Advances in Conservation Biogeography: Towards Protected Area Effectiveness under Anthropogenic Threats

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„*Die Natur muß gefühlt werden; wer sie nur sieht und abstrahiert, kann ein Menschenalter im Lebensgedränge der glühenden Tropenwelt, Pflanzen und Tiere zergliedern, er wird die Natur zu beschreiben wissen, ihr aber selbst ewig fremd sein.*“

Alexander von Humboldt

an Goethe am 3.1.1810

Contents

1 Summary

The Anthropocene is characterised by unprecedented declines in nature causing the sixth mass extinction event in earth history. The main drivers of these immense deteriorations are human land use and anthropogenic climate change.

A dilemma evolves because human welfare depends on the conservation of nature's integrity. We profit from ecosystem functioning, goods and services, which are based on biodiversity. Moreover, species have the right to exist independent of their use for us. The use and existence values of nature motivate nature conservation.

Global biodiversity hotspots are in focus of international conservation as they contain a rich inventory of species. Inventory diversity is, nevertheless, only one of three broad categories classifying diversity indices. Other diversity metrics that offer complementary information refer to differentiation or proportional diversity, and account for the dissimilarity between species assemblages.

Effective biodiversity conservation contemplates multiple measures of species diversity as well as threats to biodiversity. Anthropogenic climate change is a major threat to biodiversity that inevitably affects the entire global land in multiple ways, not only hotspots of species diversity. The change in the magnitude, timing, position and availability of climate conditions exerts influence on the demography, phenology and range of species, with unknown consequences for ecosystems worldwide. Therefore, biodiversity conservation must be applied to large geographical extents, which is the foundation of conservation biogeography.

Conservation biogeographers investigate protected areas as major tools to protect biodiversity because a high degree of biodiversity can hardly exist in unprotected landscapes that are intensively used by humans. Approximately 15% of global land is covered by protected areas. To overcome the many challenges emerging from anthropogenic pressures, protected areas need efficient and effective planning and management. Such planning and management often lacks the continuous availability of data on current states and trends of nature and threats, which can be delivered by in-situ monitoring, remote sensing and open data infrastructures. Since resources for planning and management are limited, conservationists prioritise conservation targets.

Given the rising importance of protected areas owing to expanding human land use and increasing climate change, I address the effectiveness and efficiency of terrestrial protected areas in conserving biodiversity under anthropogenic threats through the six manuscripts of this thesis. I assign each manuscript to the scientific modules of an adaptive protected area management cycle. Adaptive protected area management is an auspicious concept to ensure the enduring effectiveness of protected areas under uncertain future developments. My manuscripts provide missing scientific foundations of adaptive protected area management.

In Manuscript 1, I present a comprehensive quantification of the diversity of the European Union's priority species within major protected areas in the European Union. This quantification of inventory, differentiation and proportional diversity informs protected area management of manifold metrics of species diversity to increase protected area management effectiveness from the local to the European extent. In Manuscript 2, I prove to what degree remote sensing signals (i.e. airborne Light Detection and Ranging data, and a time series of multispectral Sentinel-2 data) reflect the compositional dissimilarity of perennial plant communities on the protected island of La Palma, Canary Islands. This study fosters efficient monitoring of differentiation diversity by remote sensing techniques. Monitoring of the biotic and abiotic environment is a scientific prerequisite of adaptive protected area management. In Manuscript 3, I developed a method to optimise in-situ surveys of biodiversity, i.e. to maximise information content and minimise sampling effort. This approach enhances the efficiency of in-situ surveys, which is required under limited management resources, such as time and funds. As a case study, I analysed the inventory diversity of alpine grassland in the Gran Paradiso National Park, Italy. I supply the data on this threatened vegetation type in an open data paper (Manuscript 4). Moreover, I show predicted changes in the availability of climate conditions (Manuscript 5) and the predicted magnitude of climate change (Manuscript 6) within the global terrestrial protected area estate for two alternative climate change scenarios in the year 2070. These two studies inform protected area management worldwide of the climate change impacts on biodiversity, to sustain protected area management effectiveness from the local to global extent. In addition, I aim at spreading this conservation-minded knowledge and data by providing open-source software and open data, and by open-access publishing. Consequently, this thesis advances the effectiveness and efficiency of protected areas in biodiversity conservation, mediated through adaptive protected area management.

Filling biogeographical knowledge gaps, improving biogeographical forecasts and promoting biodiversity conservation by communicating research are permanent tasks for conservation biogeographers. The global biodiversity crisis can be solved by local conservation strategies worldwide that are internationally coordinated. Eventually, I consider the development of a global adaptive protected area management system the most favourable future perspective in conservation biogeography to stop nature's declines and guarantee a sustainable future for the welfare of generations to come.

2 Zusammenfassung

Das Anthropozän zeichnet sich durch eine beispiellose Zerstörung der Natur aus, welche das sechste Massenaussterben in der Erdgeschichte bewirkt hat. Die wesentlichen Gründe dieser immensen Schädigung der Natur sind die menschliche Landnutzung und der anthropogene Klimawandel.

Ein Dilemma entsteht, da menschliches Wohlergehen von der Bewahrung einer intakten Natur abhängt. Wir ziehen Nutzen aus der Funktionalität von Ökosystemen, deren Gütern und Dienstleistungen, die auf Biodiversität beruhen. Darüber hinaus haben Arten das Recht, zu existieren, unabhängig von ihrem Wert für uns Menschen. Im Wert des Nutzens und der Existenz der Natur liegt der Naturschutz begründet.

Globale Hotspots der Biodiversität stehen im Fokus des internationalen Naturschutzes, da sie ein reiches Inventar an Arten beinhalten. Inventory diversity ist allerdings nur eine von drei übergeordneten Kategorien, welche Indizes der Artenvielfalt klassifizieren. Andere Kennzahlen der Artenvielfalt, welche komplementäre Informationen bieten, können der differentiation diversity oder proportional diversity zugeordnet werden und messen die Unähnlichkeit zwischen Artenzusammensetzungen.

Effektiver Schutz von Biodiversität berücksichtigt sowohl diverse Messgrößen der Artenvielfalt, als auch Bedrohungen für Biodiversität. Der anthropogene Klimawandel stellt eine wesentliche Gefahr für Biodiversität dar, der unvermeidlich sämtliche Regionen der Erde verschiedenartig beeinflusst, und nicht nur Hotspots der Artenvielfalt. Die Veränderung in der Magnitude, Zeit, Position und Verfügbarkeit von Klimabedingungen wirkt sich auf die Demographie, Phänologie und Verbreitung von Arten aus, mit ungewissen Folgen für Ökosysteme weltweit. Aus diesem Grund muss Biodiversitätsschutz auf große geographische Maßstäbe angewandt werden, was biogeographischen Naturschutz auszeichnet.

Biogeographen erforschen Schutzgebiete als wesentliche Werkzeuge zur langfristigen Bewahrung von Biodiversität auf der lokalen bis globalen Ebene, da ein großer Teil der Biodiversität kaum in ungeschützten, vom Menschen intensiv genutzten Landschaften bestehen kann. Schutzgebiete decken ca. 15% der globalen Landfläche ab. Schutzgebiete benötigen effektive und effiziente Planung und Management, um die Herausforderungen anthropogener Bedrohungen zu bestehen. Eine solche Planung und Management benötigen eine kontinuierliche Verfügbarkeit von Daten über den momentanen Stand und Trends in der Natur und deren Gefährdungen, was durch Beobachtungssysteme vor Ort, durch Fernerkundungstechniken und frei verfügbaren Dateninfrastrukturen umgesetzt werden kann. Aufgrund von limitierten Ressourcen für Planung und Management werden Naturschutzziele priorisiert.

Wegen der steigenden Bedeutung von Schutzgebieten angesichts der expandierenden menschlichen Landnutzung und des zunehmenden Klimawandels befasse ich mich in dieser Arbeit und den dazugehörigen Manuskripten mit der Effektivität und Effizienz von terrestrischen Schutzgebieten für den Erhalt der Biodiversität unter anthropogenen Bedrohungen. Ich ordne jedes meiner Manuskripte wissenschaftlichen Modulen eines Zyklus für adaptives Schutzgebietsmanagement zu. Das adaptive Management von Schutzgebieten ist ein vielversprechendes Konzept, um die anhaltende Effektivität von Schutzgebieten im Kontext zukünftiger, unsicherer Entwicklungen zu gewährleisten. Meine Manuskripte liefern fehlende wissenschaftliche Grundlagen für adaptives Schutzgebietsmanagement.

In Manuskript 1 präsentiere ich eine umfassende Quantifizierung der Vielfalt von in der Europäischen Union priorisierten Arten innerhalb großer Naturschutzgebiete der Europäischen Union. Diese Quantifizierung von inventory, differentiation und proportional diversity informiert das Schutzgebietsmanagement über vielfältige Kennzahlen der Artenvielfalt, um die Effektivität des Schutzgebietsmanagements von der lokalen bis zur europäischen Ebene zu erhöhen. In Manuskript 2 prüfe ich, inwieweit Fernerkundungsdaten, d.h. Daten eines in der Luft beförderten Light-Detection-and-Ranging-Sensors und Daten einer multispektralen Sentinel-2-Zeitreihe, die Unähnlichkeiten in den Zusammensetzungen von mehrjährigen Pflanzenarten auf der geschützten Kanareninsel La Palma widerspiegeln. Diese Studie fördert effizientes Monitoring von differentiation diversity durch Fernerkundungstechniken. Das Monitoring der biotischen und abiotischen Umwelt ist eine Voraussetzung für adaptives Schutzgebietsmanagement. Ich habe zudem eine Methode entwickelt, welche die in-situ Erfassung von Biodiversität optimiert, d.h. den Informationsgehalt maximiert und den Erfassungsaufwand minimiert (Manuskript 3). Dieses Verfahren steigert die Effizienz von in-situ Erfassungen, was notwendig ist, wenn Managementressourcen wie Zeit und finanzielle Mittel limitiert sind. Als Fallstudie habe ich die inventory diversity von alpinem Grasland im italienischen Gran Paradiso Nationalpark untersucht. Ich stelle diese Daten über einen gefährdeten Vegetationstypen in einer Open-Data-Veröffentlichung zur Verfügung (Manuskript 4). Darüber hinaus zeige ich vorhergesagte Änderungen in der Verfügbarkeit von Klimabedingungen (Manuskript 5) und die Magnitude des Klimawandels (Manuskript 6) in den globalen terrestrischen Schutzgebieten für zwei alternative Klimawandelszenarien und das Jahr 2070 auf. Diese beiden Studien informieren Schutzgebietsmanagement weltweit über Auswirkungen des Klimawandels auf gefährdete Arten, Ökosysteme und Biome, damit die Effektivität des zukünftigen Schutzgebietsmanagements von der lokalen bis globalen Ebene aufrechterhalten werden kann. Außerdem ziele ich darauf ab, dieses naturschutz-relevante Wissen und Daten aktiv zu verbreiten, indem ich meine Daten und Software kostenfrei zur Verfügung stelle, und die Manuskripte in open-access Journalen publiziere. Folglich fördert diese Arbeit die Effektivität und Effizienz von Schutzgebieten durch adaptives Schutzgebietsmanagement.

Biogeographische Wissenslücken zu schließen, biogeographische Vorhersagen zu verbessern und Naturschutz durch die Kommunikation von Wissenschaft zu unterstützen, sind permanente Aufgaben von Biogeographen im Naturschutz. Die globale Biodiversitätskrise kann überwunden werden, wenn international koordinierte Naturschutzstrategien auf lokaler Ebene in der ganzen Welt umgesetzt werden. Schließlich halte ich die Entwicklung eines globalen Systems zum adaptiven Management von Schutzgebieten weltweit für die erstrebenswerteste zukünftige Perspektive im biogeographischen Naturschutz, damit die Zerstörung der Natur gestoppt und eine nachhaltige Zukunft für kommende Generationen geschaffen werden kann.

3 Introduction

3.1 Motivation

We are currently in the midst of the sixth mass extinction event in earth history (Ceballos et al., 2015). This crisis is outstanding as the causes are not natural, such as asteroid collisions or volcanism, but the human species. About 1 million species are threatened with extinction at present and extinction rates are increasing (Díaz et al., 2019). The main drivers of this unprecedented biodiversity loss are human land use, exploitation of natural resources and organisms, anthropogenic climate change, environmental pollution and invasive species. The decline of nature is likely to continue in the near future because the driving forces result from powerful capitalistic systems and the consumptive needs of a growing human population striving after an increasing standard of living in a globalised world (Pereira et al., 2010; Díaz et al., 2019).

A dilemma evolves as human well-being depends on the protection of nature's integrity (Cardinale et al., 2012). We benefit from ecosystem functioning, goods and services, which build on biodiversity (Tilman et al., 2014). In addition, species have the right to exist independent of their benefits to humans (Wilson & Peter, 1988). The use and existence values of nature are reasons for nature conservation and motivate me as a conservation biogeographer.

I refer to conservation biogeography as 'the application of biogeographical principles, theories, and analyses, being those concerned with the distributional dynamics of taxa individually and collectively, to problems concerning the conservation of biodiversity' (Whittaker et al., 2005). Conservation biogeography combines the research disciplines of conservation biology and biogeography. Conservation biogeography has evolved from conservation biology but is deeply rooted in biogeography, which emerged as a distinct discipline as early as in the 19th century (Whittaker & Ladle, 2011). Alexander von Humboldt was the first biogeographer who raised concerns about the human impacts on nature (von Humboldt, 1845). Coincidentally, we celebrate Humboldt's 250th birthday this year.

Conservation biogeography puts biodiversity into large spatial contexts. The mapping and modelling of species diversity of conservation concern over large geographical extents and over time lie at the core of conservation biogeography (Lomolino & Heaney, 2004). The original agenda of conservation biogeography is to generate knowledge on how to optimise the conservation of biodiversity in space and time. Nowadays conservation biogeographers are facing manifold roles to stop the accelerating loss of biodiversity: they do not only generate the knowledge about biodiversity conservation in a geographical context but also implement, manage, monitor and adapt conservation initiatives in close cooperation and communication with stakeholders, such as policy-makers, managers, businesses, governmental and non-governmental organisations, local people and the general public.

Effective instruments for biodiversity conservation are protected areas (Watson et al., 2014). Protected areas are expected to be the only effective and efficient conservation tools in the future because a high degree of biodiversity will hardly be able to persist in the increasingly human-dominated landscapes of the Anthropocene (Watson et al., 2016). A proliferating number of conservationists propose setting aside half of terrestrial earth as protected areas, to compensate for the current loss of biodiversity and save our planet (Wilson, 2016). The significance of protected areas for global biodiversity conservation is also reflected in the Aichi Biodiversity Targets, which is a set of 20 global targets under the Strategic Plan for Biodiversity 2011-2020, adopted by the signatories of the Convention on Biological Diversity (CBD) in 2010. Aichi Biodiversity Target 11 particularly focuses on protected areas stating that 'by 2020, at least 17% of terrestrial and inland water areas and 10% of coastal and marine areas, especially areas of particular importance for biodiversity and ecosystem services, are conserved through effectively and equitably managed, ecologically representative and well-connected systems of protected areas.' Therefore, the effectiveness of protected areas should not only be measured by protected area coverage but also by connectivity, management success and the diversity of nature conserved.

Given my dedication to conservation biogeography and the importance of protected areas to stop biodiversity loss, it was my incentive to take protected areas as the central theme of this thesis. Within my thesis, a protected area is defined as a geographical space that is dedicated to conserve biotic and abiotic features that represent values of nature for people. I particularly focus on biodiversity conservation from the species to the biome level via terrestrial protected areas, which is increasingly challenged by human land use and anthropogenic climate change.

Successful biodiversity conservation through protected areas requires effective and efficient management of protected areas as emphasised in Aichi Biodiversity Target 11. Adaptive management can become a substantial application to ensure the enduring effectiveness and efficiency of protected areas in conserving biodiversity under uncertain future developments (Westgate et al., 2013; Gillson et al., 2019). I consequently assign each of my manuscripts in this thesis to aspects of a scientific foundation of adaptive protected area management. Adaptive management describes an iterative management approach that enables solid decision-making in a system with uncertainties. Adaptive management originates from a scientific foundation, i.e. a continual evaluation of management effectiveness and efficiency via system research and monitoring. On the grounds of this evaluation, the management efforts can be regularly adapted in order to maintain or increase the management effectiveness and efficiency.

My manuscripts provide missing scientific foundations of adaptive protected area management: the comprehensive quantification of species diversity and climate-induced threats to protected areas' biodiversity over large geographical extents, and the development and application of efficient and effective in-situ monitoring and remote sensing of species diversity. Moreover, my manuscripts aim at spreading conservation-minded data and knowledge by means of publishing open-access papers, open-source software and open data. Consequently, this thesis intends to advance the success of protected areas in biodiversity conservation mediated through adaptive protected area management. My work as a conservation biogeographer is to stimulate a growing scientific and public debate on the effectiveness of protected areas and nature conservation under anthropogenic threats, which is necessary to stop nature's decline and thus guarantee a sustainable future for the welfare of generations to come.

3.2 Structure of the thesis

I firstly introduce the values of nature as a rationale for nature conservation. Afterwards, I describe the nature conservation objectives that protected areas aim at. I generally consider biodiversity from the species to the biome level as the main conservation objectives of this thesis, but I especially concentrate on species diversity as a proxy for biodiversity because species are the crucial constituents of ecosystems. I then draw the attention to the distribution of species on earth to understand conservation hotspots. The metrics of species diversity are highlighted that are applied in the manuscripts of this dissertation. I thereupon shed light on the major threats to biodiversity in general, and on threatened species and extinction rates in particular, to stress the necessity of biodiversity conservation using protected areas.

The main part of the introduction starts with basic information about conservation biogeography as a young scientific discipline with old roots, as this needs to be understood before I devote an entire sub-chapter to terrestrial protected areas as a main objective in conservation biogeography and the central theme of the thesis. This sub-chapter includes a comprehensive review of terrestrial protected areas, ranging from their various roles, the history, designation, classification, coverage, planning, design, management and monitoring of terrestrial protected areas, to their effectiveness and future challenges.

In the synopsis, I present the adaptive management cycle for protected areas, which originates from a scientific evaluation of management effectiveness and efficiency. I explain how each of my manuscripts provides missing information for the scientific basis of adaptive protected area management. The synopsis concludes with considerations of future perspectives for protected area management and conservation biogeography in general.

The thesis ends with the characterisation of my contributions to each manuscript and the presentation of the manuscripts. Furthermore, in the appendix, I show my scientific talks and non-peer reviewed publications that relate to this thesis. The appendix also includes all my additional presentations and publications that were published during the time that I worked on my dissertation but do not relate to this thesis. I also list my activities as a scientific reviewer for peer-reviewed journals and as a lecturer while I was writing this dissertation. The main concepts and terms applied in this thesis are explained and defined in Box 1.

Box 1. Definitions and explanations of concepts and terms used in this thesis.

Adaptive management: adaptive management is an iterative management concept that enables solid decision-making in a system with uncertainty. Management effectiveness and efficiency (see definitions *effectiveness* and *efficiency*) are continuously evaluated via system monitoring (see definition *monitoring*). Based on the scientific evaluation of management effectiveness and efficiency, the management effort can be regularly adapted in order to maintain or increase management effectiveness and efficiency.

Beta diversity: beta diversity is associated with two major categories of species diversity (see definition *species diversity*): differentiation and proportional diversity (Jurasinski et al., 2009). Indicators of differentiation diversity account for species distinction and quantify the dissimilarity between species compositions (i.e. assemblages or communities). Indicators of proportional diversity do not account for species distinction because they quantify diversity by relating metrics of inventory diversity (see definition *species diversity*) from two or more different extents. In the fundamental species diversity concept of Whittaker (1960), the term *beta diversity* was introduced but defined in various ways. Since then many more metrics of beta diversity have been developed, which can be assigned to differentiation or proportional diversity (e.g. Tuomisto, 2010a, 2010b; Anderson et al., 2011; Baselga & Leprieur, 2015).

Biodiversity: biodiversity means biological diversity, i.e. the variety of life organised in taxonomic (e.g. species), ecological (e.g. ecosystems), morphological (e.g. genes) and functional (e.g. traits) entities.

Biodiversity hotspot: a biodiversity hotspot is characterised by a high degree of biodiversity (see definition *biodiversity*), e.g. a high number of species.

Biome: a biome is an ecosystem (see definition *ecosystem*) of a geographical extent larger than an ecosystem or an ecoregion (see definition *ecoregion*).

Conservation biogeography: conservation biogeography is defined as the application of biogeographical principles, theories and analyses, which are concerned with the distributional dynamics of taxa individually and collectively, to problems concerning the conservation of biodiversity (Whittaker et al., 2005).

Ecoregion: an ecoregion is an ecosystem of a geographical extent larger than an ecosystem and smaller than a biome.

Ecosystem: an ecosystem is an assemblage of biotic (e.g. species) and abiotic (e.g. climate conditions) components of nature interacting by fluxes of energy and matter.

Box 1 continued

Ecosystem services: ecosystem services are known as nature's services and constitute benefits from ecosystems to human well-being. Ecosystem services can be separated into regulating, provisioning, cultural and supporting services (Millennium Ecosystem Assessment, 2005). Regulating services refer to the regulation of ecosystem processes, e.g. climate regulation, water purification and pollination. Provisioning services are associated with ecosystem products and goods, e.g. food, water, timber and medicine. Cultural services are non-material benefits such as spiritual, intellectual, recreational and aesthetic values that people assign to ecosystems. Supporting services describe ecosystem processes that support ecosystem functioning and other services. Supporting services are, for instance, nutrient cycling, soil formation, biomass production and habitat creation for biodiversity.

Effectiveness: effectiveness describes the degree to which a target has been reached, i.e. the ratio between the actual result and the target result.

Efficiency: efficiency reflects the ratio between the result and effort to reach the result.

Extent: extent is the geographical area or space that is covered by an investigation.

Grain: grain is the spatial resolution of geographical data on a given extent, e.g. the spatial resolution of gridded raster data.

Habitat: habitat is the abiotic and biotic environment that species are able to exist in.

Monitoring: monitoring means recording something over time.

Nature: nature is the biotic and abiotic environment as opposed to human creations.

Nature conservation: nature conservation is the preservation, protection or restoration of nature by humans. Accordingly, it is a kind of human land use. Nature conservation includes the conservation of the biotic (e.g. biodiversity) and abiotic entities of nature (e.g. geodiversity). Modern approaches to nature conservation consider the conservation of biocultural diversity, i.e. the biophysical and sociocultural elements of socio-ecological systems.

Open access: open access is any kind of publication that is available to everyone at no charge.

Open data: open data are available to everyone at no charge.

Open source: open source characterises computer software that is based on source code that is available to everyone at no charge.

Priority species: since resources for species conservation are limited, conservationists select priority species. Priority species can be rare, endemic, threatened, particularly characteristic (i.e. flagship species), or key to ecosystem functioning (e.g. keystone species, ecosystem engineers or top predators) and the survival of other species (i.e. umbrella species). Priority species can be considered indicators of community and ecosystem health.

Box 1 continued

***Protected area*:** a protected area is a geographical space dedicated to conserve biotic and abiotic features of nature that represent values for humans.

***Remote sensing*:** remote sensing is the acquisition of data about an object without being in physical contact with the object. Remote sensing in nature conservation applies air- or space-born sensors that detect electromagnetic radiation emitted or reflected by objects of nature.

***Species diversity*:** species diversity is a major component of biodiversity, which is frequently used as a proxy for biodiversity. Measurements of species diversity can be assigned to three broad categories: inventory diversity, differentiation diversity and proportional diversity (Jurasinski et al., 2009). Species richness is one measure of inventory diversity. Species richness quantifies the number of species. Species abundance is another metric of inventory diversity, which combines the number of species and the number of individuals per species. In the seminal species diversity concept of Whittaker (1960), alpha diversity is defined as the species richness or abundance in the local extent, while gamma diversity expresses species richness or abundance in the regional (i.e. landscape) extent. Indicators of differentiation diversity account for species distinction and quantify the dissimilarity between species compositions (i.e. assemblages or communities). Indicators of proportional diversity do not account for species distinction because they quantify diversity by relating metrics of inventory diversity from two or more different extents. Beta diversity is associated with both, differentiation and proportional diversity (see definition *beta diversity*).

***Threatened species*:** threatened species are vulnerable or endangered, i.e. threatened with and prone to extinction, such as by human land use and anthropogenic climate change. Criteria to consider a species as threatened refer, for instance, to population and range size (IUCN, 2001).

3.3 Values of nature

We are willing to conserve nature as we value nature. Various frameworks classifying nature's values have been developed (Wallace, 2007), e.g. in the seminal studies of Daily and colleagues (Daily, 1997; Chaplin-Kramer et al., 2019), which thoroughly show the societal dependence on nature. The Economics of Ecosystems and Biodiversity (TEEB) led by the United Nations Environment Programme (UNEP) presents a widely accepted classification approach, which separates the values of nature into use, non-use and option values for humans and links these values to ecosystem services (UNEP, 2009), i.e. ecosystem benefits to human well-being (Millennium Ecosystem Assessment, 2005). I slightly adapted this categorisation as shown in Figure 1.

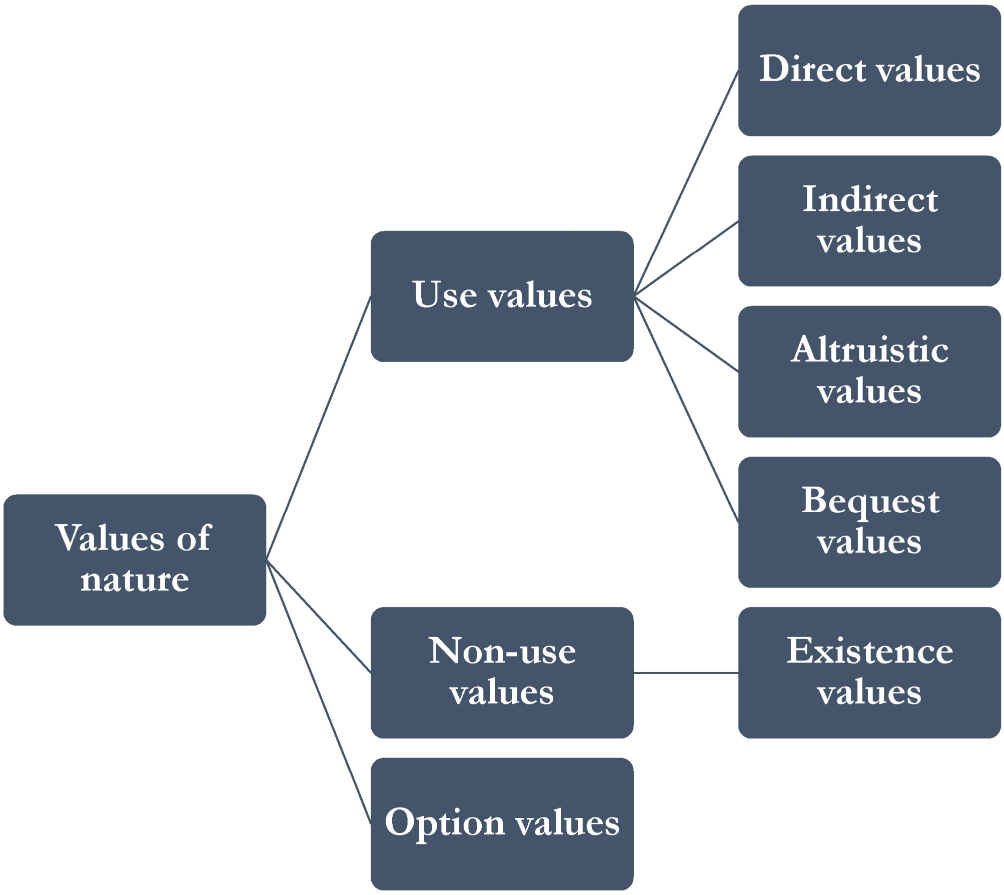

Figure 1. Categorisation of nature's values, adapted from UNEP (2009). The values of nature provide rationales for nature conservation. This dissertation and the manuscripts included address these values and contribute to nature conservation.

Because ecosystem services are defined as being useful to humans (Millennium Ecosystem Assessment, 2005), use values entail, in my adapted classification, ecosystem services, whereas non-use values do not: in contrast to the TEEB (UNEP, 2009), the existence values of nature do not refer to any use of nature to people in this thesis. Direct use values refer, however, to provisioning services such as water, food, firewood and medical plants, and cultural services such as intellectual, inspirational and spiritual values for science, education, recreation, tourism and amenity. About 70% of all cancer medicines are, for example, natural products and about four billion people depend on these direct use values (IPBES, 2019). The eco-tourism industry can even provide beneficial funds to nature conservation, but tourists cause conservation costs as well. Further, indirect use values are nature's indirect benefits to humans, i.e. regulating services (e.g. climate regulation, air and water purification, pollination and flood, pest and erosion control), and supporting services (e.g. habitat provision for species useful to humans). Ecosystem resistance, resilience and adaptation capacity under environmental changes can also be interpreted as regulating and supporting services. Moreover, altruistic and bequest values of nature are here, in contrast to the TEEB, assigned to use values since they are associated with use values to other people than oneself and to future generations respectively. In addition, I define option values not only as potential use values (e.g. new natural food sources and medicines in the future) but also as potential non-use values (e.g. new species' existence). Bioprospecting aims at turning option values into use values, but it remains unclear who owns the commercial rights to such values (Lawrence et al., 2010).

The economic values of ecosystem services are calculated, for instance, via market prices and replacement costs (UNEP, 2009). Replacement costs will appear if the ecosystem services are no longer available. The economic price of existence and option values can be determined by simply asking people how much they are willing to pay for the existence of nature's diversity and option values. The total economic value of nature was estimated to about US $145 trillion, which is about twice the value of the world's economy (Costanza et al., 2014). Hence, the values of nature are economically significant.

The components of nature differ in their economic values, leading to the fact that specific components of nature are preferably conserved (Redford & Adams, 2009). This is why ethical arguments must complement economic ones to justify the preservation of the entire natural diversity (Minteer & Collins, 2008). These ethical arguments for nature conservation are advocated by environmental philosophies, such as deep ecology (Naess & Rothenberg, 1989). They refer to the fact that humans are generally in favour of life, i.e. biophilia (Wilson, 1984). Those philosophies argue that nature has an intrinsic value that provides a rationale for its conservation irrespective of the human valuation: nature is good and consequently needs to be conserved; each component of nature has the right to exist, i.e. existence value. However, if all elements of nature are valued equally, this could cause conservation conflicts, e.g. if a species drives another species to extinction. In such cases, nature conservation can be justified by means of sustainability (Hauhs & Bogner, 2013).

3.4 Nature conservation objectives

Nature conservation is driven by value-laden human perceptions of nature. Conservation debates have consequently been loaded with emotions ever since (Trudgill, 2001). As indicated by terms like *invasive species*, conservation is not value-free. The establishment of protected areas, the extermination of invasive species, rewilding and restoration of ecosystems follow human evaluations of what is worthy of conservation. Nature conservation is therefore just one form of human land use. The role of scientists in nature conservation is not to decide on what to conserve but to inform decision-makers about how to reach different conservation goals. Accordingly, conservationists develop alternative guidelines that prioritise diverse objectives and values of nature (Brooks et al., 2006).

Conservation goals are primarily concerned with the conservation of biological diversity, which is indicated by the largest scientific society for conservation: the Society of Conservation Biology (Primack & Sher, 2016). Biological diversity is a synonym for biodiversity. The term *biodiversity* may have been first stated by Elliot Norse in a US government report in 1980 but was not scientifically established until 1988 when proceedings of the 1986 National Forum on BioDiversity were published (Wilson & Peter, 1988). This forum was organised by Walter Rosen and held in Washington, D.C. *Biodiversity* was originally meant to be a contraction of *biological diversity*, but various meanings have been associated with biodiversity since then. Even though the term *biodiversity* has promoted the raising of funds (Christie et al., 2006), it often remains unclear what biodiversity actually refers to. A general theory of biodiversity is required to comprise the multiple meanings of biodiversity (Beierkuhnlein, 2003): essentially, biodiversity describes the variability of life, i.e. the diversity of biological entities at all levels of organisation. The biotic entities are organised in taxonomic (e.g. species), ecological (e.g. ecosystems), morphological (e.g. genes) and functional entities (e.g. traits). The diversity of biotic entities is assessed quantitatively (i.e. number of entities), qualitatively (i.e. similarity or dissimilarity between entities) and functionally (i.e. ecological complexity between entities). The CBD states a definition of biodiversity, which was adopted at the United Nations Conference on Environment and Development in 1992, i.e. the 'Earth Summit' in Rio de Janeiro: 'biological diversity means the variability among living organisms from all sources including inter alia, terrestrial, marine and other aquatic ecosystems and the ecological complexes of which they are part; this includes diversity within species, between species and of ecosystems' (United Nations, 1992).

The two traditional perspectives on biodiversity conservation are the functionalist perspective and the compositionalist perspective (Callicott et al., 1999). Functionalists perceive nature as a dynamic system (i.e. flux paradigm), while compositionalists construe nature as a balanced system (i.e. balance paradigm). The functionalist perspective emphasises conserving ecological processes and functions, whereas the compositionalist perspective focuses on conserving biological composition, e.g. species assemblages. Only considering ecological functioning neglects the persistence of particular communities, while concentrating on a particular community can disregard the processes maintaining the community. In addition, the effectiveness of protecting functioning and composition is extent-dependent. Taking an ecosystem function as a conservation objective in protected area management will be inappropriate if the function is determined from outside the protected area, such as in the case of river ecosystems. Conservation implementations frequently refer to both perspectives because biological composition depends on ecological processes and vice versa (Callicott et al., 1999; Williams & Araújo, 2002).

Under both perspectives, ecological reference states are defined to measure environmental change and conservation effectiveness. For compositionalists, a specific community can be an ecological reference. Often, relict and pristine communities are used as reference states because they are rich in rare, endemic and threatened species (De Nascimento et al., 2009). Functionalists may consider an ecosystem function, e.g. productivity, as a reference state. In developing countries and North America, conservationists widely strive for the natural state as it was before human colonisation, whereas in Western Europe conservationists prefer a pre-industrial state of nature that includes a certain level of human interference (Sutherland, 2002). In the future the functionalist perspective will gain in importance since environmental changes continuously alter local species compositions, while local species richness has not significantly varied over the last few decades (Blowes et al., 2019). Globally, species richness is declining though (Ceballos et al., 2015).

Nowadays conservation approaches increasingly consider human demands on nature (Soulé, 2014) because conflicts will arise if biodiversity conservation contradicts human needs, such as poverty reduction (Ferraro et al., 2011; Minteer & Miller, 2011). Biocultural conservation combines biodiversity protection with the preservation of cultural needs in social-ecological systems (Gavin et al., 2015). Conflicts will be prevented if the people who are affected by conservation action agree to it, even though their livelihoods may be restricted (Roe et al., 2013). Although some manuscripts of this thesis include protected areas that consider biocultural conservation (Manuscript 1, 2, 5 and 6), all manuscripts are primarily concerned with the conservation of biodiversity, especially from the species to the biome level. I particularly concentrate on species because they constitute communities and ecosystems, thus ecosystem functioning and services. Species diversity is, however, only one proxy of biodiversity.

Since resources for species conservation are limited, conservationists select priority species. Taxonomists distinguish species by morphological, biological (i.e. breeding) or evolutionary aspects (i.e. DNA), but these approaches do not always agree on a species, which can impede the conservation of such species (Ryder, 1986). Selected species can be rare, endemic, threatened, particularly characteristic (i.e. flagship species), or key to ecosystem functioning (i.e. keystone species) and the survival of other species (i.e. umbrella species). Because ecosystems are organised in trophic levels, food chains or food webs, keystone and umbrella species are believed to have the ability to determine the survival of many other species by controlling biotic or abiotic interactions (Simberloff, 1998). Further, there are species that significantly modify their abiotic environments, called ecosystem engineers. The loss of such species can cause a loss of other species due to trophic and extinction cascades (Hollings et al., 2014). Thereby, conservation efforts like rewilding or restoration focus on keystone and umbrella species, such as top predators.

Inventories are built to list priority species, e.g. the Red List of threatened species initiated by the International Union for Conservation of Nature (IUCN). The IUCN has assessed 105,732 species up to now, including vertebrates, invertebrates, plants, fungi and protists. About 27% of these species are threatened with extinction (IUCN, 2019b). The Red List includes only species for which sufficient knowledge is available. In addition, laws and treaties are adopted that explicitly care for priority species, such as the Birds Directive and Habitats Directive of the European Union (EU). Under Article 12 of the Birds Directive (European Environment Agency, 2019c), 576 bird species are listed, 193 of which are particularly threatened within the EU. Under Article 17 of the Habitats Directive (European Environment Agency, 2019a), 1319 species are listed, including fish, amphibians, arthropods, mammals, molluscs, reptiles, vascular and non-vascular plants. They are rare, endemic, vulnerable or threatened in the EU. However, conservationists criticise the directives because some of those species are neither threatened nor native to Europe (Hochkirch et al., 2013; Maes et al., 2013). Setting conservation priorities is always associated with the risk of missing other conservation objectives. Above all, conservation objectives should represent conservation targets that stakeholders agree with since stakeholder agreement is essential to meet conservation goals.

The conservation of species diversity is a common facet of all manuscripts in this thesis. I integrated the products of the Birds and Habitats directives into Manuscript 1, and a product of the IUCN Red List into Manuscript 5 and 6, to assess species diversity inside protected areas. Plant species diversity plays the central role in Manuscript 2 and 3, where I demonstrate how plant species diversity is efficiently sampled. In Manuscript 4, I provide open data on threatened alpine plant species diversity. The abiotic and biotic resources that a species requires constitute the species' ecological niche and habitat. If such resources disappear from the protected area, e.g. by changing climate conditions, species will lose their habitat and may become extinct in the protected area. The loss of species diversity threatens entire ecosystems as the ecosystems' functioning depends on biodiversity (Tilman et al., 2014). Consequently, Manuscript 5 and 6 are not only about climate-induced threats to species inside protected areas but also about climate-induced threats to biodiversity, ecosystems' functioning and services in general.

3.5 Assessing species diversity

3.5.1 Global species diversity

The conservation of species requires knowledge about the existence and distribution of species. About 1.2 million species have been catalogued up to 2011, but about 8.7 million eukaryotic species are predicted to exist globally (Mora et al., 2011). The deficit of known species is referred to as the Linnean shortfall (Raven & Wilson, 1992). Especially species of inconspicuous groups remain unknown. About 20,000 new species are described each year, even in the relatively well known groups, such as birds, mammals and flowering plants (Joppa et al., 2011). New species are primarily discovered in remote and inaccessible areas, e.g. the deep sea, isolated islands and forest canopies, but also by re-inspecting samples stored in museums, herbaria and archives. According to Mora et al. (2011), 86% of terrestrial species and 91% of marine species have not been described yet.

The lack of knowledge about the precise geographical distribution of species, and therefore about the ecological niche of species, is termed the Wallacean shortfall (Lomolino & Heaney, 2004). We, however, know that the richness of most species groups increases towards the equator (Groombridge & Jenkins, 2010), i.e. the latitudinal diversity gradient (Hillebrand, 2004). The richness of many groups is positively correlated over large geographical extents and grains (Ricketts et al., 1999). Over small geographical extents and grains, this does not hold true for all groups of species because some groups prefer clearly separated local habitats. As an example, amphibians mostly prefer shady and wet habitats, while many reptiles prefer dry and sunny habitats. Species diversity is subsequently dependent on the geographical extent and grain of observation, which conservationists have to consider regarding time and cost-efficient observation techniques (Manuscript 2 and 3).

Environmental diversity is relevant for protected area planning and management (Manuscript 5 and 6) since it promotes species diversity (Irl et al., 2015) and buffers climate change impacts on species distributions (Ackerly et al., 2010; Scherrer & Körner, 2011; Comer et al., 2015; Heller et al., 2015; Lawler et al., 2015). As highlighted in Manuscript 2, environmental diversity and geographical isolation lead to high endemic richness on islands (Whittaker & Fernández-Palacios, 2007). Global richness hotspots of threatened endemic plants, mammals, birds, reptiles and amphibians are located in the tropical and Mediterranean regions (Figure 2), particularly in mountain ranges and islands of these regions (Myers et al., 2000). Tropical forests, for instance, cover only 7% of terrestrial earth but contain about half of the world's species, mainly insects (Corlett & Primack, 2011). About 40% of the global diversity of flowering plants, gymnosperms and ferns occur in tropical forests of the Americas, Africa, Asia and Australia. Several of my manuscripts address at least one of these global biodiversity hotspots. Nature conservation should, however, not only focus on biodiversity hotspots because biodiversity creates values of nature all over the globe.

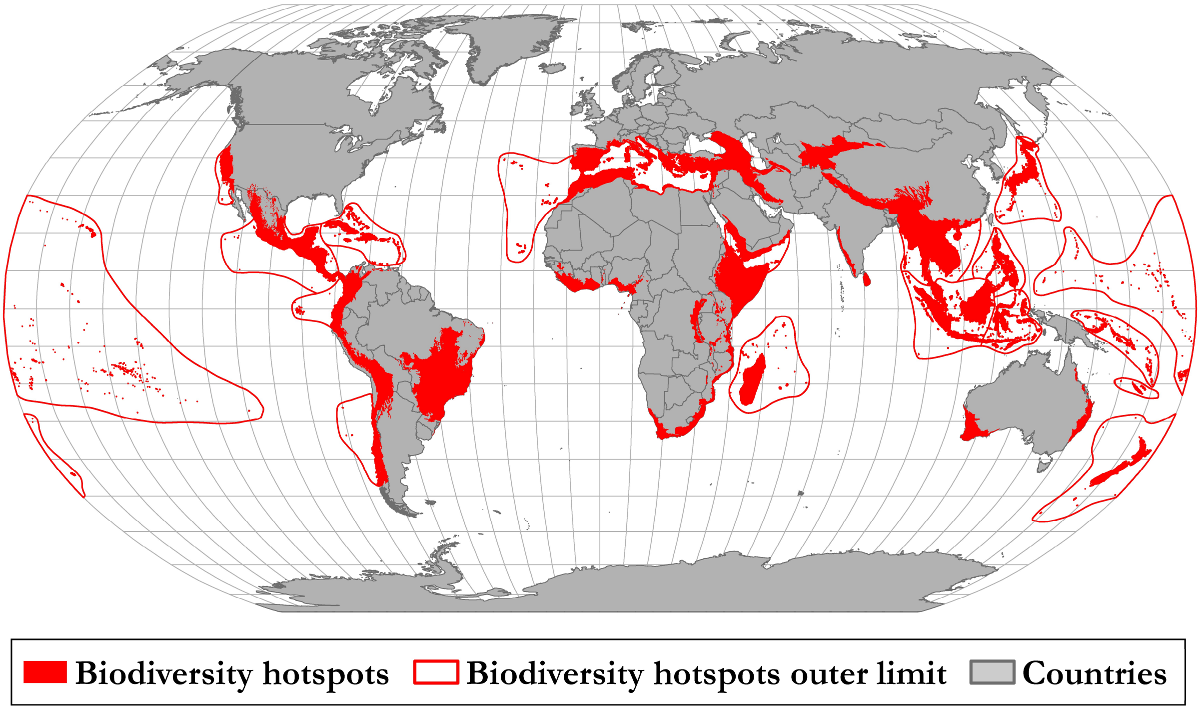

Figure 2. Terrestrial richness hotspots (red) of endemic and threatened plants, mammals, birds, reptiles and amphibians, according to Myers et al. (2000). These hotspots are of concern to conservation. Several of the manuscripts in this dissertation address at least one of these global biodiversity hotspots. The map data were retrieved from Conservation International (2004).

3.5.2 Indicators of species diversity

To evaluate the effect of conservation effort on species diversity, species diversity must be measured. There are many ways to assess species diversity (Magurran & McGill, 2013). They can be assigned to three conceptual categories according to Jurasinski et al. (2009): inventory diversity, differentiation diversity and proportional diversity (Table 1).

Table 1. Conceptual categories for species diversity indices and a selection of associated species diversity indices and concepts, according to Jurasinski et al. (2009). Each manuscript of this dissertation includes at least one of these indices.

Species diversity category	Species diversity concepts and indices
Inventory diversity	Species richness, alpha diversity, gamma diversity, species abundance, species rarity, Shannon index, irreplaceability index, residuals of the species-area relationship, dark diversity, etc.
Differentiation diversity	Compositional (dis-)similarity, beta diversity, turnover, replacement, nestedness, species richness differences, sum of squares of species matrix, gradient length in ordination, slope of distance-decay relationship, etc.
Proportional diversity	Additive beta diversity, multiplicative beta diversity, slope of the species-area relationship, etc.

The basic measurement of species diversity is counting the number of species, i.e. species richness. In this thesis, species richness was assessed inside entire protected areas (Manuscript 1) or inside sampling units within protected areas (Manuscript 2, 3 and 4). As listed in Table 1, species richness belongs to inventory diversity. The assessment of the relationship between area and species richness is not only a fundamental concept of biogeography but has also substantially contributed to species conservation. The species-area relationship is, for example, used to model species' extinction risk from climate change (Thomas et al., 2004), to design protected areas (Diamond, 1975; Chittaro et al., 2010) and to define conservation targets (Desmet & Cowling, 2004). The species-area relationship is one of the oldest ecological concepts that has been empirically investigated (Rosenzweig, 1995). Arrhenius (1921) and Gleason (1922) were the first who described the species-area relationship by mathematical formulas. In Manuscript 1, I used the residuals of the species-area relationship to estimate whether a protected area holds a surplus or deficit of species richness relative to its area (Manuscript 1). I thus developed a novel measure for the conservation value of protected areas, which is related to inventory diversity.

Species rarity is another fundamental metric of species diversity (Manuscript 1). The rarity of individual species can be expressed by the ratio between the area occupied by a species and the area of a given geographical extent (Williams et al., 1996). Species rarity belongs to inventory diversity. Rarity indices can incorporate species abundances (Preston, 1948).

The Shannon index, also known as the Shannon-Wiener index, describes the abundance of species and relates to inventory diversity as well. Species abundance integrates the number of species and the number of individuals per species. The Shannon index describes communities with one very abundant and dominant species as less diverse compared with communities of equally abundant species (Manuscript 3). The Shannon index was derived from Shannon's information entropy (Shannon, 1948), which is a central theory of informatics. Shannon's information entropy is a measure of the information content given by a number of entities, e.g. species abundance values. Into Manuscript 1, 5 and 6, I integrated an inventory diversity index that is used in conservation context and represents the irreplaceability of a protected area. This irreplaceability index is based on the overlap between ranges of 21,419 Red List species (i.e. 6240 amphibians, 9793 birds and 5263 mammals) and protected areas (Le Saout et al., 2013). It indirectly reflects the richness, abundance and rarity of threatened species inside a protected area.

In the ground-breaking species diversity concept of Whittaker (1960), the terms *alpha diversity*, *beta diversity* and *gamma diversity* were introduced, which are still widely used. Whittaker (1960) defined alpha diversity as the species richness or abundance in the local extent, while gamma diversity expresses species richness or abundance in the regional landscape extent. In this seminal work, beta diversity was already defined in different ways and many more definitions of beta diversity have been developed since then (Tuomisto, 2010a, 2010b; Anderson et al., 2011; Baselga & Leprieur, 2015). The different definitions of beta diversity either refer to differentiation or proportional diversity (Jurasinski et al., 2009). Indicators of differentiation diversity account for species distinction and quantify the dissimilarity between species assemblages in space or time. Indicators of proportional diversity do not account for species distinction because they quantify diversity by relating metrics of inventory diversity from two or more different extents.

The manuscripts of this thesis include beta diversity metrics that quantify the compositional dissimilarity between species assemblages, i.e. differentiation diversity (Jurasinski et al., 2009). The dissimilarity between two species assemblages can be calculated by pairwise beta diversity indices as a measure of distance (Legendre & De Cáceres, 2013). The Hellinger distance (Manuscript 2) is a pairwise beta diversity metric that down-weights the influence of rare species onto dissimilarity estimations (Legendre & De Cáceres, 2013). The dissimilarity between more than two species assemblages can be assessed by so-called multiple-site indices (Baselga, 2013; Ensing & Pither, 2015) and multivariate ordination techniques (Legendre et al., 2005; Legendre & De Cáceres, 2013). The latter is used in Manuscript 2. A special group of dissimilarity indices separates dissimilarity patterns into a component of species replacement (i.e. turnover), a component of species nestedness (i.e. nested species assemblages) and a component of species richness differences (Baselga & Leprieur, 2015). This separation helps to identify patterns and drivers of compositional dissimilarity (Baselga, 2013). I applied this separation to dissimilarity patterns of a protected area network (Manuscript 1).

Conservationists need to account for beta diversity in addition to other diversity metrics to identify and maintain different drivers of species diversity (Socolar et al., 2016). They can thus plan conservation efforts thoroughly, such as the design of protected area networks. Since each of the species diversity indices mentioned above provides different information about species diversity, a comprehensive assessment of species diversity has to consider a multitude of indices. In Manuscript 1, I conducted such a comprehensive assessment within a continental protected area network. The results of this study guide the management of individual protected areas towards achieving continental conservation goals, i.e. a protected area network that is representative, redundant and complementary of species diversity. Species and threats to species occur across country borders. This is why internationally coordinated conservation efforts are necessary to stop the loss of species worldwide.

3.6 Assessing threats to biodiversity

3.6.1 Types of threats

In the last few decades a tremendous loss of biodiversity has become evident which is caused by humankind (Pimm et al., 2014). The main reasons for this decline (Figure 3) are changes in land and sea use, the direct exploitation of organisms, climate change, environmental pollution and invasive species (Díaz et al., 2019). These threats act very locally but across the global extent and do not spare protected areas (Manuscript 5 and 6). The loss of biodiversity feeds back onto these threats because a decrease of biodiversity means a decrease of ecosystem stability (Tilman et al., 2014). The threats are primarily driven by capitalistic systems and the consumptive needs of developed countries in an increasingly globalised world (Pereira et al., 2010; Díaz et al., 2019). The ecological footprint of developed countries is high, but the footprints of developing countries are rapidly increasing due to population growth and economic as well as societal development. At the same time, developing countries in the tropics harbour a high degree of biodiversity. Hence, those countries are severely challenged in balancing economic development and biodiversity conservation. However, economic growth could have positive effects on conservation if economic development resulted in increasing conservation funds (Di Minin et al., 2013).

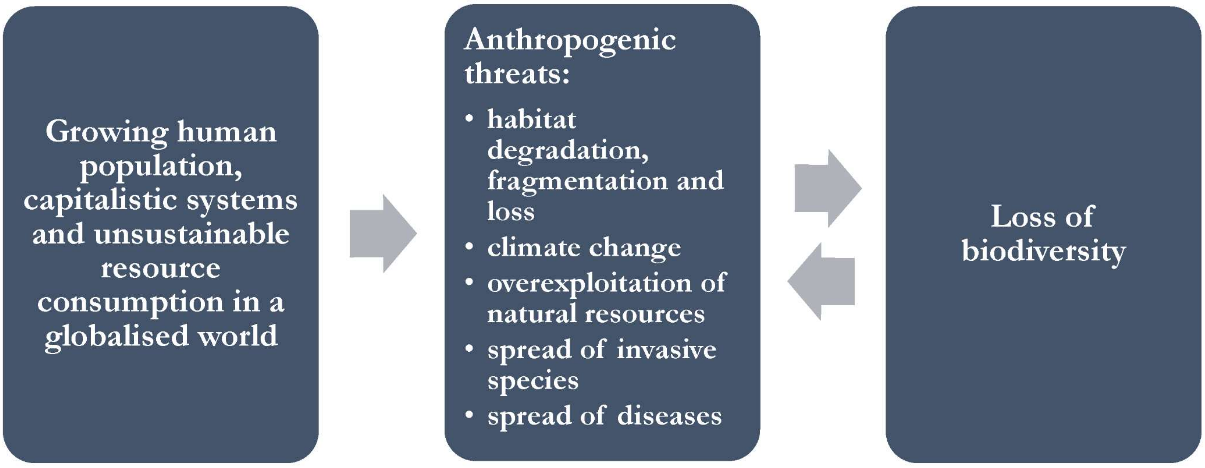

Figure 3. Drivers of biodiversity loss, adapted from Díaz et al. (2019). In the manuscripts of this dissertation, I discuss anthropogenic threats such as climate change, habitat degradation and invasive species.

Human land use is a main threat to biodiversity (Tilman et al., 2017), which has already been globally present for 3000 years (Stephens et al., 2019). About 75% of the terrestrial habitats have been significantly modified or destroyed by humans (Díaz et al., 2019). Anthropogenic land use impacts on threatened terrestrial vertebrates occur worldwide (Allan et al., 2019). Crop and livestock production are the main reasons for losing habitat (Sanderson et al., 2002), followed by commercial developments, water projects, recreational activities, environmental pollution, human infrastructure, anthropogenic disruption of fire ecology and logging (Stein et al., 2000; Wilcove & Master, 2005). The loss of tropical forests and wetlands is particularly alarming because they are extremely rich in biodiversity and act as carbon dioxide sinks counteracting global warming. Anthropogenic habitat loss is lower in protected areas, especially in those managed by local communities and indigenous people (Díaz et al., 2019). Indigenous people manage at least 25% of the global land. This area includes over one-third of the world's protected areas, as well as many other remote and unprotected regions of low human footprints. Protected areas contain the last remaining habitats of many species (Jackson & Gaston, 2008). However, anthropogenic land use is expected to expand into protected areas due to an increasing human demand for resources (Geldmann et al., 2019). The human pressures on protected areas are increasing and expansions of human land use and protected areas often conflict (Montesino Pouzols et al., 2014; Jones et al., 2018).

Human land use does not only induce habitat loss and degradation but also fragmentation. Habitat fragmentation means habitat is reduced in size and divided into fragments, e.g. by transportation infrastructure. Fragments are isolated from each other due to degraded habitat in-between. Habitat fragments are like habitat islands surrounded by human-dominated landscapes. Protected areas are perceived as habitat islands (Manuscript 1, 5 and 6). The length of habitat edges increases with fragmentation. Edges are characterised by very different abiotic conditions compared to the core zone of habitats. Edges are at higher risks of threats, such as wind throw or invasion (Murcia, 1995; Porensky & Young, 2013). The smaller the fragments and the larger the edges are, the more the fragments are prone to edge effects. Habitat fragmentation limits movement, dispersal and colonisation of species, restricts species' access to resources, reduces population sizes, and supports species invasion through disturbed habitat (Gibson et al., 2013; Fahrig, 2017; Tucker et al., 2018). Many of these fragmentation impacts on biodiversity are indirect (Wilson et al., 2016). Fragmentation is expected to proliferate in the future as about 25 million km of new paved roads are foreseen globally by 2050 (IPBES, 2019). In contrast, numerous species depend on small and isolated habitat patches (Wintle et al., 2019).

Anthropogenic climate change is the other major threat to biodiversity, which is still growing strongly (Ripple et al., 2019). Burning fossil fuels, deforestation and agricultural activities have caused a rapid and significant increase of greenhouse gas emissions since the industrialisation (IPBES, 2019). Globally, subsidies of US $345 billion are spent for fossil fuels that perversely cost US $5 trillion of externalities due to environmental degradation (IPBES, 2019). The anthropogenic greenhouse gas emissions have led to severe global warming (IPCC, 2014), even though marine and terrestrial ecosystems sequester about 60% of the annual global carbon dioxide emissions from fossil fuel burning (IPBES, 2019).

During the last century the global surface temperature has increased by 0.8 °C (IPCC, 2013). Depending on future emission scenarios, global atmospheric temperatures will further increase by 1 to 6 °C by 2100 (IPCC, 2013). The greatest and fastest temperature rise occurs at high elevation and latitudes, and over large continental masses (Garcia et al., 2014). Rising temperatures cause melting permafrost in the tundra which will additionally release greenhouse gas emissions from the soils to the atmosphere, thus enhancing climate change via a feedback-loop (Schuur et al., 2015). Importantly, anthropogenic climate change is not only about global warming. Regional precipitation patterns will change in various ways, which are hard to predict, particularly in mountain regions with few climate stations (Zandler et al., 2019). During anthropogenic climate change, a gain in global precipitation has already been measured, and wildfires and extreme weather events, such as heat waves, droughts and storms, have become more frequent (IPBES, 2019).

Anthropogenic climate change is already threatening many species (Walther et al., 2002; Parmesan & Yohe, 2003; Primack & Miller-Rushing, 2012; Nelson et al., 2013; Scheffers et al., 2016; Pecl et al., 2017). Climate change impacts on biodiversity are expected to increase in the near future, potentially outperforming the effects of human land use change on biodiversity (IPBES, 2019): the estimated proportion of species that are threatened by extinction from 2 °C future warming is 8%, and 16% at a future temperature rise of 4.3 °C; 47% of terrestrial flightless mammals and 23% of threatened birds have been already impacted by climate change.

Species with small climatic niches, e.g. tropical species, are exceptionally prone to climate change (Corlett, 2011; Şekercioğlu et al., 2012). Populations and species ranges are shrinking due to habitat loss resulting from climate shifts (Scheffers et al., 2016). Species are migrating polewards and to higher elevations to track suitable habitat (Willis et al., 2008; Chen et al., 2011; Pecl et al., 2017; Steinbauer et al., 2018). The temporal rates of habitat change likely exceed the natural dispersal rates of numerous species. Therefore, many species cannot keep up with climate change and will eventually go extinct (Jaeschke et al., 2013). A further aspect are seasonal changes. Vegetation does not only grow at higher elevation but also over longer periods per year. Flowering occurs earlier throughout the year, leading to frost damage (Muffler et al., 2016) and temporal mismatch with pollinator activity (Inouye et al., 2002; Munson & Long, 2017). Rising temperatures and more frequent and severe droughts result in increased tree mortality and detrimental insect outbreaks (Carnicer et al., 2011). Desert species are particularly endangered by droughts (Lovich et al., 2014). Thermal expansion, melting glaciers and polar ice generate sea level rise (IPCC, 2013). Rising sea levels and growing frequencies and intensities of storms threaten terrestrial mammals (Ameca y Juárez et al., 2013) and coastal species (Walls et al., 2019).

Climate change may cause non-analogue communities, i.e. communities without current analogues, because species differ in their ability to respond to climate change via dispersal, range dynamics and biotic interactions (Williams & Jackson, 2007). The functioning of such novel ecosystems is hard to predict (Hobbs et al., 2006). Impacts of recent climate change onto ecosystem functioning and services are manifold (Walther, 2010; Scheffers et al., 2016). Under climate change, the species richness and functioning of ecosystems can increase (Mascaro et al., 2012; Kueffer & Kaiser-Bunbury, 2014). Mascaro et al. (2012) shows that non-native species led to enhanced productivity, carbon storage and nutrient cycling in lowland Hawaiian rainforests. In contrast, forest carbon storage is decreasing with increasing frequencies and intensities of droughts, fires, wind throw and insect outbreaks (Seidl et al., 2011; Holmgren et al., 2013). Climate-induced changes to ecosystems generally depend on the ecosystems' exposure (i.e. magnitude of change), resistance or sensitivity (i.e. ability to remain in the original state despite change), resilience (i.e. ability to return to the original state after change) and capacity to adapt to change (Dawson et al., 2011; Magness et al., 2011; Watson et al., 2013; Bellard et al., 2014; Michalak et al., 2017; Lee et al., 2018; Li, Wu et al., 2018; Foden et al., 2019; Jentsch & White, 2019). Anthropogenic climate change can cause protected areas to contain species assemblages, ecosystems and associated services that they were not designated for (Hole et al., 2011), which is the central topic of Manuscript 5 and 6.

The human exploitation of natural resources constitutes another hazard to biodiversity. Capitalistic businesses, improved access to remote areas, technical developments and trade markets have led to the overexploitation of natural resources and biodiversity (Díaz et al., 2019). Species are driven to extinction through hunting and harvesting, even in protected areas (Redford, 1992; Doughty, 2013; Lindsey et al., 2013). Excessive hunting of mammals leads to the degradation of plant communities because seed dispersers are eliminated (Galetti & Dirzo, 2013). As soon as legal or illegal markets emerge for wildlife-related food, medicine and amenity products, unsustainable use of biological resources is likely, also in protected areas (Loucks et al., 2009). The loss of many species is rooted in the legal and illegal trade of those species (Nijman et al., 2011). In fisheries, individuals killed by by-catch and the direct exploitation of specific species, e.g. whales, are significant factors for population declines and species loss (Burgess et al., 2013). The Convention on International Trade in Endangered Species (CITES) is meant to control the trade of threatened species.

Invasive species endanger threatened species as well (Clavero & Garciaberthou, 2005; Heleno et al., 2009). Invasive species are species that establish in new and non-historical ranges and harm their environment (Mack et al., 2000), potentially causing immense costs (Pimentel et al., 2005; Marbuah et al., 2014). Invasive species are introduced in various ways, such as by human colonisation, transport, agriculture and biological controlling. Invasive species frequently occur in disturbed habitats, where biotic and abiotic conditions were altered. Therefore, climate change supports the spread of invasive species (Bradley et al., 2012). Native species can become invasive when their predators have disappeared, which is referred to as the predator release hypothesis (Davis, 2009), or when environmental conditions have been modified, e.g. by an improved availability of limiting resources (Carey et al., 2012). Invasive species abundances have increased by up to 70% across 21 countries since 1970 (Díaz et al., 2019): there, invasive species decrease native species abundances via competition, predation, parasitism and alteration of habitat conditions.

Diseases can diminish native species diversity, too. Human activities can spread such diseases. Increasing incidences of diseases are linked to increasing international travel and economic globalisation (IPBES, 2019): threatened species in human contact are particularly susceptible to diseases. Pathogens can have detrimental effects on threatened species and entire ecosystems in protected areas (Jones et al., 2008; Thogmartin et al., 2013). A high degree of biodiversity does buffer disease spread, but the accelerating loss of biodiversity poses a serious risk of disease spread, which is also increased by climate change (Siraj et al., 2014). Thus, threats to biodiversity can act simultaneously and across different spatial and temporal scales, and are more or less urgent, which requires complex conservation plans (Lawler et al., 2002; Bonebrake et al., 2019).

Adequate management can prevent or reduce many threats to biodiversity within the boundaries of protected areas. The impacts of anthropogenic climate change can, however, not be shut out from protected areas. Accordingly, climate change will unavoidably affect every protected area sooner or later. Each protected area's management consequently needs to be aware of climate change impacts.

3.6.2 Indicators of threats

Indicators of threats to biodiversity are useful for developing timely conservation action because they can warn of biodiversity loss (Failing & Gregory, 2003; Butchart et al., 2010). Indicators of threats are, for instance, climate change metrics (Garcia et al., 2014), diversity indices of invasive alien species (Clavero & Garciaberthou, 2005; Bellard et al., 2014) and quantitative estimates of natural resource extraction (Butchart, 2008). The development of indicators of threats is promoted by six of the 20 Aichi Biodiversity Targets (CBD, 2019). The removal or mitigation of threats does, however, not necessarily induce biodiversity recovery. Therefore, measuring threats should be accompanied by assessing biodiversity, such as using the IUCN Red List index to assess species reintroduction success (Shier, 2015).

Anthropogenic climate change is a growing and inevitable threat to global biodiversity (Pecl et al., 2017; Ripple et al., 2019). We know much less about the vulnerability of biodiversity to climate change than about other threats (Dawson et al., 2011). This is why Manuscript 5 and 6 are dedicated to the impacts of climate change on protected areas. These two manuscripts are the first studies in which climate change impacts inside protected areas have been investigated on the basis of a very fine grain but global extent. Such investigations are important because climate change affects local ecosystems worldwide. I accordingly provide climate impact information for each individual, terrestrial protected area worldwide. These studies support protected area management solving global climate-induced conservation problems starting in local protected areas.

There are various measures of climate change. According to the review by Garcia and colleagues (2014), these measures can be divided into metrics of local change, i.e. within a single grid cell, and metrics of regional change, i.e. considering more than one grid cell (Table 2). Metrics of local climate change are, furthermore, separated into indices of the magnitude of local climate change, i.e. local climate anomalies (e.g. Belote et al., 2018) and local change in climate extremes (e.g. Beaumont et al., 2011), and indices of the changing timing of local climates, i.e. changing seasonality (e.g. Kassam et al., 2018). The metrics of regional climate change comprise indices that are based on the changing geographical position of climates, i.e. climate change velocity, distance to analogue climates and direction to analogue climates (e.g. Hamann et al., 2015; Ordonez et al., 2016), and indices of the changing availability of climates, i.e. changing climate area, and novel and disappearing climates (e.g. Mahony et al., 2017).

Table 2. Measures of local and regional climate change linked to consequences for populations, species and species assemblages, adapted from Garcia et al. (2014). Manuscript 5 and 6 of this dissertation include metrics of local and regional climate change respectively.

Geographical extent	Type of change	Climate change measure	Biotic consequences
Local climate change	**Magnitude**	Climate anomalies	Demographic change of populations
		Change in climate extremes	Demographic change of populations
	Timing	Change in climate seasonality	Phenological and demographic change of populations, species and species assemblages
Regional climate change	**Position**	Climate change velocity	Species range displacement
		Distance to analogue climate	Species range displacement
		Direction to analogue climate	Species range displacement
	Availability	Change in climate area	Change in species range size
		Novel/disappearing climate	Novel species assemblages

Measures of climate change represent threats and opportunities for populations, species and species assemblages (Garcia et al., 2014). In the following, I want to highlight the climate change measures and corresponding biotic responses that are related to the manuscripts of this thesis. In Manuscript 5, I show predicted future climate shifts inside the world's terrestrial protected areas, by calculating the future availability of climate conditions from the extent of novel and disappearing climate conditions inside protected areas. Novel and disappearing climate conditions reflect the potential of newly formed and disrupted biotic interactions and communities.

In Manuscript 6, I highlight the climate change exposure of protected areas by predicting climate anomalies, i.e. the magnitude of climate change. Climate anomalies are defined by the climate dissimilarity between past, current and future climate conditions. Climate anomalies indicate the potential of the demographic change of species populations (Garcia et al., 2014): under local climate anomalies, species with specialised climatic requirements are especially prone to demographic changes; species living close to their lower climate tolerance limit profit from local anomalies, while species living close to their upper limit are threatened by local anomalies; the lower the capacity of species is to adapt to climate change, the more threatened are those species under climate change. The redistribution of species can, moreover, modify ecosystems and associated services (Walther, 2010; Mascaro et al., 2012; Scheffers et al., 2016).

Manuscript 5 and 6 also include the human footprint index which is another important indicator of threat (Venter et al., 2016). The human footprint index integrates remote sensing products and represents habitat degradation by human land use and land cover (Sanderson et al., 2002). The higher the human footprint is, the higher is the habitat degradation. Habitat degradation implies habitat fragmentation and isolation, which additionally prevents species migration and increases the extinction risk of species during climate change. Eventually, a comprehensive analysis of threats to protected areas and biodiversity should account for various threats, their interactions and effects.

3.7 Threatened species and extinction rates

During earth history species richness has generally increased, peaking in the present geological period but probably in pre-human times (Wiens, 2011). The rate of species speciation is not constant over time and interrupted by extinction events, such as the five main mass extinction events that determined the end of the Ordovician, Devonian, Permian, Triassic and Cretaceous period (Raup & Sepkoski, 1982; Ward, 2004; Barnosky et al., 2011). The mass extinction events of the past were caused by natural forces, e.g. volcanism and asteroid collisions, but species are also driven to extinction through competition and predation (Pimm et al., 2014).

Nowadays almost every extinction is linked to human activities (Pimm & Jenkins, 2005; Wake & Vredenburg, 2008). The ultimate reason for today’s species loss and ecosystem degradation is unsustainable resource consumption (Fischer et al., 2012). The extinction rates since the appearance of *Homo sapiens* are tenfold to hundredfold higher than the natural speciation rates (Díaz et al., 2019). Owing to this, recent rates of species loss are far from natural rates. A sixth human-induced mass extinction event is presently occurring (Barnosky et al., 2011; Ceballos et al., 2015), even though the global protected area estate has never been larger (Bingham et al., 2019).

Many species may become extinct before they have been discovered (Hoffmann et al., 2010; McClenachan et al., 2012), implying that extinction rates are underestimated. This knowledge deficit refers to the extinction estimate shortfall (Riddle et al., 2011). To estimate human-induced extinction rates, the currently observed extinction rates are compared to natural background rates revealed by fossil records. Distinguishing between human-induced extinction rates and natural background rates is, however, difficult because fossil records provide only limited information about species extinctions. The signals of mass extinction events, for example, are weaker in plant fossils (McElwain & Punyasena, 2007). During the last 150 years human-driven extinction rates have been at their highest (Pimm et al., 2014). Extinctions are more frequent on islands than on mainland (Butchart, Stattersfield et al., 2006). Extinction rates accelerate with increasing habitat destruction (Tilman et al., 1994) and climate change (Urban, 2015).

Species at high risk of extinction have narrow geographical ranges, few populations, decreasing population trends, isolated habitats and are exploited by humans (Purvis et al., 2000; Palomares et al., 2012; Di Marco et al., 2015): such species usually have slow reproduction, limited dispersal ability, little genetic variation, specialised niches, low disturbance-tolerance, no prior contact to people and relatives that are also threatened with extinction. Many vulnerable species are only found in protected areas (Jackson & Gaston, 2008).

The population size is a strong indicator of extinction risk. If a population drops below a certain minimum viable population size, an extinction vortex can apply (Figure 4), which progressively reduces population size until extinction (Palomares et al., 2012). Inside the extinction vortex, genetic and demographic factors influence the population size, in addition to natural and human threats outside the extinction vortex. Due to genetic drift, small populations lose genetic diversity faster than large populations (Primack & Sher, 2016). Small populations may face a genetic bottleneck. Stochastic variation in birth and death rates, disruption of social behaviour by low population density and random environmental impacts also decrease population sizes (Frankham et al., 2004). However, environmental stochasticity can also support population survival (Higgins et al., 2000).

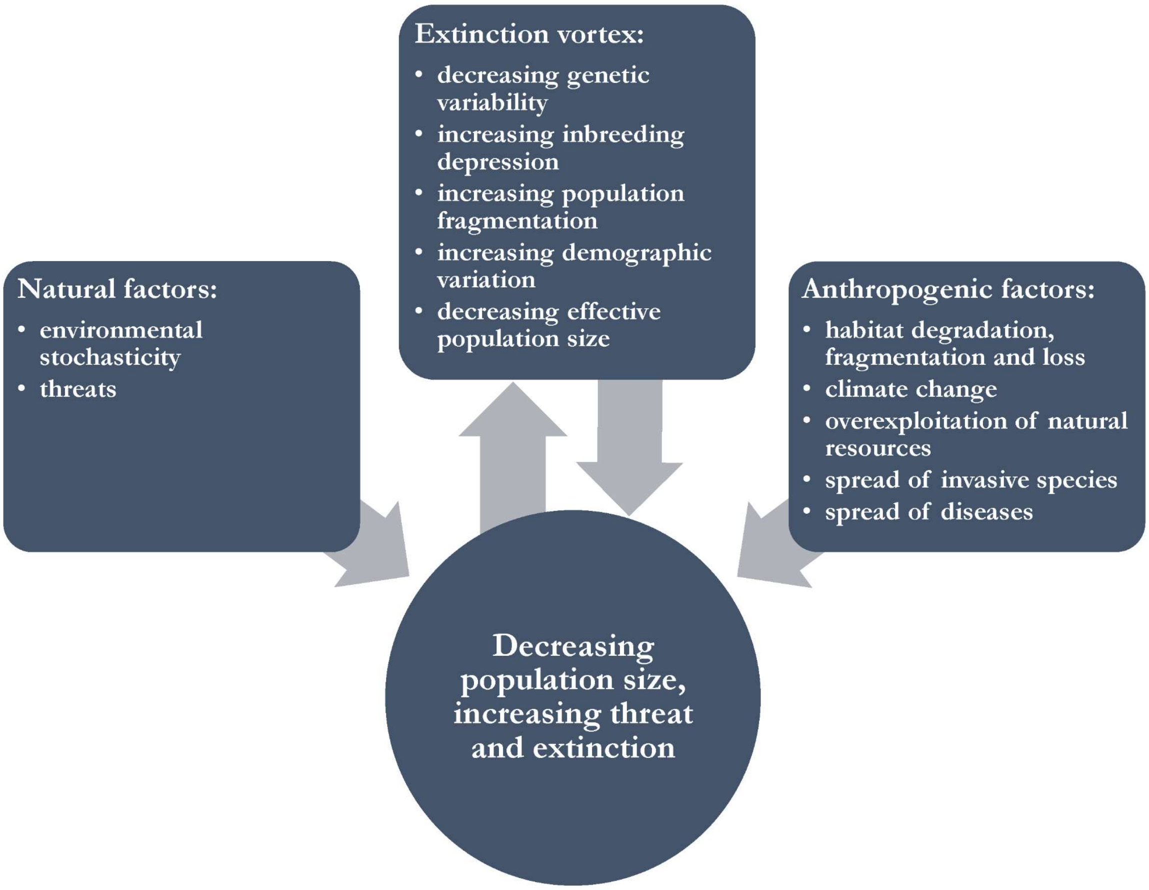

Figure 4. Factors decreasing population size and driving species to extinction, adapted from Primack & Sher (2016). The manuscripts of this dissertation aim at species conservation by assessing species diversity and anthropogenic threats inside protected areas.

The IUCN will refer to species as threatened or extinct if species-specific criteria are fulfilled, e.g. a certain population or range size (IUCN, 2001). Based on these criteria, the IUCN publishes the so-called Red Lists of threatened species. The IUCN also compiles Red Lists of threatened ecosystems (Rowland et al., 2019). These lists are fundamental tools to prioritise conservation strategies. Measures of species diversity change, such as the Red List Index (Butchart et al., 2007), the Living Planet Index (Collen et al., 2009) or the Biodiversity Intactness (Newbold et al., 2016) consider Red List species. These metrics integrate the range size of species or populations, the number of mature individuals, the number of breeding individuals and the rate of decline of population size or habitat (Hedrick, 2005; Scott et al., 2005; van Swaay et al., 2011). These assessments primarily address birds, mammals and amphibians. The Red List species have been used to calculate the aforementioned irreplaceability index of protected areas (Le Saout et al., 2013), which I included in Manuscript 1, 5 and 6.

The IUCN assessed 105,732 species including vertebrates, invertebrates, plants, fungi and protists, of which 28,338 (i.e. 27%) are threatened with extinction (IUCN, 2019b). The IUCN (2019b) estimates the proportion of threatened species per taxonomic group as follows: cycads 63%, amphibians 40%, selected dicots (i.e. magnolias, birches and cacti) 35%, selected reptiles (i.e. marine turtles, sea snakes, chameleons, crocodiles and alligators) 34%, conifers 34%, reef-forming corals 33%, sharks & rays 31%, selected crustaceans 27%, mammals 25%, birds 14%, selected gastropods (i.e. cone snails) 7.5%, selected bony fishes 7%, and selected cephalopods (i.e. octopuses) 4%.

The authors of the recent report from the 7th plenary session of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES) approximated that 1 million species are threatened with extinction (Díaz et al., 2019; IPBES, 2019). Conservationists would have to restore the habitat of over 500,000 terrestrial species to guarantee their future survival. About 10% of insect species tend to be threatened. The average abundance of native species has declined by over 20% across most terrestrial biomes since 1900. Six ungulate species would likely be extinct in the absence of conservation programmes. Moreover, 25% are the average proportion of species threatened across vertebrate, invertebrate and plant groups. Humans have driven at least 705 vertebrate species and 571 plant species to extinction since the 16th century (Díaz et al., 2019).

Research on threatened species as well as drivers, mechanisms and rates of extinction is ever important to improve conservation guidelines. Integrating paleo-ecological and present-day data will increase this knowledge further. A recent study, for instance, shows that arthropod decline is linked to human land use intensity at the landscape level (Seibold et al., 2019). Protecting the existing wilderness areas can halve the extinction rate of terrestrial species (Di Marco et al., 2019). Protected areas are therefore a promising tool to mitigate the sixth main mass extinction event in earth history.

3.8 Conservation biogeography

3.8.1 Foundations of conservation biogeography

This thesis is affiliated to the scientific field of conservation biogeography since it contributes to conserving biodiversity using terrestrial protected areas. Conservation biogeography integrates the fields of conservation biology and biogeography. Biogeography is the study of the temporal and spatial distribution of biodiversity. The core of biogeography addresses geographical extents larger than the landscape extent. Mapping and modelling spatial patterns of biodiversity over large extents lie at the heart of biogeography (Lomolino & Heaney, 2004). Biogeography relates to macroecology, but macroecology focuses on the statistical analyses of ecological data over large spatial extents rather than on the geographical patterns (Brown, 1995). Nevertheless, biogeography and macroecology largely overlap because the geographical distribution of biodiversity depends on the ecological relationships and vice versa.

Biogeography may have been one of the first interests that humans developed since the livelihoods of hunter and gatherer communities depended on knowledge about the geographical distribution of food and predators. The term *biogeography* first occurred in the 20th century, but contents of biogeography were already discussed during the early 19th century by leading scientists in the field of zoography and phytography, such as Alfred Russel Wallace, Charles Darwin, Phillip Scater, George-Louis Leclerc and Alexander von Humboldt (Whittaker & Ladle, 2011). Alexander von Humboldt laid the groundwork for several modern environmental sciences, e.g. ecology, evolution and biogeography (Schrodt, Santos et al., 2019). As a master of interdisciplinary thinking, he was the first biogeographer who raised concerns about the human impacts on nature in geographical contexts (von Humboldt, 1845). His thoughts strongly inspired the conservation and protected area movement that was later initiated by John Muir (Muir, 1901; Zimmerer, 2010). Hence, Alexander von Humboldt was a pioneer of conservation biogeography.

I refer to conservation biogeography as ‘the application of biogeographical principles, theories, and analyses, being those concerned with the distributional dynamics of taxa individually and collectively, to problems concerning the conservation of biodiversity’ (Whittaker et al., 2005). In other words, conservation biogeography generally aims at generating knowledge about the conservation of biodiversity in a geographical context. Conservation biogeography is particularly about understanding the human impacts on biodiversity and informing about how to protect and restore biodiversity across large geographical extents. Planning protected area design is therefore a typical element of conservation biogeography, for which classic components of biogeography such as the equilibrium theory of island biogeography (MacArthur & Wilson, 1967) and the metapopulation theory (Levins, 1969) are applied.

Conservation biogeography has been called a modern sub-discipline of conservation biology (Whittaker & Ladle, 2011). It is, however, deeply rooted in the natural sciences because biogeography already emerged during the 19th century, whereas conservation biology was established as a scientific field in the 1970s (Soulé, 1985). Moreover, theories of biogeography have always been applied in conservation biology, e.g. Dasmann’s biogeographical regionalisation approach to design regional protected area networks (Dasmann, 1972). The term *conservation biogeography* first appeared in a journal article by John

Grehan (1993) but without explanation. It was first defined at a conference of the International Biogeography Society in Washington in 2005 (Whittaker & Ladle, 2011).

Conservation biogeography has gained a strong momentum recently because current threats to biodiversity have led to severe losses of biodiversity worldwide. The scientific community particularly requests assessments of protected area effectiveness over large geographical extents (Watson et al., 2016). This thesis contributes to that demand via Manuscript 1, 5 and 6. Such investigations require huge amounts of biogeographical data, such as indicated in Manuscript 1, 4, 5 and 6, and efficient methods to collect and analyse these data, such as supplied by Manuscript 2 and 3. Conservation biogeographers have just started to examine the validity of data, the sensitivity of methods and the resulting uncertainty of findings (Ladle & Whittaker, 2011). There is still a huge potential for the field of conservation biogeography to grow given the increasing threats to biodiversity.

3.8.2 Protected areas

3.8.2.1 Roles of protected areas

Protected areas are the main tool for nature conservation and the common ground of all manuscripts included in this thesis. The CBD refers to a protected area in Article 2 as a 'geographically defined area, which is designated or regulated and managed to achieve specific conservation objectives' (United Nations, 1992). Similarly, Dudley (2008) defines a protected area as 'a geographical space, recognised, dedicated and managed through legal or other effective means to achieve the long-term conservation of biodiversity and associated ecosystem functions and services.' There is an agreement that both definitions have the same meaning, although Dudley's definition specifically relates to biodiversity conservation and ecosystem benefits to people (Lopoukhine & de Souza Dias, 2012). In this thesis, I refer to a protected area as a geographical space that is dedicated to conserve biotic and abiotic features that represent use, non-use and option values of nature. Moreover, this thesis concentrates on terrestrial protected areas.

The CBD (2019) manifested the significance of protected areas for biodiversity conservation in the Aichi Biodiversity Target 11: 'by 2020, at least 17% of terrestrial and inland water areas and 10% of coastal and marine areas, especially areas of particular importance for biodiversity and ecosystem services, are conserved through effectively and equitably managed, ecologically representative and well-connected systems of protected areas and other effective area-based conservation measures, and integrated into the wider landscape and seascape.' The CBD (2019) refers to other effective area-based conservation measures (OECM) as 'geographically defined area other than a protected area, which is governed and managed in ways that achieve positive and sustained long-term outcomes for the in-situ conservation of biodiversity, with associated ecosystem functions and services and, where applicable, cultural, spiritual, socioeconomic, and other locally relevant values.' A global database on OECMs has been recently launched (IUCN & UNEP-WCMC, 2019a), but it is still challenging to identify OECMs (IUCN, 2019a). The importance of protected areas is also shown by the Half-Earth project, which proposes to protect half of the global land to cope with the current biodiversity crisis (Wilson, 2016).

The global protected area estate has rapidly grown during the last few decades, which has been accompanied by stakeholders that express increasing and more diverse expectations towards protected areas (Watson et al., 2014). Protected areas were originally established to conserve sacred grounds, iconic landscapes, wildlife or natural resources. Nowadays they are expected to simultaneously conserve various biotic and abiotic features of nature, ecosystem functions, goods and services, and biocultural diversity. Intact ecosystems inside protected areas deliver services, such as providing carbon storage, drinking water, resilience to natural hazards, and resources for people and species to adapt to rapidly changing environments. Trade-offs between contrasting roles are therefore inevitable (Naughton-Treves et al., 2005). The more roles are assigned to protected areas, the more likely protected areas will miss a role. If they are ineffective, protected areas will be prone to degazettement, i.e. to a reduction in size, exploitation or status removal (Mascia & Pailler, 2011). There is, however, evidence that protected areas can fulfil multiple roles at the same time (Watson et al., 2014). Due to the ongoing threats to biodiversity and growing human demands, stakeholders will probably require protected areas to fulfil even more roles simultaneously in the future. To avoid unrealistic expectations and degazettement, it is necessary to understand what a specific protected area can provide under certain circumstances, such as limited management resources or growing threats.

3.8.2.2 Historical overview of protected areas

The establishment of protected areas traces back to restricting access and exploitation of natural resources in sacred and 'tapu' areas (Colding & Folke, 2001). Forest groves in India prevented deforestation even before the advent of agriculture (Bhagwat & Rutte, 2006). In medieval times game reserves were established enabling aristocrats to control game populations (Chape et al., 2005). In the 16th century colonial powers formed forest reserves to produce timber (Ladle et al., 2011).

Modern protected area movements emerged in the 19th century when new world views on the relationship between humans and nature appeared in Europe, North America, South Africa and Australia (Ladle et al., 2011). Protected areas were then established to conserve iconic natural features and wildlife (Phillips, 2004). In those days protected areas were often set up in areas without economic use (Runte, 1977). In 1821 the natural scientist Charles Waterton established a protected area on his private ground to prevent poaching and environmental pollution (Boettger et al., 1969). This may have been the first modern protected area worldwide. In 1836 the Prussian government bought the Drachenfels area to stop mining activities that would destroy this unique geological feature (Schmoll, 2004). This may have been Germany's first protected area (BfN, 2006). In 1864 the Yosemite Valley became the first protected area of the United States. Later, in 1872, the US Yellowstone was designated the world's first national park. The French forest of Fontainebleau became one of the first large protected areas in Europe in 1874. In Australia, the Royal National Park was established in 1879. In 1887 the New Zealand Tongariro National Park and the Canadian Banff National Park were founded. These national parks are among the oldest national parks worldwide (Winiwarter & Bork, 2015). Furthermore, state and country parks were formed during the end of the 19th century as recreation areas for urban dwellers to escape from the dust, smog and dirt of urban industries (Ladle et al., 2011). The development of state and country parks was supported by the open space movement, i.e. the amenity movement.

In 1871 the German naturalist Philipp Leopold Martin established the term *Naturschutz*, i.e. *nature conservation* (Koch & Hachmann, 2011). The maintenance of a status quo of nature was then aspired to, which led to the establishment of natural monuments as sites of aesthetic, cultural and scientific attraction (Winiwarter & Bork, 2015). In the German Empire, natural monuments were heavily promoted by the politician Wilhelm Wetekamp, the botanist Hugo Conwentz and the composer Ernst Rudorff, who are three pioneers of nature conservation (Boettger et al., 1969). The designation of natural monuments was, however, not legally binding. Since 1920 nature conservation areas are considered by German law, i.e. the Prussian law at this time (BfN, 2006). In the following year the Neandertal became one of the first legally protected areas on German ground. Later, in Nazi Germany, a law on landscape protection areas was passed. Because natural monuments were misused by nationalists and right-wing politicians during the first half of the 20th century, they have since been largely disregarded (Ladle et al., 2011).

To increase the national identity of US citizens after the American War of Independence, the painters and poets of the Hudson River School and the transcendentalist writers promoted American wilderness as a fundamental aspect of the American identity in the mid-19th century (Jepson & Whittaker, 2002). In this context, the foundation of wilderness reserves was strongly inspired by Henry David Thoreau, who refused any theology and stated that the transcendent truth was found in nature. At the end of the 19th century the American Boone and Crockett Club (B&CC) set the agenda to create wildlife refuges and sanctuaries to compensate the negative impacts of human expansion on natural environments and game populations (Jepson & Whittaker, 2002). The B&CC argued for the quality of the hunting experience rather than the number of killed animals. Wildlife conservation was thus supported by the pastimes of elite hunting societies. The B&CC was founded by Theodore Roosevelt in the United States in 1887, who later became the 26th US President.

At the beginning of the 20th century the political willingness for nature conservation was still widely missing in Europe and the United States. The Scottish naturalist John Muir then transformed the US transcendentalist movement into a broad societal movement that was able to influence policymakers (Worster, 2005). He founded the Sierra Club in 1892 that aimed at creating new protected areas to prevent nature's degradation. In 1900 European colonial powers signed the London Convention for the Preservation of Wild Animals, Birds and Fish in Africa (Ladle et al., 2011). This Convention intended to establish nature reserves in which hunting was strictly regulated, but the convention was never adopted. Later Gifford Pinchot, head of the United States Forest Service from 1905 to 1910, promoted discussions on the sustainable use of natural resources together with John Muir, who triggered the establishment of many forest and watershed reserves in America, Europe and their colonies (Brown & Pinchot, 1911). In contrast to Pinchot's rationale of sustainability, preservationist Muir applied religious arguments to achieve his conservation goals (Steiner, 2011).

The European analogue to the B&CC is the Society for Preservation of the Wild Fauna of the Empire (SPWFE), today known as Flora & Fauna International (FFI). The SPWFE was mainly concerned with game population in African colonies (Prendergast & Adams, 2003). The SPWFE and the B&CC contributed to the adoption of the Convention Relative to the Preservation of Fauna and Flora in their Natural State in 1933, the first global conservation treaty. This convention led to the creation of many more protected areas in the colonial territories of Africa and Asia (Jepson & Whittaker, 2002).

Only after World War II scientific evidence began to raise public awareness that ecosystem integrity and biodiversity strongly promotes human welfare (Ehrlich & Ehrlich, 1992). Subsequently, the conservation goals of many reserves were reformulated, from the utilitarian but sustainable exploitation of natural resources to the protection of biodiversity, ecosystem functioning and services. The United States Wilderness Act in 1964 was a result of John Muir's efforts and induced the protection of large national forests as wilderness areas (Ladle et al., 2011). The act also initiated the establishment of many more protected areas across the globe. Since the middle of the 20th century tourism inside protected areas has increasingly been permitted (Zeiger et al., 1992).

In the 1970s the in-situ conservation of species and ecosystems has come to the fore. Countries started to set up protected area networks to save nature from degradation (Watson et al., 2014). In 1970 the Nationalpark Bayerischer Wald became Germany's first national park, which I analysed in terms of conserving priority species in the European Union (EU) in Manuscript 1. The United Nations Educational, Scientific and Cultural Organization (UNESCO) launched the Man and Biosphere (MAB) Programme in 1971. The MAB programme is an intergovernmental scientific programme that works towards improving the relationship between people and nature (UNESCO, 2019). The transdisciplinary programme establishes MAB reserves, which aim at biocultural conservation. Due to their unique approach, MAB reserves are of special scientific interest. Therefore, I also investigated UNESCO MAB reserves in Manuscript 1 and 2.

Since then the rapidly growing number of protected areas led to conflicts with local communities because protected areas were often designated in top-down approaches and restricted the livelihoods of local communities living inside and in the surroundings of protected areas (Brockington et al., 2006; Agrawal & Redford, 2009). Hence, protected area management has since started to address cultural demands and human rights with efforts to decrease poverty and increase economic development. Nowadays protected areas achieve biocultural conservation (Naughton-Treves et al., 2005; Ferraro & Hanauer, 2011; Ferraro et al., 2011).

A systematic survey of peer-reviewed journals listed in the Web of Science shows that papers on protected areas date back to 1965. However, protected areas were not a continual topic in science before the 1980s (Figure 5). The amount of scientific publications on protected areas has dramatically grown since the beginning of 21st century. For this literature survey, I searched all publications listed in the Web of Science Core Collection on 26 November 2019 that address *protected area* or *protected areas* in the title, abstract or keywords using the search string '*TOPIC= "protected area" OR "protected areas"*'. A total number of 22,878 publications were found for the period 1945 to 2018. This search is simplistic and may consequently include publications that refer to *protected area* in another context than nature conservation.

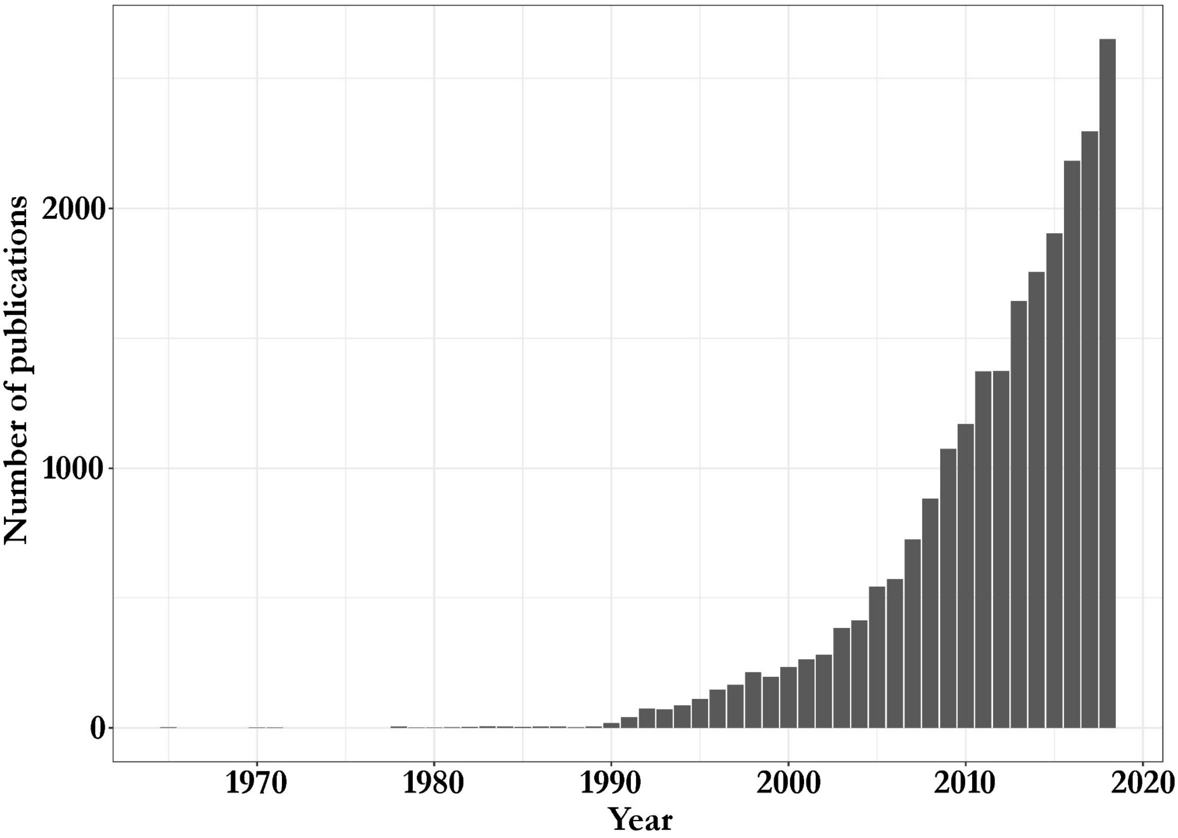

Figure 5. Number of peer-reviewed publications per year addressing *protected area* or *protected areas* in the title, abstract or keywords. The literature survey was conducted in the Web of Science Core Collection on 26 November 2019, applying the search string *'TOPIC= "protected area" OR "protected areas"'* for the period 1945 to 2018. Protected areas have been researched for about 60 years. Since the 1980s they are a continual topic in science, which has dramatically grown at the beginning of the 21st century. This search is simplistic and may consequently include publications that refer to *protected area* in another context than nature conservation. All manuscripts of this thesis refer to protected areas.

Nowadays crucial factors for the establishment of new protected areas are conservation laws and treaties at the national and international level. The UNESCO MAB Programme mentioned above is one example for this. The CBD is another renowned example (United Nations, 1992). The CBD was signed by 178 nations in 1992 and raised global awareness of the value of and threats to biodiversity. Countries committed themselves to protect their national biodiversity but were allowed to obtain profit resulting from biodiversity. Articles 8a and 8b of the CBD state that each country that signed the convention is obliged to establish and manage protected area networks on a national level. The convention is, however, not legally binding and the integration of international conventions into national law is challenging, which led to a variety of ways in which countries set up protected areas. Other treaties like the 1972 UNESCO Convention Concerning the Protection of World Cultural and Natural Heritage allowed nations to propose world heritage sites (United Nations, 1972). Many national parks became world heritage sites later on because the designation as a world heritage site causes more funds and other resources for protected area management, increasing management effectiveness

(Hockings et al., 2006). However, also unprotected areas can be proposed as world heritage site.

Other famous examples of conservation laws and treaties are the 1979 Birds Directive and the 1992 Habitats Directive of the EU. The EU member states are legally obliged to protect species of the Birds Directive by Special Protection Areas (European Environment Agency, 2019c) and species of the Habitats Directive by Special Areas of Conservation (European Environment Agency, 2019a), both of which compose the Natura 2000 protected area network. The Natura 2000 network is one of the most important conservation systems worldwide (Gaston et al., 2008; Jones-Walters et al., 2016), which is why I included it in my work. Manuscript 1 focuses on the distribution of Natura 2000 species listed in both directives. Other international treaties on biodiversity conservation address more specific concerns, e.g. the Bonn Convention (Convention on the Conservation of Migratory Species of Wild Animals), CITES, the International Treaty on Plant Genetic Resources for Food and Agriculture, or the Ramsar Convention on Wetlands. International conservation laws and conventions are required because species diversity and threats occur across country borders.

Eventually, and over time, a large variety of types of protected areas was established. Governments at the local, regional and national level designated protected areas in various ways. Citizens and organisations installed protected areas on private land. Indigenous people afforded the establishment of protected areas to ensure their own livelihoods or to preserve religious and cultural beliefs. Research and educational organisations set up protected areas for research, education and conservation. While governments do not always sufficiently enforce laws and rights regarding the establishment and management of protected areas, non-legal management regulations are sometimes applied to areas that are not legally protected but with positive conservation outcomes (Jepson et al., 2001). Hence, today's protected areas vary greatly in legal frameworks, responsible authorities, aims, attributes and governance.

3.8.2.3 Protected area designations

The denomination of protected areas often explicitly represents the purposes of the protected areas, which is comprehensively described by Jepson & Ladle (2010): game, forest and watershed reserves are to preserve game, timber and water respectively. Wilderness reserves are to protect pristine landscapes. National parks, however, do not completely disclose their conservation targets, although *national park* is probably the best-known protected area designation. National parks were originally founded to foster the national identity of people. In the United Kingdom, national parks played a key role to restore national identity after the collapse of the empire and were established in cultural landscapes adjacent to highly populated urban areas. In the United States, national parks were created, first, to preserve natural landscapes and, second, to form national identity after British colonialism. In developing countries, national parks were founded by governments to support local communities, sustainable economic development and global biodiversity targets. However, some governments have used this to improve their international reputations, to receive more conservation funds and to control remote areas under the disguise of conservation (Jepson & Ladle, 2010). I investigated national parks in Manuscript 1, 3, 4, 5 and 6.

Biosphere reserves are renowned protected areas, which have been promoted by the UNESCO MAB Programme (UNESCO, 2019). The programme's World Network of Biosphere Reserves (WNBR) consists of 701 sites in 124 countries. Biosphere reserves cover terrestrial, marine and coastal ecosystems. The management of biosphere reserves integrates biodiversity conservation and the sustainable human use of biological resources. The WNBR serves as a global observatory for climate change mitigation and adaptation. It includes monitoring of climate change impacts. The status of biosphere reserves is internationally accepted, but the national governments are responsible for their establishment and management. Three zones structure biosphere reserves. The core zone is strictly protected. It contributes to the conservation of landscapes, ecosystems, species and genetic diversity. The buffer zone around the core zone is used for ecological practices that are linked to research, monitoring, training and education. The transition area around the buffer zone allows for activities that support economic and human development in a sociologically, culturally and ecologically sustainable way. Manuscript 1, 2, 5 and 6 relate to biosphere reserves.

The increasing number of protected area designations led to a call for a globally standardised classification system. In 1994 the IUCN developed such a classification system including six categories according to protected area management targets (Dudley, 2008). The six protected area categories of the IUCN, which are applied in Manuscript 6, characterise the management of protected areas. Category I to IV means strict protection, while categories V and VI allow for the human use of natural resources, e.g. silviculture and agriculture. These so-called multi-management protected areas of category V and VI are generally larger, and integrate and benefit local people more than protected areas of other categories (Oldekop et al., 2016). Forest loss, for instance, is lower under higher protection categories (Leberger et al., 2019). The narrow focus on management goals is a main disadvantage of the IUCN categories. Protection status and management goals reflect neither protected area effectiveness nor efficiency, and vice versa (Jepson et al., 2001). Therefore, a new classification system was proposed, which is based on the measurement of biophysical variables, e.g. phylogenetic diversity, species diversity, ecological vulnerability and irreplaceability (Boitani et al., 2008). However, a purely biophysical assessment still lacks the sociological, cultural and economic dimension. A categorisation of protected area designations that combines biophysical, sociological, cultural and economic management aspects has not been developed yet.

The manuscripts of this thesis consider non-marine protected areas that fulfil Dudley's definition of protected area (Dudley, 2008). Information about these protected areas is stored in the World Database on Protected Areas (WDPA) managed by IUCN and UNEP (Bingham et al., 2019; IUCN & UNEP-WCMC, 2019b). The WDPA involves, for instance, strict nature reserves, wilderness areas, national parks, natural monuments, habitat and species management areas, protected landscapes and protected areas with sustainable use of natural resources. The WDPA also includes protected areas that are a product of specific programmes, laws and treaties, such as UNESCO world heritage sites, UNESCO MAB reserves and Natura 2000 sites.

3.8.2.4 Protected area coverage

The global protected area estate has significantly grown over the last 100 years (Watson et al., 2014; Bingham et al., 2019; Lewis et al., 2019). Among the IUCN management categories, protected areas of the categories V and VI account for the largest areal increase in the global protected area estate. It is remarkable that most of the global protected area coverage has been established over only a few decades (Watson et al., 2014).

The October 2019 version of the WDPA contains data on the boundaries of 225,161 protected areas (UNEP-WCMC et al., 2019). Out of these 225,161 protected areas, 219,438 are terrestrial and cover 15.0% of the global land area, i.e. approx. 20,210,878 km² (Figure 6). The terrestrial protected area extent is accordingly larger than South plus Central America and covers about the same area as used to grow crops globally. In Manuscript 5 and 6, I analysed the climate change impacts inside all designated terrestrial protected areas provided by the January 2018 version of the WDPA. The global protected-area estate described by the WDPA is, however, highly dynamic because of data-quality issues and on-the-ground changes (Lewis et al., 2019). The WDPA still misses many protected areas, especially those that were established by local communities, indigenous people, private persons, non-profit trusts, religious groups and corporations (Shahabuddin & Rao, 2010). Such protected areas can be very large (Peres & Nascimento, 2006).

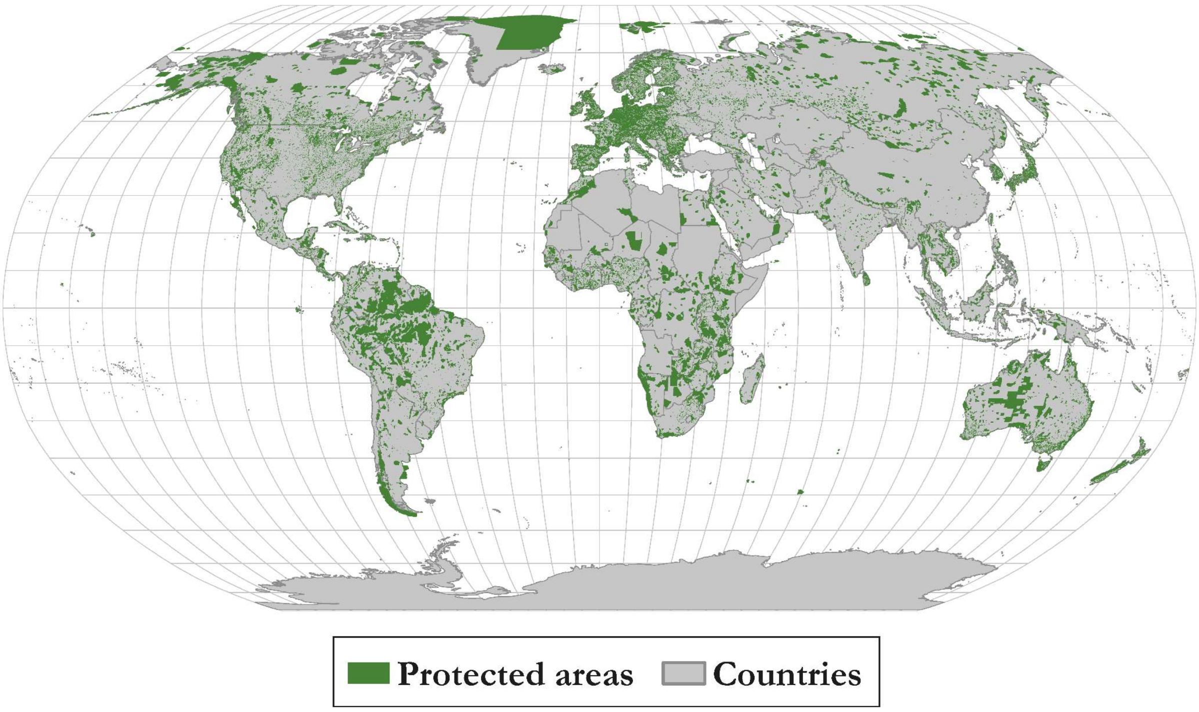

Figure 6. Non-marine protected areas (green) as provided by the October 2019 version of the WDPA, the World Database on Protected Areas (IUCN & UNEP-WCMC, 2019b). Europe seems to be entirely covered by protected areas, which is a cartographical artefact. I used the WDPA data in Manuscript 1, 5 and 6.

Almost every nation contains at least one protected area. Syria, Iraq, Haiti and Uruguay are countries with less than 1% of their land protected (UNEP-WCMC et al., 2019). Germany, Austria and the United Kingdom are countries with most protected area relative to their national area, which indicates that protected areas neither represent naturalness nor species richness hotspots but are strongly related to the socio-political framework.

Protected areas overlay 43.2% of the 821 terrestrial ecoregions, excluding Antarctica, by at least 17% (i.e. Aichi Biodiversity Target 11) of an ecoregion's land area. About 5.6% of the 821 terrestrial ecoregions have less than 1% land area under protection (UNEP-WCMC et al., 2019). Butchart et al. (2015) shows that about 78% of the Key Biodiversity Areas (KBAs) have a protected area coverage less than the Aichi Biodiversity Target 11 states, i.e. 17% for terrestrial and 10% for marine environments. Key Biodiversity Areas focus on safeguarding endangered plants and animals. They are identified using a global standard including eleven criteria organised into five categories: threatened biodiversity, geographically restricted biodiversity, ecological integrity, biological processes and irreplaceability (IUCN, 2016). Protected areas completely cover 21% of KBAs, whereas 35% of KBAs are not covered by any protected area (UNEP-WCMC et al., 2019). In addition, 5,510 IUCN Red List species occur within KBAs, which are 21% of all IUCN Red List species. Approximately 13% of the KBAs containing Red List species are completely covered by protected areas. About 31% are partially covered. Moreover, protected areas do not fulfil coverage targets for Red List species: Butchart and colleagues (2015) calculated that the global protected area estate had to double in order to reach these species-specific coverage targets.

However, KBAs and Red List species only represent a small proportion of the global biodiversity and biodiversity is not equally distributed across countries and ecoregions. Further, protected areas are often biased towards remote areas with low biodiversity and low human footprints and at high elevations (Joppa & Pfaff, 2009). For example, the Greenland National Park is the largest protected area measuring 3% of the terrestrial protected area but mostly covering ice and rock. There is consequently a risk to naively focus on such coverage targets while neglecting large proportions of biodiversity, threats and protected area management effectiveness.

3.8.2.5 Protected area planning and design

When the protected area movement took action, large land areas were already modified by humans. This is why protected areas frequently represent land that is not appropriate for human land use, such as steep slopes and infertile soils (Pressey et al., 1993). The early planning of protected area design was barely based on scientific assessments. Protected area planning became science-based when the biodiversity crisis was increasingly recognised by researchers during the second half of the 20th century (Jenkins & Joppa, 2009; Primack & Sher, 2016). Scientists then began to apply the species-area relationship and the theory of island biogeography (MacArthur & Wilson, 1967) to design protected areas. Accordingly, protected areas were seen as habitat islands isolated from each other by intense human land use (Cody & Diamond, 1975).

In the late 20th century systematic protected area planning emerged, striving for the conservation of maximal biodiversity (Margules & Pressey, 2000). Early systematic protected area planning used basic species diversity metrics, e.g. endemic species richness, to decide whether a newly established protected area would add conservation value to the existing protected area network (Margules & Usher, 1981; Shafer, 1999). Today's systematic protected area planning pursues several criteria regarding the complementarity, representativeness, persistence, redundancy, connectivity, efficiency and flexibility of protected areas in biodiversity conservation (Margules & Sarkar, 2007), also incorporating environmental change, such as climate change (Groves et al., 2012; Belote, Dietz, Jenkins et al., 2017).

Systematic protected area planning considers the protected area design because it influences conservation effectiveness. The species-area relationship and the theory of island biogeography helped to understand whether protected area characteristics are effective for biodiversity conservation (Table 3). Several effects of protected area characteristics on biodiversity conservation are examined in the manuscripts of this thesis. The manuscripts thus refer to systematic protected area planning.

Table 3. Characteristics of protected area design and their effectiveness to biodiversity conservation, adapted from Triantis & Bhagwat (2011) and Primack & Sher (2016). All manuscripts in this dissertation address at least one of these protected area characteristics.

Protected area characteristic	Low effectiveness to biodiversity conservation	High effectiveness to biodiversity conservation
Area	Small	Large
Number of protected areas	Low	High
Diversity of protected areas' sizes	Low	High
Connectivity (e.g. corridors, stepping stones)	Low	High
Area-to-edge ratio (i.e. edge effect)	Low	High
Biodiversity (e.g. species diversity)	Low	High
Environmental diversity (e.g. geodiversity)	Low	High
Threats to biodiversity (e.g. climate change)	High	Low
Control of human activities (e.g. buffer zones)	Low	High
Spatial planning extent	Local	Regional
Temporal planning period	Short-term	Long-term

The conservation community still debates whether single large or several small protected areas are more effective for biodiversity conservation given a fixed amount of conservation funds, i.e. the SLOSS debate (Soulé & Simberloff, 1986; McCarthy et al., 2006). The more and the larger the protected areas are, the higher the biodiversity is within the protected areas generally (Manuscript 1 and 5). In cultivated regions that have a long history of human land use, there is no other choice than establishing small protected areas of a given shape (Gaston et al., 2008). In semi-natural and cultivated landscapes, small protected areas can still have high conservation value (Manuscript 1). Small protected areas can be particularly effective and efficient in protecting single species, habitats, ecosystems or other natural features (Jarošík et al., 2011; Hunter et al., 2015; Richardson et al., 2015). Small protected areas can preserve high species diversity if they maintain key resources, such as ephemeral desert springs, which are essential for the survival of many desert species (Acuña et al., 2017). Large protected areas are certainly more effective in conserving populations of large mammals, for example (Newmark, 1995).

The shape of protected areas influences the edge effects on protected areas. The larger the area-to-edge ratio is, the larger the external influence is on protected areas (Yamaura et al., 2008). Edge effects are not only negative for species conservation. The transition zones (ecotones) between protected areas and unprotected surroundings can provide habitat for many species (Kellman, 1996).

Protected area networks and protected area connectivity support species migration and metapopulation dynamics, buffering detrimental effects of climate change on populations and species (Hannah, 2011; Thomas et al., 2012; Leach et al., 2013; Virkkala et al., 2014; Andrello et al., 2015; Thomas & Gillingham, 2015; Belote, Dietz, Jenkins et al., 2017; Lehikoinen et al., 2019; Peach et al., 2019; Virkkala et al., 2019): during migration populations and species can use protected areas as stepping stones and corridors. Species will be forced to migrate out of protected areas to track suitable habitat because they will lose their habitat inside the protected areas due to climate change (Manuscript 5 and 6). Under global warming species are migrating polewards and to higher elevations (Willis et al., 2008; Chen et al., 2011; Pecl et al., 2017; Steinbauer et al., 2018). The establishment of continent-wide protected area networks and migration corridors is therefore essential to safeguard numerous species (Soulé et al., 2004), such as large terrestrial mammals (Samimi & Nüsser, 2006). Presciently creating corridors, which do not necessarily require a protection status (Belote et al., 2016), supports species migration in the face of upcoming threats. Roads cause habitat fragmentation, while human constructions such as tunnels or bridges provide corridors between fragmented habitats. Nevertheless, corridors also cause differential seed predation (Orrock & Damschen, 2005) and facilitate the spread of invasive species, diseases and fire (Ogden, 2015). The effectiveness and efficiency of corridors depend on the corridor length, width and location (Gilbert-Norton et al., 2010).

In addition to protected area connectivity, spatially dynamic protected areas could also protect migrating species on the way (Hannah et al., 2007; Nuñez et al., 2013; Alagador et al., 2014), even though mobile protected areas are hard to realise in cultural landscapes. Further, new protected areas should be established in places where species will find suitable niches under climate change (Nadeau et al., 2015; Ferreira et al., 2019). Moreover, a diverse landscape matrix between protected areas generally decreases landscape resistance for species movement and gene flow (Daily et al., 2001; Rosenzweig, 2003), which can be realised by agro-forestry systems, for example (Bhagwat et al., 2008). Conservation effort outside protected areas refers to reconciliation ecology (Rosenzweig, 2003) or countryside biogeography (Daily et al., 2001).

Large protected areas can harbour more environmental diversity, i.e. the diversity of biotic and abiotic conditions (Manuscript 5 and 6). Environmental diversity includes geophysical diversity (i.e. geodiversity), such as topographic complexity and climate diversity. Environmental diversity promotes species diversity (Irl et al., 2015) and buffers impacts of threats like climate change (Ackerly et al., 2010; Scherrer & Körner, 2011; Comer et al., 2015; Heller et al., 2015; Lawler et al., 2015). Species occurring within protected areas covering large elevational and latitudinal gradients are likely to find suitable habitat within the same protected areas under climate change (Scherrer & Körner, 2011; Thomas & Gillingham, 2015). Furthermore, the planning of protected area design is increasingly concentrating on geodiversity instead of biodiversity (Schrodt, Bailey et al., 2019) because geodiversity drives biodiversity (Ackerly et al., 2010; Groves et al., 2012; Keppel et al., 2012; Comer et al., 2015; Lawler et al., 2015; Carroll et al., 2017). Hence, geodiversity indices can signal ecological change earlier than biodiversity indices (Anderson & Ferree, 2010).

The human land use density is typically lower inside larger protected areas (Wiersma et al., 2004). Human land use induces habitat fragmentation, which prevents species dispersal, splits populations, increases extinction threat and supports invasive species (Wilson et al., 2016). However, there are many species that depend on human intervention. A classic example for this is the dependence of grassland species on mowing. Vice versa, there are many people that depend on species and associated values of nature. It can consequently be sensible to integrate human activities into protected area design (Kadoya et al., 2009), such as in MAB reserves (Manuscript 1, 2, 5 and 6).

The integration of local protected area planning into a wider spatial and temporal perspective (Manuscript 1, 5 and 6), and into national and international policies would also foster individual protected areas in solving global environmental problems beyond their local conservation benefits (Kati et al., 2015; Geldmann et al., 2018; Bonebrake et al., 2019).

In reality, protected area planning and design is not only based on the conservation effectiveness of protected area characteristics but also biased by conservation costs and the demands of stakeholders, such as landowners, governments, policymakers, managers, practitioners and scientists (Scott et al., 2001; Armsworth et al., 2006; Lerner et al., 2007; Braunisch et al., 2012; Mills et al., 2014). Once the protected area plan is adopted politically, its practical implementation is yet another challenge. The socio-economic requirements of implementing protected area plans are often underestimated (Watson et al., 2016).

3.8.2.6 Protected area management

Protected area management includes and implements protected area planning and design. The flux paradigm and functionalist perspective have gained importance in protected area management over the last few decades because anthropogenic pressures have already persistently changed environments (Gillson et al., 2011). These changes have triggered the development of new theories in ecology and environmental management that acknowledge change (Wu & Loucks, 1995; Holling et al., 2002; Hobbs et al., 2010; Polasky et al., 2011; Aplet & McKinley, 2017). Those theories comprise concepts of disturbance, resilience, ecological thresholds and phase transitions (Holling, 1973; Berkes et al., 2003; Folke et al., 2004). In addition, theories applying reference states, e.g. potential natural vegetation, are called useless in ever changing environments (Chiarucci et al., 2010). In all these newer theories, ecological equilibria are assumed to be spatially restricted and temporally unstable (Whittaker et al., 2001). Under continuing human pressures and environmental changes, equilibrium-based models will probably be more and more disregarded.

It is vital to understand past dynamics to predict future developments and thus improve conservation planning and management despite permanent change (Hannah et al., 2002; Chapin et al., 2004). Ecosystem resilience, inertia, thresholds and shifts can be identified from past observations (Nogués-Bravo et al., 2008). Data on past environments are derived from fossil records, isotopes, charcoal, and archaeological and historical records. Paleo-ecological data disclosed that past climatic changes have already resulted in novel communities without modern analogues (Bush et al., 2004; Williams & Jackson, 2007). The climate change metrics applied in Manuscript 5 and 6 incorporate past climate observations to reveal the potential of community and ecosystem shifts inside protected areas in the future.

Today many theories, frameworks and guidelines for climate-smart conservation management exist (Hannah et al., 2002; Hannah, 2008; McClanahan et al., 2008; Hallegatte, 2009; Heller & Zavaleta, 2009; Hodgson et al., 2009; Hobbs et al., 2010; Conroy et al., 2011; Dawson et al., 2011; Game et al., 2011; Gray, 2011; Hole et al., 2011; Magness et al., 2011; Wintle et al., 2011; Cross et al., 2012; Groves et al., 2012; Watson et al., 2012; Gillson et al., 2013; Larson et al., 2013; Stein et al., 2013; Watson et al., 2013; Macgregor & van Dijk, 2014; Lawler et al., 2015; Aplet & McKinley, 2017; Belote, Dietz, McKinley et al., 2017; Gross et al., 2017; Michalak et al., 2017; Ando et al., 2018; Belote et al., 2018; Reside et al., 2018). This series of studies and my own research (Manuscript 5 and 6) show that recommendations for management strategies depend on many factors, e.g. the predicted climate change impacts (Dawson et al., 2011; Gillson et al., 2013), the predictions' uncertainties (Belote et al., 2018), nature's intactness (Watson et al., 2013), prevailing conservation objectives (Belote, Dietz, McKinley et al., 2017), the conservation capacity of land (Gillson et al., 2013), the management resources available (Wintle et al., 2011) and the risks of management actions (Richardson et al., 2009; Aplet & McKinley, 2017; Ando et al., 2018). The recommended management strategies are associated with management interventions that vary from low intensity, e.g. monitoring, to high intensity, e.g. assisted migration and restoration (Dawson et al., 2011; Gillson et al., 2013). Management practice may thus be conservative, innovative, flexible, reversible or experimental (Belote et al., 2018). In general, each climate-related management guideline aims either at the persistence and resistance of biodiversity despite climate change, or at the adaptation of biodiversity to climate change (Gross et al., 2017). The persistence strategy is primarily used for intact ecosystems under low to moderate pressures. If threat is imminent and conservation objectives are of utmost importance, the resistance strategy can be applied. In the face of rapid climatic changes, the resistance course can be used to save time while preparing strategies to handle the inevitable change of ecosystems. Management strategies that accommodate to unavoidable changes are required for ecosystems that will be heavily and rapidly affected by climate change (Manuscript 5 and 6). 'No-regret' strategies intend to achieve conservation benefits irrespective of climate change (Hallegatte, 2009). However, such climate-smart conservation approaches are derived from conservation literature that is biased towards specific species, ecosystems and regions (Felton et al., 2009). Consequently, those management recommendations can involve contextual drawbacks. In addition to these climate-smart strategies, protected area management is also expected to mitigate climate change by compensating greenhouse gas emissions, e.g. through forestation (MacKinnon et al., 2011; Kintisch, 2013).

Ecological restoration is recommended for ecosystems that are characterized by high climate change vulnerability (Dawson et al., 2011; Gillson et al., 2013; Watson et al., 2013) or low conservation value (Belote et al., 2018). Restoration is an intense management intervention to recreate an ecological state prior to degradation (Cairns et al., 2012). Restoration targets include the re-establishment of individual species, communities, ecosystem functions and services or other landscape features. Restoration can accordingly consider the compositionalist and functionalist perspective. Conservationists apply passive and active restoration. In passive restoration, ecosystems restore without human intervention. In protected areas, restoration increases habitat extent, quality and connectivity (Cairns et al., 2012), to buffer climate change impacts (Manuscript 5 and 6). Restoration is, however, only meaningful when the threats to restoration targets have been mitigated or removed (Venevsky & Venevskaia, 2005). Hence, restoration is difficult under persistent climate change impacts.

A special type of restoration is rewilding. Rewilding is about decreasing human intervention and increasing the self-regulatory ability of ecological and evolutionary processes focusing on the reestablishment of former species assemblages (Svenning et al., 2016). Rewilding can be applied to large extents in contrast to other conservation practices that require intensive human control. Nevertheless, rewilding is also controversial since a lack of control may lead to ecological consequences over large extents that are not intended (Corlett, 2016).

Because ecological restoration and rewilding cannot compensate for the loss of biodiversity, sustaining pre-existing biodiversity takes priority (Moreno-Mateos et al., 2015), also within protected areas (Manuscript 1, 5 and 6). There is, moreover, evidence that restoration programmes are much more expensive than protecting existing habitats (Wilson et al., 2014).

Assisted migration refers to the translocation of species and populations to safeguard those that cannot keep track with climate change velocity (Hoegh-Guldberg et al., 2008; Lunt et al., 2013; Hendricks et al., 2016). Assisted migration programmes prefer rare and endangered species, but the assisted colonization of pre-adapted ecotypes of keystone species can actually be more effective for biodiversity conservation in general (Kreyling et al., 2011). Nevertheless, assisted migration between protected areas includes the ecological risks of introducing non-native species (Olden et al., 2011). If assisted migration does not work, ex-situ conservation can be the last chance for some species to persist under climate change.

The introduction of non-native species to protected areas is also enhanced by climate change (Olden, 2006). Non-native species can cause a loss of biodiversity and ecosystem functioning (Perrings et al., 2005; Simberloff et al., 2005). The impacts of invasive species have already caused substantial economic costs (Pimentel et al., 2005; Marbuah et al., 2014). Hence, biotic homogenisation should be taken into account by protected area management (Higgins et al., 1999; Rooney et al., 2007; Hulme et al., 2014; Foxcroft et al., 2017). However, non-native species do not always induce a loss of taxonomic, genetic and functional diversity in the native communities (Olden et al., 2004). Non-native species can prevent erosion, and provide nectar and nesting ground (Kendle &

Rose, 2000; Shackelford et al., 2013). In a world being intensely altered by anthropogenic threats, conservationists increasingly tend to accept novel communities with non-native species (Hobbs et al., 2013; Hagerman & Satterfield, 2014).

Besides taking into account ecological dimensions, protected area management also needs to consider social implications. Protected areas often force the local population to change their behaviour and ways of living, which can lead to opposition. However, long-term success of protected areas depends on the acceptance of the local people. If people do not comprehend the protected area management, they may oppose the protected area concept and management staff, provoking conflicts at the expense of achieving conservation goals (Andersson et al., 2007; Mascia & Claus, 2009). Protected area management consequently needs to describe, explain and communicate conservation targets and related management implications as well as benefits to local people clearly, which also reveals whether management plans match with conservation targets (Schmidt et al., 2019).

Human activities inside protected areas increase worldwide (Geldmann et al., 2019). Hunting, recreational activities and anthropogenic modifications of the fire regime are threats to protected area effectiveness (Schulze et al., 2018). Management approaches are thereby needed that consider human demands and offer solutions to human-induced conservation problems. Biocultural conservation management accounts for cultural diversity and biodiversity alike (Gavin et al., 2018). Co-management (Gavin et al., 2015), integrated conservation development projects (Roe et al., 2013) and community-based conservation (Brooks, 2017) integrate local people into protected area management. Such protected area management allows indigenous communities and local people to sustainably use biodiversity for their livelihoods, which simultaneously supports biodiversity conservation. Biocultural management resolves conflicts between local people and animals destroying harvests, for example (Andrade & Rhodes, 2012). Such integrated management is realised by recognizing land tenure, or access and resource rights. The exploitation of natural resources within protected areas is prevented by adopting certificates for sustainable products from protected areas, by restricting the trade of wildlife, by restricting the sale of firearms, by closing roads built for logging, by adopting legal protection of wildlife, and by controlling hunting and harvesting (Cinner & Aswani, 2007; Österblom & Bodin, 2012; Moro et al., 2013). Local people can be offered other sources of income, such as being employed in the protected area management through monitoring programmes (Anadón et al., 2009), ecotourism and hunting (Naidoo et al., 2016). Revenues from protected area management can be redirected to local communities, which avoids eco-colonialism (Goodwin, 1996). There is evidence that protected areas with tourism in developing countries have positive effects on the well-being of people living in the protected area surroundings (Naidoo et al., 2019).

Protected area zoning is another possible management solution to conservation conflicts that result from human activities inside protected areas. To achieve specific conservation targets, the strict exclusion of people from protected areas can be necessary, e.g. if the human use of natural resources threatens the persistence of endangered species (Packer et al., 2013). In such cases, some protected area zones may allow human activities, whereas other zones strictly exclude humans. The MAB reserves (Manuscript 1, 2, 5 and 6) are protected areas that apply such zoning: local people are allowed to sustainably use resources in buffer zones around strictly protected core zones (UNESCO, 2019).

Eventually, protected area management requires financial resources for staff, equipment and infrastructure (Tranquilli et al., 2012; Becker et al., 2013). Income from sales of hunting licenses is a potential funding source (Crosmary et al., 2015), which is controversially discussed in terms of moral and ethical values. Killing animals for conservation purposes fosters illegal poaching and the devaluation of biodiversity (Selier et al., 2014). About US $3.4 to 4.8 billion are indispensable to improve the IUCN conservation status of all endangered Red List species by one level (McCarthy et al., 2012); the protection and management of areas harbouring those species are estimated to cost about US $76 billion annually. Funding from (inter-)national conservation organisations and governmental agencies still needs to increase (Watson et al., 2014), even though conservation funds have significantly grown over the last four decades (Zaradic et al., 2009). The World Bank spends, on average, US $275 million annually to protect areas in developing countries (Hickey & Pimm, 2011). As a comparison, the United States spent threefold the amount for military purposes in 2014 (Primack & Sher, 2016). Shifting priorities of large funding bodies to conservation issues would boost conservation effectiveness globally (Rands et al., 2010). Funds can be spent on protected area expansion and management enforcement. Funds can usually produce greatest conservation benefits if they are concurrently spent on management enforcement and protected area expansion (Kuempel et al., 2018; Adams, Iacona et al., 2019).

3.8.2.7 Prioritisation in protected area planning and management

Protected area planning and management have to prioritise conservation objectives because time and financial resources for conservation action are limited (Laurance, Koster et al., 2012; Martin et al., 2012; Wilhere, 2012; Maron et al., 2013). In the conservation context, priority species are usually charismatic, symbolic and culturally or economically important, i.e. flagship species. Priority species can be rare, endemic, endangered. Keystone and umbrella species also frequently obtain conservation priority. Another prioritisation criteria is species distinctiveness that is quantified by genetic and taxonomic dissimilarity between species (Faith, 2008). Priority species may be indicators of community and ecosystem health (Branton & Richards, 2011). In the EU, certain priority species are listed in the Birds and Habitats directives, which Manuscript 1 focuses on. The EU member states are legally obliged to protect these species through the Natura 2000 sites. Species of the Birds Directive are additionally preserved via restrictions on hunting, capture and trade, and via research, monitoring and management action (European Environment Agency, 2019c). EU member states must safeguard species of the Habitats Directive on the entire EU territory (European Environment Agency, 2019a). The exploitation of these species is legally restricted. Another tool for species conservation are Red Lists of threatened species. Into Manuscript 5 and 6, I integrated the irreplaceability index that prioritises IUCN Red List species globally (Le Saout et al., 2013). Apart from the species to be conserved, protected area management also prioritises the eradication of invasive species (Robertson et al., 2003).

Prioritisation addresses biodiversity beyond the species level as well. Tallis and Polasky (2009) show that conservation proposals prioritising ecosystem services secured more funds than proposals about priority species. Conservationists also simply focus on large wilderness areas because they are characterised by little or no human impacts, provide reference for restoration efforts and efficiently protect large mammals (Primack & Sher, 2016). Furthermore, in the hotspot approach, areas of high biodiversity obtain priority. Biodiversity hotspots are especially rich in endemic species. Global biodiversity hotspots for conservation have been identified for plants (Darbyshire et al., 2017), birds (Di Marco et al., 2016) and a mixture of species groups (Myers et al., 2000). The hotspot approach has also acquired large conservation funds (Primack & Sher, 2016).

Prioritising protected areas in receiving funds should not only be based on the size or location of protected areas inside biodiversity hotspots (Manuscript 1) but also on the prevailing threats to protected areas. Manuscript 5 and 6 guides the prioritisation of protected areas regarding the degree of potential climate change impact. To ensure protected area effectiveness and efficiency, protected area management and planning must be prioritised according to both, the biodiversity to be conserved and the threats prevailing (Visconti et al., 2010; Reside et al., 2018; Bonebrake et al., 2019).

3.8.2.8 Data for protected area planning and management

Anthropogenic pressures are quickly altering nature, which requires protected area planning and management to consider up-to-date data on the state of nature and the forces influencing it. Monitoring means recording data over time (Yoccoz et al., 2001). Monitoring is needed to measure management progress towards conservation targets (Larson et al., 2013). Some authors argue that national-level monitoring is essential to reach global conservation goals (Collen et al., 2013). However, long-term monitoring of biodiversity is currently rare (Ondei et al., 2018). The International Long-Term Ecological Research network (ILTER) is one example of long-term environmental monitoring across four continents. The BioTIME database is another global example, storing biodiversity time series (Dornelas et al., 2018). To compare results from different monitoring programmes, standardised methodology is needed. Standardised monitoring can be realised by field stations, field surveys and remote sensing techniques, and ideally combinations thereof.

Monitoring requires technical capacity that is costly. The Global Environmental Facility is one of the largest financial backers of biodiversity conservation but barely supports monitoring programmes (Primack & Sher, 2016). Since financial resources are limited, monitoring objectives are, like conservation targets, prioritised. Monitoring concentrates on ecological key components, e.g. keystone species, essential abiotic features and socio-economic developments (Lindenmayer et al., 2011; Andrade & Rhodes, 2012; Pocock et al., 2015). Nevertheless, to achieve global conservation goals as stipulated in the CBD, funding for monitoring needs to be available. Moreover, conservationists demand cost-efficient monitoring techniques (Haase et al., 2018).

Remote sensing is a quickly developing method for environmental data collection and monitoring that facilitates time- and cost-efficient biodiversity observations (Rocchini et al., 2019), which is particularly important for conservation while nature is rapidly changing (Horning et al., 2010; Turner et al., 2015). The cooperation between the remote sensing and conservation community is still evolving (Pettorelli et al., 2014). Rose and colleagues have identified ten major opportunities on how remote sensing can support conservation, addressing e.g. the monitoring of species distributions, ecosystem functioning and services, land use change, habitat degradation, climate change impacts and management effectiveness (Rose et al., 2015). Remote sensing products can also be used to plan protected area networks (Wegmann et al., 2014). Remote sensing data are used to monitor the status of protected areas, such as indicated by vegetation properties, human disturbance and the distribution of native, non-native and migratory species (Nagendra et al., 2013; Schmidtlein et al., 2014; Gillespie et al., 2015; Reynolds et al., 2017; Skowronek et al., 2018). Current advances in remote sensing technology improve such applications further. The Sentinel missions of the European Space Agency (ESA), for instance, provide space-borne radio detection and ranging (RaDAR) data as well as multi-spectral imagery, facilitating land, ocean and atmospheric monitoring with global coverage, high spatial resolutions and short revisit periods (ESA, 2019b). New developments in light detection and ranging (LiDAR) technology are able to measure two- and three-dimensional structures, which are used, for example, to monitor vegetation growth (Pettorelli et al., 2014). In Manuscript 2, I tested whether multi-spectral Sentinel-2 imagery and airborne LiDAR data are able to represent beta diversity patterns of plant assemblages. This would allow to measure the dissimilarity between plant communities in a short time and at low costs. Such time- and cost-efficient species diversity assessments support conservation planning and management across large geographical extents, where the collection of field data is not feasible.

Since field surveys are time-consuming and costly, they are required to become as efficient as possible (Rada et al., 2019). They should be designed in a way that maximises the ratio between information content and sampling effort. Information content of species data is, however, dependent on the spatial grain and extent of the data (Wiens, 1989; Levin, 1992; Rosenzweig, 1995; Peterson & Parker, 1998; Storch et al., 2008; Chave, 2013). The search for an optimal sampling design is rooted in the question of the minimal area representing communities (Hopkins, 1957). Moreover, the quantity, size, shape and spatial configuration of sampling units (i.e. plots) control species diversity estimates (Kenkel et al., 1989; Chiarucci et al., 2001; Keeley & Fotheringham, 2005; Stohlgren, 2007; Dengler, 2009; Bacaro et al., 2015; Güler et al., 2016). In Manuscript 3, I developed an approach to find an optimised sampling design for information about species diversity that improves data collection with limited resources.

Two of the most common ways to map biodiversity over large geographical extent are the grid-cell based approach (Manuscript 1) and range mapping. Range maps are usually drawn by experts who know many occurrences of the species and extrapolate those (Boakes et al., 2010). Therefore, range maps include a high degree of uncertainty. They are not useful for conservation planning based on small grain and extent, and are sometimes too coarse for modelling future range dynamics (Rondinini et al., 2006). False occurrences (i.e. errors of commission) are more likely than false absences (i.e. errors of omission) because experts tend to overestimate the species ranges when drawing (Riddle et al., 2011). In the grid-cell based approach, a grid cell will be marked occupied if the species is observed in the cell. False absences are here more likely than false occurrences because experts tend to underestimate the number of occupied cells. Analysing the sensitivity of occurrence data to sampling bias is always sensible (Manuscript 1). Geographical occurrences are less precisely locatable with increasing grain size. Owing to this, species diversity metrics that result from occurrence maps depend on the grain of occurrence data (Whittaker et al., 2005), such as demonstrated in Manuscript 1. It is consequently meaningful to analyse the sensitivity of results derived from gridded data to grain size (Manuscript 2 and 3).

Advanced techniques are emerging to record biodiversity data, e.g. automatic species identification (Barré et al., 2017), DNA barcoding (Hebert et al., 2003), non-invasive methods for individual identification, crowdsourcing for species distribution data and sampling approaches for remote and low-technology areas, including traditional knowledge from indigenous communities (Pimm et al., 2015). Species can increasingly be fitted with data loggers that track their movements and activities since these devices shrink in size due to technological advancements (Allen & Singh, 2016). Novel assessments of species diversity use acoustic data, e.g. the echolocation calls of bats, occupancy indices and even socio-economic data (Collen et al., 2013). The temporal development of threatened populations and species can, for instance, be reflected by the Red List Index (Butchart, Akcakaya et al., 2006) and the Living Planet Index (WWF, 2018). These indices integrate measures of genetic diversity, population abundance and range size to estimate extinction risk. These indices are used to prioritise species and populations for conservation efforts.

Global information systems, data repositories, databases and single data sets play a central role in fostering global conservation research and knowledge. The documentation of metadata, which sufficiently describes the data, is essential to efficiently store, search and use the growing amount of data (Wohner et al., 2019; Wüest et al., 2019). Examples used in the manuscripts of this thesis are protected area data from the WDPA (IUCN & UNEP-WCMC, 2019b), the irreplaceability index for protected areas (Le Saout et al., 2013), species occurrence data from the portal of the European Environment Information and Observation Network Eionet (European Environment Agency, 2019b), the global climate data sets from WorldClim (Hijmans et al., 2005) and TerraClimate (Abatzoglou et al., 2018), the global topographic variables from Amatulli et al. (2018), the global human footprint map (Venter et al., 2016), the global biome and ecoregion maps (Olson et al., 2001), satellite data from the Sentinel missions included in the Copernicus programme (ESA, 2019a), airborne LiDAR data from the Spanish National Geographic Institute (Spanish National Georaphic Institute, 2019), the Dynamic Ecological Information Management System to enter metadata (DEIMS; Wohner et al., 2019) and the figshare repository to store resulting data (figshare, 2019). Other prominent examples of global observation and information facilities are the Botanical Information Network and Ecology Network (BIEN), the Global Biodiversity Information Facility (GBIF), the Global Inventory of Floras and Traits (GIFT), the Map of Life, the TRY Plant Trait database, the sPlot vegetation-plot database, the Catalogue of Life, the Encyclopedia of Life, the Biodiversity Information System of Europe (BISE), the Global Earth Observation System of Systems (GEOSS), the LifeWatch infrastructure, the Data Observation Network for Earth (DataONE) and the DRYAD Digital Repository. Many such systems enable citizen scientists to contribute to data collection, monitoring and analysis, i.e. crowdsourcing (Devictor et al., 2010; Danielsen et al., 2014; Sullivan et al., 2014; McKinley et al., 2017).

3.8.2.9 Protected area effectiveness

The increasing extent of the global protected area estate is not necessarily an indicator for either effective or efficient biodiversity conservation (Barnes et al., 2018; Geldmann et al., 2019; Visconti et al., 2019). The global protected area coverage is growing, but biodiversity is still declining (Watson et al., 2014). One reason for this is the bias of protected area coverage towards remote places with low biodiversity, as discussed earlier. However, the discrepancy mentioned has also led to the development of measurements for protected area management effectiveness, i.e. the degree to which conservation targets are met by protected area management (Hockings et al., 2006). The assessment of management effectiveness requires conservation goals, but not all protected areas aim at measureable conservation targets, e.g. protected areas that enable nature to develop without human interventions. For those protected areas, management effectiveness needs to be assessed in different ways, such as by assessing the degree of human disturbances inside the protected area. Given that conservation targets need to be quantifiable, estimating management effectiveness also requires monitoring data from protected areas.

Methods to evaluate management effectiveness are manifold due to the diversity of protected area designations, their management and conservation targets (Leverington et al., 2010). The IUCN World Commission for Protected Areas established a renowned approach in which management evaluation includes the definition of assessable conservation goals, the estimation of applied resources, the selection of target indicators, the measurement of those indicators, and the analysis, interpretation and communication of results (Hockings et al., 2006). Species diversity within protected areas (all manuscripts) is, for instance, one measure of management effectiveness.

To assess and improve protected area management across protected area networks, the Global Database on Protected Area Management Effectiveness (GD-PAME) was launched (Coad et al., 2015). The GD-PAME currently includes 21,743 protected areas in 169 countries, i.e. 9.1% of the protected areas reported in the WDPA or 19.9% of the global protected area extent (UNEP-WCMC et al., 2019). The database reveals that only 21% of the countries reach the management effectiveness target, which is to evaluate at least 60% of their national protected area coverage. The management effectiveness tracking tool (METT) is related to PAME and records the quality of protected area management over time (Mascia et al., 2014). Such tools and databases are used to assess the effects of protected area management on biodiversity conservation inside protected areas (Geldmann et al., 2018). The PAME metrics are, however, criticised for insufficiently considering biodiversity outcomes (Visconti et al., 2019).

It should be noted that conservation goals per se can be more or less reasonable as a recent debate about Aichi Biodiversity Target 11 discloses (Barnes et al., 2018; Visconti et al., 2019; Woodley et al., 2019). This controversy revolves around arguments for and against setting protected area coverage as a conservation target. Protected area coverage is a measure easy to apply and to understand for policy-makers but does not account for biodiversity, ecosystem services and social equity within and around protected areas, nor for the connectivity between protected areas. Therefore, management effectiveness needs to be considered in the context of conservation targets at all times.

Recent reviews prove that protected areas can be effective in conserving biodiversity. Protected areas decrease habitat degradation (Joppa & Pfaff, 2010; Geldmann et al., 2013) and maintain species and populations better than other conservation measures (Hilborn et al., 2006; Karanth et al., 2009; Walston et al., 2010; Taylor et al., 2011; Laurance, Useche et al., 2012; Geldmann et al., 2013). At the local extent, biodiversity is higher inside protected areas than in their surroundings (Coetzee et al., 2014; Gray et al., 2016). Consequently, protected areas decelerate the decline of biodiversity, even though they cannot halt the loss completely (Laurance, Useche et al., 2012; Heino et al., 2015; Dähler et al., 2019; Geldmann et al., 2019; Leberger et al., 2019; Rada et al., 2019). Protected areas will be especially effective for global biodiversity conservation if they are located in biodiversity hotspots (Joppa et al., 2013), actively managed and well-funded (Geldmann et al., 2018; Coad et al., 2019). Protected areas can remain effective in preserving species despite climate change (Beale et al., 2013; Lawson et al., 2014; Santangeli et al., 2017; Lehikoinen et al., 2019; Virkkala et al., 2019). In addition, protected areas effectively provide ecosystem services, e.g. climate change mitigation and adaptation (Scharlemann et al., 2010; Soares-Filho et al., 2010; MacKinnon et al., 2011), natural catastrophe control and the provision of habitat and natural resources (Postel & Thompson, 2005; Palomo et al., 2013; Xu et al., 2017), tourism and recreation (Balmford et al., 2009) and poverty reduction (Andam et al., 2010). Protected areas that show no positive difference compared to their surroundings, miss their conservation targets completely, or undergo habitat degradation are called 'paper parks' since they essentially do not exist on the ground (Joppa et al., 2008).

3.8.2.10 Protected area challenges

The deficits of knowledge about nature's diversity induce uncertainties in conservation planning and management but are especially problematic to conservation because it is challenging to convince citizens and politicians of conservation action and funding via insufficient information (Funtowicz & Ravetz, 1994; Francis & Goodman, 2010; Gray, 2011). Since conservation funds are needed to fill knowledge gaps, this poses a dilemma. Open access publications, open data and open-source software help to fill this gap by gathering and sharing knowledge. All manuscripts of this thesis are open access, and include open data and software code.

If species diversity is the conservation target, protected area planning and management will have to thoroughly measure species diversity (Braunisch et al., 2012; Watson et al., 2016). However, such measurements mostly focus on single diversity indices, such as species richness or abundance, and neglect the multiple dimensions of species diversity (Socolar et al., 2016). This might mislead planning and management since species richness changes are uncoupled from changes in other species diversity metrics (Hillebrand et al., 2018). Comprehensive assessments of species diversity, including various diversity metrics, are rarely conducted but deliver complementary information for species conservation (Chiarucci et al., 2008). Manuscript 1 provides a comprehensive assessment of the diversity of priority species inside individual protected areas within a continental network. The results of this study should be used to guide the local protected area management towards conserving continental species diversity by means of representativeness, redundancy and complementarity.

Measuring species diversity inside protected areas requires data on species occurrences. However, field surveys are time-consuming and costly, while management resources for data recording are limited. Remote sensing is a time- and cost-efficient tool to assess species diversity. Inventory diversity is often estimated by remote sensing, but differentiation diversity has been widely neglected in remote sensing applications (Rocchini et al., 2018), although beta diversity is essential for conservation planning (Socolar et al., 2016). Manuscript 2 was set out to explore the ability of remote sensing signals to reflect differentiation diversity between plant communities, i.e. beta diversity. If remote sensing products are able to represent the compositional dissimilarity between species assemblages, differentiation diversity can be measured within protected areas of large extents in short time and at low costs, which benefits protected area planning and management.

The optimisation of field sampling techniques is a hot topic in conservation biogeography, too (Serra-Diaz & Franklin, 2019). Optimisation means collecting more information in shorter time and at lower costs. The ratio between the amount of information collected and sampling effort (i.e. time and costs) can be increased, particularly in vegetation surveys (Kenkel et al., 1989; Chiarucci et al., 2001; Keeley & Fotheringham, 2005; Stohlgren, 2007; Dengler, 2009; Bacaro et al., 2015; Güler et al., 2016). Manuscript 3 contributes to this topic by demonstrating a field sampling approach that maximises the ratio between the amount of species diversity information and sampling effort ,i.e. the number and size of sampling units. I applied this approach to alpine grassland, but it can be applied to any other study system. Because protected area planning and management benefits from available data on species diversity, I published these data on alpine grassland diversity as open data (Manuscript 4). This is particularly important since the alpine grassland is a climate-threatened ecosystem (Dirnböck et al., 2003).

Uncertainty in species distinction affects protected area planning and management because the geographical areas of biological and phylogenetic species can deviate (Ryder, 1986; Agapow et al., 2004). Uncertainty in species diversity estimates also results from taxonomic errors. Different species concepts lead to inconsistent species distinctions and synonymy (De Queiroz, 2007; van Dyke, 2008). Synonymy means that multiple names refer to the same species. In Manuscript 4, I show the synonymy of alpine grassland species. A growing number of taxonomists (Frobel & Schlumprecht, 2016), and modern taxonomic and phylogenetic analyses, e.g. automatic species identification (Barré et al., 2017) and DNA barcoding (Hebert et al., 2003), are needed to reduce this uncertainty in the future.

Anthropogenic climate change also induces uncertainty in protected area planning and management. Climate change is an unavoidable future challenge for protected areas (Hannah, 2008). Protected areas are exposed to climate change effects, such as rising temperatures, melting of snow and ice, more severe droughts and storms, seasonal shifts, rising sea level and increased environmental acidification (Gross et al., 2017). Climate change will thus cause gains (Berteaux et al., 2018) and losses of biodiversity within protected areas (Velazco et al., 2019). Climate change impacts may have already affected protected areas to a degree that makes it impossible to achieve their conservation targets (Hannah et al., 2002; Scheffer et al., 2015). In any case, the risk of protected area downgrading, downsizing and degazettement (PADDD) will grow if protected areas lose the biodiversity they were intended to protect (Hole et al., 2011; Thomas & Gillingham, 2015). Climate change modifies and redistributes biodiversity, thus forming novel ecosystems (Walther, 2010; Scheffers et al., 2016; Pecl et al., 2017), whose functioning and contributions to human well-being are unclear (Hobbs et al., 2006). Climate-induced changes interact with other threats to biodiversity inside protected areas, e.g. habitat degradation and fragmentation, or the spread of invasive species (Schulze et al., 2018). These threats can accumulate (Bowler et al., 2019). Consequently, climate change hinders protected area management effectiveness by modifying and potentially decreasing biodiversity, with cascading effects on ecosystem functioning and services. Moreover, the uncertainty in future climate projections limits climate-smart management planning (Midgley et al., 2007; Millar et al., 2007; Hallegatte, 2009; Conroy et al., 2011; Gray, 2011; Wang et al., 2012; Bagchi et al., 2013; Pacifici et al., 2015; Michalak et al., 2017; Belote et al., 2018).

For numerous species, protected areas are the only remaining safe site in human-dominated surroundings (Le Saout et al., 2013). Losing a suitable climate within protected areas forces species to adapt in order to survive. Species adapt via range shifts, phenotypic plasticity and natural selection. The type of adaptation depends on their adaptive capacity, i.e. on their environmental tolerance, dispersal ability and biotic interactions (Williams et al., 2008). Range shifts are a well-known response of species to climate change. If species have to move out of protected areas into uninhabitable environments, their extinction risk can increase and protected areas lose biodiversity. Already in 1985, Peters and Darling warned of the fact that protected areas may lose conservation value if species move out of protected areas due to climate change (Peters & Darling, 1985). Climate change can modify habitats inside protected areas in a way that they are no longer suitable for many species (Thomas & Gillingham, 2015). Consequently, many species shift their ranges and timing of seasonal behaviour, which may disrupt interspecific relationships. However, climate change can also positively affect species diversity in protected areas. For example, in the Kruger National Park, the population size of elephants is predicted to grow under climate change due to increasing plant productivity (Scheiter & Higgins, 2012). Such positive effects must be considered by protected area management as well, because the capacities of protected areas to maintain growing populations are limited. Protected areas at high northern latitudes are predicted to become refugia for species migrating polewards under climate change (Berteaux et al., 2018). Nevertheless, the predicted climate-induced redistribution of species suggests that many protected areas will not retain their current species diversity and composition (Araújo et al., 2004; Hannah et al., 2007; Bagchi et al., 2013; Langdon & Lawler, 2015; Barredo et al., 2016; Regos et al., 2016; Holsinger et al., 2019; Velazco et al., 2019). Species loss within protected areas is rarely compensated for by incoming taxa (Burns et al., 2003; Coetzee et al., 2009; Araújo et al., 2011; Fuentes-Castillo et al., 2019).

Studies on the geography of climate change impact are biased towards small geographical extent, large grain or specific climate variables. The climate impact is either summarised by large regions (Giorgi, 2006; Beaumont et al., 2011; Bellard et al., 2014; Habel et al., 2019) or the grid-cell resolution of climate change maps is too coarse to reflect the local climate impacts inside protected areas (Williams et al., 2007; García-López & Allué, 2013; Garcia et al., 2014; Torres & Marengo, 2014; Ordonez et al., 2016; Li, Kou et al., 2018; Li, Wu et al., 2018). The climate impact research that explicitly addresses protected areas considers a limited geographical extent only, such as China (Zomer et al., 2015), Brazil (Lapola et al., 2019), Amazonia (Feeley & Silman, 2016), the tropics (Tabor et al., 2018), North America (Batllori et al., 2017; Carroll et al., 2017; Gonzalez et al., 2018) or Europe (Barredo et al., 2016; Nila et al., 2019). A spatially high-resolution assessment of local climate change impacts inside protected areas worldwide is required to guide local protected area management towards global conservation goals (Felton et al., 2009). Loarie and colleagues provide such an assessment, but that is restricted to temperature change (Loarie et al., 2009). To fill this knowledge gap, I assessed the climate change impacts on the basis of various climate factors, a very small grain and the global extent of protected areas in Manuscript 5 and 6. The climate change indices included in these manuscripts support local protected area management across the globe, to mitigate and adapt to several climate change impacts. Protected area management plans must become robust for climate change in order to achieve their goals (Geyer et al., 2017).

To compensate for the limits of local conservation action in reaching global conservation goals, a large-extent perspective is required. Protected area networks and international agreements on species conservation are two examples of large-extent conservation. In Manuscript 1, I analysed the distribution of priority species across a protected area network in the EU. I could thus estimate the contribution of individual protected areas to the continental conservation of priority species. Manuscript 5 and 6 also provide an international perspective: I calculated the local impacts of climate change on individual protected areas all over terrestrial earth. Further, in the face of continuing threats, the temporal perspective of conservation planning needs to be long-term. Manuscript 5 and 6 reveal the impacts of climate change onto protected areas by the year 2070. Subsequently, the results of these manuscripts help to improve the management plans of individual protected areas worldwide towards reaching long-term conservation effectiveness.

4 Synopsis

4.1 Adaptive protected area management

Adaptive protected area management is a promising tool to ensure the enduring effectiveness, and also efficiency, of protected areas in the light of uncertain future developments (Rannow et al., 2014). The higher the uncertainty is, the higher is the necessity of adaptive management to achieve management effectiveness (Larson et al., 2013). The fundamental components of adaptive management are the continual evaluation of management effectiveness and the continual adaptation of management efforts to maintain or increase the management effectiveness. This iterative approach enables well-grounded decision-making in spite of uncertainties in the system. Uncertainty is reduced by regular system monitoring that is used to evaluate management effectiveness. Adaptive management thus means continuously learning about a system in order to be able to change the system. In this way, adaptive management can improve management effectiveness. The major challenge of adaptive management is to implement a reasonable balance between long-term and short-term management effectiveness. Adaptive management is an established concept of environmental management (Holling, 1978; Grumbine, 1997; Cork et al., 2000; Buck et al., 2001; Oglethorpe, 2002; Wilhere, 2002; Schreiber et al., 2004; Tompkins & Adger, 2004; Stringer et al., 2006; Allan & Stankey, 2009; van Wilgen & Biggs, 2011; Allen et al., 2011; Williams, 2011; Keith et al., 2011; Lindenmayer et al., 2011; McFadden et al., 2011; Rist et al., 2013; Westgate et al., 2013; Rannow et al., 2014; Allen & Garmestani, 2015; Reside et al., 2018).

In the following, I illustrate the principle of an adaptive management cycle for protected areas (Figure 7), which picks up aspects from the previous chapters and is grounded on a series of other studies about adaptive conservation management in the face of environmental changes (Cork et al., 2000; Wilhere, 2002; Schreiber et al., 2004; Stringer et al., 2006; Conroy et al., 2011; van Wilgen & Biggs, 2011; Williams, 2011; Wintle et al., 2011; Lindenmayer et al., 2011; Polasky et al., 2011; Watson et al., 2012; Larson et al., 2013; Stein et al., 2013; Rannow et al., 2014; Gross et al., 2017; Gillson et al., 2019). The scientific foundation of this adaptive management cycle is based on the monitoring (Section 3.8.2.8) and evaluation of management effectiveness (Section 3.8.2.9). Monitoring management effectiveness of protected areas includes assessing conservation targets (Section 3.4), such as species diversity (Section 3.5), and threats, such as climate change (Section 3.6). Since developments outside protected areas affect the interior qualities of protected areas (McNeely et al., 1990; Radeloff et al., 2010; Hellwig et al., 2019), the surroundings of protected areas should be monitored, too. Monitoring enables the evaluation of management effectiveness. Every evaluation approach is prone to contextual shortcomings, which decrease the credibility and accountability of evaluation results (Adams, Barnes et al., 2019): sophisticated evaluation methods have to consider counterfactual thinking and confounding factors. Monitoring and evaluating management effectiveness can also be used to estimate the risk of losing management effectiveness under future scenarios (Rannow et al., 2014). A lack of monitoring and research makes it difficult to evaluate progress towards management targets.

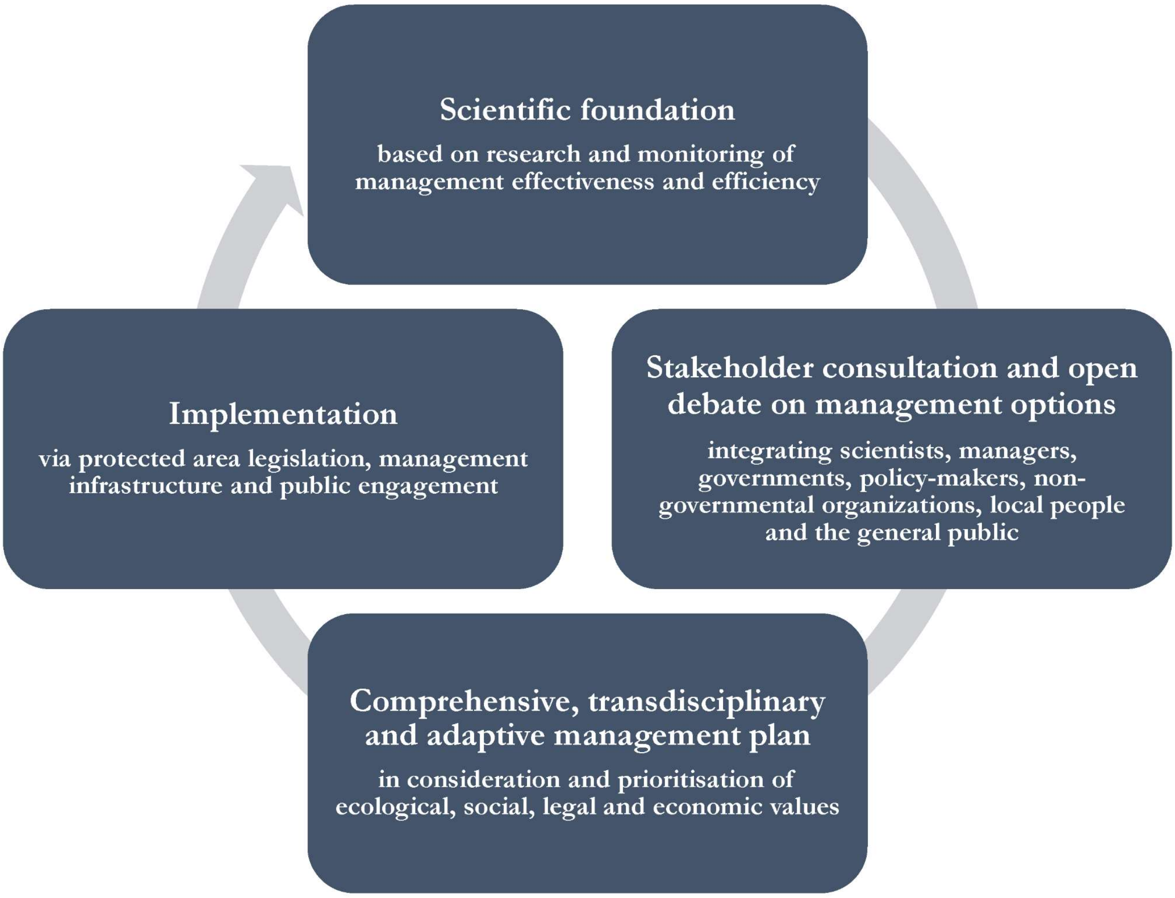

Figure 7. Adaptive management cycle for effective and efficient conservation via protected areas. Each manuscript of this dissertation contributes to the scientific foundation of adaptive protected area management.

Recent developments aim at closing the different knowledge gaps that result from a lack of monitoring. Long-term and in-situ monitoring programmes, e.g. ILTER, or new developments in remote sensing, e.g. Sentinel missions, can deliver data to observe protected areas almost continuously (Section 3.8.2.8). Citizen science can complement professional monitoring and research in disciplines where reliable data can be recorded by amateurs (Section 3.8.2.8). However, citizen science should not be a substitute for professional science. Open-access literature, open-source software and open data help to spread information and knowledge (Section 3.8.2.8).

Protected area management plans (Section 3.8.2.5 and 3.8.2.6) will be adjusted in the adaptive cycle if research and monitoring reveal deficits in management effectiveness or efficiency. Alternative management plans are then discussed, prioritised and decided on in an open and democratic debate integrating and consulting stakeholders, such as scientists, managers, governments, policy-makers, non-governmental organisations, local people and the general public. The consideration and prioritisation of ecological, social, legal and economic aspects (Section 3.8.2.7) make adaptive protected area management plans comprehensive and transdisciplinary. This process is a two-step approach moving from management goals to management options and then to management action. However, uncertain future developments may also require revisiting conservation targets. Stakeholders then agree on several management plans tracking different targets that can be followed under alternative future scenarios. Accordingly, emerging management plans can be both, reactive (i.e. responding to impacts already present) and anticipatory (i.e. preparing for future developments). Management plans should thus include a short and long-term perspective.

The implementation of resulting management plans is conducted via funding, legislation, infrastructure, equipment and the engagement of citizens (Section 3.8.2.5 and 3.8.2.6). This adaptive management cycle is closed with the execution of management plans and another cycle starts with monitoring management effectiveness and efficiency.

4.2 Synthesis of the manuscripts

In the following, I describe research gaps related to the scientific foundation of adaptive protected area management. I explain how my manuscripts address these gaps and thus advance protected area management (Table 4). Furthermore, in the Appendix, I list my talks at scientific conferences (Appendix 1) and my non-peer reviewed publications (Appendix 2) which refer to this thesis. I additionally show all other presentations (Appendix 3) and publications (Appendix 4) which I contributed to while writing my dissertation, but which are not associated with this thesis. I also included my activities as a scientific reviewer for peer-reviewed journals (Appendix 5) as well as my teaching activities while working on this thesis (Appendix 6 and 7).

Table 4. Overview of the manuscripts included in this thesis and how they advance the scientific foundation of adaptive protected area management.

Manu-script	Protected areas	Conservation objectives	Conservation threats	Data sources	Methods	Extent	Grain	Openness	Scientific advances in management
1	National parks, UNESCO MAB reserves	Diversity of the priority species listed in the EU Birds and Habitats directives	Not specified	Eionet, WDPA, Le Saout et al. (2013)	Geospatial analyses, species-area relationships, sensitivity analyses	EU	10 km, individual protected areas	Open access, open data	Be informed about multiple measures of species diversity within protected areas to increase management effectiveness from the local to continental extent
2	La Palma UNESCO MAB Reserve	Perennial plant species diversity and communities	Invasive species, human land use	In-situ survey, Copernicus, Spanish National Geographic Institute, Irl et al. (2015)	Univariate and multivariate statistics, time series and sensitivity analyses	Elevation gradient of 2,400 m	10 m	Open access, open data, open source code	Have knowledge of monitoring beta diversity efficiently using remote sensing
3	Gran Paradiso National Park	Plant species diversity of alpine grassland	Climate change	In-situ survey	Modelling information entropy	Nine 400 m^2-plots	2 m	Open access, open data	Be aware of how to increase the efficiency of biodiversity surveys under limited management resources
4	Gran Paradiso National Park	Plant species diversity of alpine grassland	Climate change, land use change	In-situ survey	In-situ survey	Nine 400 m^2-plots	2 m	Open access, open data	Acquire open data on threatened species diversity

Table 4 Continued.

Manu-script	Protected areas	Conservation objectives	Conservation threats	Data sources	Methods	Extent	Grain	Openness	Scientific advances in management
5	Terrestrial protected areas worldwide	Biodiversity with focus on biomes and IUCN Red List species	Climate change, human land use, invasive species	WDPA, WorldClim, Amatulli et al. (2018), Le Saout et al. (2013), Olson et al. (2001), Venter et al. (2016)	Temporal modelling, geospatial and sensitivity analyses	Global	ca. 1 km, individual protected areas	Open access, open data	Be informed about the potential climate change impacts on protected areas to sustain management effectiveness from the local to global extent
6	Terrestrial protected areas worldwide	Biodiversity with focus on countries, IUCN Red List species and ecosystem services	Climate change, human land use, invasive species	WDPA, WorldClim, Amatulli et al. (2018), Le Saout et al. (2013), Olson et al. (2001), Venter et al. (2016)	Temporal modelling, geospatial and sensitivity analyses	Global	ca. 1 km, individual protected areas	Open access, open data	Be informed about the potential climate change impacts on protected areas to sustain management effectiveness from the local to global extent

In conservation biogeography (Section 3.8.1), the multiple roles of protected areas are studied (Section 3.8.2.1 and 3.8.2.3), which aim at preserving values and objectives of nature (Section 3.3 and 3.4), such as species diversity (Section 3.5). The success that protected areas had during the 21st century (Section 3.8.2.2, 3.8.2.4 and 3.8.2.9) is threatened (Section 3.8.2.10), primarily by human land use and climate change (Section 3.6). Adaptive protected area management is required to guarantee effective and efficient conservation under rapid environmental changes (Section 4.1). Threats to biodiversity are occurring globally (Section 3.6) and biodiversity is rapidly lost (Section 3.7). Consequently, adaptive protected area planning and management has to consider large geographical extents to ensure biodiversity conservation worldwide (Section 3.8.2.10). To guide conservation planning and management between protected areas (Section 3.8.2.5 and 3.8.2.6), the scientific foundation of adaptive protected area management must consider protected area networks (Section 3.8.2.10). While each manuscript of this thesis contributes to a sound scientific foundation of an adaptive management cycle for terrestrial protected areas, Manuscript 1, 5 and 6 explicitly support adaptive management of protected area networks.

The scientific prerequisites of adaptive management are the research and monitoring of management effectiveness (Section 4.1). Species diversity (Section 3.5) is a reasonable indicator of protected area management effectiveness (Section 3.8.2.9). However, species diversity is not entirely known inside many protected areas (Section 3.8.2.10), because management resources are limited (Section 3.8.2.6) and thereby only priority species are considered in conservation measures (Section 3.8.2.7). In Manuscript 1, I accordingly analysed the current distributions of priority species within major protected areas in the EU. The study includes 1303 species in ten taxa. These priority species are listed in the annexes of the Birds and Habitats directives, the two most important policies for species conservation in the EU (Section 3.4 and 3.8.2.7). Member states are obliged to periodically report the occurrence of those focal species. I used these occurrence data and merged them with 285 national parks and 147 UNESCO MAB reserves, which are two major protected area designations focusing on species conservation (Section 3.8.2.3). I then applied a novel, multifunctional approach to calculate different metrics of conservation value that represent different components of species diversity, involving inventory diversity, deviation from the species–area relationship, species rarity and differentiation diversity (Section 3.5.2). I offer this approach to evaluate and regulate the representativeness, persistence, effectiveness and efficiency of protected area networks (Section 3.8.2.5). In Manuscript 1, I show that individual protected areas significantly vary in their species diversity, which is often not associated with protected area size. Protected areas around the EU periphery, harbour only few species but are key to conserving rare species. My analysis allows a multi-facetted and more accurate estimation of the conservation value of European protected areas than global-extent approaches. This study highlights the present conservation value of renowned European protected areas in terms of species diversity. It eventually supports adaptive conservation strategies for protected areas from a local to continental perspective.

In the face of the high rates of current biodiversity loss (Section 3.7), the monitoring of the biotic and abiotic environment needs to become time and cost-efficient (Section 3.8.2.10). Remote sensing is a growing, time- and cost-efficient tool for conservation (Section 3.8.2.8). In the biodiversity conservation context, remote sensing techniques have been primarily used to estimate plant species richness and abundance (i.e. alpha diversity), whereas the assessment of differentiation diversity (i.e. beta diversity) has been neglected, even though beta diversity is crucial for conservation planning (Section 3.8.2.10). Therefore, Manuscript 2 contributes to the analysis of beta diversity using remote sensing techniques. In Manuscript 2, I investigated the capability of remote sensing signals to reflect plant communities in the La Palma UNESCO MAB Reserve. If open remote sensing data are able to accurately account for the dissimilarity between species assemblages, this would allow time and cost-efficient monitoring of differentiation diversity. I calculated structural remote sensing variables from airborne LiDAR data and a time series of multispectral Sentinel-2 (S2) images. Additionally, I surveyed perennial vascular plant species abundances in three pre-defined community types: succulent scrubland, *Pinus canariensis* forest and subalpine scrubland. I show that up to 85% of beta diversity is reflected by the remote sensing variables in the wet season. The LiDAR variables explain less variation of beta diversity than the S2 variables. However, the explanatory power of S2 variables decreases with increasing grain size, while the explanatory power of LiDAR variables increases. Accordingly, I demonstrate that open remote sensing data are able to accurately reflect plant communities. Such remote sensing approaches, however, need to be complemented by field surveys to reveal the complete variation in community composition.

In contrast to remote sensing, in-situ surveys are classic approaches to assess species diversity inside protected areas (Section 3.8.2.8). In-situ sampling procedures can, however, still be improved. This leads to Manuscript 3, where I developed a time and cost-efficient sampling design for field surveys. The ongoing mass extinction of species does not allow for inefficient surveys that require a lot of time and funds. Surveys and monitoring schemes need to be optimised, that means the ratio between the amount of information collected and sampling effort has to be maximised (Section 3.8.2.10). Manuscript 3 concentrates on endangered alpine grassland in Gran Paradiso National Park, Italy, but the approach I developed can be adapted to any other ecosystem. The methodological code is attached to this open-access publication. The sampling effort in grassland increases with the number and size of sampling units (Section 3.8.2.8). To optimise sampling effort, I was searching for the size and number of sampling units (i.e. plots) that provide the maximal amount of information with minimal effort. Nine 20 m × 20 m-plots were surveyed, each consisting of 100 2 m × 2 m-subplots. Species richness and Shannon diversity (Section 3.5.2) were calculated for different sizes and quantities of subplots. I simulated larger subplot sizes by unifying adjacent 2 m × 2 m-subplots. Shannon's information entropy was then applied to measure the information content among richness and diversity values resulting from different subplot sizes and quantities. The optimal size and number of subplots is the lowest size and number of subplots returning maximal information. I found that the information content among richness values increases with subplot size which is not related to the number of subplots. Subsequently, the largest subplot size available is the optimal size for information about richness. I also show that information content among diversity values increases with subplot size when 18 or less subplots have been considered, and decreases when at least 27 subplots have been surveyed. Therefore, the subplot quantity determines whether the smallest or largest subplot size available is the optimal size, and whether the optimal size can be generalised across both, species richness and diversity. Given a 2 m × 2 m size, I estimated an optimal quantity of 54. Given a size of 4 m × 4 m, I estimated an optimal number of 36. The optimal number of plots can be generalised across both indices because it barely differed between the indices given a fixed subplot size. Effective and efficient in-situ sampling designs can be created with this approach.

In Manuscript 4, I thoroughly describe and provide open data on the alpine grassland diversity, which was studied in Manuscript 3. Manuscript 4 is to share data on this threatened vegetation type, which will support research and conservation of this ecosystem in the future. Open-access literature, open-source software and open data (Section 3.8.2.8) are key to timely conservation assessments (Section 3.8.2.10).

Threats to biodiversity must be identified inside protected areas in order to stop the loss of biodiversity from protected areas. Climate change is a major threat to biodiversity conservation (Section 3.6), which acts on the local extent of protected areas worldwide (Section 3.8.2.10). While protection status (Section 3.8.2.3) may prevent human-induced land use change and habitat degradation, the influence of anthropogenic climate change on protected areas cannot be stopped by protected area management (Section 3.8.2.6). Previous literature accounting for climate change impacts on protected areas is biased towards small geographical extent or large grain size (Section 3.8.2.10). A global assessment of the local climate change impacts on protected areas is missing but essential to guide local protected area management towards global conservation goals. Manuscript 5 and 6 address this knowledge gap. In both manuscripts, I analysed several facets of climate change impact (Section 3.6.2) onto terrestrial protected areas worldwide by the year 2070 applying a moderate and severe emission scenario.

Manuscript 5 is about predicted climate shifts within protected areas, using a fine spatial grain of approximately 1 km. I incorporated 137,432 individual protected areas, i.e. 99.9% of the world's terrestrial protected areas into Manuscript 5. If species are forced to migrate from protected to unprotected areas to track suitable climate conditions that disappeared from the protected area, they may face degraded habitats in anthropogenic landscapes (Section 3.8.2.10). Extinction threat consequently increases and protected areas lose biodiversity and associated values they were meant to provide. I found that protected areas in the temperate and northern high-latitude biomes experience especially high proportions of climate conditions that are predicted to be novel within the protected area network in a local, regional and global context by the year 2070. By relating characteristics of protected area design (Section 3.8.2.5) to the predicted climate shifts, I could estimate the future impacts of anthropogenic climate change on the performance of protected areas in biodiversity conservation. Small protected areas of temperate biomes in lowland regions with low environmental heterogeneity and high human pressure but low biotic uniqueness will lose especially high proportions of their currently protected climates. This analysis directs adaptation measures (Section 3.8.2.5 and 3.8.2.6) towards protected areas that are strongly affected by climate change, of low adaptation capacity and of high conservation value.

Manuscript 6 complements Manuscript 5 by quantifying local climate change exposure of the world's terrestrial protected areas, applying the same resolution as in Manuscript 5, i.e. ca. 1 km. In Manuscript 6, climate change was calculated by climate anomaly, i.e. the magnitude of climate change (Section 3.6.2). I show that local climate anomalies in the year 2070 are predicted to be highest inside protected areas of the (sub-)tropical and polar countries. Moreover, I found that, globally, protected areas showing large climate anomalies tend to be at high elevation and highly irreplaceable for threatened species, indicating high climate change exposure. These protected areas are relatively large in area, of high environmental heterogeneity and less pressured by humans, reducing climate change exposure. Large areas, high environmental diversity and low human pressures generally favour nature conservation under climate change (Section 3.8.2.5). This study expands Manuscript 5 by analysing a different dimension of climate change and focusing on countries instead of biomes. It informs climate-smart protected area management and policy (Section 3.8.2.6) from the local to global extent, particularly addressing national authorities.

Finally, all manuscripts of this thesis advance the scientific foundation of protected area planning (Section 3.8.2.5) and management (Section 3.8.2.5). They can thus be embedded into a transdisciplinary framework of adaptive protected area management (Section 4.1) in order to increase protected area effectiveness (Section 3.8.2.9). Nevertheless, each manuscript reflects a discrete and empirical investigation dealing with stand-alone research questions and hypotheses that are not only useful for protected area management. Furthermore, each manuscript is open-access and the data and code produced in these papers are open as well, to ensure the spread of knowledge for nature conservation.

4.3 Future perspectives

4.3.1 Towards a global protected area management system

Although global conservation efforts are growing, most of the Aichi Biodiversity Targets will not be met by 2020 (Díaz et al., 2019). Because humans progressively dominate the earth's systems, nature conservation strategies and protected area management increasingly integrate the human dimension (Minteer & Miller, 2011; Ellis, 2019), which is also recognised by the Sustainable Development Goals (SDGs), particularly by SDG 14 'Life below Water' and 15 'Life on Land'. The SDGs generally combine human development and nature conservation by addressing poverty, inequality, climate change, environmental degradation, prosperity, peace and justice. The authors of the current report from the 7th IPBES plenary session suggest diverse environmental, economic, societal and political actions that are required to attain these targets (Díaz et al., 2019; IPBES, 2019).

Many of these actions relate to protected area management: promoting sustainable resource management, agriculture and fishery; implementing hunting and fishing quotas; applying multifunctional spatial planning; establishing protected areas; reducing habitat fragmentation; reducing poverty and inequality; promoting technology, innovation and investments in conservation; generating and sharing knowledge; and promoting education. In all these examples, capacity building, integrated management and cross-sectoral approaches need to be adopted pre-emptively to account for trade-offs between stakeholders (Díaz et al., 2019; IPBES, 2019). The UNESCO MAB reserves are successful examples of such integrated and transdisciplinary conservation approaches (Section 3.8.2.3). By integrating biodiversity conservation and ecosystem services, protected areas help to reach the biodiversity and sustainable development goals alike (Ferraro & Hanauer, 2011; Di Minin et al., 2013; Butchart et al., 2015; Xu et al., 2017; Dinerstein et al., 2019).

Protected areas offer solutions to the biodiversity crisis of the Anthropocene (Section 3.8.2) and are preferred conservation policies for conservationists given climate change (Hagerman & Satterfield, 2014). My aim with this thesis is to stimulate coordinated biodiversity conservation through protected areas at the national and international level, by providing information about biodiversity and threats within individual protected areas of continental to global networks. This information guides local protected area management to reach global conservation targets. Aichi Biodiversity Target 11 sets a terrestrial protected area coverage of 17% as a conservation target, but protected area extent does not indicate protected area effectiveness (Rodrigues et al., 2004; Joppa & Pfaff, 2009; Barr et al., 2011; Kati et al., 2015; Visconti et al., 2019). For that reason, a certain degree of management effectiveness of the global protected area estate should become a legally binding global conservation target as well. Manuscript 1 refers, for instance, to protected area effectiveness as the species diversity covered by protected areas. In addition, while similar studies consider only single species diversity indices, Manuscript 1 accounts for a multitude of species diversity metrics. Manuscript 1 shows that more comprehensive conservation strategies can be delivered if inventory, differentiation and proportional diversity are integrated. Moreover, Manuscript 5 and 6 address the need to investigate multiple dimensions of threat to the effectiveness of the global protected area estate (Bonebrake et al., 2019). Both manuscripts reveal different aspects of the climate change impacts on protected areas (Section 3.6.2), which promote climate-smart planning (Section 3.8.2.5) and management (Section 3.8.2.6) of local protected areas worldwide.

Each manuscript of this thesis contributes to biodiversity conservation in a specific way. However, a comprehensive analysis that reveals the complex relationships between nature's various values (Section 3.3), conservation objectives (Section 3.4) and threats (Section 3.6) inside the global protected area estate has not been realised yet. In my opinion, this is a main future, albeit ambitious, perspective in conservation biogeography. Such a comprehensive and global analysis should be conducted frequently to ensure the long-term preservation of nature by protected areas across the globe. It is consequently necessary to establish long-term monitoring of nature and threats within protected areas all over the world. Artificial intelligence and deep learning are promising computational technologies for nature conservation since they enable an automated classification of big monitoring data (Lamba et al., 2019). Nevertheless, resources for monitoring are limited. Given that, only a selection of variables can be prioritised (Section 3.8.2.7). Scientists have recently argued for sets of essential variables that reflect states and trends of nature. These essential variables relate to climate (Bojinski et al., 2014), oceans (Constable et al., 2016), biodiversity (Pereira et al., 2013; Jetz et al., 2019), geodiversity (Schrodt, Bailey et al., 2019) and progress towards SDGs (Reyers et al., 2017). The definition of essential variables has led to advances in data collection, storage, distribution and use (Kissling et al., 2015) that are essential to big data analyses. Remote sensing (Pettorelli et al., 2016) and long-term ecological research stations (Haase et al., 2018) are sophisticated techniques to monitor essential variables.

Outcomes from such big data analyses should form the foundation of adaptive management systems of protected areas worldwide. There are many examples of adaptive management frameworks for conservation under rapid environmental changes (Section 4.1). For instance, Gillson and colleagues (2019) recently developed an advanced adaptive management cycle providing appropriate tools and approaches for integrating multiple forms of evidence to understand and manage complex dynamic systems. Such adaptive management concepts help to model future dynamics of nature with respect to social, political and economic criteria and developments. These frameworks can be applied to the global extent and local grain of protected area networks to foster local conservation effort that is globally coordinated. This could be the foundation of a globally coordinated and transdisciplinary protected area planning and management system, which is based on existing theory and practice of protected area planning (Section 3.8.2.5), management

(Section 3.8.2.6), prioritisation (Section 3.8.2.7), monitoring (Section 3.8.2.8) and effectiveness (Section 3.8.2.9), in order to cope with the biodiversity crisis (Section 3.7) and other protected area challenges (Section 3.8.2.10).

The WDPA and the Digital Observatory for Protected Areas (DOPA) could be the base of a global protected area planning and management system. The DOPA is a web based information system on the world's protected areas developed by the European Commission’s Joint Research Centre (JRC, 2019). The DOPA monitors and reports the state of and the pressures on protected areas by using global reference data sets, which reflect a multitude of indicators at country, ecoregion and protected area level. These indicators measure progress towards Aichi Biodiversity Target 11, and SDG 14 and 15. The DOPA is already able to provide a scientific foundation for a globally coordinated and adaptive management system for protected areas. I consider the development and application of such a global protected area management system as a crucial future task for conservation biogeographers, to meet the global biodiversity and sustainability targets.

4.3.2 Next generation conservation biogeography

Conservation biogeography is advancing the effectiveness of protected areas but faces many future challenges that are not related to protected areas. Filling biogeographical knowledge gaps and improving biodiversity forecasts are persistent scientific challenges. Turning theory into practice, educating, communicating and changing social values and lifestyles are common practical challenges. Accepting these challenges, conservation biogeographers need to focus on large geographical extents but small grain because threats to nature are occurring locally all over the world. Global conservation problems beyond 2020 can only be solved by local conservation strategies that are globally coordinated via international collaboration (Mace et al., 2018).

Conservation research is restricted by the unavailability of data. Growing conservation knowledge evolves from an increasing quality and quantity of data (Wüest et al., 2019). Conservation biogeographers work on the Linnean, Wallacean (Section 3.5.1) and extinction estimate shortfalls (Section 3.7) by collecting new data. However, temporal and financial resources for collecting data and monitoring are limited (Section 3.8.2.6 and 3.8.2.8). Hence, sampling and monitoring techniques need optimisation to become less time-consuming and costly (Section 3.8.2.10). Manuscript 2 and 3 follow this future agenda. Open information systems, data repositories, databases and data sets play a central role to foster global conservation research by the coming generations of conservation biogeographers (Section 3.8.2.8 and 3.8.2.10). All the data sets used and produced in my manuscripts are open data sets. Manuscript 4 explicitly describes the open data on threatened alpine grassland diversity. Varying quality, bias, noise and uncertainty within data require meta-data in order to efficiently harvest and analyse the data (Section 3.8.2.7, 3.8.2.8 and 3.8.2.10). Open-source software advances data analyses, their documentation, transparency and reproduction. Accordingly, I provide the computer code developed in Manuscript 3 in the appendix of this open-access publication. Furthermore, citizen science is a promising tool to enhance data collection, monitoring and analysis by participating citizens (Section 3.8.2.8). Citizen science brings the scientific community and the public together, which supports public education and nature conservation at the same time (Devictor et al., 2010; Danielsen et al., 2014; Sullivan et al., 2014; McKinley et al., 2017).

However, the increasing availability of data should not prevent anyone collecting new, high-quality data, especially in time of rapid environmental changes. More scientists need to be trained to enhance the quality and quantity of available data and methods in the future.

Predictions are to some degree uncertain and uncertainty may prevent decision-makers from acting (Section 3.8.2.10). There are, nevertheless, approaches to decision-making in the conservation context that account for model uncertainties (Moilanen et al., 2009; Polasky et al., 2011). A future challenge is to minimise the uncertainties of model predictions, e.g. by considering past dynamics (Di Marco et al., 2015), using sensitivity analysis and null-models (Feeley & Silman, 2010), and incorporating as many relevant hypotheses, data and models as possible (Conroy et al., 2011; Michalak et al., 2017). Forecasts are improved by refined theories as well as by the consideration of scale-dependency, inadequacies of input data and sensitivity of projections to model structure and parameterisation (Whittaker et al., 2005). However, in contrast to meteorologists, ecologists still miss a comprehensive theory to sufficiently predict complex ecosystem assemblies (Higgins, 2017), which would promote the human ability to safeguard nature.

In the view of the current rates of nature's declines, another important task for conservation biogeographers is to work harder on improving the communication and collaboration between stakeholders, such as scientists, policy-makers, managers and people (Costello et al., 2015). Publishing open-access is a substantial first step to communicate research efficiently. Nature conservation is a value-laden field (Section 3.3, 3.4 and 3.8), which can complicate communication. Studies have shown that effective conservation policy and management is based on well communicated, explained and contextualised research (Kalliola et al., 2008; Manfredo et al., 2016; Morrison, 2016). Therefore, researchers need to translate their findings into a plain language that stakeholders understand. If stakeholders recognise that their well-being depends on nature conservation, they may be willing to support conservation. Using social media is an efficient way of communicating science, though not without pitfalls (Bombaci et al., 2016). In contrast, academic media do not reach the majority of people (Knuth & Jacobson, 2000) and traditional media tend to be prone to polarisation that threatens the credibility of research. Scientists can even apply marketing techniques to reach the majority of people (Redford et al., 2015; Wright et al., 2015). Knowledge from social-psychological science helps to mainstream nature conservation (van Vugt, 2009). In these regards, conservation biogeographers should actively and adequately promote protected areas as a solution to various environmental problems (MacKinnon et al., 2011; Dinerstein et al., 2019) since protected areas safeguard biodiversity, ecosystem functioning and multiple ecosystem services (Section 3.8.2), which strengthen human well-being and represent various values of nature (Section 3.3).

If the global protected area extent grew to half of the terrestrial area on earth, new protected areas would have to be wisely planned to stop biodiversity loss (Montesino Pouzols et al., 2014; Pimm et al., 2018) and meet human demands simultaneously (Ellis & Mehrabi, 2019). Protected area expansion is, however, challenging because land is increasingly modified and used for human purposes only (Sala, 2000), which emphasises the need for nature conservation outside protected areas. A high degree of biodiversity can exist outside protected areas. Some species are even restricted to unprotected areas (Rodrigues et al., 2004), e.g. in Canada (Deguise & Kerr, 2006) and in the Mediterranean biome (Cox & Underwood, 2011). Species migrating between protected areas also depend on unprotected areas (Troupin & Carmel, 2014). Moreover, established protected areas are often taken as justification for environmental degradation in the protected area surroundings (McNeely et al., 1990; Radeloff et al., 2010; Hellwig et al., 2019). If biodiversity is lost outside protected areas, this will have, in turn, consequences for the biodiversity inside (Laurance, Useche et al., 2012; Rada et al., 2019). The smaller a protected area is, the more it is affected by unprotected surroundings (Section 3.8.2.5). Consequently, nature conservation outside protected areas is essential as well.

The sustainable use of unprotected land can complement protected areas in conserving biodiversity (Locke et al., 2019), e.g. by applying low-intensity agriculture and forestry (Kremen & Merenlender, 2018). Land sharing (i.e. sharing agricultural land with conservation efforts) and land sparing (i.e. temporally sparing agricultural land for conservation) are two strategies to merge agricultural practices and biodiversity conservation in cultural landscapes (Baudron & Giller, 2014). Private land can also be dedicated to biodiversity conservation by voluntary conservation efforts, e.g. in private gardens (Farmer et al., 2017). Such efforts refer to OECMs (Section 3.8.2.1), which are essential complements to protected areas for reaching global conservation targets (Dudley et al., 2018; Frascaroli et al., 2019).

There are numerous signs of conservation success inside and outside protected areas. Conservation efforts have, for instance, decreased the extinction risk of mammals and birds in 109 countries by 29% from 1996 to 2008 (IPBES, 2019); the average extinction risk of birds, mammals and amphibians would have been at least 20% higher without conservation initiatives; more than 107 highly threatened birds, mammals and reptiles took profit from the conservation-minded eradication of invasive mammals on islands. Many endangered species are recovering (IUCN, 2019b). The global protected area estate expands (Bingham et al., 2019) and protected areas can be effective in conserving biodiversity, even under climate change (Section 3.8.2.9). Moreover, many people do perceive nature conservation as a priority (Varma et al., 2015). Public media and institutions such as zoos, museums and botanical gardens, increasingly provide conservation-minded education programmes (Miller et al., 2004). German markets for green and sustainable products have been growing enormously (Steinemann et al., 2017). The economic value of nature is more often incorporated into economics and policy, which supports nature conservation (Bateman et al., 2013; Kubiszewski et al., 2013; Reyers et al., 2013; Waldron et al., 2017). Policy-makers increasingly discontinue perverse subsidies to environmentally harmful businesses (Merckx & Pereira, 2015). The members of the European Parliament call for legally binding biodiversity targets, equivalent to the Paris agreement on climate change (European Parliament, 2019). Cornerstone for more sustainable future policies in nature conservation would be financial and economic systems refusing the contemporary paradigm of economic growth (Díaz et al., 2019).

The societal and political values that people assign to nature are eventually decisive for nature conservation. Informed by conservation biogeographers and other experts, the societal willingness can prompt stakeholders, policy-makers and governments to induce transformative changes required for global nature conservation and sustainable development. In the future people may perceive the first decades of the 21st century as the starting point for a very successful period of nature conservation (Sodhi et al., 2011), initiated by young people, such as those involved in the movements of Voice for the Planet and Fridays for Future all over the world. However, societal trends are fickle. The task of conservation biogeographers continuously communicating their work to the people is accordingly all the more important to ensure an enduring public support for nature conservation. In the year of Alexander von Humboldt's 250th birthday, conservation biogeographers are able to produce comprehensive and integrative knowledge about our relationship to nature. I am convinced that conservation biogeographers will be more successful in converting this knowledge into policy and practice if they also follow Humboldt in experiencing and expressing the values of nature (von Humboldt, 1845).

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6 Declaration of my contributions to each manuscript

Manuscript 1

Title: Uniqueness of protected areas for conservation strategies in the European Union

Authors: Hoffmann, S., Beierkuhnlein, C., Field, R., Provenzale, A., & Chiarucci, A.

Journal and status: Scientific Reports, 8, 6445 (2018), https://doi.org/10.1038/s41598-018-24390-3

My contributions: idea and concept: 90%, data analysis and figures: 100%, writing: 95%, corresponding author

Manuscript 2

Title: Remote sensing of β-diversity: evidence from plant communities in a semi-natural system

Authors: Hoffmann, S., Schmitt, T. M., Chiarucci, A., Irl, S.D.H., Rocchini, D., Vetaas, O. R., Tanase, M. A., Mermoz, S., Bouvet, A., & Beierkuhnlein, C.

Journal and status: Applied Vegetation Science, 22, 13-26 (2019), https://doi.org/10.1111/avsc.12403

My contributions: idea and concept: 95%, field work: 75%, data pre-processing: 95%, data analysis and figures: 100%, writing: 95%, corresponding author

Manuscript 3

Title: Optimizing sampling effort and information content of biodiversity surveys: a case study of alpine grassland

Authors: Hoffmann, S., Steiner, L., Schweiger, A. H., Chiarucci, A., & Beierkuhnlein, C.

Journal and status: Ecological Informatics, 51, 112-120 (2019), https://doi.org/10.1016/j.ecoinf.2019.03.003

My contributions: idea and concept: 95%, field work: 0%, data analysis and figures: 100%, writing: 95%, corresponding author

Manuscript 4

Title: Data on alpine grassland diversity in Gran Paradiso National Park, Italy

Authors: Hoffmann, S., Steiner, L., Schweiger, A. H., Chiarucci, A., Benner, J., Provenzale, A., & Beierkuhnlein, C.

Journal and status: Data in Brief, 24, 103942 (2019), https://doi.org/10.1016/j.dib.2019.103942

My contributions: idea and concept: 100%, field work: 0%, data pre-processing: 75%, data analysis and figures: 100%, writing: 100%, corresponding author

Manuscript 5

Title: Predicted climate shifts within terrestrial protected areas worldwide

Authors: Hoffmann, S., Irl, S. D. H., & Beierkuhnlein, C.

Journal and status: Nature Communications, 10, 4784 (2019), https://doi.org/10.1038/s41467-019-12603-w

My contributions: idea and concept: 100%, data analysis and figures: 100%, writing: 95%, corresponding author

Manuscript 6

Title: Local climate change exposure of the global protected area estate from an international perspective

Authors: Hoffmann, S., & Beierkuhnlein, C.

Journal and status: Earth's Future, manuscript #: 2019EF001443 (under review, received: 2 December 2019); **Update (12 May 2020):** Diversity and Distributions, manuscript #: DDI-2020-0090 (under review with major revisions, received: 11 March 2020)

My contributions: idea and concept: 100%, data analysis and figures: 100%, writing: 99%, corresponding author

7 Manuscripts

7.1 Manuscript 1

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Uniqueness of Protected Areas for Conservation Strategies in the European Union

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Samuel Hoffmann[1], Carl Beierkuhnlein[1], Richard Field[2], Antonello Provenzale[3] & Alessandro Chiarucci[4]

Protected areas (PAs) constitute major tools in nature conservation. In the European Union (EU), the Birds and Habitats Directives are the most important policies for conservation strategy, legally preserving Europe's characteristic, rare, endemic and threatened biota. We used occurrence data for species listed in the directives' Annexes to assess the uniqueness of major PAs in the EU (National Parks, Biosphere Reserves); this is important for preserving the EU's focal species. We developed a novel, multifunctional approach to calculate different metrics of conservation value that represent different components of species diversity within the PAs, involving inventory diversity, deviation from the species–area relationship, species rarity and differentiation diversity. Applying it, we found that individual PAs frequently vary considerably in their scores on different components, which are often disconnected from PA size. PAs around the EU periphery, often containing few species, are key to conserving species that are rare in the EU. Because our analysis focuses on EU priority species and includes different components of diversity, it allows more appropriate estimation of conservation value inside PAs in context of the EU than recent, high-profile, global-level research. We offer tools to evaluate, and information to regulate, the representativeness, persistence and efficiency of PAs.

Beyond climate change, biodiversity decline is considered the major threat to human well-being in the 21st century[1]. In 2010, the Earth's nations agreed again to try to halt biodiversity loss by 2020 (Aichi Biodiversity Targets[2]), but global prospects of improvement are still slight[3]. The effectiveness of conservation action has still to increase[4].

Protected areas (PAs) represent a fundamental tool in nature conservation policies, their main purpose, often achieved, being to conserve local to regional biodiversity, particularly the characteristic or threatened species, habitats and ecosystems[5–7]. Often, PAs are the only remaining safe sites for species' populations[8], whose existence relies on PA performance. However, the Convention on Biological Diversity[2] predominantly relates to the PA surface area, stating: "By 2020, at least 17 per cent of terrestrial and inland water areas and 10 per cent of coastal and marine areas […] are conserved through effectively and equitably managed, ecologically representative and well-connected systems of protected areas" (Target 11 of Aichi Biodiversity Targets). There is thus a risk of naively focusing on the amount of area, but neglecting biodiversity protection[9,10].

The contribution of PAs to preventing habitat loss and maintaining biodiversity is debated[5,11,12]. Studies reveal poor management effectiveness[13], growing human pressures[14] and insufficient governmental support[15–17]. Changes to PAs themselves often affect their conservation role, including species invasions, pollution, acidification, nitrogen deposition and climatic change[14,18–21].

The efficiency of PAs has been studied at several scales. We refer to 'scale' as the geographical extent of the study region: 'global scale' as cross-continental extent, 'regional scale' as cross-national to continental extent, and 'local scale' to national or smaller extent. Many investigations of PA performance focus on local scales, but regional and global biodiversity cannot be maintained by a few isolated PAs[17,22,23]. Therefore, regional and global gap analyses have been applied to suggest strategies to complete protection networks[11,24–26], but gaps are unlikely to be filled if only local criteria and policies matter[27]. Moreover, local, regional and global conservation priorities

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Title: Uniqueness of protected areas for conservation strategies in the European Union

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Abstract

Protected areas (PA) constitute major tools in nature conservation. In the European Union (EU), the Birds and Habitats directives are the most important policies for conservation strategy, legally preserving Europe's characteristic, rare, endemic and threatened biota. We used occurrence data for species listed in the directives' annexes to assess the uniqueness of major PAs in the EU (national parks, biosphere reserves); this is important for preserving the EU's focal species. We developed a novel, multifunctional approach to calculate different metrics of conservation value that represent different components of species diversity within the PAs, involving inventory diversity, deviation from the species–area relationship, species rarity and differentiation diversity. Applying it, we found that individual PAs frequently vary considerably in their scores on different components, which are often disconnected from PA size. PAs around the EU periphery, often containing few species, are key to conserving species that are rare in the EU. Because our analysis focuses on EU priority species and includes different components of diversity, it allows more appropriate estimation of conservation value inside PAs in context of the EU than recent, high-profile, global-level research. We offer tools to evaluate, and information to regulate, the representativeness, persistence and efficiency of PAs.

Introduction

Beyond climate change, biodiversity decline is considered the major threat to human well-being in the 21st century [1]. In 2010, the Earth's nations agreed again to try to halt biodiversity loss by 2020 (i.e. Aichi Biodiversity Targets [2]), but global prospects of improvement are still slight [3]. The effectiveness of conservation action has still to increase [4].

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The contribution of PAs to preventing habitat loss and maintaining biodiversity is debated [5,11,12]. Studies reveal poor management effectiveness [13], growing human pressures [14] and insufficient governmental support [15,16,17]. Changes to PAs themselves often affect their conservation role, including species invasions, pollution, acidification, nitrogen deposition and climatic change [14,18,19,20,21].

The efficiency of PAs has been studied at several scales. We refer to 'scale' as the geographical extent of the study region: 'global scale' as cross-continental extent, 'regional scale' as cross-national to continental extent, and 'local scale' to national or smaller extent. Many investigations of PA performance focus on local scales, but regional and global biodiversity cannot be maintained by a few isolated PAs [17,22,23]. Therefore, regional and global gap analyses have been applied to suggest strategies to complete protection networks [11,24,25,26], but gaps are unlikely to be filled if only local criteria and policies matter [27]. Moreover, local, regional and global conservation priorities often differ greatly, and the performance of PA networks strongly depends on the geographical context they are applied to [11,28,29,30]. It is also questioned whether the global distribution and geographical density of PAs satisfy the conservation needs in the regional context [31]. Conservation effort also differs between local and global extents; continental-scale approaches are therefore considered a reasonable compromise to evaluate the real capacity for biodiversity protection of existing PA systems [17,32], particularly in Europe, where human population density is high and the legacies of land use, settlements and infrastructures allow little freedom for PA extension. Cultural landscapes and anthropogenic ecosystems (e.g. hay meadows) characterize European nature and PAs [33,34].

Since conservation aims and monitoring are primarily set for individual areas, comparing PAs' performance on larger scales is challenging. However, in the European Union (EU), the Birds and Habitats directives are legally binding conservation policies. They enforce member states to protect and report spatial records of many characteristic, endangered, vulnerable, rare and endemic species (but see Lisón et al. [35]) that are listed in the annexes of the directives. We refer to these priority species as 'reported species'. The directives also form the legal basis for the Natura 2000 PA system, which has global importance [12,22,36,37]. The reported species are focal species for conservation at the political level of the EU.

Here we use reported species data from the Birds and Habitats directives [38] to identify the individual contribution of renowned European PAs to preserve species diversity. We thus concentrate on conservation prioritization by the EU for the EU. We measure different indices to account for various components of the conservation value of PAs, including uniqueness. We do not evaluate the uniqueness of PAs against unprotected areas; we treat the PAs as self-operating and isolated sites that are, assuming the worst case, the last remaining safe sites for biodiversity in future. We focus on national parks (NP) and UNESCO Man and Biosphere reserves (MAB), because they have particularly significant benefits for biodiversity conservation in the EU due to their large areas, and integrative, intensive and effective management of biological objectives [5,7,17,34,39,40]. In total, 285 NPs, 147 MABs and 1303 species in ten taxa are considered herein, with the incidence data of species based on 10 km x 10 km grid cells. To assign species' occurrences to PAs, we developed a probabilistic approach based on the overlap of grid cells and PA polygon area.

In conservation research, uniqueness is often measured only as rarity [42]. Our evaluation is manifold, rather than relating to a single concept. We measure inventory diversity directly and accounting for the species–area relationship (SAR), species rarity and differentiation diversity. To measure the PAs' conservation value in these ways, we calculate seven indices (Tab. 1), producing a multifaceted estimation of the conservation value of major PAs for protecting focal EU species, which contrasts with a recent global approach [23]. We also performed sensitivity analyses to assess the reporting deficits of individual EU member states and how these affect measures of conservation value. The sensitivity analyses include a null model approach that compares the observed values within individual EU states to values from a random model, and to the observed values of all other EU states. Moreover, we conducted cross-validation to estimate sensitivity to reporting bias. Our methodological approaches are generally suitable for conservation assessment involving other components of biodiversity, different PAs and geographic extents. The results can guide future conservation effort to enhance the persistence and efficiency of biodiversity preservation inside single PAs and PA networks.

Table 1. Metrics of conservation value applied in this study. For details about indices' definitions and the distributions of data for them, see Methods. All the indices apply to units of space (i.e. protected areas [PA]) except conservation weight, which applies to individual species (i.e. reported species [RS]).

Name	Abbreviation	Description
Reported Species Richness	*Richness_RS*	Estimated number of reported species, calculated as the sum of the species' probabilities of occurrence, based on overlap between the PA and grid cells occupied by each species.
Area-controlled Surplus of Reported Species	*Richness_SAR_%Surplus*	Residual from modelling the species–area relationship (SAR) for the protected areas, expressed as percentage of the modelled value. Thus, if the expected *Richness_RS* of a PA based on its area is 50 and the actual *Richness_RS* is (a) 70 or (b) 35, then its *Richness_SAR_%Surplus* is (a) (70-50)/50 = 40% or (b) (35-50)/50 = -30%.
Conservation Weight	*w*	Inverse of the total number of grid cells occupied by the species in the land area of the EU. It estimates species rarity in the EU.
Rarity-weighted Richness	*Richness_Rarity_weighted*	Sum of the products resulting from the multiplication of the species' probabilities of occurrence by the species' conservation weights. It integrates reported species richness and rarity.
Average Rarity	*Rarity_Mean*	Average conservation weight of the reported species present (i.e *Richness_Rarity_weighted*/*Richness_RS*).
Total Dissimilarity	*Dissimilarity_Total*	Overall dissimilarity of species composition between protected areas, calculated using the method of Baselga (2013). It can be additively partitioned into *Dissimilarity_Balanced* and *Dissimilarity_Gradient* as described below. The dissimilarity score of a single PA is the mean of all pairwise dissimilarity values of the PA compared with all others.
Balanced Dissimilarity	*Dissimilarity_Balanced*	Dissimilarity in terms of balanced gains and losses (i.e. turnover) of species abundances between sites, calculated using the method of Baselga (2013).
Gradient Dissimilarity	*Dissimilarity_Gradient*	Dissimilarity in terms of monotonic gradients of species abundances (i.e. gains or losses) between sites, calculated using the method of Baselga (2013).

Results

Metrics of conservation value

Reported species richness in PAs broadly reflects the richness pattern in grid cells (Fig. 1), except that most PAs in Bulgaria have relatively low values. Variation in reported species richness across EU member states is apparent. The richness of reported species per grid cell (range: 0-189) appears low in Poland, the Czech Republic, Romania and Greece, and remarkably high in Bulgaria (but see the 'Sensitivity Analyses' section). We find unexpectedly low reported bird species richness in Poland, the Czech Republic, Romania and Greece (see also Supplementary Fig. S1).

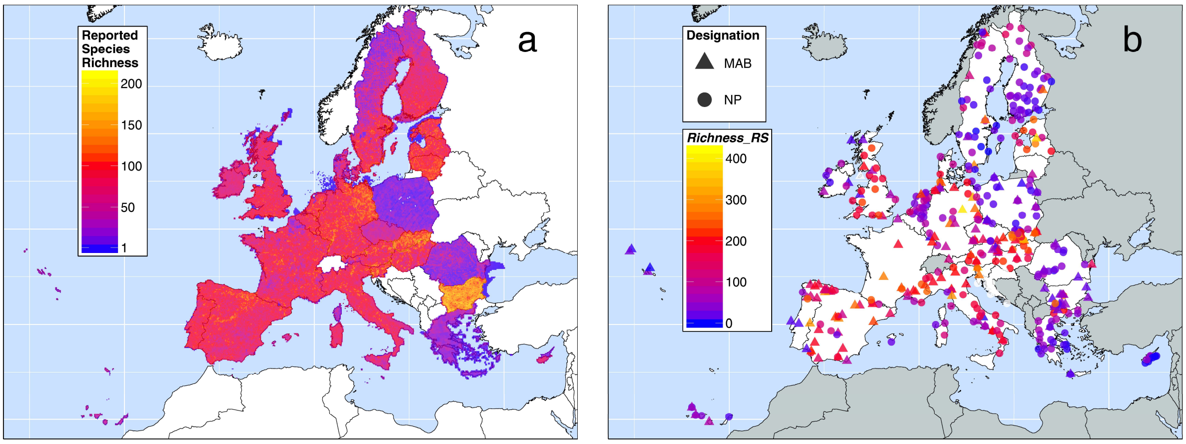

Figure 1. a) Reported richness of the 1654 annex species of the Birds and Habitats directives per 10 km x 10 km grid cell in the European Union. The 41 marine species are excluded. b) Reported species richness within 285 national parks (NP) and 147 Man and Biosphere reserves (MAB) in the European Union. The values estimate the number of annex species of the Birds and Habitats directives within these protected areas. For details see Methods section. The maps were created using open-source software R, Version 3.3.3 (https://www.R-project.org/) [60].

The other metrics of conservation value (i.e. area-controlled surplus of reported species, rarity-weighted richness, average rarity, total dissimilarity balanced dissimilarity and gradient dissimilarity; Fig. 2) only partially correlate with reported species richness (Fig. 3). For example, eastern European countries tend to have low values for most of these metrics, but high values of compositional dissimilarity. Macaronesian islands have high values for uniqueness-related metrics. High uniqueness scores are often found for clusters of PAs, especially around the periphery of the EU.

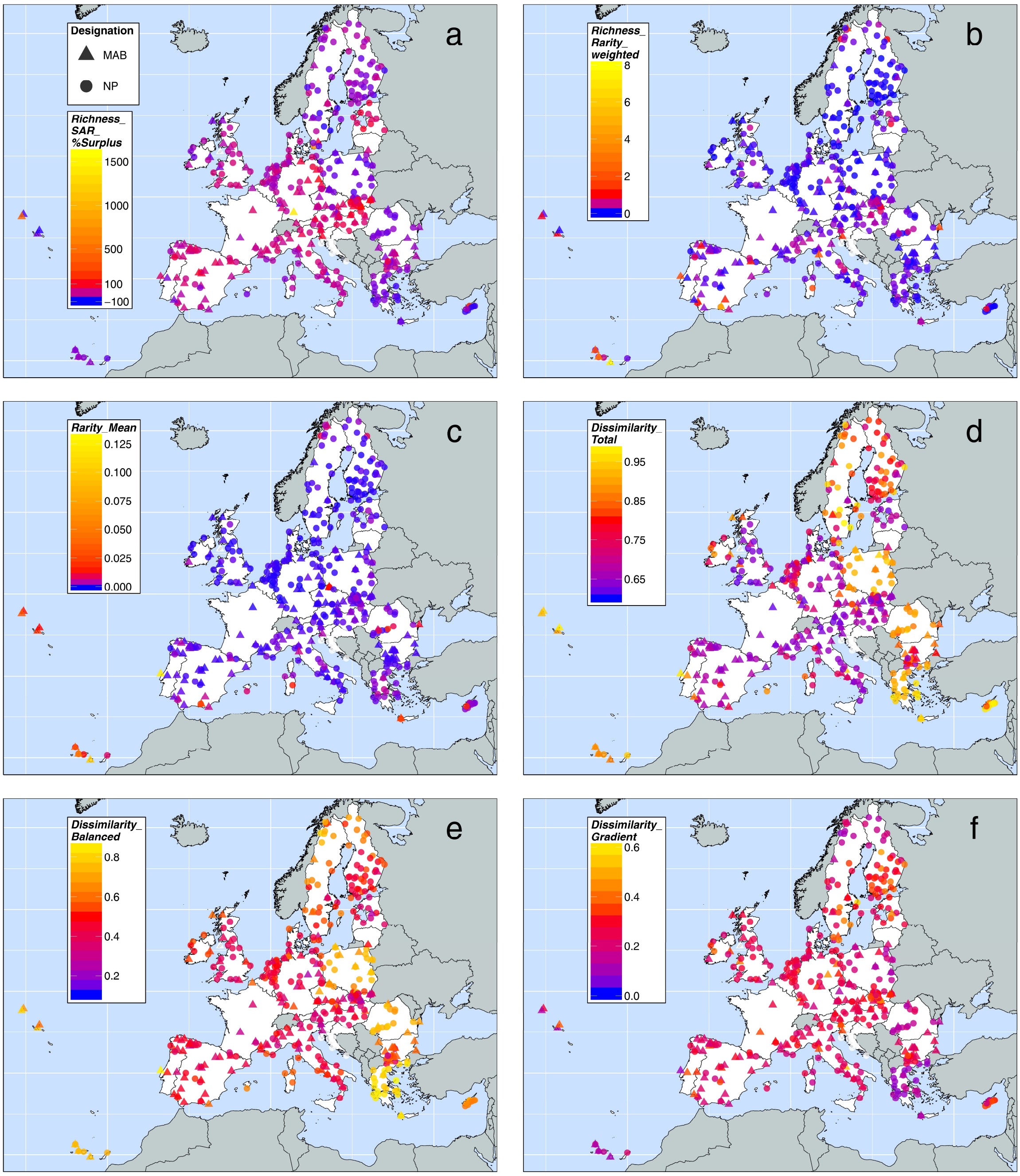

Figure 2. Metrics of conservation value for national parks (NP) and UNESCO Man and Biosphere reserves (MAB) in the European Union. a) Area-controlled surplus of reported species (*Richness_SAR_%Surplus*) accounts for the effect of area on reported species richness. It reveals the percentage deviation between observed *Richness_RS* and predicted *Richness_RS*, as modelled by the species–area relationship considering observed reported species richness and protected area. b) Rarity-weighted richness (*Richness_Rarity_weighted*) integrates reported species richness and rarity. It is a measure of the protected area's reported species richness, but weighted by the conservation weights of reported species. c) Average rarity (*Rarity_Mean*) is calculated by *Richness_Rarity_weighted* over *Richness_RS*. It represents the average rarity of reported species within the protected area. d) Total dissimilarity (*Dissimilarity_Total*) indicates beta diversity between protected areas regarding their species composition. e) Balanced dissimilarity (*Dissimilarity_Balanced*) and f) gradient dissimilarity (*Dissimilarity_Gradient*) are the additive components of total dissimilarity (Baselga, 2013). For details about indices' definition see Methods section. The maps were created using open-source software R, Version 3.3.3 (https://www.R-project.org/) [60].

Many PAs with lower reported richness than expected from their areas, i.e. negative area-controlled surplus of reported species, are in states known for low reported richness (Fig. 2a). In other EU regions, also, some PAs have such reported species deficits, for example on Macaronesian islands, in the Mediterranean Basin, in the United Kingdom, Sweden and Finland. Scattered across the EU are some PAs with strongly positive surpluses of reported species for their sizes, e.g. in Estonia, Latvia, Germany, Slovakia, Hungary, Austria, Slovenia, Bulgaria and Spain.

The values of rarity-weighted richness (<0.1-7.5) are heterogeneously distributed across EU member states (Fig. 2b). Single PAs with high rarity-weighted richness are found on Macaronesian islands, in the Mediterranean Basin, around the Black Sea, in parts of central Europe, the Baltic region and in northern Scandinavia. In most of the rest of the EU, PAs have low rarity-weighted richness. PAs with the highest average rarity tend to occur where rarity-weighted richness is also high (Fig. 2c). The range of average rarity values (<0.01–0.12) suggests that average reported species rarity is low within the PA network; reassuringly, most reported species are relatively common in the EU's PAs (see also Fig. 4a).

Total compositional dissimilarity is generally high (0.62-0.99), but is particularly high in many PAs containing few reported species (Fig. 2d). Total dissimilarity is partly decoupled from reported species richness; for example, in southern Sweden, PAs containing high reported species richness are also very dissimilar in species composition. Balanced dissimilarity, indicating species turnover between PAs, shows an analogous pattern (Fig. 2e). Nestedness-resultant dissimilarity among PAs (gradient dissimilarity; Fig. 2f) contributes less to total compositional dissimilarity than the turnover component. Furthermore, total dissimilarity of PAs with low reported species richness in Poland, Czech Republic, Romania and Greece is mainly composed of turnover-resultant dissimilarity; these PAs tend to host relatively few reported species that are unique to these areas. The standard deviation of pairwise dissimilarity values of a single PA is typically low for PAs that have high mean dissimilarity scores (i.e. total dissimilarity) and vice-versa (Supplementary Fig. S2). For a complete list of the PAs and their conservation-related metrics, see Supplementary Information.

The relationships between the metrics of conservation value (Fig. 3) reinforce the geographical patterns described above. The index 'area-controlled surplus of reported species' is strongly associated with reported species richness (r=0.41, p<0.001). Rarity-weighted richness is more strongly related to average rarity (r=0.71) than to reported species richness (r=0.22), though both correlations are significant (p<0.001; Fig. 3). Reported species richness is negatively related to total dissimilarity; this relationship is strong and non-linear (Fig. 3). Total dissimilarity is much more weakly, and positively, associated with average rarity (r=0.22, p<0.001), which suggests a small influence of species rarity on compositional dissimilarity. High balanced dissimilarity corresponds to high total dissimilarity (r=0.84, p<0.001), which indicates that dissimilarity is dominated by species turnover.

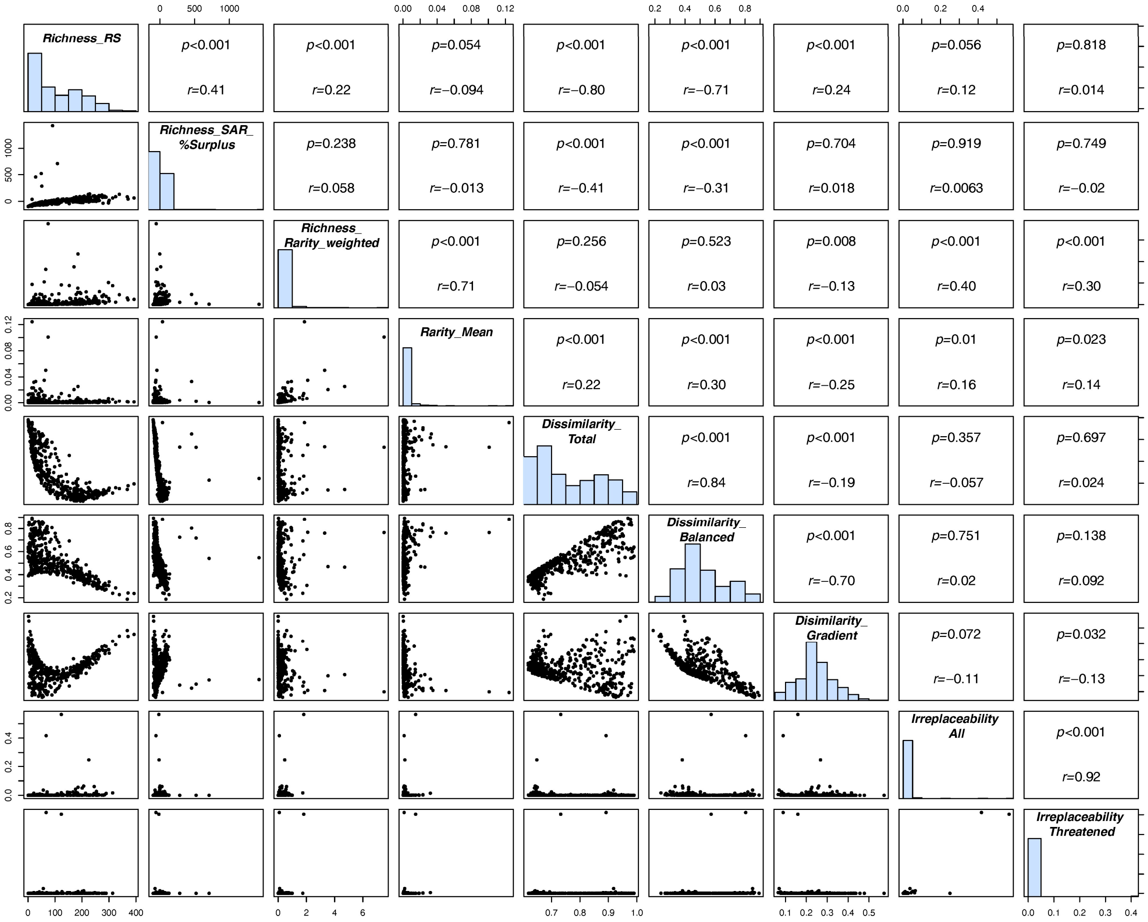

Figure 3. Correlations among metrics of conservation value of protected areas: reported species richness (*Richness_RS*)*,* rarity-weighted richness (*Richness_Rarity_weighted*), average rarity (*Rarity_Mean*), area-controlled surplus of reported species (*Richness_SAR_%Surplus*), total dissimilarity (*Dissimilarity_Total*), balanced dissimilarity (*Dissimilarity_Balanced*), gradient dissimilarity (*Dissimilarity_Gradient*), irreplaceability for all species (*Irreplaceability All*) and irreplaceability for threatened species (*Irreplaceability Threatened*). Irreplaceability values were calculated by Le Saout et al. [23]. The *r* indicates the Pearson correlation coefficient, whereas *p*-values reflect the significance of the correlation considering spatial autocorrelation. Panels at the diagonal show frequency distributions of the variables.

Sensitivity analyses

The sensitivity analyses estimate potential reporting bias of EU member states and how this influences the PAs' conservation values. The results generally show (Fig. 4b-h) that the distribution of observed values in the EU, associated with the grey line and wide grey strip, is very different from the random distribution (red line and narrow red strip). Thus, the annex species are non-randomly distributed within the entire set of PAs. The reported species richness values in Poland, Romania and Greece are significantly (i.e. $p<0.05$) lower than (i) randomly expected (red stars, Fig. 4b), and (ii) in the remaining EU states (grey stars). This supports the visually perceived paucity of reported (bird) richness in Poland, Romania and Greece (Fig. 1a, Supplementary Fig. S1), but not in the Czech Republic. For Bulgarian PAs, not only did we detect not significantly higher reported richness than in the rest of the EU, but the richness values are actually lower than expected under random species distribution. We also identified EU states that include PAs of significantly low (e.g. Cyprus, Portugal, Finland and Sweden) and high reported richness (e.g. Hungary and Slovakia), but these do not show extreme reported richness per grid cell (Fig. 1a). Other nations have *Richness_RS* values that are neither significantly distinct from randomization, nor from the rest of the EU, which does not support the existence of a bias. Moreover, the observed *Richness_RS* values are generally much lower than under the randomized null model.

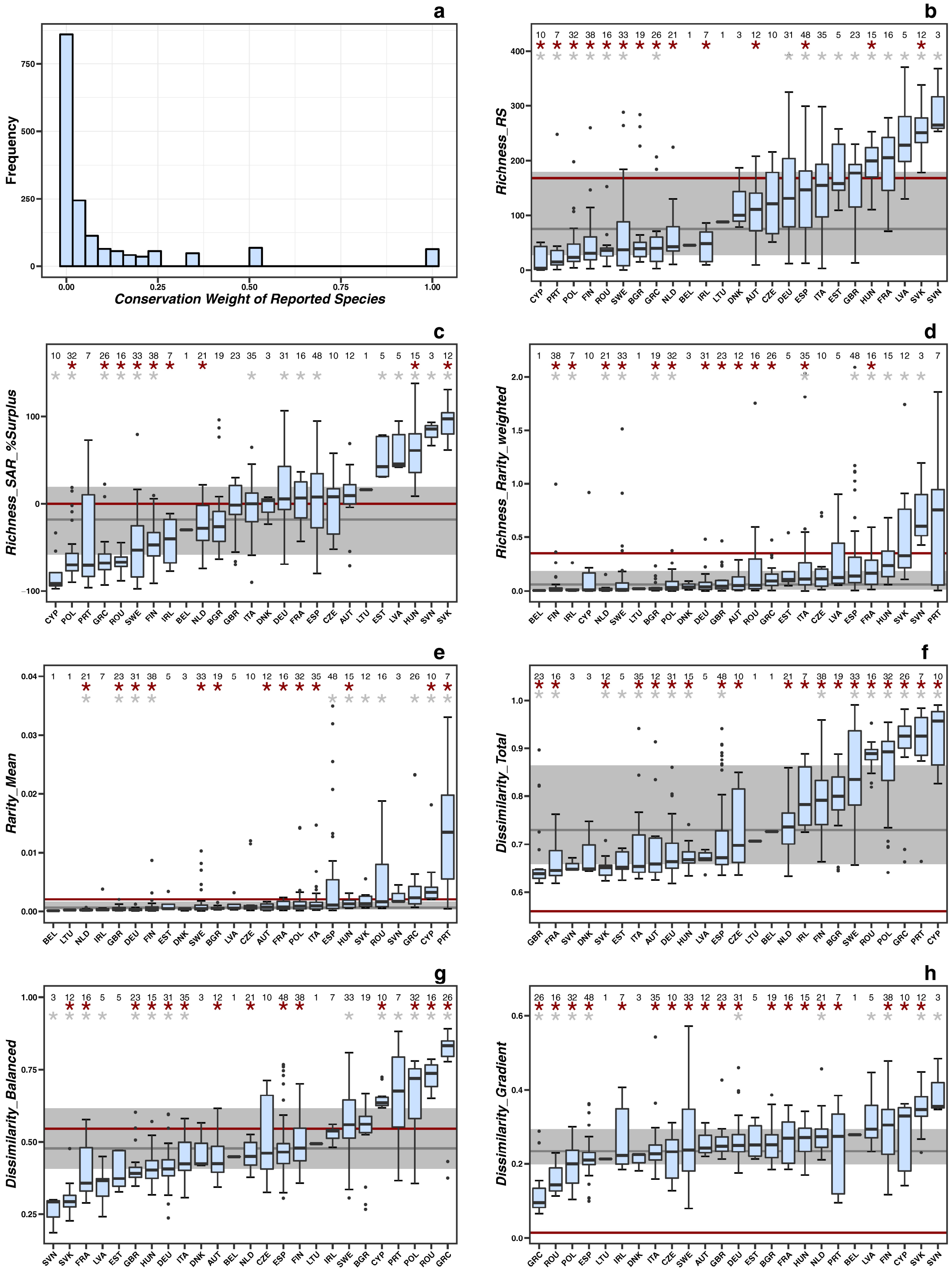

Figure 4. Sensitivity analysis to assess potential reporting bias of EU member states. a) Frequency distribution of species' conservation weight *w*, where frequency is the number of species. For annex species of the Birds and Habitats directives, *w* was calculated as the inverse of the sum of grid cells in which the species is present, within the land area of the EU. The conservation weights of reported species were maintained for the randomization procedure included in this sensitivity analysis for b) *Richness_RS*, c) *Richness_rarity_weighted*, d) *Rarity_Mean*, e) *Richness_SAR_%Surplus*, f) *Dissimilarity_Total*, g) *Dissimilarity_Balanced*, and h) *Dissimilarity_Gradient*. In b) to h) the thick black

line within blue boxes represents the median. The limits of the blue box show the lower and upper quartiles, i.e. interquartile range. The whiskers extend to the lowest to the highest values within 1.5 times the interquartile range. The black dots indicate outliers beyond the whiskers. The horizontal grey line depicts the median of the EU-wide distribution that was observed based on the original data. The corresponding grey strip shows the interquartile range of this observed distribution. The grey stars show significant differences ($p<0.05$) between the observed values within an EU member state (ISO3 code) and the rest of the EU. The horizontal red line shows the median of the EU-wide distribution that was simulated by randomization. The narrow red strip represents the interquartile range of this simulated distribution. The red stars indicate a significant difference ($p<0.05$) between the observed and randomized values per EU member state. The black number above each boxplot gives the number of data points (PAs) per EU member state. The boxplots are ordered by their median, increasing from left to right. Transboundary protected areas were excluded. For details see Methods.

Very similar results were found for the area-controlled surplus of reported species (Fig. 4c), because PA size was maintained in the null model. Furthermore, these sensitivity patterns vary little when the species' conservation weights are involved (i.e. *Richness_Rarity_weighted*, Fig. 4d) since in the null model the weights were maintained as well. The conservation weights barely changed the *Richness_RS* pattern, because most conservation weights are low (Fig. 4a). These findings are in line with sensitivity results for average rarity (Fig. 4e), which is strongly correlated to rarity-weighted richness (Fig. 3).

The total dissimilarity of PAs is, in general, significantly higher than randomly expected (Fig. 4f). *Dissimilarity_Total* is primarily driven by species turnover (Fig. 3 and 4g) rather than nestedness (Fig. 3 and 4h). Slovakia and Hungary show significantly lower total dissimilarity than the remaining EU states, while Finland, Sweden, Romania, Poland, Greece, Portugal and Cyprus indicate significantly higher values. This conforms to the sensitivity results of *Richness_RS*. The PAs of Finland, Sweden, Romania, Poland, Greece, Portugal and Cyprus include significantly fewer as well as different species than are found in the majority of other PAs. Slovakia contains PAs that are not only rich in reported species, but also significantly more similar to other PAs than are the remaining PAs in the EU. Therefore, many reported species of Slovakian PAs also occur in many other PAs that include fewer species. Hungary presents similar relationships, but turnover-resultant dissimilarity dominates here. Note that in some EU states the number of PAs was not sufficient to adequately test for significant differences between value distributions.

The cross-validation of area-controlled surplus of reported species and dissimilarity indices indicates how robust the PAs' conservation values are against potential reporting deficits of EU member states (Fig. 5). Under simulated absence of species records and PAs of various nations, the dissimilarity metrics show a small amount of variation in relation to their absolute values. The *Richness_SAR_%Surplus* index shows larger relative variation. The conservation values of many PAs in central, western, and southern Europe are less stable although we did not detect extraordinary conservation values in these nations. The extreme conservation values of eastern and western European states that we identified before, are more stable. This suggests that the conservation values of these nations are distorting the absolute conservation values of the remaining countries even if the relative deviations are small; continental patterns of uniqueness values are sustained.

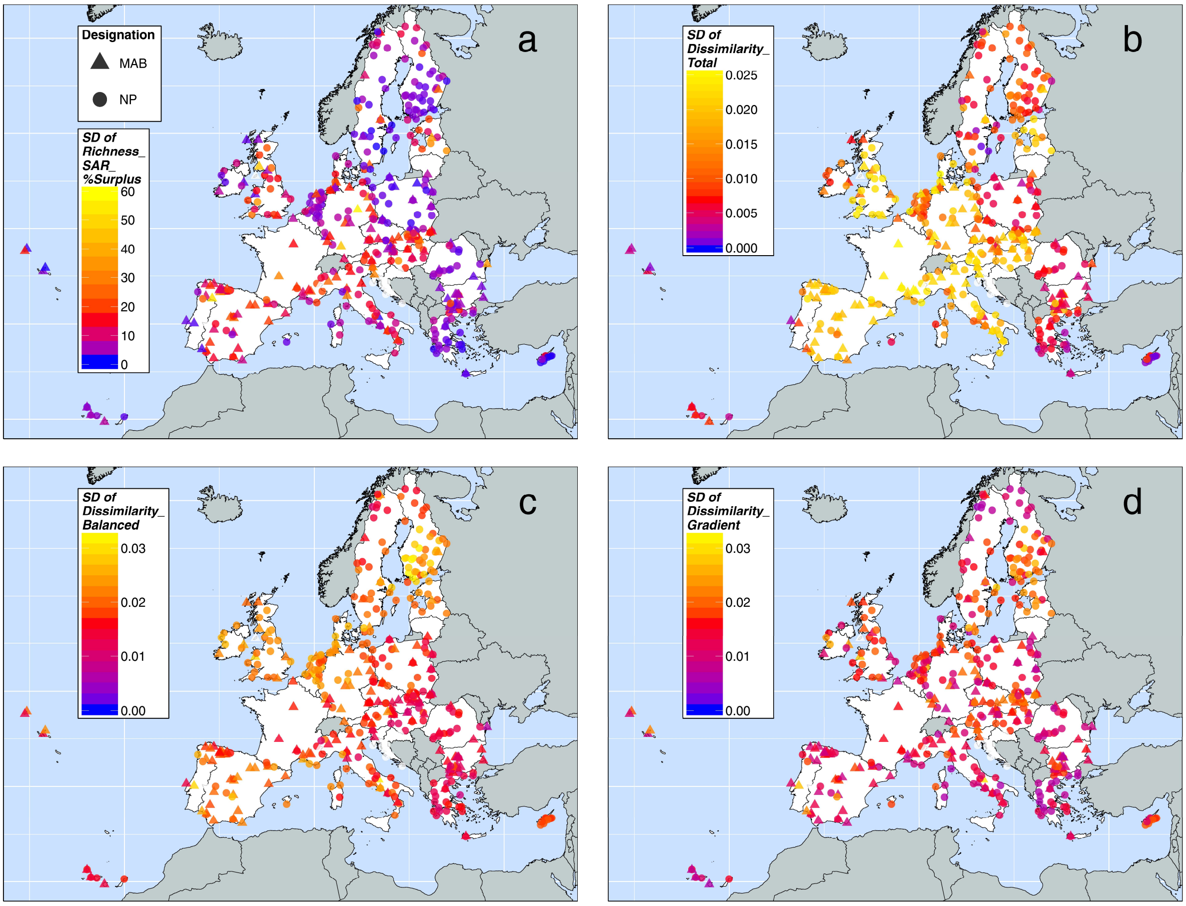

Figure 5. Cross-validation of four metrics of conservation value against potential reporting failure of EU member states. Five different nations were randomly excluded in each of 1,000 runs, to simulate the absence of biased countries and its effect on uniqueness indices. The standard deviation (SD) of resulting uniqueness values is a measure of uncertainty under reporting failure. In other words, it represents the robustness of conservation values of protected areas against potential reporting deficits of EU member states. Since we assume a lack of reported species only, we maintained the species' conservation weights in this sensitivity analysis (for details see methods section). Thus, only a) area-controlled surplus of reported species, b) total dissimilarity, c) turnover and d) nestedness are affected by this simulation procedure. Transboundary protected areas were excluded. The maps were created using open-source software R, Version 3.3.3 (https://www.R-project.org/) [60].

Irreplaceability and the metrics of conservation value

The irreplaceability scores obtained from Le Saout et al. [23] have weak positive correlations with the rarity-related metrics rarity-weighted richness and average rarity only (Fig. 3), and these correlations are driven by only a very small number of PAs. Moreover, the amount of variation in the scores from Le Saout et al. [23] is very limited for these European PAs (Fig. 3 and 6).

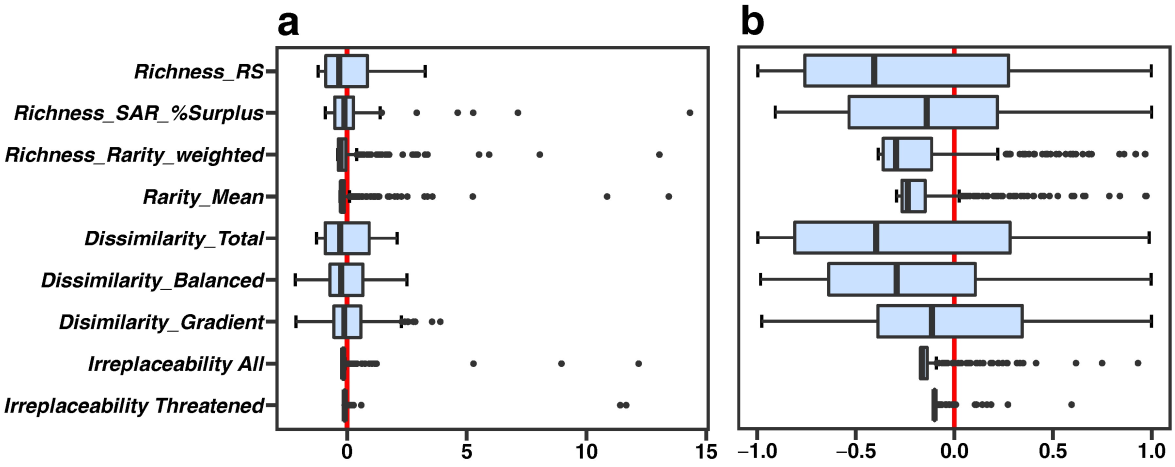

Figure 6. The standardized value range of metrics of conservation value for national parks (NP) and UNESCO Man and Biosphere reserves (MAB) in the European Union. The value range of metrics is standardized to zero mean (red line) and unit variance (horizontal axis). Boxplots as in Figure 4. The black dots indicate outliers. a) The total ranges of the values. b) Zoomed in, to display only from -1 and 1 standard deviations from the mean.

Separating national parks, biosphere reserves and taxa

We detected significant differences between the distributions of *Richness_SAR_%Surplus* values of the combined set of PAs versus the separated sets (Supplementary Fig. S3), but geographical patterns remained similar. The same is true for *Dissimilarity_Total* (Supplementary Fig. S3). Hence, *Richness_SAR_%Surplus* and dissimilarity indices are sensitive to the selection of PAs. The metrics of conservation value also depend on the species involved. When single taxa were considered separately (Supplementary Fig. S1, and S4 to S12), the uniqueness values of single PAs frequently differed from results for all taxa.

Discussion

A macroscopic perspective best guides a comprehensive conservation strategy [11,12,20,23]. Surprisingly, however, little research effort has aimed to demonstrate how biodiversity is distributed among European PAs [22], though most nature conservation funding by the EU has not been directed towards regions with urgent conservation needs [32]. With our study, we provide the first analytical approach to estimate and compare different components of species diversity across the set of European NPs and MABs. The results provide a quantitative holistic assessment conservation value of PAs and can form a basis for decision-making, conservation prioritization and targeting future field research. Funding strategies require transparent instruments to set conservation priorities for the spatial distribution of conservation effort [16,33,37,44]. Our approach enables PAs to be rated and compared, with respect to biodiversity components of conservation concern, as represented by reported species, and can be easily applied to different datasets and PA types. The results are based on data with intrinsic limitations, but represent a first and unique attempt to assess the conservation capacity of major European PAs for priority species of the EU.

The study outcomes can support EU-wide conservation planning by demonstrating strengths and weaknesses of the set of European NP and MAB sites. We found consistently high uniqueness on Macaronesian islands, the Mediterranean Basin, northern Scandinavia and parts of central and eastern Europe. The uniqueness of PAs in these regions is driven by the rarity of reported species, but most of these PAs contain relatively few species. This demonstrates a potential management conflict regarding the overall conservation value of these PAs, because it is not trivial to decide whether it is more valuable to preserve many common or few rare species. Low richness and high rarity of annex species around the periphery of the EU is probably not only related to distance decay – the increase of compositional dissimilarity of PAs with distance between PAs – but also to the occurrence of regionally endemic species in these isolated, species-poor regions. Another reason for high uniqueness in some parts of the periphery of the EU, especially eastern and north-eastern EU, is species that mostly occur beyond the EU and whose ranges extend into the EU. Many PAs in those peripheral areas are of relatively little importance for the global conservation of such species, but these PAs do contribute a lot to the conservation of these species within the EU; our study brings the EU-wide conservation effort into focus and identifies responsibilities of PAs and corresponding nations for the conservation of legally protected, priority species inside the EU. Thus, our study does not directly address the conservation needs beyond the EU, but several annex species are endemic to the EU, implying specific responsibility of the EU to preserve such species at the global scale.

We found that the size of PA is not a strong predictor of reported richness; many PAs contain considerably more or fewer species than expected from their size. The isolation of the Macaronesian islands means they relatively low species richness for their sizes, which probably explains the low SAR-related richness values of PAs on those islands. We also found clusters of PAs with distinctly different species composition from the rest, emphasizing the value of the regional perspective. Compositional dissimilarity is a crucial dimension of conservation performance of PA networks [45] that is widely neglected [46]. It is a distinct and fundamental component of biodiversity that informs about site complementarity, and is therefore highly relevant to multi-site conservation, such as PA networks. Relatively high uniqueness scores are generally more dependent on species composition rather than species richness, as it was indicated by the relationships between conservation indices, including the higher contribution of turnover than nestedness dissimilarity. Note that absolute dissimilarity values are sensitive to the selection of PAs, whereas the relative, continental patterns are not.

Mapping reported species richness per grid cell suggests variation in data quality among countries. We thus suppose under-reporting of species in Poland, Romania and Greece, particularly for birds. The conservation values of PAs in these nations may therefore be underestimated and must be interpreted with care. By applying beta diversity partitioning (i.e. turnover and nestedness), we found, nevertheless, that the reported species of these PAs are very different from the remaining nations. These uniqueness indices and average rarity indicate that rare annex species occur inside these PAs. The low uncertainties of conservation values in these countries support the idea that these PAs have distinct species composition, despite the reporting deficit. While they bias the absolute conservation values of the remaining PAs, the biogeographical patterns of uniqueness are robust against the reporting deficiency.

In the sensitivity analyses, some other PAs had conservation values very different from expectations based on species richness, with no other indication of reporting bias; we suppose that this is caused by ecological reasons. The geographically marginal location in the EU, and isolation, may reduce the number of annex species present in Portugal and Cyprus. The latitudinal richness gradient accounts for low reported richness in Finland and Sweden, and low human impact might enhance species richness found in Hungary and Slovakia. Many PAs in these areas have relatively high uniqueness values suggesting that many annex species are only found in few nations. Consequently, such nations are especially responsible for the protection of annex species in the EU and, in case of endemics, at the global scale.

Our evaluation of data deficiencies – especially the lack of (bird) species occurrences in Poland, Romania and Greece – agrees strongly with the data quality evaluation by the European Environment Agency (EEA) [49]. The EEA highlights several nations and sub-nations with serious reported data deficits, but does neither provide details nor reasoning. For Spain, the Canary Islands, Poland, the Azores, Madeira and Romania, over 5% of mandatory information under Article 12 of the Birds Directive is missing and over 25% is noted as 'absent' or 'unknown'. Mandatory data include species distribution data. With respect to the Habitats Directive, only Portugal submitted data in which over 25% of information was marked as 'unknown' or 'absent'. Data quality information for Greece is missing, probably due to the nation's delayed submission of data. These facts may explain the exceptional conservation values of PAs in Poland, Romania, Greece and Portugal even though a reporting bias in Portugal was not visually striking. The EEA also states data deficits in Spain; our sensitivity analyses do not support a lack of reported species in Spain, but indicate common conservation values of Spanish PAs. In this case, we suppose that the data deficits do not relate to species distributions. Finally, the data quality evaluation of the EEA supports the interpretation of our data quality evaluation, suggesting that Poland, Romania, Greece and Portugal failed to report the spatial distribution of all annex species present, but this under-reporting is not enough to substantially affect the EU-wide uniqueness patterns.

Using different methods and data, our findings are partially in line with, but greatly add to, a global study of irreplaceability of PAs [23]. Our study uses a wider range of metrics and more taxa, is more comprehensive within the EU and provides new tools. The uniqueness indices correlate little with the irreplaceability scores calculated by Le Saout et al. [23], which, being globally calibrated, show minimal variation for all but three European PAs, and thus have minimal discriminatory power for the EU. This again emphasizes the value of the EU-wide perspective. Recalculating global-scale conservation indices for regional-scale conservation systems can deliver more meaningful results for the regional context. In consideration of both species richness and rarity, our indices agree in the rating of PAs regarding their potential to protect species considered by the EU directives and the IUCN Red List.

Biodiversity-based indicators of conservation value strongly depend on the set of species analyzed. It is claimed that species listed in annexes of the Birds and Habitats directives were not strategically selected, i.e. their conservation status in the EU was not considered [47]. A few species of the directives are neither threatened in, nor native to Europe, and their European annex status is not always consistent with the European Red List status; but the annex species are considered 'umbrella species' for many different taxa [37,48]; a lot of other species profit from their protection. We therefore expect that our uniqueness values reflect a much higher proportion of biodiversity than annex species only. In addition, we neither use the annex status, nor the Red List status to estimate the conservation value of species in the EU. The conservation weight we applied is solely based on occurrence data, which is a simple and reproducible measure of conservation status with high spatial resolution and a metric scale.

The conservation values we calculated for individual PAs depend not only on the species involved, but also on the study extent. Our analysis quantifies conservation value inside PAs; it does not assess the conservation value of unprotected areas. Protecting all facets of biodiversity at the global extent is the ultimate goal in nature conservation, but depending on future policy and land-use change, the conservation value of protected areas, in themselves, may be crucial. Accordingly, we focus on the PAs as self-operating, isolated units in the European landscape, an approach similar to an important global study of irreplaceability focusing only on PAs and did not include data from their surroundings [23]. Applying our methods to this global data set is possible and offers further research potential, but, as we show, such global-level research can almost completely miss regional-scale patterns. An important question not addressed by our study is: how much does the conservation effort of the EU contribute to global conservation needs?

Staff deficits and financial undersupply are major challenges for European PAs [16]; such local restrictions can cause considerable bias and noise in data directly derived from park and reserve authorities, when conducting large-scale comparisons. This is a key reason why our EU-wide comparison of PAs used the standard set of species that EU member states must report. Additionally, PAs' corresponding grid cells are likely to be more extensively sampled than unprotected cells, because of monitoring and research activities by PA authorities and other parties [16]. The Birds and Habitats directives are legally binding regulations, significant and conclusive for nature conservation in the EU. The statutory duty and high importance for conservation across the EU make this dataset unique and expedient for conservation biogeography [37].

National parks and MAB reserves are cornerstones of the European PA network. Although there are many such PAs, their distribution does not conform to patterns of high biodiversity or rarity. National policies, the history and philosophy of planning, and conservation management have had strong influences on the spatial distribution of PAs [9,11,15], especially in Europe, where national biases become evident [33,36]. The current situation clearly shows differences in the distribution of NPs and MABs between countries, with large countries containing relatively few (e.g. France) and relatively small countries with many (e.g. the Netherlands). Thus, our research also demonstrates that the development of effective conservation planning at the European scale requires assessment and standardization of PA classification across the European countries, as intended by the IUCN management categories and the Natura 2000 framework, establishing Special Protection Areas (SPAs) under the Birds Directive and Special Areas of Conservation (SACs) under the Habitats Directive.

However, the SPAs and SACs are often small and lack effective management [16,44,49,50,51]. Furthermore, frequent PA designations such as habitat management areas, protected landscapes and areas for the use of natural resources are primarily not established and regulated to protect species. The European NPs and MABs are, in contrast, far from 'paper parks', because they protect biodiversity by individual, independent, intensive and integrative management [39,40] while promoting ecosystem goods and services. Thus, NPs and MABs may be more efficient in implementing new conservation insights in future [17].

Further, funds from recreational visits can be spent on conservation [52]. These are reasons why we selected NPs and MABs to study.

Conservation value goes beyond considering only species diversity; phylogenetic, trait, habitat and ecosystem diversity should be included as well. However, these other components of biodiversity are more difficult to address. Evaluating reasons for, and threats to, the measured uniqueness would need to include factors such as isolation, connectivity, anthropogenic pressure and climate change. These aspects remain for future investigations. However, our concept of uniqueness can be easily adopted for data of similar structure (e.g. ecosystem functions and services) and can serve as a common tool to judge the conservation value of PAs.

Biodiversity knows no political borders. Regional-scale nature conservation needs international coordination and implementation of integrative, yet adaptive, conservation policies, i.e. PA management plans and species protection programs. The approach we propose merges such policies to evaluate the representativeness of PAs with respect to species conservation inside a PA network. It can be easily adapted for other biodiversity aspects, from genes to ecosystem level, depending on data availability. We thus emphasize the importance of high-quality data for large-scale conservation assessments. Our study may serve as one basis for future conservation action. We encourage national authorities to cooperate and support funding beyond national boundaries to improve the adequacy of nature conservation in view of a rapidly changing world.

Methods

Protected area network and reported species

The PAs we included in the analyses were those within the EU that are designated as either 'national park' (NP) or UNESCO 'Man and Biosphere Reserve' (MAB). In some cases, MABs entirely or partly cover NPs. We therefore conducted analyses for the whole set of PAs, and separately for the NP and MAB networks. We obtained spatial data on PAs from the World Database on Protected Areas [41] and the UNESCO MAB Biosphere Reserve Directory [40]. Protected areas for which species reporting was at least partly missing (e.g. for Croatia and transboundary PAs at the EU border) were excluded from analyses. In total 432 terrestrial and semi-terrestrial PAs were considered, 285 of which are NPs and 147 are MABs. We excluded purely marine PAs, and marine species. For 7 national parks (NPs) and 120 UNESCO Man and Biosphere reserves (MABs) boundary data were not available. In this case we used circular buffers of reported PA surface area around given PA centroids (see also Le Saout et al. [23]). The PA polygons comprise all parts that officially belong to the PA, such as buffer and core zones. In total, 55 NPs overlap with 53 MABs. Ten of these 53 MABs entirely contain eight NPs. No MAB is entirely enclosed by any NP. Five MABs are identified as transboundary. The quantity of NPs and MABs is remarkably low in France, Lithuania and Belgium (Fig. 1).

We used species occurrence data published by the European Environment Agency (EEA) in fulfilment of EU legislation [38]. Known locations of annex species of the Birds Directive (2009/147/EC; Annex 1 to 5) and the Habitats Directive (92/43/EEC; Annex II, IV and V) had to be reported by EU member states for 2008–2012 under Article 12 of the Birds Directive and 2007–2012 under Article 17 of the Habitats Directive. We refer to these as 'reported species'. The annexes involve characteristic, rare, endemic, vulnerable and endangered species at the level of the EU – not necessarily global – that were selected via expert knowledge of a European Committee. Both directives require EU member states to achieve a favourable conservation status of annex species within the EU. Detailed information about the reported species and their conservation status is provided by the European Topic Centre on Biological Diversity (Eionet) [53]. According to the species lists for the reporting under Article 12 of the Birds Directive [38], EU member states reported on 576 wild bird species, which are the majority of bird species naturally occurring in the EU. Out of these species, 193 are particularly threatened within the EU, which means prone to extinction, vulnerable to habitat changes, and rare in terms of small population and range size. For these species EU member states must provide 'Special Protection Areas' (SPA), which are one type of Natura 2000 site. The other species considered by the Birds Directive are protected through hunting, capture and trade restriction, or are subject to specific research, monitoring and management regimes. Referring to the species lists for the reporting under Article 17 of the Habitats Directive [38], 1319 species of other taxa must be reported, including fish, amphibians, arthropods, mammals, molluscs, reptiles, vascular and non-vascular plants. They are rare, endemic, vulnerable or threatened in the EU. For these species the EU member states are obliged to manage 'Special Areas of Conservation' (SAC), which cover the core habitat of those species. The sites are also part of the Natura 2000 network. Moreover, a strict protection regime must be applied across the range of those species on EU territory. The exploitation of species is also legally restricted for some species listed in the Habitats Directive.

Species reporting covered all EU member states except Croatia, which joined the EU in 2013. Out of 1895 annex species that are required to be reported (see species code lists provided by the EEA [38]), we amassed occurrence records for 1695 reported species, including 41 marine species, in 10 km x 10 km grid cells across the EU, though 392 of these species did not occur in any PA that we considered here. Eventually, 1303 species were included in the PA analyses: 469 birds, 105 fish, 93 mammals, 49 amphibians, 73 reptiles, 111 arthropods, 20 molluscs, one other invertebrate, 32 non-vascular and 350 vascular plants. We performed analyses across all taxa; see Supplementary Information for within-taxon analyses.

Matching species distribution data with protected areas

Since distribution data of reported species are variable in quality and have coarse spatial resolution, we applied a probabilistic approach for assigning each reported species to each PA, comparable to methods used in Araújo et al. [20]. When a reported species was present in several grid cells partially overlapping with the PA surface, the cumulative probability that the species was present in the PA was calculated by applying chain rule probability theory. The total probability of a species being present in a PA is thus the sum of all possible chain path probabilities that result in a probability of finding the species in the PA. In other words, the total probability of a species being present in a PA is the probability that a species is present in at least one of all overlapping parts between the PA and the occupied grid. Each chain step represents one particular grid cell containing a species that is partly covered by the PA. The total probability p_i of a species i being present in a single PA j is therefore calculated by

$$p_{i;j} = c_1 + (1 - c_1)c_2 + (1 - c_1)(1 - c_2)c_3 + \cdots + (1 - c_1)(1 - c_2) \ldots (1 - c_{n-1})c_n$$

$$= 1 - (1 - c_1)(1 - c_2)(1 - c_3) \dots (1 - c_n) = 1 - \prod_{k=1}^{n}(1 - c_k)$$

where c is the PA coverage of the kth of the n grid cells where the species is present. Imagine, for instance, two cells 1 and 2 which record the presence of a given species. The PA covers 20% of cell 1 (c_1=0.2) and 50% of cell 2 (c_2=0.2). Therefore, the cumulative probability of finding the species within this PA is 1-(1-0.2)(1-0.5)=0.6.

Each reported species was thus assigned to each PA with a probability of occurrence ranging from 0 to 1. We assume that at such an extensive scale and for such large PAs, any bias or distortion of calculated species presence within PAs is acceptable, given the aims and scope of this study [54]. The limits of this approach are easily recognized, but it allows us to utilize one of the most fine-grained and freely available data sets that includes such a variety of taxa at a continental scale.

Reported species richness and adjustment for area

We calculated the richness of reported species (*Richness_RS*) for each PA j as $Richness\_RS_j = \sum_{i=1}^{RS} p_{i;j}$ with $p_{i;j}$ the probability to find the i^{th} species in the j^{th} PA. This represents the most likely number of reported species within each PA.

To account for the effect of PA size on *Richness_RS* we developed the *Richness_SAR_%Surplus* index using the species–area relationship (SAR). *Richness_SAR_%Surplus* measures the number of species present in excess of the richness expected from the best-fitting SAR model, expressed as a percentage of the expected richness. SAR modelling has rarely been used for evaluating protected areas (but see Chiarucci et al. [34]).

We modelled species–area relationships (SARs) by fitting the classic Arrhenius Power Function [55], $Richness_{RS} = b \cdot A^c$, and Gleason's Exponential Model [56], $Richness_{RS} = y + z \cdot log(A)$. In these models, b and y represent the number of species expected for unit area, while c and z represent the increase in the number of species with surface area, but with different scaling of area in the two models. We fitted the models for the whole set of PAs for which data were available and compared them to a linear null model with intercept equals 0. We performed SAR model selection using Akaike's Information Criterion (AIC), suggested to be one of the most appropriate statistical methods for comparing such models [57]. The Arrhenius model fitted best (i.e. lowest AIC; Supplementary Fig. S13) and was used as the SAR reference model for calculating the expected value of *Richness_RS*; the residuals of the SAR model were divided by the corresponding fitted values and multiplied by 100. The resulting value is therefore the number of species in the PA over and above the number expected from the species–area relationship, expressed as a percentage of the expected number; it can be labelled the 'area-controlled surplus of reported species', abbreviated as *Richness_SAR_%Surplus*. Positive values indicate PAs with more species than expected under the SAR model, and negative values indicate fewer than expected.

Conservation weight of reported species

The measures described above (i.e. *Richness_RS* and *Richness_SAR_%Surplus*) assign equal importance to all reported species. To provide a better quantification of the conservation value of each PA, we calculated a conservation weight w_i for each species i as the inverse of the sum of grid cells occupied by the species in the land area of the EU [58]. In this study, the conservation weight is also referred to as 'rarity'. The more grid cells the species is present in, the lower is its rarity and conservation weight.

Rarity-weighted richness and average rarity

Rarity-weighted richness of each PA j was calculated by $Richness\_Rarity\_weighted_j = \sum_{i=1}^{RS} p_{i;j} \cdot w_i$ where $p_{i;j}$ represents the likely presence of each reported species in the j^{th} PA and w_i is the conservation weight of the species. This index becomes 0 when no reported species are present in the PA. It increases with species richness within PAs and with the conservation weights of species. Thus, *Richness_Rarity_weighted* considers species richness and rarity simultaneously.

Since *Richness_Rarity_weighted* is partly dependent on the number of reported species within the PA, we introduce another index, the average rarity (*Rarity_Mean*). This measures the average conservation weight of reported species within the PA and is calculated as *Richness_Rarity_weighted*/ *Richness_RS*. It is set to 0 when the PA contains no reported species, and has maximum value 1. It reaches its maximum value of 1 when all the reported species in the PA are present with probability 1 and when each species only occurs in one grid cell that is entirely within the PA. A *Rarity_Mean* value of 1 means the PA is absolutely unique for preserving a set of species.

Differentiation diversity

Differentiation diversity (i.e. beta diversity) between PAs gives additional information about the conservation value of PAs [45,46]. A less unique PA has a species composition that is very similar to other PAs. We used Baselga's concept of beta diversity [43] – adapting Bray-Curtis dissimilarity index and its components – to measure the dissimilarity between sets of species occurrence probabilities of PAs. The beta diversity metrics return a dissimilarity value between two numerical vectors of the same length, no matter the meaning of the number (i.e. abundance or probability). This enables the use of the occurrence probabilities as input values for these indices, rather than forcing the probabilities into values from 1 to 0 to estimate abundances, which would implicate additional uncertainty. Thus, a dissimilarity value of 0 means the same composition of the species' occurrence probabilities, a value of 1 indicates totally different composition of probabilities. In Baselga's concept [43] the total dissimilarity (*Dissimilarity_Total*) is additively partitioned into the balanced (*Dissimilarity_Balanced,* i.e. turnover) and gradient (*Dissimilarity_Gradient,* i.e. nestedness) components, allowing a more sophisticated assessment of the PAs' conservation value. Balanced dissimilarity, *Dissimilarity_Balanced*, is equivalent to turnover between two sample sites and quantifies, in our case, a balanced change of occurrence probabilities between sites: some species gain in probability of occurrence, while others lose. Accordingly, gradient dissimilarity, *Dissimilarity_Gradient*, is equivalent to nestedness and represents monotonic increase or decrease (i.e. a gradient) of occurrence probabilities between sample sites. In order to calculate the compositional uniqueness of a given PA to all other PAs, we took the mean of all pairwise dissimilarities of the PA compared with all others. To detect the variation of pairwise dissimilarities per PA, we also calculated the standard deviation (Supplementary Fig. S2).

Sensitivity analyses

We applied sensitivity analyses to estimate the potential bias of species reporting by individual EU member states and its effect on uniqueness values of PAs. The EU nations are obliged to report on each annex species individually. We assume that a potential bias was induced by each annex species present in, but not reported by, EU states. We do not assume that the nations' reported species distributions are biased, so the species' conservation weights are the best estimate of the species' real rarity in the EU. Therefore, we maintained the weights in the sensitivity analyses. The sensitivity analyses comprise three approaches. First, we followed a null model approach to test whether observed conservation values of PAs based on the original data are significantly (i.e. $p<0.05$) different from values randomly expected, i.e. based on simulated data. Regarding the simulated data, we randomly distributed the species a thousand times (i.e. 1,000 random simulations), maintaining the frequencies of each species, i.e. the species' conservation weights in the EU. We thus simulate a quite arbitrary reporting of species occurrences in grid cells and PAs that is only restricted to the species that were originally reported, and to their total frequencies. We recalculated the metrics of conservation value for each PA and simulation run. We tested for significant differences between the observed values and the randomized values within each nation via the non-parametric, two-sided and paired Wilcoxon signed rank test. Second, we used the non-parametric, two-sided but unpaired Wilcoxon rank sum test (i.e. Mann-Whitney test) to check for significant differences between the observed values within each nation and the observed values within rest of the EU. Thus, we can estimate whether the observed conservation values of PAs within nations are rather usual or extreme (i.e. low or high) with respect to, first, arbitrary reporting and, second, conservation values at an EU-average (i.e. of all other EU nations). Third, we conducted a cross-validation procedure that accounts for the uncertainty of resulting conservation values under potential reporting bias. Here we also ran 1,000 simulations. In each simulation run, we randomly chose 20 out of 25 nations without replacement. We thus simulate reporting deficits by excluding reported species and PAs of five nations. We decided to exclude five countries, since the official data quality evaluation of the EEA [49] highlights five nations of serious reporting deficiency. Based on the remaining PAs we recalculated *Richness_SAR_%Surplus* and the *Dissimilarity* indices. Other indices are not affected by this simulated lack of species reporting, since the conservation weights are kept constant. We took the standard deviation (SD) of the 1,000 runs as a measure of uncertainty and non-robustness of conservation values against bias.

Irreplaceability and the metrics of conservation value

Our metrics of conservation value are summarized in Table 1. We investigated correlations among the metrics, and between each of these and the PAs' irreplaceability scores as calculated by Le Saout et al. [23] (Fig. 3). We used Pearson correlation and a modified t-test that accounts for spatial autocorrelation [59], to derive the *p*-values. Le Saout et al. [23]

measured irreplaceability by the overlap of each PA with species' ranges – rather than occurrence records, as here – of a subset of the taxa that we include (i.e. amphibian, mammal and bird species from the IUCN Red List of Threatened Species). We used ArcGIS (Version 10.3.1; ESRI, Redlands, CA) and R [60] (Version 3.3.3) for the geospatial and statistical analyses.

Data availability

Datasets analyzed in the current study are publicly available. Data on PAs are obtained from the World Database on Protected Areas [41] and the UNESCO MAB Biosphere Reserve Directory [40]. We used species' occurrence data published by the EEA in fulfilment of EU legislation [38]. Irreplaceability scores of PAs are taken from Le Saout et al. [23].

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Author contributions

All authors conceptualised the study idea. S.H. conducted the analyses and led the writing process. All the authors contributed to the interpretation of results and writing.

Additional information

Supplementary information Dataset 1 'Uniqueness_Data_Table.xlsx' is available online at https://doi.org/10.1038/s41598-018-24390-3.

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Supplementary information

Supplementary figures

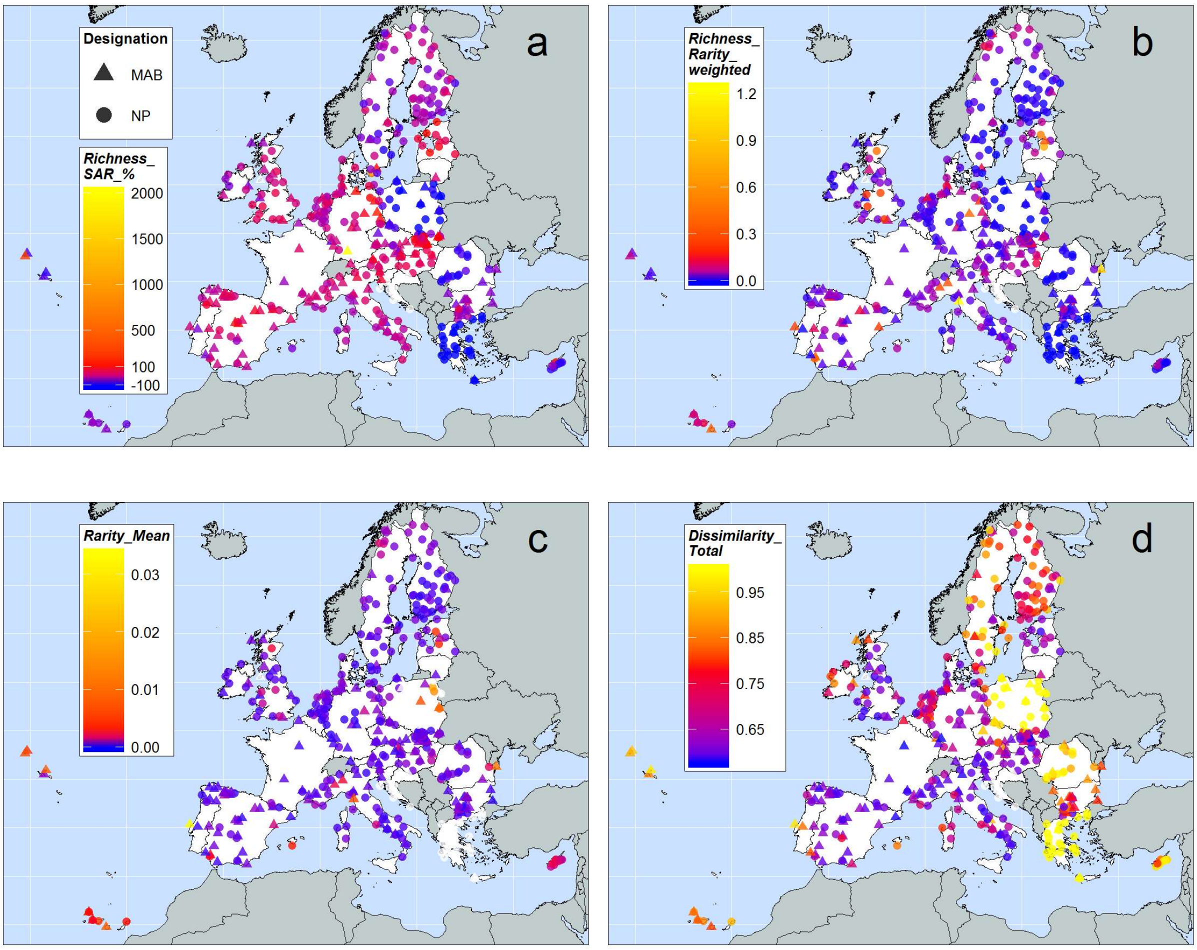

Figure S1. Uniqueness indices of protected areas calculated separately for 469 birds of the Birds Directive. a) Area-controlled surplus of reported species *Richness_SAR_%Surplus*. b) Rarity-weighted richness *Richness_Rarity_weighted*. c) Average rarity *Rarity_Mean*. d) Total dissimilarity *Dissimilarity_Total*. For details about indices' definition see Methods section. White symbols illustrate missing data. MAB: Man and Biosphere reserve; NP: national park. The maps were created using open-source software R, Version 3.3.3 (https://www.R-project.org/) [60].

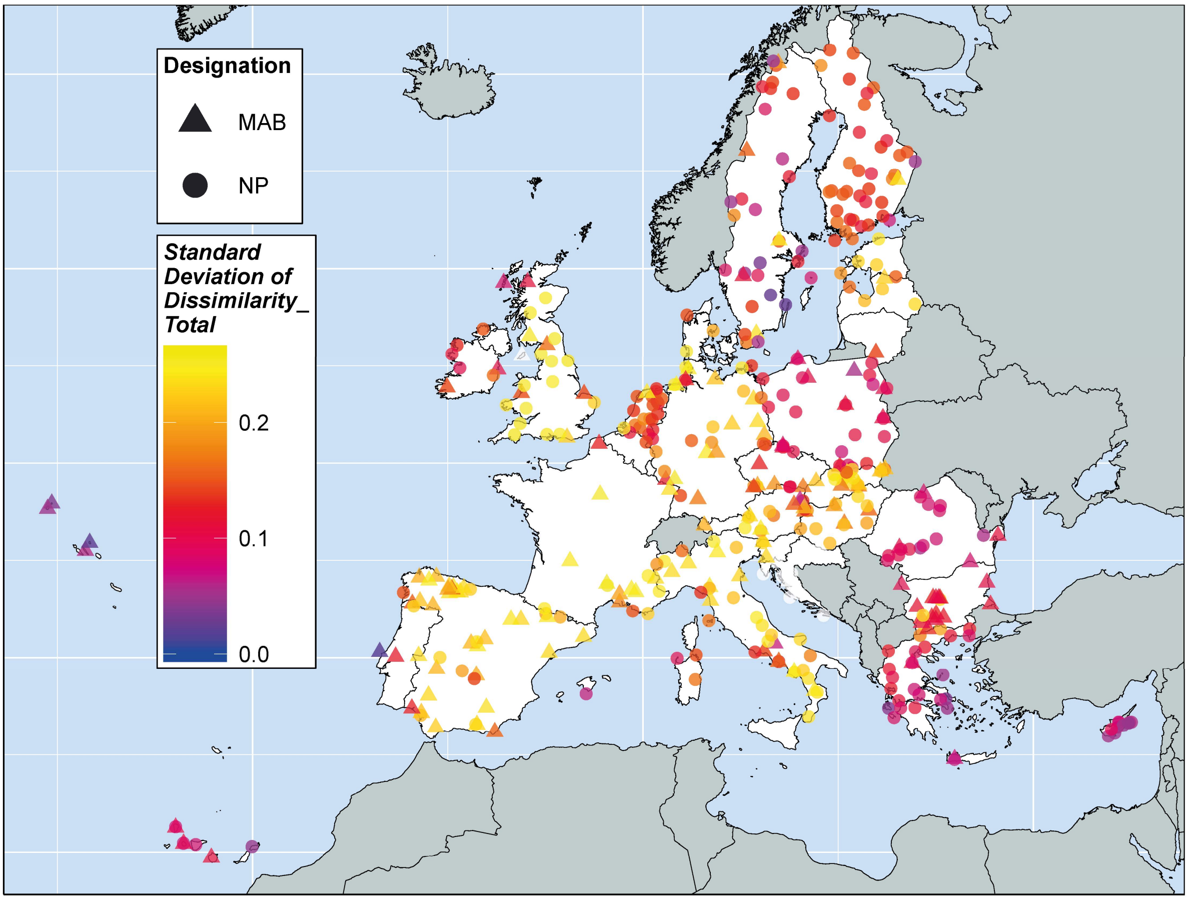

Figure S2. The standard deviation of the pairwise total dissimilarity values calculated for each national park (NP) and Man and Biosphere reserve (MAB). The mean of these pairwise total dissimilarity values results in the total dissimilarity index *(Dissimilarity_Total)* per protected area. For details about indices' definition see Methods section in main text. White symbols illustrate missing data. The map was created using open-source software R, Version 3.3.3 (https://www.R-project.org/) [60].

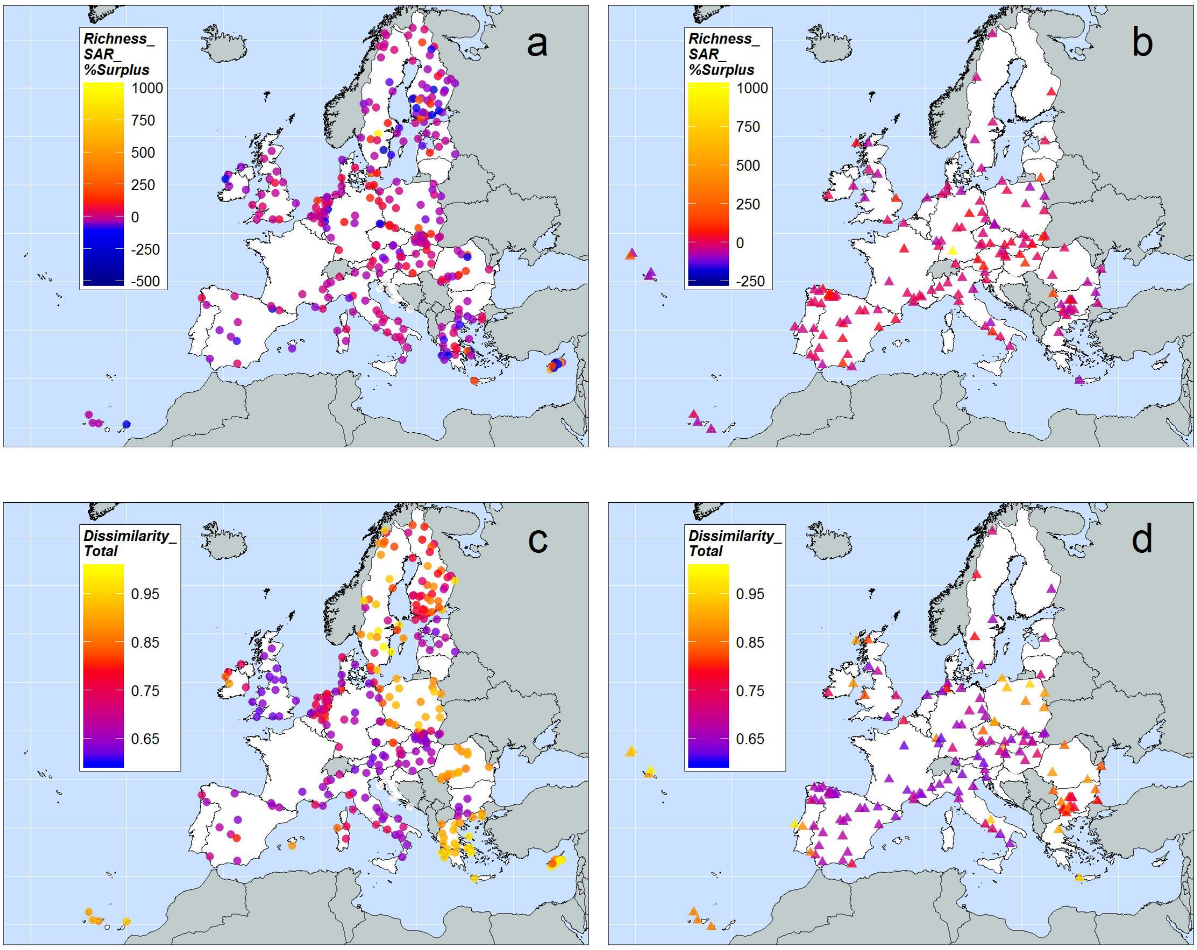

Figure S3. Area-controlled surplus of reported species (*Richness_SAR_%Surplus*) and total dissimilarity *(Dissimilarity_Total)* calculated separately for the national park (NP) and Man and Biosphere reserve (MAB) network. a) *Richness_SAR_%Surplus* values calculated for the NP network differ from NP values of the combined network (paired Wilcoxon test: $p=0.03$), but the geographic pattern is quite similar (Pearson correlation coefficient $r=0.23$). b) The same is true for *Richness_SAR_%Surplus* of the MAB network ($p<0.01$, $r=0.88$). c) *Dissimilarity_Total* of the NP network ($p<0.01$, $r=1.00$). d) *Dissimilarity_Total* of the MAB network ($p<0.01$, $r=0.99$). For details about indices' definition see Methods section in main text. White symbols illustrate missing data. The maps were created using open-source software R, Version 3.3.3 (https://www.R-project.org/) [60].

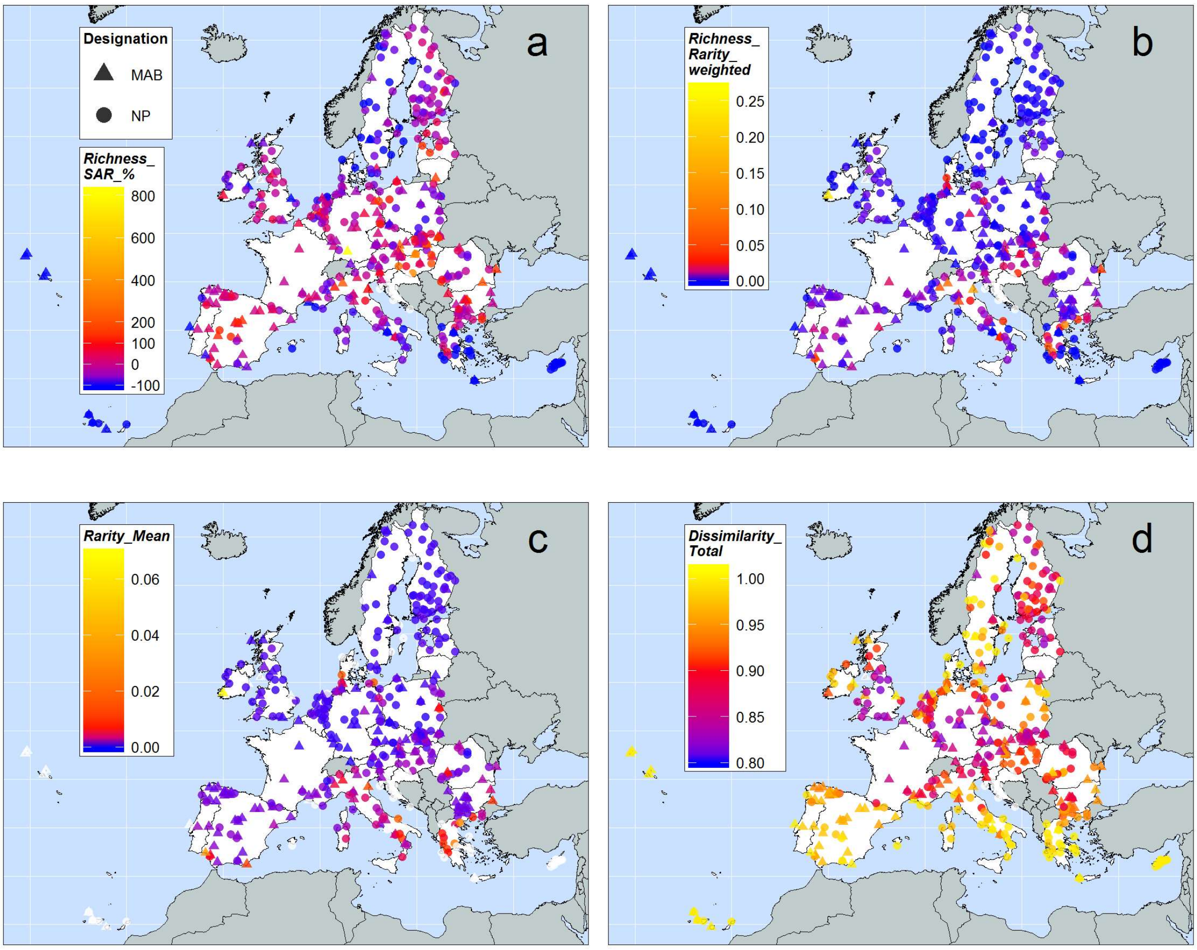

Figure S4. Uniqueness indices of protected areas calculated separately for 105 fish of the Habitats Directive. a) Area-controlled surplus of reported species *Richness_SAR_%Surplus*. b) Rarity-weighted richness *Richness_Rarity_weighted*. c) Average rarity *Rarity_Mean*. d) Total dissimilarity *Dissimilarity_Total*. For details about indices' definition see Methods section. White symbols illustrate missing data. MAB: Man and Biosphere reserve; NP: national park. The maps were created using open-source software R, Version 3.3.3 (https://www.R-project.org/) [60].

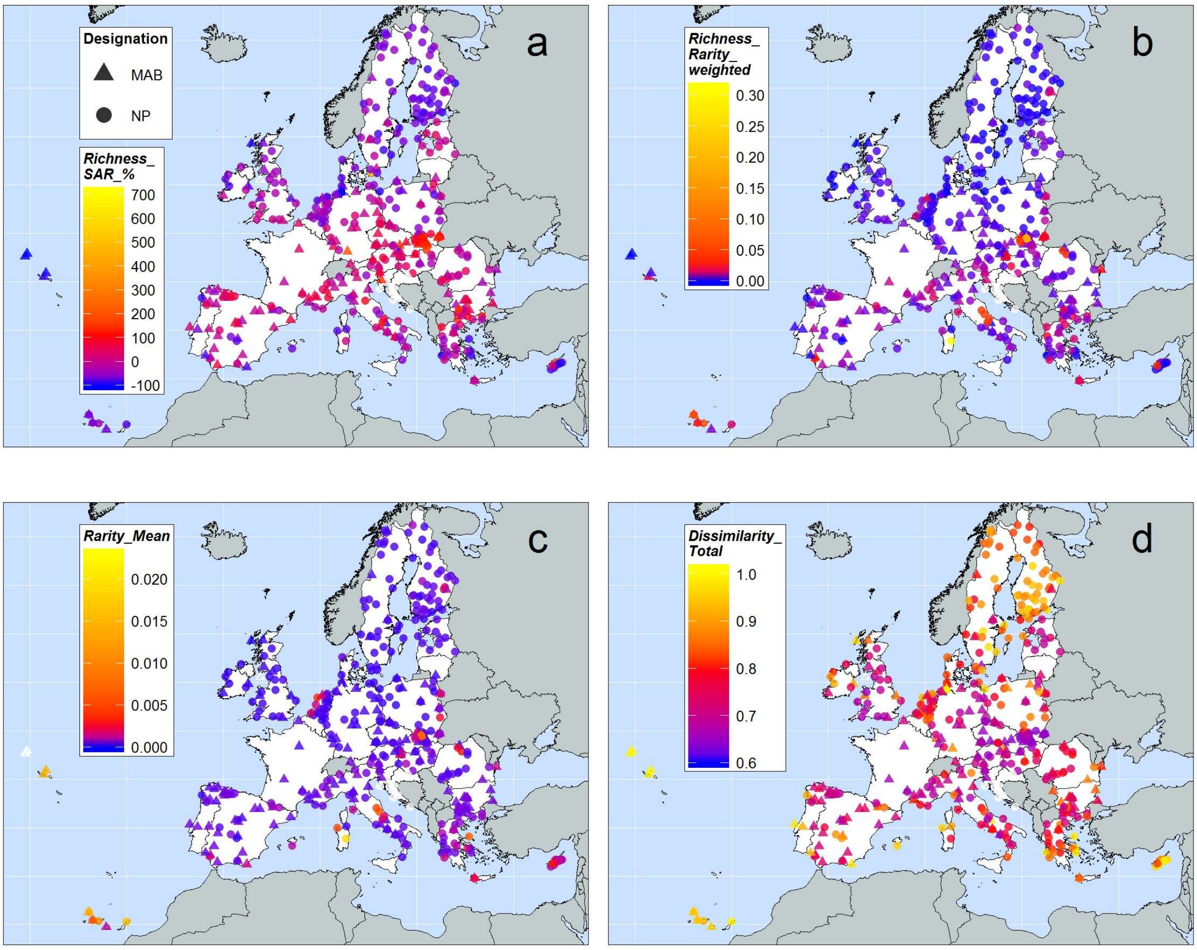

Figure S5. Uniqueness indices of protected areas calculated separately for 93 mammals of the Habitats Directive. a) Area-controlled surplus of reported species *Richness_SAR_%Surplus*. b) Rarity-weighted richness *Richness_Rarity_weighted*. c) Average rarity *Rarity_Mean*. d) Total dissimilarity *Dissimilarity_Total*. For details about indices' definition see Methods section. White symbols illustrate missing data. MAB: Man and Biosphere reserve; NP: national park. The maps were created using open-source software R, Version 3.3.3 (https://www.R-project.org/) [60].

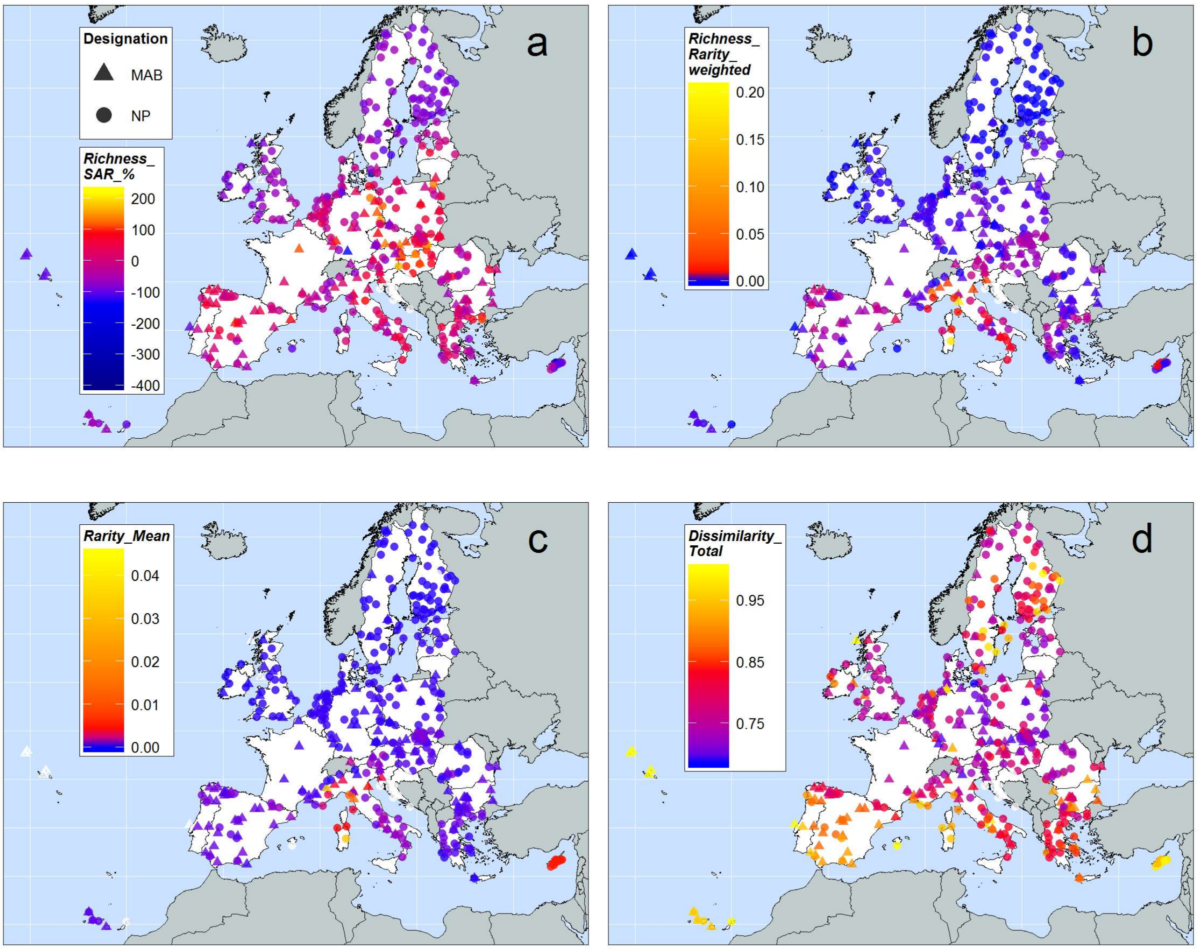

Figure S6. Uniqueness indices of protected areas calculated separately for 49 amphibians of the Habitats Directive. a) Area-controlled surplus of reported species *Richness_SAR_%Surplus*. b) Rarity-weighted richness *Richness_Rarity_weighted*. c) Average rarity *Rarity_Mean*. d) Total dissimilarity *Dissimilarity_Total*. For details about indices' definition see Methods section. White symbols illustrate missing data. MAB: Man and Biosphere reserve; NP: national park. The maps were created using open-source software R, Version 3.3.3 (https://www.R-project.org/) [60].

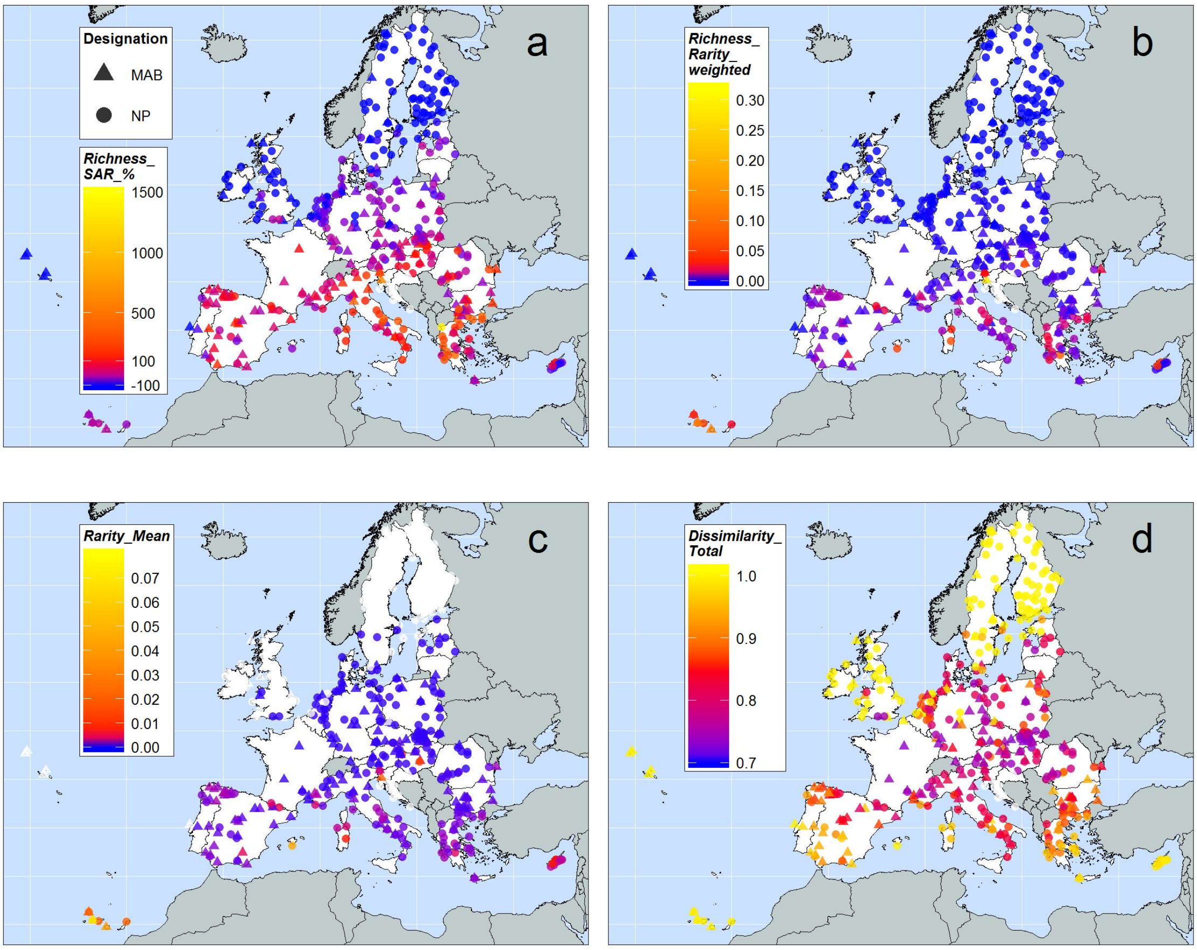

Figure S7. Uniqueness indices of protected areas calculated separately for 73 reptiles of the Habitats Directive. a) Area-controlled surplus of reported species *Richness_SAR_%Surplus*. b) Rarity-weighted richness *Richness_Rarity_weighted*. c) Average rarity *Rarity_Mean*. d) Total dissimilarity *Dissimilarity_Total*. For details about indices' definition see Methods section. White symbols illustrate missing data. MAB: Man and Biosphere reserve; NP: national park. The maps were created using open-source software R, Version 3.3.3 (https://www.R-project.org/) [60].

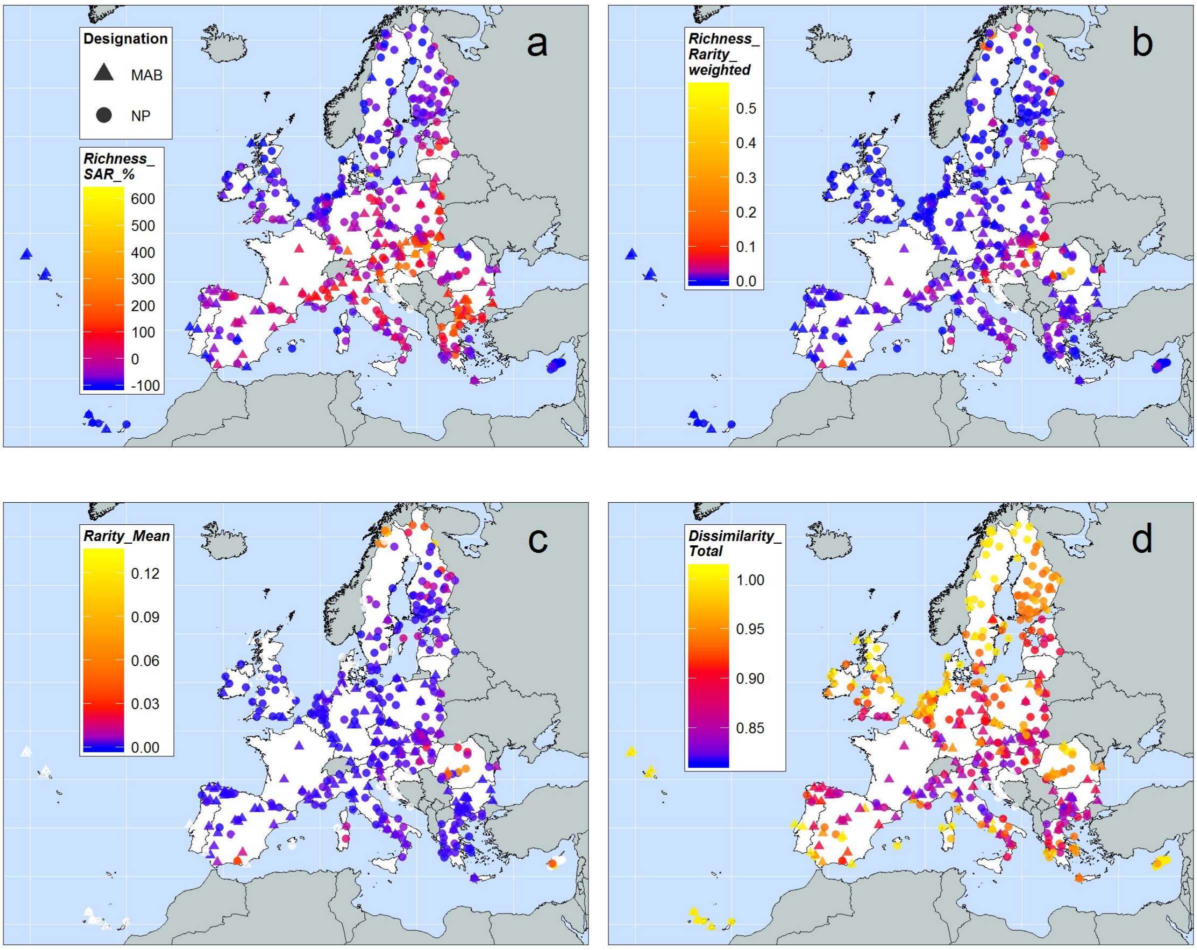

Figure S8. Uniqueness indices of protected areas calculated separately for 111 arthropods of the Habitats Directive. a) Area-controlled surplus of reported species *Richness_SAR_%Surplus*. b) Rarity-weighted richness *Richness_Rarity_weighted*. c) Average rarity *Rarity_Mean*. d) Total dissimilarity *Dissimilarity_Total*. For details about indices' definition see Methods section. White symbols illustrate missing data. MAB: Man and Biosphere reserve; NP: national park. The maps were created using open-source software R, Version 3.3.3 (https://www.R-project.org/) [60].

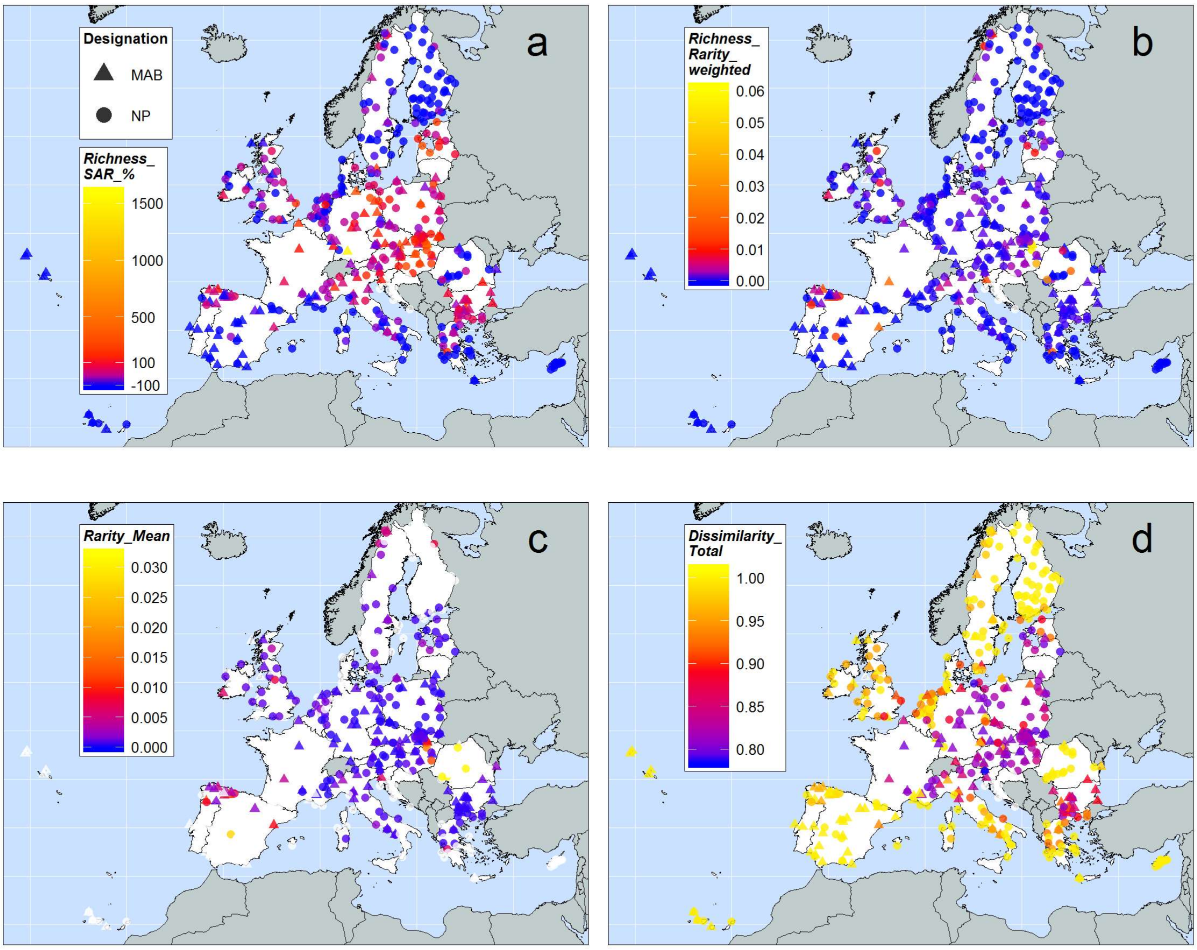

Figure S9. Uniqueness indices of protected areas calculated separately for 20 molluscs of the Habitats Directive. a) Area-controlled surplus of reported species *Richness_SAR_%Surplus*. b) Rarity-weighted richness *Richness_Rarity_weighted*. c) Average rarity *Rarity_Mean*. d) Total dissimilarity *Dissimilarity_Total*. For details about indices' definition see Methods section. White symbols illustrate missing data. MAB: Man and Biosphere reserve; NP: national park. The maps were created using open-source software R, Version 3.3.3 (https://www.R-project.org/) [60].

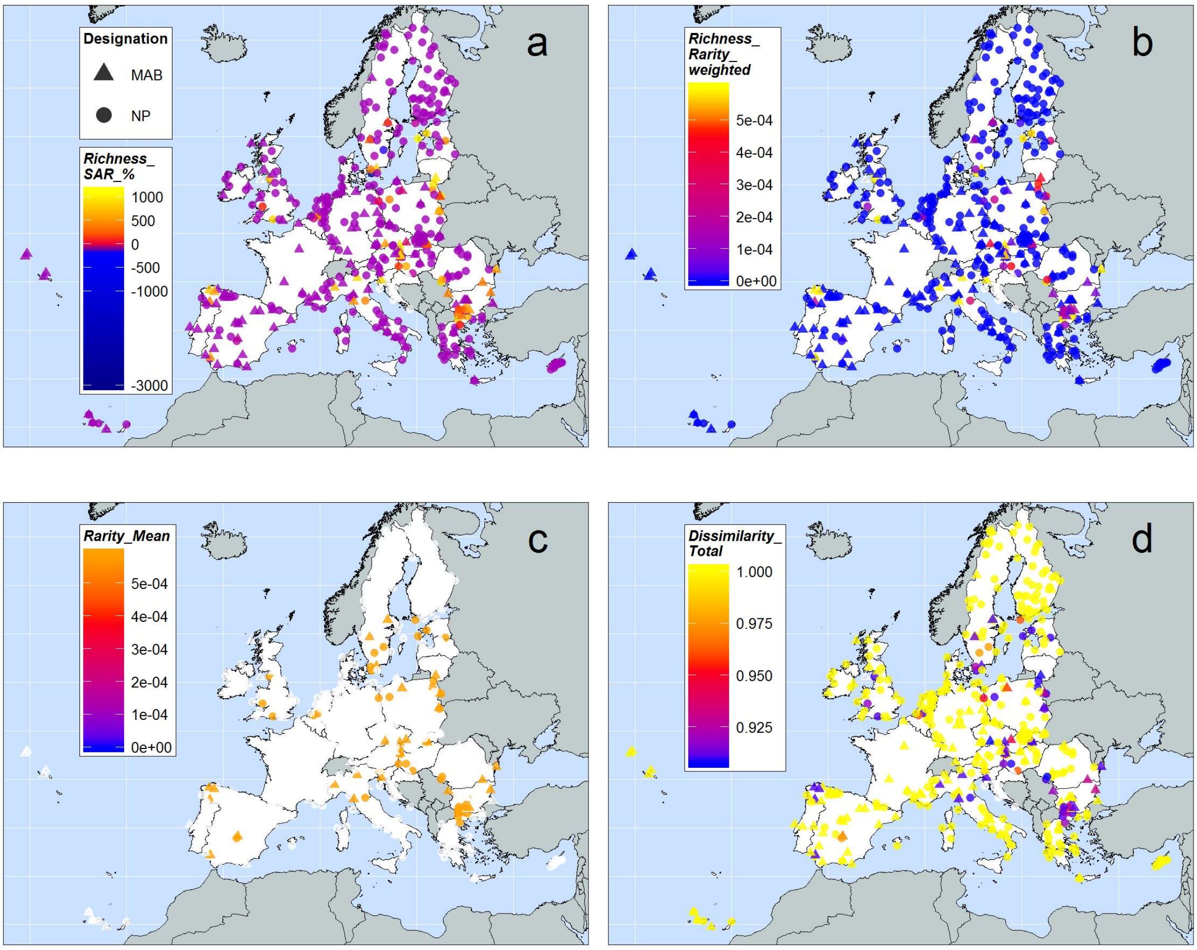

Figure S10. Uniqueness indices of protected areas calculated separately for one other invertebrate of the Habitats Directive. a) Area-controlled surplus of reported species *Richness_SAR_%Surplus*. b) Rarity-weighted richness *Richness_Rarity_weighted*. c) Average rarity *Rarity_Mean*. d) Total dissimilarity *Dissimilarity_Total*. For details about indices' definition see Methods section. White symbols illustrate missing data. MAB: Man and Biosphere reserve; NP: national park. The maps were created using open-source software R, Version 3.3.3 (https://www.R-project.org/) [60].

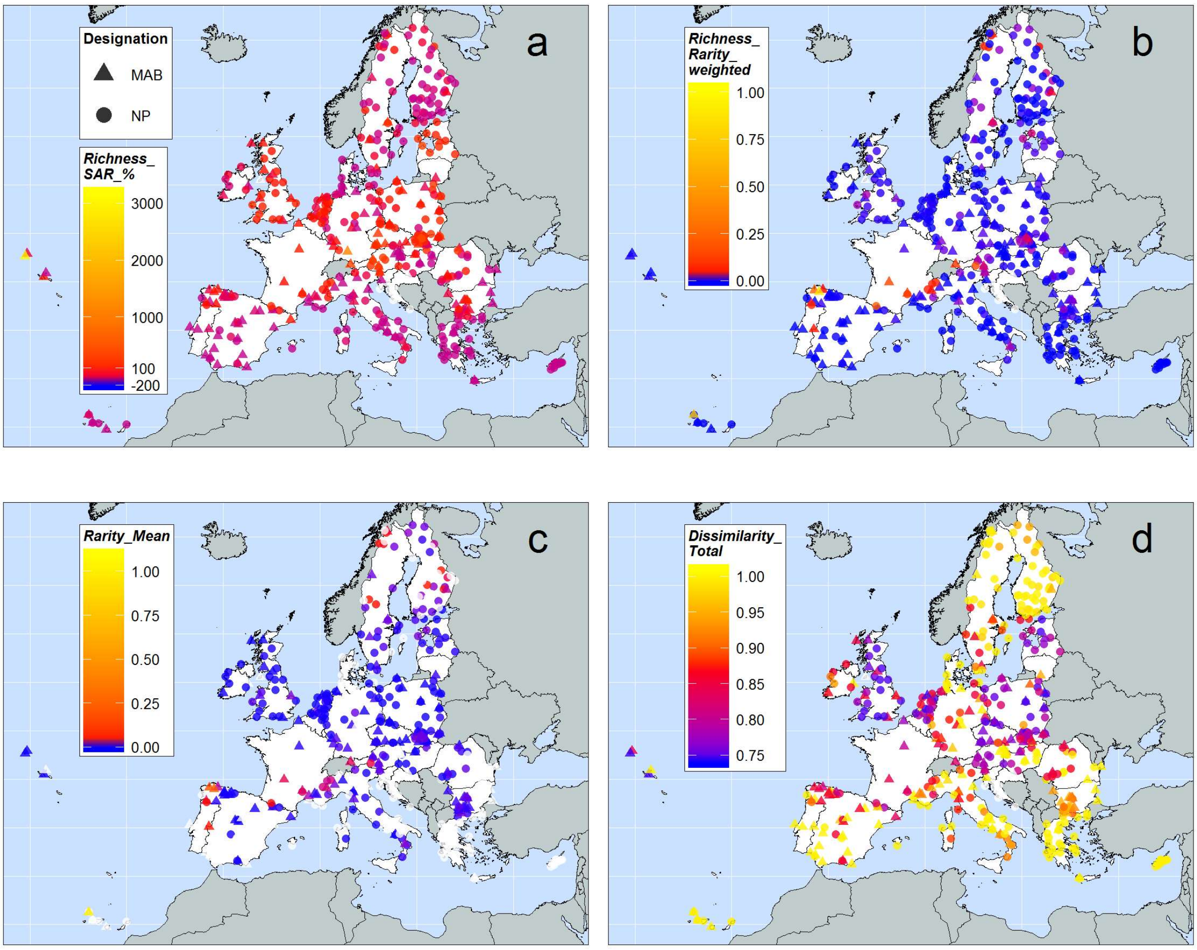

Figure S11. Uniqueness indices of protected areas calculated separately for 32 non-vascular plants of the Habitats Directive. a) Area-controlled surplus of reported species *Richness_SAR_%Surplus*. b) Rarity-weighted richness *Richness_Rarity_weighted*. c) Average rarity *Rarity_Mean*. d) Total dissimilarity *Dissimilarity_Total*. For details about indices' definition see Methods section. White symbols illustrate missing data. MAB: Man and Biosphere reserve; NP: national park. The maps were created using open-source software R, Version 3.3.3 (https://www.R-project.org/) [60].

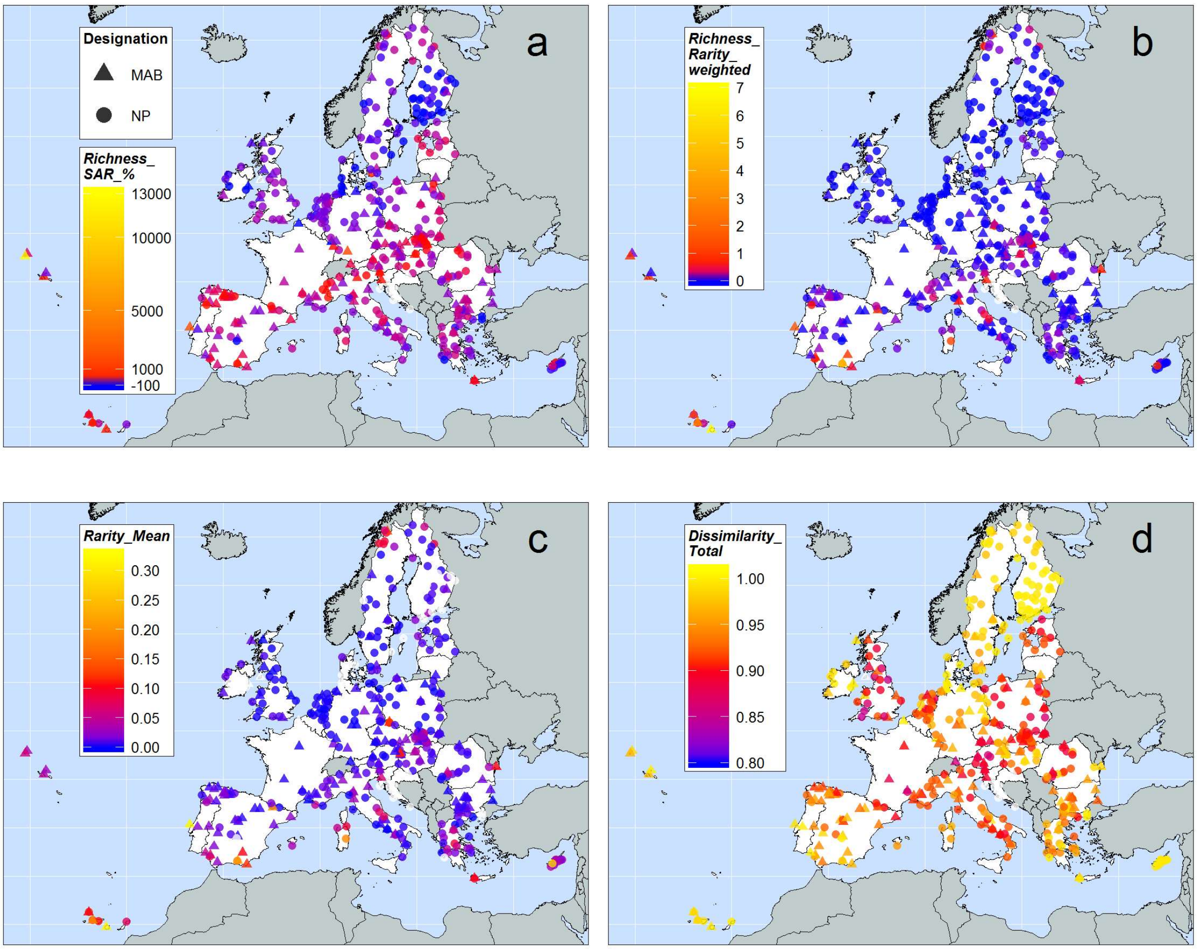

Figure S12. Uniqueness indices of protected areas calculated separately for 350 vascular plants of the Habitats Directive. a) Area-controlled surplus of reported species *Richness_SAR_%Surplus*. b) Rarity-weighted richness *Richness_Rarity_weighted*. c) Average rarity *Rarity_Mean*. d) Total dissimilarity *Dissimilarity_Total*. For details about indices' definition see Methods section. White symbols illustrate missing data. MAB: Man and Biosphere reserve; NP: national park. The maps were created using open-source software R, Version 3.3.3 (https://www.R-project.org/) [60].

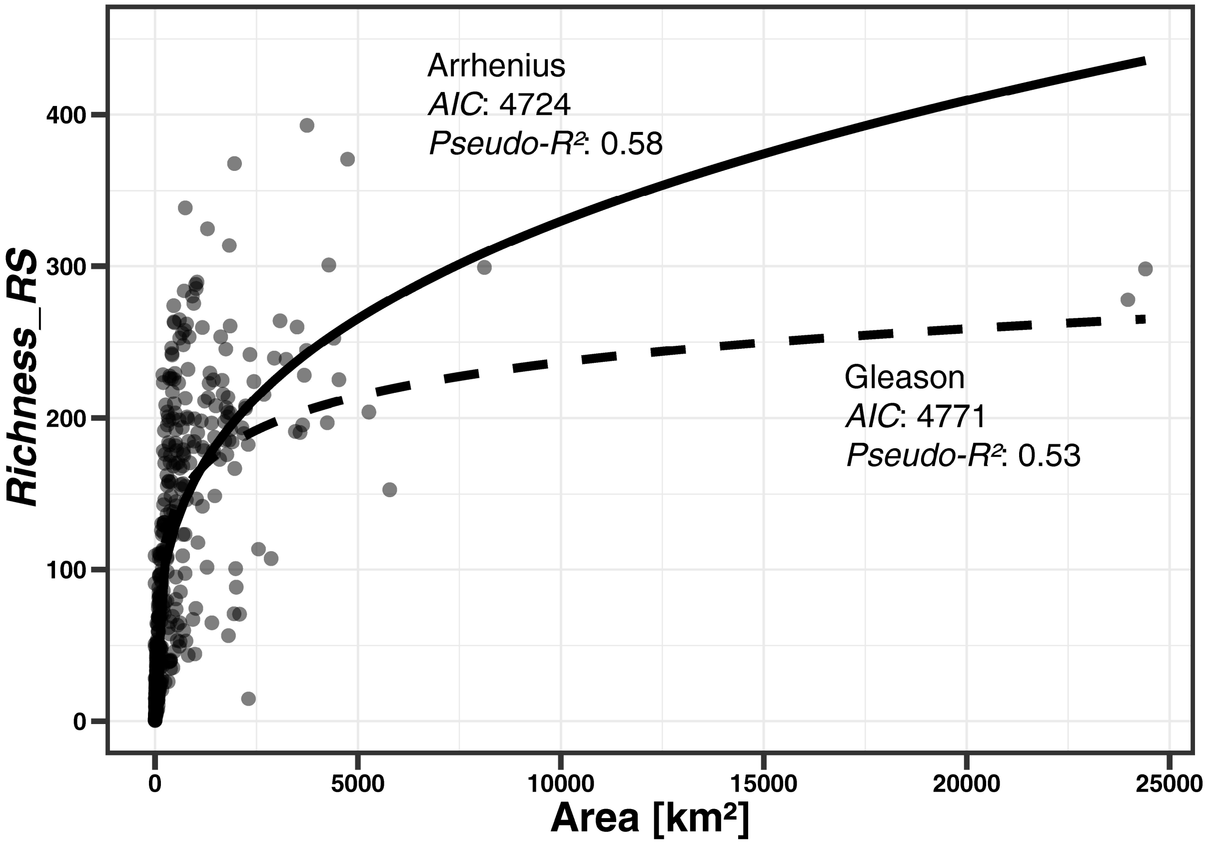

Figure S13. The species-area relationships (SAR) adapted to the set of protected areas (national parks and biosphere reserves) and reported species richness (*Richness_RS*). We compared the Arrhenius and Gleason model to a null model, i.e. the intercept-only model. The *Pseudo-R²* is calculated by 1-(*Model Deviance/Null Model Deviance*). The Arrhenius model is fitting best (i.e. lowest *AIC*) and was therefore chosen to calculate *Richness_SAR_%Surplus*. For details see methods section.

Supplementary Material

Dataset 1 'Uniqueness_Data_Table.xlsx' is available online at
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7.2 Manuscript 2

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RESEARCH ARTICLE

Remote sensing of β-diversity: Evidence from plant communities in a semi-natural system

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Abstract

Question: Do remote sensing signals represent β-diversity? Does β-diversity agree with community types?

Location: UNESCO Man and the Biosphere Reserve, La Palma, Canary Islands.

Methods: We recorded perennial, vascular plant species abundances in 69 plots (10 m × 10 m) in three pre-defined community types along an elevational gradient of 2,400 m: succulent scrubland, *Pinus canariensis* forest and subalpine scrubland. The remote sensing data consists of structural variables from airborne Light Detection and Ranging (LiDAR) and multispectral variables from a time series of Sentinel-2 (S2) images. Non-metric Multidimensional Scaling was used to assess β-diversity between plots. *K*-means unsupervised clustering was applied to remote sensing variables to distinguish three community types. We subsequently quantified the explanatory power of S2 and LiDAR variables representing β-diversity via the Mantel test, variation partitioning and multivariate analysis of variance. We also investigated the sensitivity of results to grain size of remote sensing data (20, 40, 60 m).

Results: The β-diversity between the succulent and pine community is high, whereas the β-diversity between the pine and subalpine community is low. In the wet season, up to 85% of β-diversity is reflected by remote sensing variables. The S2 variables account for more explanatory power than the LiDAR variables. The explanatory power of LiDAR variables increases with grain size, whereas the explanatory power of S2 variables decreases.

Conclusion: At the lower ecotone, β-diversity agrees with the pre-defined community distinction, while at the upper ecotone the community types cannot be clearly separated by compositional dissimilarity alone. The high β-diversity between the succulent scrub and pine forest results from positive feedback switches of *P. canariensis*, being a fire-adapted, key tree species. In accordance with the spectral variation hypothesis, remote sensing signals can adequately represent β-diversity for a large extent, in a short time and at low cost. However, in-situ sampling is necessary to fully understand community composition. Nature conservation requires such interdisciplinary approaches.

Nomenclature: Muer, Sauerbier, and Calixto (2016)

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Abstract

Question: Do remote sensing signals represent beta diversity? Does beta diversity agree with community types?

Location: UNESCO Man and Biosphere Reserve, La Palma, Canary Islands.

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Results: The beta diversity between the succulent and pine community is high, whereas the beta diversity between the pine and subalpine community is low. In the wet season, up to 85% of beta diversity is reflected by remote sensing variables. The S2 variables account for more explanatory power than the LiDAR variables. The explanatory power of LiDAR variables increases with grain size, whereas the explanatory power of S2 variables decreases.

Conclusion: At the lower ecotone, beta diversity agrees with the pre-defined community distinction, while at the upper ecotone the community types cannot be clearly separated by compositional dissimilarity only. The high beta diversity between the succulent scrub and pine forest results from positive feedback switches of *Pinus canariensis* being a fire-adapted, key tree species. In accordance with the spectral variation hypothesis, remote sensing signals can adequately represent beta diversity over large extent, in short time and at low costs. However, in-situ sampling is necessary to fully understand community composition. Nature conservation requires such interdisciplinary approaches.

Keywords: beta diversity, conservation biogeography, elevation gradient, island biogeography, LiDAR, plant community, remote sensing, Sentinel, spectral variation hypothesis, time series, treeline, vegetation indices

Introduction

The spatial and temporal rates of change in species composition, i.e. beta diversity, lie at the heart of community ecology ever since Clements (1916). However, the community definition is still largely debated (Palmer and White, 1994; Chiarucci, 2007; Ricklefs, 2008). The controversy revolves around the coherence and integrity of ecological entities through different scales of space and time (Jax, 2006). In order to assess community patterns, concepts of beta diversity are applied that quantify the compositional dissimilarity between species assemblages (Anderson et al., 2011).

Processes responsible for observed patterns of species coexistence, usually referred to as 'assembly rules', can be deterministic, stochastic, interrelated and contingent, which led Lawton (1999) to call community ecology 'a mess'. Vellend (2010) proposed the following overarching processes shaping beta diversity and community patterns: selection, drift, speciation and dispersal. These factors and anthropogenic activities determine beta diversity and thus biodiversity in general (Socolar et al., 2016), which the human well-being depends on (Cardinale et al., 2012). It is therefore important to study patterns of beta diversity as well as corresponding drivers.

The existence of communities implies the delineation of community types. Because natural boundary sharpness varies (Wilson and Agnew, 1992; Auerbach and Shmida, 1993), community distinction is not necessarily discrete. Transition between communities can be rather continuous. This is why community limits are specifically considered as transition zones also known as ecotones (Livingston, 1903). In early times, an ecotone was associated with a clear separation of plant physiognomy (Clements, 1905). The recent definition of ecotone by Lloyd et al. (2000) is based on beta diversity and describes it as a 'zone where directional change in vegetation (i.e. qualitative and quantitative species composition) is more rapid than on the other side of the zone.' Although ecotones are a standard entity in landscape ecology (Wiens et al., 1992), Hufkens et al. (2009) point out that they do not have standardized spatial and temporal units.

In order to analyse the spatial and temporal complexity of plant communities, comprehensive field sampling and monitoring are needed, which are time consuming and costly. Remote sensing (RS) can be a powerful tool to estimate beta diversity patterns over large extents, in short time and at low costs (Rocchini et al., 2016). RS sensors provide data that reveal biodiversity patterns from local to global extent as well as temporally resolved. RS sensors are used to detect changes in community composition, with changes in spectral diversity as a measure of beta diversity (Rocchini et al., 2005). This application rests on the spectral variation hypothesis (SVH) explaining the relationship between environmental heterogeneity, species diversity and spectral information (Palmer et al., 2002). Environmental heterogeneity increases habitat heterogeneity and thus species diversity (i.e. habitat-heterogeneity hypotheses; Simpson, 1949). Environmental heterogeneity also increases spectral heterogeneity. Therefore, spectral variation is associated with alpha and beta diversity (Palmer et al., 2002, Rocchini et al., 2004). However, the SVH does not apply to all ecosystems and depends on the extent of RS and in-situ data as well as the spatial, temporal and spectral resolution of RS data (Schmidtlein and Fassnacht, 2017).

This study refers to the SVH because we investigate to what degree RS signals of species assemblages can explain beta diversity, i.e. the compositional dissimilarity between species assemblages. As a case study, we sampled the semi-natural plant communities along a continuous elevational gradient on La Palma, Canary Islands. First, we test the SVH using structural RS variables from light detection and ranging (LiDAR) and multispectral variables from a time series of Sentinel-2 images (S2). Since RS sensors can hardly account for small, rare and understorey species, we expect that RS signals do not adequately explain beta diversity that is derived from in-situ observations. This combination of data and techniques has not been used before to represent beta diversity with RS products. Second, we analyse to what extent beta diversity agrees with the pre-defined community types.

Methods

Study region

The subtropical-Mediterranean island of La Palma is located at the north-western edge of the Canary archipelago in the Atlantic Ocean, approximately 400 km west of the African coast at 28° N (Fig. 1). The entire island is designated as 'UNESCO Man and Biosphere Reserve'. The elevational gradient and trade winds from the north-west constitute diverse climatic attributes leading to the existence of eight different ombrotypes ranging from hyperarid to humid within a small geographical extent (Garzón-Machado et al., 2013).

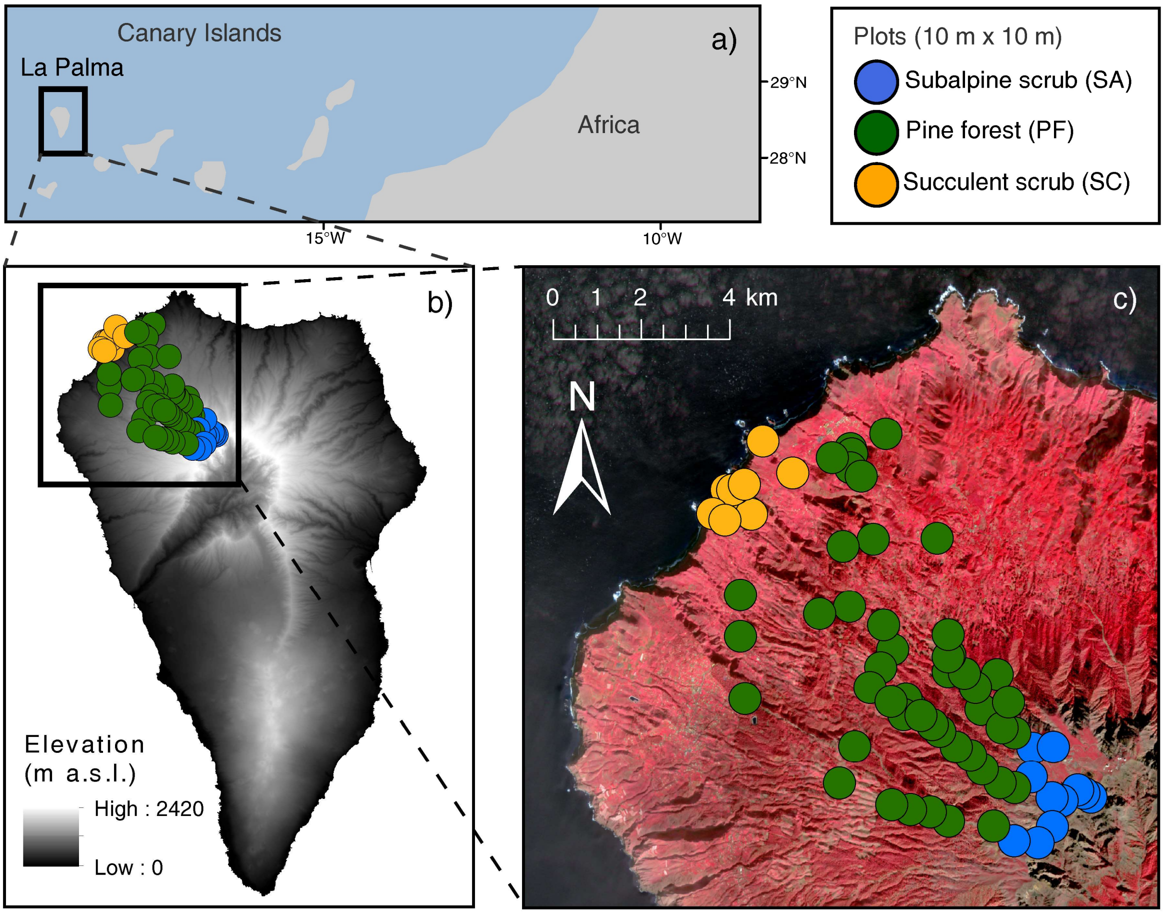

Figure 1. Location of sampling plots on La Palma, Canary Islands. a) The Canary Islands are located in the Atlantic Ocean to the west of the African continent. b) The entire island is a UNESCO Man and Biosphere Reserve. The digital elevation model (Irl et al., 2015) shows the location of the sampling plots. The plots that include *Pinus canariensis* were classified as 'Pine forest (PF)'. Plots below the pine forest without *Pinus canariensis* were classified as 'Succulent scrub (SC)', and plots above the pine forest without *Pinus canariensis* as 'Subalpine scrub (SA)'. c) The false-colour composite image supports the visual interpretation of vegetation and is based on the Sentinel-2 imagery from 14 Jan 2017 with 10 m resolution (Band 8, Band 4 and Band 3).

Field sampling

Field sampling was performed along the elevational gradient from 45 to 2400 m a.s.l., present on the north-western part of the island, where anthropogenic pressure is low, semi-natural land cover is largely preserved, edaphic conditions are homogeneous (Carracedo et al., 2001) and human activities are scarce. Field work was conducted during February and March 2017. Three main community types were crossed along elevation (Del Arco Aguilar et al., 2010). Succulent scrublands occur in semi-arid conditions at low elevation (~0-500 m) and are dominated by *Euphorbia* scrubs. The vegetation height can exceed 2 m. The vegetation cover is constantly high, but bare soil and rock can be found. The plant communities in mid elevations are dominated by the endemic *Pinus canariensis*, which also forms the treeline both towards high and low altitudes (~500-2000 m). The canopy cover and height peaks in mid elevation. The understorey consists of scrub species. The forest ground is covered by pine needles. The subalpine communities (~2000-2400 m) are characterized by the summit broom scrub *Adenocarpus viscosus subsp. spartioides* (hereafter

Adenocarpus viscosus). The vegetation height barely reaches 2 m. Bare soil, rock and deadwood are frequently found in this vegetation zone. In accordance with Del Arco Aguilar et al. (2010), we pre-classified the sampling sites including *Pinus canarie*nsis as pine forest (PF), while those without *Pinus canariensis* below the pine forest were designated as succulent scrub (SC); those above the pine forest were designated as subalpine (SA).

We applied a stratified random sampling along the elevational gradient. SC, PF and SA defined the strata. We avoided anthropogenic land use and northern slopes steeper than 20°, to prevent sites from being unnatural and appearing dark and distorted in remote sensing imagery. Due to ridges and steep slopes some sites appear linearly arranged (Fig. 1). In each sampling site, a 10 m x 10 m plot was used to record plant community data. We sampled 10 SC, 48 PF and 11 SA plots. We recorded abundances of all vascular plant species within the plots by estimating their coverage within three vertical strata, i.e. tree, scrub and herb layer. Since the presence of annual plants is driven by short-term weather events that differ locally, we only considered perennial plant species. The stochastic, short-term variation of the occurrence of annuals during the seasons makes it very difficult to conduct reliable comparison with remote sensing data that are recorded at different times. We used Muer et al. (2016) for the nomenclature of vascular plant species.

Since we are interested in changes of abundance-based species composition, we applied relative abundances to calculate beta diversity. Relative abundance per species and plot was calculated as the species' coverage divided by the sum of coverages of all species in all vertical strata. By this definition, we can accurately assess changes in species composition between plots, because land cover types other than vegetation (i.e. bare soil, rock, litter), that bias the beta diversity based on absolute abundances, are neglected. If other cover types were considered, we would notice a reduction in absolute species abundances, even if the relative species abundances remain constant. However, such cover classes and the coverage of species influence the composition of RS signals. To perform an analysis of the composition of RS signals, we used the following explanatory variables; we estimated the absolute coverages of bare soil, rock, pine needles and deadwood that are not vertically covered by any other strata in the plot. In this RS-specific analysis, we also consider the absolute coverages of the ten most abundant species that are uncovered by other strata. We refer to these coverages as 'RS-specific' coverages.

Environmental data

Since mean annual temperature and mean annual precipitation are among the most important climate variables in community ecology at the landscape scale (Whittaker, 1970), we used them to characterize the plant communities in the study region. These climatic variables were generated by the interpolation of data from meteorological stations applying linear regression kriging technique; for details see Irl et al. (2015). We extracted climate data for each plot from the grid by averaging the values of all climate cells that fall within the plot. In order to evaluate the human impact on species composition, we calculated for each plot the planar distance to the nearest anthropogenic infrastructure, i.e. roads and buildings of any kind (Fig. S1, Appendix 1).

Remote sensing data

We considered RS products that represent multispectral and structural vegetation properties, and are thus appropriate to distinguish plant communities (Xie et al., 2008; Pettorelli et al., 2014). To account for multispectral differences that may occur during the seasons, we selected 13 Sentinel-2 images (S2; European Space Agency 2017) covering the time period from February 2016 to February 2017 (Table S1, Appendix 1). We chose S2 since this sensor provides images of high radiometric (i.e. 12 bands), temporal (i.e. 5 days revisit time) and spatial resolution (i.e. 10 to 60 m) that are publicly available and free of charge (see https://sentinel.esa.int/documents/247904/685211/Sentinel-2_User_Handbook). The downloaded images were given as a geometrically and radiometrically corrected Top-of-Atmosphere (TOA) Level-1C product. We applied atmospheric, terrain and bidirectional reflectance distribution (BRDF with cosine of local solar zenith angle) correction using the Sen2Cor plugin (see http://step.esa.int/main/third-party-plugins-2/sen2cor/) within the Sentinel-2 toolbox of the Sentinel Application Platform (SNAP) to generate Bottom-Of-Atmosphere (BOA) Level-2A products. These products include a masking layer for classifying pixels affected by clouds as 'medium cloud probability', 'high cloud probability' and 'cirrus'. The cloud mask covered a maximum of two plots per image (Table S1, Appendix 1). Such plots were excluded from the analyses. Band 1 (aerosol, 60 m), Band 9 (water vapor, 60 m) and Band 10 (cirrus, 60 m) were removed by the preprocessing procedure as they are only needed for cloud-masking. The remaining bands are Band 2 (blue, 10 m), Band 3 (green, 10 m), Band 4 (red, 10 m), Band 5 (red edge, 20 m), Band 6 (red edge, 20 m), Band 7 (red edge, 20 m), Band 8 (near-infrared [NIR], 10 m), Band 8a (red edge, 20 m), Band 11 (shortwave infrared [SWIR], 20 m) and Band 12 (shortwave infrared [SWIR], 20 m).

We also applied basic vegetation indices to explore plant characteristics that lead to spectral differences. The normalized differentiation vegetation index NDVI ([Band 8-Band 4]/[Band 8+Band 4]) is one of the most popular proxies for primary productivity (Pettorelli, 2013). Higher values of the moisture stress index MSI ([Band 11/Band 8]) reveal less leaf water content (Hunt and Bock, 1989). The plant senescence reflectance index PSRI ([Band 4 – Band 2] / Band 6) increases with canopy stress (i.e. carotenoid concentration), canopy senescence and fruit ripening (Merzlyak et al., 1999). The anthocyanin reflectance index ACR1 ([1/Band 3]/[1/Band 5]) demonstrates canopy changes by growth and death (Gitelson et al., 2001). The carotenoid reflectance index CRI1 ([1/Band 2]/[1/Band 3]) represents carotenoid concentration relative to chlorophyll (Gitelson et al., 2002); carotenoid pigments increase with weakening vegetation. The photochemical reflectance index PRI ([Band 2-Band 3]/[Band 2+Band 3]) indicates light use efficiency (Gamon et al., 1997); the PRI index changes with carotenoid pigments in live foliage and thus describes productivity and stress.

Metrics derived from airborne LiDAR are able to account for both 2D and 3D vegetation structure, which helps to distinguish vegetation that differs in structural variables such as growth height and canopy cover (Pettorelli et al., 2014). Airborne laser scanning (ALS) point cloud data from April 2009 was downloaded from the Spanish National Geographic Institute (IGN). The point clouds have a density of 0.5 points per 1 m^2 (see Appendix 2). After data pre-processing, several indices were calculated with a grain size of 20 m. The canopy height model (CHM) returns the average of normalized heights above ground. The tree fraction cover (TFC) is the proportion of first ALS returns over 2 m above ground from the total amount of first ALS return in the raster cell. The vegetation fraction

(VF) reflects the number of all returns over 0.5 m height divided by the number of all returns within the cell. The return proportion (RP) indices were calculated as the number of ALS returns in different vertical strata (i.e. 0.5 m, 2 m, 5 m, 10 m, 15 m, 20 m and 25 m) divided by the total number of ALS returns in the cell. Thus, RP informs about the three-dimensional vegetation structure. The effective leaf area index (LAI) was computed based on the gap probability, but not corrected for woody elements or the clumping effect. For classifications based on RS data all, variables were standardized to zero mean and unit variance. In order to retrieve pairwise distances between plots based on these standardized RS variables, we applied the Euclidean distance measure.

To reduce the bias induced by GPS inaccuracy when extracting the RS data by plot centroids, we use RS metrics with a minimum grain size of 20 m. In addition, we evaluated the results' sensitivity to coarser grain sizes (40 m and 60 m) by aggregating the RS metrics, i.e. taking the mean value.

Statistical analyses

Our methodological approach to analyze the relationship between in-situ and RS variables is summarized in Figure 2. To describe the given plant communities and demonstrate the species' realized environmental niches, we modelled the coenoclines of the ten most abundant species. The coenocline is the response curve of the species abundance along a single gradient (Whittaker, 1967). Species with overlapping coenoclines form communities. We applied two environmental gradients: mean annual temperature and mean annual precipitation. Coenclines were generated by fitting generalized additive models (GAM) with Gaussian distribution and link function, and thin plate regression splines as the single penalty smooth class (Wood, 2017). Because we were facing unequal sample sizes between community types, we conducted non-parametric Kruskal-Wallis Analysis of Variance ANOVA (Siegel and Castellan, 1988) to identify differences in species richness (Fig. S2, Appendix 1). Linear regression models were applied to determine the relationship between species richness and environmental gradients. Model assumptions were verified visually.

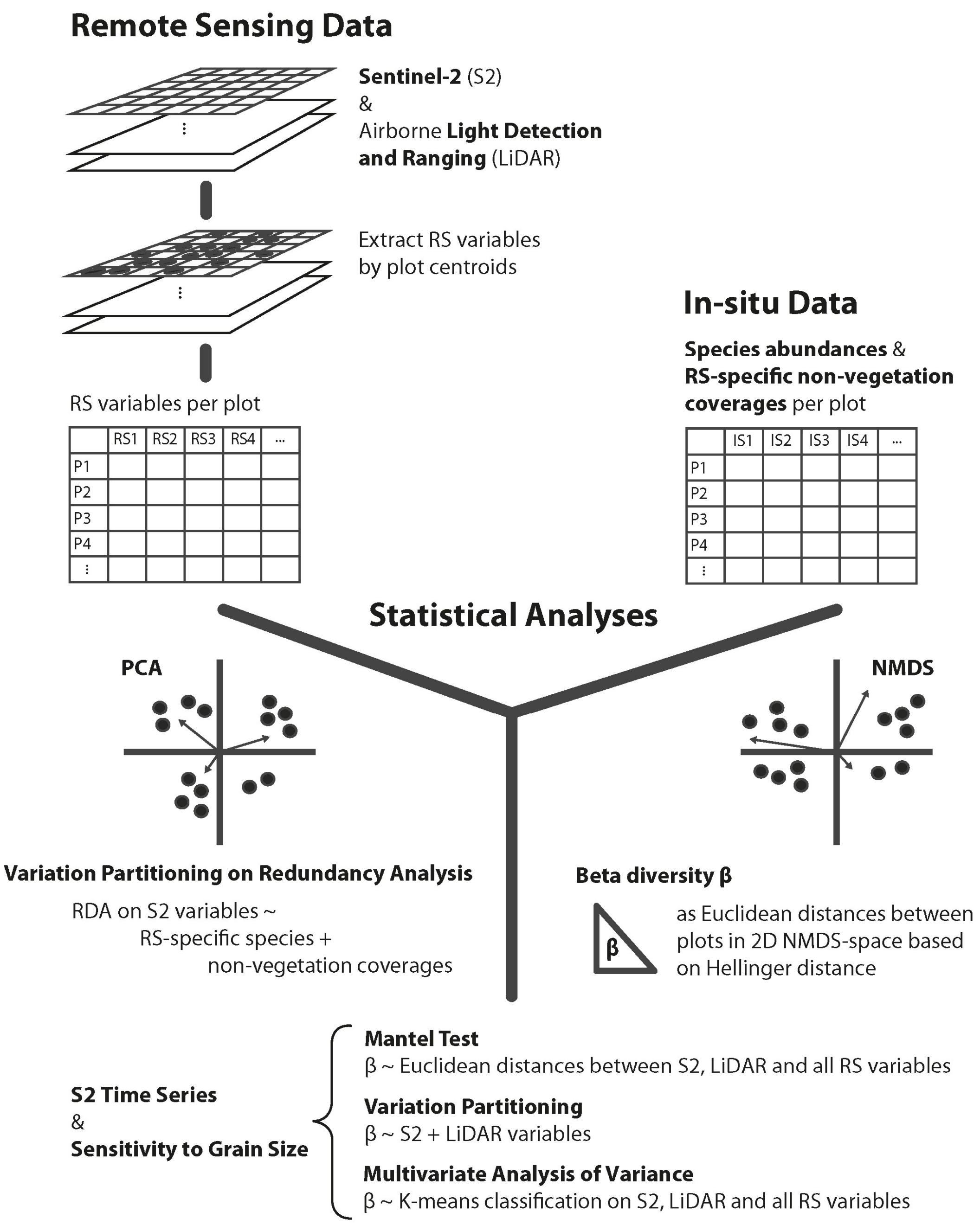

Figure 2. Flow chart describing the remote sensing and in-situ data as well as the statistical analyses to evaluate the relationship between both. For details see Methods section.

Beta diversity can be understood as the dissimilarity between plots regarding their species composition (Whittaker, 1967). We applied Non-metric Multidimensional Scaling (NMDS) to assess beta diversity and distinguish plant communities (Legendre and De Caceres, 2013). The NMDS is a distance-based, indirect ordination technique. We avoided direct ordination methods, since we were interested in unconstrained results that only rest on compositional dissimilarity (McCune and Grace, 2002). The NMDS ranks distances between input data (plots). Therefore, NMDS bypasses the linearity assumptions of metric ordination methods. Here we applied Hellinger distance to calculate the distance matrix among plots regarding their species composition (Legendre and De Caceres, 2013). The Hellinger distance down-weighs the occurrence of rare species. Thus, we controlled for overrated influence of rare species in dissimilarity calculations. We calculated a two-dimensional ordination space running 100 tries and involving random starting configurations, to find the optimal solution by NMDS, i.e. the lowest stress value. The NMDS-space was rotated to principal components; most variation in the data is shown along the first axis followed by the second. We conducted post-hoc correlation of explanatory variables to the NMDS via surface and vector fitting, to interpret the influence of explanatory variables onto the compositional dissimilarity represented by the location of plots in the NMDS-space. We eventually calculated beta diversity as the Euclidean distances between plot locations in the two-dimensional NMDS space.

Subsequently, we utilized the Mantel test (Mantel, 1967) to quantify the correlation between beta diversity and the pairwise distances between plots based on RS variables. Moreover, variation partitioning was used to reveal the combined and independent effects of S2 and LiDAR variables explaining the beta diversity (Legendre and Anderson, 1999). Variation partitioning is based on a Redundancy Analysis (RDA), which linearly models the relationship between a set of dependent variables and two sets of explanatory variables. We also employed K-means unsupervised classification algorithm (Lloyd, 1982) to distinguish three community types considering RS variables only. We aimed at creating three classes because existing vegetation maps predefine three main community types in the study region: succulent scrub, pine forest and subalpine scrub. K-means algorithm has been used before to test the SVH (Schmidtlein and Fassnacht, 2017). We then conducted Multivariate Analysis of Variance MANOVA (Anderson, 2001) to estimate how K-means classification on RS variables fits to the beta diversity.

The Mantel test, variation partitioning and MANOVA was applied to each S2 image as well as to the mean, range (|max-min|) and standard deviation of all dates. We can consequently identify seasonal variation of the explanatory power of RS signals, and account for complementarity of RS signals over time. This time series analysis was also conducted separately for each of the three vegetation types. Here we only applied the Mantel test, since the sampling size of SC and SA was too small to apply variation partitioning, and the MANOVA requires vegetation classes, which is pointless to produce within single community types. The beta diversity within vegetation types was thereby again given by the point distances in the NMDS that involves all plots (see above).

Furthermore, we applied a Principal Component Analysis PCA (Mardia et al., 1979) to the RS variables, using the S2 variables from the S2 image that showed the highest mean of the three correlational results from the Mantel test, variation partitioning and MANOVA. We thus illustrate the variation in RS signals that can best explain beta diversity, and depict the RS products that add most to this variation. As for the NMDS, we added post-hoc correlation of explanatory variables via vector fitting. In addition, variation partitioning onto a RDA was used to separate the variation among these date-specific S2 variables that can be explained by RS-specific coverages of the ten most abundant species and of non-vegetation cover types (i.e. bare soil, rock, pine needles and deadwood).

Data processing and statistical analyses were conducted using open-source R Statistics (R Core Team, 2017; Version 1.0.136) and corresponding default settings, if not mentioned differently (Table S2, Appendix 1).

Results

The responses of the ten most frequent perennial plant species to the major climatic gradients are clear and unimodal (Fig. 3a, b). In the semi-arid conditions of the low elevation zone, several species associated with succulent communities show their maximum performance with the highest temperature and lowest precipitation along the elevation gradient *(Euphorbia balsamifera*, *Retama rhodorhizoides*, *Rubia fruticosa*, *Schizogyne sericea*). *Cistus monspeliensis*, *Cistus symphytifolius* and *Erica arborea* become more abundant with decreasing temperature and increasing precipitation. They share their realized environmental niches with *Pinus canariensis*, which is most abundant at a mean annual temperature of approximately 14°C and at the highest annual precipitation found in the region (~925 mm). In the subalpine communities, *Adenocarpus viscosus* and *Arrhenatherum calderae* show their maximum abundance with decreasing precipitation and lowest temperatures.

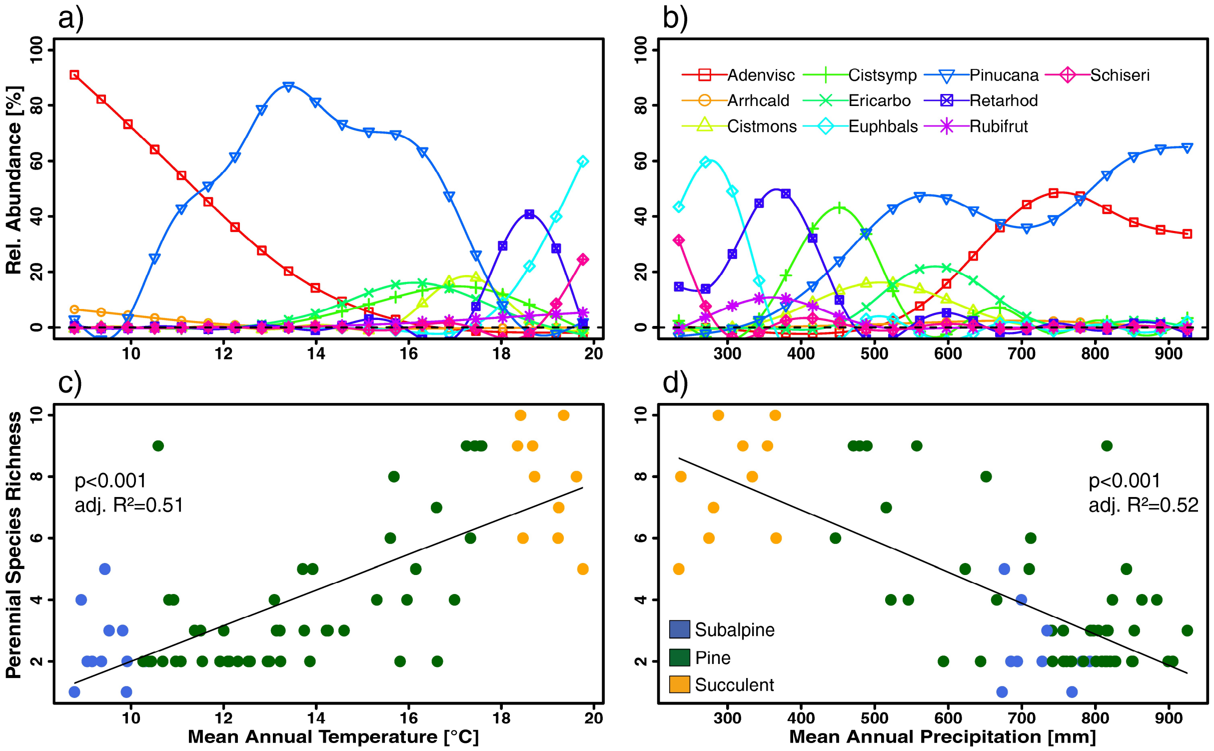

Figure 3. Species abundance versus environmental gradients. Generalized additive models (GAM) indicate the relative abundance of the ten most abundant species in the data set along a) mean annual temperature, and b) mean annual precipitation. The linear regression model demonstrates the relationship between c) perennial species richness and mean annual temperature, and between d) perennial species richness and mean annual precipitation. Species abbreviations: *Adenocarpus viscosus* (Adenvisc), *Arrhenatherum calderae* (Arrhcald), *Cistus monspeliensis* (Cistmons), *Cistus symphytifolius* (Cistsymp), *Erica arborea* (Ericarbo), *Euphorbia balsamifera* (Euphbals), *Pinus canariensis* (Pinucana), *Retama rhodorhizoides* (Retarhod), *Rubia fruticosa* (Rubifrut), *Schizogyne sericea* (Schiseri).

Species richness is also clearly related with climatic variables, i.e. a positive relation with temperature and a negative relation with rainfall (Fig. 3c, d). Despite these significant relationships, the three main vegetation types are clearly identified in the species richness versus temperature graph, but not in the species richness versus rainfall graph, which can be explained by rainfall decrease at high elevations. We did not detect a significant relationship between the relative abundance of *Pinus canariensis* and perennial species richness (not shown), but the SC plots harbour considerably more species than both other classes (Fig. S2, Appendix 1).

Figure 4a reveals that the S2 variables from 14 Jan 2017 and 20 m grain size correlate on average strongest with the beta diversity. We additionally observe a 'W'-shape; the correlation between S2 variables and beta diversity is stronger during the wet (December-March) and dry season (June-September) compared to other months. The multitemporal analysis demonstrates that neither the mean, nor the range and standard deviation of the time series reaches the highest correlation results of single image dates (Fig. 4b). Here the multitemporal mean of S2 variables yields on average strongest correlation with beta diversity compared with the multitemporal range and standard deviation. Interestingly, the multitemporal MANOVA results are weakest among the three statistical tests, but for single dates the two strongest correlations are produced by MANOVA (Fig. 4a). The Mantel test reveals a $r_{\mathrm{RS}}=0.41$ ($p<0.001$) considering all RS variables from 20 m resolution data (Fig. 4c). Considering only LiDAR variables yields a Mantel r_{LiDAR} of 0.18 ($p=0.008$). Variation partitioning of beta diversity through a combination of S2 and LiDAR variables (20 m grain) leads to a total R_{RS}^2 of 0.85 ($p<0.001$). The R_{S2}^2 resulting from independent effects of S2 signals is 0.59 ($p=0.001$). The R_{LiDAR}^2 of the independent effect of LiDAR signals is 0.01 and not significant ($p=0.111$). The combined effects of S2 and LiDAR variables produce $R_{\mathrm{S2+LiDAR}}^2=0.25$. Accordingly, $R_{\mathrm{S2}}^2 + R_{\mathrm{LiDAR}}^2 + R_{\mathrm{S2+LiDAR}}^2 = R_{\mathrm{RS}}^2=0.85$. Applying K-means classification algorithm to all RS variables leads to the differentiation of three classes that moderately explain the dissimilarities in species composition (Fig. 4c; MANOVA: $p<0.001$, $R_{\mathrm{RS}}^2=0.53$). When considering S2 variables only (Fig. 4c), K-means classification outcomes adequately reflect the beta diversity ($p<0.001$, $R_{\mathrm{S2}}^2=0.70$). A classification solely based on LiDAR variables yields a worse fit (Fig. 4c; $p=0.001$, $R_{\mathrm{LiDAR}}^2=0.19$). The correlation results between S2 variables and beta diversity decrease with increasing grain size (i.e. low resolution), while for LiDAR variables the correlation slightly increases (Fig. 4c). Except for variation partitioning, the statistical tests reveal that the correlation between all RS variables and beta diversity among 10 m plots is strongest for 20 m grain size, but resulting differences in explanatory power between grain sizes can also be marginal.

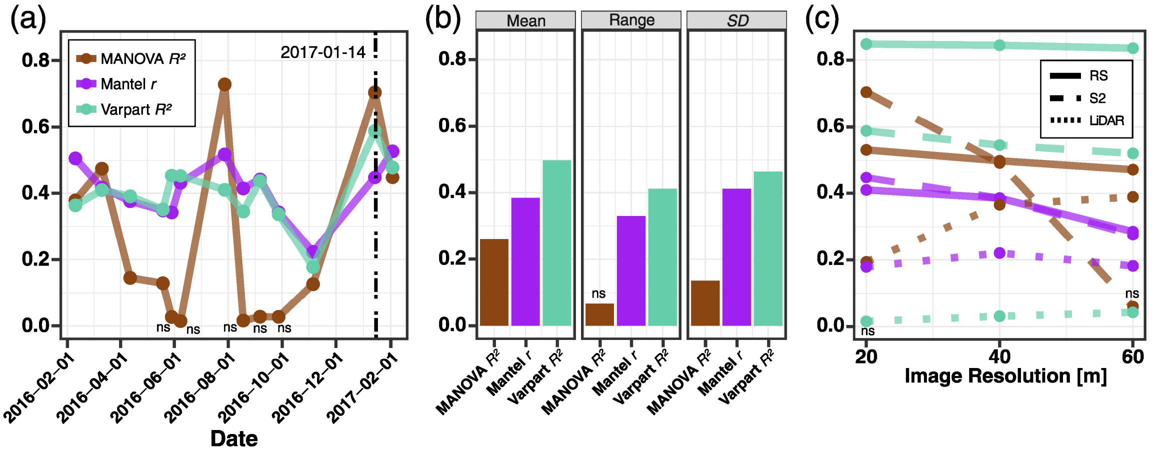

Figure 4. Time series analyses of Sentinel-2 (S2) images and sensitivity analyses concerning grain size. In a) the date-specific correlation results between the S2 variables of 13 images with 20 m grain size and the beta diversity are shown. Part b) shows the correlation results applying the multitemporal mean, range (|max-min|) and standard deviation of the time series of S2 variables. The S2 image from 14 Jan 2017 indicates the strongest correlation in view of the three statistical tests (i.e. Multivariate Analysis of Variance, Mantel test and variation partitioning). This S2 image was used for the sensitivity analysis in c). Here we show the statistical results for the coarser grain sizes 40 m and 60 m by aggregating the RS derived metrics, i.e. taking the mean value. 'Ns' highlights non-significant ($p \geq 0.05$) correlation results.

Separating the time series analyses by vegetation types resulted in Figure 5. Particularly SC undergoes temporal variation in S2 signals and shows highest Mantel *r* among communities followed by PF and SA (Fig. 5a); the SA correlations also range a lot and became even negative, but are not significant due to low sample size and very homogeneous S2 signals; the 'w'-shape is less clear for PF. The multitemporal mean of the time series produces strongest correlation for SC, followed by the multitemporal range and standard deviation (Fig. 5b); for PF, this is vice-versa.

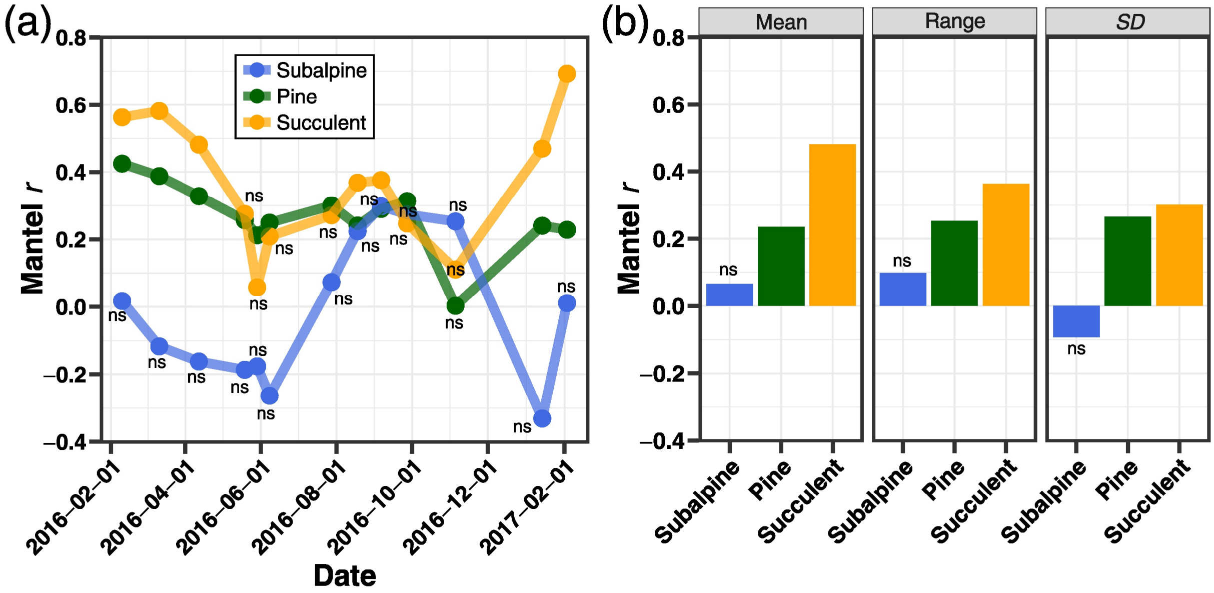

Figure 5. Time series analysis of Sentinel-2 (S2) images separated by community type. In a) the date-specific Mantel correlations between the S2 variables of 13 images with 20 m grain size and the beta diversity of the subalpine, pine and succulent community are shown. Part b) demonstrates the Mantel correlation results between the mean, range (|max-min|) and standard deviation of the time series of S2 variables and the beta diversity of the three community types. 'Ns' highlights non-significant ($p \geq 0.05$) correlation results.

The NMDS based on the species abundances (Stress=0.06) demonstrates no clear distinction between PF and SA (Fig. 6a). At lower altitudes, a considerable gap between PF and SC does become obvious. Consequently, the similarity in species composition between SA and PF is considerably higher than between SC and PF. Within PF we find an emphasized compositional variation in the lower part close to the transition to SC. Such variation along the second NMDS axis appears in the subalpine zone as well. The relationship between beta diversity and nearest distance to anthropogenic land use is very weak (Fig. S1, Appendix 1). We focus in the following on RS variables derived from RS data at 20 m spatial resolution from the S2 image acquired on 14 Jan 2017; among these RS variables, Band 3, Band 5, Band 6, Band 7, Band 8, Band 8a, NDVI, PSRI, MSI, RP0.5m, RP2m, RP5m, RP10m, LAI and VF correlate significantly ($p < 0.05$) with the NMDS scores (Fig. 6a; for details see Table S3, Appendix 1). These variables are mostly associated with the second NMDS axis, which accounts for less beta diversity than the first axis. Canopy stress, senescence or fruit ripening (PSRI), water stress (MSI) and productivity (NDVI) are associated with the first NMDS axis.

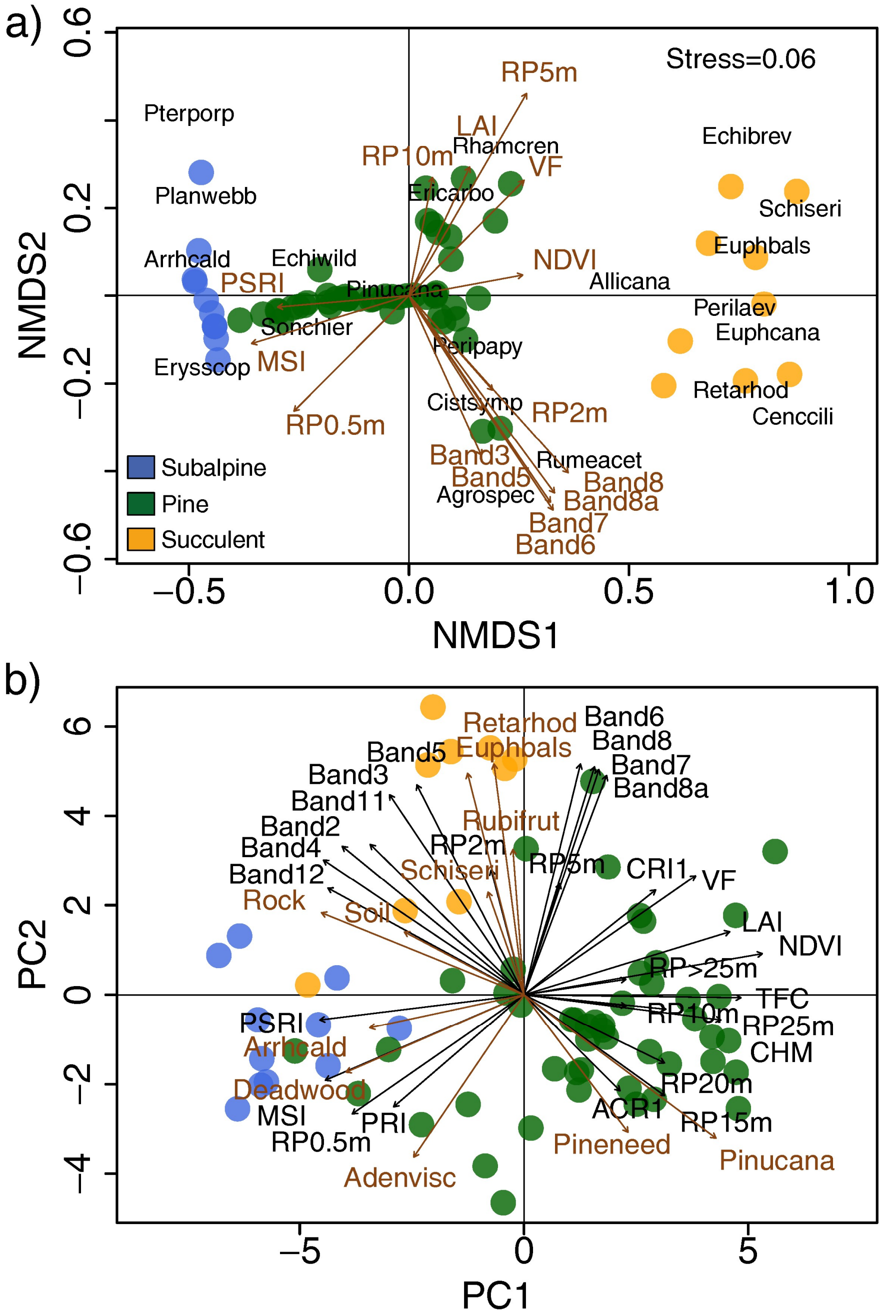

Figure 6. The location of plots in the two-dimensional ordination space calculated via Non-metric Multidimensional Scaling (NMDS) and Principal Component Analysis (PCA). a) The PC-rotated NMDS space is representing beta diversity calculated by the Hellinger distance between plots, considering the abundances of perennial plant species. The NMDS-stress value of 0.06 depicts a good fit. b) The PC-rotated PCA space is calculated by the remote sensing (RS) variables derived from the Sentinel-2 image taken on 14 Jan 2017. A proportion of 60% of total variance is explained by PC1 (39%) and PC2 (21%) (for details see Table S4, Appendix 1). The vectors of explanatory variables (brown arrows) and PCA-input variables (black arrows) were fitted after generating the ordination space (for details see Table S3, Appendix 1). Species abbreviations: *Adenocarpus viscosus* (Adenvisc), *Agrostis spec.* (Agrospec), *Allium canariense* (Allicana) *Arrhenatherum calderae* (Arrhcald), *Cenchrus ciliaris* (Cenccili), *Cistus symphytifolius* (Cistsymp), *Echium brevirame* (Echibrev), *Echium wildpretii* (Echiwild), *Erica arborea* (Ericarbo), *Erysimum scoparium* (Erysscop) *Euphorbia balsamifera* (Euphbals), *Euphorbia canariensis* (Euphcana), *Periploca laevigata* (Perilaev), *Pericallis papyracea* (Peripapy), *Pinus canariensis* (Pinucana), *Plantago webbii* (Planwebb), *Pterocephalus porphyranthus* (Pterporp), *Retama rhodorhizoides* (Retarhod), *Rhamnus crenulata* (Rhamcren), *Rubia fruticosa* (Rubifrut), *Rumex acetosa* (Rumeacet), *Schizogyne sericea* (Schiseri), *Sonchus hierrensis* (Sonchier).

The PCA based on RS variables shows that both axes contribute to the differentiation of vegetation types (Fig. 4b), but the three communities appear less clearly separated than for the species data (Fig. 4a); the distances between SC, PF and SA are not as pronounced as in the species-based NMDS ordination. Increasing S2 band values are mostly related to SC. The majority of LiDAR metrics increase along PF plots. Weakening vegetation, canopy growth or death (CRI1, ACR1), and productivity (NDVI) are also associated with the pine community. Light use efficiency (PRI), water stress (MSI) as well as canopy stress, senescence or fruit ripening (PSRI) accompany SA plots. The structural variable RP0.5m is related to SA, whereas RP2m reflects SC. The PCA axes' loadings of the RS variables are given in Table S4 (Appendix 1). Among the other explanatory variables, only the RS-specific coverage of *Cistus monspeliensis*, *Cistus symphytifolius* and *Erica arborea* are not significantly correlated with the PCA scores (Table S3, Appendix 1). The RS-specific coverages of the other species are correctly linked to their corresponding communities. RS-specific coverage of deadwood is linked to SA, of rock and bare soil to SC as well as SA.

Furthermore, variation partitioning onto the RDA explaining the variation in RS variables leads to a total R_{Total}^2 of 0.62 (p=0.001) that is the sum of the effects of the RS-specific coverages of species and non-vegetation types (i.e. rock, bare soil, deadwood and pine needles): $R_{\mathrm{Total}}^2 = R_{\mathrm{Species}}^2 + R_{\mathrm{Non\text{-}vegetation}}^2 + R_{\mathrm{Species+Non\text{-}vegetation}}^2$. Thereby, RS-specific species' coverages independently account for an R_{Species}^2 of 0.29 (p=0.001), whereas the independent effect of non-vegetation coverages scores a non-significant (p=0.067) $R_{\mathrm{Non\text{-}vegetation}}^2$ of 0.05. The combined effects of vegetation and non-vegetation coverages result in $R_{\mathrm{Species+Non\text{-}vegetation}}^2=0.28$.

Discussion

Beta diversity and remote sensing signals

Contrary to our initial expectations, we show that a combination of multispectral and structural RS variables can explain up to 85 % of beta diversity in the plant communities of the study system. The S2 variables constitute more explanatory power than the LiDAR variables we selected. These outcomes are partly in line with similar studies that consider different variables and scales. He et al. (2009) quantified the relationship between NDVI-distances, derived from MODIS with 250 m resolution, and plant beta diversity, using pairwise Bray-Curtis dissimilarity, within entire US counties. The highest Mantel *r* was achieved at the species level (r=0.4); see He and Zhang (2009) for a similar approach at the global scale. Hall and colleagues (2012) used multispectral variables derived from QuickBird imagery with a grain size of 2.4 m. They applied variation partitioning on grassland beta diversity, i.e. local-to-regional richness ratio, sampled in 0.5 m plots representative for larger sites, which resulted in an R^2 of 0.27 for the independent effect of multispectral RS variables. That is lower than the explanatory power we found, although their study scale was much smaller.

Indeed, the different extents of pixels and plots affect the correlation between RS signals and beta diversity. On the one hand, pixels larger than the plot extent imply a mixture of spectral signals that do not only originate from the plot extent (Nagendra et al., 2010). On the other hand, applying a sampling design with pixels smaller than the plot extent implies either to sample vegetation in larger plots or to use RS data with higher spatial resolution (Rocchini et al., 2010). Plots larger than 10 m by 10 m are rarely applied in vegetation ecology because the sampling effort is large, particularly in open vegetation types (Chytrý and Otýpková, 2003). Moreover, Rocchini (2007) demonstrates a Mantel *r* of 0.69 of the correlation between species diversity sampled in 10 m by 10 m plots and QuickBird data with a much smaller spatial resolution of 3 m; this Mantel *r* is not considerably larger than our findings; in case of oversampling (i.e. plots are larger than pixels) high-resolution data may contain a considerable amount of noise (Nagendra and Rocchini, 2008) even though the species composition of pixels may be inaccurate in case of undersampling (i.e. plots smaller than pixel). An increase in spectral resolution can also compensate low spatial resolution (Rocchini et al., 2007).

Usually communities that are subject to climate seasonality can be well separated by RS data (Horning et al., 2010). During the wet (i.e. December to March) and dry season (i.e. June to September), multispectral variables correlate stronger with the dissimilarity in species composition than in other months. The multitemporal variables, however, cannot explain the same amount of beta diversity than date-specific variables at maximum. That offers potential for further investigations, exploring the explanatory power of date-specific multispectral variables and vegetation indices to detect the reasons behind these findings. We assume that the dominant and stem-succulent species of the succulent zone such as *Euphorbia balsamifera* and *Euphorbia lamarckii* shed their leaves in the dry season (Muer et al., 2016). In addition, understorey species of the pine forest and subalpine species frequently show discoloration during dry spells. The highly abundant bright yellow flowers of the dominating *Adenocarpus viscosus* might also lead to multispectral differentiation of subalpine vegetation in June (Muer et al., 2016). Furthermore, during the wet season, ice-storms can cause discoloration of *Adenocarpus viscosus* as a result of leave tissue damage (Palomares Martínez et al., 2012).

In January, as our date-specific PCA showed, the vegetation indices PSRI, MSI, PRI, ACR1 and CRI1 may represent vegetation stress. Especially the high-elevation pine and subalpine community experience freezing temperatures and low precipitation. Trade winds prevent the orographic and convective rise of moist air, leading to aridity also in the subalpine zone throughout several months (González Henríquez et al., 1986). The trade-wind cloud facilitates fog-drip. The high reflectance of red light (i.e. Band 4, Band 5 and PSRI) was mostly associated with the succulent and subalpine scrub. This is an indicator for low leaf pigment content and small leaf area, but also for brown rock, soil and litter (Frampton et al., 2013). In addition, leaf water content is positively related to chlorophyll content (Sims and Gamon, 2002). Thus, leaf water content (i.e. MSI) of the succulent and subalpine scrub may be low due to aridity resulting in less chlorophyll and higher reflectance. Another reason for high reflectance in the visible spectrum refers to succulent leaf thickness, which prevents light penetration and absorption of lower leaf layers (Sims and Gamon, 2002). High NDVI values correspond to the pine forest, where annual precipitation is highest, probably indicating high biomass production. Most LiDAR-derived structural variables represent the physiognomic forest structure very well (Rees, 2007; Ørka et al., 2012). The association of structural variables representing different heights above ground (i.e. RP variables) with the community types in the date-specific PCA agrees with observed vegetation heights in the field.

In our study multispectral S2 variables explain beta diversity more accurately than structural LiDAR variables. One reason is that the vegetation coverages of both scrub types are similar, and characterized by rocky outcrops and bare soil. Considering additional LiDAR metrics that particularly differentiate the vertical scrubland structure between 0.5 and 2 m may lead to a stronger correlation between LiDAR products and beta diversity.

Besides, the LiDAR data was acquired in April 2009. Since then perennial plant coverage and structure may have slightly changed. However, increasing grain size results in increasing explanatory power of LiDAR variables applying MANOVA, while explanatory power of S2 variables decreases in all statistical tests. The low LiDAR point density and thus high variation (i.e. noise) in LiDAR variables could be responsible for the weak correlations with beta diversity at the small scale of 20 m. The noise is reduced by averaging pixel values; with increasing extent the LiDAR metrics become more stable. Hence, the average structural signatures of entire community types are rather reflected by the relatively large grain size of 60 m, which then lead to more distinct LiDAR-based classes in K-means clustering that correlate stronger with beta diversity.

A proportion of 62% of variation in S2 signals from 14 Jan 2017 can be explained by RS-specific coverages of species and non-vegetation cover, but the RS-specific coverages of bare soil, rock and litter barely add to the differentiation of plots based on S2 signals only; 38% of variation in S2 variables can neither be explained by the species' coverages, nor by non-vegetation cover types, probably because of differing spatial extents of plots and pixels and GPS-location bias.

GPS-inaccuracy affects the co-location of RS and in-situ data. For S2 imagery, a GPS-location error of 3, 6 and 18 m is given for 10, 20 and 60 m bands respectively (Baillarin et al., 2012). Due to the field-sampling conditions (i.e. cloud-free, no northern aspects, slope <20°, no obstacles), the GPS accuracy of the plot locations could be reduced to a mean of 3.6 m (±1.0 m standard deviation). However, the cardinal direction of the true location shift remains unknown. Thus, a total GPS-error of 6 m for 20 m bands plus the GPS error of the plot locations is possible and likely to cause unexplained variation when correlating RS with in-situ data. However, as the sensitivity analysis shows, the GPS bias seems to be minor, since the lowest grain size of 20 m yields equally high correlation results compared to 40 m and 60 m.

The moderate conformity of RS-based classes with the beta diversity pattern reveals that both sets of variables, S2 and LiDAR, are able to reclassify the pine forest plots, even though unsupervised classifications may be less accurate than supervised techniques (Horning et al., 2010). Both sets seem to contradict each other because the explanatory power decreases when it comes to defining vegetation classes considering a combination of both sets. Therefore, increasing the number of RS variables does not necessarily lead to more variation explained.

The RS data were not able to completely resolve the community types and beta diversity in this semi-natural system, which suggest similar RS properties of different species assemblages. Understorey species may be highly abundant and determine beta diversity, but are not detectable for RS sensors. If heterogeneous yet distinct plant communities comprise the same spectral signals (Sha et al., 2008), the potential of RS approaches in vegetation science will be limited.

Species richness and beta diversity

A series of studies describe continuous change in plant composition along an elevational gradient (Whittaker, 1956; Hamilton, 1975; Ogden and Powell, 1979; Enright, 1982; Auerbach and Shmida, 1993). In contrast, we identified two very distinct communities at low altitudes – succulent scrub and pine forest – even though the main environmental gradients do not change abruptly. The sharp ecotone appears with the presence of the

Canarian-endemic *Pinus canariensis*. Other ordination-based studies also reveal discontinuities in compositional patterns with the increasing dominance of a key tree species (Walker and Guppy, 1976; Druitt et al., 1990) inducing positive-feedback switches (Wilson and Agnew, 1992). *Pinus canariensis* influences environmental resources (e.g. water, light and nutrient availability), so that thermophilic species such as *Euphorbia balsamifera* and *Retama rhodorhizoides* do not to establish in the forest understorey. This is associated with selection, a major process shaping species communities, resulting from fitness differences and interactions between species and the environment (Vellend, 2010).

Shade-tolerant species such as *Erica arborea* and *Myrica faya* do, however, occur under humid conditions in the lower pine forest, but not in the arid conditions of the upper succulent zone. We expected a continuous transition in species composition between the succulent and the pine community according to the distribution of *Cistus monspeliensis* and *Cistus symphytifolius*, which occur in open forest stands of low elevation as well as in the upper succulent zone. Nevertheless, their abundances are too low to substantially increase compositional similarity in the lower ecotone. In contrast, the leguminous and light-demanding scrub *Adenocarpus viscosus*, which dominates above the treeline, is also abundant in open *Pinus canariensis*-stands at higher elevations. Consequently, the similarity in species composition between the pine forest and the subalpine zone is much higher than between the pine forest and the succulent scrub. This is in agreement with Hamilton and Perrott (1981) who conclude that, along elevation gradients, lower community limits are strongly influenced by competition, whereas upper limits are mostly climatically determined.

We propose that the sharp community boundary also results from different species pool sizes. The species pool size is generally smaller at higher elevation due to lower speciation rates (Ricklefs, 1987) and decreasing area with elevation (Karger et al., 2011). Dissimilarity in species composition intrinsically increases with richness differences between species assemblages because the probability of species range overlap decreases (Anderson et al., 2011). At the upper treeline, only about three perennial vascular plant species are present, whereas approximately eight species occur at the lower transition zone. Furthermore, species richness strongly decreases from the succulent scrub to the pine forest, but stays constant from the pine forest to the subalpine scrub. Hence, beta diversity is enhanced across the lower treeline, not only due to species replacement, but also due to richness differences.

The strict separation between the succulent and pine forest community might also be explained by a difference in disturbance regimes, which influence selection (Lawton, 1999), but also speciation in evolutionary time spans (Vellend, 2010). Regular occurrence of fire is common in the Canary pine forest ecosystem (Climent et al., 2004). Fire sometimes spreads into the subalpine zone (Irl et al., 2014). Contrary to thermophilic species of the succulent vegetation, *Pinus canariensis* and understorey species display adaptations to fire (i.e. pyropyhtes). *Pinus canariensis* produces epicormics shoots and basal sprouts, and serotinous cones release seeds after fire events (Climent et al., 2004). Understorey species such as *Myrica faya*, *Erica arborea*, *Cistus symphytifolius*, *Cistus monspeliensis* and *Adenocarpus viscosus* regenerate quickly after fire events (Höllermann, 2000). In accordance with field observations (burned area) and literature (Climent et al., 2004; Méndez et al., 2015; Molina-Terrén et al., 2016), short-term fire regimes do not vary among plots and long-term forest regeneration does not depend on the fire regime either (Méndez et al., 2015). Consequently, the fire regime might explain the strong compositional differentiation between pine forest and succulent scrub due to the selection and speciation of species being differently adapted to fire (Arévalo et al., 2001).

Furthermore, the European rabbit (*Oryctolagus cuniculus*), the feral goat (*Capra hircus*) and the Barbary sheep (*Ammotragus lervia*), which are introduced mammals on La Palma, induce the dominance of *Adenocarpus viscosus* at high elevation (Irl et al., 2012). Moreover, anthropogenic land use influences pine forest diversity at lower altitudes (Vellend et al., 2007). Thinning of *Pinus canariensis*-plantations for timber production enhances habitat heterogeneity, understorey species diversity, seed production and regeneration of *Pinus canariensis* (Otto et al., 2012). Although we did not find evidence for recent anthropogenic impacts, the legacy of such disturbance regimes can act over decades (Vellend et al., 2007). In any case, fire and herbivory likely contribute to the decline of species richness with elevation in the study region (Irl et al., 2015), despite precipitation increase, since rabbit densities can be high above the treeline (Cubas et al., 2018). Thus, decreasing richness differences may reduce beta diversity between the subalpine and pine community.

The vague community boundary between the pine forest and the subalpine scrub raises questions about the existence of two distinct communities. Community and respectively ecotone definition are a matter of scale (Ricklefs, 2008; Hufkens et al., 2009). Here we apply a regional approach that does not consider transition at local scale nor through time. Moreover, we did not test for causal mechanisms determining compositional (dis-)continuities (Shipley and Keddy, 1987). From a physiognomy point of view, the treeline may indicate the community limit, but in terms of species composition, limits are unclear (Walker et al., 2003). Often boundaries are human constructs. Lines on a map drawn between ecoregions do not implicitly correspond with any obvious physical discontinuities in nature (Strayer et al., 2003). Because fundamental environmental gradients were adequately covered by the plots and the relationship between beta diversity and nearest distance to anthropogenic land use was very weak, these outcomes are unlikely to be caused by sampling bias or human influence.

Conclusion

Our study demonstrated the potential of multiple RS products to represent patterns in plant community composition over large extents, in short time and at low costs. In-situ sampling was indispensable to precisely determine and understand beta diversity and community distinction. The degree of accordance between spectral and beta diversity depends not only on the studied system, but also on the methods applied (Schmidtlein and Fassnacht, 2017). Such methods that identify and map discontinuities in beta diversity are necessary for conservation planning and wildlife management (Socolar et al., 2016).

On the one hand, spatial and temporal resolution of RS data may limit the potential of linking field observation with RS data since interaction between species and environment may occur at scales finer than those that RS can deliver. In such cases, other techniques than the ones applied here may be appropriate (e.g. high spatio-temporal and hyperspectral resolution and space-borne LiDAR), but most high-quality RS data are costly. On the other hand, in-situ data are also often missing. Facing these limitations, project collaborations are necessary to bring together scientist from ecology and remote sensing to exploit the vast potential of a combination of in-situ data and earth observation for science and conservation practice.

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Author contributions

S.H. and T.S. collected the field data and processed the Sentinel-2 images. M.A.T., S.M. and A.B. processed the LiDAR data. S.H. conducted the statistical analyses and led the writing process. All authors contributed to the development of the study, the interpretation of results and the writing of the manuscript.

Data accessibility

Data and R code are available on request.

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Supporting information

Appendix 1. Supporting tables and figures

Table S1. Selected time series of Sentinel-2A images.

Date	# plots covered by cloud mask	Image Granule ID
3 February 2017	0	T28RBS_A008457_20170203T120317
14 January 2017	0	T28RBS_A008171_20170114T120212
5 November 2016	2	20161105T171456_A007170_T28RBS
26 September 2016	2	20160926T185349_A006598_T27RYM
6 September 2016	0	20160906T185710_A006312_T27RYM
17 August 2016	0	20160817T185425_A006026_T27RYM
28 July 2016	2	20160728T185358_A005740_T27RYM
8 June 2016	1	20160608T185127_A005025_T27RYM
29 May 2016	1	20160529T184805_A004882_T27RYM
19 May 2019	1	20160519T185155_A004739_T27RYM
9 April 2016	0	20160409T185621_A004167_T27RYM
10 March 2016	2	20160310T202218_A003738_T27RYM
9 February 2016	1	20160209T202004_A003309_T27RYM

Table S2. R-functions and packages used for the statistical analyses.

Statistical Analysis	R-function	R-package	Settings different from default
Generalized Additive Models	gam()	mgvc	
Non-parametric Kruskal-Wallis Analysis of Variance ANOVA	kruskalmc()	stats	
Linear Regression	lm()	stats	
Non-metric Multidimensional Scaling	metaMDS() ordisurf() envfit()	vegan	
Mantel test	mantel()	stats	Pearson's correlation coefficient, 1000 permutations
Variation Partitioning	varpart()	vegan	
K-means Unsupervised Classification	kmeans()	stats	1000 iterations of random starting configurations
Multivariate Analysis of Variance	adonis()	vegan	
Principal Component Analysis	prcomp()	stats	

Table S3. Results of post-hoc correlation of explanatory variables to the NMDS and PCA via vector fitting. For further information see main text.

	NMDS		**PCA**	
	R^2	**p**	**R^2**	**p**
Band 2	0.05	0.19	0.83	0.001
Band 3	0.14	0.009	0.88	0.001
Band 4	0.03	0.434	0.88	0.001
Band 5	0.24	0.001	0.84	0.001
Band 6	0.52	0.001	0.85	0.001
Band 7	0.49	0.001	0.85	0.001
Band 8	0.44	0.001	0.86	0.001
Band 8a	0.47	0.001	0.83	0.001
Band 11	0.08	0.059	0.70	0.001
Band 12	0.04	0.258	0.75	0.001
NDVI	0.10	0.031	0.88	0.001
PRI	0.05	0.204	0.45	0.001
ACR1	0.01	0.826	0.28	0.001
CRI1	0.04	0.277	0.43	0.001
PSRI	0.14	0.01	0.64	0.001
MSI	0.21	0.001	0.71	0.001
LAI	0.16	0.004	0.70	0.001
RP0.5m	0.21	0.001	0.66	0.001
RP2m	0.12	0.006	0.25	0.001
RP5m	0.43	0.001	0.21	0.002
RP10m	0.11	0.023	0.16	0.005
RP15m	0.02	0.532	0.45	0.001
RP20m	0.03	0.365	0.37	0.001
RP25m	0.01	0.795	0.31	0.001
RP>25m	0.00	0.997	0.16	0.005
CHM	0.00	0.873	0.59	0.001
TFC	0.07	0.088	0.71	0.001
VF	0.21	0.001	0.66	0.001
Adenocarpus.viscosus	-	-	0.29	0.001
Arrhenatherum.calderae	-	-	0.18	0.003
Cistus.monspeliensis	-	-	0.03	0.353
Cistus.symphytifolius	-	-	0.01	0.795
Erica.arborea	-	-	0.05	0.185
Euphorbia.balsamifera	-	-	0.39	0.001
Pinus.canariensis	-	-	0.43	0.001
Retama.rhodorhizoides	-	-	0.40	0.001
Rubia.fruticosa	-	-	0.16	0.004
Schizogyne.sericea	-	-	0.09	0.043
Soil	-	-	0.14	0.008
Rock	-	-	0.36	0.001
Pine.needle	-	-	0.22	0.001
Deadwood	-	-	0.28	0.001

Table S4. The PCA loadings of the RS variables, the axes' standard deviations and (cumulative) variances explained. For further information see main text.

	PC1	**PC2**	**PC3**	**PC4**	**PC5**	**PC6**	**PC7**	**PC8**	**PC9**	**PC10**	**PC11**	**PC12**
Band 2	-0.24	0.19	-0.03	0.16	-0.07	0.21	-0.07	0.18	-0.06	0.07	-0.08	0.04
Band 3	-0.19	0.28	-0.08	0.08	-0.09	0.11	-0.16	0.15	-0.07	0.07	-0.11	0.07
Band 4	-0.25	0.17	-0.06	0.15	-0.07	0.00	-0.12	0.11	-0.10	-0.02	-0.06	0.17
Band 5	-0.16	0.31	-0.05	0.16	0.13	-0.06	0.00	0.06	0.01	0.11	-0.38	0.12
Band 6	0.09	0.36	-0.07	-0.04	0.24	0.06	0.02	-0.08	-0.03	0.07	-0.06	0.03
Band 7	0.11	0.35	-0.07	-0.04	0.25	0.02	0.03	-0.05	0.00	-0.01	0.02	0.01
Band 8	0.11	0.35	-0.10	-0.03	0.10	0.15	-0.05	0.06	-0.02	-0.22	0.21	-0.06
Band 8a	0.13	0.33	-0.04	-0.05	0.26	0.04	0.07	-0.16	0.01	-0.01	-0.01	0.05
Band 11	-0.20	0.20	-0.01	0.21	0.12	-0.27	0.14	-0.16	0.08	-0.08	0.33	-0.24
Band 12	-0.24	0.13	0.00	0.24	0.01	-0.22	0.05	-0.11	0.10	-0.02	0.28	-0.29
NDVI	0.28	0.05	0.05	-0.14	0.10	0.09	0.04	-0.04	0.09	-0.05	0.21	-0.16
PRI	-0.17	-0.15	0.16	0.29	0.16	0.37	0.27	0.15	-0.05	-0.05	0.06	-0.04
ACR1	0.13	-0.13	0.20	0.15	0.44	-0.20	0.30	-0.17	0.18	0.19	-0.33	0.30
CRI1	0.17	0.14	-0.15	-0.30	-0.16	-0.39	-0.25	-0.17	0.09	0.07	-0.08	0.05
PSRI	-0.24	-0.03	-0.11	0.09	-0.11	-0.38	-0.14	-0.04	-0.15	-0.18	0.01	0.38
MSI	-0.24	-0.10	0.01	0.18	0.03	-0.31	0.15	-0.17	0.09	0.10	0.04	-0.12
LAI	0.25	0.08	0.12	0.23	-0.11	-0.01	0.01	-0.02	0.05	0.01	0.49	0.48
RP0.5m	-0.22	-0.15	-0.21	-0.13	0.22	0.17	-0.19	-0.17	0.14	0.03	0.10	0.08
RP2m	-0.05	0.19	0.29	-0.29	-0.17	-0.18	0.44	0.17	-0.28	-0.11	-0.05	-0.01
RP5m	0.06	0.17	0.40	0.14	-0.28	0.07	-0.21	0.02	0.44	0.45	0.03	-0.01
RP10m	0.12	-0.01	0.37	0.27	0.07	0.00	-0.39	-0.25	-0.07	-0.56	-0.27	-0.20
RP15m	0.18	-0.13	0.07	0.17	0.31	-0.14	-0.25	0.19	-0.50	0.17	0.25	0.17
RP20m	0.17	-0.08	-0.30	0.12	0.16	-0.25	-0.06	0.46	0.03	0.19	-0.07	-0.37
RP25m	0.17	-0.02	-0.36	0.19	-0.15	0.01	0.25	0.18	0.40	-0.42	-0.05	0.24
RP>25m	0.12	0.02	-0.26	0.21	-0.30	0.20	0.20	-0.54	-0.36	0.25	-0.06	-0.06
CHM	0.23	-0.03	-0.30	0.26	-0.12	0.00	0.07	-0.06	-0.11	0.02	-0.11	-0.09
TFC	0.25	0.00	-0.03	0.33	-0.09	-0.03	-0.15	0.05	0.03	0.04	-0.08	-0.08
VF	0.22	0.15	0.21	0.13	-0.22	-0.17	0.19	0.17	-0.14	-0.03	-0.10	-0.08
Standard deviation	3.31	2.44	1.55	1.48	1.28	1.10	1.01	0.93	0.76	0.58	0.49	0.44
Proportion of Variance	0.39	0.21	0.09	0.08	0.06	0.04	0.04	0.03	0.02	0.01	0.01	0.01
Cumulative Proportion	0.39	0.60	0.69	0.77	0.83	0.87	0.90	0.94	0.96	0.97	0.98	0.98
	PC13	**PC14**	**PC15**	**PC16**	**PC17**	**PC18**	**PC19**	**PC20**	**PC21**	**PC22**	**PC23**	**PC24**
Band 2	0.15	-0.07	-0.14	-0.07	0.39	0.06	0.20	0.03	0.06	-0.19	-0.16	-0.50
Band 3	0.16	0.00	-0.12	-0.23	0.01	0.08	0.13	-0.04	0.45	0.37	0.05	0.44
Band 4	-0.04	0.14	-0.17	0.16	0.18	-0.03	0.14	0.09	-0.12	0.16	-0.01	0.03
Band 5	0.23	-0.03	-0.10	-0.06	-0.44	-0.13	-0.50	-0.17	-0.21	-0.07	-0.04	0.02
Band 6	-0.13	-0.23	0.12	0.14	-0.43	0.40	0.31	0.40	0.08	-0.13	-0.16	-0.10
Band 7	-0.16	-0.18	0.12	0.36	0.07	-0.43	0.34	-0.51	-0.02	0.05	0.04	0.09
Band 8	-0.11	0.31	0.20	-0.65	-0.02	-0.01	0.09	-0.13	-0.27	-0.15	0.09	-0.06
Band 8a	-0.19	-0.05	0.15	0.08	0.52	0.07	-0.56	0.23	0.21	0.00	0.10	0.05
Band 11	0.14	0.11	-0.12	0.10	0.01	-0.16	0.03	0.34	-0.34	0.42	-0.07	-0.06
Band 12	0.19	0.17	-0.11	0.20	-0.02	0.23	-0.02	-0.26	0.28	-0.51	0.16	0.06

NDVI	0.11	0.35	-0.12	-0.01	-0.15	0.06	-0.04	-0.08	0.37	0.26	-0.31	0.01
PRI	-0.16	0.04	0.07	0.03	0.04	-0.03	0.06	0.19	-0.15	-0.23	-0.11	0.57
ACR1	0.05	0.31	-0.21	-0.18	0.15	0.06	0.25	-0.05	0.03	0.00	0.04	-0.05
CRI1	0.21	-0.04	-0.10	-0.08	0.21	-0.03	0.18	0.20	-0.19	-0.30	-0.08	0.42
PSRI	-0.49	0.35	0.20	0.08	-0.12	0.04	-0.02	-0.02	0.14	-0.01	-0.10	-0.01
MSI	-0.03	-0.47	0.37	-0.42	0.05	0.01	0.06	-0.10	0.17	0.12	-0.12	0.00
LAI	-0.13	-0.35	-0.44	-0.12	-0.06	0.07	-0.10	-0.10	-0.04	-0.03	-0.02	0.03
RP0.5m	0.00	-0.02	-0.06	0.00	0.02	0.09	-0.03	-0.09	-0.07	0.02	-0.11	0.02
RP2m	0.01	-0.03	-0.05	0.00	0.06	0.14	-0.02	-0.12	-0.06	0.01	-0.17	0.03
RP5m	-0.13	0.15	0.26	0.07	-0.03	0.00	0.03	0.05	-0.06	0.06	0.19	-0.02
RP10m	-0.06	-0.14	-0.15	-0.04	-0.01	-0.01	0.05	0.04	0.05	0.02	0.11	-0.01
RP15m	0.39	0.04	0.31	0.05	-0.01	-0.06	0.01	0.10	0.05	-0.01	0.15	-0.01
RP20m	-0.39	-0.05	-0.31	-0.10	-0.02	-0.11	-0.02	0.10	0.08	-0.04	0.09	-0.02
RP25m	0.27	-0.02	0.20	0.08	-0.04	-0.14	0.05	0.17	0.16	-0.04	0.11	-0.04
RP>25m	-0.06	0.11	-0.09	-0.08	-0.08	-0.29	0.04	0.12	0.13	-0.09	0.06	-0.05
CHM	0.01	0.01	0.08	0.12	0.12	0.61	0.02	-0.29	-0.31	0.26	0.20	0.08
TFC	0.04	0.06	0.14	0.06	0.13	-0.02	-0.09	-0.12	-0.06	-0.08	-0.75	0.04
VF	0.00	0.02	0.06	0.00	-0.01	-0.09	0.03	0.09	0.07	-0.02	0.11	-0.03
Standard deviation	0.37	0.34	0.25	0.21	0.16	0.14	0.14	0.11	0.08	0.07	0.06	0.05
Proportion of Variance	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Cumulative Proportion	0.99	0.99	0.99	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
	PC25	**PC26**	**PC27**	**PC28**								
Band 2	-0.25	-0.39	0.00	0.00								
Band 3	-0.26	0.23	0.00	0.00								
Band 4	0.79	0.06	0.00	0.00								
Band 5	0.02	-0.22	0.00	0.00								
Band 6	0.05	0.08	0.00	0.00								
Band 7	-0.06	-0.09	0.00	0.00								
Band 8	0.07	0.11	0.00	0.00								
Band 8a	0.02	0.02	0.00	0.00								
Band 11	-0.26	0.03	0.00	0.00								
Band 12	0.07	0.14	0.00	0.00								
NDVI	0.21	-0.52	0.00	0.00								
PRI	-0.06	-0.28	0.00	0.00								
ACR1	-0.03	0.11	0.00	0.00								
CRI1	-0.01	-0.27	0.00	0.00								
PSRI	-0.22	-0.19	0.00	0.00								
MSI	0.26	-0.19	0.00	0.00								
LAI	-0.01	-0.02	0.00	0.00								
RP0.5m	-0.02	0.03	0.42	0.68								
RP2m	-0.01	0.07	-0.29	0.50								
RP5m	-0.01	-0.08	-0.16	0.27								
RP10m	0.00	-0.08	-0.11	0.19								
RP15m	0.02	-0.05	-0.10	0.18								
RP20m	0.00	-0.04	-0.12	0.21								
RP25m	0.03	-0.01	-0.13	0.23								

RP>25m	0.02	0.01	-0.11	0.19								
CHM	-0.05	-0.19	0.00	0.00								
TFC	-0.03	0.36	0.00	0.00								
VF	0.02	-0.03	0.80	0.02								
Standard deviation	0.05	0.04	0.00	0.00								
Proportion of Variance	0.00	0.00	0.00	0.00								
Cumulative Proportion	1.00	1.00	1.00	1.00								

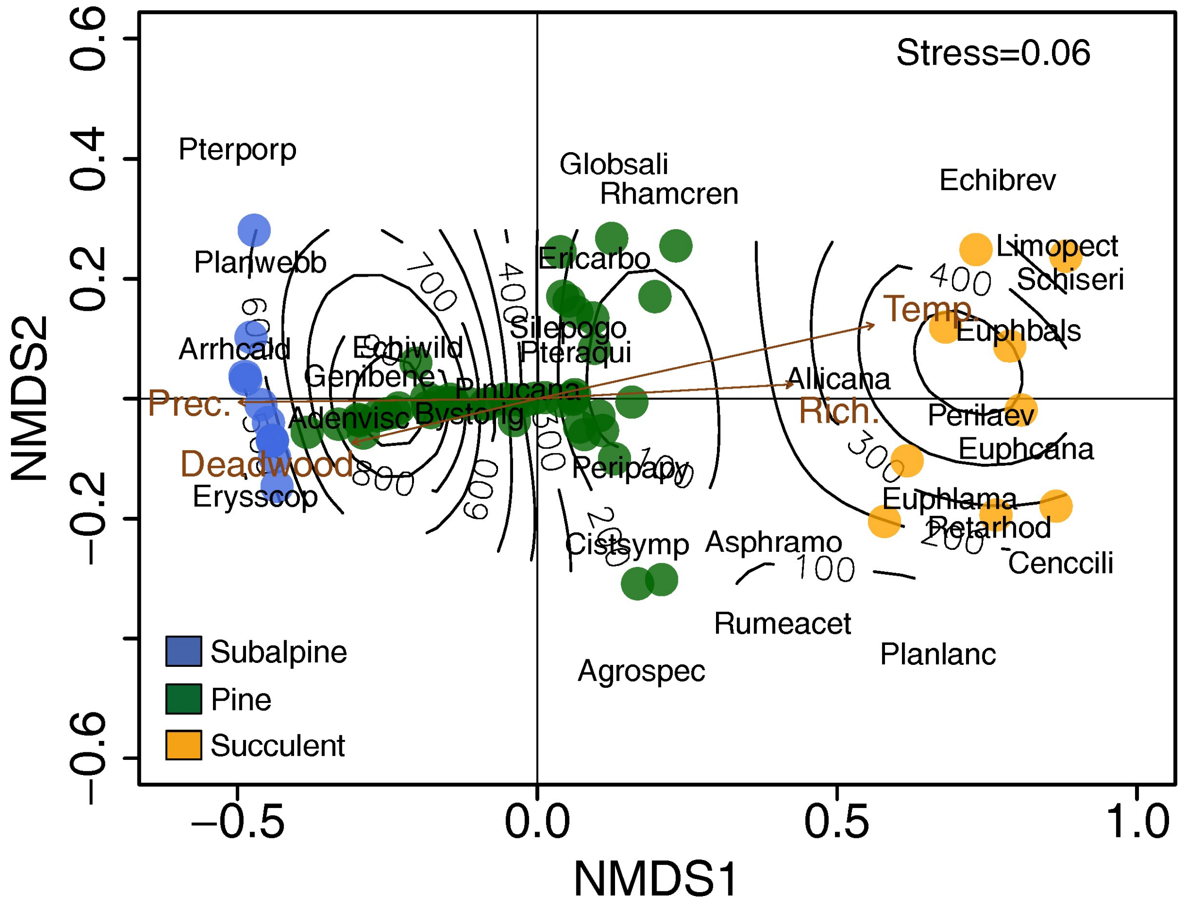

Figure S1. The location of sampling plots in the two-dimensional ordination space calculated via Non-metric Multidimensional Scaling (NMDS). The NMDS space is representing beta diversity or compositional dissimilarity calculated by Hellinger distance between sampling units considering abundances of perennial plant species. The stress value 0.06 depicts a good fit. The position of species and environmental vectors was calculated by post-hoc vector fitting. The following explanatory variables were significantly ($p<0.05$) related to NMDS axes. Temp.=Mean annual temperature, Prec.=Annual precipitation, Rich.=Perennial species richness, and Deadwood. Black contour lines depict the distance in meter to the nearest human infrastructure, i.e. roads and buildings of any kind. For further information see main text.

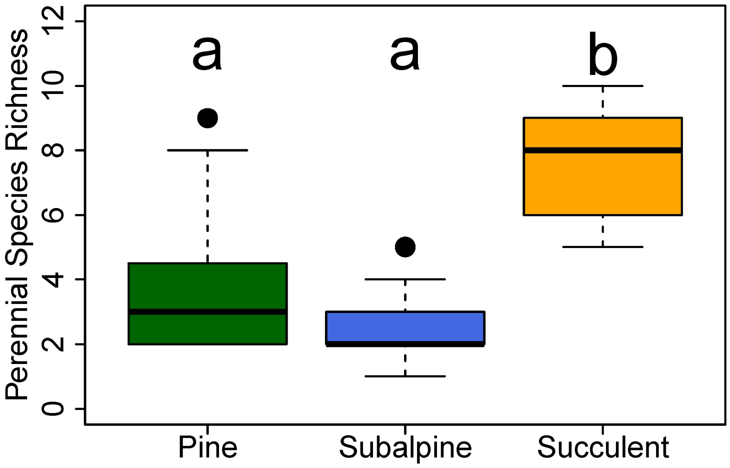

Figure S2. Species richness in three community types as defined by the occurrence of *Pinus canariensis*. Different lower cases indicate significant differences of species richness between classes as calculated by the non-parametric Kruskal-Wallis Analysis of Variance (ANOVA) test.

Appendix 2. Description of LiDAR-based metrics derived for La Palma, Canary Islands

Prepared by CESBIO in the frame of the of ECOPOTENTIAL project

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4. Latest draft: March 15th 2017

For further details regarding processing, modelling and cal/val activities please contact the CESBIO team (mihai@tma.ro, mermozs@cesbio.cnes.fr, Alexandre.Bouvet@cesbio.cnes.fr).

Version control

Version 1	Uploaded on the ECOPTENTIAL repository (March, 15th 2017)

I. Input data

1. Remote sensing data

Point cloud tiles (214, centered at 28.7N 17.87W) from Airborne Laser Scanning (ALS) were downloaded from the Spanish National Geographic Institute (IGN, in its Spanish acronym) at http://centrodedescargas.cnig.es/CentroDescargas/buscadorCatalogo.do?codFamilia=LIDAR in compressed LAZ format (Fig. S1).

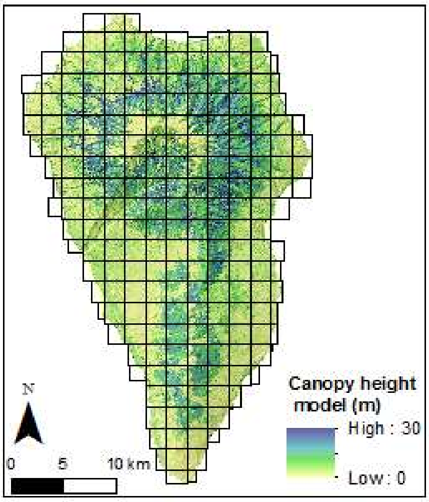

Figure S1. Extent of ALS tiles (black squares) over La Palma island.

2. In situ data

Relevant in-situ data were not available. By ‘relevant’, we mean datasets allowing for calibration and validation of LiDAR derived forest EVs, e.g. above ground biomass, canopy height, canopy cover or LAI.

II. LiDAR processing

The LiDAR data were examined for extent, point density, consistency, overlapping areas or gaps, and for the accuracy of the existing classification (Fig. S2). Several issues were noticed: i) the presence of data gaps, ii) the presence of points over sea iii) noise in shadowed areas or steep slopes, iv) overlapping flight lines and v) inaccurate point classification for the ground class. These issues were addressed as follows:

i) data gaps: no other source of ALS data was available. Therefore, two small areas of roughly 200 m by 400 m, centered at 28.5N/17.85W and 28.618N/17.844W, present gaps in the derived vegetation metrics, DEM and DSM layers. The gap size does not allow for accurate interpolation as evident when examining interpolated DEM and DSM layers. Therefore, these two areas were masked out in all layers;

ii) points over sea were eliminated using a combination of rules on height and RGB values from orthophotos, using las2las, an open source tool within the Lastools software package;

iii) noise: eliminated using a similar rule approach as for points over sea;

iv) still present in the dataset as the point clouds did not provide information on overlapping;

v) general point classification: the point classification was fairly accurate for building and vegetation classes. However, the classification does not properly differentiate between vegetation and ground points over steep slopes which resulted in flattening out most of the ridges (Fig. S3). Therefore, ground points were reclassified using the open source Multiscale Curvature Classification (MCC) algorithm (Evans and Hudak, 2007). The algorithm was designed for forested environments on rough surfaces and was proved to produce the highest success rates at identifying ground and non-ground returns for similar datasets (Montealegre et al., 2015). Depending on the tiles, different scale and curvature parameters were used. Their values were determined by iterative tests starting from the default ones. The iterative testing showed that using a scale parameter of 2 and a curvature parameter of 0.3 provides the least confusion between ground and vegetation points for most tiles. However, for 22 tiles (i.e. 214-3182, 216-3180/3182/3184, 218-3180/3182/3184/3192/3194, 220-3184, 222-3166/3190, 224-3186/3188/3190, 226-3184/3186/3188/3190 and 228-3184/3186/3188) located on the eastern slopes, the scale and curvature parameters that provide better classification results for the ground points were 1.5 and 0.4 respectively. These parameters allowed for ridges to maintain their natural shape. A combination of steep slopes, dense vegetation, low point density and flight parameters have resulted in a low number of shots hitting the ground. Ground points are therefore sparse and their interpolation inadequate when spatial resolutions below 10 m are used. As a result, the area covered by the 22 tiles presents artefacts in the high resolution DEM of 5 m. Although different tools were used to classify ground points (i.e. Fusion, MCC and Lastools), the artefacts were not completely resolved. Therefore, we advise not to use the 5 m DEM on the eastern slopes of La Palma island.

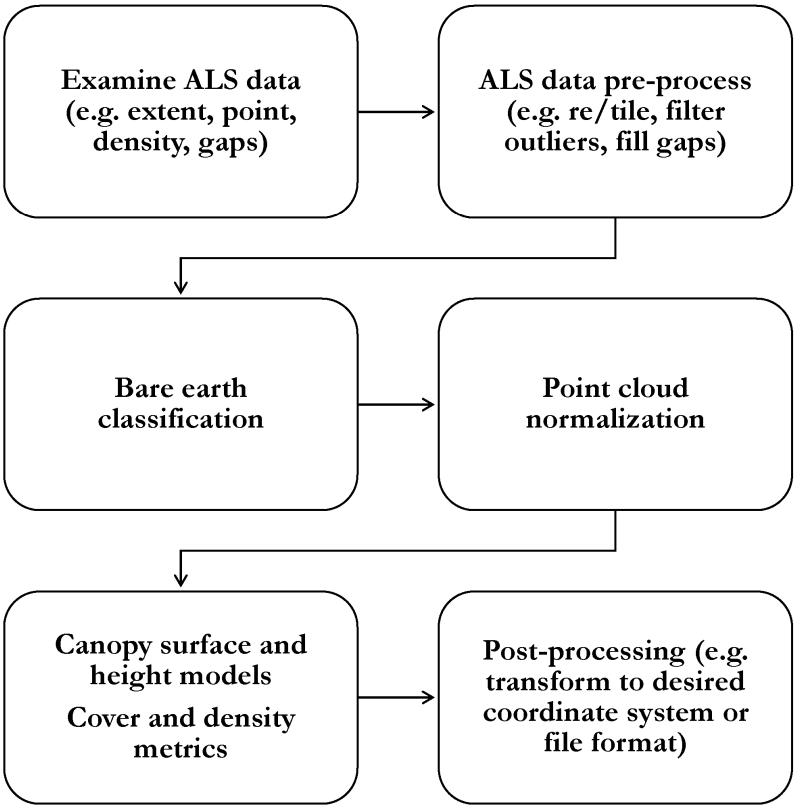

Figure S2. Flowchart of Airborne Laser Scanning (ALS) data processing and ALS-based metrics generation.

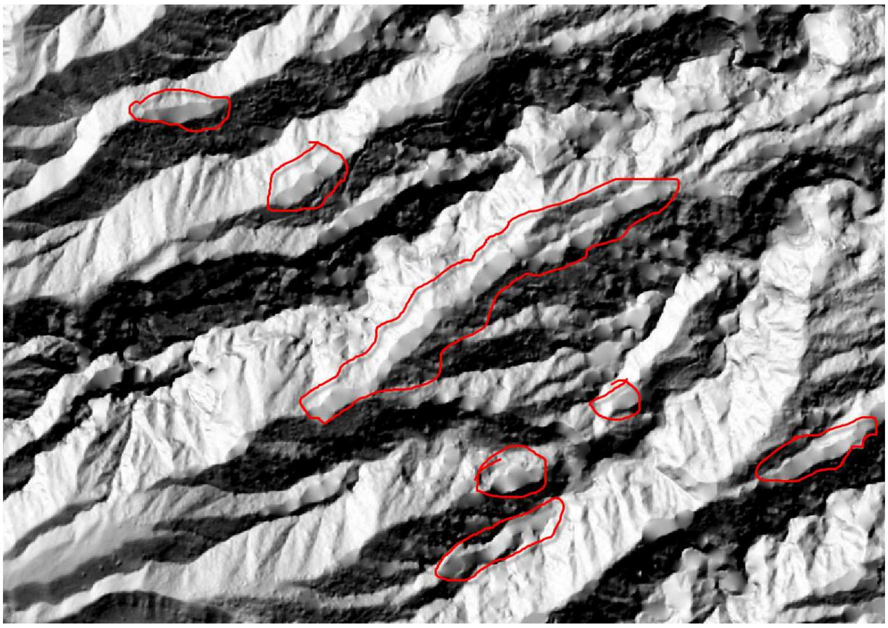

Figure S3. Flattened hill tops (circled in red) in the shaded DEM. The DEM was obtained using the original classification available in the downloaded data.

The digital elevation and surface models DEM and DSMs were interpolated in ArcGIS© at various spatial resolutions using the MCC classified ground points. The 10 m spatial resolution DEM was used to compute the height above ground (i.e. normalized height) when generating ALS-based layers characterizing forest structure (e.g., canopy height and cover). ALS-based layers where derived using the original (IGN) classification of the point cloud data to take advantage of buildings classification, which was fairly accurate. The normalized point cloud data were used to produce generic LiDAR-based metrics, e.g. canopy closure, canopy density and percentiles. Such LiDAR metrics represent proxies of forest structural characteristics and can be used with parametric or non-parametric models to derive above ground forest biomass or other structural characteristics of interest.

The LiDAR-based layers (i.e. metrics) were post-processed (i.e. masked) to eliminate areas with data gaps. A vector file showing the limits of La Palma island was used to eliminate interpolated areas around the island shore caused by the irregular patterns of available tiles. The vector file also contained the location of two areas, about 8 ha each, where data gaps in the point cloud were detected.

III. Output data

The full extent of La Palma was processed using Fusion Area Processor (AP), a suite of tools and scripts developed for large area processing. Fusion is an open software developed and maintained by the USDA Forest Service. The advantage of using AP – as compared to process individual tiles and mosaic them – is the seamless surfaces (i.e. no artifacts along border tiles) obtained through automatic buffering of the tiles. AP also offers support for multi-core processing which decreases the processing time. The metrics uploaded to the ECOPTENTIAL repository are described below. Further metrics (‘Furthermetrics.txt’, on request) were generated and are described separately (‘Gridmetrics.pdf’, on request). In addition, metrics for the following strata ('Stratametrics.txt', on request) were also computed: 0-0.5 m, 0.5-2 m, 2-5 m, 5-10 m, 10-15 m, 15-20 m, 20-25 m and >25 m. Space limitation on the ECOPTENTIAL repository impedes the storage of all these metrics. On request, these layers can be provided through other means.

Files naming: AreaName_LayerAcronymTresholds_SpatialResolution.extension

DEM: digital elevation models produced from LiDAR data.
The ALS files were re-classified using the MCC algorithm of Evans and Hudak (2007) into 'ground' and 'unassigned' points. Returns classified as 'ground' were interpolated to a raster surface at various spatial resolutions.
ALS Dataset to Raster (ArcGIS©) settings:

- Triangulation: Natural Neighbor
- Point Thinning Type: Windows Size
- Point Selection Method: Closest to Mean

Slope: slope in degree based on the above DEMs.

DSM: digital surface model based on the same LiDAR dataset as the DEM. First returns were interpolated to raster surface at various spatial resolutions. The above-mentioned ALS Dataset to Raster (ArGIS©) settings were used for interpolation.

Chm_average (i.e. canopy height model): average of normalized elevations (i.e. height above ground) within the resolution cell. Produced through Fusion AP from LiDAR point cloud data using as a reference surface the 10 m spatial resolution DEM. In areas with slopes above 50° the CHM values may exceed 60 m (i.e. the maximum height of *Pinus canariensis*) due to overhanging areas on steep slopes. Masking areas with high slopes may improve accuracy; tree type vegetation is not likely to occur on such slopes. Please notice that tree heights are generally below 30 m for all species. Pine trees above 30 m height may occur only exceptionally. Therefore, CHM values over 30 m are likely to be related to trees over steep slopes or overhanging areas and should be set to 30 m or masked out. A masking layer may be derived by combining information on slope, elevation (e.g. over 2000 m only shrub vegetation occurs) and return proportion (RP, see below) for different strata (e.g. LaPalma_RP_StrataOver25m_20m). The layer was generated for the entire island. Over developed areas, layer values correspond to infrastructure and should be masked out using an appropriate layer and/or NDVI values.

TFC (i.e. tree fraction cover in %): first returns over 2 m height divided by the total number of first returns within the resolution cell. Produced through Fusion AP from the LiDAR point cloud data using as a reference surface the 10 m spatial resolution DEM. The layer was generated for the entire island. Over developed or agricultural areas, layer values correspond to infrastructure and agriculture and should be masked out using an appropriate layer and/or NDVI values.

VF (i.e. vegetation fraction): number of all returns over 0.5 m height divided by the number of all returns within the resolution cell. Produced through Fusion AP from LiDAR point cloud data using as a reference surface the 10 m spatial resolution DEM. VF might be useful to asses cover for all vegetation types including shrubs. The layer was generated for the entire island. Over developed areas, layer values correspond to infrastructure and should be masked out using an appropriate layer and/or NDVI values.

RP (i.e. return proportion): proportion of returns from different strata with respect to the total number of returns in the resolution cell. Useful to appraise vegetation vertical structure (i.e. cover, number of strata, etc.). For percentage values, multiply with 100. The layer was generated for the entire island. Over developed areas, layer values correspond to infrastructure and should be masked out using an appropriate layer and/or NDVI values.

LAIe (i.e. effective leaf area index): computed based on the gap probability (P) as: LAIe=-ln(P). The gap probability (P) is computed as the ratio of ground returns to the total number of returns (Fieber et al., 2014). LAIe term is used to address the lack of correction for clumping effects and the presence of woody elements (Fieber et al., 2014; Fieber et al., 2016). The LAIe was set to 'no data', i.e. -9999, for pixels were no ground returns were recorded and the total number of returns was above zero. Such pixels correspond to very dense vegetation, mostly on the eastern slopes of the volcano, where shots did not reach the ground. A 30 m LAIe was also produced to reduce the presence of such pixels. Artefacts may be present in the LAIe layer particularly for the 22 tiles were the classification of the ground returns was problematic.

Notes:

- All data sets are in EPSG 4083.
- No-data areas are designated as -9999 (in *.tif files).
- Datasets covering the full extent of La Palma island were generated at various spatial resolution as indicated in the file name.
- The 5 m resolution DEM was produced to accommodate other needs, e.g. hydrological modelling. Due to the low point cloud density, such versions of the DEM may contain gaps. Please check and mask accordingly before use.
- Twenty-two tiles (see above) might present artifacts in some of the produced LiDAR metrics. These artifacts are related to the steep topography and the characteristics of the ALS flight.

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Optimizing sampling effort and information content of biodiversity surveys: a case study of alpine grassland

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ABSTRACT

Aims: Current rates of biodiversity loss do not allow for inefficient monitoring. Optimized monitoring maximizes the ratio between information and sampling effort (i.e., time and costs). Sampling effort increases with the number and size of sampling units. We hypothesize that an optimal size and number of sampling units can be determined providing maximal information via minimal effort. We apply an approach that identifies the optimal size and number of sampling quadrats. The approach can be adapted to any study system. Here we focus on alpine grassland, a diverse but threatened ecosystem.
Location: Gran Paradiso National Park, Italy.
Methods: We sampled nine 20 m × 20 m-plots. Each plot consisted of 100 2 m × 2 m-subplots. Species richness and Shannon diversity were quantified for different sizes and quantities of subplots. We simulated larger subplot sizes by unifying adjacent 2 m × 2 m-subplots. Shannon's information entropy was used to quantify information content among richness and diversity values resulting from different subplot sizes and quantities. The optimal size and number of subplots is the lowest size and number of subplots returning maximal information. This optimal subplot size and number was determined by Mood's median test and segmented linear regression, respectively.
Results: The information content among richness values increased with subplot size, irrespective of the number of subplots. Therefore, the largest subplot size available is the optimal size for information about richness. Information content among diversity values increased with subplot size if 18 or less subplots were considered, and decreased if at least 27 subplots were sampled. The subplot quantity consequently determined whether the smallest or largest subplot size available is the optimal size, and whether the optimal size can be generalized across richness and diversity. Given a 2 m × 2 m size, we estimated an optimal quantity of 54. Given a size of 4 m × 4 m, we estimated an optimal number of 36. The optimal number of plots can be generalized across both indices because it barely differed between the indices given a fixed subplot size.
Conclusions: The information content among richness and diversity values depends on the sampling scale. Shannon's information entropy can be used to identify the optimal number and size of plots that return most information with least sampling effort. Our approach can be adapted to other study systems to create an efficient in-situ sampling design, which improves biodiversity monitoring and conservation under rapid environmental change.

1. Introduction

Alpine grassland is diverse in species and equipped with various functional traits (Körner, 2003). This diversity of species and traits maintains ecosystem functions and services from which human well-being profits (Cardinale et al., 2012). Facing the rapid climate-induced

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Highlights

- The optimal sampling design provides maximal information with minimal effort.
- The optimal size/number of sampling quadrats cannot be generalized.
- Our approach is applicable to other study systems.

Abstract

Aims: Current rates of biodiversity loss do not allow for inefficient monitoring. Optimized monitoring maximizes the ratio between information and sampling effort (i.e. time and costs). Sampling effort increases with the number and size of sampling units. We hypothesize that an optimal size and number of sampling units can be determined providing maximal information via minimal effort. We apply an approach that identifies the optimal size and number of sampling quadrats. The approach can be adapted to any study system. Here we focus on alpine grassland, a diverse but threatened ecosystem.

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Conclusions: The information content among richness and diversity values depends on the sampling scale. Shannon's information entropy can be used to identify the optimal number and size of plots that return most information with least sampling effort. Our approach can be adapted to other study systems to create an efficient in-situ sampling design, which improves biodiversity monitoring and conservation under rapid environmental change.

Keywords: alpine grassland, plot size, species richness, Shannon information entropy, monitoring, sampling design

1. Introduction

Alpine grassland is diverse in species and equipped with various functional traits (Körner, 2003). This diversity of species and traits maintains ecosystem functions and services from which human well-being profits (Cardinale et al., 2012). Facing the rapid climate-induced changes of alpine plant communities (Steinbauer et al., 2018), efficient surveys and monitoring are urgently needed to explicitly inform climate-smart conservation management and policy (Rands et al., 2010). Efficient vegetation sampling represents the most ecological information that can be gathered by least sampling effort, i.e. in short time and at low costs (Stenzel et al., 2017).

Information content of ecological data is strongly dependent on temporal and spatial scales (Chave, 2013; Levin, 1992; Peterson & Parker, 1998; Rosenzweig, 1995; Storch et al., 2008; Wiens, 1989). Patterns of species diversity vary with the spatial scale of observation, with the species-area relationship being the most fundamental example (Arrhenius, 1921). Biotic drivers of species diversity generally tend to be more important at smaller scales, whereas abiotic drivers predominate at larger scales (Götzenberger et al., 2012; Schweiger & Beierkuhnlein, 2016).

In vegetation science, a single, well-founded and effective sampling design is missing so far. The disagreement on an ideal sampling design can be traced back to the fundamental question of the minimal area representing plant communities (Hopkins, 1957). In particular, the quantity, size, shape and spatial configuration of sampling units (i.e. plots) control species diversity estimates (Bacaro et al., 2015; Chiarucci et al., 2001; Dengler, 2009; Güler et al., 2016; Keeley & Fotheringham, 2005; Kenkel et al., 1989; Stohlgren, 2007). A non-directional plot shape, e.g. a quadrat, is expected to cover most phytosociological richness in homogenous stands with weak ecological gradients (Bacaro et al., 2015), but recommended quadrat sizes still vary by a factor of 10^5 (Dengler et al., 2009). Often rules of thumb are used such as the indication that plot size should be roughly proportional to vegetation height (Chytrý & Otýpková, 2003). In view of the difficulties of finding a consistent sampling design, some authors suggest to have an operational approach, with sampling scale decided on the basis of clear and repeatable criteria rather than vegetation characteristics (Chiarucci, 2007; Palmer & White, 1994).

Here we aim at identifying an optimal size and number of plots that cover the most information about species diversity with the least sampling effort. We do not analyze the relationship between sampling design and species diversity, but between sampling design and the information content among species diversity estimates. Diversity was quantified in quadratic plots of different sizes and quantities. We define the optimal size and number of plots as the smallest size and lowest quantity at which a maximum of information among species diversity values can be obtained by a minimum of sampling effort (Fig. 1). It is hypothesized that with increasing plot size and quantity information content first increases and then levels off, following the causation of the species-area relationship (Turner & Tjørve, 2005): an increasing sampling area expressed by increasing plot size or quantity means that a higher relative proportion of diversity is recorded that would result in an increasing redundancy among diversity values. Information content consequently levels off. Sampling effort is basically determined by the number and size of plots. The more and the larger the plots are, the higher is the sampling effort in terms of time and costs. As a case study, we sampled alpine grassland communities. We used Shannon's information entropy as a measure of information content captured in diversity metrics. Two fundamental metrics of biodiversity were applied that express different types of information: species richness and Shannon diversity, which integrates species richness and abundance). To our knowledge, information entropy has not been used like this before, but see Bogaert et al. (2005) for an entropy-based analysis of landscape fragmentation or Turner et al. (1989) describing a rapid loss of information for rare and dispersed land cover types with increasing sampling size. We applied a methodological approach that can be easily adapted to any study system. This makes our investigation of general interest for ecologist and conservationists.

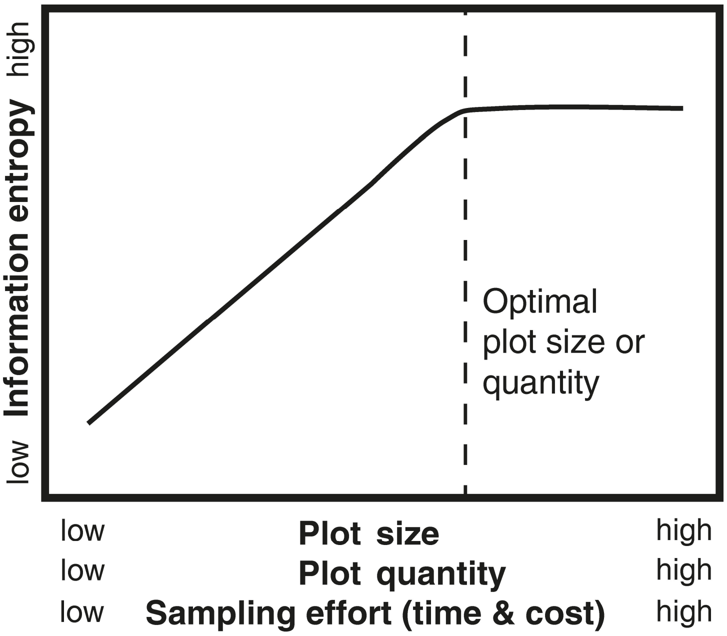

Figure 1. Theoretical background to identify the optimal size and number of sampling plots. The plot size and quantity determines the sampling effort because the size and number of plots mainly determines the time and financial ressources needed for sampling. The optimal plot size or quantity retrieves a maximum of information content by minimal sampling effort.

2. Methods

2.1. Study area and sampling design

The study area is located in the Gran Paradiso National Park in north-western Italy (Fig. 2a). This alpine environment is characterized by low human impact due to the long history of protection. The sampling covers three vegetation subtypes of alpine grassland that were identified with the support of the CORINE Land Cover map from 2012 (available at https://land.copernicus.eu/pan-european/corine-land-cover) and expert knowledge: 'pure' natural grassland, sparsely vegetated 'rocky' grassland (i.e. on rocks, scree or gravel) and 'wet' grassland (i.e. wetlands). Each vegetation subtype was sampled in three valleys (i.e. Bardoney, Colle de Nivolet and Levionaz) between 2200 and 2700 meters a.s.l. (Fig. 2b), which resulted in one plot per vegetation subtype and valley. Hence, nine plots were sampled in total.

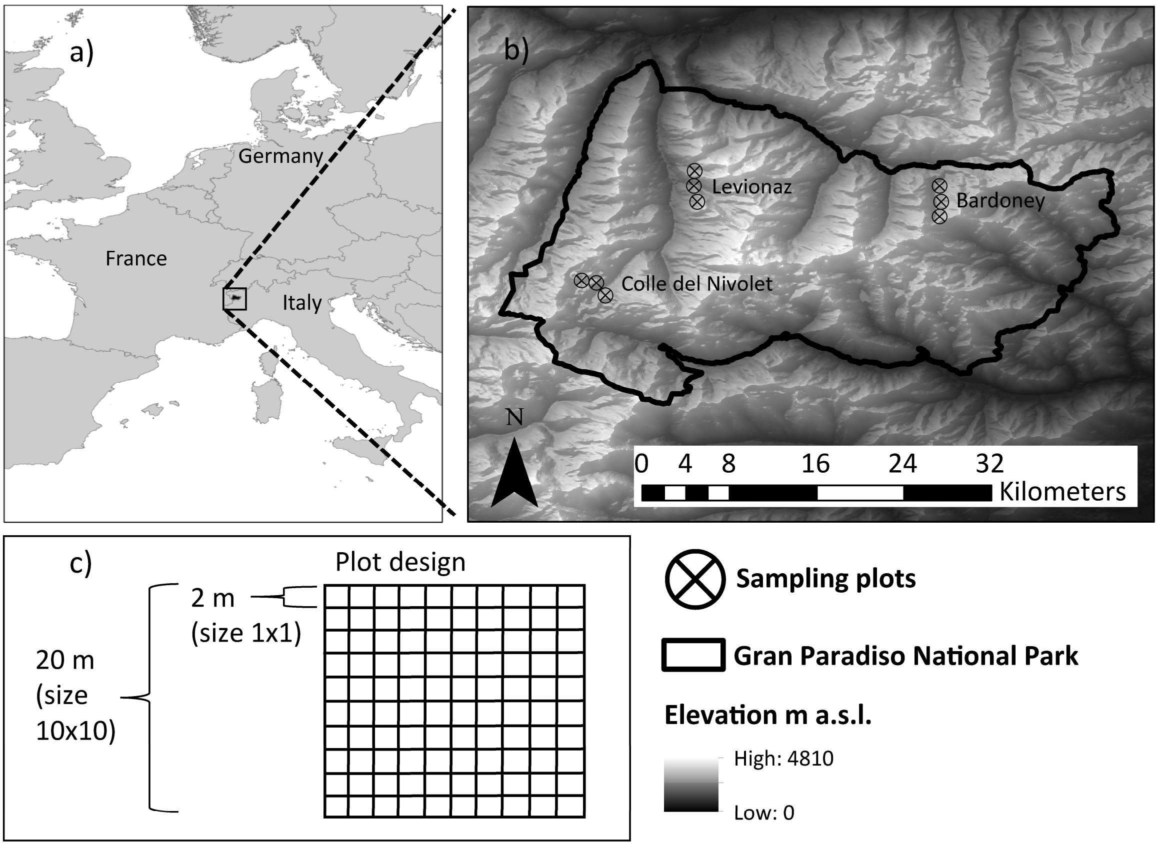

Figure 2. Geographical location of the study area. a) Gran Paradiso National Park is located in the European Alps, north-western Italy. b) Nine sampling plots were established, three in each of the three alpine grassland subtypes inside each of three valleys (i.e. Colle del Nivolet, Levionaz and Bardoney). c) The sampling plot was designed as a 20 m x 20 m quadratic square (i.e. size 10x10), subdivided into 100 subplots of 2 m x 2 m (i.e. size 1x1). Different plot sizes from 1x1 to 10x10 were simulated by unifying adjacent 2 m x 2 m-subplots.

We applied quadrats because we did not observe strong ecological gradients at any plot location (Bacaro et al., 2015). Quadrats mitigate the confounding effect of environmental heterogeneity on species diversity (Dengler, 2008). The plots were established on flat terrain. Each of the nine plots had an extent of 20 m x 20 m (i.e. 400 m^2) and was subdivided into 100 subplots measuring 2 m x 2 m (Fig. 2c). The percentage cover (i.e. abundance) of each plant species including mosses and lichens was estimated for each subplot. Cover estimates reflect the mean of two independent estimates by two people to reduce observer bias (Klimeš, 2003). The vegetation survey was conducted at the peak of the yearly vegetation development during August 2015. Species were identified using 'Flora Helvetica' (Lauber & Wagner, 1998), 'Flora Vegetativa' (Eggenberg & Möhl, 2009), 'Flora Alpina' (Aeschimann et al., 2004) and 'Guida alla flora della Valle d'Aosta' (Bovio et al., 2008).

2.2. Species diversity indices

The first fundamental measure of diversity that we applied is species richness *R*. The second index is the Shannon diversity index (Shannon, 1948), which incorporates species richness and abundance. The non-exponential version with the natural logarithm, which we used, is given by formula 1:

$$(1)\ H = -\sum_{i=1}^{R} p_i ln(p_i)$$

The number of species is given by *R* and the relative abundance of the *i*th species by p_i. The Shannon diversity *H* quantifies the uncertainty of selecting any species from the plot by chance. The Shannon diversity is maximal when each species within a plot is equally abundant. Here the percentage cover of each species was used as a measure of the relative abundance because the number of individuals cannot be recorded for clonal plants without destruction. Plants with a cover of less than 1% were set to 0.5% cover for simplification of statistical analyses. Species-specific mean cover was used to calculate the Shannon diversity *H*. We used the diversity-function within R package 'vegan' (Oksanen et al., 2018) to calculate the Shannon diversity *H*.

2.3. Shannon's information entropy of species diversity indices

Information theory, which Shannon's information entropy is an integral part of, is widely applied in the scientific fields of mathematics, statistics and system dynamics. The seminal work of Shannon (1948) has gained broad application in these fields and is widely applied in ecology as a metric of species diversity (see section 2.2). Shannon's information entropy is a central concept of information theory. It quantifies the amount of information given by a number of entities (Shannon, 1948). Information entropy increases with decreasing redundancy among entities. Ecologists and conservationists prefer to apply the size and number of sampling plots that provide most information about species diversity. If information entropy saturates with plot size and quantity, the smallest size and lowest number of plots would be preferred that still provide most information (Fig. 1) because sampling effort in terms of time and costs increases with the number and size of plots.

The Shannon's information entropy *H* is originally calculated by formula 2 including the common logarithm to base 10 instead of the natural logarithm (formula 1):

$$(2)\ H = -\sum_{i=1}^{R} p_i log(p_i)$$

with p_i being the frequency of occurrence of entity *i* of *R* unique entities. Shannon's information entropy was derived from the idea to quantify information content given by letters (i.e. entities) within a text message. Shannon species diversity incorporates species abundances instead of letter abundances. Here we used the different values of a diversity index (i.e. species richness or Shannon diversity) as entities *i*. The value of entropy, i.e. information content, depends on the number of unique entities (e.g. letters, species or unique values of a diversity index) and their frequencies of occurrence. Entropy is positive and will maximize if the abundance of each entity (e.g. a unique index value) is equal.

With increasing decimal digits of the values of diversity indices, less equal index values may be found and entropy increases, inducing bias. Since the measurement accuracy of species cover was limited to the accuracy of 2 decimal digits (e.g. 25%), we considered 2 decimal digits to be a reasonable measurement accuracy throughout the entire entropy analysis. Furthermore, the absolute values of information entropy cannot be directly compared between different diversity indices because of the different scaling of indices.

For valid comparison, which is not the intention of this study, metrics must be standardized before computing information entropy. The entropy was calculated using the entropy-function in R-package 'entropy' (Hausser & Strimmer, 2014).

2.4. Simulating plot size and quantity

First, to analyze the relationship between the information entropy of diversity indices and the plot size, we unified adjacent 2 m x 2 m (i.e. 1x1) subplots within the 20 m x 20 m (10x10) plot to simulate larger subplots sizes. Subplot sizes from 1x1 (2 m x 2 m) to 10x10 (20 m x 20 m) were considered. Accordingly, the largest subplot size of 10x10 unified 100 gridded 1x1-subplots. The larger the simulated subplot size, the less subplot-unions *n* exist that unified adjacent 1x1-subplots to a larger subplot size. For a subplot size of 2x2, *n*=81 different quadratic subplots could be generated within the 10x10-plot; *n*=64 for 3x3, *n*=49 for 4x4, *n*=36 for 5x5, *n*=25 for 6x6, *n*=16 for 7x7, *n*=9 for 8x8, *n*=4 for 9x9 and *n*=1 for 10x10.

We calculated the information entropy *H* of a given diversity index and subplot size on the basis of *m*9* randomly selected subplots, i.e. *m* from each of the nine 10x10-plots. By varying *m,* we simulated different numbers of sampled subplots. We only selected the subplot-unions within a 10x10-plot that do not share any 1x1-subplot to guarantee independent values for the entropy calculation. Accordingly, max(*m*) equals 100 for subplot size 1x1; max(*m*)=25 for 2x2, max(*m*)=9 for 3x3, max(*m*)=4 for 4x4 and 5x5, and max(*m*)=1 for 6x6, 7x7, 8x8, 9x9 and 10x10. Furthermore, given *n* subplot-unions within a 10x10-plot, there are $\prod_{k=0}^{m-1}(n-k)^9$ possibilities to combine *m* subplots from each of the nine 10x10-plots. We consequently repeated this random subplot selection procedure 10,000 times to represent an appropriate proportion of the number of possible combinations. However, repetitions of the random selection procedure were not necessary for subplot size 1x1 and *m*=100, for 2x2 and *m*=25, and for 5x5 and *m*=4, because these configurations already incorporated all independent subplot-unions available within a 10x10-plot by one single selection run. We finally computed 10,000 entropy values for each diversity index (i.e. species richness and Shannon diversity), for each subplot size (i.e. from 1x1 to 10x10) and for varying *m*: from *m*=1 to *m*=24 as well as for *m*=30, *m*=36, *m*=42, *m*=48, *m*=60, *m*=72, *m*=84, *m*=96 and *m*=99; we did not calculate entropy values of subplot size 1x1 for all subplot quantities *m* due to long computation times. Each of the 10,000 entropy values were thus calculated on the basis of *m*9* values (i.e. entities) of a diversity metric (i.e. species richness or Shannon diversity).

The effect of the spatial dispersion of sampling units onto sampling outcomes is often neglected (but see Chiarucci et al., 2009; Dengler & Oldeland, 2010). The larger the spatial area of sampling units becomes or the larger the distance between sampling units is (i.e. extent across sampling units), the more species will be detected due to the distance-decay of similarity between species communities (Steinbauer et al., 2012). We accounted for the effects of the species-area relationship (Dengler, 2008) and the species-extent relationship (Güler et al., 2016) on the sampling results by randomly selecting a given number of subplot *m* from each of nine plots that cover a constant area and extent. We also repeated this probabilistic sampling procedure 10,000 times to take the large variety of available subplot combinations into consideration.

2.5. Statistical analyses

To identify the optimal subplot size for a given number of subplots, we compared the 10,000 entropy values between subplot sizes via Mood's median test (i.e. pairwiseMedianTest-function in R package 'rcompanion'; Mangiafico, 2016). The optimal number of subplots for a given subplot size was quantified using breakpoint analyses via piecewise regression. The segmented-function inside R-package 'segmented' (Muggeo, 2003) was used to apply piecewise regression to the 5th, 50th and 95th-percentiles of the entropy distributions. The segmented linear regression fits two separate yet contiguous linear regression lines to the sampling points before and after an estimated breakpoint, which is based on the maximum likelihood of model parameterization. The breakpoint analyses onto the 5th, 50th and 95th-percentiles provided a confidence interval for the median breakpoint. As mentioned above, we did not calculate entropy values of subplot size 1x1 for all subplot quantities *m* due to long computation times. However, breakpoint estimation is sensitive to the amount of points involved. To include the entire range of *m* from 1 to 99, we applied breakpoint analysis for subplot size 1x1 onto predicted entropy values from a local polynomial regression model (i.e. loess-function in R-package 'stats'; R Development Core Team, 2016). The local regression model precisely fitted a regression line onto the points. Each subplot *m* from 1 to 99 could thus be related to an accurately predicted entropy value. These predicted entropy values were then used to detect the breakpoint along the relationship between the predicted entropy values and the subplot quantities *m*. The R-code is given in the appendix. The dataset is stored at the Dynamic Ecological Information Management System - Site and Dataset Registry (DEIMS-SDR; Wohner et al., 2019) under the UUID b549ff14-f40f-4749-8e2f-f16f6e523753 (see https://deims.org/dataset/b549ff14-f40f-4749-8e2f-f16f6e523753).

3. Results

3.1. Species richness and Shannon diversity

Species assemblages within the plots were generally representative for alpine grasslands, but specific dominance and abundance patterns were observed in the three valleys and vegetation subtypes. At Bardoney, pure grasslands were dominated by *Nardus stricta*, *Trifolium alpinum* and *Carex curvula*, whereas the wetlands were dominated by *Nardus stricta*, *Carex bicolor* and *Salix herbacea*. At Colle del Nivolet, *Oxytropis helvetica* was the dominating species in the rocky subtype along with *Silene acaulis* and *Festuca alpina*, whereas the most abundant species in the pure grassland were *Anthoxanthum alpinum*, *Carex curvula* and *Geum montanum*. In the wetlands, *Carex nigra*, *Eriophorum scheuchzeri* and *Eleocharis quinqueflora* were occurring the most. The rocky plot in Levionaz was dominated by *Salix breviserrata*, *Plantago alpina* and various grasses. *Plantago alpina* was abundant in the pure grassland along with *Festuca melanopsis* and *Hieracium pilosella agg.* The wetlands were dominated by *Carex flacca* and five moss species.

Species richness and Shannon diversity of the 1x1-subplots considerably varied within and between the nine 10x10-plots (Fig. 3). Among all nine plots, 247 plant species were recorded. Herbaceous plants were most prominent, comprising 180 species. Up to 50 species of plants were recorded per 10x10-plot. A maximum of 33 species was recorded inside a single 1x1-plot of pure grassland in the Levionaz valley (Fig. 3a); a minimum of three species was identified inside a single 1x1-plot in the wetland of the Colle del Nivolet valley. The Shannon diversity did not necessarily increase with species richness (Fig. 3b); species can be unequally abundant, compensating the positive effect of species richness on Shannon diversity.

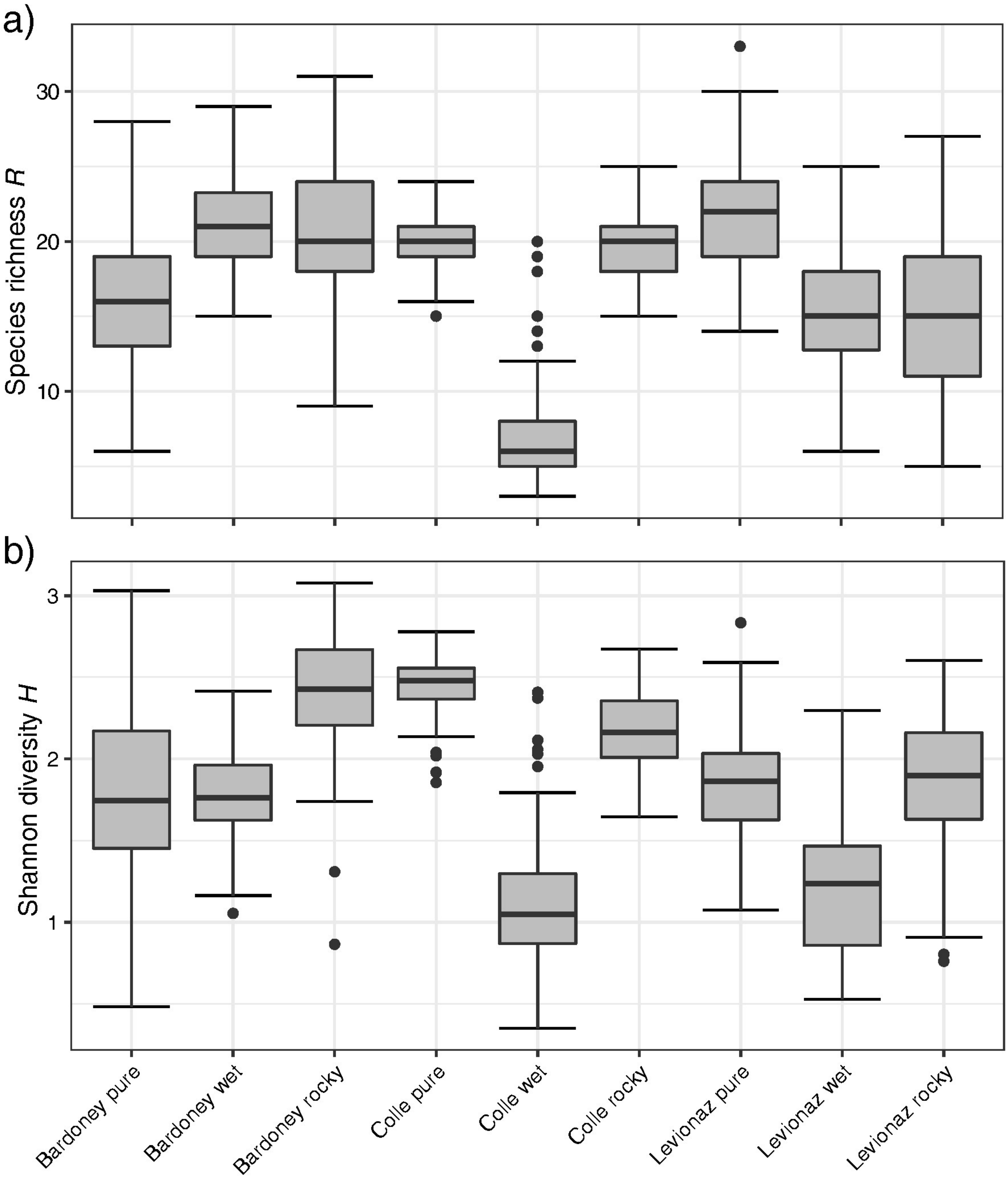

Figure 3. Species diversity within and between the nine 10x10-plots. a) Species richness *R* and b) Shannon diversity *H* of individual 1x1-subplots considerably varied among the three vegetation subtypes (i.e. pure, wet and rocky) and valleys (i.e. Bardoney, Colle del Nivolet and Levionaz). The horizontal black line within the grey box represents the median. The grey box ranges from the 1st to the 3rd quartile. The upper whisker delimits the 3rd quartile plus 1.5 times the interquartile distance (3rd quartile – 1st quartile). The lower whiskers mark the 1st quartile minus 1.5 times the interquartile distance.

3.2. Information entropy and subplot size

The information entropy of species richness *R* generally increased with increasing subplot size irrespective of the number of subplots considered (Fig. 4a). When nine subplots were considered in total (*m*=1, Fig. 4a), the information entropy between subplot sizes 4x4 and 7x7 became similar; increasing subplot size did not necessarily increase the information entropy within this range of subplot sizes. For all other *m*, the entropy significantly increased with growing subplot size.

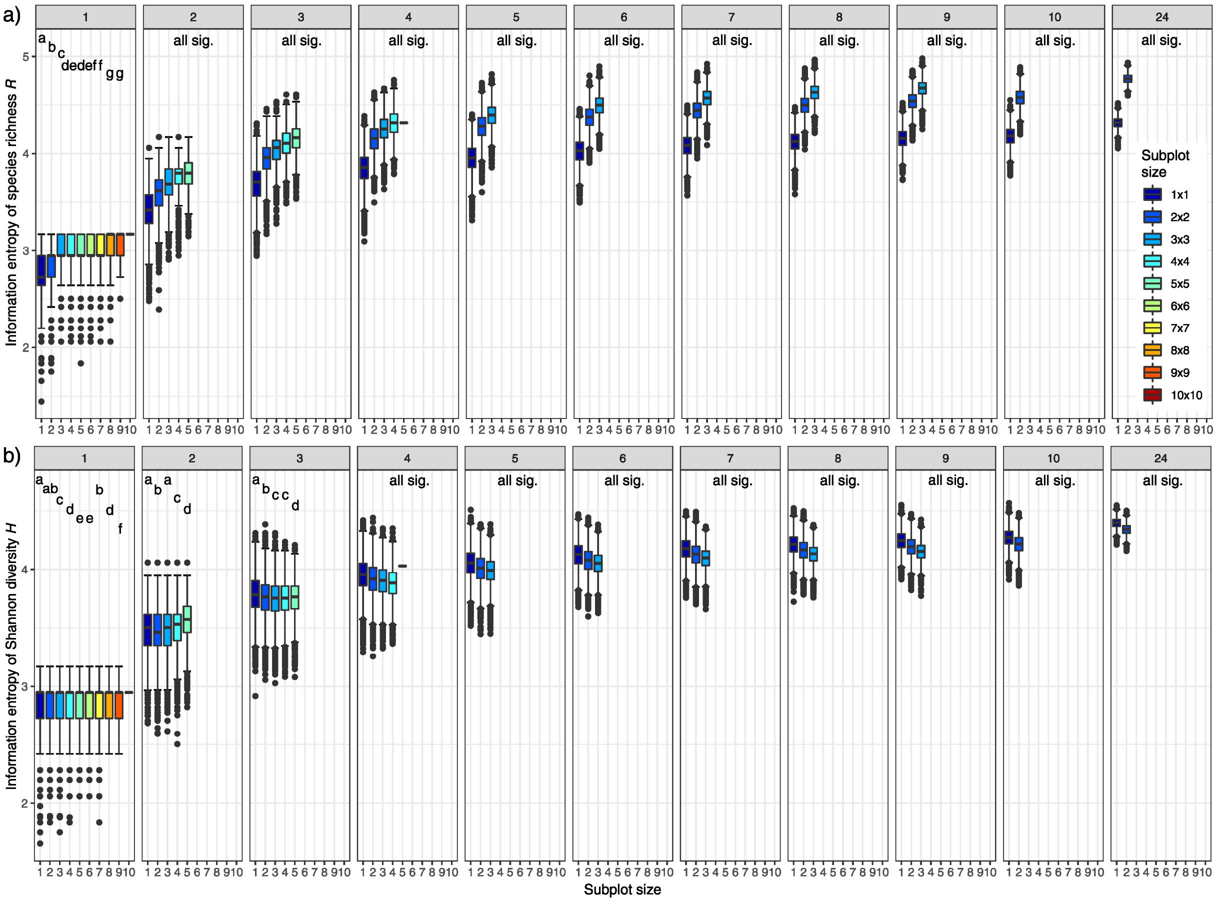

Figure 4. Information entropy versus plot size given a constant number of plots. In a) Shannon's information entropy of species richness *R* was seperately calculated for different quantities of subplots *m* (i.e. number inside grey boxes) that were randomly selected from each of the nine 10x10-plots. This random selection procedure was repeated 10,000 times, so that 10,000 entropy values were calculated per subplot size for a given constant number of subplots; see Methods section for details. In b) Shannon's information entropy of the Shannon diversity *H* was calculated; boxplots as in Fig. 3. The letters illustrate significant differences ($p<0.05$) between entropy distributions using Mood's median test. 'All sig.' indicates that all entropy distributions are significantly different from each other. For the subplot size 1x1 and *m*=100 and for 5x5 and *m*=4, repetitions of the random selection procedure were not reasonable because these configurations already incorporated all independent subplot-unions available within a 10x10-plot by one single selection run. They were excluded from Mood's median test.

The information entropy of Shannon diversity *H* increased with subplot size (Fig. 4b), but only for *m*≤2. For *m*=1, the entropy formed again a plateau along intermediate subplot sizes. For *m*=2, the entropy marginally varied between subplot size 1x1 and 3x3. For m≥3, however, the relationship between entropy and subplot size changed from positive to negative; the information entropy then decreased with increasing subplot size. For m≥4, the information entropy was significantly different between all subplot sizes.

3.3. Information entropy and subplot quantity

For the subplot sizes 1x1 and 2x2, the relationship between information entropy and the number of subplots showed a saturating behavior with an increasing number of subplots (Fig. 5). Concerning the information entropy of species richness *R* and subplot size 1x1 (Fig. 5a), the segmented regression analyses determined a median breakpoint of *m*=5.5 (95%-confidence interval: 5.1-5.8), a 5th-percentile breakpoint of *m*=7.4 (6.9-7.9) and a 95th-percentile breakpoint of *m*=5.3 (5.0-5.6). We estimated a median breakpoint of *m*=6.3 (5.9-6.7), a 5th-percentile breakpoint of *m*=6.4 (6.0-6.8) and a 95th-percentile breakpoint of *m*=4.5 (4.2-4.8) for the information entropy of Shannon diversity *H* and subplot size 1x1 (Fig. 5b). The segmented regression resulted in a median breakpoint of *m*=4.4 (3.9-4.8), a 5th-percentile breakpoint of *m*=4.4 (4.0-4.9) and a 95th-percentile breakpoint of *m*=3.5 (3.1-3.9) for the information entropy of species richness *R* and subplot size 2x2 (Fig. 5c). For the information entropy of Shannon diversity *H* and subplot size 2x2 (Fig. 5d), we calculated a median breakpoint of *m*=4.3 (3.9-4.7), a 5th-percentile breakpoint of *m*=4.3 (3.9-4.7) and a 95th-percentile breakpoint of *m*=3.3 (3.1-3.6). In a nutshell, we estimated a median subplot quantity of 6 across the diversity metrics after which information entropy of subplot size 1x1 leveled (Fig. 5a, b). For the subplot size 2x2, we estimated a median subplot quantity of 4 across both indices (Fig. 5c, d).

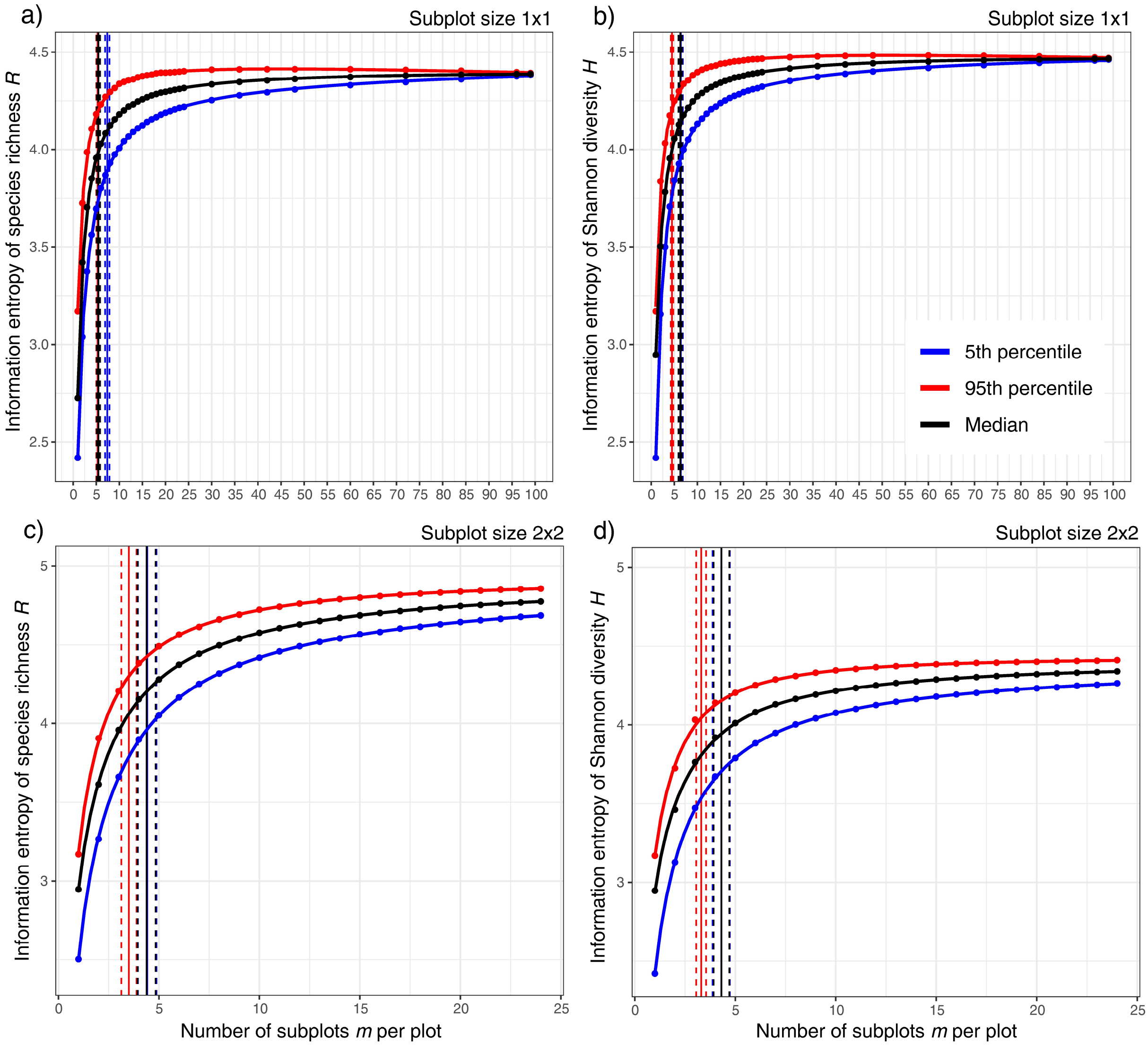

Figure 5. Information entropy versus plot quantity given constant plot size. a) The information entropy of species richness *R* given the subplot size 1x1. b) The information entropy of Shannon diversity *H* given the subplot size 1x1. c) The Information entropy of species richness *R* given the subplot size 2x2. d) The information entropy of Shannon diversity *H* given the subplot size 2x2. The curves show the local polynomial regression fits. The solid vertical lines indicate the estimated breakpoints while the stippled vertical lines span the 95%-confidence interval of those breakpoints. The 5^{th} percentile is shown in blue, the median in black and the 95^{th} percentile in red. For the subplot size 1x1 and *m*=100, and for 2x2 and *m*=25, repetitions of the random selection procedure were not reasonable because these configurations already incorporated all independent subplot-unions available within a 10x10 plot in one single selection run.

4. Discussion

As hypothesized, information content levels off with an increasing number of subplots for both diversity indices and subplot sizes, i.e. 1x1 and 2x2. Accordingly, the shape of the relationship between the information entropy and the plot quantity might be universal across plot sizes and diversity indices. In our study on alpine grassland, 54 (i.e. 6 from each of the nine 10x10-plots) was estimated to be the optimal number of 1x1-plots that cover the most information about species richness and diversity values by the minimal sampling effort. Regarding 2x2-plots, 36 (i.e. 4 from each of the nine 10x10-plots) was the optimal number of plots. Interestingly, the optimal plot quantity did not differ between the species richness and diversity indices. The optimal number of plots can consequently be generalized across both indices given a constant plot size of 1x1 or 2x2.

In contrast to our hypothesis, the information entropy did not show such saturating behavior with an increasing plot size when keeping the number of plots constant. The information content of the richness estimates clearly increased with increasing plot size. The optimal plot size in terms of richness information is therefore the largest plot size that was considered, i.e. 9x9. However, the information content among richness values did not considerably change between the intermediate plot sizes from 4x4 to 7x7. In other words, information contents significantly differed between the extremely small and between the extremely large plot sizes. Consequently, the smaller plot sizes do not necessarily provide more information about species richness. This is all the more relevant as mistakes in species sampling have a stronger impact at small plot sizes with less species diversity (Klimeš et al., 2001). Moreover, the amount of information covered by the diversity estimates increased with an increasing plot size up to 18 plots (i.e. 2 subplots were taken from each of the nine 10x10-plots), but decreased if more than 27 plots were considered (i.e. 3 subplots were taken from each of nine 10x10-plots). Hence, the number of plots determines whether the smallest or largest available plot size is the optimal size for information about diversity. A trade-off between the optimal plot size and quantity has been detected regarding information obtainable about diversity. Turner et al. (1989) showed that information content on the diversity of land cover types grows with an increasing spatial resolution of sampling units. Since this study partly confirms our findings, the general shape of the information-plot scale relationship might be consistent across study objects, e.g. species or land cover types. Our results, however, indicate that the relationship between information entropy and plot size, given constant plot quantity, is not universal across plot quantities and diversity indices. The optimal plot size for any given number of plots cannot be generalized across both diversity indices. The optimal plot size seems to depend on the number of plots considered and the diversity index applied.

Differences in the scaling of information content with plot size and quantity are driven by various factors. These include the spatial configuration of sampling units (Bacaro et al., 2015; Güler et al., 2016; Schweiger et al. 2016), dispersal mechanisms (Dengler, 2008), species density effects (Condit et al., 1996) and small-scale heterogeneity of environmental conditions (Dengler, 2008). Even at the local scale, species diversity increases with increasing distance between sampling units because habitats and environmental conditions are expected to become more similar with decreasing distance (Chiarucci et al., 2009; Dengler, 2008, 2009; Kunin, 1997; Stohlgren, 2007). Species richness also increases with decreasing dispersal limitations (Hubbell, 2001). Therefore, it is not guaranteed that our findings are true for other systems of similar diversity levels because resource availability (Olszewski, 2004; Ugland et al., 2003; Wilson & Gitay, 1995) and population dynamics (Pannell, 2012) may idiosyncratically control the spatial distribution of species abundances at small scales. In addition, regional species pool sizes may differ, which causes differences in the proportion of the pool that can be detected by local sampling units (Chao & Jost, 2012).

We additionally highlight that measuring species' abundances (i.e. cover) delivers much more information about species diversity as opposed to using species richness only (Gosselin, 2006). The shape of the relationships between information content and plot size differed between both diversity metrics, given any constant number of plots (Fig. 4). The reason for this is that the species richness index weighs all species equally. Species richness responds equally to each additional species occurring, even if species have very low cover (Stohlgren, 2007). Abundance-based measures are less sensitive to rare species whose relative coverage is marginal. Recording species richness only may be less laborious, but Shannon diversity offers additional information about species diversity by incorporating species abundances. We therefore recommend to record species abundances, especially when it comes to monitoring community composition. Because time and funds are limited for conservation management, surveys and monitoring programs should be conducted that maximize the probability of recording most species diversity with least sampling effort (Abella & Covington, 2004). Comprehensive conservation action should always be informed by a variety of diversity metrics since different metrics represent different conservation values that are given by areas of conservation concern (Hoffmann, Beierkuhnlein et al., 2018).

Our sampling design is restricted to a particular spatial configuration and shape of sampling units. Since the spatial configuration and shape of plots control the species diversity that is sampled (Bacaro et al., 2015; Güler et al., 2016; Schweiger et al., 2016), information entropy of diversity estimates may be affected by the plot shape and spatial arrangement. Moreover, assuming the nine 10x10-plots (i.e. an area of 3600 m^2) well represent the regional diversity of alpine plant communities, this study provides first estimates of the optimal plot size and number, to sample alpine grassland at a regional extent. Nevertheless, it is desirable to enlarge the study area, extent and plot scale towards larger plots and smaller subplots, in order to prove our results for alpine grassland in general. The optimal sampling design ultimately depends on the study objectives (Bacaro et al., 2015; Baffetta et al., 2007; Yoccoz et al., 2001). While we focused on the information about local diversity (i.e. alpha diversity sensu Whittaker, 1972) in alpine grassland of the regional extent, a general assessment of the information-scale relationship should consider different scales from local to global, biotic units, information types (e.g. differentiation diversity sensu Jurasinski et al. [2009]) and study objects (e.g. plant functional traits) - such as Whittaker et al. (2001) for the diversity-scale relationship. More data points will allow for a more accurate assessment of the optimal plot size and quantity by more sophisticated methods such as change point analyses (Killick & Eckley, 2014). However, due to the general fact that species diversity is monotonically increasing with sampling area, Hopkins (1957) already concluded that a minimal area representing maximal diversity is unlikely to exist for any vegetation type. It remains an open question whether this is true for information content.

5. Conclusion

Understanding the scale-dependence of information content of diversity metrics is crucial for efficient research, monitoring and conservation programs, especially for alpine ecosystems vulnerable to rapid environmental changes. An optimal sampling design should always be considered for reasons of temporal and financial efficiency. Apart from that, an optimal in-situ sampling design may also improve biodiversity assessment via Earth observation technique (Hoffmann, Schmitt et al., 2018): small-scale in-situ information can be projected to larger extents on the basis of remote sensing data with relatively low effort (Stenzel et al., 2017).

The information content among species diversity estimates is scale-dependent as we demonstrated for alpine grassland at a regional extent. Our approach can be adapted to other study systems. Nevertheless, for some diversity indices and plot quantities, a clear saturation of information content with increasing plot size might not emerge. In such cases, the smallest or largest plot size is the optimal one. The generality of our results is restricted to a single vegetation type, a particular sampling design, two diversity metrics, and a limited study area and extent. Hence, research on the scale-dependence of information entropy still offers great potential.

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Appendix

```
# R code to Hoffmann et al., Ecological Informatics: Optimizing sampling effort and
information content of biodiversity surveys: a case study of alpine grassland #

# Load packages
library(vegan)
library(entropy)
library(ggplot2)
library(colorRamps)
library(rcompanion)
library(segmented)

# Load plot x species matrix
data <- read.csv("Subplot_Data.csv")

# Remove first two columns containing plot name and subplot IDs
data <- data[,-c(1,2)]

# Separate the nine 10x10-plots
plot_1 <- data[1:100,]
plot_2 <- data[101:200,]
plot_3 <- data[201:300,]
plot_4 <- data[301:400,]
plot_5 <- data[401:500,]
plot_6 <- data[501:600,]
plot_7 <- data[601:700,]
plot_8 <- data[701:800,]
plot_9 <- data[801:900,]


# Generate subplot-unions inside the 10x10-plot for different subplot sizes
so_ids <- matrix(1:100, 10, byrow=T) # 1x1-subplot IDs within the 10x10-plot

# 1x1-subplot unions
subplot_unions_1x1 <- matrix(1:100,100,1)

# 2x2-subplot unions
subplot_unions_2x2 <- matrix(NA,0,4)

for (i in 1:9){
  for (j in 1:9){
    subplot_unions_2x2 <- rbind(subplot_unions_2x2,
                                  c(so_ids[i,j], so_ids[i,j+1],
                                    so_ids[i+1,j], so_ids[i+1,j+1]))
  }
}

# 3x3-subplot unions
subplot_unions_3x3 <- matrix(NA,0,9)

for (i in 1:8){
  for (j in 1:8){
    subplot_unions_3x3 <- rbind(subplot_unions_3x3,
                                  c(so_ids[i,j], so_ids[i,j+1], so_ids[i,j+2],
                                    so_ids[i+1,j], so_ids[i+1,j+1],
so_ids[i+1,j+2],
                                    so_ids[i+2,j], so_ids[i+2,j+1],
so_ids[i+2,j+2]))
  }
}

# 4x4-subplot unions
subplot_unions_4x4 <- matrix(NA,0,16)

for (i in 1:7){
  for (j in 1:7){
    subplot_unions_4x4 <- rbind(subplot_unions_4x4,
                                  c(so_ids[i,j], so_ids[i,j+1], so_ids[i,j+2],
so_ids[i,j+3],
                                    so_ids[i+1,j], so_ids[i+1,j+1],
so_ids[i+1,j+2], so_ids[i+1,j+3],
                                    so_ids[i+2,j], so_ids[i+2,j+1],
so_ids[i+2,j+2], so_ids[i+2,j+3],
                                    so_ids[i+3,j], so_ids[i+3,j+1],
so_ids[i+3,j+2], so_ids[i+3,j+3]))
  }
}
```

```
# 5x5-subplot unions
subplot_unions_5x5 <- matrix(NA,0,25)

for (i in 1:6){
  for (j in 1:6){
    subplot_unions_5x5 <- rbind(subplot_unions_5x5,
                                   c(so_ids[i,j], so_ids[i,j+1], so_ids[i,j+2],
so_ids[i,j+3], so_ids[i,j+4],
                                     so_ids[i+1,j], so_ids[i+1,j+1],
so_ids[i+1,j+2], so_ids[i+1,j+3], so_ids[i+1,j+4],
                                     so_ids[i+2,j], so_ids[i+2,j+1],
so_ids[i+2,j+2], so_ids[i+2,j+3], so_ids[i+2,j+4],
                                     so_ids[i+3,j], so_ids[i+3,j+1],
so_ids[i+3,j+2], so_ids[i+3,j+3], so_ids[i+3,j+4],
                                     so_ids[i+4,j], so_ids[i+4,j+1],
so_ids[i+4,j+2], so_ids[i+4,j+3], so_ids[i+4,j+4]))
  }
}

# 6x6-subplot unions
subplot_unions_6x6 <- matrix(NA,0,36)

for (i in 1:5){
  for (j in 1:5){
    subplot_unions_6x6 <- rbind(subplot_unions_6x6,
                                   c(so_ids[i,j], so_ids[i,j+1], so_ids[i,j+2],
so_ids[i,j+3], so_ids[i,j+4], so_ids[i,j+5],
                                     so_ids[i+1,j], so_ids[i+1,j+1],
so_ids[i+1,j+2], so_ids[i+1,j+3], so_ids[i+1,j+4], so_ids[i+1,j+5],
                                     so_ids[i+2,j], so_ids[i+2,j+1],
so_ids[i+2,j+2], so_ids[i+2,j+3], so_ids[i+2,j+4], so_ids[i+2,j+5],
                                     so_ids[i+3,j], so_ids[i+3,j+1],
so_ids[i+3,j+2], so_ids[i+3,j+3], so_ids[i+3,j+4], so_ids[i+3,j+5],
                                     so_ids[i+4,j], so_ids[i+4,j+1],
so_ids[i+4,j+2], so_ids[i+4,j+3], so_ids[i+4,j+4], so_ids[i+4,j+5],
                                     so_ids[i+5,j], so_ids[i+5,j+1],
so_ids[i+5,j+2], so_ids[i+5,j+3], so_ids[i+5,j+4], so_ids[i+5,j+5]))
  }
}

# 7x7-subplot unions
subplot_unions_7x7 <- matrix(NA,0,49)

for (i in 1:4){
  for (j in 1:4){
    subplot_unions_7x7 <- rbind(subplot_unions_7x7,
                                   c(so_ids[i,j], so_ids[i,j+1], so_ids[i,j+2],
so_ids[i,j+3], so_ids[i,j+4], so_ids[i,j+5], so_ids[i,j+6],
                                     so_ids[i+1,j], so_ids[i+1,j+1],
so_ids[i+1,j+2], so_ids[i+1,j+3], so_ids[i+1,j+4], so_ids[i+1,j+5],
so_ids[i+1,j+6],
                                     so_ids[i+2,j], so_ids[i+2,j+1],
so_ids[i+2,j+2], so_ids[i+2,j+3], so_ids[i+2,j+4], so_ids[i+2,j+5],
so_ids[i+2,j+6],
                                     so_ids[i+3,j], so_ids[i+3,j+1],
so_ids[i+3,j+2], so_ids[i+3,j+3], so_ids[i+3,j+4], so_ids[i+3,j+5],
so_ids[i+3,j+6],
                                     so_ids[i+4,j], so_ids[i+4,j+1],
so_ids[i+4,j+2], so_ids[i+4,j+3], so_ids[i+4,j+4], so_ids[i+4,j+5],
so_ids[i+4,j+6],
                                     so_ids[i+5,j], so_ids[i+5,j+1],
so_ids[i+5,j+2], so_ids[i+5,j+3], so_ids[i+5,j+4], so_ids[i+5,j+5],
so_ids[i+5,j+6],
                                     so_ids[i+6,j], so_ids[i+6,j+1],
so_ids[i+6,j+2], so_ids[i+6,j+3], so_ids[i+6,j+4], so_ids[i+6,j+5],
so_ids[i+6,j+6]))
  }
}

# 8x8-subplot unions
subplot_unions_8x8 <- matrix(NA,0,64)

for (i in 1:3){
  for (j in 1:3){
    subplot_unions_8x8 <- rbind(subplot_unions_8x8,
                                   c(so_ids[i,j], so_ids[i,j+1], so_ids[i,j+2],
so_ids[i,j+3], so_ids[i,j+4], so_ids[i,j+5], so_ids[i,j+6], so_ids[i,j+7],
```

```
                                     so_ids[i+1,j], so_ids[i+1,j+1],
so_ids[i+1,j+2], so_ids[i+1,j+3], so_ids[i+1,j+4], so_ids[i+1,j+5],
so_ids[i+1,j+6], so_ids[i+1,j+7],
                                     so_ids[i+2,j], so_ids[i+2,j+1],
so_ids[i+2,j+2], so_ids[i+2,j+3], so_ids[i+2,j+4], so_ids[i+2,j+5],
so_ids[i+2,j+6], so_ids[i+2,j+7],
                                     so_ids[i+3,j], so_ids[i+3,j+1],
so_ids[i+3,j+2], so_ids[i+3,j+3], so_ids[i+3,j+4], so_ids[i+3,j+5],
so_ids[i+3,j+6], so_ids[i+3,j+7],
                                     so_ids[i+4,j], so_ids[i+4,j+1],
so_ids[i+4,j+2], so_ids[i+4,j+3], so_ids[i+4,j+4], so_ids[i+4,j+5],
so_ids[i+4,j+6], so_ids[i+4,j+7],
                                     so_ids[i+5,j], so_ids[i+5,j+1],
so_ids[i+5,j+2], so_ids[i+5,j+3], so_ids[i+5,j+4], so_ids[i+5,j+5],
so_ids[i+5,j+6], so_ids[i+5,j+7],
                                     so_ids[i+6,j], so_ids[i+6,j+1],
so_ids[i+6,j+2], so_ids[i+6,j+3], so_ids[i+6,j+4], so_ids[i+6,j+5],
so_ids[i+6,j+6], so_ids[i+6,j+7],
                                     so_ids[i+7,j], so_ids[i+7,j+1],
so_ids[i+7,j+2], so_ids[i+7,j+3], so_ids[i+7,j+4], so_ids[i+7,j+5],
so_ids[i+7,j+6], so_ids[i+7,j+7]))
  }
}

# 9x9-subplot unions
subplot_unions_9x9 <- matrix(NA,0,81)

for (i in 1:2){
  for (j in 1:2){
    subplot_unions_9x9 <- rbind(subplot_unions_9x9,
                                   c(so_ids[i,j], so_ids[i,j+1], so_ids[i,j+2],
so_ids[i,j+3], so_ids[i,j+4], so_ids[i,j+5], so_ids[i,j+6], so_ids[i,j+7],
so_ids[i,j+8],
                                     so_ids[i+1,j], so_ids[i+1,j+1],
so_ids[i+1,j+2], so_ids[i+1,j+3], so_ids[i+1,j+4], so_ids[i+1,j+5],
so_ids[i+1,j+6], so_ids[i+1,j+7], so_ids[i+1,j+8],
                                     so_ids[i+2,j], so_ids[i+2,j+1],
so_ids[i+2,j+2], so_ids[i+2,j+3], so_ids[i+2,j+4], so_ids[i+2,j+5],
so_ids[i+2,j+6], so_ids[i+2,j+7], so_ids[i+2,j+8],
                                     so_ids[i+3,j], so_ids[i+3,j+1],
so_ids[i+3,j+2], so_ids[i+3,j+3], so_ids[i+3,j+4], so_ids[i+3,j+5],
so_ids[i+3,j+6], so_ids[i+3,j+7], so_ids[i+3,j+8],
                                     so_ids[i+4,j], so_ids[i+4,j+1],
so_ids[i+4,j+2], so_ids[i+4,j+3], so_ids[i+4,j+4], so_ids[i+4,j+5],
so_ids[i+4,j+6], so_ids[i+4,j+7], so_ids[i+4,j+8],
                                     so_ids[i+5,j], so_ids[i+5,j+1],
so_ids[i+5,j+2], so_ids[i+5,j+3], so_ids[i+5,j+4], so_ids[i+5,j+5],
so_ids[i+5,j+6], so_ids[i+5,j+7], so_ids[i+5,j+8],
                                     so_ids[i+6,j], so_ids[i+6,j+1],
so_ids[i+6,j+2], so_ids[i+6,j+3], so_ids[i+6,j+4], so_ids[i+6,j+5],
so_ids[i+6,j+6], so_ids[i+6,j+7], so_ids[i+6,j+8],
                                     so_ids[i+7,j], so_ids[i+7,j+1],
so_ids[i+7,j+2], so_ids[i+7,j+3], so_ids[i+7,j+4], so_ids[i+7,j+5],
so_ids[i+7,j+6], so_ids[i+7,j+7], so_ids[i+7,j+8],
                                     so_ids[i+8,j], so_ids[i+8,j+1],
so_ids[i+8,j+2], so_ids[i+8,j+3], so_ids[i+8,j+4], so_ids[i+8,j+5],
so_ids[i+8,j+6], so_ids[i+8,j+7], so_ids[i+8,j+8]))
  }
}

# 10x10-subplot unions
subplot_unions_10x10 <- matrix(1:100,1,100)


# Calculate information entropy among species richness and Shannon diversity values
for different subplot sizes and quantities
# Major step 1: Randomly sample a number of subplots m of a given size from each of
nine 10x10-plots
# Major step 2: Calculate entropy on the basis of the m*9 species richness and
Shannon diversity values
# Repeat procedure 10,000 times

set.seed(123)

size <- "1x1" # Select the subplot size from 1x1 to 10x10
subplot_unions_xxx <- subplot_unions_1x1 # Select the subplot-unions for the given
subplot size
```

```
for(m in 1:100){ # m the number of randomly sampled subplot-unions from each of
nine 10x10-plots

  # The m subplot-unions are not allowed to share any 1x1-subplot to guarantee
independent richness and diversity values as input into the entropy calculation.
  # Therefore, max(m) depends on the size of the subplot-union.
  # For 1x1 max(m)=100, for 2x2 max(m)=25, for 3x3 max(m)=9, for 4x4 max(m)=4, for
5x5 max(m)=4, for 6x6 and larger subplot-unions max(m)=1.

  random_entropy_runs <- matrix(NA, 0,2) # Empty matrix that will be filled

  for (i in 1:10000) { # Repeat 10,000 times

    random_subplots_richness_diversity_plot_1 <- matrix(NA,0,3) # Empty matrix that
will be filled
    random_subplots_richness_diversity_plot_2 <- matrix(NA,0,3)
    random_subplots_richness_diversity_plot_3 <- matrix(NA,0,3)
    random_subplots_richness_diversity_plot_4 <- matrix(NA,0,3)
    random_subplots_richness_diversity_plot_5 <- matrix(NA,0,3)
    random_subplots_richness_diversity_plot_6 <- matrix(NA,0,3)
    random_subplots_richness_diversity_plot_7 <- matrix(NA,0,3)
    random_subplots_richness_diversity_plot_8 <- matrix(NA,0,3)
    random_subplots_richness_diversity_plot_9 <- matrix(NA,0,3)

    random_rows_subplot_unions <- c() # Emtpy vector that will be filled

    # Major step 1: Loop to randomly select m subplot-unions from each of nine
10x10-plots with the condition that the m subplot-unions do not share any 1x1-
subplot inside a 10x10-plot

    for(j in 1:9) {

      if(m!=1){

        repeat {
          random_rows <- sample(1:nrow(subplot_unions_xxx), m, replace=F)
          random_subplot_unions <- as.matrix(subplot_unions_xxx[random_rows,])
          intersect_random_subplot_unions <-
Reduce(intersect,split(random_subplot_unions, seq(nrow(random_subplot_unions))))
          if(length(intersect_random_subplot_unions)==0) {break}}

        random_rows_subplot_unions <- c(random_rows_subplot_unions, random_rows)

      } else {

        random_rows <- sample(1:nrow(subplot_unions_xxx), m, replace=F)
        random_subplot_unions <- as.matrix(subplot_unions_xxx[random_rows,])
        random_rows_subplot_unions <- c(random_rows_subplot_unions, random_rows)

        }
    }

    random_subplot_unions <-
as.matrix(subplot_unions_xxx[random_rows_subplot_unions,])

    for(l in 1:m) { # Loops to extract and unify 1x1-subplot data, and to calculate
species richness and Shannon diversity
      random_subplots_richness_diversity_plot_1 <-
rbind(random_subplots_richness_diversity_plot_1,
                                                        c(1,
specnumber(apply(plot_1[random_subplot_unions[l,],], 2, mean)),
diversity(apply(plot_1[random_subplot_unions[l,],], 2, mean))))
    }
    for(l in (1+1*m):(2*m)) {
      random_subplots_richness_diversity_plot_2 <-
rbind(random_subplots_richness_diversity_plot_2,
                                                        c(2,
specnumber(apply(plot_2[random_subplot_unions[l,],], 2, mean)),
diversity(apply(plot_2[random_subplot_unions[l,],], 2, mean))))
    }
    for(l in (1+2*m):(3*m)) {
      random_subplots_richness_diversity_plot_3 <-
rbind(random_subplots_richness_diversity_plot_3,
                                                        c(3,
specnumber(apply(plot_3[random_subplot_unions[l,],], 2, mean)),
diversity(apply(plot_3[random_subplot_unions[l,],], 2, mean))))
    }
    for(l in (1+3*m):(4*m)) {
```

```
      random_subplots_richness_diversity_plot_4 <-
rbind(random_subplots_richness_diversity_plot_4,
                                                            c(4,
specnumber(apply(plot_4[random_subplot_unions[l,],], 2, mean)),
diversity(apply(plot_4[random_subplot_unions[l,],], 2, mean))))
    }
    for(l in (1+4*m):(5*m)) {
      random_subplots_richness_diversity_plot_5 <-
rbind(random_subplots_richness_diversity_plot_5,
                                                            c(5,
specnumber(apply(plot_5[random_subplot_unions[l,],], 2, mean)),
diversity(apply(plot_5[random_subplot_unions[l,],], 2, mean))))
    }
    for(l in (1+5*m):(6*m)) {
      random_subplots_richness_diversity_plot_6 <-
rbind(random_subplots_richness_diversity_plot_6,
                                                            c(6,
specnumber(apply(plot_6[random_subplot_unions[l,],], 2, mean)),
diversity(apply(plot_6[random_subplot_unions[l,],], 2, mean))))
    }
    for(l in (1+6*m):(7*m)) {
      random_subplots_richness_diversity_plot_7 <-
rbind(random_subplots_richness_diversity_plot_7,
                                                            c(7,
specnumber(apply(plot_7[random_subplot_unions[l,],], 2, mean)),
diversity(apply(plot_7[random_subplot_unions[l,],], 2, mean))))
    }
    for(l in (1+7*m):(8*m)) {
      random_subplots_richness_diversity_plot_8 <-
rbind(random_subplots_richness_diversity_plot_8,
                                                            c(8,
specnumber(apply(plot_8[random_subplot_unions[l,],], 2, mean)),
diversity(apply(plot_8[random_subplot_unions[l,],], 2, mean))))
    }
    for(l in (1+8*m):(9*m)) {
      random_subplots_richness_diversity_plot_9 <-
rbind(random_subplots_richness_diversity_plot_9,
                                                            c(9,
specnumber(apply(plot_9[random_subplot_unions[l,],], 2, mean)),
diversity(apply(plot_9[random_subplot_unions[l,],], 2, mean))))
    }

    random_subplots_richness_diversity <-
rbind(random_subplots_richness_diversity_plot_1,

random_subplots_richness_diversity_plot_2,

random_subplots_richness_diversity_plot_3,

random_subplots_richness_diversity_plot_4,

random_subplots_richness_diversity_plot_5,

random_subplots_richness_diversity_plot_6,

random_subplots_richness_diversity_plot_7,

random_subplots_richness_diversity_plot_8,

random_subplots_richness_diversity_plot_9)

    # Major step 2: Calculate Shannon's information entropy among the resulting
species richness and Shannon diversity values
    random_entropy_runs <- rbind(random_entropy_runs,

c(entropy(as.vector(table(random_subplots_richness_diversity[,2])), unit="log2"),

entropy(as.vector(table(round(random_subplots_richness_diversity[,3], digits=1))),
unit="log2")))

    print(i)

  }

  random_entropy_runs <- as.data.frame(random_entropy_runs)
  colnames(random_entropy_runs) <- c("entropy_richness", "entropy_diversity")

  write.csv(random_entropy_runs,
paste(size,"_10000_random_entropy_of",m,"per9.csv", sep=""))
```

```
  gc()

  print(m)

}


# Load and rbind() entropy tables for different subplot sizes and quantities

entropy_1x1_1per9 <- read.csv("1x1_10000_random_entropy_of1per9.csv", row.names=1)
entropy_1x1_1per9 <- data.frame(entropy_1x1_1per9, random_run=1:10000,
subplot_size=1, subplots_per_plot=1)

entropy_1x1_2per9 <- read.csv("1x1_10000_random_entropy_of2per9.csv", row.names=1)
entropy_1x1_2per9 <- data.frame(entropy_1x1_2per9, random_run=1:10000,
subplot_size=1, subplots_per_plot=2)

entropy_1x1_3per9 <- read.csv("1x1_10000_random_entropy_of3per9.csv", row.names=1)
entropy_1x1_3per9 <- data.frame(entropy_1x1_3per9, random_run=1:10000,
subplot_size=1, subplots_per_plot=3)

entropy_1x1_4per9 <- read.csv("1x1_10000_random_entropy_of4per9.csv", row.names=1)
entropy_1x1_4per9 <- data.frame(entropy_1x1_4per9, random_run=1:10000,
subplot_size=1, subplots_per_plot=4)

entropy_1x1_5per9 <- read.csv("1x1_10000_random_entropy_of5per9.csv", row.names=1)
entropy_1x1_5per9 <- data.frame(entropy_1x1_5per9, random_run=1:10000,
subplot_size=1, subplots_per_plot=5)

entropy_1x1_6per9 <- read.csv("1x1_10000_random_entropy_of6per9.csv", row.names=1)
entropy_1x1_6per9 <- data.frame(entropy_1x1_6per9, random_run=1:10000,
subplot_size=1, subplots_per_plot=6)

entropy_1x1_7per9 <- read.csv("1x1_10000_random_entropy_of7per9.csv", row.names=1)
entropy_1x1_7per9 <- data.frame(entropy_1x1_7per9, random_run=1:10000,
subplot_size=1, subplots_per_plot=7)

entropy_1x1_8per9 <- read.csv("1x1_10000_random_entropy_of8per9.csv", row.names=1)
entropy_1x1_8per9 <- data.frame(entropy_1x1_8per9, random_run=1:10000,
subplot_size=1, subplots_per_plot=8)

entropy_1x1_9per9 <- read.csv("1x1_10000_random_entropy_of9per9.csv", row.names=1)
entropy_1x1_9per9 <- data.frame(entropy_1x1_9per9, random_run=1:10000,
subplot_size=1, subplots_per_plot=9)

entropy_1x1_10per9 <- read.csv("1x1_10000_random_entropy_of10per9.csv",
row.names=1)
entropy_1x1_10per9 <- data.frame(entropy_1x1_10per9, random_run=1:10000,
subplot_size=1, subplots_per_plot=10)

entropy_1x1_11per9 <- read.csv("1x1_10000_random_entropy_of11per9.csv",
row.names=1)
entropy_1x1_11per9 <- data.frame(entropy_1x1_11per9, random_run=1:10000,
subplot_size=1, subplots_per_plot=11)

entropy_1x1_12per9 <- read.csv("1x1_10000_random_entropy_of12per9.csv",
row.names=1)
entropy_1x1_12per9 <- data.frame(entropy_1x1_12per9, random_run=1:10000,
subplot_size=1, subplots_per_plot=12)

entropy_1x1_13per9 <- read.csv("1x1_10000_random_entropy_of13per9.csv",
row.names=1)
entropy_1x1_13per9 <- data.frame(entropy_1x1_13per9, random_run=1:10000,
subplot_size=1, subplots_per_plot=13)

entropy_1x1_14per9 <- read.csv("1x1_10000_random_entropy_of14per9.csv",
row.names=1)
entropy_1x1_14per9 <- data.frame(entropy_1x1_14per9, random_run=1:10000,
subplot_size=1, subplots_per_plot=14)

entropy_1x1_15per9 <- read.csv("1x1_10000_random_entropy_of15per9.csv",
row.names=1)
entropy_1x1_15per9 <- data.frame(entropy_1x1_15per9, random_run=1:10000,
subplot_size=1, subplots_per_plot=15)

entropy_1x1_16per9 <- read.csv("1x1_10000_random_entropy_of16per9.csv",
row.names=1)
entropy_1x1_16per9 <- data.frame(entropy_1x1_16per9, random_run=1:10000,
subplot_size=1, subplots_per_plot=16)
```

```
entropy_1x1_17per9 <- read.csv("1x1_10000_random_entropy_of17per9.csv",
row.names=1)
entropy_1x1_17per9 <- data.frame(entropy_1x1_17per9, random_run=1:10000,
subplot_size=1, subplots_per_plot=17)

entropy_1x1_18per9 <- read.csv("1x1_10000_random_entropy_of18per9.csv",
row.names=1)
entropy_1x1_18per9 <- data.frame(entropy_1x1_18per9, random_run=1:10000,
subplot_size=1, subplots_per_plot=18)

entropy_1x1_19per9 <- read.csv("1x1_10000_random_entropy_of19per9.csv",
row.names=1)
entropy_1x1_19per9 <- data.frame(entropy_1x1_19per9, random_run=1:10000,
subplot_size=1, subplots_per_plot=19)

entropy_1x1_20per9 <- read.csv("1x1_10000_random_entropy_of20per9.csv",
row.names=1)
entropy_1x1_20per9 <- data.frame(entropy_1x1_20per9, random_run=1:10000,
subplot_size=1, subplots_per_plot=20)

entropy_1x1_21per9 <- read.csv("1x1_10000_random_entropy_of21per9.csv",
row.names=1)
entropy_1x1_21per9 <- data.frame(entropy_1x1_21per9, random_run=1:10000,
subplot_size=1, subplots_per_plot=21)

entropy_1x1_22per9 <- read.csv("1x1_10000_random_entropy_of22per9.csv",
row.names=1)
entropy_1x1_22per9 <- data.frame(entropy_1x1_22per9, random_run=1:10000,
subplot_size=1, subplots_per_plot=22)

entropy_1x1_23per9 <- read.csv("1x1_10000_random_entropy_of23per9.csv",
row.names=1)
entropy_1x1_23per9 <- data.frame(entropy_1x1_23per9, random_run=1:10000,
subplot_size=1, subplots_per_plot=23)

entropy_1x1_24per9 <- read.csv("1x1_10000_random_entropy_of24per9.csv",
row.names=1)
entropy_1x1_24per9 <- data.frame(entropy_1x1_24per9, random_run=1:10000,
subplot_size=1, subplots_per_plot=24)

entropy_1x1_25per9 <- read.csv("1x1_10000_random_entropy_of25per9.csv",
row.names=1)
entropy_1x1_25per9 <- data.frame(entropy_1x1_25per9, random_run=1:10000,
subplot_size=1, subplots_per_plot=25)

entropy_1x1_30per9 <- read.csv("1x1_10000_random_entropy_of30per9.csv",
row.names=1)
entropy_1x1_30per9 <- data.frame(entropy_1x1_30per9, random_run=1:10000,
subplot_size=1, subplots_per_plot=30)

entropy_1x1_36per9 <- read.csv("1x1_10000_random_entropy_of36per9.csv",
row.names=1)
entropy_1x1_36per9 <- data.frame(entropy_1x1_36per9, random_run=1:10000,
subplot_size=1, subplots_per_plot=36)

entropy_1x1_42per9 <- read.csv("1x1_10000_random_entropy_of42per9.csv",
row.names=1)
entropy_1x1_42per9 <- data.frame(entropy_1x1_42per9, random_run=1:10000,
subplot_size=1, subplots_per_plot=42)

entropy_1x1_48per9 <- read.csv("1x1_10000_random_entropy_of48per9.csv",
row.names=1)
entropy_1x1_48per9 <- data.frame(entropy_1x1_48per9, random_run=1:10000,
subplot_size=1, subplots_per_plot=48)

entropy_1x1_50per9 <- read.csv("1x1_10000_random_entropy_of50per9.csv",
row.names=1)
entropy_1x1_50per9 <- data.frame(entropy_1x1_50per9, random_run=1:10000,
subplot_size=1, subplots_per_plot=50)

entropy_1x1_60per9 <- read.csv("1x1_10000_random_entropy_of60per9.csv",
row.names=1)
entropy_1x1_60per9 <- data.frame(entropy_1x1_60per9, random_run=1:10000,
subplot_size=1, subplots_per_plot=60)

entropy_1x1_72per9 <- read.csv("1x1_10000_random_entropy_of72per9.csv",
row.names=1)
```

```
entropy_1x1_72per9 <- data.frame(entropy_1x1_72per9, random_run=1:10000,
subplot_size=1, subplots_per_plot=72)

entropy_1x1_84per9 <- read.csv("1x1_10000_random_entropy_of84per9.csv",
row.names=1)
entropy_1x1_84per9 <- data.frame(entropy_1x1_84per9, random_run=1:10000,
subplot_size=1, subplots_per_plot=84)

entropy_1x1_96per9 <- read.csv("1x1_10000_random_entropy_of96per9.csv",
row.names=1)
entropy_1x1_96per9 <- data.frame(entropy_1x1_96per9, random_run=1:10000,
subplot_size=1, subplots_per_plot=96)

entropy_1x1_99per9 <- read.csv("1x1_10000_random_entropy_of99per9.csv",
row.names=1)
entropy_1x1_99per9 <- data.frame(entropy_1x1_99per9, random_run=1:10000,
subplot_size=1, subplots_per_plot=99)

entropy_1x1_100per9 <- read.csv("1x1_entropy_of100per9.csv", row.names=1)
entropy_1x1_100per9 <- data.frame(entropy_1x1_100per9, random_run=1,
subplot_size=1, subplots_per_plot=100)


entropy_2x2_1per9 <- read.csv("2x2_10000_random_entropy_of1per9.csv", row.names=1)
entropy_2x2_1per9 <- data.frame(entropy_2x2_1per9, random_run=1:10000,
subplot_size=2, subplots_per_plot=1)

entropy_2x2_2per9 <- read.csv("2x2_10000_random_entropy_of2per9.csv", row.names=1)
entropy_2x2_2per9 <- data.frame(entropy_2x2_2per9, random_run=1:10000,
subplot_size=2, subplots_per_plot=2)

entropy_2x2_3per9 <- read.csv("2x2_10000_random_entropy_of3per9.csv", row.names=1)
entropy_2x2_3per9 <- data.frame(entropy_2x2_3per9, random_run=1:10000,
subplot_size=2, subplots_per_plot=3)

entropy_2x2_4per9 <- read.csv("2x2_10000_random_entropy_of4per9.csv", row.names=1)
entropy_2x2_4per9 <- data.frame(entropy_2x2_4per9, random_run=1:10000,
subplot_size=2, subplots_per_plot=4)

entropy_2x2_5per9 <- read.csv("2x2_10000_random_entropy_of5per9.csv", row.names=1)
entropy_2x2_5per9 <- data.frame(entropy_2x2_5per9, random_run=1:10000,
subplot_size=2, subplots_per_plot=5)

entropy_2x2_6per9 <- read.csv("2x2_10000_random_entropy_of6per9.csv", row.names=1)
entropy_2x2_6per9 <- data.frame(entropy_2x2_6per9, random_run=1:10000,
subplot_size=2, subplots_per_plot=6)

entropy_2x2_7per9 <- read.csv("2x2_10000_random_entropy_of7per9.csv", row.names=1)
entropy_2x2_7per9 <- data.frame(entropy_2x2_7per9, random_run=1:10000,
subplot_size=2, subplots_per_plot=7)

entropy_2x2_8per9 <- read.csv("2x2_10000_random_entropy_of8per9.csv", row.names=1)
entropy_2x2_8per9 <- data.frame(entropy_2x2_8per9, random_run=1:10000,
subplot_size=2, subplots_per_plot=8)

entropy_2x2_9per9 <- read.csv("2x2_10000_random_entropy_of9per9.csv", row.names=1)
entropy_2x2_9per9 <- data.frame(entropy_2x2_9per9, random_run=1:10000,
subplot_size=2, subplots_per_plot=9)

entropy_2x2_10per9 <- read.csv("2x2_10000_random_entropy_of10per9.csv",
row.names=1)
entropy_2x2_10per9 <- data.frame(entropy_2x2_10per9, random_run=1:10000,
subplot_size=2, subplots_per_plot=10)

entropy_2x2_11per9 <- read.csv("2x2_10000_random_entropy_of11per9.csv",
row.names=1)
entropy_2x2_11per9 <- data.frame(entropy_2x2_11per9, random_run=1:10000,
subplot_size=2, subplots_per_plot=11)

entropy_2x2_12per9 <- read.csv("2x2_10000_random_entropy_of12per9.csv",
row.names=1)
entropy_2x2_12per9 <- data.frame(entropy_2x2_12per9, random_run=1:10000,
subplot_size=2, subplots_per_plot=12)

entropy_2x2_13per9 <- read.csv("2x2_10000_random_entropy_of13per9.csv",
row.names=1)
entropy_2x2_13per9 <- data.frame(entropy_2x2_13per9, random_run=1:10000,
subplot_size=2, subplots_per_plot=13)
```

```
entropy_2x2_14per9 <- read.csv("2x2_10000_random_entropy_of14per9.csv",
row.names=1)
entropy_2x2_14per9 <- data.frame(entropy_2x2_14per9, random_run=1:10000,
subplot_size=2, subplots_per_plot=14)

entropy_2x2_15per9 <- read.csv("2x2_10000_random_entropy_of15per9.csv",
row.names=1)
entropy_2x2_15per9 <- data.frame(entropy_2x2_15per9, random_run=1:10000,
subplot_size=2, subplots_per_plot=15)

entropy_2x2_16per9 <- read.csv("2x2_10000_random_entropy_of16per9.csv",
row.names=1)
entropy_2x2_16per9 <- data.frame(entropy_2x2_16per9, random_run=1:10000,
subplot_size=2, subplots_per_plot=16)

entropy_2x2_17per9 <- read.csv("2x2_10000_random_entropy_of17per9.csv",
row.names=1)
entropy_2x2_17per9 <- data.frame(entropy_2x2_17per9, random_run=1:10000,
subplot_size=2, subplots_per_plot=17)

entropy_2x2_18per9 <- read.csv("2x2_10000_random_entropy_of18per9.csv",
row.names=1)
entropy_2x2_18per9 <- data.frame(entropy_2x2_18per9, random_run=1:10000,
subplot_size=2, subplots_per_plot=18)

entropy_2x2_19per9 <- read.csv("2x2_10000_random_entropy_of19per9.csv",
row.names=1)
entropy_2x2_19per9 <- data.frame(entropy_2x2_19per9, random_run=1:10000,
subplot_size=2, subplots_per_plot=19)

entropy_2x2_20per9 <- read.csv("2x2_10000_random_entropy_of20per9.csv",
row.names=1)
entropy_2x2_20per9 <- data.frame(entropy_2x2_20per9, random_run=1:10000,
subplot_size=2, subplots_per_plot=20)

entropy_2x2_21per9 <- read.csv("2x2_10000_random_entropy_of21per9.csv",
row.names=1)
entropy_2x2_21per9 <- data.frame(entropy_2x2_21per9, random_run=1:10000,
subplot_size=2, subplots_per_plot=21)

entropy_2x2_22per9 <- read.csv("2x2_10000_random_entropy_of22per9.csv",
row.names=1)
entropy_2x2_22per9 <- data.frame(entropy_2x2_22per9, random_run=1:10000,
subplot_size=2, subplots_per_plot=22)

entropy_2x2_23per9 <- read.csv("2x2_10000_random_entropy_of23per9.csv",
row.names=1)
entropy_2x2_23per9 <- data.frame(entropy_2x2_23per9, random_run=1:10000,
subplot_size=2, subplots_per_plot=23)

entropy_2x2_24per9 <- read.csv("2x2_10000_random_entropy_of24per9.csv",
row.names=1)
entropy_2x2_24per9 <- data.frame(entropy_2x2_24per9, random_run=1:10000,
subplot_size=2, subplots_per_plot=24)

entropy_2x2_25per9 <- read.csv("2x2_entropy_of25per9.csv", row.names=1)
entropy_2x2_25per9 <- data.frame(entropy_2x2_25per9, random_run=1, subplot_size=2,
subplots_per_plot=25)


entropy_3x3_1per9 <- read.csv("3x3_10000_random_entropy_of1per9.csv", row.names=1)
entropy_3x3_1per9 <- data.frame(entropy_3x3_1per9, random_run=1:10000,
subplot_size=3, subplots_per_plot=1)

entropy_3x3_2per9 <- read.csv("3x3_10000_random_entropy_of2per9.csv", row.names=1)
entropy_3x3_2per9 <- data.frame(entropy_3x3_2per9, random_run=1:10000,
subplot_size=3, subplots_per_plot=2)

entropy_3x3_3per9 <- read.csv("3x3_10000_random_entropy_of3per9.csv", row.names=1)
entropy_3x3_3per9 <- data.frame(entropy_3x3_3per9, random_run=1:10000,
subplot_size=3, subplots_per_plot=3)

entropy_3x3_4per9 <- read.csv("3x3_10000_random_entropy_of4per9.csv", row.names=1)
entropy_3x3_4per9 <- data.frame(entropy_3x3_4per9, random_run=1:10000,
subplot_size=3, subplots_per_plot=4)

entropy_3x3_5per9 <- read.csv("3x3_10000_random_entropy_of5per9.csv", row.names=1)
entropy_3x3_5per9 <- data.frame(entropy_3x3_5per9, random_run=1:10000,
subplot_size=3, subplots_per_plot=5)
```

```
entropy_3x3_6per9 <- read.csv("3x3_10000_random_entropy_of6per9.csv", row.names=1)
entropy_3x3_6per9 <- data.frame(entropy_3x3_6per9, random_run=1:10000,
subplot_size=3, subplots_per_plot=6)

entropy_3x3_7per9 <- read.csv("3x3_10000_random_entropy_of7per9.csv", row.names=1)
entropy_3x3_7per9 <- data.frame(entropy_3x3_7per9, random_run=1:10000,
subplot_size=3, subplots_per_plot=7)

entropy_3x3_8per9 <- read.csv("3x3_10000_random_entropy_of8per9.csv", row.names=1)
entropy_3x3_8per9 <- data.frame(entropy_3x3_8per9, random_run=1:10000,
subplot_size=3, subplots_per_plot=8)

entropy_3x3_9per9 <- read.csv("3x3_10000_random_entropy_of9per9.csv", row.names=1)
entropy_3x3_9per9 <- data.frame(entropy_3x3_9per9, random_run=1:10000,
subplot_size=3, subplots_per_plot=9)


entropy_4x4_1per9 <- read.csv("4x4_10000_random_entropy_of1per9.csv", row.names=1)
entropy_4x4_1per9 <- data.frame(entropy_4x4_1per9, random_run=1:10000,
subplot_size=4, subplots_per_plot=1)

entropy_4x4_2per9 <- read.csv("4x4_10000_random_entropy_of2per9.csv", row.names=1)
entropy_4x4_2per9 <- data.frame(entropy_4x4_2per9, random_run=1:10000,
subplot_size=4, subplots_per_plot=2)

entropy_4x4_3per9 <- read.csv("4x4_10000_random_entropy_of3per9.csv", row.names=1)
entropy_4x4_3per9 <- data.frame(entropy_4x4_3per9, random_run=1:10000,
subplot_size=4, subplots_per_plot=3)

entropy_4x4_4per9 <- read.csv("4x4_10000_random_entropy_of4per9.csv", row.names=1)
entropy_4x4_4per9 <- data.frame(entropy_4x4_4per9, random_run=1:10000,
subplot_size=4, subplots_per_plot=4)


entropy_5x5_1per9 <- read.csv("5x5_10000_random_entropy_of1per9.csv", row.names=1)
entropy_5x5_1per9 <- data.frame(entropy_5x5_1per9, random_run=1:10000,
subplot_size=5, subplots_per_plot=1)

entropy_5x5_2per9 <- read.csv("5x5_10000_random_entropy_of2per9.csv", row.names=1)
entropy_5x5_2per9 <- data.frame(entropy_5x5_2per9, random_run=1:10000,
subplot_size=5, subplots_per_plot=2)

entropy_5x5_3per9 <- read.csv("5x5_10000_random_entropy_of3per9.csv", row.names=1)
entropy_5x5_3per9 <- data.frame(entropy_5x5_3per9, random_run=1:10000,
subplot_size=5, subplots_per_plot=3)

entropy_5x5_4per9 <- read.csv("5x5_entropy_of4per9.csv", row.names=1)
entropy_5x5_4per9 <- data.frame(entropy_5x5_4per9, random_run=1, subplot_size=5,
subplots_per_plot=4)


entropy_6x6_1per9 <- read.csv("6x6_10000_random_entropy_of1per9.csv", row.names=1)
entropy_6x6_1per9 <- data.frame(entropy_6x6_1per9, random_run=1:10000,
subplot_size=6, subplots_per_plot=1)


entropy_7x7_1per9 <- read.csv("7x7_10000_random_entropy_of1per9.csv", row.names=1)
entropy_7x7_1per9 <- data.frame(entropy_7x7_1per9, random_run=1:10000,
subplot_size=7, subplots_per_plot=1)


entropy_8x8_1per9 <- read.csv("8x8_10000_random_entropy_of1per9.csv", row.names=1)
entropy_8x8_1per9 <- data.frame(entropy_8x8_1per9, random_run=1:10000,
subplot_size=8, subplots_per_plot=1)


entropy_9x9_1per9 <- read.csv("9x9_10000_random_entropy_of1per9.csv", row.names=1)
entropy_9x9_1per9 <- data.frame(entropy_9x9_1per9, random_run=1:10000,
subplot_size=9, subplots_per_plot=1)


entropy_10x10_1per9 <- read.csv("10x10_entropy_of1per9.csv", row.names=1)
entropy_10x10_1per9 <- data.frame(entropy_10x10_1per9, random_run=1,
subplot_size=10, subplots_per_plot=1)


entropy_df <- rbind(entropy_1x1_1per9, entropy_1x1_2per9, entropy_1x1_3per9,
entropy_1x1_4per9, entropy_1x1_5per9,
```

```
                    entropy_1x1_6per9, entropy_1x1_7per9,entropy_1x1_8per9,
entropy_1x1_9per9, entropy_1x1_10per9,
                    entropy_1x1_11per9, entropy_1x1_12per9, entropy_1x1_13per9,
entropy_1x1_14per9, entropy_1x1_15per9,
                    entropy_1x1_16per9, entropy_1x1_17per9, entropy_1x1_18per9,
entropy_1x1_19per9, entropy_1x1_20per9,
                    entropy_1x1_21per9, entropy_1x1_22per9, entropy_1x1_23per9,
entropy_1x1_24per9,
                    entropy_1x1_30per9, entropy_1x1_36per9, entropy_1x1_42per9,
entropy_1x1_48per9, entropy_1x1_60per9,
                    entropy_1x1_72per9,entropy_1x1_84per9,entropy_1x1_96per9,
entropy_1x1_99per9, entropy_1x1_100per9,

                    entropy_2x2_1per9, entropy_2x2_2per9, entropy_2x2_3per9,
entropy_2x2_4per9, entropy_2x2_5per9,
                    entropy_2x2_6per9, entropy_2x2_7per9,entropy_2x2_8per9,
entropy_2x2_9per9, entropy_2x2_10per9,
                    entropy_2x2_11per9, entropy_2x2_12per9, entropy_2x2_13per9,
entropy_2x2_14per9, entropy_2x2_15per9,
                    entropy_2x2_16per9, entropy_2x2_17per9, entropy_2x2_18per9,
entropy_2x2_19per9, entropy_2x2_20per9,
                    entropy_2x2_21per9,
entropy_2x2_22per9,entropy_2x2_23per9,entropy_2x2_24per9, entropy_2x2_25per9,

                    entropy_3x3_1per9, entropy_3x3_2per9, entropy_3x3_3per9,
entropy_3x3_4per9, entropy_3x3_5per9,
                    entropy_3x3_6per9, entropy_3x3_7per9, entropy_3x3_8per9,
entropy_3x3_9per9,

                    entropy_4x4_1per9, entropy_4x4_2per9, entropy_4x4_3per9,
entropy_4x4_4per9,

                    entropy_5x5_1per9, entropy_5x5_2per9, entropy_5x5_3per9,
entropy_5x5_4per9,

                    entropy_6x6_1per9, entropy_7x7_1per9, entropy_8x8_1per9,
entropy_9x9_1per9, entropy_10x10_1per9)

write.csv(entropy_df, "entropy_df.csv")

# Load entropy_df.csv
df <- read.csv("entropy_df.csv", row.names=1)

# Plot information entropy among species richness values for different numbers and
sizes of subplots

df_sub <- subset(df, df$subplots_per_plot%in%c(1:10, 24)) # Select numbers of plots
m to be shown

ggplot(data=df_sub, aes(x=as.factor(subplot_size), y=entropy_richness,
fill=as.factor(subplot_size)))+
  stat_boxplot(geom ='errorbar') +
  geom_boxplot()+
  scale_fill_manual(values = matlab.like(10))+
  facet_grid(~subplots_per_plot)+
  theme_bw()

ggplot(data=df, aes(x=as.factor(subplots_per_plot), y=entropy_richness,
fill=as.factor(subplot_size)))+
  stat_boxplot(geom ='errorbar') +
  geom_boxplot()+
  scale_fill_manual(values = matlab.like(10))+
  facet_grid(~subplot_size)+
  theme_bw()


# Plot information entropy among Shannon diversity values for different numbers and
sizes of subplots

df_sub <- subset(df, df$subplots_per_plot%in%c(1:10, 24)) # Select numbers of plots
m to be shown

ggplot(data=df_sub, aes(x=as.factor(subplot_size), y=entropy_diversity,
fill=as.factor(subplot_size)))+
  stat_boxplot(geom ='errorbar') +
  geom_boxplot()+
  scale_fill_manual(values = matlab.like(10))+
  facet_grid(~subplots_per_plot)+
  theme_bw()
```

```
ggplot(data=df, aes(x=as.factor(subplots_per_plot), y=entropy_diversity,
fill=as.factor(subplot_size)))+
  stat_boxplot(geom ='errorbar') +
  geom_boxplot()+
  scale_fill_manual(values = matlab.like(10))+
  facet_grid(~subplot_size)+
  theme_bw()


# Mood's median test

df_sub <- subset(df, df$subplots_per_plot==2) # Select number of subplots m, e.g.
m=2

median_test(entropy_richness ~ as.factor(subplot_size), data = df_sub, distribution
= approximate(B = 10000))
PT <- pairwiseMedianTest(entropy_richness ~ as.factor(subplot_size), data =
df_sub,method = "BH")
cldList(p.adjust ~ Comparison, data = PT, threshold = 0.05)


# Breakpoint analysis via segmented linear regression

# Subplot size 1x1 as an example

df_sub <- subset(df, df$subplot_size==1 & !(df$subplots_per_plot%in%c(100))) #
Exclude max(m)=100 fir subplot size 1x1

# Calculate median, 5th and 95th percentile of entropy distributions resulting from
the 10,000 repetitions
df_sub_median <- aggregate(df_sub, by=list(df_sub$subplots_per_plot), median)
df_sub_5 <- aggregate(df_sub, by=list(df_sub$subplots_per_plot), function(x)
quantile(x, 0.05))
df_sub_95 <- aggregate(df_sub, by=list(df_sub$subplots_per_plot), function(x)
quantile(x, 0.95))
df_sub_med_5_95 <- as.data.frame(cbind(df_sub_median$subplots_per_plot,
df_sub_median$entropy_richness, df_sub_median$entropy_diversity,
                                       df_sub_5$entropy_richness,
df_sub_5$entropy_diversity,
                                       df_sub_95$entropy_richness,
df_sub_95$entropy_diversity))
colnames(df_sub_med_5_95) <- c("subplots_per_plot", "median_entropy_richness",
"median_entropy_diversity",
                               "perc5_entropy_richness", "perc5_entropy_diversity",
                               "perc95_entropy_richness",
"perc95_entropy_diversity")

# Median breakpoint for species richness

# Fit loess model and predict for m=1:99
y <- df_sub_med_5_95$median_entropy_richness
x <- df_sub_med_5_95$subplots_per_plot
model <- loess(y~log(x))
pred <- predict(model, log(seq(1,99,1)))

# Apply segmented linear regression
y <- pred
x <- 1:99
lin.mod <- lm(y~x)
seg.mod <- segmented(lin.mod, seg.Z=~x, psi=10)
sp_median_rich_1x1 <- seg.mod$psi[2]
sp_confint_median_rich_1x1 <- confint.segmented(seg.mod)

# 5th percentile breakpoint for species richness
y <- df_sub_med_5_95$perc5_entropy_richness
x <- df_sub_med_5_95$subplots_per_plot
model <- loess(y~log(x))
pred <- predict(model, log(seq(1,99,1)))
y <- pred
x <- 1:99
lin.mod <- lm(y~x)
seg.mod <- segmented(lin.mod, seg.Z=~x, psi=10)
sp_5_rich_1x1 <- seg.mod$psi[2]
sp_confint_5_rich_1x1 <- confint.segmented(seg.mod)

# 95th percentile breakpoint for species richness
y <- df_sub_med_5_95$perc95_entropy_richness
x <- df_sub_med_5_95$subplots_per_plot
```

```
model <- loess(y~log(x))
pred <- predict(model, log(seq(1,99,1)))
y <- pred
x <- 1:99
lin.mod <- lm(y~x)
seg.mod <- segmented(lin.mod, seg.Z=~x, psi=10)
sp_95_rich_1x1 <- seg.mod$psi[2]
sp_confint_95_rich_1x1 <- confint.segmented(seg.mod)


# Median for Shannon diversity
y <- df_sub_med_5_95$median_entropy_diversity
x <- df_sub_med_5_95$subplots_per_plot
model <- loess(y~log(x))
pred <- predict(model, log(seq(1,99,1)))
y <- pred
x <- 1:99
lin.mod <- lm(y~x)
seg.mod <- segmented(lin.mod, seg.Z=~x, psi=10)
sp_median_div_1x1 <- seg.mod$psi[2]
sp_confint_median_div_1x1 <- confint.segmented(seg.mod)

# 5th percentile for Shannon diversity
y <- df_sub_med_5_95$perc5_entropy_diversity
x <- df_sub_med_5_95$subplots_per_plot
model <- loess(y~log(x))
pred <- predict(model, log(seq(1,99,1)))
y <- pred
x <- 1:99
lin.mod <- lm(y~x)
seg.mod <- segmented(lin.mod, seg.Z=~x, psi=10)
sp_5_div_1x1 <- seg.mod$psi[2]
sp_confint_5_div_1x1 <- confint.segmented(seg.mod)

# 95th percentile for Shannon diversity
y <- df_sub_med_5_95$perc95_entropy_diversity
x <- df_sub_med_5_95$subplots_per_plot
model <- loess(y~log(x))
pred <- predict(model, log(seq(1,99,1)))
y <- pred
x <- 1:99
lin.mod <- lm(y~x)
seg.mod <- segmented(lin.mod, seg.Z=~x, psi=10)
sp_95_div_1x1 <- seg.mod$psi[2]
sp_confint_95_div_1x1 <- confint.segmented(seg.mod)


# Plot the breakpoints
# Species richness
ggplot(data=df_sub_med_5_95) +

  geom_vline(xintercept = sp_confint_5_rich_1x1$x[1], col="blue")+
  geom_vline(xintercept = sp_confint_5_rich_1x1$x[2], lty=2 , col="blue")+
  geom_vline(xintercept = sp_confint_5_rich_1x1$x[3], lty=2 , col="blue")+

  geom_vline(xintercept = sp_confint_95_rich_1x1$x[1], col="red")+
  geom_vline(xintercept = sp_confint_95_rich_1x1$x[2], lty=2 , col="red")+
  geom_vline(xintercept = sp_confint_95_rich_1x1$x[3], lty=2 , col="red")+

  geom_vline(xintercept = sp_confint_median_rich_1x1$x[1], col="black")+
  geom_vline(xintercept = sp_confint_median_rich_1x1$x[2], lty=2 , col="black")+
  geom_vline(xintercept = sp_confint_median_rich_1x1$x[3], lty=2 , col="black")+

  geom_point(aes(x=subplots_per_plot, y=perc5_entropy_richness), col="blue")+
  geom_smooth(aes(x=subplots_per_plot, y=perc5_entropy_richness, col="5th
percentile"), method="loess", formula=y~log(x), se=F)+

  geom_point(aes(x=subplots_per_plot, y=perc95_entropy_richness), col="red")+
  geom_smooth(aes(x=subplots_per_plot, y=perc95_entropy_richness, col="95th
percentile"), method="loess", formula=y~log(x), se=F)+

  geom_point(aes(x=subplots_per_plot, y=median_entropy_richness), col="black")+
  geom_smooth(aes(x=subplots_per_plot, y=median_entropy_richness, col="Median"),
method="loess", formula=y~log(x), se=F)+

  scale_colour_manual(name="",values=c("blue", "red", "black"))+
  scale_x_continuous(breaks=seq(0,100,5))+
  scale_y_continuous(limits=c(2.4,4.5))+
  theme_bw()
```

```
# Shannon diversity
ggplot(data=df_sub_med_5_95) +

  geom_vline(xintercept = sp_confint_5_div_1x1$x[1], col="blue")+
  geom_vline(xintercept = sp_confint_5_div_1x1$x[2], lty=2 , col="blue")+
  geom_vline(xintercept = sp_confint_5_div_1x1$x[3], lty=2 , col="blue")+

  geom_vline(xintercept = sp_confint_95_div_1x1$x[1], col="red")+
  geom_vline(xintercept = sp_confint_95_div_1x1$x[2], lty=2 , col="red")+
  geom_vline(xintercept = sp_confint_95_div_1x1$x[3], lty=2 , col="red")+

  geom_vline(xintercept = sp_confint_median_div_1x1$x[1], col="black")+
  geom_vline(xintercept = sp_confint_median_div_1x1$x[2], lty=2 , col="black")+
  geom_vline(xintercept = sp_confint_median_div_1x1$x[3], lty=2 , col="black")+

  geom_point(aes(x=subplots_per_plot, y=perc5_entropy_diversity), col="blue")+
  geom_smooth(aes(x=subplots_per_plot, y=perc5_entropy_diversity, col="5th
percentile"), method="loess", formula=y~log(x), se=F)+

  geom_point(aes(x=subplots_per_plot, y=perc95_entropy_diversity), col="red")+
  geom_smooth(aes(x=subplots_per_plot, y=perc95_entropy_diversity, col="95th
percentile"), method="loess", formula=y~log(x), se=F)+

  geom_point(aes(x=subplots_per_plot, y=median_entropy_diversity), col="black")+
  geom_smooth(aes(x=subplots_per_plot, y=median_entropy_diversity, col="Median"),
method="loess", formula=y~log(x), se=F)+

  scale_colour_manual(name="",values=c("blue", "red", "black"))+
  scale_x_continuous(breaks=seq(0,100,5))+
  scale_y_continuous(limits=c(2.4,4.5))+

  theme_bw()
```

7.4 Manuscript 4

Data in brief 24 (2019) 103942

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Data Article

Data on alpine grassland diversity in Gran Paradiso National Park, Italy

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ABSTRACT

The diversity of alpine grassland species and their functional traits constitute alpine ecosystem functioning and services that support human-wellbeing. However, alpine grassland diversity is threatened by land use and climate change. Field surveys and monitoring are necessary to understand and preserve such endangered ecosystems. Here we describe data on abundances (percentage cover) of 247 alpine plant species (including mosses and lichens) inside nine 20 m by 20 m plots that were subdivided into 2 m by 2 m subplots. The nine plots are located in Gran Paradiso National Park, Italy. They cover three distinct alpine vegetation subtypes (‘pure’ natural grassland, sparsely vegetated ‘rocky’ grassland, and wetland) in each of three valleys (Bardoney, Colle de Nivolet and Levionaz) between 2200 and 2700 m a.s.l., i.e. above the treeline. The vegetation survey was conducted in 2015 at the peak of vegetation development during August. The dataset is provided as

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Abstract

The diversity of alpine grassland species and their functional traits constitute alpine ecosystem functioning and services that support human-wellbeing. However, alpine grassland diversity is threatened by human land use and climate change. Field surveys and monitoring are necessary to understand and preserve such endangered ecosystems. Here we describe data on abundances (i.e. percentage cover) of 247 alpine plant species, including mosses and lichens, inside nine 20 m by 20 m plots, which were subdivided into 2 m by 2 m subplots. The nine plots are located in Gran Paradiso National Park, Italy. They cover three distinct alpine vegetation subtypes (i.e. 'pure' natural grassland, sparsely vegetated 'rocky' grassland, and wetland) in each of three valleys (i.e. Bardoney, Colle de Nivolet and Levionaz) between 2200 and 2700 meters a.s.l. and above the treeline. The vegetation survey was conducted in 2015, at the yearly peak of vegetation development during August. The dataset is provided as supplementary material and associated with the research article 'Optimizing sampling effort and information content of biodiversity surveys: a case study of alpine grassland' [1]. See [1] for data interpretation.

Keywords: alpine grassland, species diversity, plot data, cover, abundance, vegetation survey, vegetation monitoring

Specifications table

Subject area	Biogeography, vegetation ecology, biodiversity conservation
More specific subject area	Community ecology
Type of data	Plant species cover-abundance within a quadratic and gridded plot design
How data was acquired	Field observation
Data format	Table
Experimental factors	Mosses and lichens are included. The cover of litter, deadwood, bare soil, rocks, gravel and water are given. Uncertain species identities are noted.
Experimental features	Two independent observers estimated the cover-abundance of each plant species. The mean of these two estimates is given.
Data source location	Gran Paradiso National Park, Italian Alps
Data accessibility	The dataset is provided as supplementary material.
Related research article	S. Hoffmann, L. Steiner, A.H. Schweiger, A. Chiarucci, C. Beierkuhnlein, Optimizing sampling effort and information content of biodiversity surveys: a case study of alpine grassland, Ecol. Inform. 51 (2019) 112–120. https://doi.org/10.1016/J.ECOINF.2019.03.003. [1]

Value of the data

- Since alpine plant diversity is threatened by human land use and climate change, but provide ecosystem functioning and services [2,3], vegetation surveys and monitoring of the endangered vegetation types above the treeline are needed to inform conservation management and policy.
- The sampling design and data allows for various investigations on the relationship between sampling scale and species diversity (e.g. [4,5]).
- Due to the sampling design, the dataset is suitable to be linked to remote sensing data in order to analyze the relationship between plant species diversity and spectral signals (e.g. [6]). Such investigations can facilitate large scale vegetation mapping by relatively low effort [7].
- The data can be integrated into macroecological analyses.

1. Data

The data presented here involves cover-abundance of alpine grassland species in Gran Paradiso National Park, Italy (Fig. 1a, b). We estimated percentage cover of plant species including mosses and lichens, and of litter, deadwood, bare soil, rocks, gravel and water inside nine 20 m by 20 m plots, which were subdivided into 100 2 m by 2 m subplots (Fig. 1c). The nine plots cover three vegetation subtypes (i.e. ‘pure’ natural grassland, sparsely vegetated ‘rocky’ grassland and wetland) in each of three valleys (i.e. Bardoney, Colle de Nivolet and Levionaz) between 2200 and 2700 meters a.s.l. (Fig. 1b). The vegetation survey was conducted in the middle of the yearly vegetation period during August 2015. The plots’ boundary lines were north-south and east-west aligned according to Universal Transverse Mercator reference system (UTM Zone 32N) coordinates. The Global Positioning System (GPS) coordinates of the plots’ corner points are given in the UTM Zone 32N. The dataset is given as supplementary material and is additionally registered at the Dynamic Ecological Information Management System - Site and Dataset Registry (DEIMS-SDR) [8] under the UUID b549ff14-f40f-4749-8e2f-f16f6e523753 (see https://deims.org/dataset/b549ff14-f40f-4749-8e2f-f16f6e523753).

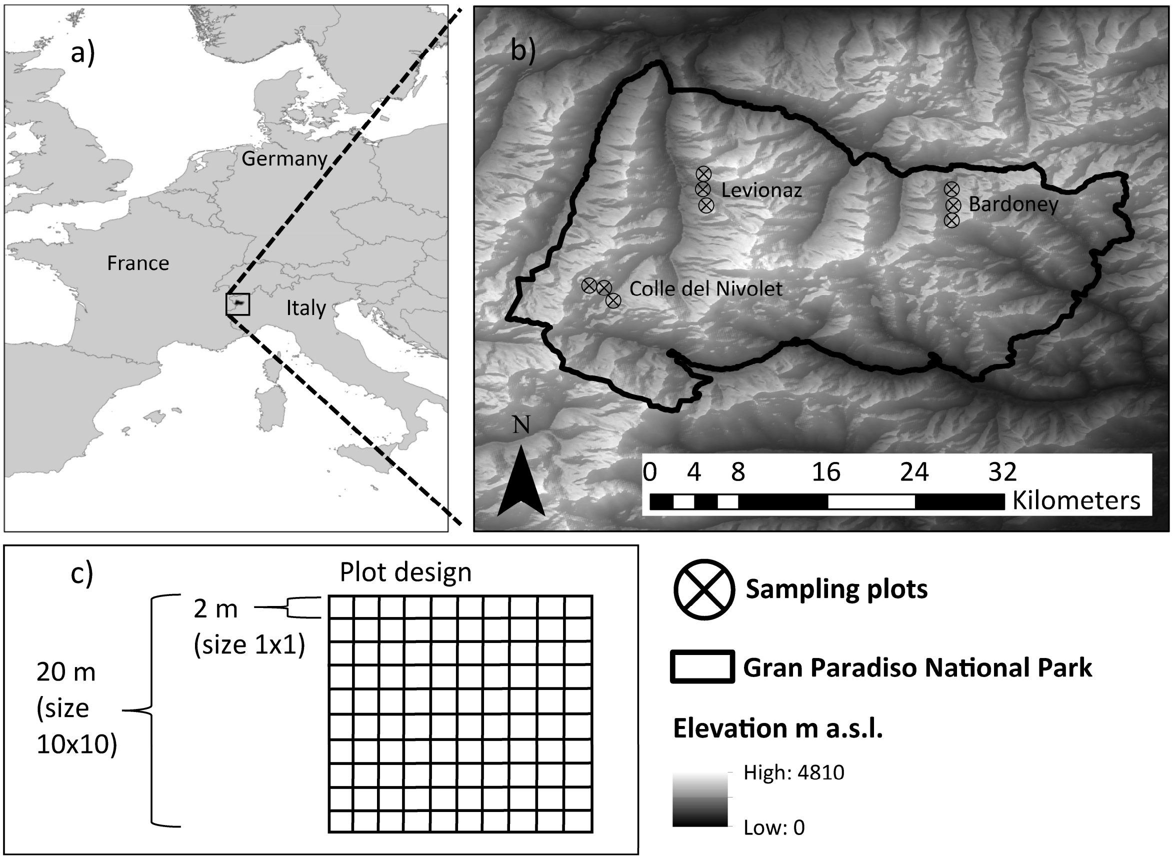

Figure 1. Geographical location of the study area. a) Gran Paradiso National Park is located in the European Alps, north-western Italy. b) Nine sampling plots were established, three in each of the three alpine grassland subtypes inside each of three valleys (i.e. Colle del Nivolet, Levionaz and Bardoney). c) The sampling plot was designed as a 20 m by 20 m quadratic square subdivided into 100 subplots of 2 m by 2 m. Figure adapted from [1].

2. Experimental design, materials and methods

We established nine quadratic plots in the Gran Paradiso National Park in north-western Italy (Fig. 1a). Quadrats mitigate the confounding effect of environmental heterogeneity on species diversity [9]. The plots cover three subtypes of alpine vegetation, which were located with the support of the CORINE Land Cover map from 2012 (available at https://land.copernicus.eu/pan-european/corine-land-cover) and expert knowledge. The three vegetation subtypes are 'pure' natural grassland, sparsely vegetated 'rocky' grassland and 'wet' grassland (i.e. wetlands). Each vegetation subtype was sampled in each of three valleys (i.e. Bardoney, Colle de Nivolet, Levionaz; Fig. 1b), which resulted in one plot per vegetation subtype and valley. The plots were established on flat terrain. Each of the nine plots had an extent of 20 m by 20 m (i.e. 400 m^2) and was subdivided into 100 subplots measuring 2 m by 2 m (Fig. 1c).

The plot boundaries were marked with cord and the plot corners with four pegs. The first two pegs were aligned to north-south with a compass. The aberration between 32 UTM to north in the Aosta valley is -2.33°. The aberration between north and the magnetic north is -2°. To compensate these aberrations, we revised the north on the compass with -4°. The quadratic squares were built by three measuring tapes and trigonometric functions.

The percentage cover-abundance of each plant species including mosses and lichens, and of litter, dead wood, bare soil, rock, gravel and water were estimated for each subplot. Ordinal cover estimates from 0 to 100% were done independently by two people to reduce observer bias [10]. We then took the mean of these two cover estimates, which was rounded to no decimal places. Plants with a cover of less than 1% were set to 0.5% cover for simplification of statistical analyses. The vegetation survey was conducted in the middle of the yearly vegetation period during August 2015. Species were identified using 'Flora Helvetica' [11], 'Flora Vegetativa' [12], 'Flora Alpina' [13] and 'Guida alla flora della Valle d'Aosta' [14]. The taxonomic names of species were standardized using TCL-function in R package 'taxonstand' [15], which refers to 'The Plant List' website (www.theplantlist.org). The resulting taxonomic information are provided as a separate table in addition to the plot data.

The plots were established on flat terrain and the plot boundaries were north-south and east-west aligned based on UTM-coordinates in reference system WGS 84, i.e. the subplots IDs are ordered from the north-west corner to the south-east corner. GPS coordinates were taken at each plot corner. We used Garmin Montana 600 to determine the GPS coordinates of the plots' corner points. To get the date and time of the strongest GPS signal (i.e. most satellites available at position), the GPS-satellites' Almanach data was queried. Waypoint averaging was applied to improve the positioning accuracy of the Garmin Montana 600. The position accuracy is given in meters. Additionally, all corners were marked by burying magnets in a soil depth of about 20 cm. This allows precise relocation and long-term monitoring.

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Additional information

The dataset is available online at https://doi.org/10.1016/j.dib.2019.103942.

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7.5 Manuscript 5

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ARTICLE

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Predicted climate shifts within terrestrial protected areas worldwide

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Protected areas (PA) are refugia of biodiversity. However, anthropogenic climate change induces a redistribution of life on Earth that affects the effectiveness of PAs. When species are forced to migrate from protected to unprotected areas to track suitable climate, they often face degraded habitats in human-dominated landscapes and a higher extinction threat. Here, we assess how climate conditions are expected to shift within the world's terrestrial PAs ($n = 137{,}432$). PAs in the temperate and northern high-latitude biomes are predicted to obtain especially high area proportions of climate conditions that are novel within the PA network at the local, regional and global scale by the end of this century. These PAs are predominantly small, at low elevation, with low environmental heterogeneity, high human pressure, and low biotic uniqueness. Our results guide adaptation measures towards PAs that are strongly affected by climate change, and of low adaption capacity and high conservation value.

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Abstract

Protected areas (PA) are refugia of biodiversity. However, anthropogenic climate change induces a redistribution of life on Earth that affects the effectiveness of PAs. When species are forced to migrate from protected to unprotected areas to track suitable climate, they often face degraded habitats in human-dominated landscapes and a higher extinction threat. Here we assess how climate conditions are expected to shift within the world's terrestrial PAs (n=137,432). PAs in the temperate and northern high-latitude biomes are predicted to obtain especially high area proportions of climate conditions that are novel within the PA network at the local, regional and global scale by the end of this century. These PAs are predominantly small, at low elevation, with low environmental heterogeneity, high human pressure, and low biotic uniqueness. Our results guide adaptation measures towards PAs that are strongly affected by climate change, and of low adaption capacity and high conservation value.

Keywords: climate change, novel climate, disappearing climate, conservation biogeography, species conservation, protected area, conservation management

Introduction

Protected areas are essential tools to achieve international biodiversity targets [1]. However, anthropogenic climate change will induce a fundamental redistribution of life on earth that affects the effectiveness of PAs [2] as well as ecosystem functioning and human welfare [3]. Species shift and resize their ranges under climate change, mainly migrating poleward and towards higher elevation as they track suitable habitats [4]. The dynamics of climate change-induced range shifts are in contrast to PAs which are spatially static. As a result, species may lose suitable climatic conditions within PAs and move into unprotected and human-dominated surroundings [5–7] making extinction rates potentially higher than projected [8]. Currently we lack fine-scale resolution on changing climatic conditions within PAs [9], particularly at the global extent [6,10–12].

As the global climate shifts, the climatic conditions found within a given PA may become novel relative to any existing PA (hereafter, 'novel climate conditions'). Conversely, climate change may result in the loss of particular combinations of climatic conditions that are represented among the world's PAs (hereafter, 'disappearing climate conditions'). Here, we sought to quantify these gains and losses in climate conditions in the global network of terrestrial PAs. We did so by collating globally available climate data (i.e. temperature and precipitation parameters) at the 1 km resolution, projecting the change in distribution of these climate conditions under various emission scenarios, and calculating the percentage of PA land with novel and disappearing climate conditions.

For each of 137,432 PAs (Fig. 1), we computed the 'novel climate index' and the 'disappearing climate index'. The novel and disappearing climate indices were calculated at three different scales: local, regional and global. For the local scale, the novel climate index was quantified by the proportion of raster cells of a single PA that hold climate classes in the future scenarios but are currently not present inside the same single PA (i.e. local-scale). For the regional scale, the novel climate index was quantified by the proportion of raster cells of a single PA that hold climate classes in the future scenarios but are currently not present inside the entire PA network of the respective biome (i.e. regional-scale). For the global scale, the novel climate index was quantified by the proportion of raster cells of a single PA that hold climate classes in the future scenarios but are currently not present inside the global PA network (i.e. global-scale). The disappearing climate index was calculated by using the proportion of raster cells inside a single PA that hold climate classes currently but are absent in the future scenarios.

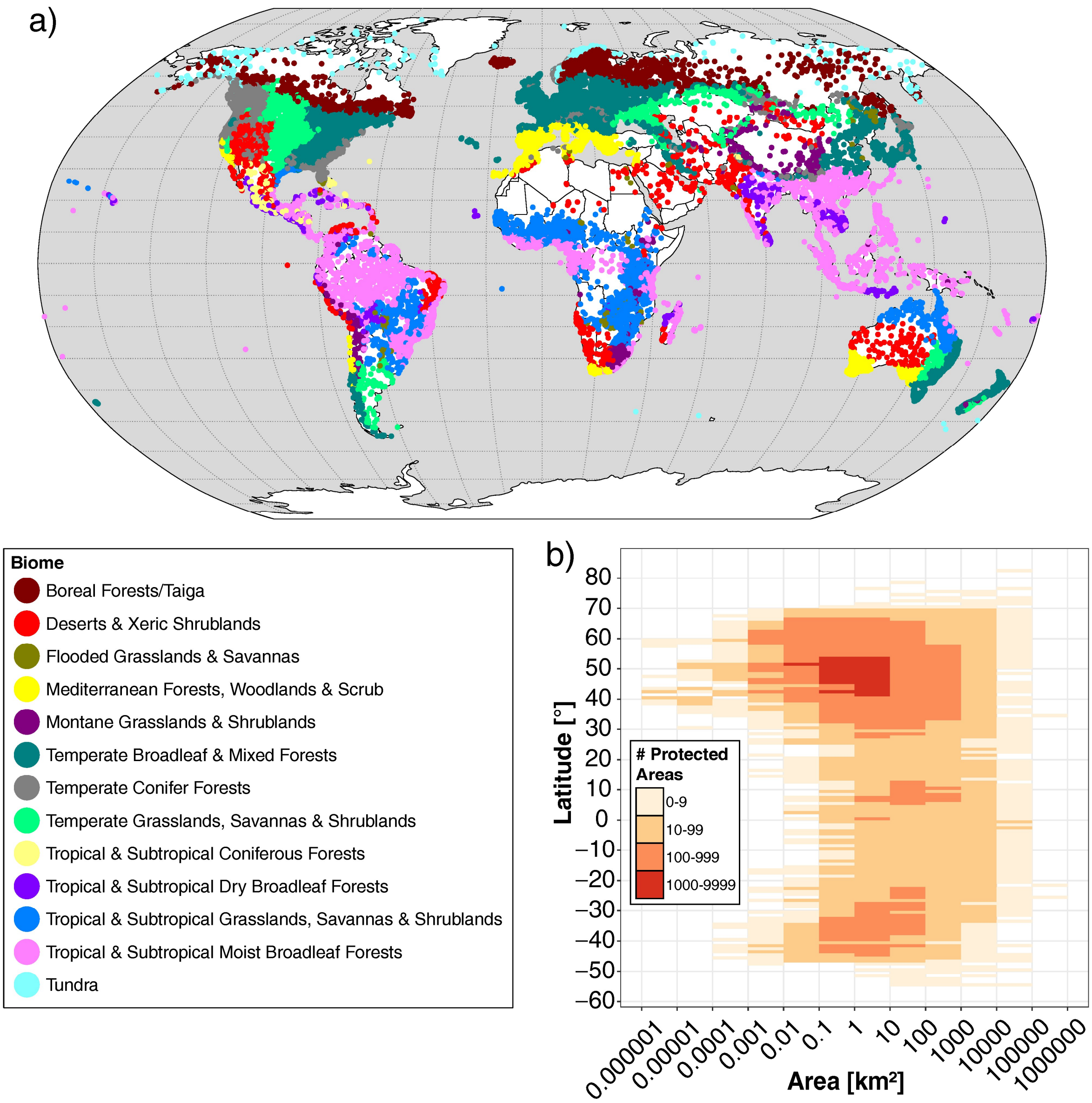

Figure 1. Terrestrial protected areas of the Earth's biomes. a) The climate change analyses involve 137,432 terrestrial PAs that cover 20,658,583 km², which is about 14% of the global land area including Antarctica, and 99.9% of the global PA area. The colored dots represent the centroids of these PAs. The color indicates the biome of the PA. The map was created using open-source software R [16]. b) The majority of PAs are located between 40° and 50° north. Their areas range between 0.1 and 10 km².

To calculate the novel and disappearing climate indices, we assigned a current and a future climate class to each raster cell within each PA by applying the algorithm of Carroll et al. [13]. In contrast to other linear, distance-based climate change algorithms (e.g. Williams et al. [14]), this approach classifies cells in a non-linear fashion with respect to their current and future climate conditions. The climate classifications were based on five independent climate variables that resulted from a principal component analysis (PCA) built on 19 bioclimatic variables. The five-dimensional PCA space (i.e. climate space) was subdivided into climate classes. Each PA raster cell was assigned to a current climate class according to its current climate conditions and to a future climate class according to its future climate conditions. The novel and disappearing climate indices were then calculated based on the cells' current and future climate classes.

We calculated the climate change indices for the year 2070 accounting for future climate projections of the two Representative Concentration Pathways RCP 4.5 and 8.5, and ten different Global Climate Models (GCM). The RCP scenarios are trajectories for atmospheric greenhouse gas concentrations from the Fifth Assessment Report (AR5) of the International Panel on Climate Change (IPCC). The numbers 4.5 and 8.5 indicate the radiative forcing value in Watt per m^2. The moderate scenario RCP 4.5 is associated with a mean global temperature increase of 1.8 °C, while the 'business-as-usual' scenario RCP 8.5 represents continued high greenhouse gas emission, i.e. a high mean global warming of 3.7 °C by the end of the 21st century [15]. We show the mean and standard deviation (sd) of the PAs' novel and disappearing climate indices throughout the ten GCMs for each RCP scenario.

We additionally examined correlations between the local-scale novel and disappearing climate indices and PA characteristics to identify PA attributes that are associated with novel and disappearing climate conditions inside PAs. The PA attributes we examined are area, elevation, topographic heterogeneity (i.e. terrain ruggedness), human pressure (i.e. the human footprint) and biotic uniqueness (i.e. irreplaceability). Environmental heterogeneity includes climate diversity and increases with the area and topographic heterogeneity. Environmental heterogeneity buffers climate-induced biodiversity loss at the local scale [9,11,17,18]. We expect the degree of climate change inside individual PAs to increase with decreasing environmental heterogeneity (i.e. with decreasing PA size, decreasing elevation and decreasing terrain ruggedness). This is because completely novel/disappearing climate conditions are less likely under high environmental and climate diversity. The human footprint quantifies anthropogenic land use and habitat loss that can prevent biodiversity conservation under climate change [18]. Irreplaceability is a measure of biotic uniqueness. It quantifies the overlap of PA area with ranges of global Red List species [19] and thus the current conservation value of PAs regarding threatened species worldwide. We assume that the vulnerability of individual PAs to climate change (i.e. the risk of losing irreplaceability under climate change) increases with the magnitude of climate change (i.e. with increasing area of novel/disappearing climate conditions), with decreasing climate change buffer (i.e. with decreasing environmental heterogeneity) and with increasing human pressure and irreplaceability. Mean values of the local-scale novel and disappearing climate indices were highly correlated (RCP 4.5: Pearson's coefficient r=0.96, RCP 8.5: r=0.97). We subsequently concentrated on the novel climate index in the main text; see Supplementary Figures 1-5 for the disappearing climate index.

We find that PAs in the temperate and northern high-latitude biomes are predicted to experience particularly high proportions of climate conditions that are novel within the PA network on a local, regional and global scale. These PAs are predominantly small, at low elevation, with low environmental heterogeneity, high human pressure, and low biotic uniqueness. These results guide adaptation measures towards PAs that are not only strongly affected by climate change, but also of low adaption capacity and high conservation value.

Results

Novel climate conditions within PAs

PAs could experience, on global average, 41% (±9% sd) of local-scale novel climate conditions until 2070, following RCP 4.5, and 54% (±10% sd) according to RCP 8.5 (Fig. 2a, b). The mean values of the local-scale novel climate index are also moderately correlated with the standard deviations of the local-scale novel climate index (Fig. 2c, d; RCP 4.5: $r=0.56$, $p<0.001$ using a modified t-test accounting for spatial autocorrelation [20]; RCP 8.5: $r=0.43$, $p<0.001$). Under both scenarios, 'Montane Grasslands & Shrublands' and 'Tropical & Subtropical Coniferous Forests' are biomes that include PAs with, on average, the lowest predicted proportions of novel climate conditions at the local scale (Fig. 3a, b). In contrast, the biomes 'Temperate Conifer Forests' and 'Temperate Grasslands, Savannas & Shrublands' contain PAs with the highest predicted proportions of novel climate conditions at the local scale. The standard deviation shows a very similar order at both extremes (Fig. 3c, d).

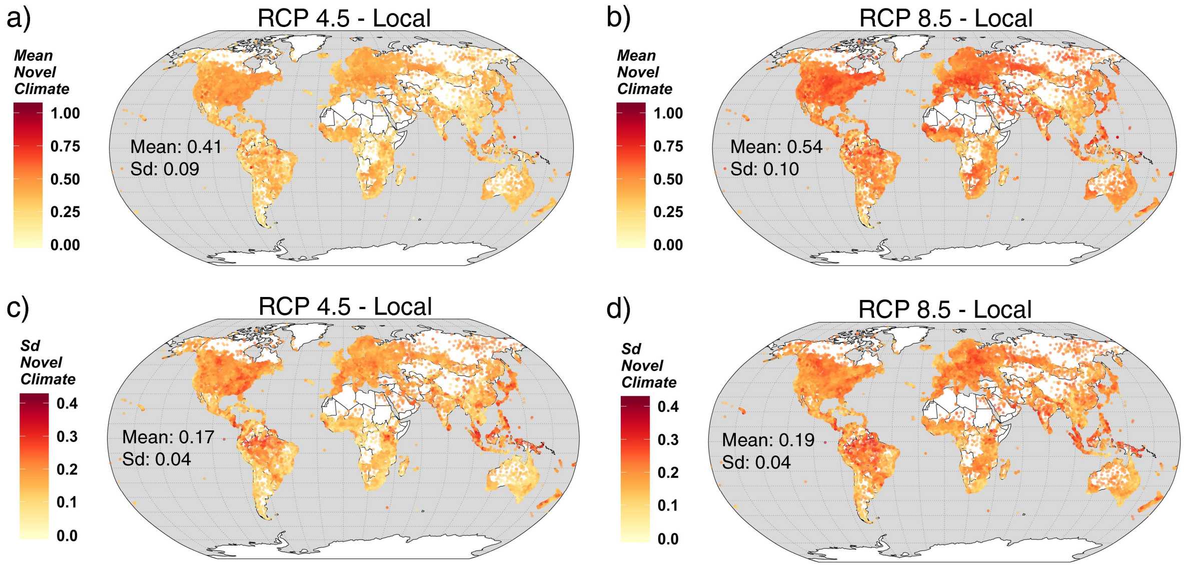

Figure 2. Local-scale novel climate index of terrestrial protected areas worldwide. The local-scale novel climate index shows the proportion of raster cells inside a PA that hold climate classes in the future which are currently not present in the PA. The mean (panels a and b) and standard deviation (panels c and d) of the local-scale novel climate index comprise future climate data from ten GCMs under RCP 4.5 and 8.5. Sd represents the variation of the local-scale novel climate index resulting from ten GCMs. a) Mean of the local-scale novel climate index under RCP 4.5. b) Mean of the local-scale novel climate index under RCP 8.5. c) Sd of the local-scale novel climate index under RCP 4.5. d) Sd of the local-scale novel climate index under RCP 8.5. For each metric in a) to d), the mean and standard deviation across all 137,432 PA values are also given inside the global maps. Data on climate change metrics and other characteristics per PA are given as Supplementary Data 1. The maps were created using open-source software R [16].

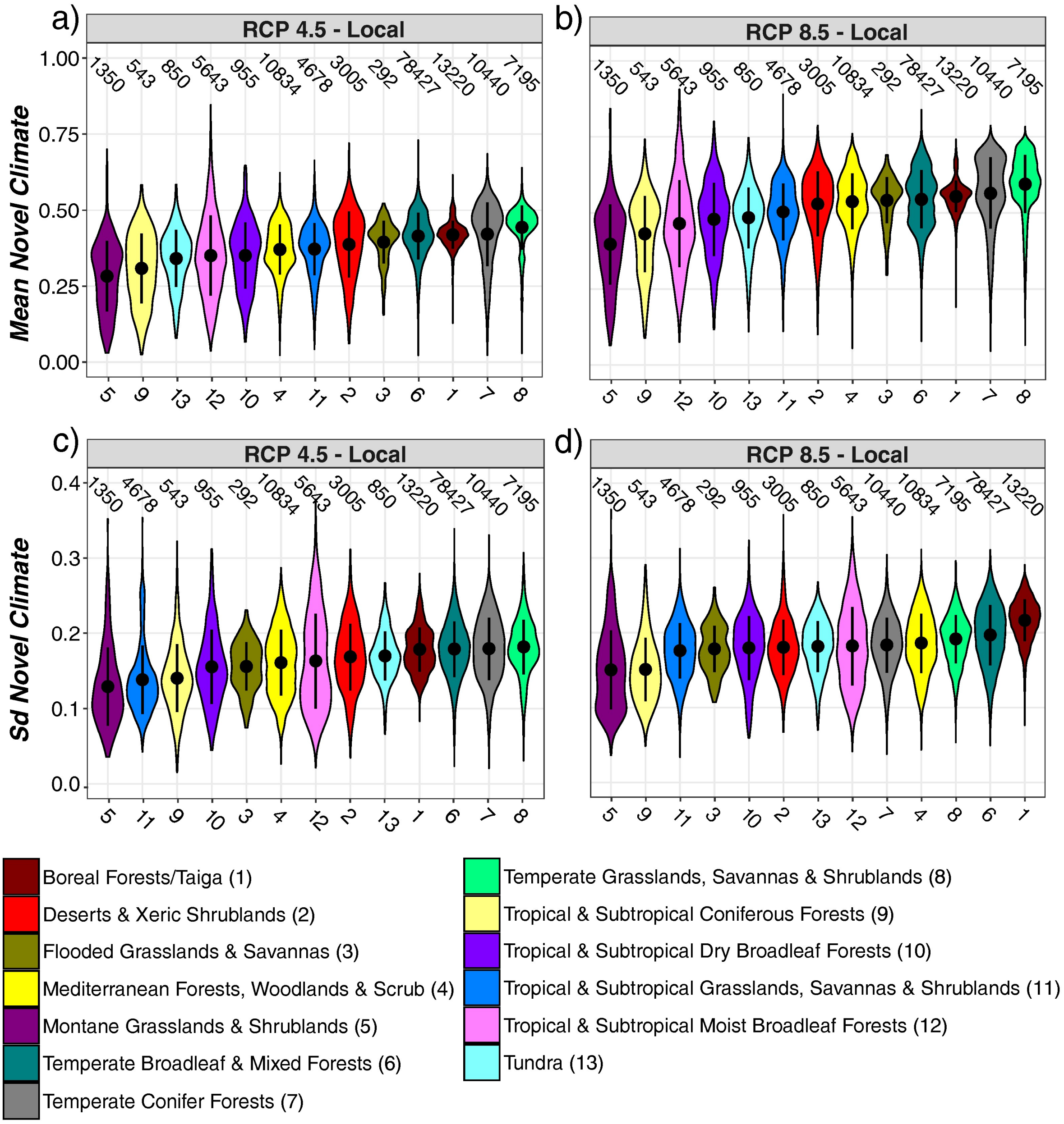

Figure 3. Local-scale novel climate index of terrestrial protected areas worldwide, summarized by biomes. The mean of the local-scale novel climate index under a) RCP 4.5 and b) RCP 8.5. The standard deviation (sd) of the local-scale novel climate index under c) RCP 4.5 and d) RCP 8.5. Sd represents the variation of the local-scale novel climate index resulting from ten GCMs. Violins are ordered by increasing mean. Black dots and attached lines within violins represent the mean ± standard deviation. Black numbers above violins indicate the number of PAs within the respective biome. Data on climate change metrics and other characteristics per PA are given as Supplementary Data 1. Source data are provided as a Source Data file.

The values of the regional and global-scale novel climate indices demonstrate similar geographical patterns (Fig. 4 and 5). The regional-scale index reveals higher values than the global-scale index. The biomes 'Temperate Grasslands, Savannas & Shrublands' and 'Flooded Grasslands & Savannas' contain PAs with, on average, the highest predicted proportions of novel climate conditions on the regional scale, while 'Tropical & Subtropical Moist Broadleaf Forests' and 'Tropical & Subtropical Coniferous Forests' contain PAs with the lowest predicted proportions of novel climate conditions at the regional scale (Fig. 5a, b). The biomes 'Flooded Grasslands & Savannas' and 'Temperate Grasslands, Savannas & Shrublands' include PAs with, on average, the highest predicted proportions of novel climate conditions at the global scale, whereas 'Tundra' and 'Tropical & Subtropical Coniferous Forests' include PAs with the lowest predicted proportions at the global scale (Fig. 5c, d). Note, however, that the novel and disappearing climate indices may over- or underestimate ecological change associated with climate change in some biomes due to the different number of eco-regions within biomes (Supplementary Fig. 8). The climate change metrics may overestimate the ecological change within PAs in 'Montane Grasslands & Shrublands', 'Temperate Broadleaf and Mixed Forests', 'Temperate Conifer Forests', 'Tropical & Subtropical Coniferous Forests' and 'Tropical & Subtropical Grasslands, Savannas & Shrublands'. The indices may underestimate the ecological change in 'Deserts & Xeric Shrublands' and 'Mediterranean Forests, Woodlands & Scrub'. The number and size of PAs (Fig. 1) differ substantially between biomes.

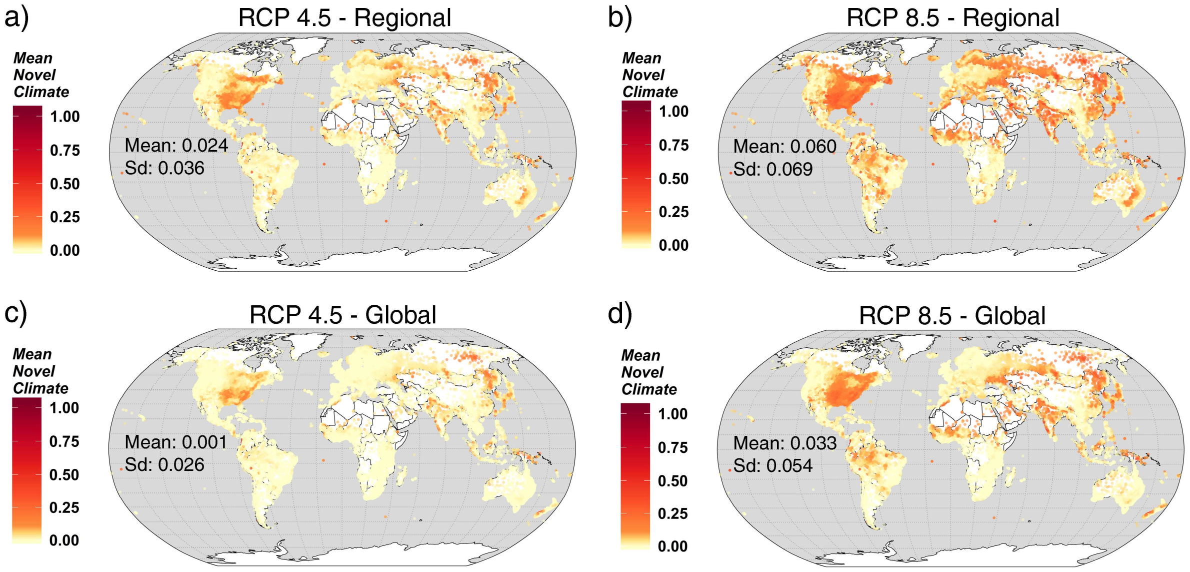

Figure 4. Regional and global-scale novel climate index of terrestrial protected areas worldwide. The regional-scale novel climate index shows the proportion of raster cells inside a PA that hold climate classes in the future which are currently not present in the entire PA network of the respective biome. The global-scale novel climate index indicates the proportion of raster cells inside a PA that hold climate classes in the future which are currently not present in the global PA network. The mean of the novel climate indices comprises future climate data from ten GCMs under RCP 4.5 and 8.5. a) Mean of the regional, biome-specific novel climate index under RCP 4.5. b) Mean of the regional, biome-specific novel climate index under RCP 8.5. c) Mean of the global-scale novel climate index under RCP 4.5. d) Mean of the global-scale novel climate index under RCP 8.5. For each metric in a) to d) the mean across all 137,432 PA values are also given inside the global maps. Data on climate change metrics and other characteristics per PA are given as Supplementary Data 1. The maps were created using open-source software R [16].

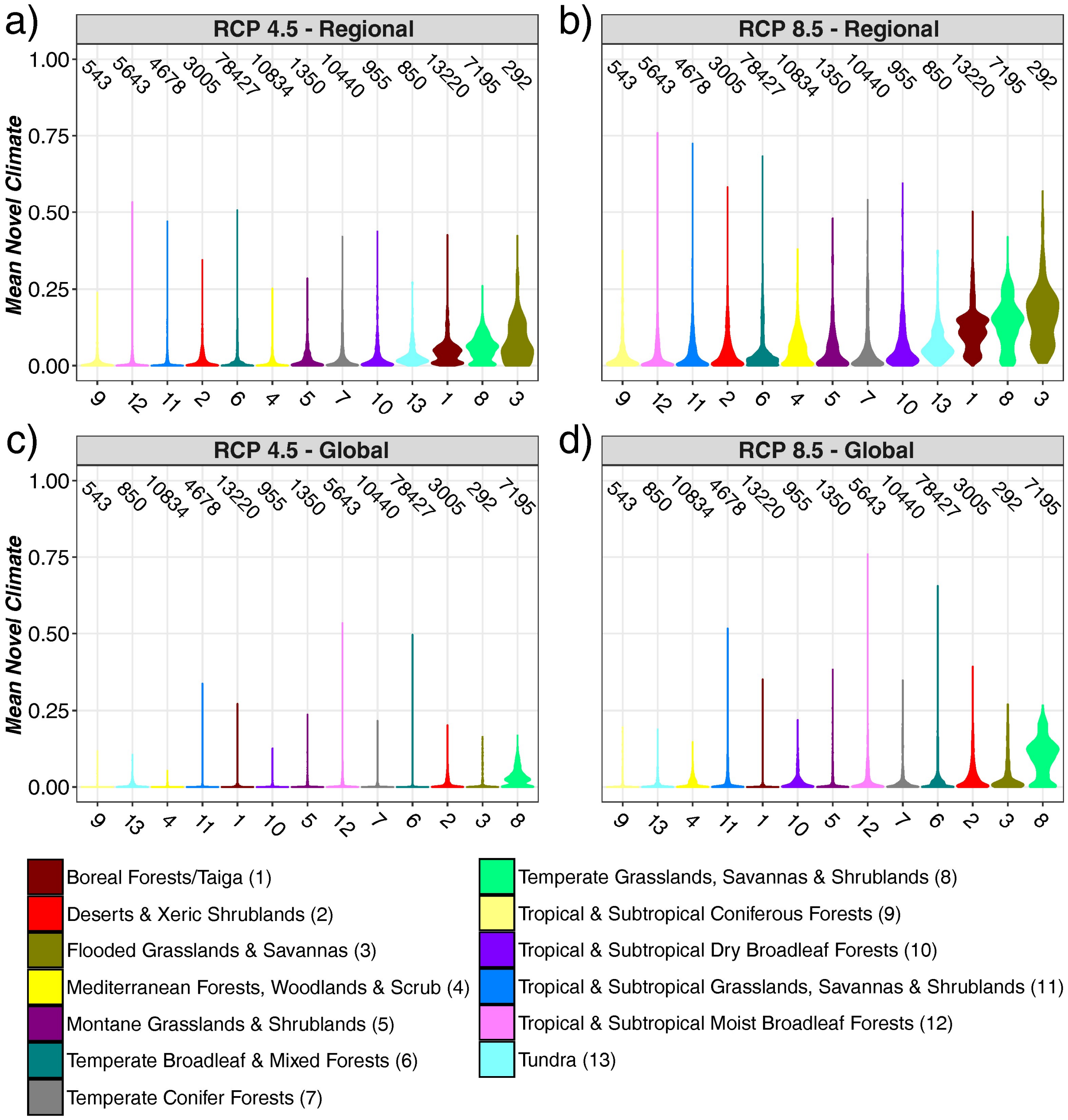

Figure 5. Regional and global-scale novel climate index of terrestrial protected areas worldwide, summarized by biomes. The mean of the regional-scale novel climate index across ten GCMs under a) RCP 4.5 and b) RCP 8.5. The mean of the global-scale novel climate index across ten GCMs under c) RCP 4.5 and d) RCP 8.5. Violins are ordered by increasing mean. Black numbers above violins indicate the number of PAs within the respective biome. Data on climate change metrics and other characteristics per PA are given as Supplementary Data 1. Source data are provided as a Source Data file.

Relationships between novel climate conditions and PA characteristics

We found negative significant ($p<0.05$ using a modified t-test accounting for spatial autocorrelation [20]) correlations when pooling PAs worldwide (Fig. 6, 'Overall'): between area (RCP 4.5: $r=-0.15$; RCP 8.5: $r=-0.13$), between elevation (RCP 4.5: $r=-0.19$; RCP 8.5: $r=-0.1$), and between irreplaceability and the local-scale novel climate index (RCP 4.5: $r=-0.13$, RCP 8.5: $r=-0.13$). Even though the global correlations between the local-scale novel climate index and topographic heterogeneity as well as the human footprint show equally high *r*-values for both scenarios, the modified t-test revealed no significance due to spatial autocorrelation. Inside individual biomes, the local-scale novel climate index mainly negatively correlates with topographic heterogeneity and positively correlates with the human footprint index.

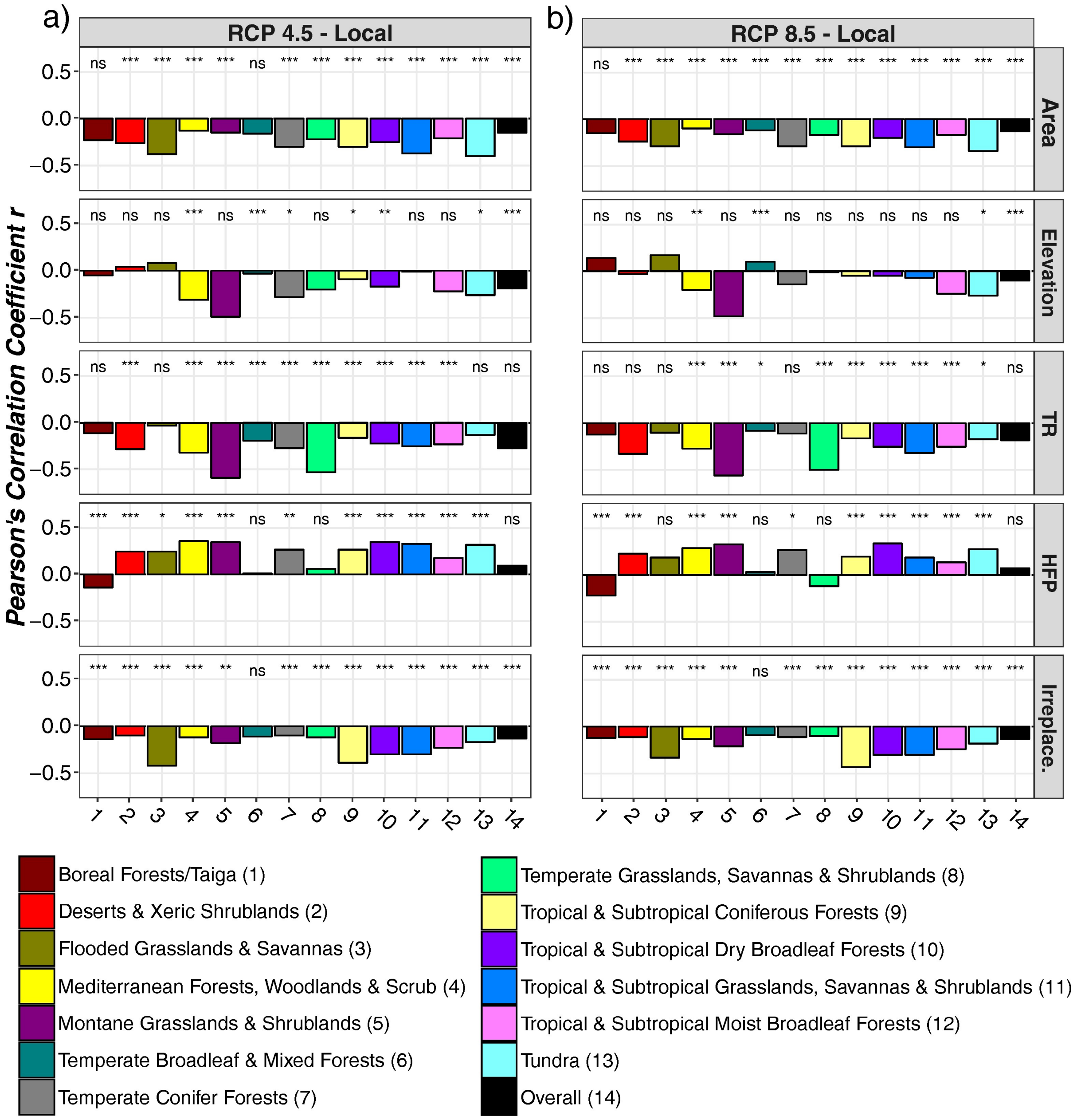

Figure 6. Correlation between the mean values of the local-scale novel climate index and protected area characteristics, separated by biome and RCP scenario. a) RCP 4.5 and b) RCP 8.5. Bars show Pearson's correlation coefficients *r*. Asterisks represent the significance level considering a modified t-test accounting for spatial autocorrelation [20] (*: $p≤0.05$, **: $p≤0.01$, ***: $p≤0.001$), while 'ns' implies non-significant ($p>0.05$) correlation. Note that 'TR' stands for terrain ruggedness, 'HFP' for the human footprint index and 'Irreplace.' for irreplaceability. Data on climate change metrics and other characteristics per PA are given as Supplementary Data 1. Source data are provided as a Source Data file.

Discussion

We found that PAs of temperate and northern high-latitude biomes are predicted to experience large proportions of novel climate conditions at the local, regional and global scale. Large proportions of novel climate conditions at the regional and global scale could also appear in PAs of flooded grasslands and savannas. Protected areas that are potentially affected by high proportions of locally novel climate conditions tend to contain low topographic heterogeneity and a large human footprint, suggesting increased vulnerability. However, irreplaceability tends to decrease with an increase in locally novel climate conditions. Hence, PAs that are very important for the conservation of Red List species seem to be less affected by local-scale novel climate conditions.

Novel and disappearing climate conditions indicate novel and disappearing habitat conditions. When PAs gain novel habitats, potentially invasive species might migrate into PAs [21]. When PAs lose habitats, species are likely to migrate out of PAs into unprotected surroundings [5–7]. In both cases, the communities inside PAs are modified with unknown consequences for ecosystem functioning. Since ecosystem functioning depends on biodiversity [22], the integrity of ecosystems inside PAs is at risk when species diversity decreases through invading and migrating species. Novel and disappearing climate metrics are basic indicators of such risks.

Our findings can be compared to Loarie et al. [23], who demonstrated that large PAs in the desert biome will widely retain their current temperature conditions, while small PAs in the Mediterranean biome and in temperate coniferous forests will largely lose their current temperature conditions. Several studies agree that the magnitude of anthropogenic climate change, i.e. the degree of dissimilarity between current and future climate, is predicted to be highest in the tropics, subtropics, and a few northern high-latitude regions [14,23–31]. The (sub-)tropical biomes and northern high-latitude regions could primarily experience novel, non-analogue climates (i.e. future climates without modern analog) [14,25,26,29–31]. The velocity of climate change may be lowest in mountainous regions and highest in continental plains [23,26,30]. Li et al. [27] illustrated that climate change vulnerability is expected to be highest in plains such as deserts and xeric shrublands, whereas intact boreal and tropical forests as well as polar regions can be capable of mitigating future climate impacts. These authors revealed that low environmental heterogeneity and small temperature gradients imply high biotic attrition in continental basins under climate change. In addition, areas of high northern latitudes are predicted to become climate-vulnerable in the future. However, a direct comparison of the approach taken by Li et al. with our study is not feasible due to the methodological differences.

We do not indicate that mountain ecosystems inside PAs are less prone to climate change, even though novel climate conditions at the local scale decreases with the increasing elevation of PAs. Climate change may even have a disproportional impact on mountain biomes as exemplified by current melting glaciers and permafrost or increasing mass movements [32]. However, at the landscape scale of mountain PAs, the heterogeneity of site conditions may maintain high biodiversity under climate change, in contrast to PAs of lowland biomes [11]. Mountain PAs play an important role for future biodiversity conservation. They are characterized by large areas, high topographic and thus climatic diversity, low human pressure, and high irreplaceability, qualifying them as places for future climate refugia.

We found the numbers and sizes of PAs to explain the proportion of novel and disappearing climate conditions at the local scale inside PAs. This applies strongly to PAs in the temperate zone that include well-developed industrial nations with high population densities limiting the options to set aside large areas for nature conservation. Temperate biomes exhibit a large number of small PAs at the lower elevation not covering a wide range of environmental conditions (i.e. heterogeneity) that could compensate high proportions of novel and disappearing climate conditions. Particularly in the temperate regions of Europe, the legacy of land use, high population density, and highly fragmented landscapes are reflected in the establishment of many comparatively small PAs [6].

The outcomes of this study suggest several implications for conservation action. The negative relationships between climate change indices and PA attributes such as size, elevation, and topographic heterogeneity emphasize the importance of expanding and establishing large-scale PAs. Such PAs should cover high climatic and environmental diversity that can buffer climate change impacts on biodiversity. The biotic uniqueness of PAs is also a major criterion for the conservation value of PAs [33]. Protected areas showing a high proportion of locally novel or disappearing climate conditions seem to be less unique for the global conservation of Red List species to date (i.e. low irreplaceability). This relationship may result from the fact that species richness generally decreases towards the poles, while high-latitude regions warm fastest under anthropogenic climate change. However, the positive relationships between the climate change indices and the human footprint indicate that high proportion of human land use will hinder the adaption and migration of species under climate change. These findings should direct policy towards the restoration and maintenance of habitat quality and connectivity, not only within, but also between PAs. The co-occurrences of threatened biota, high human pressure, low climate-buffer capacity and high magnitudes of climate change suggest a high vulnerability of PAs, based on which conservation strategies need to be developed and prioritized [13,25,27]. While the management of PAs varies across the globe, particularly the management effectiveness of climate-vulnerable PAs should be enhanced. Current conservation actions focusing on the management of single habitats and species neglects the majority of biota; revising current conservation policy and pro-active biodiversity management (e.g. habitat restoration, connection, and species translocations) will be essential adaption strategies in view of the climate change velocity [17,34]. We also suggest establishing climate-proof PA networks to overcome the static applications of spatial conservation; climate-proof PA systems implement spatially and temporally dynamic PAs that track the ecological niche of species under climate change [35]. Relocated niches can also be translated into trans-PA conservation schemes [10]. Importantly, early action will be more efficient and less expensive than no or delayed interventions [36].

Nevertheless, our approach has limitations. Because climate niches of species can extend beyond protected areas, novel climate conditions relative to the climate pool of protected areas does not necessarily mean the entire habitat for species inside a protected area will be lost. Novel climate conditions may have even positive effects, e.g. when threatened species migrate into PAs [2]. We did not consider unprotected surroundings where species may also migrate and persist. Still, protected areas are the main tools for biodiversity conservation [19]. Here we highlight only novel and disappearing climate conditions, but there are many more dimensions of climate change to which species react [26]. The novel and disappearing climate indices do not account for historic inter-annual climate variability. Past inter-annual climate variability increases with latitude and is associated with large-ranged species, while climate stability characterizes areas with many small-ranged species, such as those at low latitudes [37]. Small-range species, especially those found in the lowland tropics, are at a higher risk of range attrition under climate change than species at higher latitudes [38]. Ecosystems that have experienced high, historical inter-annual climate variability are expected to be more resilient to climate change [9]. However, the effect of inter-annual climate variability on ecosystems can hardly be generalized across ecosystems [39]. Climate data resolution may also underestimate micro-refugia (i.e. local habitats) [40]. The detection of climate change velocity inside PAs might additionally foster climate-proof conservation strategies [9]. Furthermore, climate is not the only factor that determines species' habitats. Habitat can be degraded by other means such as human land use. To account for all these aspects in future studies and to meet global conservation goals, financial support must increase by at least one order of magnitude [41].

This study serves as an information resource for climate-smart conservation policy and management at local to global extent. The results can guide the distribution of conservation funds and prioritization. However, recommending an optimal investment strategy for biodiversity conservation under climate change requires a complex analytical framework including ecological and economic factors [42]. High rates of climatic displacement within PAs in the temperate biomes do not suggest focusing conservation efforts only here. Protected areas in less developed countries harbor more biodiversity and are often less effectively managed due to lack of conservation laws, staff, funds, and political willingness [1]. International conservation strategies need to include the demands of a complex setting considering all aspects of climate change as well as biodiversity and socio-economic factors. Nevertheless, it is time to realize the impact of climate change on PAs when discussing conservation policy [43]. Variation in future trends can be quantified, e.g. through the variation in climate models or the deviation between scenarios, but should not be a hindrance for inaction. For this purpose, it is important to increase societal and political awareness about the consequences of climate change for biodiversity and human well-being.

Methods

Protected area data

The World Database on Protected Area (WDPA) [44] includes boundary (i.e. polygon) data for 201,464 purely terrestrial designated PAs. These PAs cover 20,702,558 km², amounting to around 15% of the Earth's land surface. We rasterized these PA polygons in the same resolution as the climate data (30 arc seconds, i.e. approx. 900 m at the equator) via cell center coverage. Thus, relatively small PAs and PAs which have an elongated shape may cover only a few or even no raster cells. After rasterization, 137,735 PAs remained, from which another 303 PAs were excluded because the centroids of those 303 PAs were located in the 'Mangroves' biome [45] and are consequently assumed to be coastal PAs. Eventually, we considered 26,038,594 cells that are covered by 137,432 PAs, which still comprise a total area of 20,658,583 km² (i.e. 14% of the global terrestrial surface and 99.9% of the global PA area on land). We refer to these raster cells as 'protected cells'.

To identify PA attributes that are particularly associated with climate change inside PAs, we related several PA characteristics to the novel and disappearing climate indices. We assigned each PA to its biome by overlaying the PA centroids and the biome polygons provided by Olson et al. [45]. Coastal mangrove PAs were excluded. The biome informs us about dominant ecosystem types. The PA area is given by the WDPA. The size of the PA influences the number of resources for species' adaption and migration in response to climate change. We extracted the median elevation of each PA from a digital elevation model with a resolution of 30 arc seconds provided by Amatulli et al. [46]. The median elevation indicates the geographical location of PAs in highland or lowland regions. The Terrain Ruggedness Index (TR) is a measure of topographic heterogeneity. This product is based on 90 m elevation data from the Shuttle Radar Topography Mission and has a final resolution of 30 arc seconds [46]. The TR was calculated as the mean of the absolute differences in elevation between a protected cell and its eight adjacent protected cells. Planar area has a TR of 0 m. The TR of mountain areas can be as high as 2000 m in the Himalaya region [46]. We used the median of the TR values inside PAs to represent the topographic heterogeneity of each PA. Topographic heterogeneity implies elevational gradients as well as climatic and habitat heterogeneity. Topographic heterogeneity reflects the adaptive capacity of PAs' biodiversity to impacts of climate change [17]. The probability of species tracking suitable environmental conditions within the same PA – via adaptation or migration – is higher in areas with more heterogeneous conditions. Environmental heterogeneity buffers climate change effects on ecosystems [9]. The human footprint index 2009 comprises eight indicators of human impact on natural systems that stem from in-situ and remotely sensed data [47]: population density, buildings, electric infrastructure, roads, railways, navigable waterways, cropland and pasture. The human footprint of a PA was calculated by the median human footprint of the raster cell values that fall within the PA. The irreplaceability of PAs is a measure of biotic uniqueness and quantifies the degree of overlap between each PA and the range of species of the IUCN Red List [19]. In total, 21,419 species were considered: 6240 amphibians, 9793 birds and 5263 mammals. Since irreplaceability was calculated for the WDPA (Version October 2012), we could link the irreplaceability index to our PA data by the WDPA ID.

Climate data

We used global climate data with a resolution of 30 arc seconds (i.e. approx. 1 km) provided by the WorldClim project (Global Climate Data Version 1.4, Hijmans et al. [48]). The current climate data was produced by interpolations of observed data of the time period between 1960 and 1990. The future climate data were downscaled from Global Climate Models (GCMs) of the Coupled Model Intercomparison Project Phase 5 (Intergovernmental Panel on Climate Change, Fifth Assessment Report). We implemented the Representative Concentration Pathway RCP 4.5 and 8.5, and the following GCMs for the year 2070, i.e. the average of period 2061-2080: BCC-CSM1-1, CCSM4, CNRM-CM5, GFDL-CM3, HadGEM2-AO, INMCM4, IPSL-CM5A-LR, MIROC5, MPI-ESM-LR and MRI-CGCM3. We chose pathways RCP 4.5 and 8.5 because they delimit a range of future climate conditions that are likely to occur. We only considered raster cells that hold information about each of the 19 bioclimatic variables provided for current and future climate conditions. We refer to these raster cells as 'climate cells' hereafter.

Climate change analyses

We calculated the novel and disappearing climate indices of each PA for each GCM and RCP. The calculation of the novel and disappearing climate indices is only based on climate cells that are covered by a protected area (i.e. protected climate cells). One reason for this approach is that PAs are expected to be the only remaining isolated sites for global biodiversity conservation in future [49]. Another reason refers to the enormous computing capacity that would be required when considering the climate pool of the global land surface at a spatial resolution of 1 km. Nevertheless, the climate pool of the global PA network well represents the climate pool of the global land surface because the PAs are distributed worldwide (Fig. 1). However, this approach entails disadvantages that are discussed in the main text.

To identify protected climate cells that considerably change climate conditions between the present and future, we adapted the algorithm of Carroll et al. [13], which is based on Hamman et al. [50]. Accordingly, we applied a Principal Component Analysis (PCA). We constructed the PCA space based on a random sample of 10,000,000 (i.e. 40% of the total amount of protected climate cells). This representative sample is still computationally manageable. The random sampling implies that each climate type is sampled proportionally to its extent. The PCA was built on both current and future climate information because all possible climate conditions now and in the future are supposed to be represented by the PCA [10]. We considered the first five PCA axes for further analyses to reduce the climate information from 19 bioclimatic variables to five independent variables. As an example, the first five PCA axes partially built on future climate data from BCC-CSM1-1 under RCP 8.5 account for 92% of the variation in the 19 original bioclimatic variables. These first five axes correspond to thermal and hydraulic variables alike (Supplementary Table 1 and 2). We then predicted for each protected climate cell the current and future position on the first five PCA axes. Subsequently, each protected climate cell received a current and future position in the five-dimensional climate space. The five-dimensional climate space was then subdivided into climate classes. To create those classes, each of the first five PCA axes was subdivided into equally sized bins. Then the bins along each axis were grouped according to their spatial intersection in the five-dimensional space. Finally, each group of intersecting bins was taken to constitute a climate class. Each climate cell could now be assigned to a current climate class based on the cell's current position in the PCA space and to a future climate class based on the cell's future position in the PCA space. Hence, each cell holds a current and future climate class. If current and future cell positions fall within the same class, it is assumed the climate of that cell will not change. Since the delimitation of classes in the five-dimensional PCA space is crucial for the result, we randomly shifted the bin limits 30 times around the actual bin limits within the range of the bin width, and took the mean of the 30 different outcomes, which was adapted from Carroll et al. [13].

This non-linear classification approach needs less computing capacity and time than classic and linear distance methods (e.g. Williams et al. [14]) because in the non-linear classification method there is no need to calculate pairwise distances between very large numbers of grid cells [50]. Very large numbers of grid cells are given when the spatial resolution is high. This non-linear classification approach has several drawbacks. It does not account for distance or dissimilarity between current and future climate conditions in an ordinal way because ordinal distances between climate classes are not considered. The non-linear classification algorithm does also not incorporate historic inter-annual climate variability, which could improve the assessment of future climate distance/dissimilarity [14].

The number of PCA axes considered and the bin width used for subdividing the PCA axes determine the total number of climate classes. The novel and disappearing climate indices are sensitive to the number of axes and the bin width because the indices are based on the number of climate classes. Carroll and colleagues [13] state that applying five axes and a bin width of 2 PCA units are appropriate for the Western Hemisphere. Here we conducted another sensitivity analysis that demonstrated the relationship between the bin width and the resulting number of climate classes given by five PCA axes. We accounted for five PCA axes because they explain 92% of the variation in the original climate data and are still computationally manageable. For the sensitivity analysis, climate data from BCC-CSM1-1 under RCP 8.5 were taken as an example. The more climate classes are defined, the more sensitive are the indices to future changes, i.e. the higher are the index values eventually. In our example, a bin width of 2 PCA units yielded 430 climate classes worldwide (Supplementary Fig. 7a, red line); 320 classes are defined by current climate conditions, and 372 by future conditions; the present and future conditions shared 262 classes. The threshold of 2 PCA units (Supplementary Fig. 7b, red line) balances underestimation of climate change by very broad climate classes and overestimation of climate change by very narrow classes. Consequently, we agree with Carroll et al. [13] not only for reasons of comparability, and use five PCA axes and a PCA bin width of 2 PCA units. Additionally, the resulting climate change metrics depend on the number of climate variables put into the PCA and the spatial resolution of climate data. The geographic patterns of climate change estimates, however, are robust against these user choices [50]; this makes this approach useful for prioritizing conservation management.

To assess the degree of ecological differentiation between climate classes resulting from a bin width of 2 PCA units, we compared the number of climate classes to the number of ecoregions worldwide [45]. Taking again BCC-CSM1-1 under RCP 8.5 as an example, 320 classes were calculated for current climate conditions worldwide. Olson et al. [45] describe 867 present ecoregions nested within 14 biomes. Because the ecoregion richness is almost three times as high as the number of current climate classes, our climate change metrics underestimate, at the global scale, the ecological change that is associated with changes of the climate class. However, at the biome scale, the relation between the number of ecoregions and current climate classes may be different. We therefore related the number of climate classes to the number of ecoregions per biome. This comparison serves as a caveat that our metrics may overestimate climate-induced ecosystem change in some biomes and underestimate in others. Because of the number of ecoregions deviating from the number of current climate classes to more than 25% (Supplementary Fig. 8), the climate change metrics may considerably overestimate the ecological change within PAs in ’Montane Grasslands & Shrublands’, ‘Temperate Broadleaf and Mixed Forests’, ‘Temperate Conifer Forests’, ‘Tropical & Subtropical Coniferous Forests’ and ‘Tropical & Subtropical Grasslands, Savannas & Shrublands’, and underestimate in ‘Deserts & Xeric Shrublands’ and ‘Mediterranean Forests, Woodlands & Scrub’.

Our cell classification procedure allows for the calculation of a variety of climate change indices. Here we focused on two indices of fundamental importance [9,14,51,52]: the novel climate index and the disappearing climate index. We calculated the novel climate index and the disappearing climate index for each PA at the local, regional and global scale. We defined the local-scale novel climate index as the proportion of cells within a single PA that hold climate classes in the future projections which do currently not exist within the same single PA (i.e. at the local scale). We defined the regional-scale novel climate index as the proportion of cells within a single PA that hold climate classes in the future projections which do currently not exist within the entire PA network of the respective biome (i.e. at the regional scale). We defined the global-scale novel climate index as the proportion of cells within a single PA that hold climate classes in the future projections which do currently not exist within the global PA network (i.e. at the global scale). The disappearing climate index was calculated by the proportion of cells within a single PA that currently hold climate classes which do not exist in the future. The climate of a protected climate cell can be novel and disappearing at the same time. The indices are based on cell counts and do not hold any unit. Since the raster cells represent area, the indices can be perceived as an estimate of proportional area of novel and disappearing climate conditions inside individual PAs. The local-scale novel and disappearing climate indices are more sensitive indicators of climate change than the regional and global-scale indices because the local-scale indices were calculated based on a smaller geographical extent including fewer climate classes. The fewer climate classes are found inside a geographical extent, the more likely are novel and disappearing climate classes inside this extent, which will increase the novel and disappearing climate indices. The regional and global-scale indices of disappearing climate conditions are less sensitive indicators of climate change because they represent the proportion of climate inside a PA that is in the future not only lost from the PA (i.e. local-scale), but also from the entire PA network of the biome (i.e. regional-scale) or from the global PA network (i.e. global-scale). Both indices exhibit several weaknesses for the benefit of computational feasibility: they do not represent climate distance or dissimilarity in an ordinal way. While they indicate the spatial extent of novel and disappearing climate conditions, they do not show how dissimilar the future climate will be compared to the current climate. Furthermore, the metrics do not account for historic inter-annual climate variability. Inter-annual climate variability increases with latitude and is associated with large-range species, while climate stability characterizes areas with small-range species, such as those at low latitudes [37]. The effects of inter-annual climate variability on ecosystems cannot be generalized and depend on the current ecosystem state [39]. Small-range species, however, are at particular risk of range attrition under global warming [38]. We calculated the mean and standard deviation of the indices over ten GCMs per RCP. The standard deviation and value range between RCP 4.5 and 8.5 are estimates of variation, i.e. uncertainty in climate predictions.

Statistical analyses

We tested for correlations between climate change indices as well as between climate change indices and PA characteristics by using Pearson's correlation coefficient *r* and a modified t-test accounting for spatial autocorrelation [20].

Data availability

All data used in this study are open. Data produced in this study are attached as Supplementary Data 1 and stored in the figshare repository (https://doi.org/10.6084/m9.figshare.9804350). See Carroll et al. [13] for R code. The source data underlying Figures 3, 5 and 6 as well as Supplementary Figures 2, 4, 5, 6, 7 and 8 are attached as a Source Data file.

Code availability

The algorithm we used to calculate climate change is adapted from Carroll et al. [13].

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Author contributions

S.H. conceived the idea, conducted the analysis and led the writing. S.I. and C.B. contributed to the writing.

Competing interests

The authors declare no conflicts of interests.

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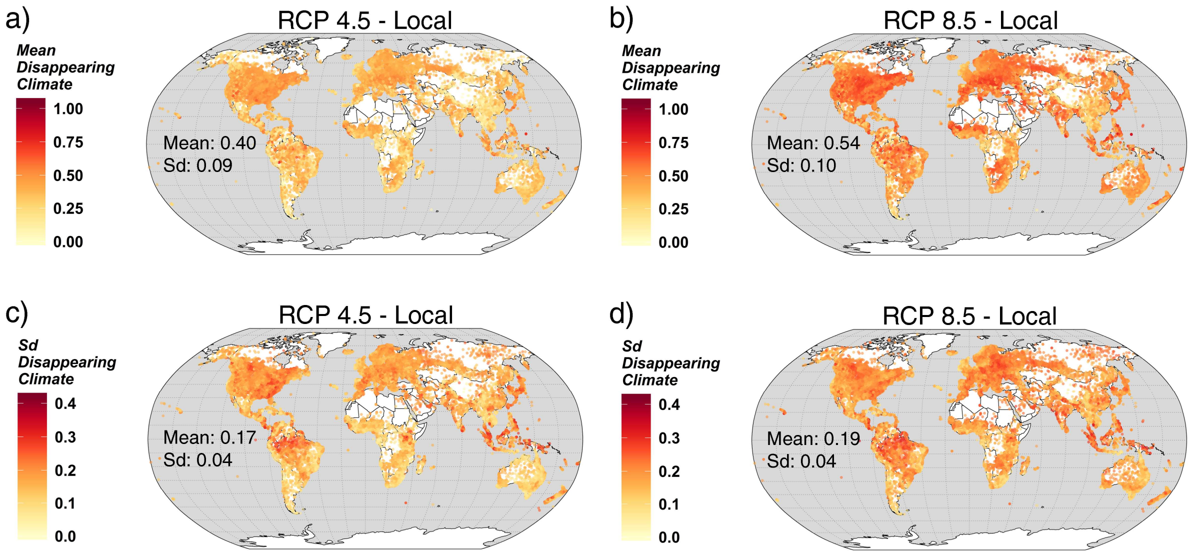
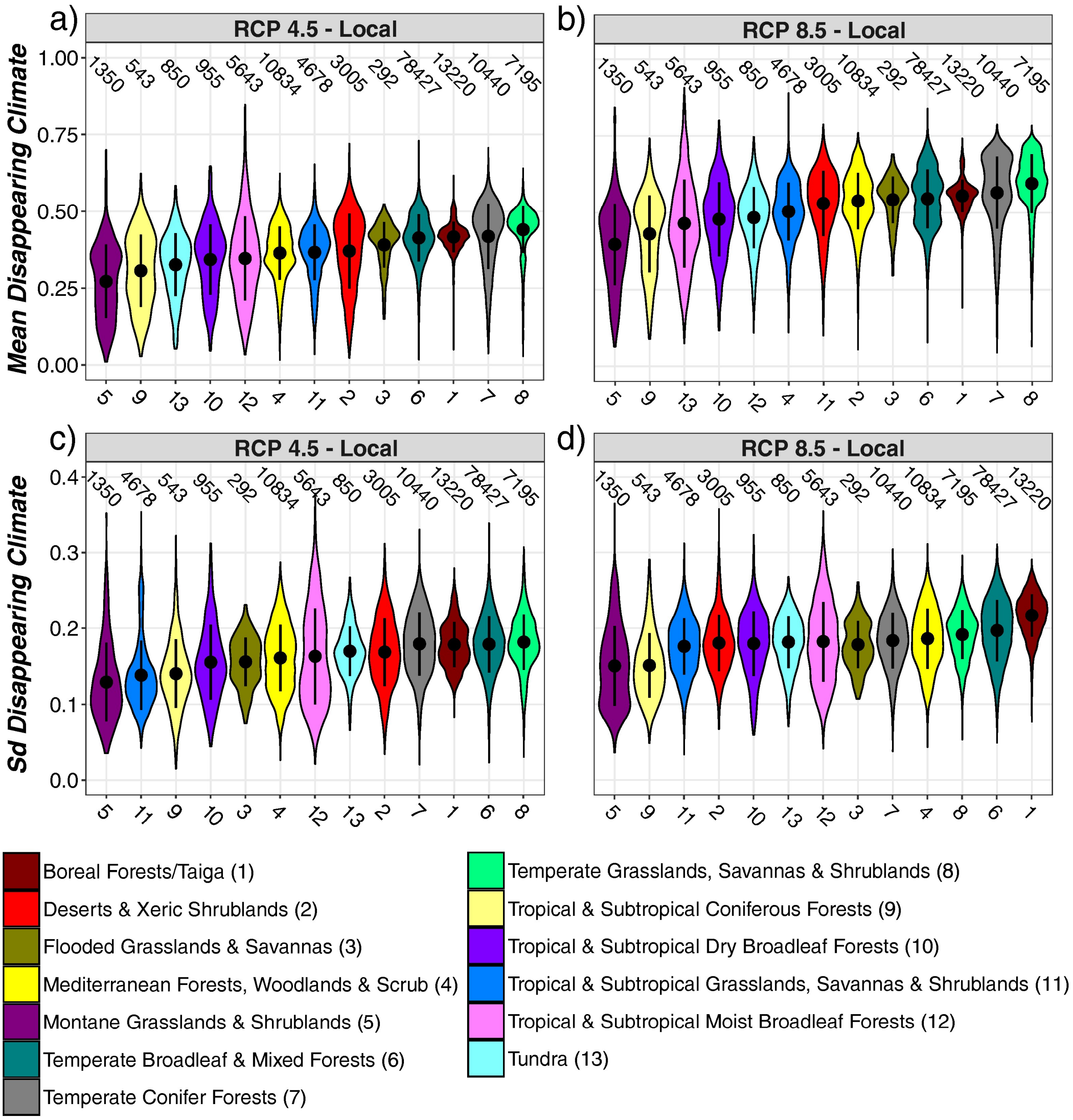
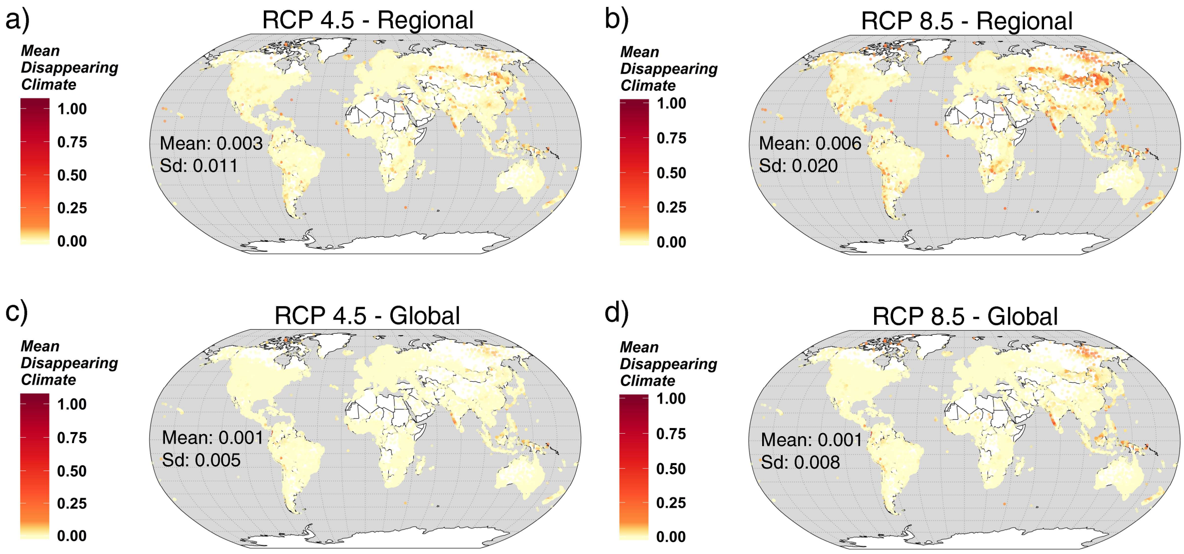
Supplementary information



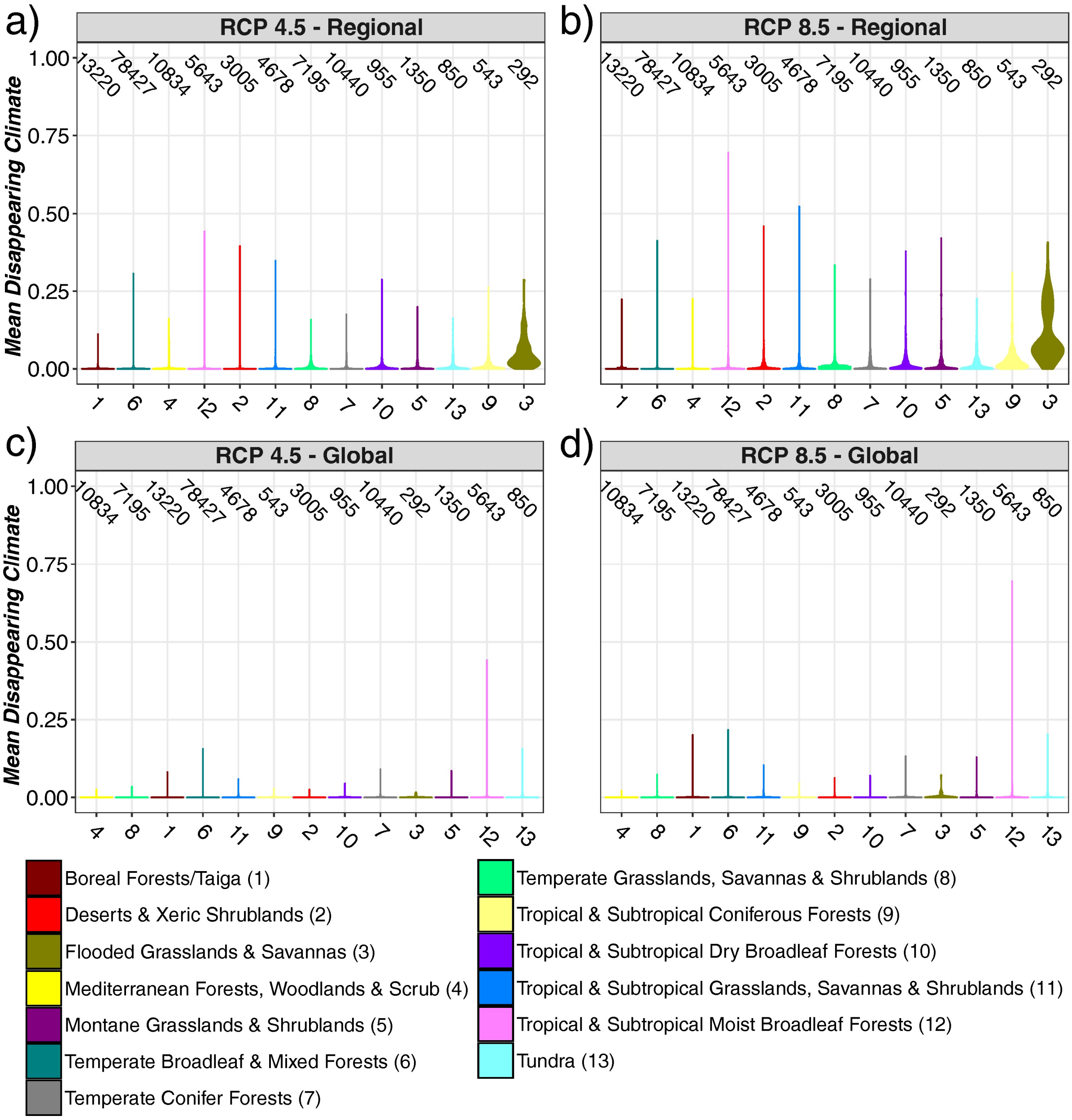
Supplementary Figure 1. Local-scale disappearing climate index of terrestrial protected areas worldwide. The local-scale disappearing climate index shows the proportion of raster cells inside a PA that currently hold climate classes which will disappear from the PA in the future. The mean and standard deviation (sd) of the local-scale disappearing climate index comprise future climate data from ten GCMs under RCP 4.5 and 8.5. Sd represents the variation of the local-scale disappearing climate index resulting from the ten GCMs. a) Mean of the local-scale disappearing climate index under RCP 4.5. b) Mean of the local-scale disappearing climate index under RCP 8.5. c) Sd of the local-scale disappearing climate index under RCP 4.5. d) Sd of the local-scale disappearing climate index under RCP 8.5. For each metric in a) to d), the mean and standard deviation across all 137,432 PA values are also given inside the global maps. Data on climate change indices and other characteristics per PA are given as Supplementary Data 1. The maps were created using open-source software R [1].



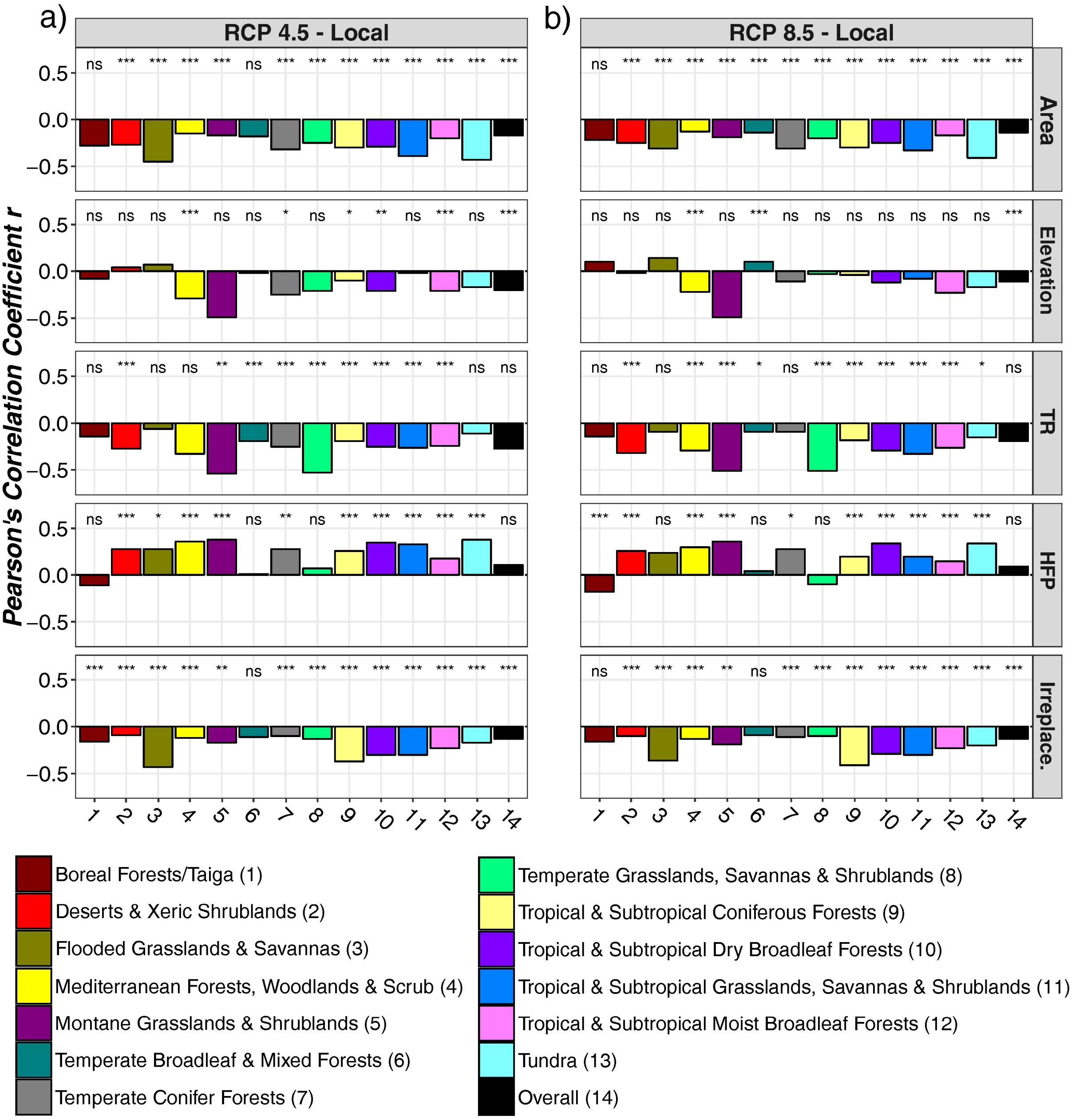
Supplementary Figure 2. Local-scale disappearing climate index of terrestrial protected areas worldwide, summarized by biomes. The mean of the local-scale disappearing climate index across ten GCMs under a) RCP 4.5 and b) RCP 8.5. The standard deviation (sd) of the local-scale disappearing climate index across ten GCMs under c) RCP 4.5 and d) RCP 8.5. Violins are ordered by increasing mean. Black dots and attached lines within violins represent the mean ± standard deviation. Black numbers above violins indicate the number of PAs within the respective biome. Source data are provided as a Source Data file.



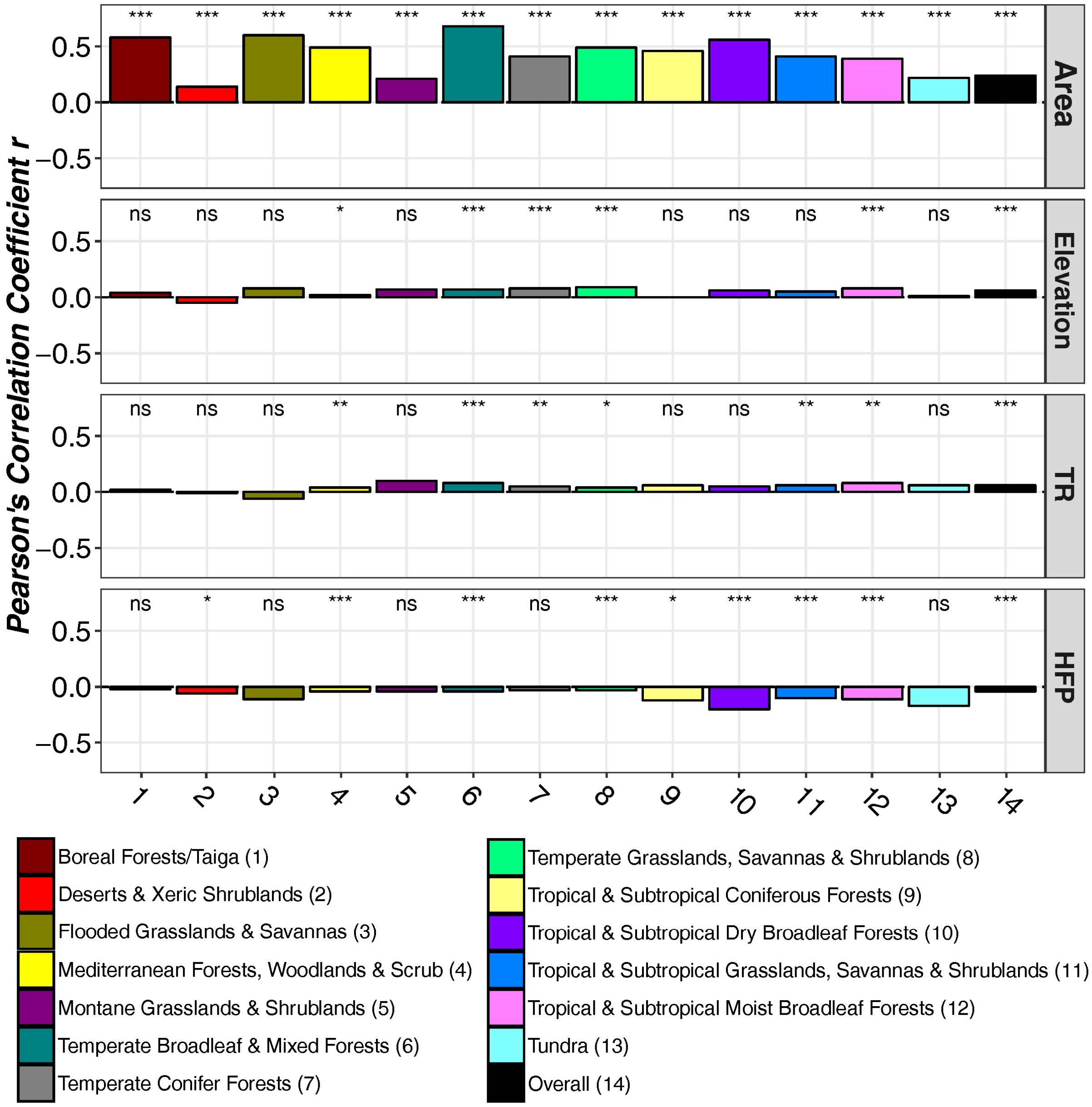
Supplementary Figure 3. Regional and global-scale disappearing climate indices of terrestrial protected areas worldwide. The regional-scale disappearing climate index shows the proportion of raster cells inside a PA that currently hold climate classes which will disappear from the entire PA network of the respective biome in the future. The global-scale disappearing climate index indicates the proportion of raster cells inside a PA that currently hold climate classes which will disappear from the global PA network in the future. The mean of the disappearing climate index comprises future climate data from ten GCMs under RCP 4.5 and 8.5. a) Mean of the regional-scale disappearing climate index under RCP 4.5. b) Mean of the regional-scale disappearing climate index under RCP 8.5. c) Mean of the global-scale disappearing climate index under RCP 4.5. d) Mean of the global-scale disappearing climate index under RCP 8.5. For each metric in a) to d) the mean across all 137,432 PA values are also given inside the global maps. Data on climate change indices and other characteristics per PA are given as Supplementary Data 1. The maps were created using open-source software R [1].



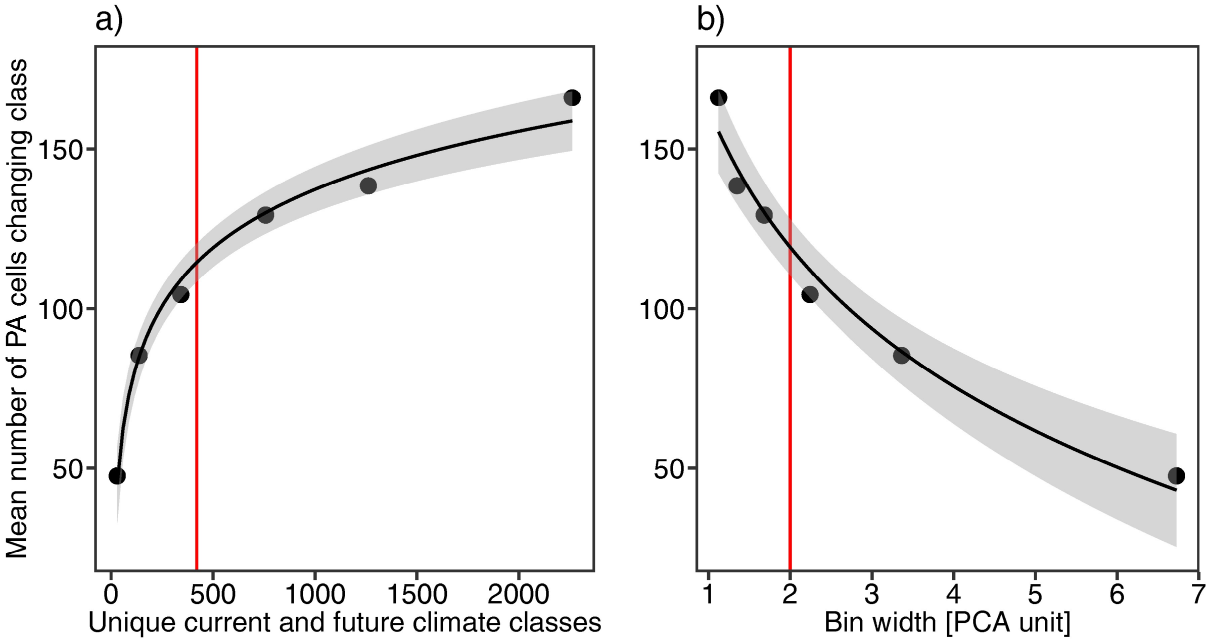
Supplementary Figure 4. Regional and global-scale disappearing climate indices of terrestrial protected areas worldwide, summarized by biomes. The mean of the regional-scale disappearing climate index across ten GCMs under a) RCP 4.5 and b) RCP 8.5. The mean of the global disappearing climate index across ten GCMs under c) RCP 4.5 and d) RCP 8.5. Violins are ordered by increasing mean. Black numbers above violins indicate the number of PAs within the respective biome. Source data are provided as a Source Data file.



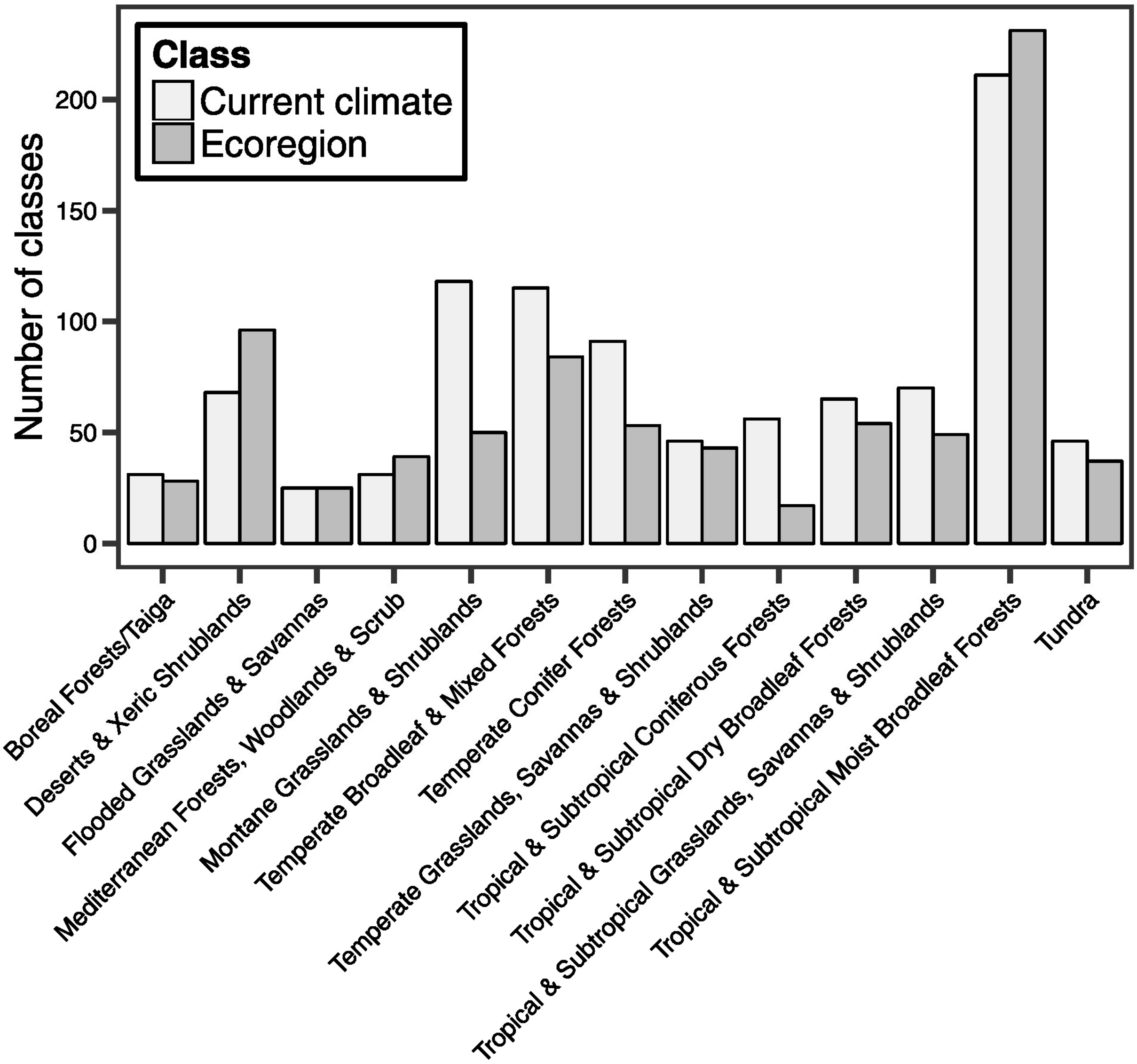
Supplementary Figure 5. Correlation between the mean values of the local-scale disappearing climate index and protected area characteristics, separated by biomes and RCP scenarios. a) RCP 4.5 and b) RCP 8.5. The proportion of local-scale disappearing climate inside PAs increases with decreasing area, elevation, topographic heterogeneity (terrain ruggedness [TR]) and irreplaceability (Irreplace.), and with increasing human footprints (HFP), globally and to a varying degree among biomes. Bars show Pearson's correlation coefficients *r*. Asterisks represent the significance level considering a modified t-test accounting for spatial autocorrelation [2] (*: $p \leq 0.05$, **: $p \leq 0.01$, ***: $p \leq 0.001$), while 'ns' implies non-significant ($p > 0.05$) correlation. Source data are provided as a Source Data file.



Supplementary Figure 6. Correlation between the protected areas' irreplaceability and other characteristics, separated by biome. Irreplaceability increases with area, elevation and topographic heterogeneity (terrain ruggedness [TR]), and decreases with the human footprint (HFP), globally and to a varying degree among biomes. Bars show Pearson's correlation coefficients r. Asterisks represent the significance level considering a modified t-test accounting for spatial autocorrelation[2] (*: $p \leq 0.05$, **: $p \leq 0.01$, ***: $p \leq 0.001$), while 'ns' implies non-significant ($p > 0.05$) correlation. Source data are provided as a Source Data file.



Supplementary Figure 7. Sensitivity of changes in cell classes to climate class width. a) Relationship between the defined number of current and future climate classes and the mean number of cells that change climate class inside all protected areas. b) Relationship between the defined bin width in PCA space and the mean number of cells that change climate class per protected area worldwide. The red line indicates a PCA climate bin width of 2 PCA units, which results in 430 current and future climate classes. The black lines are logarithmic functions fitted to the data; the grey band equals the 95% confidence interval.



Supplementary Figure 8. Comparison between the number of current climate classes applied in this study and the number of ecoregions inside terrestrial biomes as described by Olson et al. [3]. The positive and negative differences between both numbers indicate respectively over- and underestimation of ecological change within biomes, which is associated with climate class changes over time.

Supplementary Table 1. Exemplary PCA outcomes that the climate change indices are resulting from. The standard deviation and variance of the first eleven PCA axes are shown. As an example, this PCA is based on future climate data from the Global Climate Model BCC-CSM1-1 for RCP 8.5 and the year 2070, i.e. the average of the time period 2061-2080.

	PC1	**PC2**	**PC3**	**PC4**	**PC5**	**PC6**	**PC7**	**PC8**	**PC9**	**PC10**	**PC11**
Standard deviation	4.539	2.970	1.593	1.385	1.091	1.031	0.812	0.649	0.429	0.351	0.327
Proportion of variance	0.542	0.232	0.067	0.050	0.031	0.028	0.017	0.011	0.005	0.003	0.003
Cumulative proportion	0.542	0.774	0.841	0.892	0.923	0.951	0.968	0.979	0.984	0.987	0.990

Supplementary Table 2. Exemplary PCA outcomes that the climate change indices are resulting from. The PCA loadings of the first five axes are shown, which are used for the calculation of climate change indices. As an example, this PCA is based on future climate data from the Global Climate Model BCC-CSM1-1 for RCP 8.5 and the year 2070, i.e. the average of the time period 2061-2080.

Time	**Bioclimatic variable**	**PC1**	**PC2**	**PC3**	**PC4**	**PC5**
Current	Annual Mean Temperature	-0.204	-0.119	-0.066	-0.012	0.037
Current	Mean Diurnal Range	-0.022	-0.255	0.019	-0.144	-0.501
Current	Isothermality	-0.201	-0.029	0.017	0.120	-0.176
Current	Temperature Seasonality	0.201	0.027	0.026	-0.267	0.095
Current	Max Temperature of Warmest Month	-0.157	-0.193	-0.098	-0.244	0.097
Current	Min Temperature of Coldest Month	-0.211	-0.067	-0.073	0.106	0.038
Current	Temperature Annual Range	0.196	-0.028	0.040	-0.302	0.008
Current	Mean Temperature of Wettest Quarter	-0.162	-0.143	0.027	-0.250	0.134
Current	Mean Temperature of Driest Quarter	-0.199	-0.096	-0.117	0.085	0.007
Current	Mean Temperature of Warmest Quarter	-0.173	-0.165	-0.091	-0.211	0.144
Current	Mean Temperature of Coldest Quarter	-0.209	-0.089	-0.056	0.091	-0.001
Current	Annual Precipitation	-0.172	0.191	0.098	-0.067	0.004
Current	Precipitation of Wettest Month	-0.174	0.122	0.270	-0.046	0.088
Current	Precipitation of Driest Month	-0.099	0.252	-0.200	-0.126	-0.222
Current	Precipitation Seasonality	-0.006	-0.212	0.388	0.050	-0.202
Current	Precipitation of Wettest Quarter	-0.175	0.129	0.255	-0.048	0.082
Current	Precipitation of Driest Quarter	-0.106	0.253	-0.189	-0.120	-0.206
Current	Precipitation of Warmest Quarter	-0.123	0.178	0.218	-0.169	-0.091
Current	Precipitation of Coldest Quarter	-0.131	0.178	-0.071	-0.010	0.004
Future	Annual Mean Temperature	-0.203	-0.121	-0.068	-0.019	0.060
Future	Mean Diurnal Range	-0.037	-0.252	-0.015	-0.134	-0.491
Future	Isothermality	-0.201	-0.033	0.019	0.123	-0.181
Future	Temperature Seasonality	0.197	0.012	0.007	-0.296	0.069
Future	Max Temperature of Warmest Month	-0.149	-0.195	-0.111	-0.270	0.097
Future	Min Temperature of Coldest Month	-0.211	-0.061	-0.069	0.106	0.069
Future	Temperature Annual Range	0.190	-0.049	0.019	-0.330	-0.028
Future	Mean Temperature of Wettest Quarter	-0.156	-0.149	0.061	-0.253	0.103
Future	Mean Temperature of Driest Quarter	-0.197	-0.091	-0.142	0.080	0.038
Future	Mean Temperature of Warmest Quarter	-0.167	-0.169	-0.105	-0.232	0.151
Future	Mean Temperature of Coldest Quarter	-0.209	-0.086	-0.054	0.091	0.025
Future	Annual Precipitation	-0.165	0.203	0.118	-0.083	0.002
Future	Precipitation of Wettest Month	-0.166	0.130	0.289	-0.054	0.097
Future	Precipitation of Driest Month	-0.082	0.258	-0.203	-0.138	-0.232
Future	Precipitation Seasonality	-0.022	-0.209	0.382	0.071	-0.204
Future	Precipitation of Wettest Quarter	-0.168	0.138	0.277	-0.056	0.086
Future	Precipitation of Driest Quarter	-0.091	0.260	-0.192	-0.134	-0.217
Future	Precipitation of Warmest Quarter	-0.096	0.179	0.252	-0.191	-0.099
Future	Precipitation of Coldest Quarter	-0.137	0.177	-0.051	-0.017	0.022

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7.6 Manuscript 6

Title: Local climate change exposure of the global protected area estate from an international perspective

Submitted to: Earth's Future, manuscript #: 2019EF001443 (under review, received: 2 December 2019); **Update (12 May 2020):** Diversity and Distributions, manuscript #: DDI-2020-0090 (under review with major revisions, received: 11 March 2020)

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Key Points

- Protected areas are crucial to conserve biodiversity and ecosystem benefits under increasing human pressures of the Anthropocene.
- Climate change redistributes biodiversity worldwide with unknown consequences for biodiversity and ecosystems within protected areas.
- We predicted the climate change exposure of the global terrestrial protected areas to support national conservation policy and management.

Summary

Protected areas are essential to conserve biodiversity and ecosystem benefits to society under increasing human pressures of the Anthropocene. Anthropogenic climate change, however, threatens the enduring effectiveness of protected areas in conserving biodiversity and providing ecosystem services, because it modifies and redistributes biodiversity with unknown consequences for ecosystem functioning within protected areas. Here we assess the climate change exposure of the global terrestrial protected area estate. We predict climate anomalies between the present and 2070 using ten global climate models, two alternative emission scenarios and the finest spatial resolution available for global climate projections. We found climate anomalies highest in protected areas of tropical and polar countries. Globally, protected areas showing large climate anomalies tend to be at high elevation and highly irreplaceable for threatened species, indicating high climate change exposure. These protected areas are relatively large in area, of high environmental heterogeneity and less pressured by humans, reducing climate change exposure. Such correlations differ between countries. This study is to support climate-smart conservation policy and management, particularly national to local authorities, to ensure the future effectiveness of protected areas in preserving biodiversity and ecosystem benefits to human well-being.

Keywords: climate change, protected area, biodiversity, conservation policy, environmental management, ecosystem services

1 Introduction

Protected areas (PAs) are effective in conserving biodiversity, ecosystem functioning and services under increasing human pressures of the Anthropocene. Local biodiversity is generally higher inside than outside PAs (Gray et al., 2016). PAs preserve species and populations better than other conservation measures (Geldmann et al., 2013). PAs are particularly effective for global biodiversity conservation when they are located in biodiversity hotspots (Joppa et al., 2013), actively managed and funded (Coad et al., 2019). PAs cannot stop but decelerate the global biodiversity loss (Geldmann et al., 2019). Further, PAs safeguard ecosystem services such as climate change mitigation and adaptation (MacKinnon et al., 2011); natural catastrophe control and the provision of natural resources (Xu et al., 2017); tourism and recreation (Balmford et al., 2009); and poverty reduction (Andam et al., 2010). They are consequently considered crucial tools to meet the Sustainable Development Goals (SDG) and Aichi Biodiversity Targets (Mace et al., 2018). Conservationists perceive PAs as the most important policy for biodiversity conservation in the face of climate change (Hagerman & Satterfield, 2014).

Already in the 1980s scientists have warned of climate change being an inevitable threat to PA effectiveness (Peters & Darling, 1985). PAs are exposed to various direct and indirect climate change effects, e.g. increasing temperatures, melting of snow and ice, more severe droughts and storms, seasonal shifts, rising sea level and increased environmental acidification (Gross et al., 2017). Climate change is predicted to cause gains (Berteaux et al., 2018) and losses of biodiversity within PAs (Velazco et al., 2019). In any case, the risk of PA downgrading, downsizing and degazettement (PADDD) increases for PAs that lose the biodiversity they were meant to protect (Thomas & Gillingham, 2015). Climate change modifies and redistributes biodiversity and thus forms novel ecosystems whose functioning and contributions to human well-being are unclear (Pecl et al., 2017). Climate change additionally co-occurs with other threats to biodiversity, such as human land use, implying interactive effects (Schulze et al., 2018). Therefore, the future effectiveness of PAs in preserving biodiversity and ecosystem services under climate change is uncertain.

Predicting the future climate inside PAs is required to inform conservation management and policy-makers of potential climate change impacts on PAs (Rannow et al., 2014). Conservation management and policy is mainly adopted at the national to local scale. However, global studies about climate change impact neither address national authorities nor represent the local extent of PAs (Williams et al., 2007; Beaumont et al., 2011; García-López & Allué, 2013; Bellard et al., 2014; Garcia et al., 2014; Ordonez et al., 2016; Li, Wu et al., 2018; Li, Kou et al., 2018); and the climate change research that focuses on PAs comprises a limited geographical extent only, e.g. North America (Batllori et al., 2017) or Europe (Nila et al., 2019). A recent biogeographical investigation predicting climate shifts within PAs worldwide does not contemplate the governmental level either (Hoffmann et al., 2019). A national view of the local climate change impact on individual PAs worldwide is missing but vital to support local to national conservation policy and management in reaching global conservation goals beyond 2020 despite climate change (Watson et al., 2016).

Here we approach this research gap by assessing the climate change exposure of the terrestrial PAs worldwide at the highest spatial resolution for which global climate data is available, i.e. approximately 1 km. In a first step, we assessed the climate anomalies predicted for the year 2070 (i.e. average of 2061-2080) within each grid cell covered by a

PA. We considered ten global climate models (GCMs), and the moderate and 'business as usual' emission scenarios RCP 4.5 and 8.5 respectively. The climate anomaly is a fundamental metric of the climate change magnitude at a given location, i.e. the difference in climate parameters between present and future conditions, which is associated with demographic changes in species populations, particularly of species living close to their climatic tolerance limits and having low adaptation capacity (Garcia et al., 2014). Our climate parameters compose five independent climate variables, i.e. five principal components resulting from 19 bioclimatic variables. We then calculated climate anomaly by the standardized Euclidean distance (SED) between the mean current (1960-1990) and the mean future (2061-2080) climate parameters, which was relativized by the 1960-1990 interannual variability of the climate parameters. The SED applied to independent variables equals the Mahalanobis distance (Mahony et al., 2017). In a second step, we summarized the climate anomalies by each PA using the median, and present the PAs' median climate anomalies by country and management category. The IUCN management categories from I to VI cover a gradient of human integration, from strict human exclosure to sustainable human land use respectively (Dudley, 2008). In a third step, we calculated country-specific correlations between median climate anomalies and other PA characteristics. The PA characteristics 'area', 'elevation' and 'terrain ruggedness' indicate the PAs' capacity to buffer climate change impact; 'irreplaceability' represents the PAs' importance for the conservation of globally threatened species. By relating the predicted climate anomalies to these PA characteristics, we additionally estimate the climate change exposure of PAs, i.e. potential impacts of climate change on PAs' effectiveness. We assume PAs to be particularly exposed to climate change when the predicted climate anomalies, the human footprint and irreplaceability are high, while area, elevation and terrain ruggedness are low. The outcomes help to develop proactive management that can compensate for negative impacts of climate change on PA effectiveness (Game et al., 2011). Our work sets out to support climate-smart policy and management of PAs, particularly at the national to local level.

2 Materials and Methods

2.1 Protected area data

The World Database on Protected Area (version January 2018) includes boundary data for 201,464 PAs excluding marine, coastal (i.e. semi-terrestrial) and non-designated PAs (IUCN & UNEP, 2018). Non-designated PAs are PAs without legal recognition whose effectiveness is dubious. We rasterized the PA polygons by the same resolution as the climate data (30 arc seconds, i.e. approximately 1 km at the equator) via cell center coverage. We thus produced a global raster grid containing all cells that are covered by any of the PAs we selected. Because small PAs may cover no cell centroids, 137,735 PAs remained after rasterization, which compose 26,038,594 cells and 20,658,583 km², i.e. 14% of the global terrestrial surface and 99.9% of the terrestrial area under protection.

The area and IUCN management category of each PA was retrieved from the WDPA. We consider PA area as a proxy for the amount of available resources for biodiversity to adapt to climate change within PAs. The IUCN management categories I to IV mean stricter protection, while categories V and VI allow for the sustainable use of natural resources, e.g. via silviculture and agriculture (Dudley, 2008). We applied the Terrain Ruggedness index (TR) as a measure of topographic heterogeneity. The TR index has also a resolution of 30 arc seconds (Amatulli et al., 2018). Planar area has a TR of 0 m, whereas mountain areas can have a TR of up to 2000 m in the Himalayas (Amatulli et al., 2018). The median of the TR values inside PAs was used to represent the topographic heterogeneity of each PA. The median is more robust against extreme values than the mean. Terrain ruggedness is a proxy for climate and habitat diversity, and thus of resource availability and the adaptation capacity of PAs' biodiversity to impacts of climate change (Lawler et al., 2015). The human footprint index 2009 is the most recent global indicator of human pressure and involves eight indicators of human land use (Venter et al., 2016a): population density, buildings, electric infrastructure, roads, railways, navigable waterways, cropland and pasture. We calculated the median human footprint of each PA by taking the median of the raster cell values that fall within each PA polygon. The irreplaceability index provided by Le Saout et al. (Le Saout et al., 2013) reflects the conservation value of PAs in terms of the species diversity covered by PAs (Hoffmann et al., 2018). This irreplaceability index represents the degree of overlap between each PA included in the WDPA (version October 2012) and the ranges of species on the IUCN Red List (Le Saout et al., 2013). The index involves ranges of 21,296 species; 6240 amphibians, 9793 birds, and 5263 mammals.

2.2 Climate data

We used the WorldClim global climate data provided by Hijmans et al. (2005) including 19 bioclimatic variables with a resolution of 30 arc seconds. The 19 bioclimatic variables cover the full climate spectrum relevant for biodiversity, from annual trends (e.g. mean annual temperature and annual precipitation) to seasonal trends (e.g. annual range in temperature and precipitation) and extreme conditions (e.g. temperature of the coldest and warmest month, and precipitation of the wettest and driest quarters of the year). The 19 bioclimatic variables are listed in Table S1. Each current bioclimatic variable represents the mean value across the years 1960 to 1990; each future bioclimatic variable represents the mean value across the years 2061 to 2080, i.e. of 2070. WorldClim's current climate data was generated by interpolating climate station data. WorldClim's future climate data was downscaled from the GCMs of the Coupled Model Intercomparison Project Phase 5 (Intergovernmental Panel on Climate Change, Fifth Assessment Report). We considered projected data for the Representative Concentration Pathways (RCP) 4.5 and 8.5 as well as ten GCMs: BCC-CSM1-1, CCSM4, CNRM-CM5, GFDL-CM3, HadGEM2-AO, INMCM4, IPSL-CM5A-LR, MIROC5, MPI-ESM-LR and MRI-CGCM3. The RCPs represent future scenarios for atmospheric greenhouse gas concentrations. The moderate scenario RCP 4.5 projects a mean global temperature increase of 1.8 °C, while the 'business-as-usual' scenario RCP 8.5 forecasts mean global warming of 3.7 °C by the end of the 21st century (IPCC, 2013). The numbers 4.5 and 8.5 depict the radiative forcing value in Watt per m^2. We refer to raster cells that hold complete climate data from all variables as 'climate cells' hereafter.

Since WorldClim does not provide a monthly time series of mean climate variables for the period 1960-1990, we used the monthly time series provided by Abatzoglou et al. (2018). This data represents locally observed interannual climate variability (ICV), i.e. the standard deviation of mean monthly climate data of each year from 1960 to 1990. The ICV data has a resolution of 2.5 arc minutes. To assign the ICV data to the mean climate data of current and future conditions, we disaggregated the ICV data to the resolution of 30 arc seconds. For the ICV data, we calculated the 19 bioclimatic parameters via the biovars function of R package dismo (Hijmans et al., 2017).

2.3 Calculating climate anomaly

We calculated climate anomaly of each climate cell covered by a PA as the Mahalanobis distance between the mean current (1960-1990) and mean future (2061-2080) climate conditions relative to the current ICV (1960-1990). We computed the Mahalanobis distance by the standardized Euclidean distance (SED) applied to independent climate variables (Mahony et al., 2017). The SED is a widely applied metric to estimate future climate anomaly (Williams et al., 2007; Bellard et al., 2014; Garcia et al., 2014; Ordonez et al., 2016; Mahony et al., 2017). The standardization of climate distance by the ICV makes the SED robust against distance inflation due to high interannual climate variability. The Mahalanobis distance is a more robust measurement of deviations from historical climate variability than the SED, especially when many climate variables are incorporated, because the Mahalanobis distance avoids variance inflation resulting from intercorrelated climate variables (Mahony et al., 2017).

To produce independent climate variables, we projected the mean current, mean future and ICV climate data onto the first five principal components of the ICV data. We thus reduced the 19 bioclimatic variables to five independent climate variables. We log10-transformed the precipitation variables before we conducted the principal component analysis (PCA) to represent non-linearity of ecological effects along precipitation gradients. The PC space was built on the ICV data of all climate cells covered by a PA (*n*=26,038,594). The first five PCA axes account for 92% of the variation in the ICV data. The PC loadings are shown in Table S1.

We defined the following parameters to calculate the SED: [*A*] is a (*n* x *K*) matrix of *n* climate cells of *K* mean climate variables for the period 1960-1990. [*B*] is a (*n* x *K*) matrix of *n* climate cells of *K* mean climate variables for the period 2061-2080. Each climate cell *i* thus represents a mean climate value a_{ik} and b_{ik} for a period of time and a climate variable *k*. [C_i] is a (*T* x *K*) matrix of *T* annual mean observations (31-year time series) and *K* climate variables of a climate cell *i*. c_{itk} is the mean value of climate variable *k* at year *t*, i.e. of the ICV reference period 1960–1990). s_{ik} is the standard deviation of the ICV reference period at cell *i* in variable *k* across the 31 c_{itk} values. The SED of cell *i* based on independent climate variables, i.e. the Mahalanobis distance, can finally be calculated by $\mathrm{SED_i} = \sqrt{\sum_{k=1}^{K} \frac{(b_{ik}-a_{ik})^2}{s_{ik}^2}}$.

The fewer climate variables are considered in measuring climate distance, the lower is the risk of Type I inference error (i.e. overestimating climate distance) and the higher is the risk of Type II inference error (i.e. underestimating climate distance). By considering five independent climate variables, we tried to balance the risk of both inference errors. However, because five variables are relatively few to represent all dimensions of the climate space, our results may underestimate the climate change impact in regions of low climate anomaly (Mahony et al., 2017). We adapted the R code of Mahony et al. (2017) to compute the Mahalanobis distance.

2.4 Estimating climate change exposure

We summarized the cell-based climate anomalies by individual PAs using the median, grouped the resulting median climate anomalies of each PA by country, and correlated the median anomalies of PAs to other PA characteristics (see section 'Protected area data`). We tested for correlations by using Pearson's correlation coefficient r and a modified t-test accounting for spatial autocorrelation (Dutilleul et al., 1993). The correlations between climate anomalies and PA characteristics estimate the climate change exposure of PAs. PAs are assumed to be particularly exposed to climate change when the predicted median climate anomalies positively correlate with the human footprint and irreplaceability scores; and negatively correlate with area, elevation and terrain ruggedness. The data on PAs' median climate anomalies and characteristics are supplied under DOI 10.6084/m9.figshare.10329929 and linked to the WDPA via the WDPA ID.

3 Results

The predicted mean climate anomaly under RCP 4.5 (Fig. 1a, b) and 8.5 (Fig. 1e, f) is highest inside tropical and subtropical PAs between -25° and 25° latitude, but also remarkably high in polar PAs at high northern latitudes. The standard deviation of the climate anomalies across the ten GCMs represents the variation of predicted climate anomalies among the ten GCMs. The geographic pattern of the standard deviation (Fig. 1c, d, g, h) largely conforms to the pattern of the mean (Fig. 1a, b, e, f): the larger the predicted climate anomaly is, the higher is the uncertainty of the prediction.

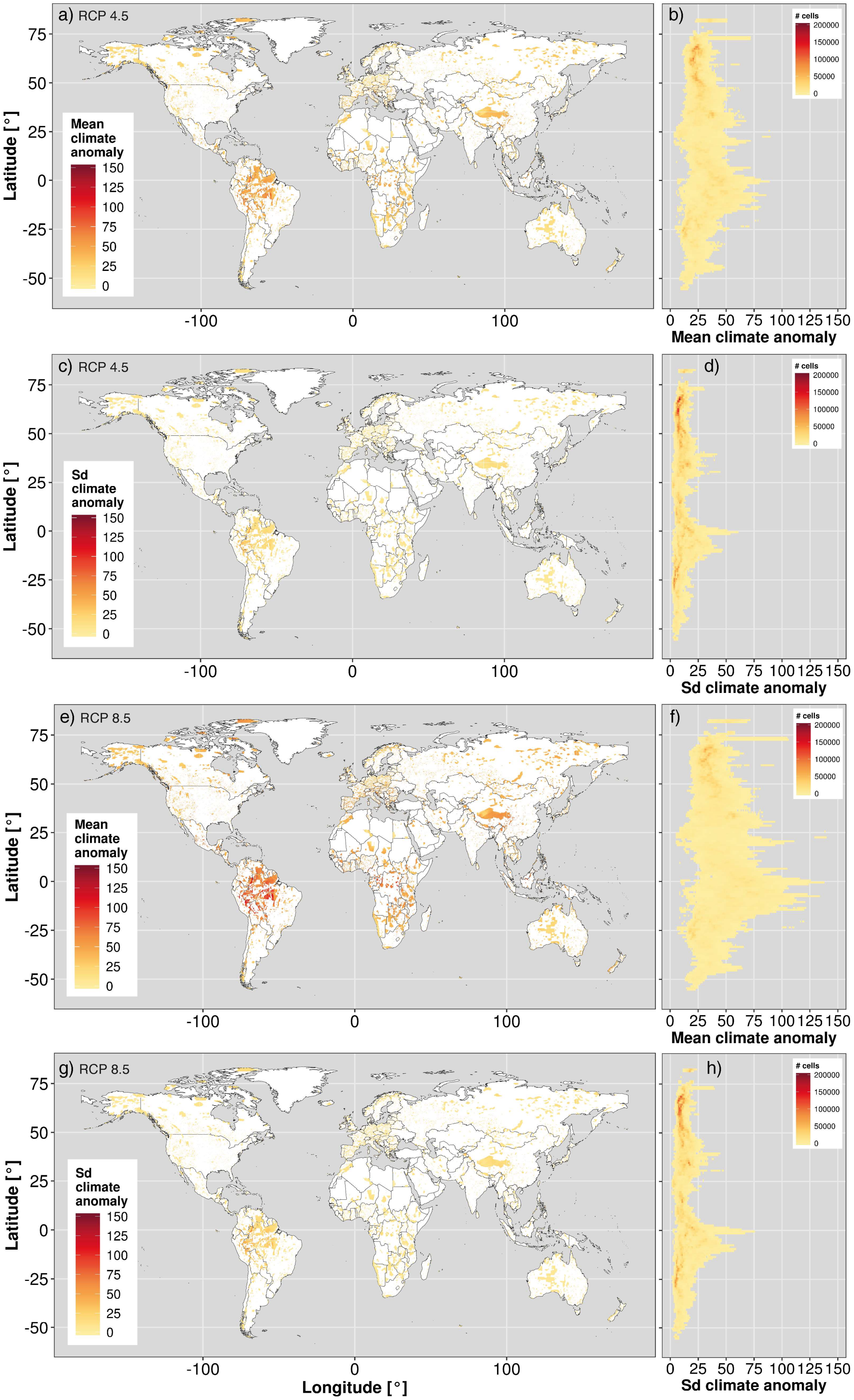
a) RCP 4.5
b)
c) RCP 4.5
d)
e) RCP 8.5
f)
g) RCP 8.5
h)
Latitude [°]
75
50
25
0
-25
-50
-100
0
100
Longitude [°]
Mean climate anomaly
Sd climate anomaly
150
125
100
75
50
25
0
cells
200000
150000
100000
50000
0
0 25 50 75 100 125 150

Figure 1. Predicted climate anomalies within the terrestrial PA estate for the year 2070 under the moderate emission scenario RCP 4.5 and the 'business as usual' scenario RCP 8.5. The climate anomaly represents the magnitude of future climate change at a given location. Climate anomalies were calculated for each grid cell of approximately 1 km resolution, using the Mahalanobis distance between the current and future climate conditions. Here we show the mean and standard deviation (sd) of climate anomalies resulting from future climate projections of ten global climate models. The sd is a measure of the variation among future climate predictions. a) Mean climate anomalies under RCP 4.5. b) Density distribution of mean climate anomalies by degree latitude under RCP 4.5. c) Sd climate anomalies under RCP 4.5. d) Density distribution of sd climate anomalies by degree latitude under RCP 4.5. e) Mean climate anomalies under RCP 8.5. f) Density distribution of mean climate anomalies by degree latitude under RCP 8.5. g) Sd climate anomalies under RCP 8.5. h) Density distribution of sd climate anomalies by degree latitude under RCP 8.5.

From a national perspective, Albania, Bhutan, Bolivia, Bosnia and Herzegovina, Burundi, Cameroon, Central African Republic, Colombia, Congo, Equatorial Guinea, French Guiana, Guatemala, Guinea, Guyana, Macedonia, Malawi, Malaysia, Mexico, Montenegro, Nepal, Nicaragua, Palestine, Peru, Rwanda, Sierra Leone and Uganda are among the top ten countries containing PAs of any IUCN management category with on average highest median climate anomalies under RCP 4.5 (Fig. 2); see Figure S1 in Supporting Information for RCP 8.5. Considering the global pool of PAs (see 'Global' in Fig. 2), the median climate anomalies of PAs marginally differ between management categories.

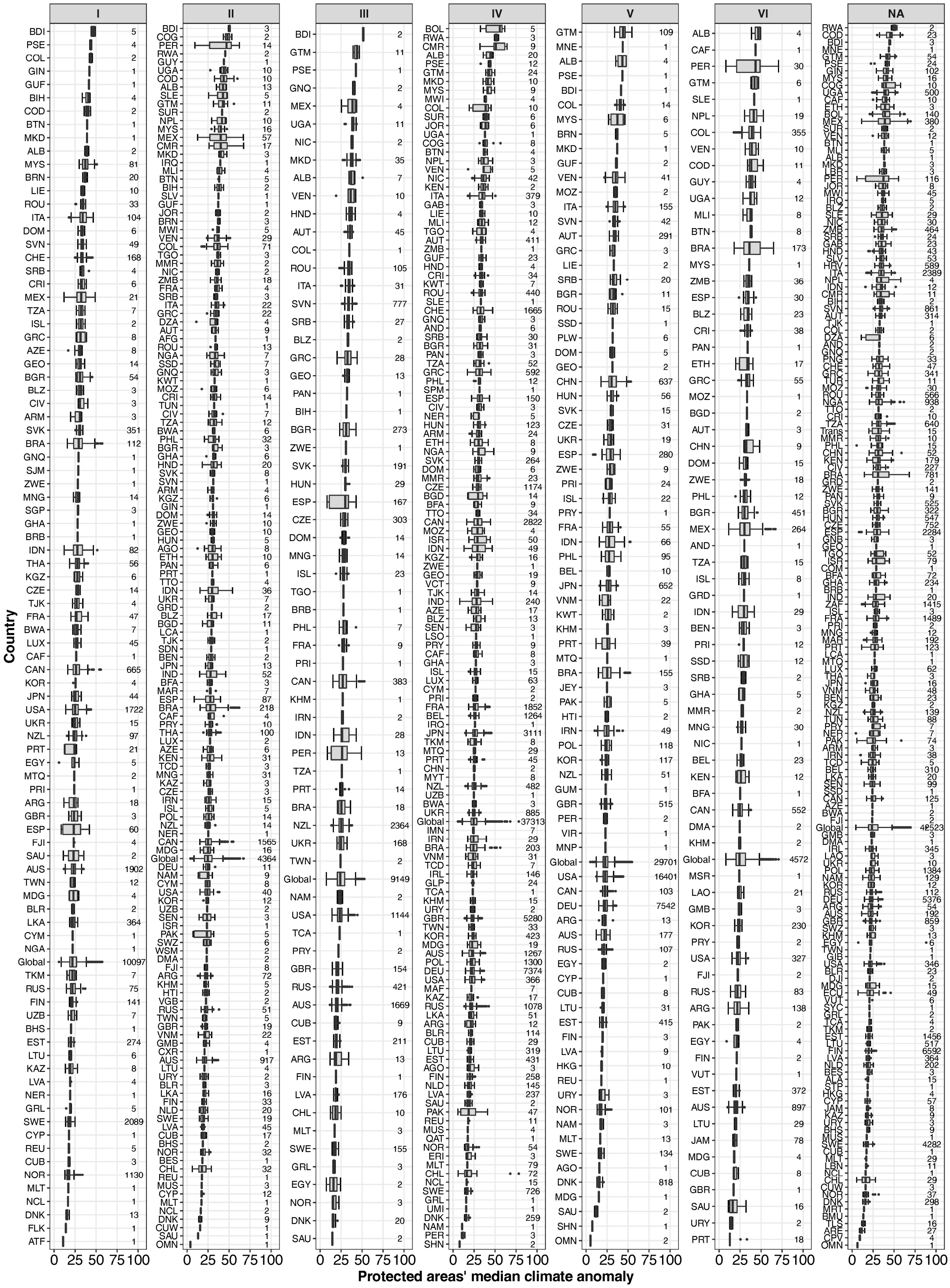

Figure 2. Predicted climate anomalies (2070, RCP 4.5) of PAs grouped by country and IUCN management category; see Figure S1 for results of RCP 8.5. We summarized the mean climate anomalies (Fig. 1) for each PA using the median. The IUCN management categories from I to VI cover a gradient of human integration, from strict human exclosure to sustainable human land use respectively. The black numbers represent the number of PAs within the countries and IUCN management categories. 'NA' means no management category was available. The boxplots were

ordered by decreasing median. The limits of the grey box show the lower and upper quartiles, i.e. the interquartile range. The whiskers extend to the lowest and highest values within 1.5 times the interquartile range. The black dots indicate outliers beyond the whiskers. The alpha-3 country codes are given (i.e. ISO 3166). 'Global' composes all PAs, while 'Trans' refers to transboundary PAs.

At the global scale, the median climate anomalies of PAs under RCP 4.5 correlate positively with PA area (r=0.05, p<0.001), elevation (r=0.40, p<0.001), terrain ruggedness (r=0.32, p<0.001) and irreplaceability (r=0.06, p<0.001) (see 'Global' in Fig. 3). There is no significant global correlation between climate anomaly and the human footprint under RCP 4.5; see Figure S2 in Supporting Information for results of RCP 8.5. Those worldwide correlations were weak. The country-scale relationships are on average stronger than the global relationships and even change direction. They differ considerably between countries. Few countrywide correlations are significant.

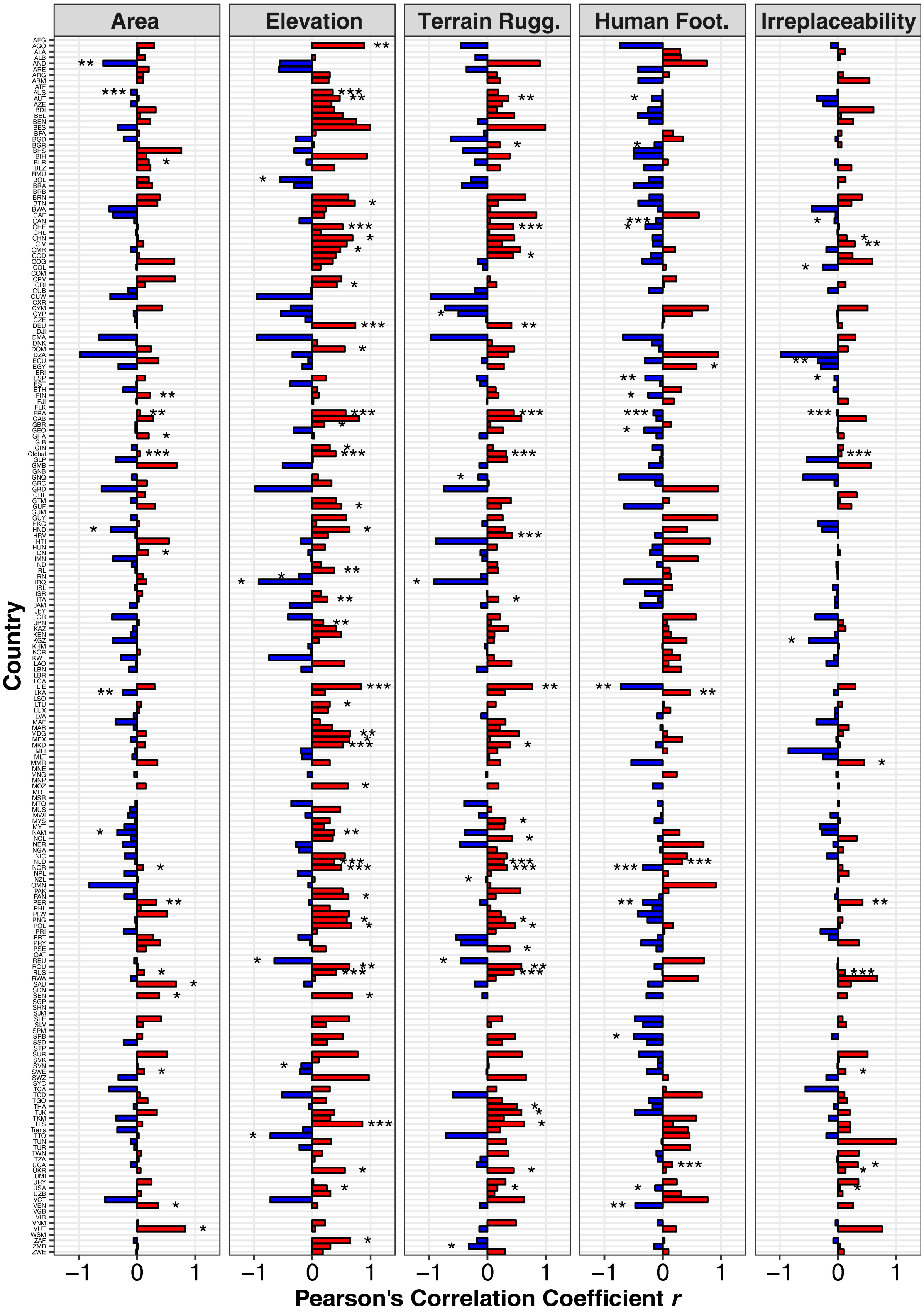

Figure 3. Global and country-specific correlations of the PAs' median climate anomalies (2070, RCP 4.5) with PA characteristics; see Figure S2 for results of RCP 8.5. The PA characteristics 'area', 'elevation' and 'terrain ruggedness' indicate the PAs' capacity to buffer the climate change impact; 'irreplaceability' represents the PAs' importance for the conservation of globally threatened species.

By relating the predicted climate anomalies to the PA characteristics, we estimate the climate change exposure of PAs, i.e. potential impacts of climate change on PAs' effectiveness. PAs are assumed to be particularly exposed to climate change when the predicted climate anomalies, the human footprint and irreplaceability are high, while the area, elevation and terrain ruggedness are low. Bars reflect Pearson's correlation coefficients *r*; red for positive and blue for negative coefficients. Asterisks represent the significance level considering spatial autocorrelation (*: $p \leq 0.05$, **: $p \leq 0.01$, ***: $p \leq 0.001$), while no asterisk means non-significant correlation ($p > 0.05$). The alpha-3 country are given codes (i.e. ISO 3166). 'Global' composes all PAs, while 'Trans' refers to transboundary PAs.

Conclusions

We found hotspots of climate anomaly in tropical, subtropical and polar PAs. Our climate anomaly metric integrates future changes of multiple thermal and hydraulic variables. Previous investigations have disentangled the roles of temperature and precipitation in forming these climate change hotspots: temperature change is projected largest in tropical regions, while precipitation change might be greatest in polar regions (García-López & Allué, 2013; Garcia et al., 2014; Li, Kou et al., 2018). We predicted high-resolution patterns of climate anomaly inside PAs worldwide, which geographically agree with other global climate predictions based on different methods and coarser spatial resolution (Williams et al., 2007; Beaumont et al., 2011; García-López & Allué, 2013; Garcia et al., 2014; Ordonez et al., 2016; Li, Wu et al., 2018; Li, Kou et al., 2018).

Our study adds to previous research in global climate change by applying a promising new climate change metric to the finest spatial resolution for which global climate data is available. The Mahalanobis distance is a more robust metric of climate anomaly than the renowned SED (Williams et al., 2007; Bellard et al., 2014; Garcia et al., 2014; Ordonez et al., 2016) because the Mahalanobis distance avoids variance inflation resulting from intercorrelated climate variables (Mahony et al., 2017). Our findings complement another global analysis of climate change within PAs (Hoffmann et al., 2019) by predicting local climate anomalies instead of changes in the areal proportion of climate zones, and by addressing national authorities instead of biogeographical regions. In contrast to the areal changes of large climatic zones, the high-resolution map of local climate anomalies can guide spatial conservation management even inside individual PAs. Since conservation policy is mainly adopted at the national and smaller level, it is reasonable to highlight national responsibilities for climate-smart conservation. PAs are the cornerstones of conservation effort, but extending our high-resolution approach to the entire terrestrial surface would be extremely useful for environmental management worldwide. We highly recommend to follow this future perspective, although the computational burdens are enormous and the computational capacities required are hardly available.

Climate anomalies imply various consequences for biodiversity and ecosystems. Given that all other factors are constant, high climate anomalies are more likely to modify biodiversity and ecosystems than low anomalies. The impact of climate anomalies depends on the magnitude of anomaly and on the ecological systems themselves. In general, low climate anomalies suggest locations in which present biodiversity and ecosystem functioning is likely to persist under ongoing climate change. Novel species assemblages and interactions are expected to emerge under high climate anomalies (Ordonez et al., 2016). High local climate anomalies can lead to physiological, morphological and behavioural changes of individuals and demographic changes of populations (Peñuelas et al., 2013). Species living close to their climatic tolerance limits and having low adaptation capacity are most affected by climate anomalies (Garcia et al., 2014), potentially leading to population declines (Foden et al., 2007) and local extinctions (Sinervo et al., 2010). Local climate anomalies can also positively affect biodiversity. Rising temperatures cause increasing plant diversity in high latitudes (Hill & Henry, 2011) and elevations (Steinbauer et al., 2018). The fitness of mountain lizards can increase due to warming (Chamaille-Jammes et al., 2006). High-latitude PAs are projected to gain biodiversity under global warming (Berteaux et al., 2018). In Kruger National Park, climate change is expected to increase plant productivity and thus elephant populations (Scheiter & Higgins, 2012).

Climate anomalies cause new, non-analogue communities, i.e. communities without current analogues, because species differ in their ability to respond to climate change via dispersal, range dynamics and biotic interactions (Williams & Jackson, 2007). The functioning of such novel communities remains largely unknown (Hobbs et al., 2006). Impacts of recent climate change onto ecosystem functioning and services are manifold (Scheffers et al., 2016). Mascaro et al. (2012) shows that non-native species led to increased productivity, carbon storage and nutrient cycling in lowland Hawaiian rainforests. In contrast, forest carbon storage is decreasing with increasing frequency and intensity of droughts, fires, wind throw and insect outbreaks (Seidl et al., 2011; Holmgren et al., 2013). Climate-induced changes to ecosystem functioning and services depend on the ecosystems' exposure (i.e. magnitude of change), resistance or sensitivity (i.e. ability to remain in the original state despite change), resilience (i.e. ability to return to the original state after change) and capacity to adapt to change (Dawson et al., 2011).

We revealed that increasing climate anomalies are, at the global scale, linearly related to increasing PA area, elevation, terrain ruggedness and irreplaceability. We do not want to overestimate these weak global relationships. However, some of the country-specific correlations were strong, suggesting particularly low or high climate change exposure of national PA estates, depending on whether correlations were positive or negative respectively. When management resources are limited, PAs that are most exposed to climate change should obtain priority by conservation effort.

PA area, elevation and terrain ruggedness correspond to environmental, climate and habitat diversity, reflecting the adaptive capacity of PAs' biodiversity to impacts of climate change (Lawler et al., 2015). Generally, a positive correlation between climate anomalies and these characteristics is beneficial for conservation. However, not each particular conservation objective of PAs might be supported by environmental heterogeneity. The human footprint represents habitat fragmentation. A small footprint is thus advantageous for species migration under high climate anomalies. Irreplaceability accounts for the PAs' importance in conserving endangered species globally. The higher the irreplaceability, the more valuable are PAs for species conservation. We assume that climate change exposure increases with climate anomaly and irreplaceability.

Conservation planning and management is more challenging in areas where climate anomaly is higher, all else being equal. We warn of naively applying common management responses to climate change. They involve contextual drawbacks since they are biased towards specific species, ecosystems and regions (Felton et al., 2009). Management responses must be developed in the context of individual PAs because the climate predictions, their uncertainties (Belote et al., 2018), ecosystem intactness (Watson et al., 2013), conservation targets (Belote et al., 2017), the conservation capacity of land (Gillson et al., 2013), the management resources available (Wintle et al., 2011) and the risks of management actions (Ando et al., 2018) differ between PAs. Our findings contribute to the development of climate-smart management implications for individual PAs worldwide. Climate-smart management guidelines generally aim at the persistence and resistance of present biodiversity despite climate change, or at the adaption of biodiversity to climate change (Gross et al., 2017). Reasonable management interventions can vary from low intensity, e.g. monitoring, to high intensity, e.g. assisted migration and restoration (Dawson et al., 2011; Gillson et al., 2013). Appropriate management practice may be conservative, innovative, flexible, reversible or experimental (Belote et al., 2018). Alternatively, 'no-regret' strategies could be applied, which intend to achieve conservation benefits irrespective of climate change (Hallegatte, 2009). In any case, adaptive PA management is a promising tool to ensure the enduring effectiveness and efficiency of PAs in the light of uncertain future developments (Rannow et al., 2014).

Our methodological approach implies assumptions that limit the implications of our findings. While we estimated variation among future climate projections, an uncertainty of the predictions remains that is inherent in the climate models and practically incalculable. Further, climate anomaly is a sophisticated indicator of climate change impact, but cannot reveal the entire complexity of biodiversity and ecosystem responses to climate change (Garcia et al., 2014). This indicator does not reflect shifts in seasonal climate nor climate extremes, which are both extremely relevant for biodiversity, ecosystem functioning and services (Scheffers et al., 2016; Pecl et al., 2017). Moreover, the climate data resolution of approximately 1 km does not consider microclimate, which can buffer climate change impact (Suggitt et al., 2018). Interacting effects between climate change and other threats to biodiversity and ecosystem functioning are neglected as well. In addition, the human footprint index from 2009 and the irreplaceability index from 2012 are out of date. Nevertheless, given that human land cover (Venter et al., 2016b) and species loss (Johnson et al., 2017) are increasing globally, our application of the human footprint and irreplaceability index may even underestimate the climate change exposure of PAs.

We here delivered a simplistic assessment of the climate change exposure of the global PA estate that is intuitive and can thus be easily understood by stakeholders and policy-makers. This study is to inform national and local authorities of the potential climate change impact on PAs. This work does, however, not to reveal the complex responses of conservation objectives to climate change and other factors within global PAs, which is important to derive well-grounded management recommendations for individual PAs under rapid environmental changes worldwide. Such a comprehensive analysis could be the foundation of a globally coordinated and adaptive PA planning and management system. Adaptive protected area management is a promising tool to ensure the enduring effectiveness, and also efficiency, of protected areas in the light of uncertain future developments (Westgate et al., 2013; Rannow et al., 2014; Gillson et al., 2019). Adaptive management requires environmental monitoring. As resources for monitoring are limited, only a selection of variables can be prioritised. Scientists have identified sets of essential variables describing states and trends of climate (Bojinski et al., 2014), biodiversity (Jetz et al., 2019), geodiversity (Schrodt et al., 2019) and progress towards SDGs (Reyers et al., 2017). Remote sensing (Pettorelli et al., 2016) and long-term ecological research stations (Haase et al., 2018) are promising techniques to monitor essential variables. Artificial intelligence and deep learning are promising computational technologies that enable automated processing of big monitoring data (Lamba et al., 2019). Moreover, there are web based information systems such as the Digital Observatory for Protected Areas (DOPA) that could be the digital basis for a global PA management system. The DOPA already monitors PAs across the globe in progressing towards Aichi Biodiversity Target 11 and the SDG 14 and 15 (JRC, 2019). We perceive the development and application of a global adaptive PA management system as a major future task to reach global conservation and sustainability targets, and safeguard human well-being of generations to come.

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Data and software availability

All data used in this study are open data (see Materials and Methods). The data we produced for each PA are available online at https://doi.org/10.6084/m9.figshare.10329929 and linked to the WDPA via the WDPA ID. The R code we used to compute the Mahalanobis distance was adapted from Mahony et al. (2017).

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Supporting information

Table S1. Bioclimatic variables and PC loadings. The PCA was built on the interannual climate variability (ICV) data from 1960-1990.

Bioclimatic variable	**Description**	**PC1**	**PC2**	**PC3**	**PC4**	**PC5**
1	Annual Mean Temperature	0.319	-0.090	-0.098	-0.058	-0.027
2	Mean Diurnal Range	0.061	-0.306	0.112	-0.273	0.175
3	Isothermality	0.295	-0.017	0.014	0.177	-0.077
4	Temperature Seasonality	-0.303	-0.018	0.012	-0.364	0.028
5	Max Temperature of Warmest Month	0.251	-0.188	-0.148	-0.414	0.062
6	Min Temperature of Coldest Month	0.324	-0.028	-0.099	0.131	-0.020
7	Temperature Annual Range	-0.288	-0.077	0.044	-0.432	0.065
8	Mean Temperature of Wettest Quarter	0.255	-0.119	0.028	-0.354	-0.396
9	Mean Temperature of Driest Quarter	0.307	-0.065	-0.165	0.081	0.174
10	Mean Temperature of Warmest Quarter	0.273	-0.152	-0.152	-0.349	-0.005
11	Mean Temperature of Coldest Quarter	0.325	-0.054	-0.074	0.099	-0.022
12	Annual Precipitation	0.182	0.328	0.226	-0.085	0.108
13	Precipitation of Wettest Month	0.211	0.256	0.358	-0.073	0.185
14	Precipitation of Driest Month	-0.019	0.373	-0.256	-0.140	-0.098
15	Precipitation Seasonality	0.029	-0.261	0.514	-0.017	0.393
16	Precipitation of Wettest Quarter	0.201	0.275	0.349	-0.076	0.139
17	Precipitation of Driest Quarter	0.000	0.385	-0.222	-0.185	0.080
18	Precipitation of Warmest Quarter	0.063	0.303	0.364	-0.165	-0.517
19	Precipitation of Coldest Quarter	0.053	0.337	-0.273	-0.140	0.513

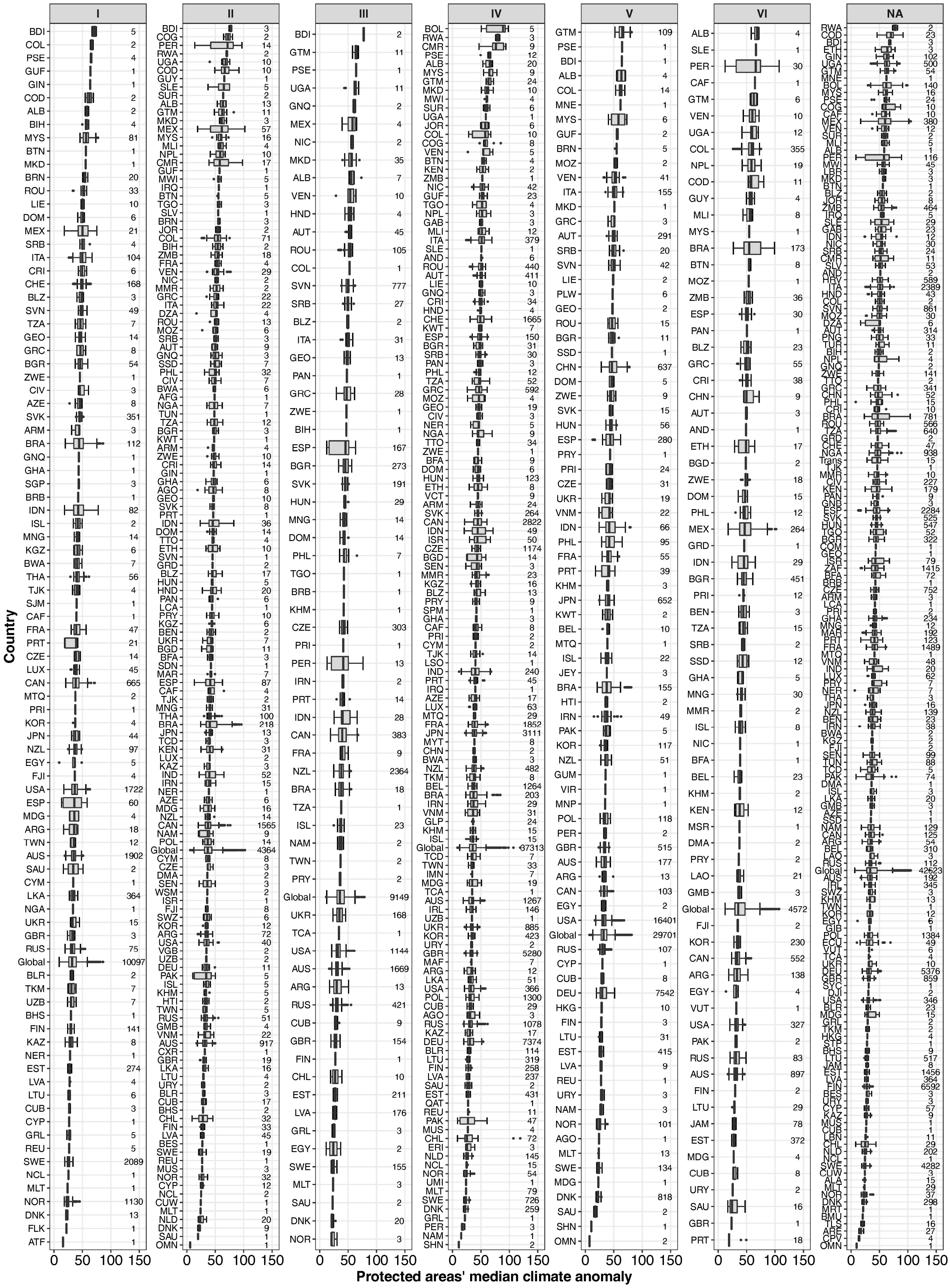

Figure S1. Predicted climate anomalies (2070, RCP 8.5) of PAs grouped by country and IUCN management category; see Figure 2 in the main text for RCP 4.5. We summarized the mean climate anomalies (Fig. 1) for each PA using the median. The IUCN management categories from I to VI cover a gradient of human integration, from strict human exclosure to sustainable human land use respectively. The black numbers represent the number of PAs within the countries and IUCN management categories. 'NA' means no management category was available. The boxplots were ordered by decreasing median. The limits of the grey box show the lower and upper quartiles, i.e. the interquartile range. The whiskers extend to the lowest and highest values within 1.5 times the interquartile range. The black dots indicate outliers beyond the whiskers. The alpha-3 country codes are given (i.e. ISO 3166). 'Global' composes all PAs, while 'Trans' refers to transboundary PAs.

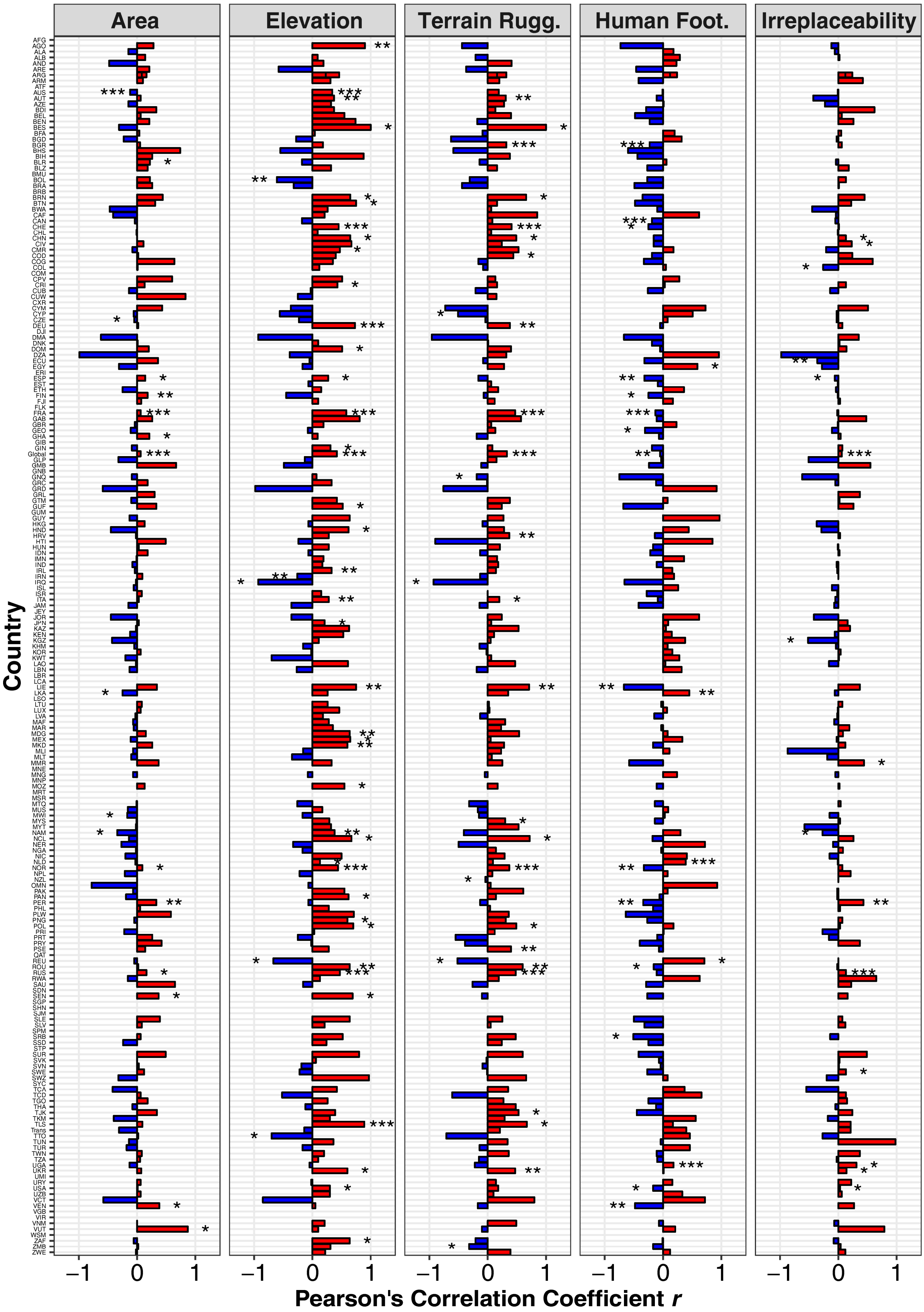

Figure S2. Global and country-specific correlations of the PAs' median climate anomalies (2070, RCP 8.5) with PA characteristics; see Figure 3 in the main text for RCP 4.5. The PA characteristics 'area', 'elevation' and 'terrain ruggedness' indicate the PAs' capacity to buffer the climate change impact; 'irreplaceability' represents the PAs' importance for the conservation of globally threatened species. By relating the predicted climate anomalies to the PA characteristics, we estimate the climate change exposure of PAs, i.e. potential impacts of climate change on PAs' effectiveness. PAs are assumed to be particularly exposed to climate change when the predicted climate anomalies, the human footprint and irreplaceability are high, while the area, elevation and terrain ruggedness are low. At the global scale, the median climate anomalies of PAs under RCP 8.5 correlate positively with PA area (r=0.06, p<0.001), elevation (r=0.42, p<0.001), terrain ruggedness (r=0.32, p<0.001) and irreplaceability (r=0.06, p<0.001); and negatively with the human footprint (r=-0.05, p=0.008) (see 'Global' in Fig. S2). Bars reflect Pearson's correlation coefficients r; red for positive and blue for negative coefficients. Asterisks represent the significance level considering spatial autocorrelation (*: p≤0.05, **: p≤0.01, ***: p≤0.001), while no asterisk means non-significant correlation (p>0.05). The alpha-3 country codes are given (i.e. ISO 3166). 'Global' composes all PAs, while 'Trans' refers to transboundary PAs.

8 Acknowledgements

First of all, I would like to express my gratitude to Prof. Dr. Carl Beierkuhnlein for igniting my passion for biogeography. I am inspired by his caring manner of teaching and giving advice not only about science. He provided me with the freedom to work on the open questions in ecology and biogeography that I was most fascinated by.

I also want to give thanks to all my co-authors and colleagues, especially Severin, Andreas, Asja and Reinhold, for the scientific guidance, stimulating discussions and technical support. I have learned a lot from these folks.

Moreover, I want to thank my wife Lena for her enduring support and love. She knows how to slow me down, particularly at times I am stubborn. Her enthusiasm for nature and an eco-friendly lifestyle motivates me every day to contribute to nature conservation. I am very grateful to be able to share my passion for nature with someone I love so much.

I am also very grateful for the continuous support of my parents during my entire career.

I would also like to show my appreciation to the editors and anonymous reviewers of my papers for their constructive criticism.

Finally, I would like to thank everyone who is dedicated to nature conservation. Nowadays such people are needed more than ever to preserve the values of nature for the generations to come. Let's keep on!

9 Appendix

Appendix 1. List of my talks at scientific conferences that are related to this thesis.

Conference	Date and location	Title	Authors
Jahrestagung des Arbeitskreis Biogeographie im Verband der Geographen an deutschen Hochschulen	05/2017, Erlangen, Germany	ECOPOTENTIAL - Protected Areas in a Continental Perspective	**Hoffmann, S**; Beierkuhnlein, C; Provenzale, A
6th International Symposium for Research in Protected Areas	11/2017, Salzburg, Austria	Uniqueness of protected areas based on priority species as a potential driver of conservation strategies in Europe	**Hoffmann, S**; Beierkuhnlein, C; Field, R; Provenzale, A; Chiarucci, A
Jahrestagung des Arbeitskreis Biogeographie im Verband der Geographen an deutschen Hochschulen	05/2018, Bonn, Germany	Plant community patterns along an elevation gradient of 2500 m: Do remote sensing signals conform to beta diversity?	**Hoffmann, S**; Schmitt, T; Chiarucci, A; Irl, S; Rocchini, D; Vetaas, OR; Tanase, MA; Mermoz, S; Bouvet, A; Beierkuhnlein, C
9th Biennial Conference of The International Biogeography Society	01/2019, Malaga, Spain	Climate change inside terrestrial protected areas worldwide	**Hoffmann, S**; Irl, S; Beierkuhnlein, C
Jahrestagung des Arbeitskreis Biogeographie im Verband der Geographen an deutschen Hochschulen	05/2019, Frankfurt, Germany	Climate change impact inside terrestrial protected areas across the globe	**Hoffmann, S**; Beierkuhnlein, C
Deutscher Kongress für Geographie	09/2019, Kiel, Germany	The geography of climate change inside the earth's terrestrial protected area	**Hoffmann, S**; Beierkuhnlein, C

Appendix 2. List of my publications related to this thesis but published in non-peer reviewed newsletters, journals or conference proceedings.

Newsletter, journal or conference proceedings	Publisher	Title	Authors
Ecopotential Newsletter, August 2016, http://ecopotential-newsletter.igg.cnr.it/2016/09/climatic-representativeness-of-ecopotential-protected-areas/	Ecopotential Project - European Union's Horizon 2020 research and innovation programme, grant agreement No 641762	Climatic Representativeness of ECOPOTENTIAL Protected Areas	**Hoffmann, S**; Beierkuhnlein, C; Provenzale, A
6th International Symposium for Research in Protected Areas – Conference Volume, 237-238 (2018), https://doi.org/10.1553/np_symposium2017s1	Salzburger Nationalparkfonds	Evaluating the potential of protected areas to preserve biodiversity at large scales	**Hoffmann, S**; Beierkuhnlein, C
Spektrum, 14(1), 36-39 (2018), https://epub.uni-bayreuth.de/3846/1/spektrum_ausgabe_01_2018.pdf	University of Bayreuth	Europäische Schutzgebiete - Neue Studie zeigt facettenreiche Beiträge zur biologischen Vielfalt	**Hoffmann, S**; Beierkuhnlein, C; Chiarucci, A
Deliverable No: 5.5, Ecopotential Project, https://www.ecopotential-project.eu/images/ecopotential/documents/D5.5.pdf	Ecopotential Project - European Union's Horizon 2020 research and innovation programme, grant agreement No 641762	Datasets following standard requirements	**Hoffmann, S**; Peterseil, J; Poursanidis, D; Beierkuhnlein, C

Appendix 3. My conference contributions to other topics while working on my dissertation. The asterisk marks the presenting author.

Conference	Date and location	Title	Authors	Type
46th Annual Meeting of the Ecological Society of Germany, Austria and Switzerland	09/2016, Marburg, Germany	The same, only different: Analysing the world‘s grassland heterogeneity in terms of productivity and beta diversity	**Hoffmann, S***; Fraser, LH; Pither, J; Jentsch, A; Sternberg, M; Zobel, M; Stahlmann, R; Beierkuhnlein, C	Talk
8th Biennial Conference of the International Biogeography Society	01/2017, Tucson, USA	ECOPOTENTIAL – Protected Areas in a Continental Perspective	Beierkuhnlein, C*; **Hoffmann, S**; Provenzale, A	Talk
EU BON Final Meeting	03/2017, Brussels, Belgium	Protected Areas and Biodiversity at the Continental Scale	Beierkuhnlein, C*; **Hoffmann, S**; Provenzale, A	Talk
International Biogeographical Society meeting: Climate Change Biogeography	03/2018, Evora, Portugal	Challenges for Networks of Protected Areas in a Rapidly Changing Climate	Beierkuhnlein, C*; **Hoffmann, S**; Hanz, D; Kienle, D; Weiser, F; Lawrence, A; Bernd, A; Zennaro, Barbara; Chiarucci, A; Vetaas, OR; Field, R; Provenzale, A	Talk
EuroGEOSS Workshop	09/2018, Geneva, Switzerland	ECOPOTENTIAL: Protected Areas and Earth Observation	Beierkuhnlein, C*; **Hoffmann, S**; Weiser, F; Stahlmann, R; Provenzale, A	Poster
9th Biennial Conference of the International Biogeography Society	01/2019, Malaga, Spain	ECOPOTENTIAL – Protected Areas and Earth Observation	Beierkuhnlein, C*; **Hoffmann, S**; Weiser, F; Stahlmann, R; Provenzale, A	Poster
9th Biennial Conference of the International Biogeography Society	01/2019, Malaga, Spain	How environment modulates primary succession dynamics	Irl, S*; Schweiger, A; **Hoffmann, S**; Fernández-Palacios, JM; Steinbauer, MJ; Beierkuhnlein, C; Jentsch, A	Talk

Appendix 4. Peer-reviewed publications on other topics that I contributed to during the time that I wrote my dissertation. The asterisk marks authors that contributed equally.

Irl, SDH; Schweiger, AH; **Hoffmann, S**; Beierkuhnlein, C; Hartmann, H; Pickel, T; Jentsch, A: Spatiotemporal dynamics of plant diversity and endemism during primary succession on an oceanic-volcanic island, *Journal of Vegetation Science*, *30*(4), 587-598, (2019), https://doi.org/10.1111/jvs.12765

Nila, MUS; Beierkuhnlein, C; Jaeschke, A; **Hoffmann, S**; Hossain, ML: Predicting the effectiveness of protected areas of Natura 2000 under climate change, *Ecological Processes*, 8(13) (2019) https://doi.org/10.1186/s13717-019-0168-6

Irl, SDH; Schweiger, AH; **Hoffmann, S**; Beierkuhnlein, C; Dewenter, J; Fernández-Palacios, JM; Hartmann, H; Müller, CL; Nuppenau, JN; Pickel, T; Steinbauer, MJ; Jentsch, A: How environment modulates primary succession dynamics, *American Naturalist*, (resubmission)

Raharivololoniaina, A; **Hoffmann, S**; Jaeschke, A; Beierkuhnlein, C: Madagascar' protected area network: under threat of novel and disappearing climate? (in prep.)

Kidane, Y; **Hoffmann, S**; Jaeschke, A; Beloiu, M; Beierkuhnlein, C: Current and future distribution of *Erica arborea*: a keystone species of Bale Mountains and other East African mountain ecosystems, (in prep.)

Pither, J*; **Hoffmann, S***; Beierkuhnlein, C; Bartha, S; Bennett, JA; Boldgiv, B; Bork, EW; Cabido, M; Cahill, JF; Carlyle, C; Campetella, G; Csergő, AM; Díaz, S; Enrico, L; Ensing, DJ; Fidelis, A; Foster, BL; Garris, H; Henry, HAL; Jentsch, A; Jurasinski, G; Mitchell, R; Moora, M; Overbeck, GE; Pillar, VD; Reinhart, K; van Rooyenx, M; Stotz, GC; Tungalag, R; Undrakhbold, S; Wellstein, C; Zobel, M; …; Fraser, L: The spatial scaling of plant taxonomic beta diversity in grasslands worldwide, *Global Ecology and Biogeography*, (in prep.)

Appendix 5. While writing my dissertation I was active as a scientific reviewer for the following journals: *Environmental Research*, *Applied Vegetation Science*, *Plant Ecology*, *Diversity*, *PeerJ*, *Journal of Mountain Science*, *Folia Geobotanica* and *Sustainability*.

Appendix 6. Bachelor and Master theses that I supervised while working on my dissertation.

Student	Year	Thesis type	Title
Franziska Hauch	2017	Bachelor	Eine Beta-Diversitätsanalyse verschiedener Waldtypen im Nationalpark Bayerischer Wald
Bernd Köppel	2017	Bachelor	Auswirkungen von Veränderungen in der Vegetationsperiode auf die Biomasseproduktion in mitteleuropäischen Wiesen
Viola Hipler	2018	Bachelor	Die räumliche Skalierung des Distance Decay in einem alpinen Tundraökosystem
Daniel Resch	2018	Bachelor	Klimabedingungen europäischer biogeografischer Regionen und ihrer Natura 2000-Gebiete
Maximilian Milbert	2019	Bachelor	Wirkung paneuropäischer und nationalstaatlicher Unterschiede auf die räumlichen Dimensionen europäischer Nationalparks
Mst Umme Salma Nila	2017	Master	Natura 2000 in Times of Climate Change: An Analysis across Biogeographical Regions in Europe
Bravedo Mudenda Mwaanga	2017	Master	Geographical analysis of habitat richness in European protected areas for conservation of biodiversity
Ange Raharivololoniaina	2018	Master	Climate change threats to protected areas in Madagascar

Appendix 7. My teaching activities while working on my dissertation.

Course	Term	Course type	Study degree
Seminar Physische Geographie: Biogeographie	Winter term 2017/18, 2018/19	Seminar	Bachelor
Seminar Nachbereitung La Palma Science School	Summer term 2016	Seminar	Mixed
Arbeitsmethoden zur Physischen Geographie	Summer term 2019	Seminar	Bachelor
Trends in Biogeography	Summer term 2018, 2019 Winter term 2018/19, 2019/20	Seminar	Mixed
Scientific Writing in Biogeography and Disturbance Ecology	Summer term 2018, 2019 Winter term 2018/19, 2019/20	Seminar	Mixed
Theories in Environmental Geography and Ecology	Winter term 2018/19, 2019/20	Seminar	Master
Fundamentals of Biodiversity Research	Winter term 2019/20	Exercise	Master
Geoökologisches Freilandpraktikum: Standortkundliche Feldmethoden	Summer term 2016, 2017, 2018, 2019	Practical course	Bachelor
Geländeübung zur Physischen Geographie	Summer term 2016, 2017, 2018, 2019	Exercise	Bachelor

10 Eidesstattliche Versicherungen und Erklärungen

(§ 8 Satz 2 Nr. 3 PromO Fakultät)

Hiermit versichere ich eidesstattlich, dass ich die Arbeit selbstständig verfasst und keine anderen als die von mir angegebenen Quellen und Hilfsmittel benutzt habe (vgl. Art. 64 Abs. 1 Satz 6 BayHSchG).

(§ 8 Satz 2 Nr. 3 PromO Fakultät)

Hiermit erkläre ich, dass ich die Dissertation nicht bereits zur Erlangung eines akademischen Grades eingereicht habe und dass ich nicht bereits diese oder eine gleichartige Doktorprüfung endgültig nicht bestanden habe.

(§ 8 Satz 2 Nr. 4 PromO Fakultät)

Hiermit erkläre ich, dass ich Hilfe von gewerblichen Promotionsberatern bzw. –vermittlern oder ähnlichen Dienstleistern weder bisher in Anspruch genommen habe noch künftig in Anspruch nehmen werde.

(§ 8 Satz 2 Nr. 7 PromO Fakultät)

Hiermit erkläre ich mein Einverständnis, dass die elektronische Fassung der Dissertation unter Wahrung meiner Urheberrechte und des Datenschutzes einer gesonderten Überprüfung unterzogen werden kann.

(§ 8 Satz 2 Nr. 8 PromO Fakultät)

Hiermit erkläre ich mein Einverständnis, dass bei Verdacht wissenschaftlichen Fehlverhaltens Ermittlungen durch universitätsinterne Organe der wissenschaftlichen Selbstkontrolle stattfinden können.

…………………………………………………………………………………….

Ort, Datum, Unterschrift