The future of protected areas: towards a multiscale management strategy enabling movement in face of climate change

DISSERTATION

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1 Summary

Despite growing societal awareness and rising political will to protect the planet's biodiversity, we are still in the midst of a biodiversity crisis. Habitat loss and fragmentation from anthropogenic development is considered the primary driver of species extinctions worldwide. In addition, human induced climate change is projected to severely decrease global biodiversity and markedly reduce the effectiveness of protected areas as nature conservation tools. In many cases, climate change will lead to shifts in species distributions by compelling migration poleward and towards higher elevations as species attempt to track suitable climatic conditions. Hence, the synergistic impacts of anthropogenic climate change – forcing species to move – and habitat loss from fragmentation – preventing species from moving – can be detrimental to species persistence and severely reduce the effectiveness of current protected areas.

In this thesis I formulate concrete recommendations for protected area expansion and management suited to the EU biodiversity strategy for 2030, which are primarily built on the objective of preserving large areas in the last remaining low fragmented lands on one of the world's most anthropogenically modified continents. I demonstrate that topographic diversity is correlated with climate change resilience in protected areas because climatic conditions can move within the boundaries of topographically diverse protected areas, allowing mobile species to establish new habitats within extant protected areas. I further present options for Europe to foster movement of individuals, populations, and species by expanding protected areas into low fragmented surroundings. Finally, I present current and future potentialities to preserve the capacity for species movement in existing protected areas in the EU.

These recommendations offer insights into landscape conservation strategies capable of maximizing the ability of species to move as local climatic conditions change (manuscript 1). Hence, I argue in this thesis that conservationists and policymakers should prioritize expanding protected areas so as to stem the impacts of additional fragmenting infrastructure (manuscript 2) while also managing existing protected areas by prioritizing anti-fragmentation approaches (manuscript 3). This strategy has the potential to directly and indirectly tackle two major threats to biodiversity: loss and fragmentation of habitat as well as climate change. This strategy is simultaneously applicable on multiple scales while also being relatively easy for policymakers to understand and is therefore translatable to actual conservation practice

2 Zusammenfassung

Naturschutzbemühungen zum Erhalt der globalen Biodiversität haben in den letzten Jahren an Aufmerksamkeit und Unterstützung stark gewonnen, sowohl in Gesellschaft als auch in Politik. Nichtsdestotrotz sinken die Zahlen der weltweit dokumentierten Arten rapide ab. Dies ist hauptsächlich auf den Verlust und die Fragmentierung von natürlichen Lebensräumen zurückzuführen. Desweiteren, trägt der durch den Menschen hervorgerufene Klimawandel einen erheblichen Teil zum Artensterben bei und verringert unter Anderem die Effektivität von Schutzgebieten. Um sich dem wandelnden Klima anzupassen, verlagern viele Arten Ihre Lebensräume in grössere Höhen bzw. weiter Richtung Pole. Während Klimawandel Arten dazu bringt sich auf Wanderschaft zu begeben, verhindert eine durch menschliche Siedlungen und Straßen fragmentierte Landschaft oft genau diese Form der Klimawandelanpassung. Daher ist es ein Leichtes sich vorzustellen, wie Klimawandel und Fragmentierung eine fatal Kombination für unsere globale Biodiversität sein können.

In dieser Dissertation lege ich konkrete Vorschläge für eine Vergrößerung und ein verbessertes Managment von Schutzgebieten in Europa dar. Diese Vorschläge entsprechen den Zielen der vor Kurzem verabschiedeten EU Biodiversitätsstrategie für 2030 und beinhalten eine Erweiterung des europäischen Schutzgebietsnetzwerks in Gegenden mit geringer Landschaftszersiedelung und -fragmentierung. Zudem weise ich eine höhere Klimawandelresistenz für topographisch heterogenere Schutzgebiete nach. Diese Klimawandelresistenz besteht darin, dass es wanderungsfähigen Arten in topographisch heterogenen Schutzgebieten theoretisch möglich ist neue Habitate innerhalb des gleichen Schutzgebiets zu finden ohne dieses verlassen zu müssen. Mit konkreten Vorschlägen zur Erweiterung von Schutzgebieten in gering fragmentierte Regionen der EU präsentiere ich eine praxisorientierte Option für die Förderung von klimabedingten Artwanderungen. Abschließend lege ich dar durch welche Praktiken im Naturschutzmanagment ein Erhalt der Artwanderungsmöglichkeit in bereits bestehenden Schutzgebieten sichergestellt werden kann.

Diese Empfehlungen erweitern unser Verständnis zu großräumigen Naturschutzmaßnahmen, welche die Fähigkeit von klimabedingten Wanderungen massgeblich verbessern. Basierend auf den Ergebnissen dieser Dissertation empfehle ich eine Erweiterung von bestehenden Schutzgebieten in gering fragmentierte Regionen. Dies brigt das Potential sowohl den Folgen des Klimawandels (Manuskript 1), als auch der Bedrohung durch zusätzlich fragmentierende Infrastruktur (Manuskript 2) Einhalt zu gebieten. Beides hat jedoch nur langfristig eine Aussicht auf Erfolg wenn Naturschutzmanagment in bestehenden Schutzgebieten ein weiteres Fortschreiten von Landschaftszersiedelung und -fragmentierung innerhalb von Schutzgebieten verhindert (Manuskript 3). Diese Naturschutzempfehlung hat somit eine erfolgversprechende Aussicht zwei der größten Bedrohungen unserer Biodiversität direkt und indirekt anzusprechen: Die Bedrohung durch den Verlust und die Fragmentierung von Lebensräumen sowie die Bedrohung durch den Klimawandel. Die empfohlenen Naturschutzmaßnahmen dieser Dissertation können gleichzeitig auf versiedenen räumlichen Skalen angewandt werden und sind zusätzlich leicht für Politiker verständlich und daher in der Praxis leicht umsetzbar.

3 Introduction

3.1 Motivation

Global biodiversity is poised to face unprecedented levels of threat in the coming decades. The challenge for conservationists is that addressing these threats requires working on and responding to challenges at multiple scales. On the global scale, human-caused climate change will force species to move or adapt to very different environmental conditions than they have faced in the recent past. At the regional scale, anthropogenic landscape fragmentation encroaches on and destroys habitats while preventing animal species from easily relocating to new areas. At the local level, conservation managers often lack proper legal tools as well as adequate financial resources paired properly with actionable, science-based criteria for expanding, maintaining, or hardening protections for threatened species and habitats. This thesis represents an attempt to address these multi-scalar pressures by synthesizing global, regional, and local threats to conservation, and offer steps toward integrating approaches to conserving protected areas at these different scales.

3.2 Structure of this thesis

In this thesis I first introduce biodiversity as it is the core of most recent conservation efforts and the target of threats analyzed in this thesis. I elaborate on its definition and assessment methods as well as its current state of rapid decline. Causes for the current biodiversity crisis are manifold, but two of the most dire threats are climate change and habitat loss and fragmentation. I first give a broad overview of human-caused climate change before I lay out biological responses to those changes observed. One of those responses is species or population movement to track suitable climate conditions, which presents the biological basis for the implications and suggestions drawn from all my manuscripts. Yet, while movement is a crucial adaptation strategy to respond to climate change, it is often obstructed by fragmented landscapes. Following the description of biological responses to climate change, I describe in greater detail the main processes and consequences of landscape fragmentation, the subject of manuscript 2 and 3. I first give an overview of terminology before I describe the consequences of landscape fragmentation to our globe's biota, directly through habitat loss, degradation, and isolation, as well as indirectly through altered species interactions. I include a separate section on the scientific debate over the consequences of habitat amount versus habitat configuration for biodiversity, and clarify the relation of my thesis results towards this debate. Since this thesis makes concrete suggestions for protected area establishment, design, and management, I introduce the historical background of protected areas as well as the objectives for their existence. Clarifying the objective for protected areas is crucial when making decisions on protected area establishment, design, and management, which form the core suggestions of my manuscripts. Further, I detail different management options, how they can be classified globally, and how management can be adapted to rapid global change. I briefly lay out which management options are supported by my thesis results. The section on protected areas ends with a short overview of their spatial distribution around the world. The introduction closes with the most recent conservation agreements on an international, as well as on an EU stage. I clarify how my manuscripts directly address commitments made by some of these treaties.

In the synopsis, I demonstrate how my manuscripts address potential avenues for improved conservation practices facing the synergetic threats of climate change and landscape fragmentation to biodiversity on different scales. I show how topographic diversity is correlated with climate change resilience in protected areas, since climatic conditions can move within the boundaries of topographically diverse protected areas. I further present the option for Europe to foster movement of individuals, populations, and species by expanding protected areas into low fragmented surroundings. And finally, I present the current state and future perspectives to preserve the ability of movement in already existing protected areas in the EU. In the outlook, I point to existing research gaps beyond the scope of this thesis and argue that managing landscapes for conservation purposes, as it is the goal of conservation biogeography, needs to include a management of protected areas for movement, especially in the light of high uncertainty for future environmental conditions.

The thesis ends with a description of my contributions to each manuscript followed by the presentation of the manuscripts. In the appendix, I list my scientific talks related to this thesis as well as 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 lecturer while I was writing this dissertation. The main concepts and terms applied in this thesis are explained and defined in **Box 1**.

Glossary: Definitions and explanations of concepts and terms used in this thesis.

Adaptation: A change or the process of change by which an organism or species becomes better suited to its environment.

Biodiversity: Biodiversity describes the variety of life and comprises genes, individuals, demes, populations, metapopulations, species, communities, ecosystems, and the interactions between these entities. Biodiversity considers the number of these entities as well as the differences between these entities.

Climate change: Climate change is a change in global or regional climatic patterns. In this thesis I focus on a change in climatic patterns predicted to occur in the mid to late 20th century attributed to global warming, a long-term heating of Earth’s surface observed since the pre-industrial period (between 1850 and 1900) due to human activities primarily fossil fuel burning, which increases heat-trapping greenhouse gas levels in Earth’s atmosphere (NASA, 2022).

Dispersal: Dispersal is any movement of individuals or propagules that has potential consequences for gene flow across space (Ronce, 2007). This includes the process by which individuals move from the immediate environment of their parents to establish in an area more or less distant from them (Traveset and Rodriguez-Peres, 2019).

Ecological niche: An ecological niche describes biotic and abiotic conditions enabling a species to persist within a certain space and time. There are three main niche concepts: Grinnellian’s, Eltonian’s, and Hutchinson’s niche concept. Grinnell describes a niche as the sum of a species needs towards its abiotic environment or habitat that allows the species to persist and reproduce within its habitat (Grinnell, 1917). Elton emphasizes the forms of biotic interactions, e.g., foraging and predation, which need to be fulfilled for a species to be able to persist in a habitat (Elton, 1927). Hutchinson’s niche concept describes a set of biotic and abiotic conditions (also called n-dimensional hypervolume) to which a species is adapted. This niche concept is not tied to a geographic location (Hutchinson, 1957). In this dissertation I most closely orientate on Hutchinson’s niche concept (section 3.4.2).

Edge effect: The change in biotic and abiotic conditions that appear at an ecosystem boundary and within adjacent ecosystems (Lindenmayer and Fischer, 2006).

Effectiveness: Effectiveness describes the degree to which a goal has been reached or an intended result been produced.

Efficacy: Efficacy describes the ability of reaching a goal or an intended result.

Efficiency: Efficiency reflects the ability to reach a goal or produce a result with little to no waste of energy, effort, or resources.

Habitat isolation: The isolation of species-specific habitat patches.

Habitat: Habitat is a geographic location (Krebs, 1985) where the environment is suitable for a species to survive and reproduce (Block and Brennan, 1993). Habitat, in contrast to landscape, is a species-specific entity. Contrary to habitat and landscape, a niche is not tied to a geographic location (Hutchinson, 1957). The fundamental niche of a species is the set of physical limits within which a species can live and reproduce.

Habitat fragmentation: Habitat fragmentation or habitat subdivision is the process of subdividing a single large area of habitat into several smaller areas. Habitat fragmentation or habitat subdivision is a species-specific entity (see definition Habitat). Contrary to habitat fragmentation, landscape fragmentation is a subdivision of areas of a certain land cover type, mostly vegetation cover.

Habitat isolation: The isolation of species-specific habitat patches.

Habitat loss: Habitat loss describes the loss of suitable habitat for a species, making the area unsuitable for the species survival and reproduction.

Landscape: In this thesis I use the human perspective on landscape (contrary to the species perspective on a landscape). Landscape perceived as experienced by humans, usually distinguishes between different patches of varying land cover, including vegetation cover, and their spatial arrangement.

Landscape fragmentation: Landscape fragmentation or landscape subdivision is the process of subdividing areas of vegetation cover within a landscape from a human perspective (Lindenmayer and Fischer, 2006).

Matrix: A matrix, in the context of a patch-matrix landscape, describes the space around and in between focal patches, not part of a focal patch itself.

Migration: Movement of animals from one place to another, usually seasonal.

Natura 2000: Natura 2000 is a network of protected areas in the EU. The aim of the network is to ensure the long-term survival of Europe's most valuable and threatened species and habitats, listed under both the Birds Directive and the Habitats Directive (European Commission [EC], 2022).

Protected area: An area of land and/or sea especially dedicated to the protection and maintenance of biological diversity, of natural and associated cultural resources, and managed through legal or other effective means (Dudley and Stolton, 2008).

Protected area surrounding: Protected area surrounding is the area immediately adjacent to a protected area. In this thesis protected area surrounding describes the terrestrial area in a 5 km buffer surrounding a protected area.

Resilience: Resilience describes the ability to maintain a good condition, or return to a previously good condition, after distress or change.

SLOSS: “SLOSS” stands for “Single Large or Several Small” and refers to the scientific debate on whether single large or several small protected areas are more effective for biodiversity conservation given a fixed amount of habitat area (Fahrig et al., 2022).

Topographic diversity: Topographic diversity, or topographic heterogeneity can be broadly defined as the diversity, size, and spatial arrangement of focal patches or landscapes. In manuscript 1 I investigate the topographic diversity of protected areas using three distinct characteristics: protected area size; maximal elevational difference i.e., elevational difference between highest and lowest point in a PA; and median terrain ruggedness (a median of small-scale elevational diversity).

3.3 Biodiversity

3.3.1 Concept, definitions, and measurement

Biodiversity or biological diversity, as the terms are used in this thesis, describe the variety of life and comprise genes, individuals, demes, populations, metapopulations, species, communities, ecosystems, and the interactions between these entities. Biodiversity considers the number of these entities as well as the differences between these entities. At the pioneering 'Earth Summit' the United Nations Conference on Environment and Development in 1992 in Rio de Janeiro, the Convention on Biological Diversity (CBD) defined biodiversity as '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 [UN], 1992).

First coined in 1988 (Wilson & Peter, 1988), the term biodiversity has experienced much attention while it's many definitions and meanings are often divergent at parts and lack a general theory behind them (Beierkuhnlein, 2003). In fact, the term biodiversity is regularly used as a catch-all term covering any of the multiple entities of biological diversity (Ferrier, 2002). Despite the lack of a concise and agreed-upon scientific definition, the measurement and monitoring of biodiversity is a pervasive practice in ecology, in part because biodiversity can function as an indicator for ecosystem health and ecosystem functioning (Tilman et al. 2014). In times of global change there is a growing concern for the maintenance of ecosystem health and ecosystem functioning on our planet. Hence, monitoring biological responses, e.g., in the form of biodiversity measures, to human-induced environmental changes has gained increased attention. In this thesis I do not measure biodiversity or the effects of human-induced environmental changes. Instead, I measure patterns of human-induced environmental change, i.e., shifted environmental conditions due to climate change (**manuscript 1**) and landscape fragmentation in (**manuscript 3**) and around (**manuscript 2, 3**) protected areas, with implications for biodiversity conservation. These changes in landscape patterns can have tremendous effects on biodiversity (Fahrig, 2003; Bellard et al., 2012). Thus, monitoring biodiversity, especially during a time of sharp biodiversity decline worldwide (section 3.3.2), should be complementary instead of opposed to monitoring a change in environmental patterns.

In general, measuring biodiversity is extremely challenging as it cannot be condensed through a single metric (Liu et al., 2018; Williams and Araújo, 2002). To combat this dilemma ecologists regularly measure a small subset of biodiversity to act as a proxy for other aspects of biological diversity not explicitly assessed (Lewandowski et al., 2010; Davies & Cadotte, 2011). The most commonly used metric to measure biodiversity is species richness (Marshall et al., 2020), which simply records the number of species in a given area. Measuring species richness is a relatively straightforward and easily interpretable method. Other common metrics for biodiversity assessment include species abundances or diversity indices combining species richness and abundance. Less common metrics include functional diversity, genetic diversity, or phylogenetic diversity (Marshall et al., 2020). Rarely is a species biology or population process (e.g., phenotypic plasticity, dispersal, migration, etc.) included since these measurements would add further complexity to biodiversity evaluations (Ferrier & Drielsma, 2010). Depending on which kind of biodiversity metric is used there can be differing results even for the same spatial location (Gascón et al., 2009). This can play an important role when it comes to conservation management. For example, when targeting conservation efforts towards the protection of species richness, all species are given equal status, sometimes even eliminating differences between highly threatened, endemic species and ubiquitous, introduced species (Milledge et al., 1991). In addition, all diversity assessments are scale dependent, whether assessed on a patch or a landscape level. Unfortunately, this scale dependency is often not conceded in conservation management and decisions. An example for a scale dependent species assessment is the dwarf-pine (*Pinus mugo*), categorized as early-warning stage in Bavaria (Landesamt für Umwelt [LfU] 2021), it is classified as not threatened (LfU 2021) for the whole Alpine region, and even stable for its global extend (IUCN 2022). Since conservation decisions are usually conducted on a national (**see manuscript 2**) or a local scale (see implications **manuscript 3**), biodiversity measures when intended to inform concrete conservation decisions need to be conducted on the appropriate spatial scale. In summary, to avert oversimplifications in assessing a subset of biodiversity, it is essential to determine an appropriate metric, and identify appropriate taxa or species assemblages, as well as determining an appropriate spatial scale when measuring biodiversity to inform conservation practices. Or in other words: we should always be aware that in the end “we do not conserve diversity indices,” Gilmore (1990, p. 384).

3.3.2 Global biodiversity crisis

Current scientific consensus holds that Earth has undergone five mass extinction events since the Cambrian period (e.g., Sepkoski, 1996; McElwain & Punyasena, 2007; Ceballos et al., 2015). “Mass extinction events” refers to brief geological periods in which comparatively stable background extinction rates of the past 540 million years are interrupted by sudden, precipitous spikes in species loss reaching over 75% of estimated species (Barnosky et al., 2011). These mass extinction events are believed to have resulted from an array of causes (Bond & Grasby, 2017). Today the primary drivers of species extinction are habitat loss due mainly to human population growth and infrastructure, and disproportionate resource consumption by humans as well as climate change (Millenium Ecosystem Assessment, 2005). Scientists anticipate that climate change will be the primary cause of biodiversity loss in the foreseeable future (Urban 2015). Conservation scientists generally increasingly embrace the hypothesis that we may be on the cusp of a sixth mass extinction directly brought on by the advent of the Anthropocene, a new geologic epoch characterized by the escalating global ecological and biogeochemical impacts exerted by human civilization (Steffen et al., 2015).

This sixth mass extinction is a loss of global biodiversity that is unprecedented within the timescale of human history (Barnosky et al., 2011). Its existence is indicated by contemporary rates of species loss far higher than the background rate estimated for the Holocene overall, much faster than the rate of compensatory evolutionary (speciation) that would be necessary to maintain steady rates of biodiversity (Barnosky et al., 2011; Ceballos et al., 2015; Cowie et al., 2022).

Large-scale assessments of extinction rates have used approaches based on species–area relationship (SAR) (section 3.5.5). These use spatial projections for lost habitat area, which are then used to model the proportional loss of species assumed to depend on that spatial pattern (Pimm & Raven, 2000). This collection of approaches has the benefit of avoiding the need for data on individual species extinctions, which are often biased to vertebrates or vascular plants (Cowie et al. 2022, Eisenhauer et al., 2019). However, SAR has been criticized for its use as a kind of blunt-instrument in predicting species loss, apparently over- or under-estimating future extinction rates, sometimes by wide margins (Simberloff, 1992; Harte et al., 2004; Thomas et al., 2004; He & Hubbell, 2013). Still, studies based on SAR-based approaches generally concur that loss of habitat is, and will continue to be, a significant contributor to biodiversity loss (Cowie et al., 2022).

Approaches based on individual species are more difficult to employ based on constraints of data collection but offer an invaluable tool to scientists by providing hard data against which SAR models can be judged and calibrated (Cowie et al. 2022). To provide a worldwide general assessment of biodiversity trends, The Living Planet Index, a joint initiative of the World Wildlife Fund and the Zoological Society of London, has monitored population trends of 4911 species and 27963 individual populations since 1970 (LPI 2022). The Index indicates and overall species decline of 68% within the last 50 years (World Wildlife Fund [WWF], 2020). The International Union for Conservation of Nature (IUCN) Red List (IUCN, 2022) is the global standard for evaluation of extinction risk (Lacher & Roach, 2017). The Red List assesses entire taxonomic groups facing high levels of threat. Classified as near threatened, vulnerable, endangered, critically endangered, extinct, or extinct in the wild are 26% of all animals, 30% of mammals, 41% of amphibians, 25% of insects, 46% of all plants, 50% of conifers, 44% of monocots, including grasses, 61% of asteracea (IUCN, 2022). Further, Red List Assessments are updated as new data becomes available. This allows trends in risk assessment to be observed over time (Butchart et al., 2007; Lacher & Roach, 2017). IUCN Red List data are the standard and basis for most transnational conservation initiatives such as the United Nations Environment Program, the Convention on International Trade in Endangered Species of Fauna and Flora, and the Convention on Biological Diversity (Lacher & Roach, 2017). Ominously, nearly every taxonomic group assessed has evinced consistently worsening status over time (IUCN 2022).

Broadly, expert consensus holds that this crisis of biodiversity has the grim distinction of being the first entirely anthropogenic mass extinction (Wake & Vredenburg, 2008; Ceballos et al., 2015; Schachat & Labandeira, 2021; Rull, 2022) Crucially, however, this biodiversity crisis has not yet developed into an anticipated mass extinction event. While current trends may indicate the imminence of a catastrophic mass extinction event, there remains an active scientific consensus that avoiding such a mass die-off remains theoretically plausible if substantial and holistic efforts are made (MacLeod, 2014). Therefore, research in biodiversity is more needed than ever before, including taxonomic research to assess the existing biodiversity before it is lost, biogeographical research assessing the distribution of biodiversity and its threats, conservation research assessing the methods most suited for the protection of biodiversity, and social-political research assessing the tools necessary to integrate different interest groups when proceeding with conservation efforts. With this thesis I attempt to advance biodiversity conservation by formulating concreate conservation suggestions. I have used toolsets founded in biogeographical research to address two of the most severe threats to biodiversity worldwide: habitat loss and fragmentation as well as climate change. With this thesis I hope to contribute to a better understanding of the spatial patterns of threats diminishing our biodiversity worldwide and to provide a roadmap for adjusted conservation efforts functioning as an early-onset intervention of biodiversity loss in the EU and globally.

3.4 Climate change

3.4.1 Overview

Anthropogenic climate change is one of the main drivers of the current biodiversity crisis (Ripple et al., 2019). While the earth has always been subject to climatic variations, intensive agriculture, deforestation, and the burning of fossil fuels have emitted an excess in greenhouse gases such as CO_2 and CH_4 into our atmosphere (Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services [IPBES], 2019). Since the industrial revolution, around the year 1750, there has been a sharp increase in greenhouse gas emissions now accumulating in the planet's atmosphere at unprecedented rates. In 2019, atmospheric CO_2 concentrations reached a possible peak within the last two million years of 440 ppm (parts per million) compared to just 50 years earlier where concentrations ranged around 320ppm (Intergovernmental Panel on Climate Change [IPCC], 2021). As a result, global average temperatures are rising alarmingly fast, especially since the midst of the 20th century (IPCC 2021). Average global surface temperature for the month of August was 0.9°C higher in 2022 compared to the average for the 20th century, and therefore ranks among the six warmest Augusts ever measured (National Oceanic and Atmospheric Administration [NOAA], 2022). The IPCC (2021) report predicts global average surface temperature will rise an additional 1 to 5°C by the end of the 21st century depending on future emission scenarios (IPCC, 2022). While these alarming rates of average surface temperature rise reflect a rapid global trend, they do not inform about conditions on smaller scales, e.g., continental or regional scales. In fact, terrestrial lands, especially in the northern hemisphere, as it is the focus of **manuscript 2** and **3**, are expected to experience greater rates of warming compared to the global average. In addition, surface temperatures at the poles and in high elevations are expected to increase especially fast. Climate impacts and risks in these regions are already advanced and likely to become irreversible (IPCC, 2022). Melting of glaciers and ice sheets giving way to land or water in those regions can cause a stark decrease in albedo, further accelerating global warming (Deser et al., 2000).

Another feedback loop is created by the melting of permafrost, which contains additional greenhouse gases e.g., CH_4, that, if melting occurs are released into the atmosphere adding to the greenhouse effect (Schuur et al., 2015). However, climate change does not only increase global average temperatures. Other dynamics and their associated climatic parameters, including maximum temperatures, precipitation, water balance etc., are also predicted to experience dramatic shifts (IPCC 2021). Those parameters are often more challenging to predict compared to temperature, especially for certain locations on more local or regional scales (Shepherd 2014, Zandler et al., 2019).

A similar challenge exists for the prediction of extreme events, e.g., hurricanes, droughts, and wildfires. While their overall frequency on a global scale is predicted to increase during the 21st century, the spatial and temporal specifics of these extreme events are subject to high uncertainty (IPCC, 2021; IPCC, 2022). Despite the high uncertainty for local climatic changes (Shepherd 2014), a call to action to safeguard our natural environment from detrimental effects of climate change is almost ubiquitous. This is mainly sparked by the already apparent evidence for climate change impacts on species and their habitat. As such, species are shifting their distributional ranges poleward or towards higher elevations (Chen et al., 2011; Pecl et al., 2017; Steinbauer et al., 2018; IPCC, 2022). While this change in distributional range can be a climate change adaptive strategy for some organisms, it often is not for others, depending on a myriad of factors, biotic and abiotic (section 3.4.2). Further, with rising temperatures phenological events, such as flowering (Muffler et al., 2016) or breeding (Bonamour et al, 2018) occur earlier in the season, often disrupting essential species interactions. Extreme events such as droughts have repeatedly been shown to result in increased tree mortality (Adams et al., 2009; Allen et al., 2010; Beierkuhnlein, 2021; Beloiu et al., 2022), sometimes leading to entire forest die-offs (Anderegg et al, 2013; Senf et al. 2020). Rising sea levels can also lead to the disappearance of entire habitats (Iwamura et al., 2013; Mukul et al. 2019). The impacts of climate change on species are manifold and are likely to cause severe declines in biodiversity of all levels including organisms, populations, ecological networks, ecosystems, and biomes (Bellard et al., 2012, Urban 2015). However, uncertainty in climate change predictions confounds efforts by conservationists to protect what is left of biodiversity today. For example, based on species-specific differences in climate change responses (section 3.4.2) climate change will likely lead to novel community assemblages, i.e., communities without current analogues (Williams & Jackson, 2007). Consequently, protected areas might contain species assemblages and ecosystems for which they were not designated originally (Hoffmann et al., 2019; Hoffmann & Beierkuhnlein, 2020).

Today's protected areas are static and fixed in space while climatic conditions and species distributional ranges are changing. Protected areas have traditionally been established to protect species or landscapes from human destruction (section 3.6.1) and if well managed (compare suggestions made in **manuscript 3**), can be effective in limiting threats to biodiversity caused by habitat loss and fragmentation. However, their inflexibility in the face of species' mobility could severely hinder their overall effectiveness in reducing extinctions tied to climate change (Araújo et al., 2011; Gaüzère et al., 2016; Hoffmann et al., 2019). Which existing protected areas will remain effective (**manuscript 1**), and how we can design future protected areas to stay effective (**manuscript 2**) as tools for biodiversity conservation in a changing climate, are key questions that need to be answered to develop robust long-term conservation strategies (Johnston et al., 2013; Lehikoinen et al., 2019).

3.4.2 Adaptation to climate change

Climate change is projected to influence all ecosystems worldwide (Scheffers et al., 2016) and future persistence of suitable climatic conditions is critical for species survival (Hannah et al., 2007; Loarie et al., 2009). All species are adapted to specific ecological niches. According to Hutchinson (1957) a species occurrence depends on environmental conditions and interspecific interactions. Today this niche concept has been refined to include – among other dependencies - the possible dependency on dispersal movement to colonize otherwise available niche space (Holt 2009). As Hutchinson's (1957) niche concept states, a species occurrence depends on the environmental conditions to which the species is adapted. If those environmental conditions change, because of climate change, species have three major ways to cope with this change if not going extinct: (1) "adapting genetically via microevoloution" (2) "adjustments through phenotypic plasticity" or (3) "moving to areas where conditions are still favorable to them" (Gienapp & Merilä, 2017).

One of the biggest problems with (1) adapting genetically to changing climatic conditions via microevolution, is time. The evolutionary process is a long process over several generations, it works through genetic variation, e.g., genetic mutation or recombination. This genetic variation can cause a change in an individual's characteristic. If this characteristic is better suited to the existing environmental conditions, including changed environmental conditions due to climate change, it is more likely to manifest in successive generations and eventually across entire populations. Hence, the speed to which a population or even an entire species can adapt to climate change through evolution is slow and depends strongly on a species' life cycle and reproduction rate (Jentsch and Beierkuhnlein 2008). The so-called 'evolutionary rescue' (Carlson et al., 2014) might, however, profit from certain extreme events (e.g., storms, fires, floods) in the sense that these disturbances can remove inertia from a system (e.g. non-reproductive long-lived individuals) and support accelerated establishment of new species and structures, potentially enabling species populations to adapt more quickly to changing climatic conditions (Jentsch & Beierkuhnlein, 2003). However, even if disturbance events accelerate a species turn-over, an evolutionary adaptation of species or populations to climate change strongly depends on reproduction rate. Especially if resistant genotypes must appear through mutation, evolutionary adaptation may require more time than available, given the speed at which climatic conditions are changing (Griffiths & Kelly, 2017).

Another way in which adaptation to climate change might be possible is (2) adjustments through phenotypic plasticity. Phenotypic plasticity is the ability of a genotype to express different phenotypes depending on the environmental conditions in its habitat. One example are genetically identical water flea (*Daphnia*) clones that vary in morphology depending on the absence or presence of potential predators (Gienapp & Merilä, 2017). Phenotypic plasticity in morphology or behavior has generally evolved to increase fitness under differing environmental conditions. It allows individuals or genotypes to adjust their phenotypes to cope with varying environmental conditions (Gienapp & Merilä, 2017). Hence, phenotypic plasticity has the potential to allow adjustments to changed environmental conditions due to climate change within the lifetime of a single individual compared to successive generations of a species. However, outside of a laboratory experiment, ecosystem complexity limits the abilities of phenotypic plasticity to function as a successful strategy to cope with climatic changes (Cohen et al. 2018). A prominent example are predator-prey relationships. If a predator's life cycle has evolved around a prey's life cycle, a phenotypic plasticity not synchronized between predator and prey likely decreases the predator's fitness (Cohen et al., 2018; Bonamour et al., 2019). In their review Thackeray et al. (2010) were able to show how the phenology at lower trophic levels has advanced consistently at faster rates than that at higher trophic levels. This further emphasizes the point that phenotypic plasticity may allow populations and species to adjust to environmental changes in the short term, but there may be limits to the expression of plasticity making long-term persistence through this mechanism impossible (Gienapp & Merilä, 2017, Cohen et al., 2018).

Another way in which adaptation to climate change might be possible is (3) the movement of populations and species to areas where the environmental conditions are favorable. On the global average, climate change has led to an increase in temperature (IPCC 2022). However, on a local or regional scale, as relevant for species distribution and population's habitat suitability, climate change can bring a multifarious change in environmental conditions besides a rise in average temperature. As such, variation, e.g., in precipitation, seasonality, or evaporation, are additional consequence of global warming (Konapala et al., 2020). Indirectly, climate change can also lead to altered environmental conditions apart from climate, e.g., changes in salinity of water and soil, or changes in habitat availability through rising sea levels. As is mentioned above, species' niches are determined by specific environmental conditions (Hutchinson, 1957). If climate change causes a change in environmental conditions outside a species niche, and adaptation through plasticity or evolution is not sufficient, relocating to another area where the environmental conditions describing a species' niche are present is often the only alternative to extinction. As such, there is an increasing body of literature documenting species' range shifts theoretically (e.g., Berteaux et al., 2018) and empirically (e.g., Chen et al., 2011; Root et al., 2003).

In a meta-analysis Chen et al. (2011) calculated an average speed of 16.9 km/decade for species range shifts into higher elevations. In another meta-analysis Parmesan and Yohe (2003) estimated an average range shift speed of 6.1 km/decade toward the poles. While these numbers nicely showcase the urgency of biological response to a rapidly changing climate, they have little meaning for individual species or populations. The ability of a species to track its suitable climatic condition depends strongly on species-specific characteristics, e.g., dispersal ability, as well as landscape characteristics, e.g., fragmentation. Dispersal abilities between species can vary tremendously, and whether a relocation to an area with suitable environmental conditions is possible depends almost entirely on whether suitable habitat is present within the typical dispersal distance of a species (Jaeschke et al., 2013).

In mountainous regions, high heterogeneity in elevation, aspect, and slope often results in a diversity of climates such that species can make smaller spatial adjustments to track suitable climatic conditions, compared to low-elevation areas (Carroll et al., 2017; Littlefield et al., 2017). Yet species or populations already living at the limit of their distributional range, for example on mountain tops, can often not evade climate change by dispersal. Landscape features, such as insurmountable environmental barriers, or anthropogenic constructions and landscape fragmentation, can further prevent successful climate tracking (Littlefield et al., 2017; Lehikoinen et al., 2019). Even considering these limits, dispersal as a biological response to climate change is still a crucial way to evade extinction with shifting environmental conditions, proven by the simple fact that it has already been repeatedly recorded in nature (Parmesan & Yohe, 2003; Root et al., 2003, Chen et al., 2011; Steinbauer et al., 2018).

Although climate change is not the only reason behind species extinctions (section 3.5), climate change is certainly one of them, with often detrimental consequences for a huge variety of species (Chivian & Bernstein, 2008; Chen et al., 2011; Urban, 2015). Urban (2015) even predicts that climate change alone could put one-sixth of all species at risk of extinction. This demonstrates the risk biodiversity is facing due to climate change and exemplifies that biological responses to climate change are not optional but rather critical. While we, as humans, have little control over a species microevolution, phenotypic plasticity, or dispersal ability, we do – however - have some control over anthropogenic landscape fragmentation acting as dispersal barriers for many species. Hence, I argue in this thesis that we should prioritize a reduction in additional fragmenting structures by expanding protected areas (**manuscript 2**) and managing for anti-fragmentation policies within protected areas (**manuscript 3**). This strategy has the potential to directly and indirectly tackle two major threats to biodiversity: loss and fragmentation of habitat as well as climate change (**manuscript 1**).

3.5 Landscape fragmentation

This thesis is meant to address potential avenues for improved conservation practices facing the synergetic threats of climate change and landscape fragmentation to biodiversity on different scales. Hence, this thesis does not address any specific species directly and therefore does not look at any habitat – which is a species-specific entity – directly. Instead, when addressing landscape fragmentation in this thesis I address a landscape-scale process encompassing the loss and fragmentation of vegetation cover through anthropogenic structures, i.e., build-up area, roads, and rail lines. Using effective mesh density (s_{eff}) as metric (**manuscript 2, 3**), I thereby measure (a) the reduction in total area of vegetation cover, (b) the increase in the number of patches containing vegetation cover, and (c) decrease in sizes of patches containing vegetation cover. I do not consider the degree of patch isolation. Thus, I measure loss and fragmentation of areas containing vegetation cover as a unified phenomenon rather than measuring fragmentation per se (Fahrig, 2003). While the effects of fragmentation per se on biodiversity are debated, habitat loss and fragmentation are unilaterally accepted as the primary driver of our current global biodiversity crisis (section 3.3.2). Habitat loss and fragmentation are a highly common result of landscape fragmentation as defined in **Box 1**.

Most definitions for landscape or habitat fragmentation involve breaking a habitat patch into two or more smaller patches. Smaller patches of vegetation and/or habitat are often unable to support viable populations (Shaffer 1981) and depending on their degree of isolation, do not support metapopulation exchange (Chesson, 2001). Landscape fragmentation, i.e., the loss and fragmentation of vegetation cover, means for most species a loss and fragmentation of habitat (McGarigal & Cushman, 2002; Fahrig, 2003). Landscape fragmentation can quickly lead to species extinction when remnant habitat patches are too small to support species persistence. In this case the habitat has been lost entirely. However, if a population can survive and persist within the remaining habitat patches, it still often faces severe threats from habitat degradation, including edge effects, habitat isolation, or altered species interactions. In addition, random fluctuations in abiotic conditions (environmental stochasticity), within the small remnant population (demographic stochasticity), and within the gene pool of these small remnant population (genetic stochasticity), can often aggravate the threats posed by landscape fragmentation. In the following I outline the most critical outcomes of landscape fragmentation on species' habitats, as well as species responses to those threats.

3.5.1 Habitat loss

In contrast to landscape, habitat is defined as a species-specific entity, i.e., the geographic location (Krebs, 1985) where the environment is suitable for a species to survive and reproduce (Block & Brennan, 1993). Habitat loss is, therefore, also a species-specific entity describing the loss of suitable habitat for a species, making the area unsuitable for the species to survive and reproduce. Hence, it is not too surprising that habitat loss is the foremost driver of population declines and species extinctions worldwide (Lindenmayer & Fischer, 2006). Reasons for habitat loss can be either natural or human induced. Examples for natural causes of habitat loss are volcanic eruptions (Croizat 1960; Weiser et al. 2022), wildfires (Agee 1999; Bradstock et al., 2002), or coastal erosions (Paprotny et al., 2021, Vitale et al., 2021). Examples for human induced habitat loss include landscape modification, for example through logging, excavation, or construction of roads and build-up areas. In both cases it is important to be aware that habitat loss is not a synonym for the loss of vegetation. While a loss of vegetation can be a loss of habitat for many species, it does not need to be a loss of habitat for all species (Fahrig, 2003). The amount of suitable habitat may in some cases even increase, e.g., for certain generalist species (Devictor et al., 2008). However, in most cases loss of vegetation results in the loss of habitat and consequently leads to species' decline (Kattan, 1994; Radford et al., 2005; Mayani-Paras et al., 2021).

In this thesis, I do not focus on any specific species, therefore I do not measure habitat loss or habitat fragmentation directly, since habitat is a species-specific entity. Instead, I measure landscape modification by humans, i.e., the loss and fragmentation of vegetation cover through build-up area, roads, and rail lines. Indirectly this type of landscape modification is highly associated with habitat loss, habitat degradation, habitat fragmentation, and habitat isolation, as well as changed species interactions (Lindenmayer & Fischer, 2006). Further, these processes occur on multiple spatial scales and can be highly threatening to species survival and persistence in an area. In addition, measuring landscape modification from a human perspective allowed me to derive results on multiple spatial scales (**manuscript 1** global, **manuscript 2 and 3** continental) as well as formulate concrete suggestions for conservationists focused on the preservation of biodiversity rather than single species (**manuscript 1, 2, 3**).

3.5.2 Habitat degradation

According to the IPBES (2019), habitat degradation is a "general term describing the set of processes by which habitat quality is reduced. Habitat degradation may occur through natural processes (e.g., drought, heat, cold) and through human activities (forestry, agriculture, urbanization)". In this thesis I focus on human-caused landscape fragmentation. Hence, in the following I briefly illustrate possible reasons and results of habitat degradation through human activities within patches of vegetation cover in a fragmented landscape.

Once a landscape is fragmented and vegetation cover is lost, the remaining patches of vegetation, habitat to the species that persist within them, often suffer various forms of habitat degradation. These forms include pollution of air, soil, and water, disturbance through light or noise, altered physical conditions at the edges of habitat patches, increase in poaching activity, increase in invasive species etc. A common result of landscape fragmentation is the increase in the length of boundaries or edges of the remaining patches (Burgess & Sharpie, 1981). Edges usually experience altered biological or physical conditions, i.e., edge effects (Matlack et al., 1993). Edge effects can be manifold and include changes in microclimatic conditions, e.g., changes in temperature, water vapor, or wind speed (Lovejoy 1986), altered biological conditions, e.g., changes in reproduction, biomass production, or disease dynamics (Hobbs & Yates, 2003; Wilkin et al., 2007; Lawrence et al., 2018), and altered biochemical processes, e.g., changes in nutrient cycles (Weathers et al., 2001). These edge effects at the boundaries often permeate into the interior of a remaining patch, in some cases even throughout the entire patch, often leading to severely degraded habitats (Laurance, 2000).

The quality of the surrounding matrix of a patch also has a strong influence on the state of ecosystems or their degree of degradation within patches (Clerici et al., 2007; Watling et al., 2011; Rider et al., 2018). As such, anthropogenic pressures in the surroundings of protected area ‘patches’ are often closely mirrored within protected areas themselves (Laurance et al., 2012; Perello et al., 2012). Landscape fragmentation as a form of anthropogenic pressure is no exception to this relation of matrix-patch quality, as I show in **manuscript 3**. Human constructions and roads as drivers of landscape fragmentation have led to sever habitat degradation overall.

Roads have immense consequences for ecosystems, even beyond their direct impact on habitat loss and fragmentation. In a comprehensive review, Trombulak and Frissel (2000) have shown that roads can heavily alter environmental conditions in areas adjacent to the actual road itself. As such, roads can lead to changes in soil density, temperature, soil water content, light levels, dust, surface waters, patterns of runoff, and sedimentation, as well as adding heavy metals (especially lead), salts, organic molecules, ozone, and nutrients to roadside environments. Roads also have been shown to increase the presence of exotic species, and often facilitate the spread of invasive species. Since roads provide access to formerly remote regions, legal or illegal hunting, trapping, and poaching often increases remarkably after road construction. On a population level, roads can change the demography of species by increasing mortality through vehicle collisions or changing animal behavior. While Trombulak and Frissel (2000) do not explicitly focus on roads or settlements in protected areas, or mention the need for species movement in times of climate change, the results of my thesis derives the same implication as Trombulak and Frissel (2000) derive from their review: Avoid construction in areas with no or little roads and settlements and where possible remove existing roads to benefit conservation outcomes.

It is important to emphasize that I do not assess habitat degradation from a species perspective. For example, I do not distinguish an old-growth forest home to many species from a forest plantation. Yet, such differences in habitat quality can have immense consequences for species survival and persistence (Franklin, 1981). In my thesis I formulate concrete suggestions for conservation actions, i.e., the expansion of protected area size (**manuscript 1, 2**), prioritizing low fragmented areas when establishing new protected areas (**manuscript 2**), and managing for preventing additional fragmentation inside protected areas (**manuscript 3**). These suggestions are geared towards allowing species movement with shifting environmental conditions with the ultimate goal of preserving biodiversity in times of global change. Yet, it is important to note that this research and these suggested conservation actions are just a first step in achieving the goal of biodiversity preservation. While a direct measurement of biodiversity (section 3.3.1.) or habitat degradation lies beyond the scope of this thesis, follow-up studies including such measurements to further narrow down spatial priority areas for the establishment of future protected areas, are urgently needed, especially considering the chronically limited budget in nature conservation (section 3.7).

3.5.3 Habitat isolation

The main threat posed by habitat isolation is the hindrance of movement for species, populations, and individuals between habitat patches. Yet movement is often essential for the survival and persistence of a species in a given area. Plants' dispersal can be dramatically impaired based on the distances between habitat patches (Hanski 1994, Duncan & Chapman, 1999). While animals are generally more mobile than plants, their movement occurs on several spatial and temporal scales, i.e., day to day movement, dispersal movement, migration movement, or even movement due to range shifts under climate change (Lindenmayer & Fischer, 2006).

Several studies have documented animal day to day behavioral changes due to habitat isolation. When primary habitat is broken up into smaller habitat patches, a single patch alone might not hold enough resources for an animal of a particular species to survive. In this case the animal needs to cross unsuitable matrix to travel from patch to patch for foraging. This increases total distance covered as well as total foraging time spent (Boone & Hunter, 1996). Consequently, home range sizes can increase, as it was empirically shown for coyotes and bobcats in North America (Riley et al., 2003), or giraffes in Tanzania (Knüsel et al., 2019). The increase in total distance covered and time spent on foraging can lead to an overall increase in energy spent on foraging (Doherty & Driscoll, 2018). In some cases, this can even cause a reduction in overall fitness of a species (Haapakoski & Ylönen, 2010).

In addition to phenomena related to day-to-day movement, altered dispersal due to habitat isolation has been extensively studied for plants and animals. If habitat is subdivided into several smaller patches, these smaller patches are then to different degrees isolated from each other, and dispersal between the patches is impaired. In such a case a formerly connected population can likewise be divided into subpopulations, which together can form a metapopulation with its own dynamics of dispersal (**Box 2**). The division of a single large patch into several small patches increases habitat isolation from which two major consequences arise. One, possibly suitable habitat patches might remain uninhabited by certain species simply because the distance to the next inhabited patch is too big to be overcome (Burkey, 1989; Pither & Taylor, 1998).

Box 2: Metapopulation

In fragmented landscapes the habitat of a given species is often subdivided into several habitat patches. Hence the individuals living in these habitat patches form spatially separated populations, also called subpopulations. When these spatially separated subpopulations show population dynamics independent from each other, but are in limited and infrequent contact, e.g., through dispersal, the sum of these subpopulations is called a ‘metapopulation’ (Levins, 1970; Hanski, 1997; 1999). Within a metapopulation, extinction and recolonization of patches occurs frequently. A formerly occupied patch can become empty when a subpopulation goes extinct. Contrary, an empty patch can be recolonized (also called rescue-effect) and therefore be again a part in the metapopulation habitat (Hanski & Gyllenberg, 1993). There exist several metapopulation models. The classical metapopulation model assumes habitat patches of roughly the same size with roughly the same functions among subpopulations (Levins, 1970). The island-mainland metapopulation model is based on the theory of island biogeography (MacArthur and Wilson, 1963) and describes one large ‘mainland’ patch and one or more small ‘island’ patches (Hanski, 1999). This model also inspired the source-sink metapopulation model. This model distinguishes between ‘source’ patches and ‘sink’ patches. ‘Source’ patches are characterized by populations with high reproduction rates and a population growth beyond their capacity that function as source of individuals, which frequently disperse and recolonize other patches. ‘Sink’ patches, on the other hand, are characterized by populations with low reproduction rates (lower than 1) which would not be able to sustain permanent viable populations without frequent recolonization events from nearby ‘source’ patches (Pulliam, 1988; Hanski, 1999). Metapopulation models are a concept inherently tied to a landscape-scale perspective (section 3.5). They are often used to assess species extinction risks for conservation in fragmented landscapes.

Secondly, if the subdivision of suitable habitat into smaller and more distant patches impairs dispersal, then gene flow between populations is reduced (Epps et al., 2005). However, distance alone does not define the possibility or impossibility of dispersal. The type of barrier that needs to be crossed to travel from one patch to the other can have tremendous impacts on species’ movement. One prominent example is the puma (*Puma concolor*) population in southern California. Isolated by a major highway, the population on the western side of the highway has become extremely isolated and inbred to the degree that a single puma crossing in 15 years has markedly changed the genetics of the whole population, raising heterozygosity to levels similar to the much larger puma population on the eastern side of the highway (Gustafson et al., 2017).

Landscape fragmentation and resulting habitat fragmentation can also pose a severe threat to migrating species. The most common migrations occur across latitudes, e.g., the migration of many diurnal bird species from north to south and vice versa (Sockman & Hurlbert, 2020), or across altitudes, such as ungulate migration into lower altitudes to reach accessible feeding grounds in winter (Smolok et al., 2018). Other types of seasonal migration include migrations tracking food sources (Price et al., 1999) or migration from and to breeding grounds, as common among amphibians (Matos et al., 2019). All of these types of migration require at least short-term suitable habitat for the spaces used in between the start and end point of a migration route. Examples for possible conservation solutions targeted towards migrating species include narrow corridors or steppingstones, allowing species to use these spaces as travelling passages on their way to their seasonal habitat grounds (Scharf et al., 2018; Myslayek et al., 2020; Rocha et al., 2021).

Another rather innovative conservation approach attempts to institute short-term nature preserves in places where permanent protection of land is not feasible, e.g., due to private ownership. As such, Reynolds et al. (2017) proposes to put flooded rice fields under temporary protection, ranging between a few days to a couple of weeks, to allow a stop-over for migrating birds on otherwise continuously used agricultural fields. A special case of migration movement constitutes the movement due to range shifts under climate change. While range shifts associated with climatic shifts have been usually slow in the past, current anthropogenic climate change demands a much faster speed for range shifts if they are to be successful (Thomas et al., 2004; Loarie et al., 2009).

All forms of movement described here are species specific. In this thesis I attempt to derive concrete suggestions for conservation actions from a landscape perspective capable of maximizing the ability of species to move. While this holds the benefit of being applicable on multiple scales as well as relatively easy understandable, and therefore translatable into actual conservation practice, it does not address any species-specific conservation actions. Movement – whether it is day to day movement, dispersal movement, migration movement, or movement due to range shifts under climate change – is always species-specific. Impacts of landscape and habitat fragmentation are dependent on the species mobility, mode of movement, as well as the relative spatial scale of species body and home range sizes. (Chepko-Sade & Halpin, 1987; Hanski, 1994; Lindenmayer et al., 2005). Hence, biogeographical conservation research with a landscape perspective – as it is the focus of this thesis - should be complementary and not opposed to species-specific research on the effects of landscape fragmentation. I contend that individual species responses to modified habitat, e.g., habitat loss, fragmentation, degradation, and isolation are a critical piece in our understanding of the effects of rapid and ongoing human landscape modification on biodiversity. Therefore, it is crucial to extend and deepen our knowledge in this field. However, I also acknowledge that given the pace of ongoing landscape modification paired with a rapidly changing climate, fast and comprehensive actions from nature conservationists are required. Taking on a landscape perspective and deriving implications and suggestions for conservation action as I present it in this thesis might not always provide the most suitable solutions for certain species based on our current knowledge gaps regarding species responses to landscape modification and climate change. However, these are immediate and executable solutions capable of keeping track with the speed of land-use and climate change threatening our global biodiversity.

3.5.4 Altered species interactions

Species interactions such as mutualism, competition, predation, and parasitism, are often altered due to habitat loss and fragmentation (Lindenmayer & Fischer, 2006). Mutualism is defined as interspecific interactions that benefit both species (Bronstein, 1994). Often one or both species are to such a degree dependent on the goods or services the mutualistic partner provides that they are severely reduced in their fitness, or in some cases cannot survive without the mutualistic partner. One common example are plants and their pollinators. While most plants can be pollinated by at least a few different species, some plants rely on very few, or in the case of the yucca plant, on one single species for their reproduction (Pellmyr & Huth, 1994). If one of the mutualistic partners responds to habitat loss and fragmentation through spatial range shifts, the other mutualistic partner needs to respond in the same way or face extinction risk, even if they might not have been directly impaired by habitat loss or fragmentation.

Competition occurs in an environment containing a limited resource. Competition is the interaction between two species which both require the resource, but the interaction between the two species lowers the fitness of both species. Habitat loss and fragmentation can cause spatial shifts in species ranges, forcing species to ‘share’ habitat with limited resources resulting in new forms of competition. One example is partitioning the time of activity, as has been empirically shown for deer species in Brazil (Ferreguetti et al., 2015), or mule deer, moose, grizzly bear, and wolverine in a shared boreal forest habitat (Frey et al., 2017).

Predation is the interaction in which one organism or species, the predator, consumes all or part of the body of another organism, the prey. Predation interactions can be highly sensitive to habitat loss and fragmentation, as shown on behavioral predation responses of an apex predator the Puma (*Puma concolor*) in a highly fragmented landscape in central California. Smith et al. (2016) have shown that Pumas in highly fragmented areas shift their preferences for prey to smaller animals, including domesticated animals. In addition, the traditional prey - black-tailed deer (*Odocoileus hemionus columbianus*) - experienced an up to 36% higher kill rate by pumas (Smith et al., 2015). This increased predation pressure was correlated with a decrease in distance to human housing resulting in an ‘ecology of fear’ in which pumas spend shorter times feeding on a killed deer out of fear from humans (Smith et al., 2017). This short feeding time results in a decreased energy intake from each individual kill, which is compensated by higher predation rates (Smith et al., 2015).

Parasitism is the interaction in which one organism, the parasite, causes harm to another, the host, which the parasite utilizes as habitat and depends on for resource acquisition (Raffel et al., 2008). If a host’s spatial distribution is altered due to habitat loss and fragmentation, this directly affects the parasite. One example for this can be found in the eastern United States, where human settlement and agriculture, and mining lead to extensive logging and large-scale land-clearing. A sharp decline in wildlife population, such as white-tailed deer (*Odocoileus virginianus*) and even the extinction of many apex predators, such as puma or wolf were the consequence (Wayne & Jenks, 1991; Brookman, 2006). However, in the 19th and 20th centuries land use trends changed, agricultural practices declined, and many cropland, pasture, and other cleared lands were abandoned. An ensuing reforestation followed (Drummond & Loveland, 2010). With regrowing forests and the absence of apex predators, deer population increased rapidly and along with them the associate parasite species, the deer tick (*Ixodes spp.*) (Wilson et al., 1985; Allen et al., 2003). However, deer ticks are not deer-specific parasites. They feed on a variety of hosts, including humans. One of the diseases transmitted from deer tick to humans is Lyme disease. Today, the eastern United States is considered a hotspot for Lyme disease cases, with Lyme disease affecting an estimated 300,000 people per year (Centers for Disease Control and Preventions [CDC] 2022). This is just one of many examples demonstrating how habitat loss and fragmentation can have a rippling effect through the complexity of altered species interactions. There is much empirical evidence showing that species dependent on highly complex biological processes and species interactions are often more vulnerable to landscape fragmentation simply because the likelihood that one of the components of these highly complex processes and interactions is disrupted is higher, compared to species with less complex processes and interactions.

To summarize, landscape fragmentation often coincides with the loss, degradation, and isolation of habitat which can have tremendous effects on species survival and persistence. Sometimes those effects are easy to grasp, for example in the case of the Formosan clouded leopard (*Neofelis nebulosa*) in Taiwan declared extinct in 2012, Père David's Deer (*Elaphurus davidianus)* in China declared extinct in 2016, or *Nymphaea thermarum* in Rwanda declared extinct in 2019 (IUCN, 2022). In other cases, interspecific interactions such as predation, competition, mutualism, parasitism, and disease transmission can be altered due to landscape fragmentation and can indirectly cause extinctions, arguably in the case of the St Helena Olive (*Nesiota elliptica)* on St. Helena Island, declared extinct in 2016, or the Splendid Poison Frog (*Oophaga speciosa)* in Panama declared extinct in 2020. Similarly to habitat loss and fragmentation, species range shifts due to climate change (section 3.4.2) can also lead to changes in species compositions and therefore altered species interactions, such as described in this section. The reasons for an extinction are manifold and often difficult to track or tease apart. Sometimes extinctions can follow many decades after a disturbance event, such as habitat loss or fragmentation. This is referred to as the 'extinction debt' (Tilman et al., 1994; Kuussaari et al., 2009) and creates an additional, often-unrecognized challenge for biodiversity conservation. However, this complexity behind extinctions should be an added motivation for halting habitat destruction and degradation and putting efforts into protecting what is left of natural habitat and the biodiversity within.

3.5.5 Habitat amount versus habitat configuration

The main tool in nature conservation is the establishment of protected areas. Certain areas of the land or sea are designated as protected to preserve species from extinction. However, the protection of land or seascapes has, and will always, stand in competition with other land use interests, and nature conservation has, and will always, suffer from a lack of financial resources. Hence, trying to optimize the outcome of conservation efforts given a limited budget is of high concern for theoretical and applied conservation science. One prominent goal in nature conservation is the protection of biodiversity. The need to achieve this goal under restricted financial resources has sparked a vigorous debate among conservationists: The so called SLOSS debate. Assuming that a limited budget determines the total amount of area that can be preserved, the SLOSS "Single Large or Several Small" debate centers around the question of whether a single large, protected area can conserve more species, i.e., higher biodiversity, compared to several small, protected areas, given that the total habitat amount stays the same.

Ecological theory, developed as early as the 1920s, has been used in trying to solve this question. Among the most prominent theoretical concepts in the SLOSS debate are the species-area relationship (Arrhenius, 1921; Gleason, 1922), island biogeography theory (MacArthur and Wilson 1963, 1967), and habitat amount hypothesis (Fahrig, 2013). Species-area relationship (SAR), often referred to as the species-area curve, describes the relationship between patch area or patch size, and species richness. Whereby, the number of species within a taxonomic group tends to increase with area (Connor & McCoy, 1979; Hanski, 1994). This relationship, regardless of its concrete shape (e.g., whether a linear, exponential, or power function), has been empirically confirmed across different spatial scales, different ecosystems, and different taxonomic groups (Kjoss & Litvaitis, 2001; Chen et al., 2019; Gooriah et al., 2020; Moradi et al., 2020). The underlying theory behind this relationship is the theory of island biogeography, which was originally developed to explain species occurrences on true oceanic islands. MacArthur and Wilson (1967) describe how islands retain a dynamic equilibrium between immigration and extinction rates. While an increase in island area decreases extinction rates, an increase in distance between island and mainland decreases immigration rates. Since the theory has been put forward it has been further applied to fragmented habitat patches in terrestrial systems (Lomolino & Smith, 2003; Lawrence et al., 2018; Lu et al., 2022) and used to inform protected area design (Higgs, 1981). However, applying island biogeography theory to terrestrial ecosystems can be problematic. When comparing oceanic islands to patches of vegetation cover on land, those patches of vegetation cover do not equal habitat patches, since habitat is a species-specific entity. Yet, measuring species richness is by definition not species-specific.

Delineating the borders of a patch on land can be much more challenging compared to islands. A clear delineation of unsuitable habitat in the matrix around a patch is also at times problematic since habitat is – again - species-specific. In many cases the matrix between patches is at least to some degree permeable for certain species. Hence, testing island biogeography theory as well as SAR in terrestrial ecosystems requires a careful and stringent research design keeping the distinction between vegetation patch and habitat patch in mind. Even though transferring island biogeography theory to terrestrial systems can be challenging, the resulting species-area relationship has been empirically tested and confirmed across different spatial scales, different ecosystems, and different taxonomic groups (Kjoss & Litvaitis, 2001; Chen et al., 2019; Gooriah et al., 2020; Moradi et al., 2020). This evidence resulted in the common view among ecologist that at least in theory single large (SL) patches or protected areas should hold more species than several small (SS) protected areas, accounting for all other factors. When trying to answer the question which protected area design maximizes species richness: Single large or several small (SLOSS), the question centers around an inherent biogeographical question in the sense that, given a constant habitat amount, habitat configuration, i.e., SLOSS, is in question.

Most ecologists believe that large and unfragmented stretches of natural land are highly desirable for habitat conservation, partly based on the assumption that SL holds higher species richness compared to SS. However, this should not diminish the importance of smaller, already fragmented habitats which are likewise essential for biodiversity protection (Fahrig et al., 2019; Wintle et al., 2019; Riva & Fahrig, 2022). Fahrig (2003; 2013; 2021) and Fahrig et al. (2017; 2019; 2022) have consistently challenged the view of SL being more desirable for conservation compared to SS, by trying to disentangle the effects of habitat amount and habitat configuration. Assuming a landscape with formerly continuous vegetation cover is broken up into patches of vegetation cover, we expect a decline in species richness. Yet, this can be an effect of habitat loss, habitat fragmentation, or both. Studying the effects of habitat loss versus habitat fragmentation on biodiversity is an extremely difficult endeavor since both – habitat loss and fragmentation – usually go hand in hand.

In Fahrig's (2003) landmark review on the effects of habitat fragmentation on biodiversity, she examines existing evidence for the effects of habitat fragmentation per se, i.e., the effects of spatial arrangement of habitat patches independent from the amount of habitat lost. Fahrig (2003) concludes that the total amount of habitat is far more important for biodiversity compared to the degree of fragmentation, and fragmentation per se has in most cases no effect on biodiversity, or sometimes even positive effects for biodiversity if habitat amount is held constant. This led to the formulation of the habitat-amount-hypothesis (HAH) (Fahrig, 2013), which predicts that variation in species richness among sampling sites can be explained by the amount of habitat in the local landscape around the sites, while the spatial configuration of habitat (e.g., fragmentation per se) makes little difference. This interpretation of the HAH has been vigorously debated ever since (Hanski, 2015; Haddad et al., 2017; Fahrig et al., 2017; Saura, 2021; Fahrig, 2021). Resulting in publications titled 'Is habitat fragmentation good for biodiversity?' (Fletcher et al., 2018), 'Is habitat fragmentation bad for biodiversity?' (Fahrig, 2019), 'The habitat amount hypothesis predicts that fragmentation poses a threat to biodiversity: A reply to Fahrig' (Saura, 2021) and 'What the habitat amount hypothesis does and does not predict: A reply to Saura' (Fahrig, 2021). To summarize, the HAH and further publications by Fahrig try to disentangle the effects on biodiversity by habitat amount vs. habitat configuration or habitat loss vs. fragmentation per se, broadly concluding that configuration or fragmentation per se have little, no, or positive effects on biodiversity. Yet these results have been theoretically as well as empirically challenged (Fletcher et al., 2018; Saura, 2021; Haddad et al., 2017). More importantly their implications for conservation are highly controversial because they potentially lead to a skewed concept of neutral or positive effects of fragmentation per se on biodiversity (Fletcher et al., 2018, Haddad et al., 2017). In reality the effects of fragmentation per se are nearly inseparable from the effects of habitat loss which is considered the primary threat to biodiversity and should therefore be in the focus of conservationist efforts to preserve biodiversity levels. In this thesis I measure habitat loss and fragmentation as one unified phenomenon, which is widely accepted as a major threat to biodiversity (Hanski, 2015; Haddad et al., 2017) and one of today's main objectives for protected area establishment (section 3.6.2).

3.6 Protected areas

3.6.1 History

For most of human history people have lived in direct contact with nature. Human survival depended on the ability of nature's provision of food, water, building resources, spiritual connections and so forth. Hence, humans have always designated parts of the land and the sea for spiritual use or to control resources (Colding & Folke, 2001). As such, parts of forests set aside to prevent deforestation or control for timber production could be considered as the first protected areas (Bhagwat & Rutte, 2006; Ladle et al., 2011). However, protected areas inscribed into law as we know them today have emerged only in the 19th century (Ladle et al., 2011). During this time, the industrial revolution brought a change to human lives. More people lived in urban areas and lost direct contact with nature, resulting in a romanticized view of it. Protected areas were then established to conserve iconic natural features and wildlife (Phillips, 2004; Watson et al., 2014). As such, Yellowstone national park was designated the world's first national park in 1872. The Forty-Second Congress of the United States of America wrote into law that a certain tract of land lying near the headwaters of the Yellowstone River

> "[…] is hereby reserved and withdrawn from settlement, occupancy, or sale under the laws of the United States, and dedicated and set apart as a public park or pleasuring-ground for the benefit and enjoyment of the people;" (Yellowstone Establishment Act, 1872)

Conserving natural features and wildlife, particularly through the creation of protected areas (PAs), is inherently political (Adams & Hutton, 2007), and protected areas, i.e., national parks, wildlife sanctuaries, conservation areas, nature preserves, etc., need to be understood as a characteristic of the modern nation state (Jepson & Whittaker, 2002). After the United States designated Yellowstone as a national park in 1872, other nations followed swiftly, establishing their own iconic national parks.

In Europe, Sweden was the first country to create national parks in 1909. In fact, the nation legally designated nine national parks at once, i.e., Hamra, Garphyttan Ängsö, Gotska Sandon, Abisko, Pieljekaise, Sarek, Stora sjöfallet and Sonfjället (Naturvardsverket, 2022). Framed as an environmental history, Jepson and Whittaker (2002) describe how nature conservation and the creation of protected areas in the late 19th and early 20th century is, at its core, a social movement with the goal of developing and maintaining values in society related to the human-nature-relationship. Jepson (2019) further describes two narratives recognizable as the main motives for nature conservation and the creation of protected areas in the late 19th and early

20th century. One aspirational narrative links nature conservation with the act of realizing and executing civilized values. In this sense, protecting nature from human exploitation is considered a moral duty reflecting civilized ideals of compassion, stewardship, and moral consideration to the non-human world (Jepson & Whittaker, 2002). The second narrative described by Jepson (2019) is a risk-based narrative focusing on the threats to social, economic, and territorial instability because of damage to watersheds, soil erosion, and resource depletion, which – at the time – was believed to be an unavoidable consequence of economic development.

In particular, this second narrative can be related to the concept of ecosystem services today. Ecosystem services are defined as nature's services and ecosystem benefits to human well-being (Millennium Ecosystem Assessment, 2005). This includes regulating, provisioning, cultural and supporting services. Regulating services refer to the regulation of ecosystem processes, e.g., water purification and pollination; Provisioning services to the provision of – for example - food and timber; Cultural services to non-material benefits to people by ecosystems, e.g., spiritual and recreational benefits; and finally Supporting services to ecosystem processes that support ecosystem functioning and other services, e.g., nutrient cycling and soil formation. Hence, if this second narrative according to Jepson (2019) is understood as part of the concern about preserving ecosystem services, it is still prominent even in the 21st century, e.g., within the goals and targets set by the Convention on Biological Diversity [CBD] or the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services [IPBES].

Next to the protection of ecosystem services, there is another argument for the maintenance of current, and the establishment of new, protected areas: the preservation of biodiversity. Soon after the term biodiversity arose in 1988 (Wilson, 1988), political actors treated biodiversity as a new form of natural resource that could be systematically monitored, mined, and developed (Haila & Kouki, 1994) to continue to produce the ecosystem services required for sustainable development (Jepson, 2019). As part of this biodiversity narrative, which we still experience today, governmental and intergovernmental agencies attempt to fulfill their role as authorities to act responsibly and competently in advancing the preservation of biodiversity by, among other ways, the maintenance of current, and the establishment of new, protected areas. Assessing the state of nature, the cause of its possible deterioration, and the consequences that must be drawn to conserve what is left is thereby a common narrative logic applied in in many conservation and development projects, such as the 1992 Convention on Biological Diversity (Jepson, 2019).

3.6.2 Current objectives for protected areas

While protected areas emerged mainly as a characteristic of the modern nation state around the turn of the century, today protected areas encompass a variety of objectives (Watson et al., 2014). Beyond the conservation of iconic land and seascapes as well as habitat for endangered wildlife, the creation of protected areas today is also set to achieve biodiversity or spatial coverage targets in the context of international agreements (**manuscript 2**), prevent habitat loss and fragmentation (**manuscript 2, 3**), play a key role in the mitigation of, and adaptation to, climate change (**manuscript 1**), contribute to human well-being, raise the livelihood of local communities, boost tourism revenues, restock natural resources such as timber and fisheries, and so forth (Dudley & Stolton, 2010; Watson et al, 2014). Part of the reason for this expansion in protected areas objectives is the variety of financial sources behind protected areas. Funded through national governments, the collective decisions of several governments, local communities, NGOs, and even private people, the expectations toward protected areas have dramatically increased (Watson et al., 2014). This variety of expectations for protected areas makes them – however - susceptible to accusations of failure to accomplish one or more of these objectives. One example is protected areas managed specifically for the protection of certain species. While these protected areas can be highly successful in fulfilling the objective of preserving the species in focus, e.g., waterbirds (Wauchope et al., 2022), protected areas designated to, and managed for the protection of specific species can – on the other hand – be quite ineffective in the mitigation of climate change outcomes as I show in **manuscript 1**. This multitude of objectives in protected area establishment, design, and management might lead to a failure in obtaining certain objectives. However, it might also be the reason for the increased support of PAs, not just at a local or national scale, but internationally as well (section 3.7). This might be an important reason for the current rapid expansion of protected areas (Watson et al., 2014).

In the 21st century – a time of rapid global change – one common objective among the many varying goals for protected areas is the preservation of biodiversity (Butchart et al., 2015). The rationale behind preserving biodiversity, especially in times of rapid change, is strongly supported by the "insurance theory" (Yachi & Loreau, 1999; Loreau et al., 2021). This theory states that "biodiversity insures ecosystems against declines in their functioning because many species provide greater guarantees that some will maintain functioning even if others fail" (Yachi & Loreau, 1999). This theory has been further expanded to include not only species diversity but also genetic diversity, diversity of functional types, diversity of species interactions, complexity of food webs, etc. (Pires et al., 2018, Wagg et al., 2019; Brooker et al., 2021; Yacine et al., 2021). All lead up to the prediction that diverse ecosystems are likely to increase stability and contribute to the persistence of ecosystem functioning even when the effects of global change, and in particular climate change, are tied to insecurity. Partly based on this theory, as well as the fact that biodiversity is in the midst of an unprecedented crisis (section 3.3.2), political conservation goals (3.10) are increasingly addressing biodiversity preservation as a main objective for PAs.

3.6.3 Management and effectiveness

Naturally, protected area management and effectiveness strongly depends on the objective for each protected area individually. To create a somewhat comparable system of management practices for protected areas the IUCN assigned all global protected areas to one of seven different management categories (for IUCN management categories see **Tab. 1** of **manuscript 1**) (Dudley, 2008; IUCN & UNEP, 2022). For example, protected areas classified as IUCN management category IV are referred to as areas to protect particular species or habitats, where management reflects this priority. Protected areas classified as IUCN management category Ia are referred to as strict nature reserves, where human visitation, use and impacts are strictly controlled and limited to ensure protection of the conservation values (Dudley, 2008). Having large, low fragmented protected areas under strict protection, e.g., IUCN category Ia might be beneficial for the preservation of certain species or ecological processes sensitive to human disturbance, but not for example for tourism and recreation.

In Europe a long history of modified landscapes, also called cultural landscapes or "Kulturlandschaften," poses a special challenge to conservation. These historical land use practices often resulted in the development of unique ecosystems (Peterken & Francis, 1999; Erikson, 2013; Poschlod et al., 2017). For example, the traditional grazing practices on timberline grasslands in the Alps prevent shrub and tree encroachment, hence creating unique ecosystems with high habitat heterogeneity (Patthey et al., 2012). Similarly, cork harvesting in Spain and Portugal has led to the development of open woodland cork plantations (Ferreras, 2001). Other examples are hedges, hollow ways (sunken lanes), hay-meadows, stone walls, and quarries (Eriksson, 2013; Poschlod et al., 2017), The dynamics of these cultural landscape practices often have significant impacts on biota. As such brood-rearing success of black grouse (*Tetrao tetrix*) is closely tied to the timberline grasslands (Patthey et al., 2012). Open woodland cork plantations are an important habitat component to the endangered Iberian lynx (*Lynx pardinus*) (Ferreras, 2001).

These traditional land use practices pose a special case in conservation management. In the case of cultural landscapes in Europe, especially those part of the N2k network, effective protected area management cannot entail the exclusion of humans as characterized by IUCN category Ia. These examples emphasize the need for clear objectives for protected areas before their management is addressed and evaluated for effectiveness. In this thesis I broadly presume preservation of biodiversity as the main objective for protected area conservation efforts, as it has been the focus of recent political agreements (section 3.7). To meet this objective, conservationists need to plan for the spatial location of protected areas (section 3.6.4 and **manuscript 1, 2**), the spatial configuration, e.g., connectedness, or size (**manuscript 1**), as well as the proper management of protected areas (see implications **manuscript 3**) (Margules & Pressey, 2000). According to Margules & Pressey (2000), protected areas should function as a basic separator between elements of biodiversity and processes that threaten those elements in the wild.

In their influential insight review paper Margules & Pressey (2000) differentiate between two central goals when attempting the preservation of biodiversity with protected areas as tools. Namely, representativeness and persistence. Representativeness describes the representation of the full variety of biodiversity or at least of a sample of biodiversity within a protected area. Persistence describes the need for protected areas to secure the long-term survival of the contained elements of biodiversity through the maintenance of natural processes and viable populations and the exclusion of threats. While my dissertation does not address representativeness, it strongly focuses on persistence. Yet, management for persistence of biodiversity contained within protected area is subject to additional complexity given global change. While protected areas may be effective in limiting threats to biodiversity caused by further land use changes, e.g., additional landscape fragmentation, their effectiveness in reducing extinctions tied to climate change are much more questionable (Araújo et al., 2011; Gaüzère et al., 2016; Hoffmann et al., 2019).

If protected areas should foster the persistence of biodiversity through the exclusion of threats (Margules & Pressey, 2000), protected areas need to be adaptable to climatic changes and their management needs to reflect this approach. Examples for adaptive management of protected areas to climate change include somewhat exotic examples such as assisted migration or relocation. Assisted migration describes the active translocation of species from one location threatened to become unsuitable habitat due to climatic changes to another location more fitted to the species' niche under future climatic conditions (Thomas, 2011). Another example is "dynamic conservation" or temporary reserves, where areas are under protection only for short periods of time. A system that can be described as "protected areas on demand". This flexible approach has the benefit of reducing conflict with other human land-use interests, e.g., through private ownership or agricultural practices, and creating short-term protected areas capable of filling temporal and spatial gaps in habitat for species on the move, reacting to changed environmental conditions (Bull et al., 2013; Reynolds et al., 2017). While these approaches might be necessary, they are also highly debated, especially since these approaches usually focus on a single species or functional group but cannot address the full complexity of species interactions (Kreylinger et al., 2011; Vila & Hulme, 2011; Neff & Larson, 2014)

I suggest a different strategy by advocating for the expansion of existing protected areas in size as well as the prioritization towards, and management for low fragmented landscapes. This double-sided approach addressing movement under climate change can reduce major anthropogenic barriers to movement, i.e., fragmenting structures, lands with no protection status subject to human disturbances and disruptions, for all entities of biodiversity. In addition, the results of **manuscript 1 and 2** indicate that threats due to climate change and anthropogenic landscape fragmentation are smallest in protected areas large in size (**manuscript 1**) and with large elevational gradients (**manuscript 1, 2**), therefore, making these areas a unique target for conservation efforts. This result is in line with studies by Scherrer & Körner (2011) and Thomas & Gillingham (2015) which have shown that species occurring in protected areas covering large elevational gradients are more likely to successfully track changing climatic conditions without having to leave the borders of the protected area. Recent political efforts such as the EU's biodiversity strategy for 2030 (section 3.7.2), including additional financial support, makes our suggestions for a climate-adaptive protected area management. i.e., a prioritization for the expansion of protected areas into low fragmented surroundings (**manuscript 2**), especially in topographically diverse regions more resilient to climate change (**manuscript 1**) and their follow-up management towards fostering species movement by reducing anthropogenic barriers (**manuscript 3**), possible.

3.6.4 Spatial distribution

As of today, countries worldwide have legally designated over 271,000 protected areas covering 17% of Earth's terrestrial and 8% of the Earth's marine surface, thereby achieving Aichi target 11 for the first time in 2021. Within the last decade alone, 21 million km^2 of our planet's surface area has received protection status of one kind or another, which means that 42% of the area now part of the protected area network has been added since 2010 (UNEP-WCMC & IUCN, 2021).

Yet quantity does not always mean quality. Protected area conservation targets such as Aichi target 11 (section 3.7.1) (Secretariat of the Convention on Biological Diversity, 2020) or the EU's biodiversity strategy for 2030 (section 3.7.2) (EC, 2020) focus both on coverage, i.e., Aichi target 11 on the protection of 17% of terrestrial land worldwide and the EU on 30% of the terrestrial land in the EU. Such targets, however, often result in a common and politically pragmatic conservation strategy in which areas of low political and economic interest are prioritized for protection (Joppa & Pfaff, 2009; Margules & Pressey, 2000). Examples are regions in polar climate zones or regions dominated by steep, high-elevation terrain.

Protecting areas in marginal lands (also known as "rock and ice" conservation strategy (Joppa & Pfaff, 2009) or "worthless land hypothesis" (Hall, 1988) avoids competition with other economic and societal interests and has become a popular and politically viable way for nations worldwide to reach their coverage targets. The largest terrestrial Natura 2000 sites in the EU, for example, are Kaldoaivi Wilderness area at a latitude of 69°N in Finland, followed by Torneträsk-Soppero fjällurskog, at a latitude of 68°N in Sweden (European Environmental Agency [EEA], 2021). Instead of prioritizing science-backed conservation goals such as minimizing habitat loss and fragmentation (**manuscript 2, 3**), or aiming for climate change adaptation capacities (**manuscript 1**), a "rock and ice" conservation strategy is rather based on political expediency. Protected areas are not randomly distributed across space and neither are the targets of conservation efforts, e.g., biodiversity, nor the threats to those targets, e.g., landscape fragmentation. Hence before conservation decisions are made, a clear consensus on the objectives of protected areas should be formulated on both sides - the scientific and the political. In this thesis I formulate concrete recommendations for protected area expansion and management suited to the EU biodiversity strategy for 2030, which are primarily built on the objective of preserving large areas in the last remaining low fragmented lands on one of the world's most anthropogenically modified continents.

3.7 Conservation policy

3.7.1 International conservation agreements

The transnational environmental movement gained momentum in the mid-twentieth century. Popular books like Rachel Carson's Silent Spring (Carson et al., 1962), which brought the potentially calamitous ecological consequences of unmanaged land use practices to the attention of the wider public were published during this time. Several major international organizations were founded, including the IUCN (1948) and WWF (1961). Publication of the IUCN Redlist in 1963 raised awareness of the threat of extinction looming over many of the world's species (Walter & Gillett, 1998). To push back against this biodiversity loss, national and local governments increasingly protected some areas in the form of national parks, green spaces, wildlife management areas, and other legal designations intended to insulate certain spaces from human pressures (Dudley, 2008).

In 1971, the Ramsar Convention was signed, forging the first cooperative transnational network of protected areas. In 1992 the United Nations held a Conference on Environment and Development [UNCED] in Rio de Janeiro, better known as the "Earth Summit." This pivotal conference marks the beginning for many current political agendas and agreements in conservation politics. As such, participating nations reached an agreement on the Climate Change Convention which in turn led to the Kyoto Protocol and the Paris Agreement. The Kyoto Protocol was adopted during the 5th meeting of the Conference of the Parties [COP], in Kyoto, Japan. COP meetings by the United Nations Framework Convention on Climate Change [UNFCCC] usually meet every year to evaluate emission inventories and national communications by the signatory countries, i.e., 198 nations today. Signed at the COP3 in 1994, and contrary to the Paris Agreements, the Kyoto Protocol legally binds the European Union, as well as 37 additional industrialized countries, to meet emission reduction targets. The Paris Agreement approved 11 years later at the COP21 in Paris was signed by 196 countries, which committed to the goal of keeping global warming under 2°C compared to pre-industrial levels (UNFCCC, 2022).

In addition to addressing climate change, the "Earth summit" also marked the beginning of the Convention on Biological Diversity [CBD], which was opened for signature in 1992 (CBD, 2022a) and counts 196 members today (CBD, 2022b). The CBD meets regularly to set goals and targets for further improving biodiversity conservation. These meetings are also referred to as Conferences of the Parties [COP] with the first COP meeting (COP1) held in Nassau, Bahamas, in 1994 and the most recent meeting, COP15, held in 2021/2022 in Kunming, China and Montreal, Canada. In 2010, the COP10 meeting in Nagoya, Japan was arguably one of the most thematized meetings by the CBD so far, since it produced 20 concrete, but voluntary, targets for the protection of biodiversity, the so-called "Aichi targets." Relevant to this thesis are especially targets 5, 11, 12, and 20.

Target 5

> “*By 2020, the rate of loss of all natural habitats, including forests, is at least halved and where feasible brought close to zero, and degradation and fragmentation is significantly reduced.*”

Target 11

> “*By 2020, at least 17 per cent of terrestrial and inland water areas and 10 per cent 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*.”

Target 12

> “*By 2020 the extinction of known threatened species has been prevented and their conservation status, particularly of those most in decline, has been improved and sustained*.”

Target 20

> “*By 2020, at the latest, the mobilization of financial resources for effectively implementing the Strategic Plan for Biodiversity 2011–2020 from all sources, and in accordance with the consolidated and agreed process in the Strategy for Resource Mobilization, should increase substantially from the current levels. (Specific targets: (1) to double international financial flows to developing countries; (2) to include biodiversity in national priorities or development plans; (3) to report on domestic spending, needs, gaps, priorities; (4) to prepare national finance plans and assess the multiple values of biodiversity; and to mobilize domestic financial resources*.”

Since the formulation of those targets, much improvement happened on the political side as well as on the scientific research front. Concrete suggestions on how to reach these targets by implementing concrete conservation strategies were formulated, leading to a huge body of literature on protected area establishment, design, and management geared towards achieving Aichi biodiversity targets (Joppa et al., 2013; Visconti et al., 2015; Bicknell et al., 2017; Gannon et al., 2017; Mappin et al., 2019;). On the political side, the European Union for example, expanded its network of protected areas to successfully reach target 11. On 15 September 2020, the United Nations Convention on Biological Diversity (CBD) issued its latest periodic report on the state of the world’s biological diversity, the Global Biodiversity Outlook (GBO-5) (Secretariat of the Convention on Biological Diversity, 2020). This publication evaluates the world’s progress toward achieving the Aichi Biodiversity Targets. Tragically, according to the GBO-5 report (Secretariat of the Convention on Biological Diversity, 2020), the society of nations failed to achieve a single Aichi Target. The GBO-5 summarizes the achievements made for all targets including target 5, 11, 12, and 20.

Target 5

> “*The recent rate of deforestation is lower than that of the previous decade, but only by about one third, and deforestation may be accelerating again in some areas. Loss, degradation and fragmentation of habitats remains high in forest and other biomes, especially in the most biodiversity-rich ecosystems in tropical regions. Wilderness areas and global wetlands continue to decline. Fragmentation of rivers remains a critical threat to freshwater biodiversity. The target has not been achieved (high confidence).*”

Target 11

> “*The proportion of the planet’s land and oceans designated as protected areas is likely to reach the targets for 2020 and may be exceeded when other effective area-based conservation measures and future national commitments are taken into account. However, progress has been more modest in ensuring that protected areas safeguard the most important areas for biodiversity, are ecologically representative, connected to one another as well as to the wider landscape and seascape and are equitably and effectively managed. The target has been partially achieved (high confidence).*”

Target 12

> “*Species continue to move, on average, closer to extinction. However, the number of extinctions of birds and mammals would likely have been at least two to four times higher without conservation actions over the past decade. Among well-assessed taxonomic groups, nearly one quarter (23.7%) of species are threatened with extinction unless the drivers of biodiversity loss are drastically reduced, with an estimated total of one million threatened species across all groups. Wild animal populations have fallen by more than two-thirds since 1970, and have continued to decline since 2010. The target has not been achieved (high confidence).*”

Target 20

> “*There have been increases in domestic resources for biodiversity in some countries, with resources remaining broadly constant for others over the past decade. Financial resources available for biodiversity through international flows and official development assistance have roughly doubled. However, when all sources of biodiversity finance are taken into account, the increase in biodiversity financing would not appear to be sufficient in relation to needs. Moreover, these resources are swamped by support for activities harmful to biodiversity. Progress on identifying funding needs, gaps and priorities and the development of national financial plans and assessments of biodiversity values has been limited to relatively few countries. The target has been partially achieved (high confidence).*”

To summarize, progress towards slowing habitat loss, fragmentation, and degradation (target 5) has been made to some extent, however human modification of natural landscapes remains a disproportionate threat to biodiversity and urgently needs further addressing. Similar, progress towards slowing species extinction (target 12) has been made to some extent, but biodiversity decline still progresses astonishingly fast. Substantial progress has been made expanding and establishing new protected areas worldwide (target 11). However, focusing on coverage often results in a common and politically expedient conservation strategy of protecting areas in marginal lands (also referred to as "rock and ice") where political and economic interests are smallest (Joppa & Paff, 2009) (section 3.6.4). Areas of high biodiversity conservation value are still not sufficiently covered. Financial support for conservation (target 20) remains a severe challenge for biodiversity conservation efforts, even after small improvements. This still makes a prioritization in conservation action mandatory.

Currently the CBD discusses a post-2020 agreement. Having taken notice of the further global decrease in biodiversity levels and the failure in achieving the previously placed Aichi targets, the 21 post-2020 targets are slightly more ambitious than the previous 20 Aichi targets but remain under discussion.

Target 1

> "*Ensure that all land and sea areas globally are under integrated biodiversity-inclusive spatial planning addressing land- and sea-use change, retaining existing intact and wilderness areas*."

Target 3

> "*Ensure that at least 30 percent globally of land areas and of sea areas, especially areas of particular importance for biodiversity and its contributions to people, 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 landscapes and seascapes*."

Target 4

> "*Ensure active management actions to enable the recovery and conservation of species and the genetic diversity of wild and domesticated species, including through ex situ conservation, and effectively manage human-wildlife interactions to avoid or reduce human-wildlife conflict*."

Target 8

> "*Minimize the impact of climate change on biodiversity, contribute to mitigation and adaptation through ecosystem-based approaches, contributing at least 10 GtCO2e per year to global mitigation efforts, and ensure that all mitigation and adaptation efforts avoid negative impacts on biodiversity*."

Target 19

> "*Increase financial resources from all sources to at least US$ 200 billion per year, including new, additional and effective financial resources, increasing by at least US$ 10 billion per year international financial flows to developing countries, leveraging private finance, and increasing domestic resource mobilization, taking into account national biodiversity finance planning, and strengthen capacity-building and technology transfer and scientific cooperation, to meet the needs for implementation, commensurate with the ambition of the goals and targets of the framework.*"

(Secretariat of the UN Convention on Biological Diversity, 2021)

These five CBD's preliminary 2030 action targets relate directly to this thesis by a) prioritizing biodiversity conservation as the main objective for protected areas (**manuscript 1, 2, 3)**; b) expanding protected areas to cover 30% of terrestrial area (**manuscript 2)**; c) minimizing impacts of climate change on biodiversity (**manuscript 1**); and d) increasing financial input as required for effective conservation management (**manuscript 3)**. Hence the most recent international agreements such as the CBD's preliminary 2030 action targets, give hope that concrete conservation suggestions, as made in this thesis, have a realistic chance of being put into practice.

3.7.2 EU conservation agreements

Europe as a whole is anything but an untouched wilderness. It is a densely settled and highly urbanized continent that has been subject to human modification for millennia. European ecosystems are crisscrossed by roads, railways, powerlines, fences, and footpaths. Its exurban landscapes are dotted by townships and much of its rural land is given over to monoculture of one form or another. There exists almost nowhere on the continent that is more than a few kilometers from human settlement (Pereira & Navarro, 2015).

The use of protected areas for the specific purpose of safeguarding biodiversity in Europe began with the European Comission's Directive on the Conservation of Wild Birds, approved in 1979 (EC, 1979). The directive required signatories to designate Special Protection Areas (SPAs), considered important for the migration of rare and/or threatened species as designated in Annex I of the Directive (EC, 1979). The unique mobility of birds and their inclination to ignore political borders in their movements necessitated and normalized transnational cooperation in European conservation efforts. (Evans, 2012). In a pivotal moment for the history of nature conservation in Europe, a Directive on the conservation of natural habitats and of wild fauna and flora was adopted on 21 May 1992 (EC, 1992). This Directive is typically referred to as the Habitats Directive. It called for stringent safeguards of certain species and their habitats (listed in Annex IV), requiring the designation of protected areas, originally called Sites of Community Importance (SCIs) and later Special Areas of Conservation (SACs). These protected areas combined with the SPAs established by the Birds Directive (EC, 1979), formed the Natura 2000 network (N2k). This network of currently more than 27,000 protected areas is the largest conservation network in the world, covering more than 18% of the EU's terrestrial area (EEA, 2021).

On 20 May 2020, the European Commission announced an updated strategy to safeguard the continent's biodiversity as part of the European Green Deal (EC, 2019). The topline aspiration of this new strategy is to protect 30% of the EU's terrestrial and 30% aquatic area by 2030 with 10% of terrestrial and 10% of sea surface area under strict protection. The EU's Biodiversity Strategy for 2030 explicitly contains the goal of enlarging the Natura 2000 network with strict protection for areas of very high biodiversity and climate value. Having realized the threat from a global biodiversity crisis the extension of knowledge, monitoring, and protection of biodiversity and biodiversity hotspots has taken a central role in this latest EU agreement. Similarly prominent are the aims made towards climate change as well as the realization that the current biodiversity crisis and the climate crisis are intrinsically linked as should be their solutions (EC, 2020). One of the EU's main goals of this Biodiversity Strategy for 2030 is a better protection of biodiversity and a mitigation of climate change impacts – among others - via monitoring progress in biodiversity conservation and climate change impacts, an expansion of the existing protected area network, an implementation of more strict protection regulations, and better monitoring on the enforcement of those regulations and the progress towards these goals. To this end, the EU will put at least 20 billion EUR toward expanding and restoring the N2k network (EC, 2020). A key question animating this dissertation is: how can these resources be used to achieve the goals made by the EU and to safeguard the integrity of Europe’s protected areas in the most efficient and efficacious manner.

4 Synopsis

4.1 Synthesis of the manuscripts

In the following, I describe research gaps related to effective protected area designation, expansion, and management under the threats of climate change and landscape fragmentation. I explain how my manuscripts address these gaps relevant on a global, continental, national and local scale. I clarify how my manuscripts provide a set of theoretically coherent spatial models that can be applied to protected area policies in real-world contexts across different scales (**Tab. 1**), recognizing the vast array of trade-offs that are involved in safeguarding spaces of biodiversity today and in the future.

Furthermore, in the Appendix, I list my talks at scientific conferences related to this dissertation (**Appendix 1**) as well as my talks thematically not related to this dissertation (**Appendix 2**). In **Appendix 3,** I list all peer-reviewed articles published during my work on this dissertation, but not part of this dissertation. Finally, I included my teaching activities while working on this dissertation (**Appendix 4** and **5**).

Manuscript	**Protected areas**	**Threats**	**Methods**	**Scientific advances**	**Management suggestions**
1	Terrestrial protected areas globally	Climate change	univariate and multivariate statistic	Topographic diversity, i.e., area and elevational diversity is linked to climate change resilience in protected areas	Global scale implication, expansion of protected area size, prioritization of protected area establishment in mountainous regions.
2	Terrestrial protected areas part of Natura 2000 in the EU	Landscape fragmentation, climate change (indirectly)	Geospatial analysis, univariate and multivariate statistic	Protected areas in remote and mountainous regions with low population density are least fragmented in their surroundings, hence have a high potential for protected area expansion	Continental and national scale implication, expansion of protected areas into low fragmented surroundings
3	Terrestrial protected areas part of Natura 2000 in the EU	Landscape fragmentation	Geospatial analysis, Temporal analysis, univariate and multivariate statistic	Protected areas are highly fragmented and fragmentation inside protected areas is strongly linked with fragmentation in their surroundings independent of time	National and local scale implications, inscribing construction bans in protected areas into law, monitoring and enforcing the law

Traditionally protected areas have been designated to protect and conserve threatened species, habitats, and ecosystems (Pimm et al., 2014; Langdon & Lawler, 2015; Gray et al., 2016) (section 3.6.1). Yet even with growing political will, and to some degree success in increasing protected area coverage and quality (section 3.7), the planet is still in the midst of a biodiversity crisis (Barnosky et al., 2011; Ripple et al., 2019; Cowie et al., 2022) (section 3.3.2). Around one million of all described species (representing 25% of all assessed species) are estimated to be threatened (IPBES 2019) despite current conservation efforts (Delso, Fajardo & Muñoz 2021). Habitat loss and fragmentation from anthropogenic development is still considered the primary driver of species extinctions worldwide (section 3.5). In addition, human induced climate change is projected to severely decrease global biodiversity (Bellard et al., 2012; IPBES, 2019) (section 3.4) and can markedly reduce the effectiveness of protected areas as nature conservation tools (Hoffmann & Beierkuhnlein, 2020; Hoffmann et al., 2019; Johnston et al., 2013).

In many cases, climate change will lead to shifts in species distributions by compelling migration poleward and towards higher elevations as species attempt to track suitable climatic conditions (Berteaux et al., 2018; Chen et al., 2011) (section 3.4.2). Therefore, it is easy to imagine how the synergistic impacts of anthropogenic climate change – forcing species to move - and habitat loss and fragmentation - preventing species from moving - can be detrimental (Oliver et al., 2017; Synes et al., 2020; Lehikoinen et al., 2021) leading to species and population extinctions worldwide (Travis, 2003; Thomas et al., 2006; Jackson & Sax, 2010).
In contrast to species distributional ranges, protected areas are static and fixed in space. Therefore, species' mobility could severely hinder protected area's overall effectiveness in reducing extinctions tied to climate change (Araújo et al., 2011; Gaüzère et al., 2016; Lehikoinen et al., 2021).

Which existing protected areas allow for species movement and show resilience towards climatic changes (**manuscript 1**), how we can improve climate change resilience by designating new protected areas (**manuscript 2**), and how we should manage protected areas for preserving this resilience in the future (**manuscript 3**), are key questions I attempt to answer in my thesis with the goal of contributing to the development of robust and sustainable conservation strategies.

In **manuscript 1** I take advantage of openly accessible data on the disappearing climate index (DCI). DCI provides a measure of the relative area (percent of total area) within a protected area that exhibits certain climatic conditions that will either disappear entirely or move outside the boundaries of the protected area at focus by the year 2070. I show that all terrestrial protected areas on earth will experience a change of climatic conditions within the next 50 years. Certain climatic conditions within the boundaries of any given protected area will disappear, while others expand or change locations. This can severely reduce biodiversity conservation and other measures of protected area effectiveness. Under moderate climate change (RCP 4.5) global terrestrial protected areas will lose between 1%-85% of their relative land surface area exhibiting certain climatic conditions which will no longer be part of the protected area at focus by the year 2070. On the other hand, topographic diversity is highly correlated with climate change resilience, i.e., lower DCI values, in protected areas worldwide. I examined the correlation of DCI with three different protected area characteristics - protected area area, maximal elevational difference, and median terrain ruggedness. All three characteristics are highly correlated with a decrease in DCI. protected area size and maximal elevational difference alone explain 63% of the variance observed in DCI among the world's terrestrial PAs. While it is harder to manage for increasing elevation, i.e., maximal elevational difference, within protected areas, expanding protected area size is a viable conservation option.

In **manuscript 1** I demonstrate that increasing protected area size, a politically feasible option, is significantly related to decreasing DCI, hence an improved climate change resilience within protected areas. This result is in line with previous studies suggesting small protected areas are more vulnerable to climatic changes compared to larger ones (Langdon & Lawler, 2015; Loarie et al., 2009). Large protected areas are more likely to harbor diverse climatic conditions allowing for internal climate displacement such that some portion of the protected area is more likely to exhibit prior climatic conditions (Loarie et al., 2009; Thomas & Gillingham, 2015). In addition, I show in **manuscript 1** that the strong correlation between protected area size, maximal elevational difference and terrain ruggedness with DCI also hold true across protected area management practices. IUCN management category IV (habitat/species management area) and V (protected landscape/seascape) exhibit on average the highest DCI values. This result is of special interest since protected areas managed under IUCN category IV are explicitly designated to protect "particular species or habitats, where management reflects this priority" (Dudley, 2008). Yet, while the management in those protected areas might be effective for the protection of specific species and habitats, today our results suggest that those management practices will not be effective in mitigating climate change in the future. Other strategies such as protected area size expansion may be necessary to booster climate change resilience in protected areas.

When we accept that protected area size should be as large as politically feasible (Halpin, 1997; Lemieux et al., 2011; Lehikoinen et al., 2021) and protected areas should be as little as possible fragmented to allow large-scale ecological and evolutionary processes such as gene flow, migration, and species range shifts to persist, the question remains where an expansion in protected area size is still possible. In **manuscript 2** I make concrete suggestions for possible protected area expansions into low fragmented surroundings in Europe. I show that currently large areas surrounding Natura 2000 protected areas still consist of natural, low fragmented lands. While the EU has recognized the severity of climate and land use change for the continents biodiversity, the European Commission [EC] has set an ambitious goal of establishing additional protected areas protecting at least 30% of the land and 30% of the sea area (section 3.7.2). To provide science-based guidance for possible protected area expansions, I investigated in **manuscript 2** the state and the spatial distribution of anthropogenic landscape fragmentation around existing Natura 2000 protected areas across the EU. In **manuscript 2** I show that most of central Europe, i.e., latitudes between 40°N and 60°N and longitudes between -5°W and 15°E have generally high degrees of fragmentation and are arguably less well suited for protected area expansion if our focus is on safeguarding intact and connected habitats. By contrast, there are still relatively low fragmented lands to be found in Europe, especially in remote and mountainous regions in the north and the east of the continent. Many of these regions are currently not a part of the Natura 2000 network. While the degree of fragmentation in Natura 2000 surroundings is highly correlated with national population density, economic wealth, as measured by GDP per capita, is less important and has no significant effect on the degree of fragmentation in Natura 2000 surroundings.

From an ecological standpoint it might be wise to approach nature conservation decisions from a larger scale –e.g., a global or continental scale –as the EU Biodiversity Strategy for 2030 attempts to do. However, the political structure of the EU dictates that most real-world conservation decisions are implemented on a national level and subject to the pragmatic and multifarious decision-making processes of democratic governments. One consequence of this incongruity between continental-scale goals and national-scale implementation is the tremendous difference in government spending on Natura 2000 protected areas. In **manuscript 2** I provide a country-level comparison of available resources to Natura 2000 preservation among the different EU member states. I show data depicting the vast incongruity in resource availability and spending practices for Natura 2000 conservation among EU countries. The most striking example is Romania, which exhibits the lowest levels of fragmentation in its current Natura 2000 protected area surroundings and at the same time preserves and manages over 8000 times more Natura 2000 land per one million Euro spent compared to the Netherlands. Similar results can be found for many Eastern European countries, e.g., Bulgaria and the Baltic countries. The results of **manuscript 2** show that some of the least-well funded national protected area networks also hold the highest potential for expanding current Natura 2000 protected areas into low fragmented lands. In this sense our results could be used to formulate pragmatic conservation decisions, while also ensuring high ecological quality of protected area additions in the face of climate change.

However, expanding protected area size in itself does not ensure the persistence of habitat quality and therefore protected area effectiveness in biodiversity protection (Joppa & Pfaff 2009, Hoffmann et al., 2018). Based on **manuscript 1** I argue that an expansion of the protected area network, as proposed by the EU's Biodiversity Strategy for 2030, should aim for maximizing protected area size to enhance climate change resilience within PAs. In **manuscript 2** I focus on protected area size expansion and argue that apart from species or ecosystem focused conservation approaches, a landscape-focused conservation approach which prioritizes the expansion of existing protected areas into low fragmented surroundings is a viable and pragmatic pathway to secure the possibility for species migration and redistribution within protected areas under climate change. Yet establishing new protected areas, even under ecologically relevant criteria, still does not ensure long-term habitat quality or overall effectiveness of protected areas in biodiversity protection (Joppa & Pfaff, 2009; Hoffmann et al., 2018). Even within protected areas, ecosystems are threatened due to increasing human pressure 'spilling over' from the surrounding matrix (Maiorano et al., 2008; Laurance et al., 2012). To this day, the relationship between the quality of the surrounding matrix and the quality of habitat within the boundaries of protected areas is a neglected field of research.

A few studies of tropical ecosystems have shown that pressures stemming from the surrounding matrices of protected areas are evident within protected areas (Laurance et al., 2012; Perello et al., 2012). It is still unclear to what extent these findings can be transferred to extratropical regions. As the historical cradle of industrialization and transportation infrastructure, Europe has one of the world's heaviest human footprints. High anthropogenic pressure faces ecosystems across the continent (Selva et al., 2011; Perello et al., 2012; Jones et al., 2018). The current dearth of broad-scale modelling approaches to analyze anthropogenic pressures in and around European protected areas severely limits our understanding of effective biodiversity conservation on a continental scale (Orlikowska et al., 2016).

In **manuscript 3** I investigate anthropogenic fragmentation inside and around Natura 2000 protected areas across the EU and quantify the degree to which Natura 2000 protected areas are insulated from development pressures. I used a comprehensive dataset of effective mesh density (*seff*) to measure aggregate fragmentation inside and within a 5 km buffer surrounding Natura 2000 protected areas. Despite their protected status, I could show that Natura 2000 protected areas are substantially fragmented. A quarter of all Natura 2000 sites are classified as highly to very-highly fragmented. Moreover, fragmentation within Natura 2000 protected areas strongly correlates with the fragmentation of their surroundings ($R^2 = 0.78$). This result applies to all biogeographical regions in Europe. Only a narrow majority (58.5%) of Natura 2000 protected areas are less fragmented than their surroundings. Remote and mountainous regions in northern Europe, the Alps, parts of Spain, and parts of eastern Europe show the lowest levels of fragmentation. These regions tend to hold the largest Natura 2000 protected areas as measured by area. In contrast, central and western Europe show the highest fragmentation levels within and around Natura 2000 protected areas. Time since initial protection of Natura 2000 protected areas does not correlate with the difference in exterior and interior fragmentation of Natura 2000 protected areas. These results indicate that anthropogenic pressures in the surrounding matrix are in fact closely mirrored within protected areas themselves. I conclude that Natura 2000 protected areas in Europe are not sheltered from anthropogenic pressures leading to fragmentation and legal concepts addressing anthropogenic fragmentation need to be incorporated into current and future Natura 2000 management to strengthen its long-term viability for continent-wide biodiversity conservation. In fact, it is essential to take pre-emptive action against encroaching anthropogenic fragmentation now by a) inscribing a ban of additional development inside Natura 2000 sites into law; b) putting additional resources into enforcing bans on constructions inside Natura 2000 sites; and c) where possible, removing extant fragmenting infrastructure.

4.2 Outlook

4.2.1 Insurance theory and the need to manage for movement

Conservation biogeography research is focused on “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 recent years a consensus arose within the field of conservation biogeography stating that with growing insecurity about future abiotic and biotic conditions, preservation of biodiversity rather than single target species should be prioritized. This concept was manifested in the “insurance theory” suggesting that “biodiversity insures ecosystems against declines in their functioning because many species provide greater guarantees that some will maintain functioning even if others fail” proposed by Yachi and Loreau (1999). Yachi and Loreau (1999) further explain that “such an effect is expected because different species respond differently to environmental changes, hence the contribution of some species to ecosystem processes may decrease while that of others may increase when the environment changes. Thus, greater species richness should lead to a decreased variability in ecosystem processes because of compensation among species.” While Yachi and Loreau (1999) focus on species richness, diversity in abiotic conditions, diversity in community compositions, functional types, and genetic diversity can support the stability and functioning of ecosystems under varying environmental conditions. Intraspecific variability can – for example - lead to differentiated reactions to climatic changes (Beierkuhnlein et al., 2011), and genetic variability within populations can potentially lessen the effects of climatic extremes (Reusch et al., 2005; Malyshev et al., 2016). Yet, populations living in isolated habitat patched, whose movement is severely hindered by unpassable barriers in fragmented landscapes, can quickly experience an interruption in gene flow. With time this will inevitably lead to a decrease, and eventually depletion, of genetic variability.

Conservationists (in any field) should be aware that preserving biodiversity does not only include preserving species diversity, but also diversity of genes, and ecosystems, as well as their interactions and functions. Even today, there still exists a prominent research gap in global change ecology addressing other forms of diversity, besides species diversity. Investigating the patterns and dynamics of these other forms of diversity over different spatial scales and introducing avenues for preserving diversity in the future will be one of the biggest challenges, but also one offering the biggest rewards in conservation science of the 21st century. In my thesis I show how protected areas could be designed and managed for promoting movement, necessary to preserve diversity among species, within populations and even individuals. **In manuscript 1** I show how topographic diversity is correlated with climate change resilience. This is partly since climatic conditions can move within the boundaries of topographically diverse protected areas. In **manuscript 2** I show an option for Europe to foster movement of individuals, populations, and species by expanding protected areas into low fragmented surroundings. In **manuscript 3** I point out the current state and future perspectives to preserve the ability of movement in already existing protected areas. Hence, I argue that managing landscapes for conservation purposes, as it is the goal of conservation biogeography needs to include a management of protected areas for movement.

Manuscript 1, 2 both suggest a prioritization of large protected areas covering large elevational gradients. Pairing the priority of conserving such abiotically diverse stages with the priority of conserving low fragmented landscapes to allow for species movement can be a promising avenue for future conservation biogeography. However, it is important to note that representing heterogeneity alone is unlikely to preserve specific species or certain aspects of biodiversity. While this thesis follows a landscape focused conservation approach and therefore allows to infer results on a local, continental, and a global scale, it does not consider information on specific species, communities, or populations. When inferring direct measures for species conservation, landscape indices - e.g., DCI (**manuscript 1**) or s_{eff} (**manuscript 2 and 3**) - should be paired with biological information on species movement routes to predict the best suited protected area network for biodiversity conservation. Underlying mechanisms such as dispersal limitations, demographic shifts, species interactions, and evolution need to be included when assessing the future perspective of biotic responses to climate and land use changes (Littlefield et al., 2017; Urban, 2015).

4.2.2 Limitations of the thesis and possibilities for future research

This thesis focuses on, among other things, the benefits and options to increase protected area size as a climate-smart conservation approach. However, it is also understood that expanding protected areas in size is often not feasible due to limited funds, human land use pressures, depleted natural habitats, political will, and a myriad of other factors (Hoffmann et al., 2019; Langdon & Lawler, 2015; Thomas & Gillingham, 2015). In such cases protected area management might profit from new, more flexible approaches towards biodiversity conservation, for example assisted migration (Thomas, 2011), i.e. translocating individuals between populations to increase gene flow or dynamic conservation, i.e., establishing temporary short-term nature reserves outside the traditional protected area network to support species transitions or migrations (Reynolds et al., 2017). Further, it is important to note that this thesis makes an important assumption in treating protected areas as islands, assuming that species will not be conserved outside protected areas and that species are unable or severely hindered in moving through non-protected area territory into other protected areas for example to track their climatic niche. While there is a vast body of research which looks at the optimal shape and connectivity of protected areas and their effects on species movement (Heller &

Zavaleta, 2009; Hodgson et al., 2009; Wegmann et al., 2014; Ward et al., 2020), further research on the use of unprotected lands by organisms of all taxa is still surprisingly little researched. While species movement is already tremendously restricted by human activity, climate change is projected to further constrain potential movement routes while simultaneously creating a higher need for species movement (Littlefield et al., 2017). In order to put connectivity-enhancing strategies forward, future climate projections, landscape permeability due to human modification, and dispersal capabilities need to be considered simultaneously (Littlefield et al., 2017; Urban et al., 2013).

Another limitation to the research design of this thesis includes spatial resolution, which was partly determined using preprocessed open data. While in **manuscript 1** only protected areas whose polygons overlapped with the center point of a 30 arcsecond-sized raster cell were included, in **manuscript 2 and 3** only protected area polygons which overlapped with the center point of at least one 1 km^2 raster cell were included. In both cases, very small protected areas and protected areas with elongated shapes are more likely to elude the center point of any raster cell and therefore were not included in the final dataset. Despite their requisite exclusion, these small protected areas are an important component of the global (**manuscript 1**) and the continental (**manuscript 2 and 3**) protected area network. They can be vital habitats for confined or for small-range species, or they may contribute to landscape complementation and overall habitat diversity (Wintle et al., 2019). In the case of Europe, it has also been shown that small protected areas are unevenly distributed across the continent (Friedrichs et al., 2018] and might therefore play an outsized role in nature conservation for some countries relative to others. While large and low fragmented stretches of natural land are highly desirable for habitat conservation, this should not diminish the importance of smaller, already fragmented habitats which are likewise essential for biodiversity protection (Wintle et al., 2019; Fahrig et al., 2019; Fahrig, 2022]. Additional research is needed to quantify the pressures from climate change and anthropogenic fragmentation for small protected areas and to show ways of allowing species movement even within spatial restrictions. Only then can we gain a comprehensive understanding of climate and land use changes posing pressures to the protected area network as a whole and thus better design climate change resilient protected areas, as well as develop anti-fragmentation management plans, especially at the national level.

Clearly, today there is still a disjuncture between scientific theories of biodiversity protection and the practice of conservation policymaking. To some extent, this may reflect a failure on the part of conservation interest groups and scientific researchers to integrate the drivers of anthropogenic pressure into their biodiversity protection models. Even where the political will to increase and harden protections for natural spaces exists, there is surprising scarcity of actionable scientific literature that would tell policymakers how and where to expand protections. There is often a disjuncture between biogeographical theory, conservation policy, and on-the-ground management practices.

This thesis is an attempt to unify the theory and practice of biodiversity conservation via protected area designation, expansion, and management. It aims to provide a set of theoretically cogent spatial models that can be applied to protected area policies in real-world contexts, recognizing the vast array of trade-offs – fiscal, political, humanitarian, and ecological – that are involved in safeguarding spaces of biodiversity today and in the future. Accepting the existence of these trade-offs without compromising the integrity of conservation theory is essential if biodiversity is to be preserved to the maximum extent plausible.

5 Declaration of my contributions to each manuscript

Manuscript 1

Title: Topographic diversity as an indicator for resilience of terrestrial protected areas against climate change

Authors: Lawrence, A., Hoffmann, S., Beierkuhnlein, C.

Journal and status: Global Ecology and Conservation, 25, e01445 (2021),

https://doi.org/10.1016/j.gecco.2020.e01445

My contributions: idea and concept: 60%, data analysis and figures: 85%, writing: 90%, corresponding author

Contribution of Samuel Hoffmann: idea and concept: 15%, data analysis and figures: 15%, writing: 10%

Contribution of Carl Beierkuhnlein: idea and concept: 25%, writing: 10%

Manuscript 2

Title: Detecting low fragmented sites surrounding European protected areas - implications for expansion of the Natura 2000 network

Authors: Lawrence, A., & Beierkuhnlein, C.

Journal and status: Biological Conservation, in review

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

Contribution of Carl Beierkuhnlein: idea and concept: 10%, writing: 10%

Manuscript 3

Title: Landscape fragmentation of the Natura 2000 network and its surrounding areas

Authors: Lawrence, A., Friedrich, F., & Beierkuhnlein, C.

Journal and status: PLoS One, 16(10), e0258615 (2021), https://doi.org/10.1371/journal.pone.0258615

My contributions: idea and concept: 75%, data analysis and figures: 80%, writing: 70%, corresponding author

Contribution of Fabian Friedrich: data analysis and figures: 20%, writing: 20%

Contribution of Carl Beierkuhnlein: idea and concept: 25%, writing: 10%

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7 Manuscripts

7.1 Manuscript 1

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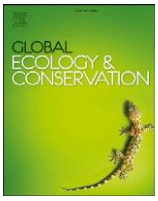

Topographic diversity as an indicator for resilience of terrestrial protected areas against climate change

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Abstract

Habitat loss from unrelenting human pressure is causing an unprecedented decline in global biodiversity. Protected areas (PAs) are meant to counteract loss and fragmentation of ecosystems and today PAs form the backbone of conservation strategies worldwide. However, anthropogenic climate change can severely reduce the effectiveness of PAs. Conservation professionals are in need of concrete spatial information on climatic changes within PAs in order to put forward practicable strategies to safeguard PA effectiveness in the face of climate change. In this study, we take advantage of openly accessible data on the disappearing climate index (DCI) to examine which PA characteristics are linked to climate change resilience on a global scale. DCI provides a measure of the relative area (percent of total area) within a PA that exhibits certain climatic conditions that will either disappear entirely or move outside the boundaries of the PA by the year 2070. Our results show that topographic diversity is highly correlated with reduced climate change impacts in PAs worldwide. We analysed three different PA characteristics representing topographic diversity: PA area, maximal elevational difference (MED) and median terrain ruggedness (TR). All three characteristics are highly correlated with a decrease in the disappearing climate index (DCI). These results hold true across localities and even PA management practices. IUCN management category IV (habitat/species management area) and V (protected landscape/seascape) exhibit on average the highest DCI values. As an indicator for PA resilience under climate change, topographic diversity can be assessed easily through publicly available data and remote sensing products. This ease-of-use leaves topographic diversity standing in marked contrast to overall environmental diversity as an actionable conservation metric. Of course, topographic diversity alone is not a sufficient criterion on which to base conservation decisions. However, neither should the potential usefulness of topographic diversity be underestimated. As an actionable and complementary metric in combination with biological information topographic diversity can be an exceptional tool for decision making by PA managers, conservation practitioners and politicians.

Introduction

Anthropogenic pressure and the associated loss and fragmentation of natural habitats are the primary cause of species extinctions and the rapid decline in biodiversity worldwide (Millennium Ecosystem Assessment 2005; IUCN 2010; Cardinale et al. 2012; Crooks et al. 2017). To counteract these negative developments, protected areas (PAs) function as the backbone of conservation strategies (Gaüzère et al., 2016; Hoffmann et al., 2018; Pimm et al., 2014) by preserving valuable habitat for rare and threatened species (Gray et al., 2016; Langdon & Lawler, 2015; Nila et al., 2019).

However, anthropogenic climate change can severely reduce the effectiveness of PAs as nature conservation tools (Hoffmann & Beierkuhnlein, 2020; Hoffmann et al., 2019; Johnston et al., 2013). Climate change is projected to influence all ecosystems worldwide (Scheffers et al., 2016) and future persistence of suitable climatic conditions is critical for species survival (Hannah et al., 2007; Loarie et al., 2009). In many cases, climate change will lead to shifts in species distributions by compelling migration poleward and towards higher elevations as species attempt to track suitable climatic conditions (Berteaux et al., 2018; Chen et al., 2011; Root et al., 2003; Scheffers et al., 2016; Thomas & Gillingham, 2015). In contrast to species distributional ranges, PAs are static and fixed in space. While PAs may be effective in limiting threats to biodiversity caused by habitat loss and fragmentation, their inflexibility in the face of species' mobility could severely hinder their overall effectiveness in reducing extinctions tied to climate change (Araújo et al., 2011; Gaüzère et al., 2016; Hoffmann et al., 2019)

Whether existing protected areas will remain effective as the climate changes is a key question that needs to be answered to develop robust long-term conservation strategies (Johnston et al., 2013; Lehikoinen et al., 2019).

A number of recent studies have dealt with the challenges PAs face under climate change and consider strategies PA managers might take to adapt their conservation efforts (Batllori et al., 2017; Hannah et al., 2007; Langdon & Lawler, 2015; Monzón et al., 2011). Unfortunately, scientific recommendations for effective PA management are often too theoretical or vaguely defined to be implementable in practice (Halpin, 1997; Monzón et al., 2011). Even well-structured recommendations are often based on little or no scientific data. As result, these recommendations can be prohibitively difficult to apply, are targeted to certain areas (Langdon & Lawler, 2015) or are based on a limited sample of case studies (Monzón et al., 2011), if any at all.

To determine which PA characteristics lead to a reduced effect of changing climatic conditions, much more information on interactions between projected climate scenarios, PA characteristics, and adaptive management strategies is needed. Information of this kind has long been unavailable on a global scale. Today, however, widely accessible future climate projections, improved climate modelling techniques, global satellite data and more open-access platforms for sharing administrative and scientific data, create the opportunity to empirically test previously stated assumptions about the relationship between PA characteristics and climate change.

It has been suggested that small PAs are more vulnerable to climatic changes than large ones, leading to greater loss of species and ecological systems as PA area decreases (Hoffmann et al., 2019; Langdon & Lawler, 2015). Therefore, it is recommended that PA area should be as large as politically feasible (Halpin, 1997; Lemieux et al., 2011).Both environmental diversity and species diversity can buffer against climate change and in particular against climatic extremes (Ackerly et al., 2010; Isbell et al., 2015; Lawler et al., 2015). Hence, environmentally heterogeneous PAs are expected to allow for adaptation or migration of species under climate change (Thomas and Gillingham 2015). While PAs located in mountainous regions are expected to experience some of the largest climatic changes (Monzón et al., 2011; Root et al., 2003), they also cover some of the most diverse environmental conditions (Carroll et al., 2017; Langdon & Lawler, 2015). Mountainous PAs that show a high topographic heterogeneity can create a high environmental diversity due to – for example - differences in solar radiation, precipitation and wind exposure (Scherrer & Körner, 2011). Heterogeneity in elevation, aspect, and slope result in a diversity of climates such that species can make smaller spatial adjustments to track suitable climatic conditions (Carroll et al., 2017; Littlefield et al., 2017). In addition, mountainous landscapes are especially prone to natural disturbance events like mud flows or avalanches. These disturbances can remove inertia from a system (e.g. non-reproductive long-lived individuals) and support accelerated establishment of new species and structures, enabling species populations to adapt more quickly to changing climatic conditions (Jentsch & Beierkuhnlein, 2003). Diversity in environmental conditions can indicate the resilience and adaptive capacity of PAs in the face of climate change (Loarie et al. 2009; Langdon and Lawler 2015; Lawler et al. 2015). High topographic heterogeneity within a PA also increases the likelihood that shifting climatic conditions still remain within the boundaries of PAs (Thomas and Gillingham 2015).

As climate changes, certain climatic conditions hitherto found within a given PA may disappear. Hoffmann, Irl, and Beierkuhnlein (2019) previously calculated the percentage of PA surface with disappearing climate conditions expressed by the so-called “disappearing climate index" (DCI). DCI closely relates to climate change velocity in that both indices assess the speed of climate change for certain areas in a way that is relevant to the ability of species to track their suitable climates. Climate change velocity measures the instantaneous local velocity (km yr^{-1}) along Earth's surface needed to maintain constant temperatures (Loarie et al., 2009). In other words, it measures the speed at which organisms would have to migrate on a 2D surface to keep up with climate change. DCI measures the percent of total area within each PA that exhibits a loss of certain climatic conditions. In that sense DCI is easier to apply and to interpret for PAs. Hence, when combined with biological information on species and habitats, DCI as an indicator for PA resilience against climate change can be a useful tool for conservation managers.

The DCI was calculated for all terrestrial PAs and is publicly available (Hoffmann et al., 2019). In our study, we hypothesize that (a) PAs which cover larger areas will show a decrease in DCI, (b) PAs with a high maximal elevational difference (MED) will show a decrease in DCI and (c) PAs with an increased terrain ruggedness (TR) will show a decrease in DCI. Further, we hypothesize that MED and TR differ in their strength affecting DCI within PAs. While TR measures a median of small-scale elevational diversity, MED simply measures the difference between the highest and the lowest elevation within a PA. Hence, especially for bigger PAs MED is measured on a larger scale compared to TR. The differing scales at which MED and TR are calculated affect their relationships with environmental diversity. We expect that MED – the large-scale measurement – correlates more strongly with DCI than TR. It is known that climatic data is correlated with elevational data at local and landscape scale. Elevational data is even built into climate data projections. Yet we believe that quantification of the relationship between climatic and elevational data across almost all of the world's PAs is useful since it has never been done with such scope and clarity.

Beyond revealing general correlations between PA characteristics and DCI we also analysed these correlations separately for different PA management categories. The IUCN divides all global PAs into seven different management categories (**Tab. 1**) (Dudley 2008; IUCN and UNEP 2018).

Tab. 1: IUCN management categories. Adapted from Dudley 2008

IUCN category	Name	Description
Ia	Strict nature reserve	Human visitation, use and impacts are strictly controlled and limited to ensure protection of the conservation values.
Ib	Wilderness Area	Usually large unmodified or slightly modified areas, retaining their natural character and influence, without permanent or significant human habitation.
II	National park	Large natural or near-natural areas protecting large-scale ecological processes with characteristic species and ecosystems, which also have environmentally and culturally compatible spiritual, scientific, educational, recreational and visitor opportunities
III	Natural monument or feature	Areas set aside to protect a specific natural monument, which can be a landform, sea mount, marine cavern, geological feature such as a cave, or a living feature such as an ancient grove
IV	Habitat/species management area	Areas to protect particular species or habitats, where management reflects this priority.
V	Protected landscape or seascape	Areas where the interaction of people and nature over time has produced a distinct character with significant ecological, biological, cultural and scenic value: and
VI	PAs with sustainable use of natural resources	Areas which conserve ecosystems, together with associated cultural values and traditional natural resource management systems. Generally large, mainly in a natural condition, with a proportion under sustainable natural resource management

We hypothesize no strong differences in DCI among management categories since DCI is generally driven by large-scale geographic patterns and therefore it is independent of individual PA management. However, it is conceivable that some types of PA are on average more topographically diverse than others. For example, establishing PAs in mountainous landscapes is often easier and cheaper since there is less pressure to use this land for agriculture or urban expansion. In addition, especially scenic mountain landscapes often attract tourists. This may be more relevant to some IUCN management categories than others. Hence, we hypothesize higher topographic diversity among strictly protected PAs (IUCN Ia, Ib and II) linked to lower DCI values. Analysing IUCN management categories separately can demonstrate which types of PAs are more or less affected by climate change and where conservation efforts should be focussed.

Methods

Protected area data

This study is based on the dataset produced by Hoffmann, Irl, and Beierkuhnlein 2019. The dataset is derived from the World Database on Protected Area (WDPA) (IUCN and UNEP 2018). The original WDPA dataset was condensed to include only terrestrial PAs. Hoffmann et al. 2019 then rasterized the original PA polygons into a dataset of the same resolution (30 arcseconds, approx. 900m at the equator) as the climate data used for identification of the areas experiencing disappearing climate conditions for each PA. Rasterization was processed via cell-center coverage. In other words, PA polygons were only included in the final dataset when the center point of a 30 arcsecond-sized raster cell falls within that polygon. Very small PAs and PAs with elongated shapes are more likely to elude the center point of any raster cell and therefore were not included in the final dataset. While this procedure was necessary in order to calculate reliable DCI values, it might distort the results since very small PAs are expected to experience high DCI values. After processing, a total of 137,432 PAs remained, comprising a total area of 20,658,583 km^2 (This is 14% of the global terrestrial surface and 99.9% of total PA-status area as of January 2018). For more details see Hoffmann, Irl, and Beierkuhnlein 2019.

Disappearing climate index

We used the open access (https://doi.org/10.6084/m9.figshare.9804350) disappearing climate index (DCI) calculated for the local scale by Hoffmann, Irl, and Beierkuhnlein (2019). This index measures the proportion of 30 arcsecond cells within a given PA that contain climate classes which will not exist within the same PA in the future. In other words, the DCI provides a measure of the relative area (percent of total area) within each PA that exhibits certain climatic conditions that will either disappear entirely or move outside the boundaries of the PA in the future. To calculate the DCI, Hoffmann, Irl, and Beierkuhnlein (2019) used global climate data with a resolution of 30 arcseconds provided by the WorldClim project (Hijmans et al. 2005). Future climate data were downscaled from ten different general circulation models (GCMs) for the Representative Concentration Pathways RCP 4.5 covering the year 2070, i.e., the average of period 2061–2080. For further details on the calculation of DCI see Appendix A.

Protected area characteristics

To identify PA characteristics that are especially associated with climate change inside PAs, we related three distinct PA characteristics – PA area, maximal elevational difference, and terrain ruggedness - to the DCI. PA area is given by the WDPA dataset. Maximal elevational difference (MED) was calculated as the absolute difference between maximal elevation and minimum elevation for each PA. Maximal and minimum elevation data was obtained from two separate global raster datasets by Amatulli et al. 2018. These two remote sensing products (maximal elevation and minimum elevation) are based on 90 m elevation data from the Shuttle Radar Topography Mission and have a final resolution of 30 arcseconds (Jarvis, Reuter and Nelson 2008; Reuter, Nelson and Jarvis 2007). We than calculated the highest minus the lowest point of each PA at 30 arcsecond resolution. Terrain ruggedness index (TR) of each PA is given by the original dataset of Hoffmann, Irl, and Beierkuhnlein 2019 (https://doi.org/10.6084/m9.figshare.9804350). This data was extracted from open-source digital elevation model data provided by Amatulli et al. (2018). It is based on 90 m elevation data and has a final resolution of 30 arcseconds. TR was calculated as the mean of the absolute differences in elevation between a cell within a PA and its eight adjacent cells inside the PA. It is important to note that a resolution of 30 arcsecond will show variation in grain size with latitude, which can bias or distort TR values to some degree. Hoffmann, Irl, and Beierkuhnlein 2019 assigned each PA one TR value by calculating the median of all TR values inside a single PA. For further details see Hoffmann, Irl, and Beierkuhnlein 2019.

IUCN management categories

We further analyzed the correlations between PA characteristics and DCI for separate PA management categories. The IUCN divides all global PAs into different management categories ranging from strictly protected (Ia) to PAs with sustainable use of natural resources (VI) (**Tab. 1**). This data is provided by the original WDPA dataset (IUCN and UNEP, 2018). We hypothesized no strong differences among management categories since DCI is generally driven by large-scale geographic patterns and therefore it is largely independent of individual PA management. However, our results can reveal which types of PAs are more severely affected by climate change and therefore might impact decisions about where to concentrate future conservation efforts.

Statistical analyses

Statistical analyses were performed in R v. 3.6.2 (R Core Team 2019). We tested frequency distribution of our data visually by using histograms as well as qqplots. To assess the effects of PA characteristics on DCI we conducted a generalized linear model (GLM). We selected three distinct characteristics as explanatory variables, PA area, maximal elevational difference (MED), and median terrain ruggedness (TR). To account for spatial autocorrelation we assigned each PA to one of 32 climate zones based on Koeppen-Geiger climate classification (Rubel & Kottek, 2010). We initially conducted separate linear mixed models (LMMs) with disappearing climate index as response variable, PA characteristics as fixed effects and Koeppen-Geiger climate zone as random effect. In all three cases, variance explained by Koeppen-Geiger climate zone was below 0.01. This implies that our model is robust for differences in climate and the effect of spatial autocorrelation in our data is negligible. After clarifying the status of spatial autocorrelation, we conducted generalized linear model analyses (GLM) using the *glm* function in R. DCI functioned as response variable while log (PA area), MED and TR and their interactions PA area*MED, PA area*TR and MED*TR were predicting variables in our model. All predicting variables were poisson distributed and below the 0.7 threshold value for the Pearson correlation test. Stepwise, forward selection was used to select the most parsimonious model. Since most goodness-of-fit measures are not well suited for such large data sets we based our model selection on a threshold of an increase in R^2 of at least 2% for each degree of freedom used by the model. R^2 was calculated using the *rsq* package (Zhang 2020). The assumptions for linear regressions were tested via diagnostic plots and met in all cases presented in this study.

To see if different IUCN management categories have significantly different DCI values, we calculated an one-way ANOVA test with IUCN category as explanatory variable and DCI as response variable. For this test we excluded PAs, which follow under one of the following IUCN categories, “Not applicable”, “Not assessed”, “Not reported”, which amounted to a total of 37784 (27.5%). The remaining 99648 PAs were analyzed. All DCI values within the seven IUCN groups followed a normal distribution. The assumptions for ANOVA were tested via diagnostic plots and met in all cases presented in this study. In addition, we performed a Tukey’s Honestly Significant Difference (Tukey’s HSD) post-hoc test for pairwise comparisons of DCI among IUCN categories using a 95% confidence interval.

To test whether PA characteristics differ significantly among IUCN management categories, we performed a Kruskal-Wallis test between IUCN category and a) area, b) MED and c) TR. We performed a posthoc pairwise.wilcox.test() for pairwise comparisons of PA characteristics among IUCN categories.

To test how IUCN categories interact with PA characteristics in their effects on DCI we conducted three separate GLMs with poisson distribution: DCI~area*IUCN; DCI~MED*IUCN; and DCI~TR*IUCN. This analysis of IUCN management categories in relation to abiotic terrain variables should allow a description of the relative characteristics of each category. To preserve the clarity of interpretation we separated the analysis in three models, one for each abiotic terrain variable, instead of fitting all variables into a single model. We plotted our data with the *interact_plot* function from the package *interactions* (Long 2019) and included 80% confidence intervals. We chose 80% confidence intervals instead of 95% confidence intervals to improve the interpretability of the graphics.

Results

All terrestrial protected areas worldwide will experience a change of climatic conditions in the future. Under moderate climate change (RCP 4.5) global terrestrial PAs will lose between 1%-85% of their relative land surface area exhibiting certain climatic conditions which will no longer be part of this PA by 2070. The best-fit model for predicting DCI within global terrestrial PAs included PA area (log-transformed) and maximal elevational difference (MED) (R^2=0.63) (**Tab. 2**).

Tab. 2: Generalized linear model results of PA characteristics as predictors of DCI. R^2=0.63

Variable	Estimate	Standard Error	z-value	p-value
DCI				
PA area (log)	-0.0398	0.003	-11.50	<0.000001 ***
MED	-0.0003	< 0.001	-15.91	<0.000001 ***

Significance codes as indicated are "*" <0.05, "**" <0.01 "***" <0.001

Including TR as predicting variable in the model resulted in an R^2 increase of only 0.9% even though TR had a significant effect on DCI (p=0.000002) (**Appendix B, Tab. B1**).

The one-way ANOVA test showed significant differences in DCI for IUCN categories (p<0.000001). With a 95% confidence interval, Tukey's Honestly Significant Difference (Tukey's HSD) post-hoc test for pairwise comparisons showed a significant difference in DCI between all IUCN categories except for Ib (wilderness area) and VI (PAs with sustainable use of natural resources) **(Fig. 1).**

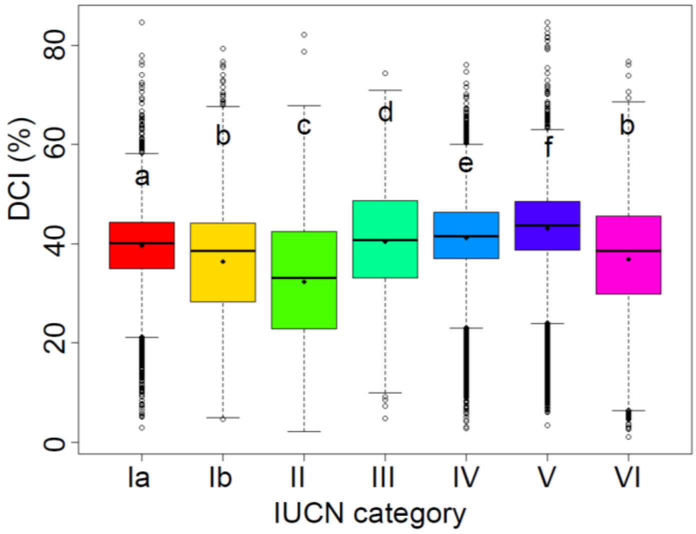

Fig. 1: DCI for IUCN management category. IUCN categories differ significantly in their DCI values. Black lines represent the median, black dots the mean, and error bars show 95% confidence intervals. Statistical significance (p<0.000001) is indicated by different letters below the bars. Tukey's HSD post-hoc test showed a significant difference in DCI between all IUCN categories except for Ib (wilderness area) and VI (PAs with sustainable use of natural resources). IUCN management category IV (habitat/species management area) and V (protected landscape/seascape) exhibit on average the highest DCI values.

When testing the differences in PA characteristics for each IUCN category **(Tab. 3)** we found area differed significantly (p<0.000001) for all IUCN categories except IUCN Ia (strict nature reserve) and V (protected landscape or seascape) (Ia: p=0.14). The largest median areas were found in category II (66 km^2), the smallest in category IV (1 km^2).

Tab. 3: The difference of PA area among PAs of different IUCN management categories. We performed a Kruskal-Wallis Test excluding PAs, which follow under one of the following IUCN categories, “Not applicable”, “Not assessed”, “Not reported”.

	Ia	Ib	II	III	IV	V	VI
Median in km^2	2	40	66	1	1	2	9
Mean in km^2	118	467	918	22	63	67	968
p-value:							
Ib	$<0.001^{***}$						
II	$<0.001^{***}$	$<0.001^{***}$					
III	$<0.001^{***}$	$<0.001^{***}$	$<0.001^{***}$				
IV	$<0.001^{***}$	$<0.001^{***}$	$<0.001^{***}$	$<0.001^{***}$			
V	0.140	$<0.001^{***}$	$<0.001^{***}$	$<0.001^{***}$	$<0.001^{***}$		
VI	$<0.001^{***}$	$<0.001^{***}$	$<0.001^{***}$	$<0.001^{***}$	$<0.001^{***}$	$<0.001^{***}$	

Significance codes as indicated are “*” <0.05, “**” <0.01 “***” <0.001

MED differed significantly ($p<0.000001$) for all IUCN categories except IUCN Ia (strict nature reserve) and III (natural monument or feature) ($p=0.51$) as well as Ib (**wilderness Area**) and II (national park) ($p=0.83$). The largest median MED was found in category Ib (400m), the smallest in category V(50m) (**Tab. 4**).

Tab. 4: The difference of MED among PAs of different IUCN management categories. We performed a Kruskal-Wallis Test excluding PAs, which follow under one of the following IUCN categories, “Not applicable”, “Not assessed”, “Not reported”.

	Ia	Ib	II	III	IV	V	VI
Median in km^2	87	400	292	95	73	50	180
Mean in km^2	248	594	634	198	173	154	378
p-value:							
Ib	$<0.001^{***}$						
II	$<0.001^{***}$	<0.83					
III	<0.51	$<0.001^{***}$	$<0.001^{***}$				
IV	$<0.001^{***}$	$<0.001^{***}$	$<0.001^{***}$	$<0.001^{***}$			
V	0.140	$<0.001^{***}$	$<0.001^{***}$	$<0.001^{***}$	$<0.001^{***}$		
VI	$<0.001^{***}$	$<0.001^{***}$	$<0.001^{***}$	$<0.001^{***}$	$<0.001^{***}$	$<0.001^{***}$	

Significance codes as indicated are “*” <0.05, “**” <0.01 “***” <0.001

TR differed significantly ($p<0.000001$) for all IUCN categories except IUCN III (natural monument or feature) and VI (PAs with sustainable use of natural resources) ($p=0.31$). The largest median TR was found in category Ib (10m), the smallest in category V(3m) (**Tab. 5**).

Tab. 5: The difference of TR among PAs of different IUCN management categories. We performed a Kruskal-Wallis Test excluding PAs, which follow under one of the following IUCN categories, “Not applicable”, “Not assessed”, “Not reported”.

	Ia	Ib	II	III	IV	V	VI
Median in km^2	4	10	7	6	4	3	6
Mean in km^2	9	12	11	10	7	6	10
p-value:							
Ib	$<0.001^{***}$						
II	$<0.001^{***}$	$<0.001^{***}$					
III	$<0.001^{***}$	$<0.001^{***}$	$<0.001^{***}$				
IV	$<0.001^{***}$	$<0.001^{***}$	$<0.001^{***}$	$<0.001^{***}$			
V	$<0.001^{***}$	$<0.001^{***}$	$<0.001^{***}$	$<0.001^{***}$	$<0.001^{***}$		
VI	$<0.036^{*}$	$<0.001^{***}$	$<0.001^{***}$	<0.305	$<0.001^{***}$	$<0.001^{***}$	

Significance codes as indicated are “*” <0.05, “**” <0.01 “***” <0.001

When we tested the interaction of IUCN category with PA area (DCI ~ PA area * IUCN) we found that compared to the strictest protection status Ia (strict nature reserve) the other IUCN categories do not exhibit significant differences in the effects of area on DCI. Within category II (national park) we see a weak, yet insignificant trend (p=0.054) in area linked with a stronger decrease in DCI compared to IUCN Ia (**Tab. 6**). This might be due to the large sizes of PAs found in category II (**Tab. 3**). Within category IV we also see a weak, but insignificant trend (p=0.058) in area linked with a less strong decrease in DCI compared to IUCN Ia (**Tab. 6**).

Tab. 6: Generalized linear model results on the interaction of PA area and IUCN category as predictors for DCI.

Variable	Estimate	Std Error	z-value	P-value
DCI				
PA area (log):IUCN_Ib	-0.0325	0.023	- 1.42	0.154
PA area (log):IUCN_II	-0.0363	0.019	- 1.93	0.054
PA area (log):IUCN_III	-0.0163	0.023	- 0.72	0.471
PA area (log):IUCN_IV	0.0295	0.016	1.89	0.058
PA area (log):IUCN_V	0.0059	0.016	0.36	0.721
PA area (log):IUCN_VI	-0.0091	0.019	- 0.48	0.629

Significance codes as indicated are “*” <0.05, “**” <0.01 “***” <0.001

The relationship between DCI and PA area for the different IUCN categories is shown in **Fig. 2**.

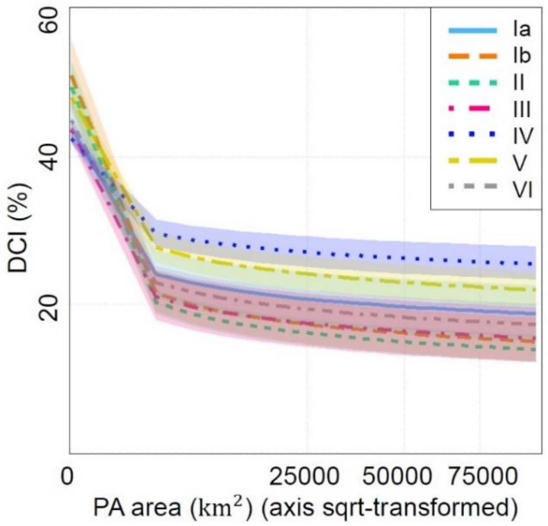

Fig. 2: Decreasing DCI with increasing PA area among all IUCN management categories. Colored sections around the trendlines represent an 80% confidence interval. Compared to the strictest protection status Ia (strict nature reserve) the other IUCN categories do not exhibit significant differences in the effects of area on DCI.

When we tested the interaction of IUCN category with MED (DCI ~ MED * IUCN) we found that compared to the strictest protection status Ia (strict nature reserve) IUCN category Ib (wilderness area) exhibits a significantly stronger decrease of DCI with MED (p=0.25) (**Tab. 7**). Within category II (national park), V(protected landscape or seascape) and VI (PAs with sustainable use of natural resources) we see a weak, yet insignificant trend in MED linked with a stronger decrease in DCI compared to IUCN Ia (II: p=0.059, V:p=0.052, VI:p=0.065). All five IUCN categories (Ia, Ib, II, V and VI) were significantly different from each other in their levels of MED except for IUCN category Ib and II (**Tab. 4**) which both resulted in a stronger decrease of DCI with MED compared to IUCN Ia (**Tab. 7**).

Tab. 7: Generalized linear model results on the interaction of MED and IUCN category as predictors for DCI.

Variable	Estimate	Std Error	z-value	P-value
DCI				
MED:IUCN_Ib	-0.0002	<0.001	- 2.25	0.025*
MED:IUCN_II	-0.0002	<0.001	- 1.89	0.059
MED:IUCN_III	<0.0001	<0.001	<0.01	0.999
MED:IUCN_IV	<0.0001	<0.001	0.66	0.511
MED:IUCN_V	-0.0001	<0.001	- 1.94	0.052
MED:IUCN_VI	-0.0002	<0.001	- 1.85	0.065

Significance codes as indicated are “*” <0.05, “**” <0.01 “***” <0.001

The relationship between DCI and MED for the different IUCN categories is shown in **Fig. 3.**

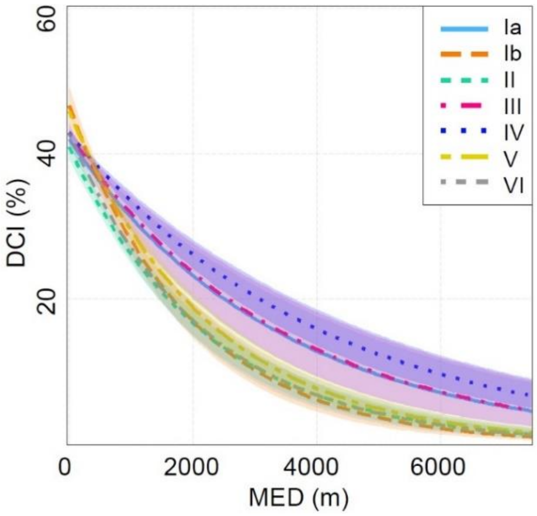

Fig. 3: Decreasing DCI with increasing MED among all IUCN management categories. Colored sections around the trendlines represent an 80% confidence interval. Compared to the strictest protection status Ia (strict nature reserve) IUCN category Ib (wilderness area) exhibits a significantly stronger decrease of DCI with MED (p=0.25).

When we tested the interaction of IUCN category with TR (DCI ~ TR * IUCN) we found that compared to the strictest protection status Ia (strict nature reserve) IUCN category Ib (wilderness area), II (national park), V(protected landscape or seascape) and VI (PAs with sustainable use of natural resources) exhibits a significantly stronger decrease of DCI with TR (Ib:p=0.009, II: p<0.001, V:p=0.040, VI:p=0.038) (**Tab. 8**). All five IUCN categories (Ia, Ib, II, V and VI) were significantly different from each other in their levels of TR (**Tab. 4**).

Tab. 8: Generalized linear model results on the interaction of TR and IUCN category as predictors for DCI.

Variable	Estimate	Std Error	z-value	P-value
DCI				
TR:IUCN_Ib	-0.0110	0.004	- 2.61	0.009**
TR:IUCN_II	-0.0198	0.004	- 5.25	<0.001***
TR:IUCN_III	-0.0011	0.003	- 0.39	0.699
TR:IUCN_IV	0.0017	0.002	0.67	0.501
TR:IUCN_V	-0.0056	0.003	- 2.05	0.040*
TR:IUCN_VI	-0.0069	0.003	- 2.07	0.038*

Significance codes as indicated are “*” <0.05, “**” <0.01 “***” <0.001

The relationship between DCI and TR for the different IUCN categories is shown in **Fig. 4**.

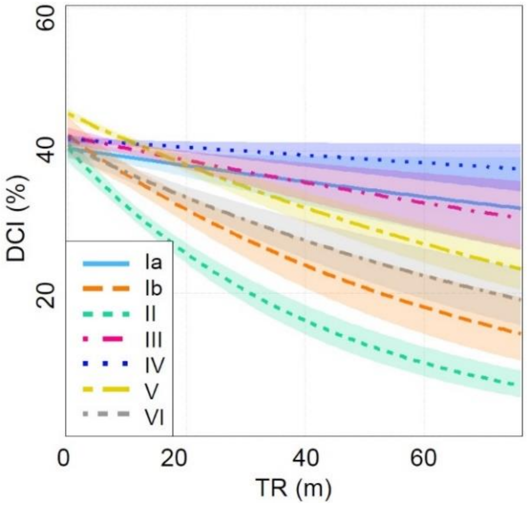

Fig. 4: Decreasing DCI with increasing TR among all IUCN management categories. Colored sections around the trendlines represent an 80% confidence interval. compared to the strictest protection status Ia (strict nature reserve) IUCN category Ib (wilderness area), II (national park), V(protected landscape or seascape) and VI (PAs with sustainable use of natural resources) exhibits a significantly stronger decrease of DCI with TR (Ib:p=0.009, II: p<0.001, V:p=0.040, VI:p=0.038). Category IV (habitat/species management area) exhibits a less strong decrease in DCI compared to IUCN category Ia, this weak trend is – however – not significant (p=0.501).

Discussion

All terrestrial protected areas (PAs) on earth will experience a change of climatic conditions in the near future. Certain climatic conditions within the boundaries of any given PA will disappear while others expand or change locations. This can severely reduce biodiversity conservation and other measures of PA effectiveness. Under moderate climate change (RCP 4.5) global terrestrial PAs will lose between 1%-85% of their relative land surface area exhibiting certain climatic conditions which will no longer be part of this PA by the year 2070. The disappearing climate index (DCI) is a measure of the amount of land surface area that will lose current climatic conditions by 2070. Higher topographic diversity within PAs is strongly linked to lower DCI values. We found that all three investigated PA characteristics representing topographic diversity –PA area, maximal elevational difference (MED) and terrain ruggedness (TR)– are correlated with a significant decrease in DCI. PA area and MED alone explain 63% of the variance observed in DCI among the world's terrestrial PAs. IUCN management category IV (habitat/species management area) and V (protected landscape/seascape) exhibit on average the highest DCI values.

In our study we analyzed the relationship between DCI and topographic diversity using the resolution of 30 arcseconds, determined by the preexisting data of DCI. To our knowledge this is the highest spatial resolution for which global climate data is available. While this allowed us to look at all terrestrial PAs worldwide, the resolution of 30 arcseconds – approximately 1 km – probably underestimates the potential for microclimates and microclimatic refugia (Suggitt et al., 2018). Therefore, a 30 arcsecond resolution might underestimate climate change indices such as DCI by overlooking fine-scale topoclimatic patterns, especially in rugged terrain and by not-detecting fine-scale sites decoupled from the regional climate (Heikkinen et al., 2020). While MED and TR values are based on elevation data of 90 m resolution, we analyzed them in a final resolution of 30 arcseconds determined by the preexisting data of DCI.

This allowed us to create computationally manageable values for all terrestrial PAs worldwide. These values however are likely to underestimate the full range of topographic diversity present in any given PA.

As hypothesized, our research demonstrates that increasing PA area is significantly related to decreasing DCI. This backs up previous studies suggesting small PAs are more vulnerable to climatic changes compared to larger ones (Hoffmann et al., 2019; Langdon & Lawler, 2015; Loarie et al., 2009). Large PAs are more likely to harbor diverse climatic conditions allowing for internal climate displacement such that some portion of the PA is more likely to exhibit prior climatic conditions (Loarie et al., 2009; Thomas & Gillingham, 2015).

Our research also demonstrates that increases in both MED and TR are significantly linked to decreases in DCI. This builds on previous studies which have suggested that mountainous areas are less vulnerable to climatic changes (Lawler et al., 2015; Loarie et al., 2009). High topographic diversity leads to high climatic and thus environmental diversity (Carroll et al., 2017; Halpin, 1997; Langdon & Lawler, 2015), which increases the likelihood that species will be able to find suitable nearby habitat as climate changes (Carroll et al., 2017), for example by shifting their ranges towards higher elevations (Halpin, 1997; Scheffers et al., 2016)Further, our results show that MED is much stronger correlated with DCI and adds a higher explanatory power to DCI compared to TR

To our knowledge, the effects of TR and MED on climate change indices have never before been analyzed separately. One reason for this lacuna could be a paucity of available data. Alternatively, TR and MED are often assumed to be too closely correlated to differ significantly in their effects on climate change indices. In our study of 137,432 terrestrial protected areas MED and TR were just below the 0.7 threshold value for the Pearson correlation test. Even if MED and TR are often correlated, they still represent two different aspects of mountainous landscapes that must be studied independent of one another. MED measures the difference between the lowest and highest elevations within a PA. TR, by contrast, is the mean of the absolute differences in elevation between a raster cell located within a PA and its eight adjacent cells inside the PA. Consequently, TR represents the roughness of a terrestrial surface independent of its altitudinal range or zonation. As such, PAs with low overall elevational difference can still have high TR. As we have hypothesized MED is linked with a much stronger decrease in DCI compared to TR. One possible explanation for this phenomenon is that MED is a more large-scale measurement compared to TR. Testing whether MED also leads to higher environmental diversity compared to TR would require additional analysis not attempted in this paper.

DCI differs significantly among all IUCN categories. IUCN management category IV (habitat/species management area) shows a generally high DCI (second highest mean and median DCI after IUCN management category V). Regardless of whether or not this difference can be explained by topographic diversity this is an important finding, since PAs managed under IUCN category IV are specifically designated to protect “particular species or habitats, where management reflects this priority” (Dudley 2008, **Tab 1**). Yet, while the management in those PAs might be effective for the protection of particular species and habitats today our results suggest that those management practices will not be effective in mitigating climate change in the future. Therefore, we advocate for the incorporation of climate change indices, such as DCI, during decision making regarding PAs managed under IUCN category IV. The lowest mean and median DCI value was found in category II (national park). PAs within category II – however - also exhibit the largest range of DCI values. Overall IUCN category II has the highest median PA area, the second highest median MED and the second highest median TR (the order of mean values is comparable). This might be a result of political interests in preserving especially large and scenic mountain landscapes as national parks. IUCN category Ib (wilderness area) exhibits the second highest median values in PA area and the highest in MED and TR. This may be due to less pressure from land use by agriculture or urban expansion in mountainous landscapes, which creates room for larger, more strictly protected PAs. The highest DCI values are found in category V (protected landscape or seascape), which usually consists of small (median area = 2 km^2) and flat areas with the lowest median MED and TR values among all IUCN categories.

We found no strong differences in the interactions of IUCN categories and PA characteristics in its effects on DCI. However, there was one notable exception: IUCN management category II (national parks) exhibits lower DCI values compared to even the strictest protection status Ia (strict nature reserve) based on all three PA characteristics. While the interaction of IUCN II and PA area is not quite significant (p=0.054) there is a weak trend in decreasing DCI by an additional 3.6% for each km^2 PA area increases compared to IUCN Ia (strict nature reserve). The interaction of IUCN II and MED shows a weak trend (p=0.059) in decreasing DCI for an additionally 0.02% for each additional 1 m increase in MED compared to IUCN Ia. The interaction of IUCN II and TR shows a significant decrease in DCI (p<0.000001) for an additionally 2% for each additional 1 m increase in TR. IUCN management category IV (habitat/species management area) shows a generally high DCI and tends to reduce the decrease of DCI with increasing PA area, MED and TR. However, none of these relationships tested significant (PA area*IUCN IV: p=0.058, MED* IUCN IV: p=0.511, TR*IUCN IV: p=0.501). While our results demonstrated no significant effect of the interactions of PA area, MED and TR with IUCN category IV it nevertheless showed elevated levels of DCI. For future research it is worth examining the factors driving climate change indices especially within IUCN category IV since these PAs are specifically designated to protect “particular species or habitats, where management reflects this priority” (Dudley 2008, **Tab 1**). Thus, if we want to preserve specific species or habitats, we need to consider doing this during times of climatic change, so that species can still profit from PAs currently listed under IUCN management category IV. DCI as a climate index is generally driven by large-scale geographic patterns and it is therefore independent of individual PA management. However, our results show which types of PAs are more affected by climate change compared to others. Our study demonstrates which PA characteristics are most influential in determining DCI for different PA management categories. However, DCI can vary tremendously between individual PAs even if they are part of the same IUCN management category. Therefore, IUCN management category alone cannot be used to inform practitioners of individual PAs about potential future strategies in reducing DCI. The results of our study are the first to demonstrate topographic diversity as a meaningful and practicable guide for conservation managers to design effective PA’s in the face of climate change.

Previous studies have projected tremendous differences in the degree of climatic change individual PAs will experience (Langdon & Lawler, 2015; Loarie et al., 2009; Wiens et al., 2011). While some studies show a projected increase in biodiversity for certain areas under climate change, either through direct or indirect means (Lim et al., 2018; Pawson et al., 2013), most research predicts negative effects of climatic changes on overall biodiversity in the long-term. Environmentally heterogeneous PAs are expected to allow for adaptation or migration of species under climate change (Scherrer & Körner, 2011; Thomas & Gillingham, 2015). Hence, environmental diversity within PAs is considered to act as a buffer in climatic change (Ackerly et al., 2010; Heller et al., 2015; Lemieux et al., 2011). Our goal was to assess if and how topographic diversity may buffer the impacts of climate change. We found three meaningful PA characteristics representing topographic diversity –PA area, maximal elevational difference (MED) and terrain ruggedness (TR)– that are strongly linked to a decrease in DCI. This robust correlation holds true for all terrestrial PAs worldwide and all IUCN management categories.

Hence, topographic diversity can be used as an indicator for the resilience and, to some extent, the effectiveness of PAs under climatic change as it is based on evidence from many climatic regimes which shows that different geophysical settings can maintain distinct ecological communities under a wide range of climates (Jones et al., 2016). In this way our results support the theory of Conserving Nature's Stage (CNS), which advocates for conserving an abiotically diverse stage, which is considered to exhibit high climate change resilience and is easier to identify and measure than biotic diversity (Lawler et al., 2015). However, it is important to note that representing heterogeneity alone is unlikely to preserve specific species or aspects of biodiversity that are most threatened by climate change. Hence, representing heterogeneity within PAs should be complemented by specific conservation approaches which will incorporate biological information to conserve individual species or communities (Jones et al., 2016; Tingley et al., 2014).Applying topographic diversity as an indicator for PA resilience under climate change is an important first step toward climate smart conservation that will be especially useful for PA managers, conservation practitioners and politicians because topographic diversity can be assessed easily through publicly available data and remote sensing products. This ease-of use puts topographic diversity in marked contrast to overall environmental diversity as an actionable metric. Assessing overall environmental diversity is a much more complex undertaking, usually demanding intensive and costly fieldwork for which most conservation practitioners are understaffed, underfunded, and underequipped. Thus, in most circumstances, topographic diversity is a better measure for designing and managing effective PAs.

In the age of "big data," topographic diversity offers a relatively simple and inexpensive guide for estimating climate change resilience in PAs worldwide. It can help in maintaining effectiveness of current and future PAs given projected climatic changes. Most mountainous PAs with high MED and TR are relatively well situated to cope with climatic change while PAs located in flat terrain likely experience higher DCI values. Wessely et al. (2017) suggests that habitat restoration has high potential to mitigate species loss due to climate change in the lowlands of Europe but limited potential in high mountain landscapes. The likely reason is that semi-natural habitats are restricted to remnant patches in Central European lowlands while they still represent the matrix at (sub-) alpine elevations. Pairing practical and applied conservation studies like this with our results on the spatial distribution of climate change resilient PAs based on topographic heterogeneity might help guide conservationists in distributing limited funds in preparing current PAs for remaining their effectiveness under climate change. Beyond managing current PAs our results have the potential to help in designing new PAs with an eye to climate-smart conservation strategies. Our results concur with Lawler et al. 2020, who also point out that creating new PAs in mountainous regions with the intention of providing future climatic refugia will be relatively inexpensive, making the protection of rare climate refugia a low-cost adaptation strategy. However, while managing for topographic diversity is a comparatively simple approach, conservation decisions also need to be based on other criteria such as biological diversity, quality of habitat inside the PA, or the uniqueness of its species (Heikkinen et al., 2020; Hoffmann et al., 2018).

While we investigated the correlation of topographic diversity on DCI we did not include information on species movement. DCI does inform about the disappearing climatic conditions comparable to climate velocity or climate anomaly indices, however these are based on abiotic conditions and processes. When inferring direct measures for species conservation climatic indices should be paired with biological information on species movement in order to predict future climate refugia or biodiversity hotspots. Underlying mechanisms such as dispersal limitations, demographic shifts, species interactions, and evolution, however play key roles in mediating biotic responses to climate change (Littlefield et al., 2017; Urban, 2015). In addition to mountain-top extinction or low-elevation bottlenecks, physical structures, such as insurmountable environmental barriers, can further prevent successful climate tracking (Littlefield et al., 2017; Reside et al., 2018).

Our results underscore the findings of previous studies that suggest future-oriented conservation approaches that maximize environmental diversity to buffer impacts of climate change (Ackerly et al., 2010; Heller et al., 2015; Lawler et al., 2015; Scherrer & Körner, 2011). However, maximizing environmental diversity is difficult to put into practice. One often-used proxy for environmental diversity is PA size. While it is widely acknowledged that increasing PA area leads to a reduction in climatic change impacts within PAs it is also understood that expanding PA area is often unfeasible due to limited funds, human land use pressures, depleted natural habitats, political will, and other factors (Hoffmann et al., 2019; Langdon & Lawler, 2015; Thomas & Gillingham, 2015). In such cases PA management might profit from new, more flexible approaches to PA management and design. However, it is important to note that in this study we focused on PAs only and did not analyze the surroundings of PAs. In this sense we treated PAs as islands, assuming that species will not be conserved outside PAs and that species are unable to move through non-PA areas into other PAs to track their climatic niche. There is a vast body of research which looks at the optimal shape and connectivity of PAs and their effects on species movement (Heller & Zavaleta, 2009; Hodgson et al., 2009; Ward et al., 2020; Wegmann et al., 2014). While species movement is already tremendously restricted by human activity, climate change is projected to further constrain potential movement routes while simultaneously creating a higher need for species movement (Littlefield et al., 2017). In order to put connectivity-enhancing strategies forward, future climate projections, landscape permeability due to human modification, and dispersal capabilities need to be considered simultaneously (Littlefield et al., 2017; Urban et al., 2013).

Broadly, PAs exist to preserve global biodiversity. But at the local and regional level, PAs are geared toward the preservation of characteristic species, populations, and ecosystems within static boundaries. Unfortunately, these principles appear increasingly anachronistic in the face of global climate change. The mosaic of PAs worldwide comprises a vast array of biota and habitats that need flexible principles of design to adapt to large-scale environmental changes (Abrahms et al., 2017; Thomas, 2011; Timberlake & Schultz, 2017). By focusing – as a first step - on topographic diversity as an indicator for PA resilience in the face of climate change, practitioners will have an easier, more reliably implementable guide in designing, formulating and establishing effective PAs.

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7.2 Manuscript 2

Detecting low fragmented sites surrounding European protected areas - implications for expansion of the Natura 2000 network

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Abstract

Preserving land with low anthropogenic pressures is essential for achieving biodiversity conservation outcomes. In response, EU member states have set an ambitious goal of establishing additional protected areas (PAs) preserving at least 30% of the land and 30% of the sea by 2030, specifying that these additions should be of high ecological quality. A targeted selection of existing PA expansions into surroundings, which are marginally fragmented by human infrastructure, may be a uniquely efficacious strategy to secure high ecological quality by maximizing PA area, accommodating species movement, and boosting climate change resilience. We used high-resolution data on effective mesh density, a metric for the degree of landscape fragmentation, in the vicinity of Natura 2000 PAs (N2k) to assess their potential for PA expansion. Our results show that contrary to most of Central Europe, mountainous and remote territories exhibit the lowest degree of fragmentation in N2k surroundings. Fragmentation in N2k surroundings is highly correlated with national population density, while economic wealth, measured by GDP per capita, plays a less important role. To address the long-standing dilemma of where scarce economic resources in nature conservation have the potential to do the most-good, we conducted a country-level comparison between fragmentation in N2k surroundings and national expenditures on nature conservation relative to N2k area. Our results show a vast incongruity in resource availability and spending practices for nature conservation among EU countries. Eastern European states, especially Romania, host some of the least-well funded national PA networks while holding the highest potential for expanding N2k PAs into low fragmented lands. If protecting low fragmented lands to expand N2k PAs is accepted as an efficacious strategy to meet EU Biodiversity targets our results could be used to formulate pragmatic conservation decisions, while also ensuring high ecological quality of PA additions in the face of climate change.

Highlights

- Expanding existing protected areas (PA) into surroundings, which are marginally fragmented by human infrastructure, may be a uniquely efficacious strategy to safeguard biodiversity by maximizing PA area, accommodating species movement, and boosting climate change resilience.
- Within the European Natura 2000 network (N2k), mountainous and remote territories exhibit the lowest degree of fragmentation in N2k surroundings and therefore show arguably the highest potential for PA expansion.
- There exists a vast incongruity in resource availability and spending practices for nature conservation among EU countries.
- Eastern European states, especially Romania, host some of the least-well funded national PA networks while holding the highest potential for expanding N2k PAs into low fragmented lands.
- If protecting low fragmented lands to expand N2k PAs is accepted as an efficacious strategy to meet EU Biodiversity targets our results could be used to formulate pragmatic conservation decisions, while also ensuring high ecological quality of PA additions in the face of climate change.

Keywords: Natura 2000, landscape fragmentation, EU Biodiversity Strategy for 2030, protected area expansion, protected area surroundings, climate change, pragmatic conservation, Eastern Europe

Introduction

Stemming habitat degradation is the key to salvaging what biodiversity the globe has left. Unless societies find ways to effectively protect natural spaces from habitat destruction and mitigate anthropogenic fragmentation of terrestrial landscapes, catastrophic rates of biodiversity loss are likely to continue or worsen (Millennium Ecosystem Assessment 2005, IUCN 2010, Cardinale et al. 2012, Crooks et al. 2017). Urban expansion and the concomitant extension of human infrastructure into zones of wildland leads to the breakdown of ecosystems, biodiversity loss, and the deterioration of both ecosystem functions and ecosystem services (Barnosky et al. 2012, Wu 2013, Haddad et al. 2015). In the 21st century, when measurable human pressure has touched 75% of the world's terrestrial land (Venter et al. 2016), protected areas (PAs) are critical for biodiversity conservation (Saura et al. 2018). Well designed and managed PA systems can provide a safe haven for species in a changing environment, buffering them against preventable habitat loss and fragmentation (UNEP-WCMC and IUCN 2016).

Expanding and carefully managing PAs is regarded as one of the most efficient and effective strategies for safeguarding biodiversity worldwide (Thomas and Gillingham 2015). However, successfully insulating some terrestrial areas from anthropogenic fragmentation and habitat loss requires policymakers and conservation practitioners to manage PAs not just with the goal of biodiversity protection in mind but also within the context of divergent policy agendas as well as fiscal and political constraints (Venter et al. 2014, Watson et al. 2014). Given budgetary restrictions, economic incentives, and the projected continued expansion of urban infrastructure, policymakers and conservation practitioners need to know where scarce economic resources have the potential to do the most good (Wintle et al. 2011, Watson et al. 2014). The question these decision-makers face is clear: where can PAs be established or expanded so as to be most efficacious in conserving current and future habitats?

In the European Union, the Natura 2000 (N2k) network is the backbone of continent-wide conservation efforts. N2k is the world's largest coordinated network of PAs, covering 18.5% of the EU's terrestrial and almost 10% of its marine area (CEC 1992, EC 2020). Since the establishment of N2k in 1992, the network has increased both PA coverage and interconnectivity of PAs in the European Union (Maiorano et al. 2008). However, even this widespread PA coverage is insufficient to adequately protect European biodiversity (Baillie and Zhang 2018). One reason that the N2k network must expand even further is human-induced climate change. Changing climatic conditions force species to either adapt to the changing conditions of their local habitat or to shift their geographic ranges to trace their preferred climatic conditions (Thuiller et al. 2005, Gonzales et al. 2013, Chen et al. 2011). Absent either of these possibilities, species face extinction (Bennett and Classen 2020). Where habitats are small and fragmented, species' ability to relocate to preferred climatic conditions is hindered severely, if not precluded altogether (Robillard et al. 2015). Hence, the synergistic effects of climate change and habitat fragmentation may be detrimental to biodiversity (Travis 2003) and initiate a turnover in the composition and functional diversity of wildlife communities, (Lawler et al. 2009, Lehikoinen et al. 2021).

To maintain intact natural ecosystems under climatic changes it has consistently been recommended to expand PAs (Peters and Joan 1985, Hannah 2008, Loarie et al. 2009, Watson et al. 2014, Pringle 2017). As such the N2k network must expand its coverage by growing PAs and connecting existing PAs to allow species to shift geographic ranges with minimal interference from anthropogenic infrastructure. Expanding PAs in size is likely to boost climate change resilience (Lawrence et al. 2021a), increase biodiversity protection and help maintain ecosystem services (Griscom et al. 2017, Dinerstein et al. 2019). European member states have set an ambitious goal of establishing additional PAs and protecting at least 30% of the land and

30% of the sea area with 10% of EU land and 10% of EU sea under strict protection. It is important that these additions to the future expansion of the N2k network will rely on careful environmental assessments to ensure additions to the PA network are of high ecological quality and relevance to nature conservation (EC 2020). However, the limits of fiscal resources that EU member states intend to devote to nature conservation need to be considered in designing future N2k expansion potentially forcing conservation goals towards more pragmatic, utilitarian approaches that are typically understood as less than ideal from a pure biodiversity conservation standpoint. Among other “pragmatic” approaches are calls for protection of areas of uniquely high biodiversity, especially the tropical and sub-tropical marine and terrestrial ecosystems in the EU’s outermost regions, the protection of carbon-rich ecosystems such as peatlands or old-growth forests, and the construction of narrow ecological corridors to connect existing PAs (EC 2020). While the EU Biodiversity Strategy for 2030 does not explicitly mention the need to consider landscape fragmentation as a criterion in designing PA additions, targeted selection of existing PA expansion into low fragmented surroundings may be a uniquely efficacious strategy to secure high ecological quality in PA additions capable of boosting climate change resilience.

Within low fragmented and intact habitats species have an enhanced chance of maintaining fundamental ecological and evolutionary mechanisms such as dispersal, migration, gene flow, and species range shifts. These mechanisms are essential for the persistence of viable populations, possibly evading extinction due to climate and land-use changes (Kuussaari et al. 2009, Krosby et al. 2010, Saura et al. 2018).

Expanding already existing PAs into low fragmented surroundings can foster species movement by increasing total PA area (Loarie et al. 2009, Langdon and Lawler 2015, Saura et al. 2018). Currently, even in Europe large areas surrounding N2k PAs consist of natural, low fragmented lands (Lawrence et al. 2021b). It has been recommended that PA area should be as large as politically feasible to facilitate species movement and contribute to higher PA resilience against climate change (Halpin, 1997, Loarie et al. 2009, Lemieux et al., 2011, Lawrence et al. 2021a). However, until today, the spatial potential for an extension of European PAs has not been fully utilized yet.

To provide science-based guidance for future PA expansions we investigate the spatial distribution of anthropogenic fragmentation around existing N2k PAs across the EU. Hereby, we define fragmentation as a landscape-scale process that includes (a) reduction in total habitat area, (b) increase in the number of habitat patches, and (c) decrease in sizes of habitat patches. We do not consider the degree of patch isolation. Thus, we measure habitat loss and fragmentation as a unified phenomenon rather than measuring fragmentation per se (Fahrig 2003). This is an important distinction because habitat loss is known to be a primary threat to biodiversity while the effects of landscape configuration, such as fragmentation per se, are debated (Fletcher et al. 2018, Fahrig et al. 2019, Saura 2020, Fahrig 2021). In this study, we measure habitat loss and fragmentation as one unified syndrome linking processes with spatial patterns, which is widely accepted as a major threat to biodiversity (Hanski 2015, Haddad et al. 2017).

Our study relates to member states of the EU, responsible for implementing the EU Biodiversity Strategy 2030, as well as biogeographical regions, which are useful in ecology-based decision making for nature conservation. While national borders are usually clearly defined, there is more ambiguity around the delineation of biogeographical regions (Beierkuhnlein and Fischer 2021). In fact, there is no common standard for large-scale biogeographical units such as biogeographical regions or biomes. In consequence, assessments on the basis of these regions can differ based on the applied criteria for classification (Fischer et al. 2022). In this study we analyzed fragmentation of N2K PA surroundings for the nine different biogeographical regions as they are defined for official use by EU institutions.

Here, we hypothesize that (a) degree of fragmentation in N2k PA surroundings differ significantly among biogeographical regions of the EU. Assuming that remote northern locations as well as mountainous regions of Europe are less suited to infrastructure development due to their climate and topography, we further hypothesize that (b) the degree of fragmentation of N2k PA surroundings is negatively correlated with latitude and elevation but not correlated with longitude. In addition, we hypothesize that (c) degree of fragmentation in N2k PA surroundings differ significantly among countries and that (d) the degree of fragmentation of N2k PA surroundings is positively correlated with population density as well as GDP, based on the assumption that highly populated, wealthier countries exhibit more expansive infrastructure systems and thus higher degrees of landscape fragmentation. These hypotheses test the link between geographic, i.e., latitude, longitude, elevation, and anthropogenic, i.e., population density and GDP, characteristics with the degree of fragmentation of N2k PA surroundings. Our focus lies on low-fragmented N2k surroundings, as they hold a high potential harboring intact ecosystems not-yet part of the N2k network. Our goal is to provide spatial information on the location of such low-fragmented N2k surroundings. Addressing the divergent fiscal and economic constraints among EU member states, we compare national expenditures on nature conservation relative to N2k PA area covered by each country in order to determine gaps in N2k preservation funding. This country-level information combined with data on the location of low-fragmented N2k surroundings can provide a roadmap on where protection of comparatively low fragmented landscapes can be efficiently achieved within the context of national budgetary restrictions.

Methods

Study area

To assess the potential for PA expansion in the EU and the UK, we used open-access data (DOI: 10.6084/m9.figshare.13513902) to examine landscape fragmentation within a 5 km buffer zone around N2k PAs, hereafter referred to N2k surroundings, in Europe (Fig 1). The N2k network spans 27 countries and nine distinct biogeographical regions, as defined for official use by EU administrations (Fig 2). In total, the degree of landscape fragmentation within the surroundings of 15390 terrestrial PAs ranging in size from 1 km² to 5556 km² was investigated. All PAs at the core of the buffer zones analysed in this study are part of the European N2k network, the world's largest coordinated network of PAs.

Effective Mesh Size and Effective Mesh Density

In this study, we used open access data by Lawrence et al. (2021b) showing the degree of fragmentation within a 5 km buffer surrounding N2k PAs (DOI: 10.6084/m9.figshare.13513902).

Effective mesh density, a landscape-scale metric developed by Jaeger (Jaeger 2000) was used to quantify the degree of fragmentation. Jaeger et al. (Jaeger et al. 2007) defined a series of 'fragmentation geometries' (FGs) which include different types of barriers. This study focuses on major and medium anthropogenic constructions –such as roads, railways, and buildings. This coincides with fragmentation geometry A2 (FG-A2) described in more detail by Jaeger et al. (2011).

To quantify fragmentation within a landscape, Jaeger (2000) developed the landscape metric known as effective mesh size (m_{eff}), which is based on the probability that two randomly chosen points within a defined area will be connected (i.e., located in the same patch). This probability can be understood as the probability that two theoretical and perfectly mobile individuals can find each other inside the defined area without crossing a barrier. By multiplying this probability by the total area under study, the result represents the size of an area: the effective mesh size. Hence, m_{eff} can be interpreted as the expected size of the area that is accessible to an individual animal located at a random point inside the defined area without encountering a barrier (Jaeger 2000, Moser et al. 2007).

As the number of barriers from fragmentation increases, the mesh size diminishes, and therefore m_{eff} decreases. m_{eff} has a value of 0 km² if barriers cover a landscape entirely. Originally, m_{eff} was calculated using the cutting-out (CUT) procedure. However, this method is affected by the "boundary problem" because the boundaries of the reporting units, e.g., the borders of raster cells, are considered additional barriers. To overcome this limitation, a new method called the "cross-boundary connections" (CBC) procedure attributes the connections between two points located in different reporting units to both reporting units. The CBC procedure is independent of the size and administrative boundaries of reporting units (Moser et al. 2007). The open access data used in this study follows the CBC procedure to avoid the classification of the 5 km buffer edges as additional barriers.

Within a defined landscape – e.g., 5 km buffer zones around N2k PAs – it is possible to calculate effective mesh density (s_{eff}), by taking the inverse of the effective mesh size (m_{eff}) of the defined landscape (Eq 1) (Jaeger et al. 2007).

$$seff = \frac{1}{meff} \tag{1}$$

The m_{eff} value gives information about the size of uninterrupted spaces and s_{eff} about the density of these uninterrupted spaces. In ecological context, the phenomena measured by m_{eff} and s_{eff} impact the mobility of species within a given range. Thus, these concepts directly address landscape fragmentation and make it possible to quantify the reduction in landscape connectivity (Jaeger et al. 2011) as ambulatory species experience it.

Data collection

For our model, we used previously published open access data on effective mesh density (s_{eff}) within the surroundings, a 5 km wide buffer zone of terrestrial N2k PAs (DOI: 10.6084/m9.figshare.13513902). This data was originally calculated based on m_{eff} raster data in a 1 km^2 resolution covering the entire EU and UK (EEA 2014).

Data on N2k PAs encompass the Special Areas of Conservation (SAC) and the Special Protection Areas (SPAs) of the European Union and the UK (EEA 2019). For each N2k PA surrounding, information on the core PA's biogeographical region is included in the dataset (DOI: 10.6084/m9.figshare.13513902) and formerly derived from the EU classification of biogeographical regions (EEA 2016). In the original dataset, marine N2k PAs were excluded and N2k PAs were further filtered to ensure each N2k PA covered at least one cell-center of the 1 km^2 raster dataset showing fragmentation in the EU. Hence, N2k PAs which did not cover at least one raster cell-center, i.e., particularly small and elongated N2k PAs were excluded from the original dataset. This resulted in a dataset comprised of 15390 N2k PAs, i.e., 55.3%, of the original 27845 N2k PAs, with their respective surroundings (for more details see Lawrence et al. 2021b).

We analysed a buffer zone of 5 km around each of these N2k PAs. For small-scale analyses focusing on specific species, buffer size is often determined by home range sizes, migration, or dispersal distances of those species (Alexandre et al. 2010). However, the most appropriate spatial scale to analyse a species' survival and persistence probabilities vary tremendously depending on the species in question, even within the same family (Holland et al. 2004). While it is nearly impossible to determine a uniform buffer size best suited to conserve biodiversity on a continental scale, we used publicly available data with a fixed 5 km buffer size as a politically achievable and environmentally meaningful (Cai and Pettenella 2013, Hermoso et al. 2018, Lawrence et al 2021b) buffer size suitable for PA expansion. We determined the latitude and longitude of the center-point of each N2k PA. In addition, we used the open-source Copernicus digital elevation model (EEA 2021) with a resolution of 25 m to calculate maximum elevational difference (MED) (Eq 2) for each N2k PA surrounding, applying zonal statistics in ArcGIS 10.6.1.

$$MED = max.elevation - min.elevation \tag{2}$$

Data on population density and per capita gross domestic product (GDP) per country was taken from the European Union's own dataset (Eurostat 2021a, Eurostat 2021b). In this study, population density data as well as GDP data was based on the year 2014 to match the date of record of the fragmentation data used in this study. Since population density and GDP data does not exist on a 1 km^2 resolution as the original base for s_{eff} calculations, we assessed the relationship between population density, GDP, and fragmentation in N2k surroundings on a national level. We therefore calculated the mean of s_{eff} in N2k surroundings per country.

To calculate N2k area per one million Euros (km^2) we used publicly available data for N2k area under preservation as well as expenditure for nature conservation per country. N2k area per country was determined in ArcGIS using Natura 2000 spatial data (EEA 2020) including all PAs that are part of the N2k network in the year 2020. Expenditure for nature conservation per country was assessed using the European statistic for government expenditure (Eurostat 2022). Herby only values for expenditure on "protection of biodiversity and landscape" for the year 2020 have been included. By dividing the area of N2k PAs by the expenditure spent on the protection of biodiversity and landscape, we derived a value hereafter referred to as 'N2k area per one million Euros (km^2)' expended. All spatial data were processed using ESRI ArcGIS 10.6.1 in ETRS 89 Lambert Azimuthal Equal Area (LAEA) Projection.

Statistical analysis

Statistical analysis and data visualization were performed in R v. 4.1.2 (R Core Team 2021) using the packages ggbreak (Xu et al. 2021), ggplot2 (Wickham 2016), Hmisc (Harrell and Dupont 2021), lmtest (Zeileis and Hothorn 2002), multcompView (Graves et al. 2019), plyr (Wickham 2011), relaimpo (Groemping 2006).

One-way ANOVA

To test for significant differences between s_{eff} of N2k surroundings among biogeographical regions, we used a one-way ANOVA with s_{eff} as dependent variable and biogeographical region as independent variable. We performed a Tukey's Honestly Significant Difference (Tukey's HSD) post-hoc test for pairwise comparisons of s_{eff} values among biogeographical regions. To test for significant differences in s_{eff} between countries we used a one-way ANOVA with s_{eff} as dependent variable and country as independent variable. We performed a Tukey's HSD post-hoc test for pairwise comparisons of s_{eff} values among countries. In both cases, the assumptions for ANOVA were tested via diagnostic plots and met in all cases presented in this study. For both Tukey’s HSD post-hoc tests, we used a 95% confidence interval.

Linear regressions

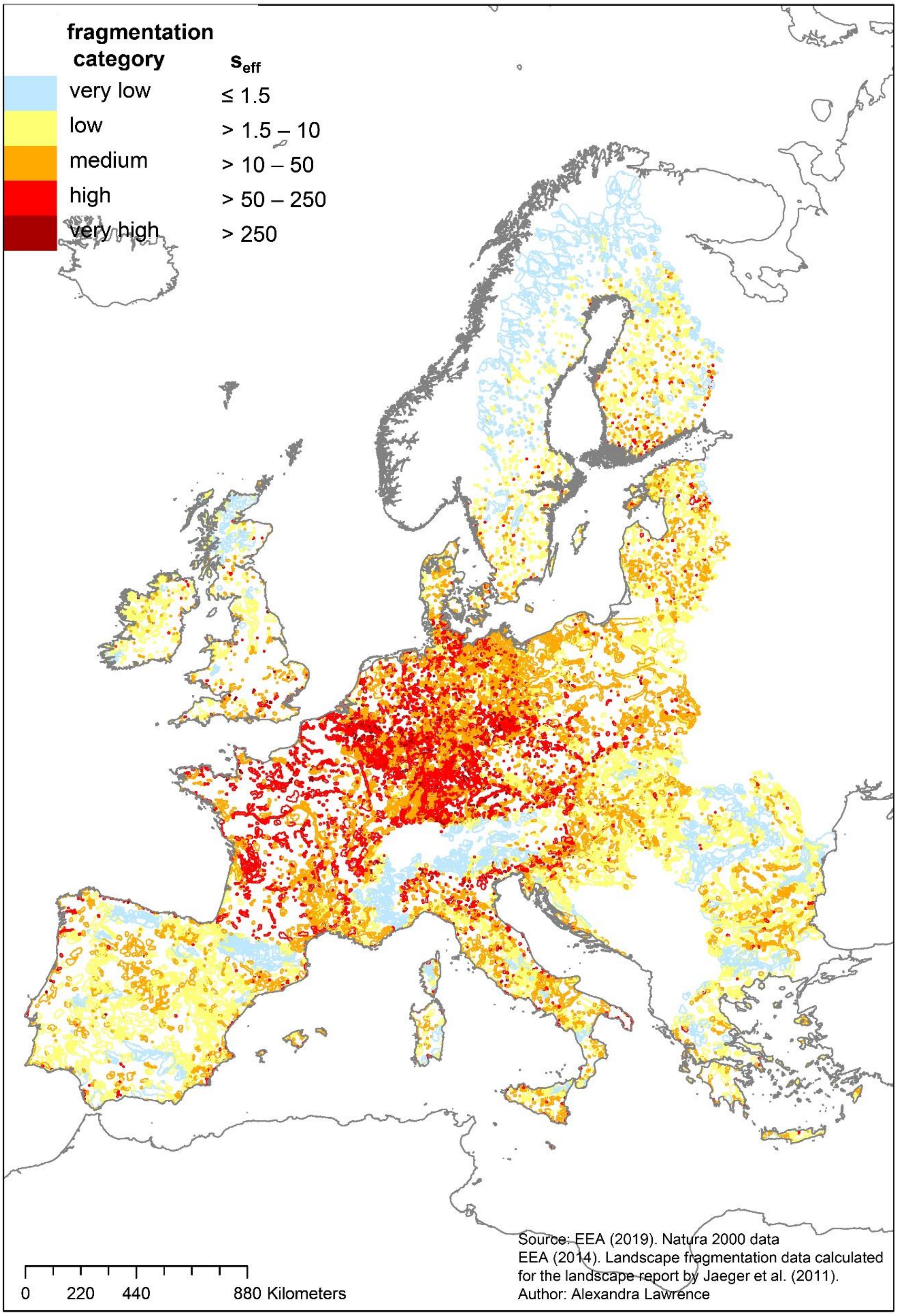
We conducted a multiple linear regression to analyze the relationship between the independent variables MED, latitude and longitude, and the dependent variable s_{eff} of N2k surroundings. According to Pearson correlation coefficients, correlation between independent variables was below 0.7 for all pairwise comparisons. We further log-transformed s_{eff} of N2k surroundings to meet normality requirements. The best fit model was determined by backward selection and based on the lowest AIC value as well as the highest R^2 value accounting for a difference of at least 2% increase in R^2 for each degree of freedom lost. Using diagnostic plots (*plot(linear model)*) confirmed that assumptions for linear regressions were met.

To test the relationship between anthropogenic predictors and s_{eff} of N2k surroundings we calculated the mean of s_{eff} of N2k surroundings per country since predictive variables were only available on at a national scale. Median values of s_{eff} per country are reported in Tab S1. To meet normality requirements, we log-transformed mean s_{eff} values and confirmed normality using a Shapiro-Wilk test. We conducted a multiple linear regression with mean s_{eff} of N2k surroundings as response variable and population density and GDP per capita as explanatory variables. Both explanatory variables were log-transformed to fulfill linear regression assumptions. We used diagnostic plots, the Shapiro-Wilk test, and the Breusch-Pagan test (Zeileis and Hothorn 2002) to confirm linear regression assumptions. According to Pearson correlation coefficients, correlation between independent variables was below 0.7. The best fit model was determined by backward selection and based on lowest AIC value as well as the highest R^2 value.

To quantify the relative importance (RI) of variables in in each model we used the relaimpo package v. 2.2.6 (Groemping 2006). The relaimpo package is based on variance decomposition for multiple-linear-regression models. We chose the most commonly used method named “Lindeman–Merenda– Gold” (lmg; Grömping 2006) from the methods provided by the relaimpo package. This method allowed us to quantify the contributions, i.e., relative importance (RI), of explanatory variables in our multiple linear regression model. For second- and third-order polynomial variables, we reported the cumulative RI for each variable over all polynomial orders.

Results

Anthropogenic fragmentation in the vicinity of existing N2k PAs varies tremendously in state and distribution across the EU. All EU classified categories from very low to very high degrees of fragmentation are represented within the surroundings of N2k PAs (Fig 1).



Source: EEA (2019). Natura 2000 data
EEA (2014). Landscape fragmentation data calculated for the landscape report by Jaeger et al. (2011).
Author: Alexandra Lawrence

Fig 1. Varying degrees of fragmentation in the direct surroundings (5 km buffer) of European Natura 2000 protected Areas. Natura 2000 protected areas themselves are not depicted in this figure.

Some countries and regions, e.g., northern Scandinavia have a few large Natura 2000 protected areas, while other countries such as Germany are characterized by many small Natura 2000 protected areas and consequently more densely packed surroundings. All fragmentation categories classified by the EU (EEA 2018) are represented within 5 km buffer zones surrounding Natura 2000 protected areas in Europe. In contrast to the EEA classification fragmentation categories “anthropogenic” and “very high” were combined into one category “very high” due to the relatively small number of Natura 2000 protected areas within the anthropogenic category. Categories range from very low fragmented (light blue) to very highly fragmented (dark red) and are based on values for effective mesh density, representing number of meshes per 1000 km² (s_{eff} values). Map generated in ArcGIS 10.6.1 (http://www.esri.com/software/arcgis/ arcgis-for-desktop).

However, there are significant differences in the degree of fragmentation represented in N2k PA surroundings for the different biogeographical regions. The alpine region, which covers among others the Alps, the Scandinavian mountains, the Pyrenees, and the Carpathians (Fig. 2a) is the biogeographical region with the lowest levels of fragmentation in N2k PA surroundings (Fig 2b), followed by the Steppic and Boreal regions (Fig 2b). The Steppic and Pannonian regions are in general little fragmented but also characterized through low sample sizes (Fig 2b). The Steppic and Pannonian regions cover only small parts of the EU (Fig 2a). The Atlantic and Continental regions show the highest degrees of fragmentation in N2k surroundings.

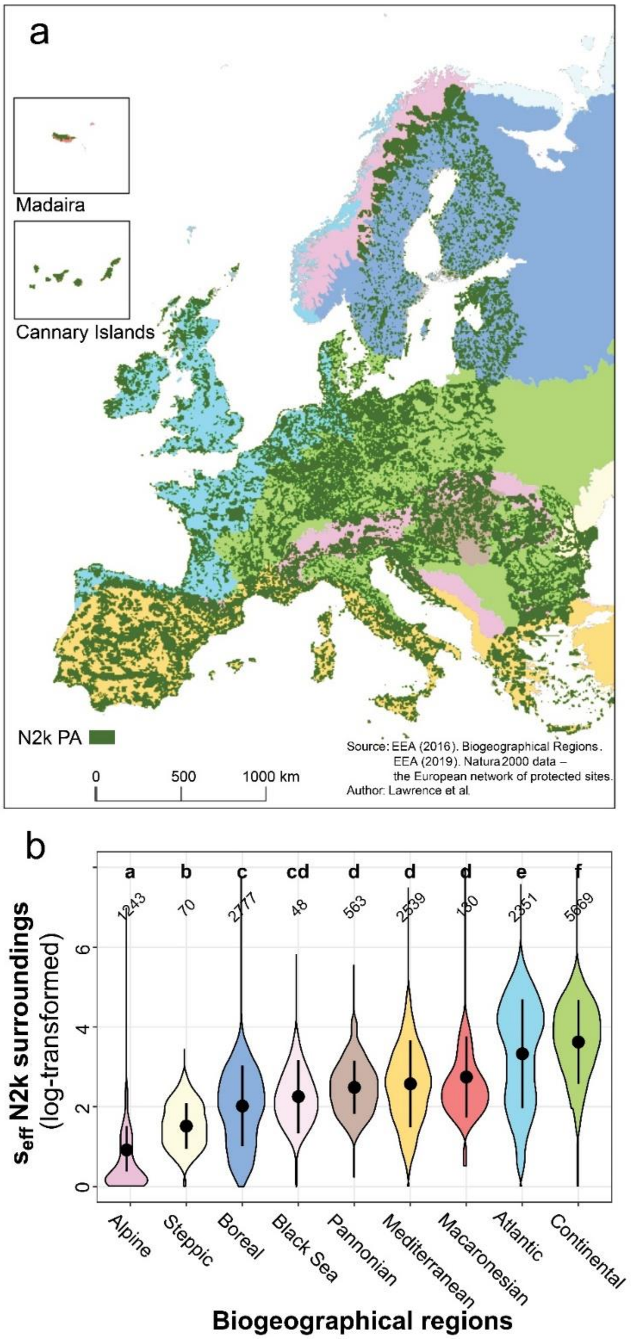


Fig 2. Fragmentation of Natura 2000 protected area surroundings within the nine defined biogeographical regions of the EU. In this study we analyzed the surroundings of 15390 terrestrial Natura 2000 protected areas across the nine biogeographical regions defined by the EU. (a): Dark green polygons represent Natura 2000 protected areas and the nine biogeographical regions are color coded as indicated in b). (b): Biogeographical regions differ significantly in their degrees of fragmentation for Natura 2000 protected area surroundings. 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 Natura 2000 protected area surroundings analyzed within each biogeographical region and black letters above violins indicate the significant difference between biogeographical regions according to Tukey HSD post-hoc test. Map generated in ArcGIS 10.6.1. Graphic generated in R v. 4.1.2 with the packages ggplot2 (Wickham 2016) and multcompView (Graves et al. 2019).

The best-fit model for predicting fragmentation (s_{eff}) of N2k surroundings based on geographical variables within the EU included maximal elevational difference (MED), latitude (third-order polynomial), and longitude (second-order polynomial) ($R^2=0.485$, $p<0.001$) (Tab 1).

Tab 1: Linear model results of geographic characteristics as predictors of fragmentation in Natura 2000 protected area surroundings. The best fit model was determined by backward selection and based on lowest AIC value as well as the highest R^2 value accounting for a difference of at least 2% increase in R^2 for each degree of freedom lost. P-values less than 0.05 were considered significant. Highly significant p-values are marked as ***.

	Estimate	**Std. Error**	**t-value**	**p-value**
s_{eff} of N2k surroundings (log-transformed)				
Intercept	3.482	0.011	316.06	<0.001 ***
MED	-0.001	<0.001	- 84.38	<0.001 ***
Latitude (poly 1)	-0.524	1.191	- 44.02	<0.001 ***
Latitude (poly 2)	-0.207	1.202	- 17.22	<0.001 ***
Latitude (poly 3)	-0.243	1.085	- 22.40	<0.001 ***
Longitude (poly 1)	-0.214	1.114	- 19.21	<0.001 ***
Longitude (poly 2)	-0.523	1.218	- 42.99	<0.001 ***

Relative importance analysis of our linear regression model based on geographical variables ($R^2=0.485$, $p<0.001$) revealed that MED, latitude, and longitude contribute 46.2% (Fig 3a), 30.7% (Fig 3b), and 23.1% (Fig 3c) to the overall model (Tab 1) explaining variance in s_{eff} of N2k surroundings, respectively. PA surroundings with higher maximal elevational differences (MED) are linked with lower degrees of fragmentation (low s_{eff} values) (Fig 3a). Contrary latitudes around 52°N, e.g., the latitudes of Amsterdam or Berlin, show the highest levels of fragmentation. Latitudes north of 52°N are linked with a sharp decrease in s_{eff} values and latitudes south of 52°N are linked with a moderate decrease in s_{eff} values (Fig 3b), as described by a third order polynomial regression (Tab 1). Longitudes around 6°E, e.g., the longitude of the city of Luxembourg, show on average the highest levels of fragmentation in N2k surroundings. Longitudes further west or east are linked with lower s_{eff} values (Fig 3c).

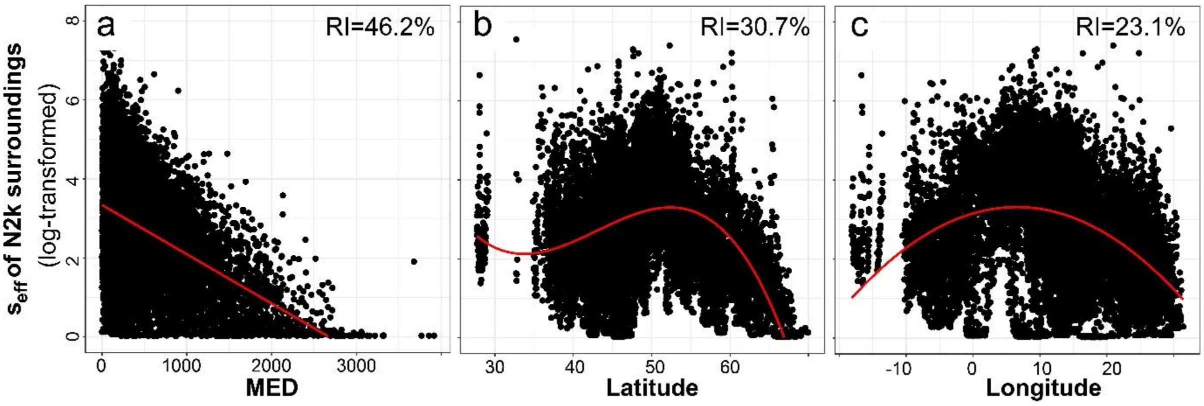


Fig 3. Relative importance of geographical variables in explaining fragmentation (s_{eff}) in Natura 2000 protected area surroundings. Maximal elevational difference (MED) (a), longitude (b) and latitude (c) explain 48.5% of the variance observed in fragmentation (s_{eff}) of Natura 2000 protected area surroundings. While increasing MED (a) is linked to a significant decrease in s_{eff}, MED has a relative importance (RI) of 46.2% in the overall model (compare Tab 1). Latitude has a RI of 30.7% and latitudes between 50°N and 55°N are linked with the highest values in s_{eff} while lower or higher latitudes are linked with a decrease in s_{eff} (b). Longitude has an RI of 23.1% and longitudes around 6°E are linked with the highest values in s_{eff} while lower or higher longitudes are linked with a decrease in s_{eff} (c). Graphic generated in R v. 4.1.2 with the packages ggplot2 (Wickham 2016).

The best-fit model for predicting fragmentation (s_{eff}) of N2k surroundings based on anthropogenic variables within the EU included population density (PD) and gross-domestic product per capita (GDP) (third-order polynomial) (R^2=0.563, p<0.001) (Tab 2). The response variable was log-transformed to meet normality requirements and both explanatory variables were log-transformed as well to fulfil linear regression assumptions of homoscedasticity.

Tab 2. Linear model results of anthropogenic characteristics as predictors of fragmentation in Natura 2000 protected area surroundings. Mean fragmentation (s_{eff}) in Natura 2000 protected area surroundings functioned as response variable while population density (PD) and gross domestic product per capita (GDP) functioned as explanatory variables for 27 countries in the EU. The best fit model was determined by backward selection and based on lowest AIC value as well as the highest R^2 value. Population density (PD) had a significant effect on fragmentation (s_{eff}) in N2k surroundings (p<0.001) and showed a relative importance (RI) of 82.5% towards the overall model. Gross domestic product per capita (GDP) had no significant effect on fragmentation (s_{eff}) in N2k surroundings (p=0.099) but improved the model fit. GDP plays a minor role in the overall model with a relative importance (RI) of 17.5%.

	Estimate	**Std. Error**	**t-value**	**p-value**	**RI (%)**
s_{eff} of N2k surroundings (log-transformed)					
Intercept	- 0.316	0.469	- 0.673	0.507	
PD (log-transf.)	0.174	0.034	5.099	<0.001 ***	82.5
GDP (log-transf.)	0.083	0.048	1.713	0.099	17.5

Our One-way ANOVA and Tukey post-hoc test showed significant differences in the degree of fragmentation (s_{eff}) represented in N2k PA surroundings for the different European Countries (Fig 4) confirming our original hypothesis. Romania (RO) and Sweden (SE) are the countries with the lowest levels of fragmentation in N2k PA surroundings, followed by Finland (FI), Bulgaria (BG), and Slovakia (SK) (Fig 4). The highest average degree of fragmentation in N2k surroundings is found in Luxembourg (LU), Belgium (BE), and Malta (MT). A full list of country abbreviations and Tukey post-hoc HSD test results is provided in Tab S1.

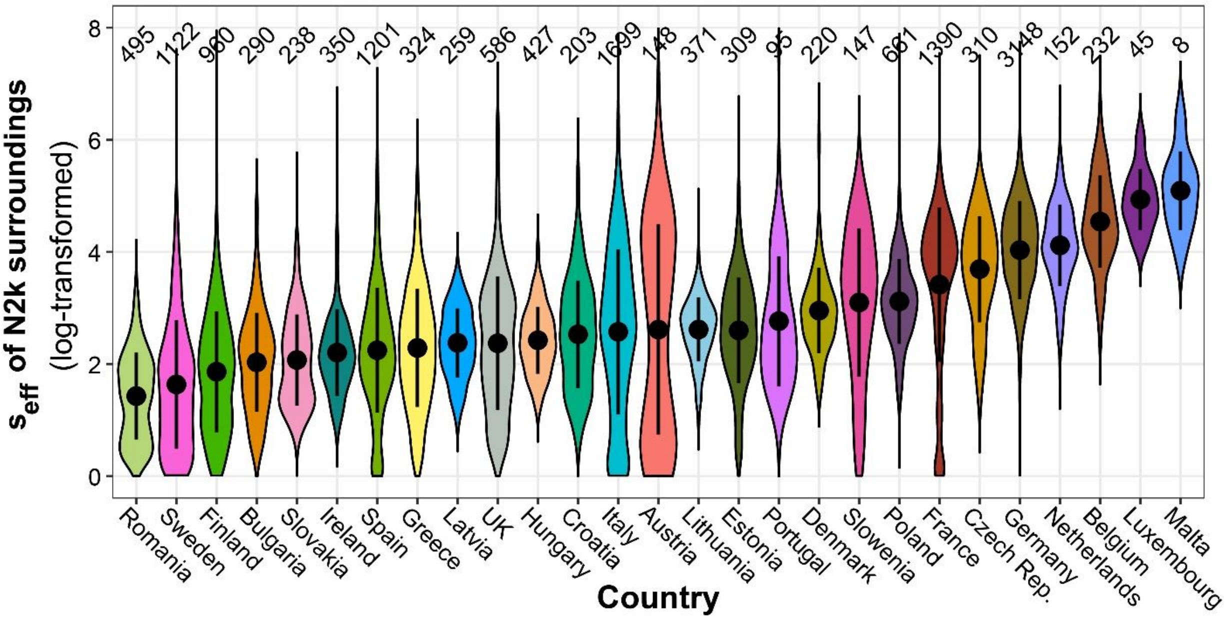


Fig 3. Differences in fragmentation of Natura 2000 protected area surroundings among European countries. We analyzed the fragmentation (s_{eff}) of Natura 2000 protected area surroundings of 15390 terrestrial Natura 2000 protected areas for 27 European countries. Raw values for mean, standard deviation, and median s_{eff} of Natura 2000 protected area surroundings, and Tukey HSD post-hoc test results on significant differences among countries are reported in Tab S1. 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 N2k PAs surroundings analyzed within each country. Graphic generated in R v. 4.1.2 (R Core Team 2021) with the packages ggplot2 (Wickham 2016).

In Fig 4 we provide information on country level differences in the degree of fragmentation in N2k surroundings, a possible proxy for N2k expansion potential of the different EU countries. In Fig 5 we present information on countries expenditure for nature conservation in relation to the N2k network. The value 'Preserved N2k area per one million Euros (km^2)' indicates how much PA area is preserved and managed for one million Euros spent on preservation of biodiversity and landscape on a national level. We found striking difference between 'N2k area per one million Euros' for the different countries (Fig 5).

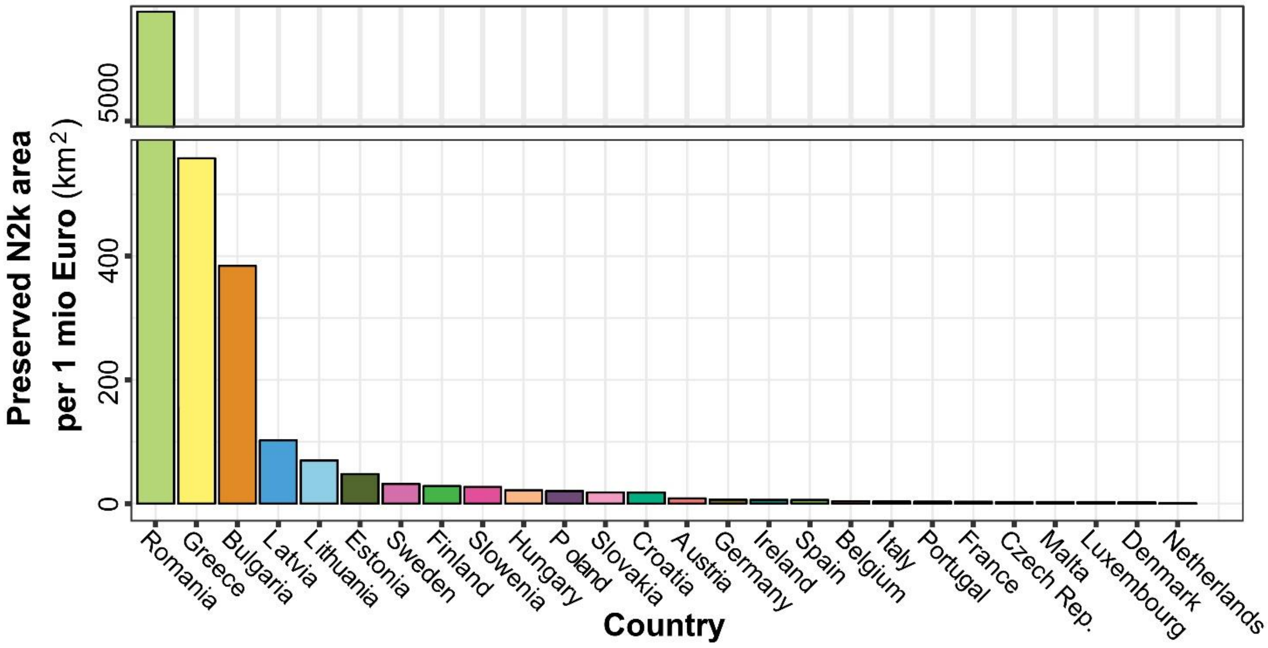


Fig 4. Countries expenditure for nature conservation in relation to the Natura 2000 network. The value 'N2k area per one million Euros (km^2)' was calculated by dividing the area of all Natura 2000 protected areas per country by the government expenditure for 'protection of biodiversity and landscape' for each country. Values were taken from the year 2020 and include all protected areas part of the Natura 2000 network. Graphic generated in R v. 4.1.2 (R Core Team 2021) with the packages ggplot2 (Wickham 2016) and ggbreak (Xu et al. 2021).

For one million Euros spent on 'protection of biodiversity and landscape' the Netherlands (NL) only preserve and manage only 0.6 km^2, Denmark (DK) 2.0 km^2 and Luxembourg (LU) 2.5 km^2 of N2k PA area per one million Euros. Contrary, countries located further east in Europe such as Latvia (LV) 102.5 km^2, Bulgaria (BG) 384.5 km^2, or Greece (GR) 558.2 km^2 preserve and manage much more PA area relative to the same amount of money. By far the most N2k PA area per one million Euro is preserved and managed in Romania (RO) with 5167.6 km^2. This demonstrates huge differences in money available for the management and preservation of N2k PAs in the EU.

Discussion

Anthropogenic fragmentation around existing N2k PAs varies tremendously among the national territories that comprise the EU. If protecting low fragmented lands while expanding currently existing N2k PAs is widely accepted as an efficacious strategy to meet the EU Biodiversity Strategy for 2030, there remains the question of determining which N2k sites provide the most conservation value relative to the resource investments necessary for expansion. Most of Central Europe, i.e., latitudes between 40°N and 60°N and longitudes between -5°W and 15°E exhibit generally high degrees of fragmentation and are arguably less well suited for PA expansion if our focus is on safeguarding intact and connected habitats. By contrast, there are still relatively low fragmented lands to be found in Europe, especially in remote and mountainous regions in the north and the east of the continent. Many of these regions currently remain excluded from the N2k network. While the degree of fragmentation in N2k surroundings is highly correlated with national population density, economic wealth, as measured by GDP per capita, is less important and has no significant effect on degree of fragmentation in N2k surroundings. As an example, Ireland and Bulgaria, which have very similar population densities, are not significantly different in their degree of fragmentation in N2k surroundings, despite vastly differing GDP per capita.

From an ecological standpoint it might be wise to approach nature conservation decisions from a larger scale –e.g., a global or continental scale –as the EU Biodiversity Strategy for 2030 attempts to do. However, the political structure of the EU dictates that most real-world conservation decisions are implemented on a national level and subject to the pragmatic and multifarious decision-making processes of democratic governments. One consequence of this inconsistency between continental-scale goals and national-scale implementation is the tremendous difference in government spending on N2k PAs. For example, compared to the Netherlands, Romania preserves and manages over 8000 times more N2k land per one million Euro spent on nature preservation. This reflects a vast incongruity in resource availability and spending practices for nature conservation among EU countries. Our study addresses both, available finances for nature conservation and guidance for high ecological quality in possible PA additions. Hence, these results suggest viable pathway for achieving the EU Biodiversity Strategy for 2030 by specifying areas where PA expansion maximizes both cost-effectiveness and ecological quality.

In this study we develop guidelines for the expansion of current N2k PAs into low fragmented surroundings. While we argue that an expansion in PA area has the benefit of fostering movement of species, populations, and individuals (Saura et al. 2018) and therefore helps maintain important ecological processes in the face of climate change (Loarie et al. 2009, Venter et al. 2014, Watson et al. 2014), it is important to note that small PAs are still a crucial component in continent-wide conservation efforts. They can be vital habitats for small-range species, contribute to landscape complementation, and increase overall habitat diversity (Fahrig 2017, Wintle et al. 2019). In addition, other conservation tools enhancing connectivity between PAs, such as establishing PAs as stepping-stones, building corridors or wildlife crossing structures have been proven to enhance species movement and dispersal (Scharf et al. 2018, Myslayek et al. 2020, Rocha et al. 2021) and markedly contribute to biodiversity conservation under many climate change scenarios (Heller and Zavaleta 2009). Therefore, research on where to expand existing PAs should be complemented by research on how to best connect PAs (Stewart et al. 2019). Taking this dual approach as a baseline will allow policy makers to formulate guidelines that can fulfilling conservation targets such as the EU's Biodiversity Strategy for 2030.

The results of this study demonstrate that there are still considerable amounts of low-fragmented area surrounding current PAs, especially in Northern and Eastern Europe as well as in selected parts of the Mediterranean region. However, these low fragmented surroundings are not part of the N2k network as it is currently constituted.

Anthropogenic landscape fragmentation is a good indicator of the intensity of human activities and disturbance (Hawbaker et al. 2006, Laurance et al. 2009) and low fragmented lands have been shown to exhibit lower rates of land use change, habitat degradation, and biodiversity loss (Trombulak and Frissell 2000, Hawbaker et al. 2006). As such, we concur with Selva et al. (2011) that a prioritization of low fragmented, roadless and low-traffic areas in Europe – historically a highly developed, fragmented, and crowded continent (Pullin et al. 2009) –should be emphasized in future conservation decisions.

Based on these results, we argue that the expansion of N2k PAs into low fragmented surroundings has a high potential to improve biodiversity conservation into the foreseeable future by addressing the synergistic impacts of landscape fragmentation and anthropogenic climate change. Shifting climate patterns force species to move in search of suitable climatic conditions but habitat loss and fragmentation –prevent this means of survival. The synergy of anthropogenic climate change and anthropogenic fragmentation is therefore akin to relocating suitable habitats while locking biota in place. To combat this destructive trajectory, our study suggests a rational course of action is to follow a landscape-scale conservation approach, bearing landscape patterns such as habitat amount, connectivity, and fragmentation in mind to reach sustainable conservation goals (Redford et al. 2003, Lindenmayer et al. 2008). This contrasts a patch-scale conservation approach which focusses on single patch content and quality (Lindenmayer et al. 2008) or single flagship species part of these patches (Redford et al. 2003). Landscape-scale conservation approaches that center around the preservation of large-scale patterns and ecological processes, can potentially address the needs of a variety of targets across different spatial scales (Redford et al. 2003) especially considering uncertainty created through climate change.

However, we recognize that this landscape-focused approach does not consider more granular information on species, communities, or populations. Beyond mobility and habitat availability, numerous mechanisms play key roles in maintaining biodiversity under climate change. These include phenomena such as dispersal limitations, demographic shifts, species interactions, and evolution (Urban 2015, Littlefield et al. 2017). In addition to mountain-top extinction or low-elevation bottlenecks, physical structures, such as insurmountable environmental barriers, can further prevent successful climate tracking even in anthropogenically low fragmented lands (Littlefield et al. 2017, Reside et al. 2018). To formulate effective conservation policy and ensure new or expanded PA designations are of high ecological quality, the results from this study should be paired with biological data on species movement such as biologging data, species diversity data such as data on biodiversity hotspots, and up-to-date climate change models that predict locations of climate refugia.

Because the EU operates through national implementation of transnational policy agenda, fiscal constraints faced by constituent national governments must be considered in formulating actionable conservation guidelines to achieve the EU Biodiversity Strategy for 2030 targets. Other things being equal low-cost approaches that can achieve comparable conservation goals are more likely to be successfully implemented at scale. If we accept the existence of these political constraints, the results of our study should be welcome news to policymakers and managers. Our results show that low-fragmented areas surrounding current N2k PAs mostly occur in European areas where the per-km cost of biodiversity and landscape preservation is lowest. The implication of this correlation is that future expansion of PAs of the high ecological quality, measured by landscape fragmentation, can be done relatively inexpensively.

The most striking example is Romania, which exhibits the lowest levels of fragmentation in its current N2k PA surroundings and protects the most N2k area per-Euro spent. Similar results can be found in Bulgaria, Greece, and the Baltic countries. Contrary Malta, the Netherlands and Luxembourg exhibits the highest levels of fragmentation in its current N2k PA surroundings while protecting the least N2k area per-Euro spent (Fig 3 and Fig 4). Importantly, the factors behind these low expenditures could undermine their future potential as sites of expanded protection. Low costs of labour, land and low population densities in these countries are likely the main drivers of these apparent efficiencies in the state’s capacity to protect large swaths of land for relatively little money. As these economies grow labour and land costs are likely to increase, thereby diminishing the cost-effectiveness of nature conservation practices

(Pullin et al. 2009, Hartel et al. 2014). The obvious implication of these growth projections is to conserve as much land in these areas as possible while it remains inexpensive to do so. However, this approach presents a moral quandary. It is clearly exploitative to take advantage of higher poverty rates in some countries by removing large swaths of land from potential economic exploitation – and thereby diminishing potential economic growth in the future – simply on the grounds that wealthier countries have failed to properly husband their low fragmented lands in the past. Another possible reason for the apparent fiscal efficiency with which these countries have protected land is that the land is only nominally protected in the first place. Low expenditures on nature conservation are likely an indicator for comparatively little management, restoration, or enforcement of conservation law leading to shortfalls in biodiversity conservation overall (Craigie and Pressey 2022). The supranational institutions of the EU currently have few, if any, mechanisms to enforce fidelity to the stated goals of biodiversity conservation at the national level (EC 2020). Therefore, it is essential that any future N2k expansions that rely on these low-cost countries to meet EU targets are done with financial support as well as substantial political support from the residents of those countries. This may mean incentivizing these expansions with additional external funding, supporting efforts of citizen-led conservation, and considering ways of compensating these lower-income countries for the future loss of economically exploitable land.

The results of this study show that some of the least- well funded national PA networks also hold the highest potential for expanding current N2k PAs into low fragmented lands. In this sense our results could be used to formulate pragmatic conservation decisions, while also ensuring high ecological quality of PA additions in the face of climate change.

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Data Accessibility

Country-level data used in this study is available in the Supplementary material Data S1

Supplementary Materials

The following materials are available as part of the supplementary material

Tab S1. Fragmentation of N2k PA surroundings of European countries

Data S1. Country-level data on N2k PAs, population density, gross domestic product per capita, and expenditure by the government for the “protection of biodiversity and landscape”

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Tab S1. Fragmentation of N2k PA surroundings of European countries. To provide information on the potential for PA expansion into unfragmented surroundings for each EU country (including the UK) we calculated the mean, standard deviation (SD), and median s_{eff} values per country. Countries are ordered from lowest to highest mean s_{eff} value. Significant differences among countries were calculated via Tukey post-hoc test.

Country	Mean s_{eff} of N2k surroundings	SD for s_{eff} of N2k surroundings	Median s_{eff} of N2k surroundings	Significant difference
Romania	1.43	0.77	1.46	m
Sweden	1.64	1.15	1.53	m
Finland	1.87	1.10	1.83	l
Bulgaria	2.03	0.88	2.08	kl
Slovakia	2.07	0.81	2.03	jkl
Ireland	2.23	0.92	2.14	hijk
Spain	2.25	1.11	2.21	ijk
Greece	2.29	1.05	2.22	hijk
Latvia	2.38	0.62	2.39	ghij
United Kingdom	2.41	1.33	2.34	ghi
Hungary	2.42	0.59	2.40	ghi
Croatia	2.53	0.96	2.49	ghi
Italy	2.58	1.48	2.64	g
Austria	2.61	1.88	2.92	fgh
Lithuania	2.62	0.57	2.69	fg
Estonia	2.62	0.99	2.61	fg
Portugal	2.77	1.16	2.57	efg
Denmark	2.95	0.76	2.91	ef
Slovenia	3.1	1.32	3.29	de
Poland	3.12	0.76	3.11	e
France	3.42	1.38	3.82	d
Czech Rep.	3.69	0.95	3.79	c
Germany	4.03	0.88	4.09	b
Netherlands	4.12	0.73	4.12	b
Belgium	4.54	0.82	4.47	a
Luxembourg	4.94	0.54	4.86	a
Malta	5.09	0.69	5.14	abc

Data S1. Country-level data on Natura 2000 protected areas, population density, gross domestic product per capita, and expenditure by the government for the "protection of biodiversity and landscape".

N2k area and number per country was determined in ArcGIS using Natura 2000 spatial data (EEA 2020) including all PAs that are part of the N2k network in the year 2020. Data on population density (PD) and per capita gross domestic product (GDP) per country is based on the year 2014 to match the date of record of the fragmentation data used in this study. Data on PD and GDP was obtained from publicly available data provided by the European Union (Eurostat 2021a, Eurostat 2021b). Environmental protection expenditure (EPE) per country was assessed using the European statistic for government expenditure (Eurostat 2022). Herby only values for expenditure on “protection of biodiversity and landscape” for the year 2020 have been included. By dividing the area of N2k PAs by the expenditure spent on the protection of biodiversity and landscape, we derived a value called ‘N2k area per one million Euros (km^2)’. All spatial data were processed using ESRI ArcGIS 10.6.1 in ETRS 89 Lambert Azimuthal Equal Area (LAEA) Projection.

Country	**N2k Area 2020 (km^2)**	**Number of N2k PAs 2020**	**PD 2014 (persons per km^2)**	**GDP per capita 2014 (Euros)**	**EPE 2020 (mio. Euros)**	**N2k Area per 1 mio. EPE**
Romania	2070.69	495	86.6	7040	0.4	5176.725
Sweden	5015.11	1122	23.8	41180	157.3	31.88245391
Finland	3910.43	960	18	34390	138	28.33644928
Bulgaria	1230.4	290	66.3	5470	3.2	384.5
Slovakia	1143.52	238	110.5	13600	63.3	18.06508689
Ireland	1680.34	350	67.8	40010	278.9	6.024883471
Spain	5948.09	1201	92.5	22210	1013	5.871757157
Greece	1674.58	324	82.5	16830	3	558.1933333
Latvia	840.19	259	32	11290	8.2	102.4621951
United Kingdom	NA	NA	266.4	31290	NA	NA
Hungary	1724.23	427	108.1	10800	80.3	21.47235367
Croatia	1520.32	203	74.9	10430	84.5	17.99195266
Italy	7845.72	1699	206	25620	2266	3.462365402
Austria	684.33	148	103.7	36130	81	8.448518519
Lithuania	1251.01	371	46.8	10260	17.9	69.88882682
Estonia	1160.99	309	30.3	12960	24.3	47.77736626
Portugal	556.81	95	112.8	16260	180.6	3.083111849
Denmark	1173.39	220	131.5	44890	586.1	2.00203037
Slovenia	626.92	147	102.4	17620	23.2	27.02241379
Poland	2896.7	661	123.7	10440	143.2	20.22835196
France	5997.98	1390	104.6	31320	1982	3.026226034
Czech Rep.	1372.79	310	136.3	15480	500.2	2.744482207
Germany	12547.41	3148	226.5	33920	1941	6.464404946
Netherlands	685.48	152	500.9	38580	1089	0.629458219
Belgium	1139.96	232	369.6	33870	293.5	3.884020443
Luxembourg	174.64	45	215.1	82590	68.9	2.534687954
Malta	98.43	8	1375.2	18610	36.2	2.719060773

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RESEARCH ARTICLE

Landscape fragmentation of the Natura 2000 network and its surrounding areas

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Abstract

Habitat loss from anthropogenic development has led to an unprecedented decline in global biodiversity. Protected areas (PAs) exist to counteract this degradation of ecosystems. In the European Union, the Natura 2000 (N2k) network is the basis for continent-wide conservation efforts. N2k is the world's largest coordinated network of protected areas. However, threats to ecosystems do not stop at the borders of PAs. As measured by a landscape fragmentation metric, anthropogenic development can affect the interiors of PAs. To ensure the long-term viability of the N2k network of PAs, this paper attempts to quantify the degree to which N2k sites are insulated from development pressures. We use a comprehensive dataset of effective mesh density (*seff*) to measure aggregate fragmentation inside and within a 5 km buffer surrounding N2k sites. Our results show a strong correlation ($R^2 = 0.78$) between fragmentation (*seff*) within and around N2k sites. This result applies to all biogeographical regions in Europe. Only a narrow majority (58.5%) of N2k sites are less fragmented than their surroundings. Remote and mountainous regions in northern Europe, the Alps, parts of Spain, and parts of eastern Europe show the lowest levels of fragmentation. These regions tend to hold the largest N2k sites as measured by area. In contrast, central and western Europe show the highest fragmentation levels within and around N2k sites. 24.5% of all N2k sites are classified as highly to very-highly fragmented. N2k PA age since initial protection does not correlate with the difference in exterior and interior fragmentation of N2k PAs. These results indicate that PAs in Europe are not sheltered from anthropogenic pressures leading to fragmentation. Hence, we argue that there is a high potential for improving PA efficacy by taking pre-emptive action against encroaching anthropogenic fragmentation and by targeting scarce financial resources where fragmentation pressures can be mitigated through enforced construction bans inside PAs.

Introduction

Habitat loss from anthropogenic development is the primary driver of species extinctions worldwide, resulting in a rapid decline in global biodiversity [1-4]. As cities grow and transportation infrastructure expands, ecosystems are degraded, biodiversity is lost, and critical ecological functions are impaired [5-7]. To some degree, landscapes are fragmented by natural barriers. However, unlike most natural barriers, rapid growth of man-made infrastructure subdivides habitats into artificially small and isolated patches. This development has been illustrated in the first figure of the seminal book *Theory of Island Biogeography* [8], one of the foundational texts of modern nature conservation and planning. Nevertheless, there is still a deficit in the scientific understanding of the effects of fragmentation on biodiversity. Large and unfragmented stretches of natural land are highly desirable for habitat conservation. This should not diminish the importance of smaller, already fragmented habitats which are likewise essential for biodiversity protection [9,10]. Yet increasingly small and isolated habitat patches are often ill-suited to achieve certain conservation goals, such as providing opportunities for species movement as an adaptive strategy in response to climate change [11]. Therefore, to counteract the adverse effects of rapid infrastructure development, protected areas (PAs) have been designated to protect and conserve threatened species, habitats, and ecosystems [12-14].

In 1992 the European Union established a special protected area network, Natura 2000 (N2k), which covers 18% of the EU's terrestrial and 9.5% of its marine area [15]. This PA network includes Special Protection Areas (SPAs) (Birds Directive) and Special Areas of Conservation (SACs) (Habitats Directive). Together, they are considered to be among the most substantive international strategies for nature protection [16]. This network functions as a vital tool for the EU that is supposed to ensure the long-term persistence of Europe's most threatened species and habitats [17].

The N2k network also meets Aichi Target 11, according to which every UN member nation except the United States agreed to protect 17% of terrestrial surface area and 10% of coastal and marine areas by 2020 (Target 11 of Aichi Biodiversity Targets) [18]. As part of the European strategy for green infrastructure, the N2k network further aims to improve connectivity between protected areas [19]. Overall, the establishment of the N2k network has increased both PA coverage and interconnectivity of PAs in the European Union [20]. To maximize spatial coverage of protected areas, policy makers frequently establish PAs within remote and mountainous regions where economic development pressures are typically less pronounced [21]. However, this emphasis on spatial coverage does not in itself ensure habitat quality, regulation enforcement, or overall effectiveness of PAs in biodiversity protection [21,22]. Notably, there currently exists no EU-wide regulation strictly preventing new infrastructure from being built inside N2k PAs. Prevention of new infrastructure within N2k PAs is thus left to regulation and enforcement at the local and national level [23].

Within the borders of PAs, ecosystems are threatened due to increasing human pressure [20,24]. The quality of PA surroundings has a strong influence on ecosystems within PAs [25-27]. Genetic diversity, for example, is severely impacted when dispersal of species from PAs is hampered by surrounding fragmentation [28,29]. Conversely, healthy ecosystems in the vicinity of a PA may reduce isolation and contribute to population size and species persistence within the PA [28,30,31]. Research has shown that anthropogenic disturbances have steadily increased within PAs in the last decades, and smaller PAs are especially at risk of losing their effectiveness in conserving biodiversity in the face of ongoing infrastructure development [9,32,33].

To this day, the relationship between the quality of the surrounding matrix and the quality of habitat within the boundaries of PAs is a neglected field of research. A few studies of tropical ecosystems have shown that pressures stemming from the surrounding matrices of PAs are evident within PAs [24,34]. It is still unclear to what extent these findings can be transferred to extratropical regions. As the historical cradle of industrialization and transportation infrastructure, Europe has one of the world's heaviest human footprints. High anthropogenic pressure faces ecosystems across the continent [33,34,35]. The current dearth of broad-scale modelling approaches to analyse anthropogenic pressures in and around European PAs severely limits our understanding of effective biodiversity conservation on a continental scale [36].

In this study, we investigate anthropogenic fragmentation inside and around N2k sites across the EU. We define fragmentation as a landscape-scale process that includes (a) reduction in total habitat area, (b) increase in the number of habitat patches, and (c) decrease in sizes of habitat patches. We do not consider the degree of patch isolation. Thus, we measure habitat loss and fragmentation as a unified phenomenon rather than measuring fragmentation per se [37]. This is an important distinction because habitat loss is known to be a primary threat to biodiversity while the effects of landscape configuration, such as fragmentation per se, are debated [10,38-40]. The most common view among ecologists is that both habitat amount and fragmentation per se result in negative consequences for biodiversity [7,38,41]. Fahrig [42] challenges this view by proposing the habitat amount hypothesis (HAH). The HAH predicts that variation in species richness among sampling sites can be explained by the amount of habitat in the local landscape around the sites, while the spatial configuration of habitat (e.g., fragmentation per se) makes little difference. This interpretation of the HAH has both defenders and critics [40-44]. In a review of 118 studies reporting significant ecological responses to fragmentation per se, Fahrig [45] shows that 70% of ecological responses to fragmentation per se are non-significant. Among the 381 significant ecological responses, 76% showed positive effects towards fragmentation per se, such as increased species abundance and richness. However, this study has been challenged for reliance on a small sample size of species and landscapes under study. Likewise, the study's overall implications for conservation are controversial because they potentially lead to a skewed concept of neutral or positive effects of fragmentation per se on biodiversity [38,44]. Unlike the contention surrounding the effects of fragmentation per se, habitat loss and fragmentation as one unified phenomenon, as measured in this study, is widely accepted as a major threat to biodiversity [41,44].

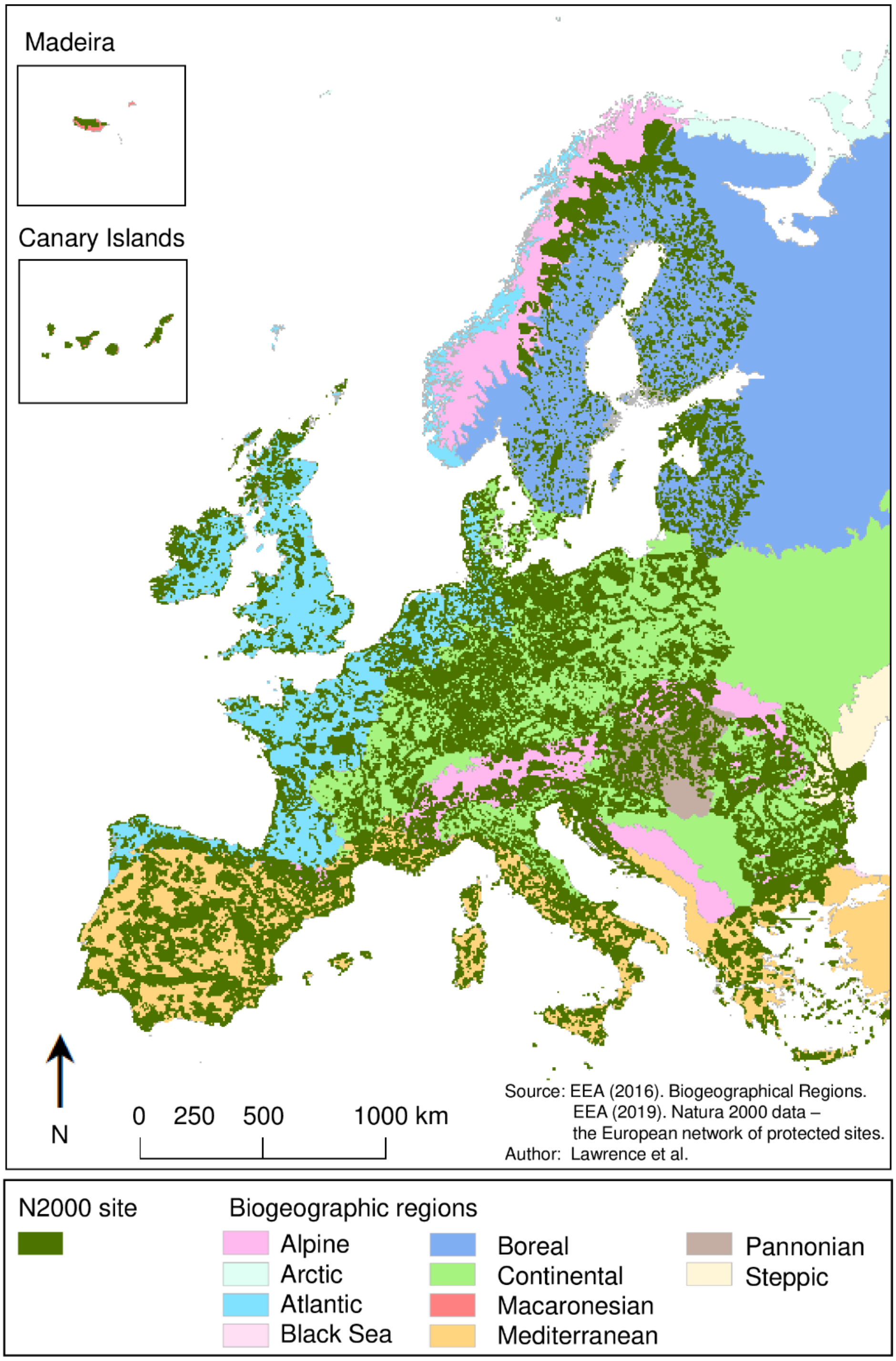
Preliminary analysis by the EEA [46], investigating habitat loss and fragmentation as one unified phenomenon, suggest that N2k sites are, in general, less fragmented relative to their surroundings, and fragmentation varies among biogeographical regions. However, the EEA did not publish any quantitative data in support of this conclusion. Thus, conservation strategies based on these findings are missing critical information needed to address anthropogenic pressures in and around PAs.

This study seeks to investigate the relationship between fragmentation around N2k sites and fragmentation within N2k sites. We hypothesized that A) N2k sites are less fragmented than their surroundings; B) the least fragmented sites are located in remote and mountainous regions; and C) the degree of fragmentation within N2k sites correlates positively with the degree of fragmentation in the sites' surroundings for all biogeographical regions. Further, we expected protected status to curb additional fragmentation within PAs while development continues relatively unabated in surrounding areas. Therefore, we hypothesized that (D) the difference between exterior and interior fragmentation of N2k sites has increased with time since N2ksites first gained protected status, from here on referred to as “age“.

Methods

Study area

This study quantifies landscape fragmentation within and around the European N2k network, the world's largest coordinated network of PAs [15]. The N2k network spans 27 countries and nine different biogeographical regions (Fig 1).



Source: EEA (2016). Biogeographical Regions.
EEA (2019). Natura 2000 data – the European network of protected sites.
Author: Lawrence et al.

Fig 1. The European N2k network across nine biogeographical regions. Dark green polygons represent terrestrial N2k sites analysed in this study [47]. Map generated in ArcGIS 10.6.1 (http://www.esri.com/software/arcgis/ arcgis-for-desktop).

Our analysis covers a total of 15390 terrestrial PAs that range in size from 1 km² to 5556 km² (Table 1) and range between 2 and 37 years in age. The N2k network is a heterogenous network of PAs that shows considerable differences in the distribution of PA numbers, sizes, ages, and relative area-coverage among the biogeographical regions (Table 1).

Table 1. The N2k network across biogeographical regions of the EU. The distribution of N2k PAs in terms of number, size, age, and relative coverage by number and area varies considerably among biogeographical regions. The Alpine and the Black Sea regions host the largest N2k PAs by area, while the Continental region hosts the highest number of N2k PAs. "Age of N2k PAs" refers to the time since PAs first gained protected status. "Relative number of N2k PAs" refers to the number of N2k PAs within a biogeographical region relative to the total number of N2k PAs. "Relative area of N2k PAs" refers to the total area covered by N2k PAs within a biogeographical region relative to the total area covered by all N2k PAs.

Biogeo-graphical region	Number of N2k PAs	Mean size of N2k PAs (km²)	Min-max. size of N2k PAs (km²)	Mean age of N2k PAs (years)	Relative number of N2k PAs	Relative area of N2k PAs
Alpine	1243	144	1-5556	19	8.1 %	22.5 %
Atlantic	2350	36	1-3465	22	15.3 %	10.8 %
Black Sea	48	209	1-4344	14	0.3 %	1.2 %
Boreal	2777	20	1-3095	19	18.0 %	7.1 %
Continental	5665	38	1-2915	18	36.8 %	26.9 %
Macaronesian	130	29	1- 404	25	0.8 %	0.5 %
Mediterranean	2539	87	1-2186	22	16.5 %	27.6 %
Pannonian	568	41	1-1102	15	3.7 %	2.9 %
Steppic	69	66	1- 577	12	0.4 %	0.6 %
Total	15390	52	1-5556	20	100 %	100 %

Effective Mesh Size and Effective Mesh Density

In this study, we measured fragmentation by calculating effective mesh density, a landscape-scale metric developed by Jaeger [48]. Effective mesh density represents the degree of fragmentation in a landscape [48,49]. Jaeger et al. [50] defined a series of 'fragmentation geometries' (FGs) which include different types of barriers. This study focuses on major and medium anthropogenic constructions –such as roads, railways, and buildings. This coincides with fragmentation geometry A2 (FG-A2) described in more detail by Jaeger et al. [51].

To quantify fragmentation within a landscape, Jaeger [48] developed the landscape metric effective mesh size (*meff*), which is based on the probability that two points chosen randomly within a defined area will be connected (i.e., located in the same patch). This can be interpreted as the probability that two animals can find each other inside the defined area without crossing a barrier. Multiplying this probability by the total area of the area under study, it is converted into the size of an area: the effective mesh size. Hence, *meff* can be interpreted as the expected size of the area that is accessible for an individual animal from a randomly chosen point inside the defined area without encountering a barrier [48,52].

As the number of fragmentation barriers increases, the mesh size diminishes, and therefore *meff* decreases in its value. If anthropogenic barriers cover a landscape entirely, *meff* has a value of 0 km². Originally, *meff* was calculated using the cutting-out (CUT) procedure. However, this method is affected by the boundary problem because the boundaries of the reporting units, e.g., the borders of raster cells, are considered additional barriers. To overcome this limitation, a new method called the "cross-boundary connections" (CBC) procedure attributes the connections between two points located in different reporting units to both reporting units. The

CBC procedure is independent of the size and administrative boundaries of reporting units [52]. In this study, we used the CBC procedure.

Within a defined landscape – e.g., 1 km² grid cell – it is possible to calculate effective mesh density (*seff*), by taking the inverse of effective mesh size (*meff*) (Eq 1) [51].

$$seff = \frac{1}{meff} \tag{1}$$

The value of *meff* informs about the size of uninterrupted spaces and *seff* about the density of these uninterrupted spaces. Translated into an ecological context, the phenomena measured by effective mesh size and density impact the mobility of animals within a given range. Thus, this concept directly addresses landscape fragmentation and makes it possible to quantify the reduction in landscape connectivity [51].

Data collection

In this study, we used a raster dataset showing the state of fragmentation in 2012/2014 for the European Union (Table 2). This dataset is based on 2012 Corine Land Cover (CLC) data and 2014 Teleatlas data and available on demand from the EEA [53]. Each raster cell has a resolution of 1 km^2 and contains a value representing effective mesh size (*meff*) calculated via CBC procedure [52]. The administrative units refer to the 2016 Nomenclature of Territorial Units for Statistics (*Nomenclature des unités territoriales statistiques*, NUTS), which divides each EU Member State into three hierarchical regions. The data set comprises all countries at a 1:1 million scale. We used NUTS level 3 to investigate landscape fragmentation across the EU. Data on N2k sites encompass the Special Areas of Conservation (SAC) and the Special Protection Areas (SPAs) of the European Union, including the UK. In addition, each N2k site has information listed on its location within Europe's biogeographical regions. To determine the age of N2k PAs, we used information provided by the World Database of Protected Areas (WDPA) (Table 2). From the WDPA database, only information from entries containing geographical data and reporting a PA's protection status as "designated" was used.

Table 2: Processed Data. In this study, we used open-access data to derive information on fragmentation within and around Natura 2000 (N2k) PAs, N2k PA locations within one of nine biogeographical regions, their locations within specific administrative units, and PA age.

Dataset	Information	Resolution	Date	Source	Open access
Fragmentation	Effective mesh size (*meff*) and density (*seff*)	1 km^2	2012/ 2014	EEA [53]	Yes, on demand
Administrative units	NUT-3 regions	Vector data	2016	ESTAT [54]	Yes
Natura 2000	PA borders, PA size, biogeographical region	Vector data	2018	EEA [47]	Yes
WDPA	PA age	Vector data	2019	UNEP [55]	Yes

Spatial data processing with GIS

All spatial data were processed using ESRI ArcGIS 10.6.1 and QGIS 2.18.25 in ETRS 89 Lambert Azimuthal Equal Area (LAEA) Projection. To calculate *meff* values for each N2k site, we first filtered the N2k site dataset to ensure each N2k covers at least one cell center of the *meff* raster dataset. To do so, we rasterized all N2k sites via cell center coverage using the 1-km^2-resolution of the original *meff* dataset. This method entailed excluding N2k sites which did not cover at least one raster cell center. These were particularly small and elongated N2k sites. We also reduced our analysis to terrestrial PAs by excluding marine N2k sites. These exclusions resulted in a dataset comprised of 15390 N2k sites of the original 27845 N2k sites (55.3%).

We created a buffer zone of 5 km around each of these N2k sites. We further applied the same rasterization process to these buffer zones as to the N2k sites using cell center coverage based on the 1-km^2-resolution of the original *meff* dataset. This approach has the advantage that each cell of the *meff* dataset is assigned only once and never to both a N2k site and a buffer. For fine-scale analyses focusing on the effects of PA surroundings on specific species, buffer size is often determined by migration or dispersal distances or habitat size requirements of those species [56]. However, as Holland et al. [57] have shown, the most appropriate spatial scale to analyse species' responses to environmental variables varies tremendously between species even within the same family. As this is a landscape-focused study, the chosen buffer size does not consider species-specific indicators and instead is homogenous for all N2k sites. Still, it is nearly impossible to determine a uniform buffer size best suited to analyse anthropogenic fragmentation around a PA relative to its interior. The most appropriate buffering distance varies according to location and the conservation focus of each PA. In this study, we consider a 5 km buffer around each N2k site following previous studies investigating landscape factors such as surrounding agriculture [58] and surrounding land cover changes [59]. As in those studies, our focus is on surrounding areas close to N2k sites, rather than comparing them against distant areas which presumably have a less immediate influence on ecosystems inside PAs.

To calculate effective mesh size (*meff*) and effective mesh density (*seff*) for each N2k site individually, we first summed up the *meff* values of all grid cells (1-*n*), the cell centers of which fell within the N2k site. Since *meff* is area-proportionately additive [52], we calculated an individual *meff* value for each N2k site by dividing the sum of *meff* values within the N2k site by *n*, the total number of cells within the N2k site (Eq 2).

$$meff = \frac{\sum_{i=1}^{n} meff_i}{n} \tag{2}$$

Taking the inverse of the new site-specific *meff* value resulted in one site specific *seff* value (Eq 1). *seff* values represent the number of meshes per km^2. In order to follow EEA standards, we report final *seff* values in meshes per 1000 km^2 [51]. We used the same steps as described above for determining *seff* values for the 5 km buffer zone around each N2k site.

We further calculated the median *seff* value of N2k sites and of their surroundings for each NUTS-3 region. Obtaining the median fragmentation value per NUTS-3 region allowed us to present the data on a broader spatial scale compared to presenting the data for each N2k PA individually (S1 Fig). This presentation also allowed for better visual comparison of regions within the EU relative to the presentation of raw data. The median instead of the mean was used to lessen the impact of outliers. It is important to consider that one large fragmented N2k site has the same influence on the median of the NUTS-3 region as a small N2k site. For more detailed information on individual N2k sites, we published our raw data (https://doi.org/10.6084/m9.figshare.13513902) and added figure S1 to the supporting information. To minimize information loss, statistical analysis was performed exclusively on raw data instead of using medians.

Many of the N2k sites were already protected prior to the establishment of the N2k network in 1992. We used each site's age since first designation as a PA. To determine the age of N2k sites, data on protected areas from the World Database of Protected Areas (WDPA) [55] were intersected with N2k data. N2k sites commonly overlap with other protected areas, such as national parks or biosphere reserves. In case a single N2k site overlapped with several protected areas, the earliest date of designated protection was used to calculate the age of the N2k site. Of our total 15390 N2k sites, we identified the age for 15335 N2k sites (99.6%).

Statistical analysis

Statistical analysis was performed in R v. 3.6.2 [60]. We assigned each N2k site and each 5 km buffer zone to one of five fragmentation categories following previous EEA reports [46] (Table 3). This categorization was used primarily for the visualization of the data.

Table 3: Categories of effective mesh density (*seff*). In contrast to the EEA [46], the fragmentation categories "anthropogenic" and "very high" were combined into one category “very high” due to the relatively small number of N2k sites within the anthropogenic category.

Effective mesh density (number of meshes per 1000 km²)	**Fragmentation Category**
≤ 1.5	Very low
> 1.5 – 10	Low
> 10 – 50	Medium
> 50 – 250	High
> 250	Very high

We conducted linear regressions using the lm function to examine the relationship between fragmentation of N2k sites and their surroundings. The effective mesh density of the surroundings of N2k sites ($seff_{surrounding}$) served as the predictor variable and the effective mesh density within the N2k sites ($seff_{within}$) as the response variable. The data were log (x+1) transformed to meet normality requirements. We also created nine individual linear regression models relating $seff_{surrounding}$ and $seff_{within}$ to the nine biogeographical regions covered by N2k sites. To analyse the relationship between the area of N2k sites and fragmentation within N2k sites, we conducted linear regressions using N2k site area as the predictor and $seff_{within}$ as the response variable.

To test for correlation between site age and the difference of fragmentation within and around N2k sites, we first calculated the difference between mesh density inside a N2k site ($seff_{within}$) and outside a N2k site ($seff_{surrounding}$) by subtracting $seff_{within}$ from $seff_{surrounding}$ for each N2k site separately (Eq 3).

$$seff_{diff} = seff_{surrounding} - seff_{within} \tag{3}$$

We then conducted linear regression using age as predictor and $seff_{diff}$ as response variable. For all linear regressions, the assumptions of linear regressions were verified by using diagnostic plots (*plot(linear model)*) showing linearity, homoscedasticity, and no substantial influence of extreme values.

Results

Fragmentation within and around N2k sites

Based on absolute *seff* values, 58.5% of all N2k sites are less fragmented than their surroundings, 0.9% are equally fragmented, and 40.6% are more fragmented than their surroundings. When categorized according to EEA standards (Table 3), N2k sites exhibit all levels of fragmentation from very low to very high (S1 Fig). Most N2k sites and their surroundings show a medium level of fragmentation, and only a few N2k sites and their surroundings show very low or very high levels of fragmentation (Fig 2). Surroundings of N2k sites are mostly within the same fragmentation category as N2k sites themselves (Fig 2).

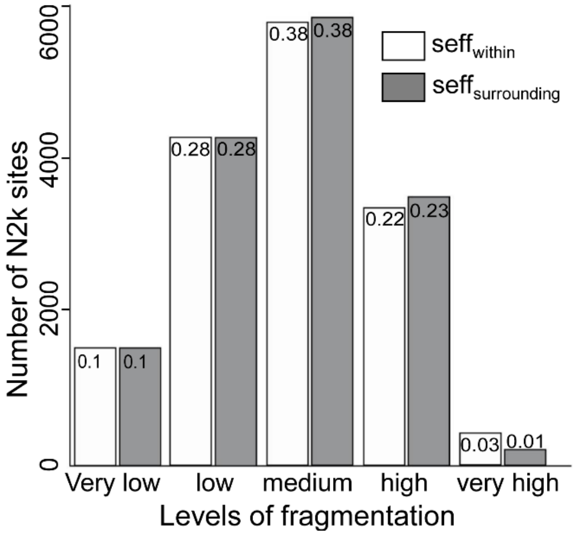
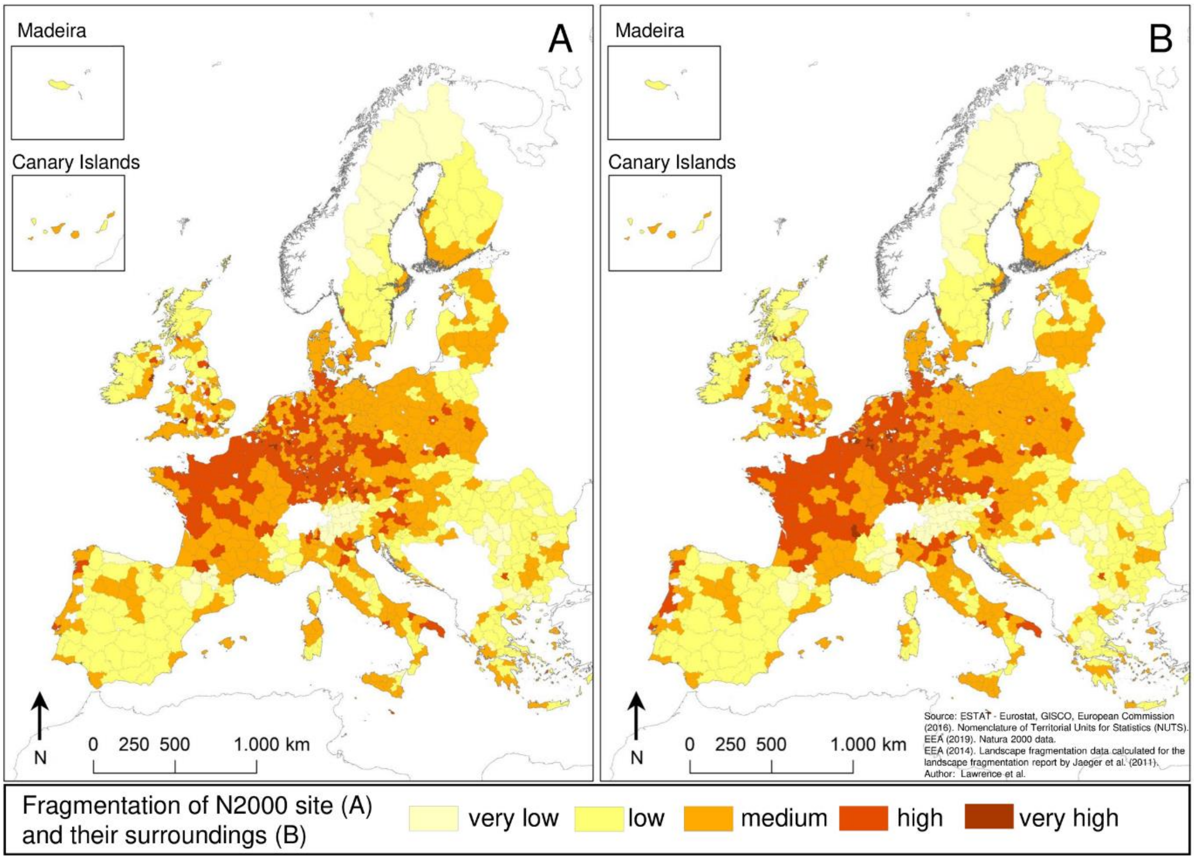


Fig 2. Number of N2k sites and their surroundings per fragmentation category. Fragmentation categories are based on EEA standards for effective mesh density (Table 3). Decimal numbers represent the relative amount of N2k sites which fall in one of the five fragmentation categories. The total number of N2k sites analyzed was 15390 (55.3% of N2k sites).

Fragmentation patterns of N2k sites across the EU

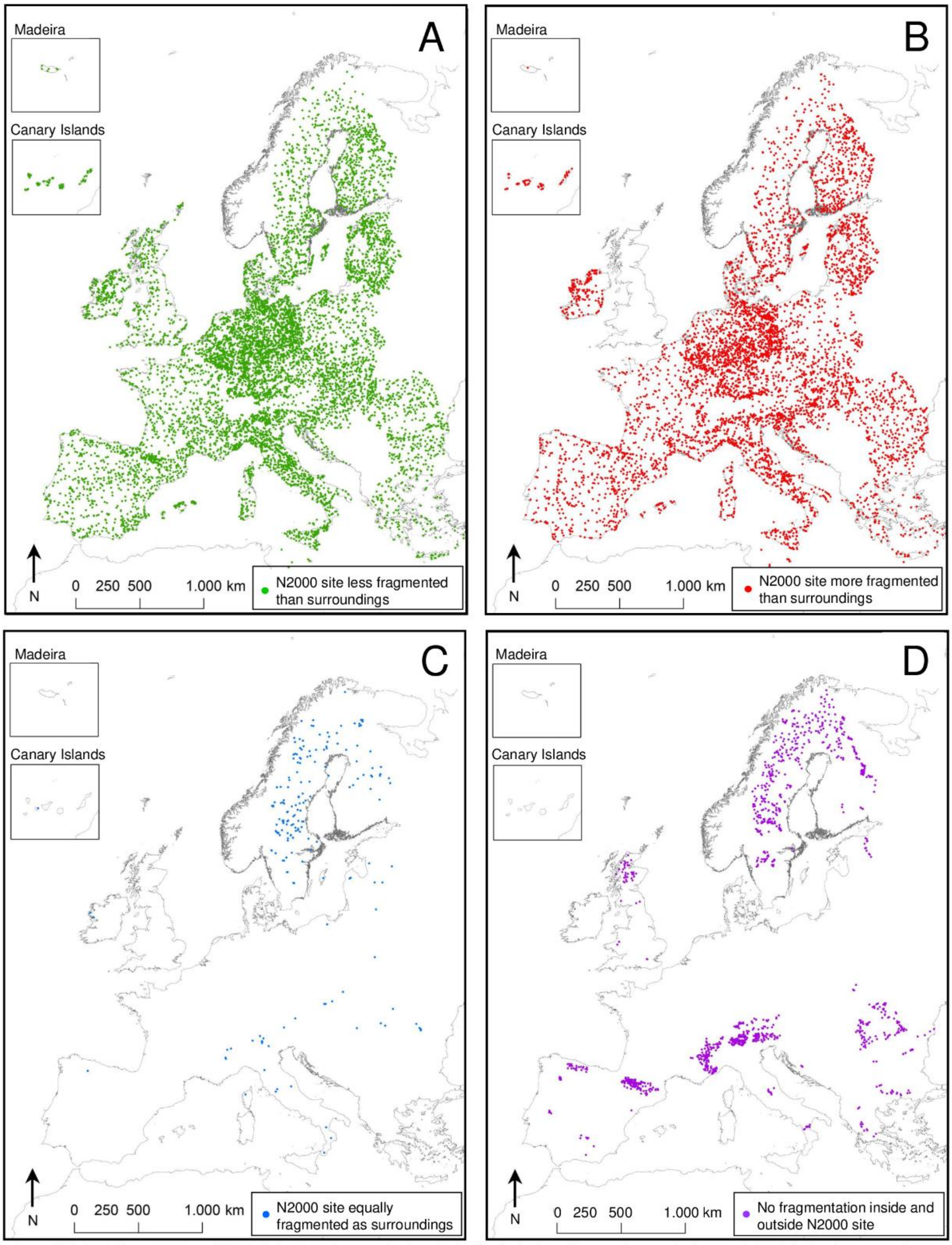
All five fragmentation categories are represented when taking the median for $seff_{within}$ (Fig 3A) and $seff_{surrounding}$ (Fig 3B) for each NUTS-3 region. Fragmentation inside and outside N2k sites is highest in central Europe, especially in France, Belgium, the Netherlands, Luxembourg, Germany, and the Czech Republic (Figs 3A-B). N2k sites and their surroundings showing very low levels of fragmentation are predominantly located in remote and/or mountainous regions of the EU, such as large parts of Sweden, Finland, Romania, the border between Bulgaria and Greece, the French, Italian and Austrian Alps, and the French and Spanish Pyrenees (Figs 3A-B). For most NUTS-3 regions, the category of interior fragmentation does not differ from the category of fragmentation for N2k sites' surroundings. Some NUTS-3 regions in France, Italy, and along the coast in Portugal show lower fragmentation categories inside N2k sites (Fig 3A) compared to N2k surroundings (Fig 3B).



Source: ESTAT - Eurostat, GISCO, European Commission (2016). Nomenclature of Territorial Units for Statistics (NUTS).
EEA (2019). Natura 2000 data.
EEA (2014). Landscape fragmentation data calculated for the landscape fragmentation report by Jaeger et al. (2011).
Author: Lawrence et al.

Fig 3. Fragmentation within N2k sites ($seff_{within}$) (A) and in their surroundings ($seff_{surrounding}$) (B) for NUTS-3 regions. The value for each NUTS-3 region was obtained by calculating the median of $seff_{within}$ (A) and the median of $seff_{surrounding}$ (B) of N2k sites for each NUTS-3 region. The area-wide coloration on the map reflects only the degree of fragmentation within (A) or in the surroundings of (B) N2k sites rather than the area-wide fragmentation throughout the NUTS-3 regions. Map generated in ArcGIS 10.6.1 (http://www.esri.com/software/arcgis/ arcgis-for-desktop).

According to the absolute difference between $seff_{surrounding}$ and $seff_{within}$ (Eq 3), 58.5% of N2k sites are less fragmented than their surroundings and those sites are distributed throughout the EU (Fig 4A). Similarly, N2k sites which are more fragmented than their surroundings (40.6%) are also represented throughout the EU (Fig 4B). N2k sites for which $seff_{within}$ and $seff_{surrounding}$ are exactly equal are rare (0.9%) and mainly located in northern Europe, the Alps, and parts of Romania (Fig 4C). N2k sites that exhibit no or only marginal fragmentation inside their boundaries as well as in their immediate surroundings ($seff_{within}$ and $seff_{surrounding} \leq 0.9$ meshes per 1000 km^2) (6.9%) are almost exclusively found in remote and mountainous regions of the EU (Fig 4D). This includes large parts of Sweden, Finland, parts of Romania, the French, Italian and Austrian Alps, the French and Spanish Pyrenees, and parts of the Scottish Highlands.

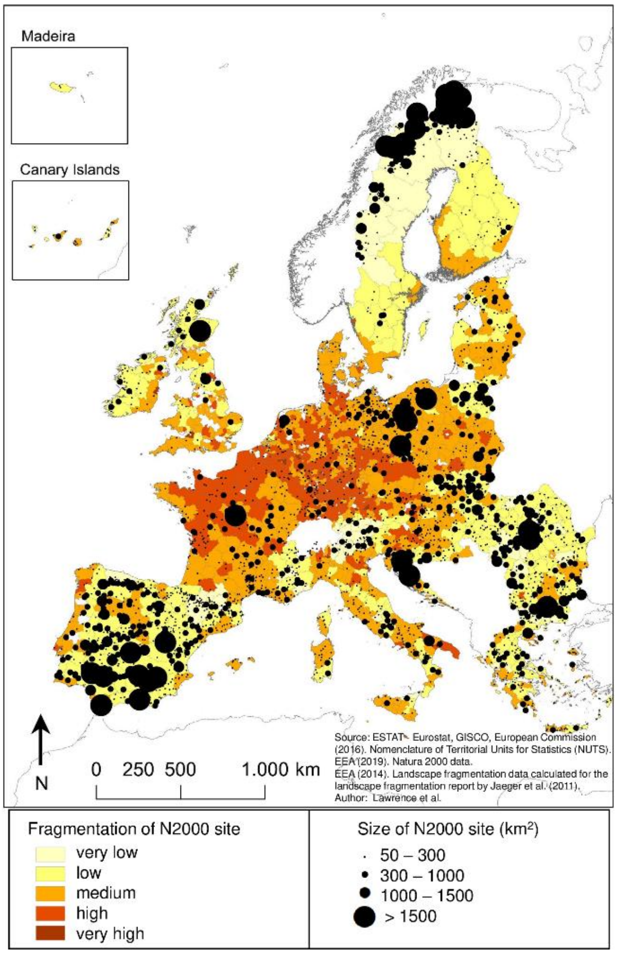


Source: EEA (2019). Natura 2000 data; EEA (2014). Landscape fragmentation data calculated for the landscape fragmentation report by Jaeger et al. (2011). Author: Lawrence et al.

Fig 4. Fragmentation difference between N2k sites and their surroundings. Each point represents the centroid of a N2k site: when calculating $seff_{diff} = seff_{surrounding} - seff_{within}$, 58.5% of N2k sites are less fragmented than their surroundings ($seff_{diff} > 0$ meshes per 1000 km^2) (A); 40.6% of N2k sites are more fragmented than their surroundings ($seff_{diff} < 0$ meshes per 1000 km^2) (B); 0.9% of N2k sites are equally fragmented as their surroundings ($seff_{diff} = 0$ meshes per 1000 km^2) (C); and independent from $seff_{diff}$, no or only marginal fragmentation within and in the surrounding of N2k sites ($seff_{within}$ and $seff_{surrounding} \leq 0.9$ meshes per 1000 km^2) exists for 6.9% of N2k sites (D). Map generated in ArcGIS 10.6.1 (http://www.esri.com/software/arcgis/ arcgis-for-desktop).

Size and area coverage of fragmented N2k sites

The sizes of the N2k sites analysed in this study vary greatly between the smallest (1 km²) and largest site (5556 km²). The majority (90.1%) of all N2k sites cover an area between 1 km² (5% quantile) and 243 km² (95% quantile). Large N2k sites are mainly located in remote and mountainous regions of the EU (Fig 5). N2k sites larger than 1500 km^2 are found predominately north of the polar circle in Sweden and Finland, in eastern Europe in parts of Poland, Romania and the Balkans, as well as in southern Spain (Fig 5). N2k area and fragmentation within N2k sites ($seff_{within}$) are negatively correlated ($R^2 = 0.09$, $p < 0.001$).



Source: ESTAT - Eurostat, GISCO, European Commission (2016). Nomenclature of Territorial Units for Statistics (NUTS). EEA (2019). Natura 2000 data. EEA (2014). Landscape fragmentation data calculated for the landscape fragmentation report by Jaeger et al. (2011). Author: Lawrence et al.

Fig 5. Size of N2k sites and fragmentation within N2k sites ($seff_{within}$). The value for each NUTS-3 region was obtained by calculating the median of $seff_{within}$ of N2k sites for each NUTS-3 region. The area-wide coloration on the map reflects only the degree of fragmentation within N2k sites rather than the area-wide fragmentation throughout the NUTS-3 regions. Large N2k sites are predominantly located in remote and mountainous regions, which tend to exhibit low fragmentation. Map generated in ArcGIS 10.6.1 (http://www.esri.com/software/arcgis/ arcgis-for-desktop).

We also compared the number of N2k sites to the cumulative area covered by N2k sites for the different fragmentation categories (Fig 6). N2k sites of low and very low fragmentation are few in number (37.9%) but they cover over 66.3% of the total area within the N2k network analyzed in this study (Fig 6). In contrast, N2k sites that show fragmentation levels in the categories medium, high, and very high, amount to 62.1% of the total number of N2k sites analyzed but cover only 33.7% of the cumulative area of N2k sites analyzed in this study.

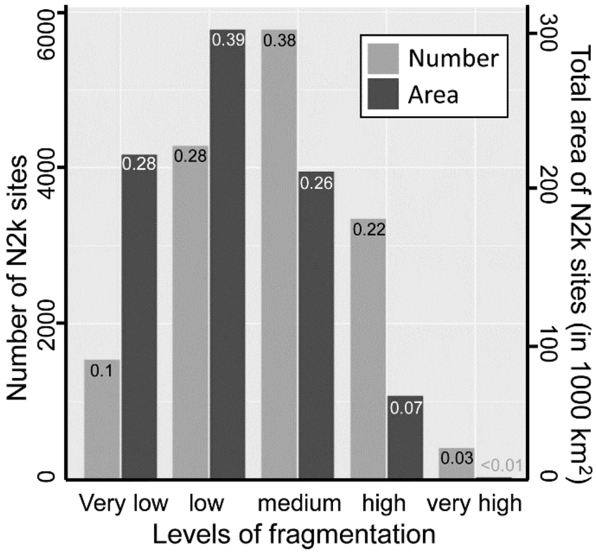


Fig 6. Number and area coverage of N2k sites per fragmentation category. Bars in light grey represent absolute numbers of N2k sites analyzed in this study. Bars in dark grey represent absolute area coverage in 1000 km^2 of N2k sites analyzed in this study. Black decimal numbers represent the relative amount of sites for each of the five fragmentation categories. White decimal numbers represent the relative amount of area covered by N2k sites for each of the five fragmentation categories. The total number of N2k sites analyzed was 15390 (55.3% of N2k sites). The total area covered by N2k sites analyzed was 796637 km^2 (79.5% of the total area covered by N2k sites). Fragmentation categories are based on EEA standards for effective mesh density (Table 3).

Interior and exterior fragmentation of N2k sites for the biogeographical regions of the EU

Linear regression was used to predict interior fragmentation of N2k sites ($seff_{within}$) based on the fragmentation of their surroundings ($seff_{surrounding}$). The results show a strongly significant relationship between $seff_{surrounding}$ and $seff_{within}$ ($seff_{within} = 0.9\ seff_{surrounding} + 0.3$, $p < 0.001$, $R^2 = 0.78$) (Fig 7). We also analysed the relationship between $seff_{within}$ and $seff_{surrounding}$ for each biogeographical region separately using linear regressions. Our results demonstrate that $seff_{within}$ significantly increases with increasing $seff_{surrounding}$ for all nine biogeographical regions (Fig 7). $seff_{surrounding}$ explains 67% or more of the variance observed in $seff_{within}$ for all biogeographical regions, except for the Black Sea ($R^2 = 0.62$), Macaronesian ($R^2 = 0.32$) and Pannonian ($R^2 = 0.46$) regions, which are also characterized by relatively small sample sizes (Fig 7). For all nine biogeographical regions, except for the Black Sea, Boreal, and Steppic region, the regression slope is slightly below 1, i.e., an increase by 1 mesh per 1000 km^2 in $seff_{surrounding}$ results in an increase of slightly less than 1 mesh per 1000 km^2 in $seff_{within}$. For the Black Sea, Boreal, and Steppic regions, the regression slope is slightly above 1. This means that an increase in $seff_{surrounding}$ by 1 mesh per 1000 km^2 results in an increase of slightly more than 1 mesh per 1000 km^2 in $seff_{within}$ (Fig 7).

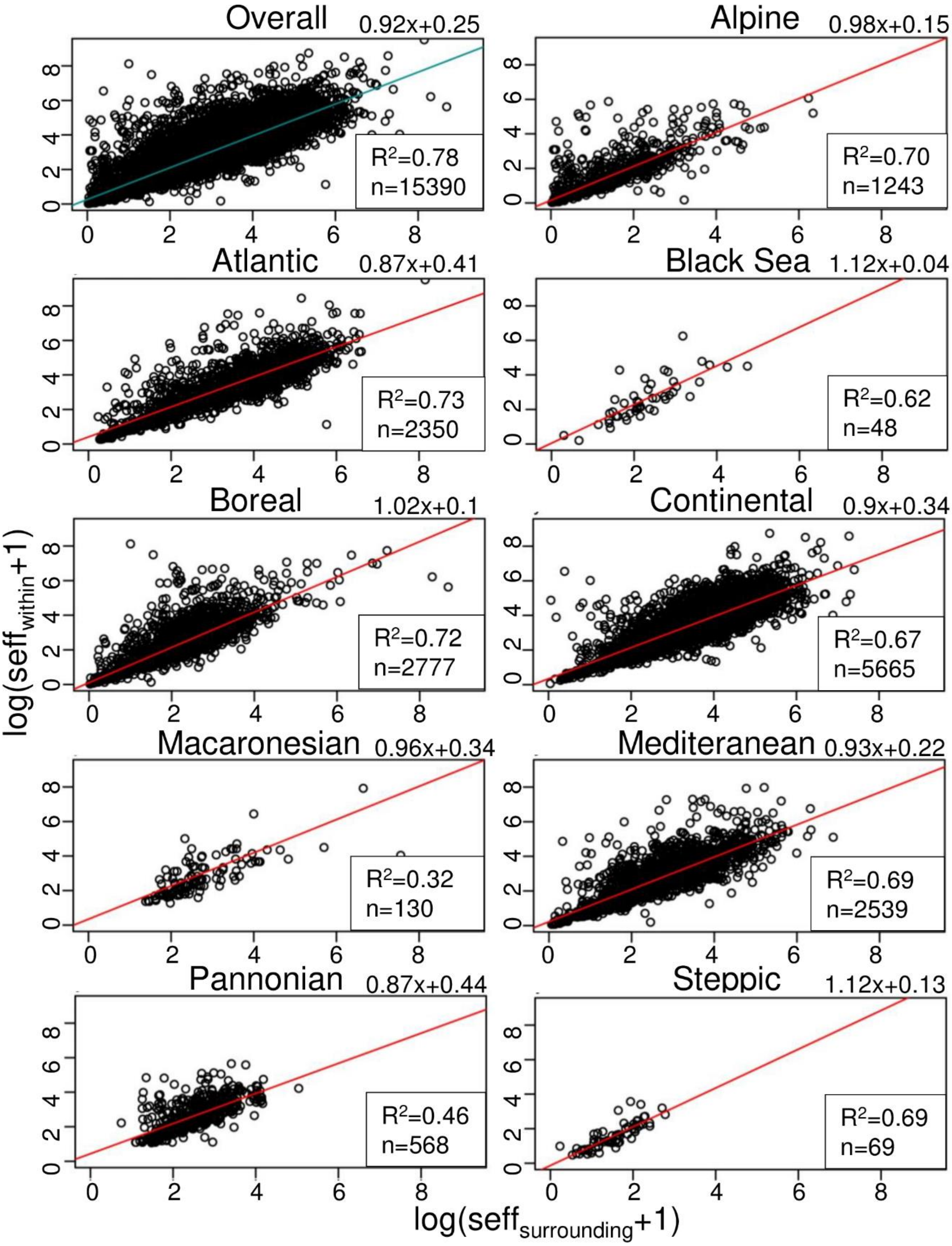
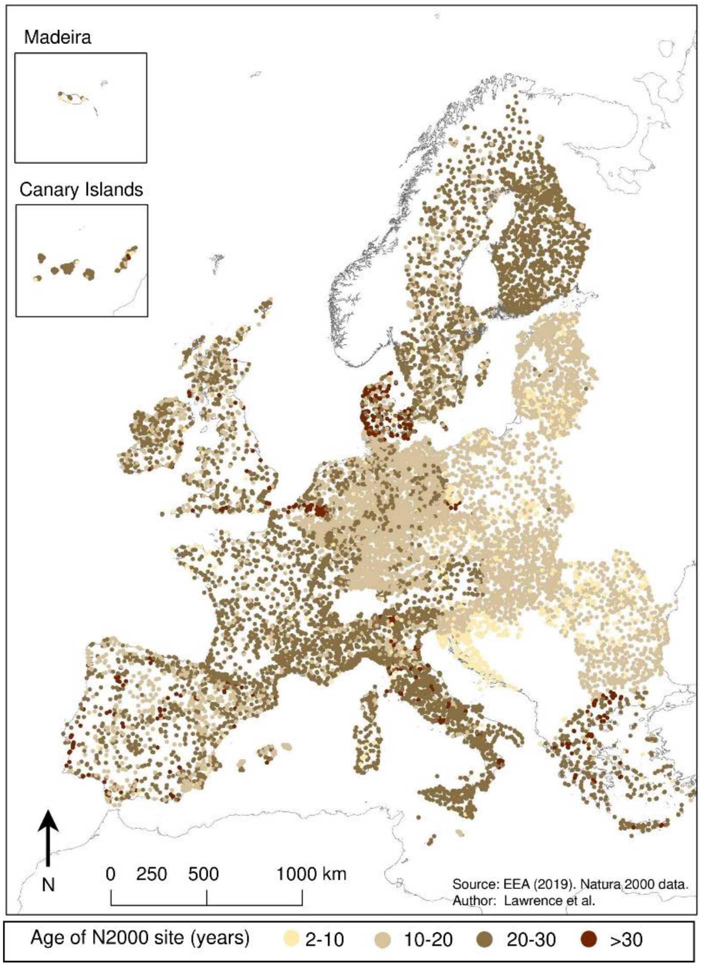


Fig 7. Correlation between effective mesh density (*seff*) within and around N2k sites for the nine biogeographical regions of the EU. $seff_{within}$ significantly correlates with $seff_{surrounding}$ for all nine biogeographical regions. For each biogeographical region, the R^2 value, the number of sites (*n*), and the linear regression formula with $x = seff_{surrounding}$ are provided.

Difference in interior and exterior fragmentation of N2k sites in relation to site age

N2k sites analysed in this study differed in age between 2 and 37 years. Young N2k sites are predominantly located in eastern European member states, especially Croatia, which joined the EU in recent years. In contrast, the oldest N2k sites are predominantly located in Spain, France, Italy, Greece, Denmark, and the Netherlands (Fig 8).



Source: EEA (2019). Natura 2000 data.
Author: Lawrence et al.

Fig 8. Age of N2k sites. Recently protected PAs within the N2k network are predominantly located in eastern European member states which joined the EU since 2004 (Status 2017) [55]. Map generated in ArcGIS 10.6.1 (http://www.esri.com/software/arcgis/ arcgis-for-desktop).

There is no significant correlation between N2k age and the absolute difference in effective mesh density ($seff_{diff}$) within and around N2k sites ($R2 < 0.001$, $p = 0.58$). In other words, N2k sites are not significantly less fragmented compared to their surroundings the longer their protected status has been in place. This result contradicts our original hypothesis.

Discussion

Despite their protected status, our results show that N2k sites are very fragmented. Moreover, fragmentation within N2k sites strongly correlates with the fragmentation of their surroundings. This correlation applies to all nine biogeographical regions in the EU. Remote and mountainous regions show the lowest levels of fragmentation within and around N2k sites. These remote and mountainous regions also tend to hold the largest N2k sites by area. Further, N2k PA age does not correlate with the difference in exterior and interior fragmentation of N2k PAs. Our results suggest that there is high potential for improving PA efficacy by taking pre-emptive action against encroaching anthropogenic fragmentation and by targeting scarce financial resources in nature conservation where fragmentation pressures can be mitigated feasibly through enforced construction bans inside PAs.

Limitations to analysing fragmentation of N2k sites

While N2k sites form a network of PAs designated for nature conservation and biodiversity preservation, each site's conservation value is largely based on land use history. These local histories can include long periods of anthropogenic changes as in areas formerly exploited for agricultural production or resource extraction. The biota that have established and evolved within these cultural landscapes are no less crucial for biodiversity compared to those that have evolved within landscapes which have experienced little or no anthropogenic change [16,59]. Linear structures such as historic roads or canals are intrinsic features of many N2k sites that host high numbers of species adapted to these unique habitats [61]. Therefore, it is to be expected that some degree of fragmentation exists within much of the N2k network. However, these land use histories do not account for the high degree of fragmentation we found within N2k sites. Economic development is the main driver of European landscape fragmentation [51], and our results suggest that N2k sites are not sufficiently sheltered from contemporary fragmentation pressures.

While our data show that the vast majority of N2k sites (93.1%) are fragmented to some degree, limitations in our study design led to the exclusion of a large number of sites from our analysis. We used pre-processed data on the effective mesh size (*meff*) and effective mesh density (*seff*), with a resolution of 1 km². However, it was necessary to apply a filter to ensure that each N2k site analysed covers at least one 1 km^2 raster cell-center containing information on *meff* and *seff*. This led to the exclusion of several small or elongated N2k sites. Despite their requisite exclusion, these small N2k sites are an important component of the N2k network. They can be vital habitats for confined or for small-range species, or they may contribute to landscape complementation and overall habitat diversity [9,45]. Further, small N2k sites are unevenly distributed across Europe [62] and might therefore play an outsized role in nature conservation for some countries relative to others. The range and distribution of differently-sized PAs within the N2k network is a result of political considerations, societal criteria, and the regional patterns of high conservation value habitats [63-65]. There is no single standard criterion that was applied in the designation of N2k sites across Europe [65]. As a consequence, the regional and biogeographical specifics in PA size, naturalness, as well as in fragmentation, are simultaneously constraints and inherent qualities of the N2k network. With additional research quantifying the degree of fragmentation for small N2k sites - by, for example, calculating *meff* and *seff* directly using OpenStreetMap (OSM) data [66], - we could gain a comprehensive understanding of fragmentation pressures posed to the N2k network as a whole and better design anti-fragmentation management plans at the national level.

Anthropogenic fragmentation inside N2k sites

Previous studies have demonstrated the N2k network's low effectiveness in protecting certain target species [67-69]. Our study is the first to quantify fragmentation differences between the interior of N2k sites and their surroundings, and our results suggest that failure to account for fragmentation in and around N2k sites may contribute to these sites' subpar effectiveness. Fragmentation within N2k sites strongly correlates with the fragmentation of their surroundings ($R^2 = 0.78$). Indeed, only a narrow majority of N2k sites are less fragmented than their surroundings.

We hypothesized the difference between exterior and interior fragmentation of N2k PAs to be bigger the longer protected status has been in place, reflecting effective PA management even if anthropogenic fragmentation in PA surroundings continues unabated. However, contrary to our original hypothesis, no correlation between PA age and the difference of fragmentation outside and inside the PA ($seff_{diff}$) was found. It is possible that too little time has passed since PAs within the N2k network gained PA status for protection to have had a measurable effect in mitigating fragmentation pressures. The oldest PAs tested are no more than 37 years old and many N2k sites have only recently acquired protected status. This is especially true for N2k sites located in eastern European member states such as Bulgaria, Czech Republic, Estonia, Hungary, Latvia, Lithuania, Poland, Romania, Slovakia and Slovenia, which have been members of the EU only since 2004 [70]. It will be interesting to see if and how differences between fragmentation of PAs and their matrix do or do not change over time. In general, eastern European countries have lower population densities, have experienced delayed economic development, and have sparser road networks compared to central or western Europe. However, transportation infrastructure and urbanization have developed quickly in these countries since their accession to the EU [35]. This rapid development is likely to result in conflicts with conservation objectives in the future [16]. Therefore, we recommend a continuous monitoring of fragmentation within and around N2k PAs.

With a well-enforced nature conservation strategy, it should be possible to shelter existing N2k sites from encroaching anthropogenic fragmentation. Spatial concepts and priorities need to be developed in due course. This does apply not only to eastern Europe but to the entire EU. Our study provides information on the location of N2k sites most threatened from fragmentation. These results can be combined with projections of future economic development and projections of PA climate sensitivity to develop criteria for priority areas where conservation resources can be most efficaciously applied. This can provide a roadmap for N2k planners to ensure the continued viability of the crucial ecosystems located within the current N2k network. To shelter N2k sites from the deleterious effects of habitat loss and fragmentation, we suggest, based on our results: a) inscribing a ban of additional development inside N2k sites into law; b) putting additional resources into enforcing bans on constructions inside N2k sites; and c) where possible, removing extant fragmenting infrastructure.

Distribution of low-fragmented N2k sites and implications for future conservation strategies

Our data show that large N2k sites of low fragmentation tend to be located where topography limits human infrastructure development. One reason for this phenomenon might be that establishing PAs in sparsely populated, mountainous, and far-northern landscapes is often easier and cheaper than in alternative locations. There is typically less pressure to use this land for agriculture or urban expansion. Low fragmentation is mainly found in remote regions, such as the Black Sea, Steppic, Macaronesian, Pannonian, or Boreal regions, as well as in mountainous regions such as the Alpine region. In fact, many N2k sites in mountainous regions have escaped anthropogenic fragmentation altogether, within and around N2k sites, highlighting the effect of topographical constraints.

At the country level, Sweden, Finland, and Romania manifest low or very low levels of fragmentation. However, in contrast to Sweden and Finland, Romania is in the process of expanding its road and rail infrastructure which will increase fragmentation in the future [51]. Some of this infrastructure may cut through existing PAs and will likely increase habitat fragmentation and species population decline, threatening – among others - the survival of several large mammal populations protected under the Habitats Directive such as bears, wolves, and lynx [51,71]. Given the importance of Romania's ecosystems for European biodiversity, Romania's relatively untouched N2k sites need careful monitoring and active management to protect them from future fragmentation. One existing legal framework for this effort is the Carpathian Convention (2003), which explicitly addresses regulations on traffic and development [35]. We argue that similar legal concepts addressing anthropogenic fragmentation should be incorporated into N2k management in order to strengthen its long-term viability for continent-wide biodiversity conservation.

Target 11 of Aichi Biodiversity Targets, which aims to protect 17% of terrestrial area in each signatory country, results in a common and politically expedient conservation strategy of protecting those areas in which political and economic development pressures are weakest [21]. Protecting areas in marginal lands (also referred to as "rock and ice" [21]) to avoid competition with other economic and societal interests is a popular and politically viable way for countries to achieve their 17% target. This strategy is based on political expediency rather than science-backed conservation goals such as minimizing biodiversity loss. Given the essential contribution of smaller and often more fragmented PAs to biodiversity [9], this "rock and ice" strategy is dangerously inadequate as a conservation policy without including scientific findings on effective biodiversity preservation. However, our research suggests that strict enforcement of anti-fragmentation policies, such as those outlined above, can have immense benefits in those large, remote, and mountainous PAs that are already protected. These benefits derive from the fact that non-arable and sparsely populated areas, such as far northern or mountainous landscapes, are not well-suited to anthropogenic land use today, but economic and development interests of these areas may expand as a result of climate change. Therefore, today's politically expedient solution of conserving large sections of remote, low-fragmented areas can, if strictly maintained and enforced, help prevent fragmentation pressures from undercutting conservation efforts in the future. By focusing on enforcement of construction bans inside PAs as an inexpensive and comparatively uncontroversial strategy, conservationists can take this opportunity to guard PAs against future anthropogenic pressure.

Acknowledgment

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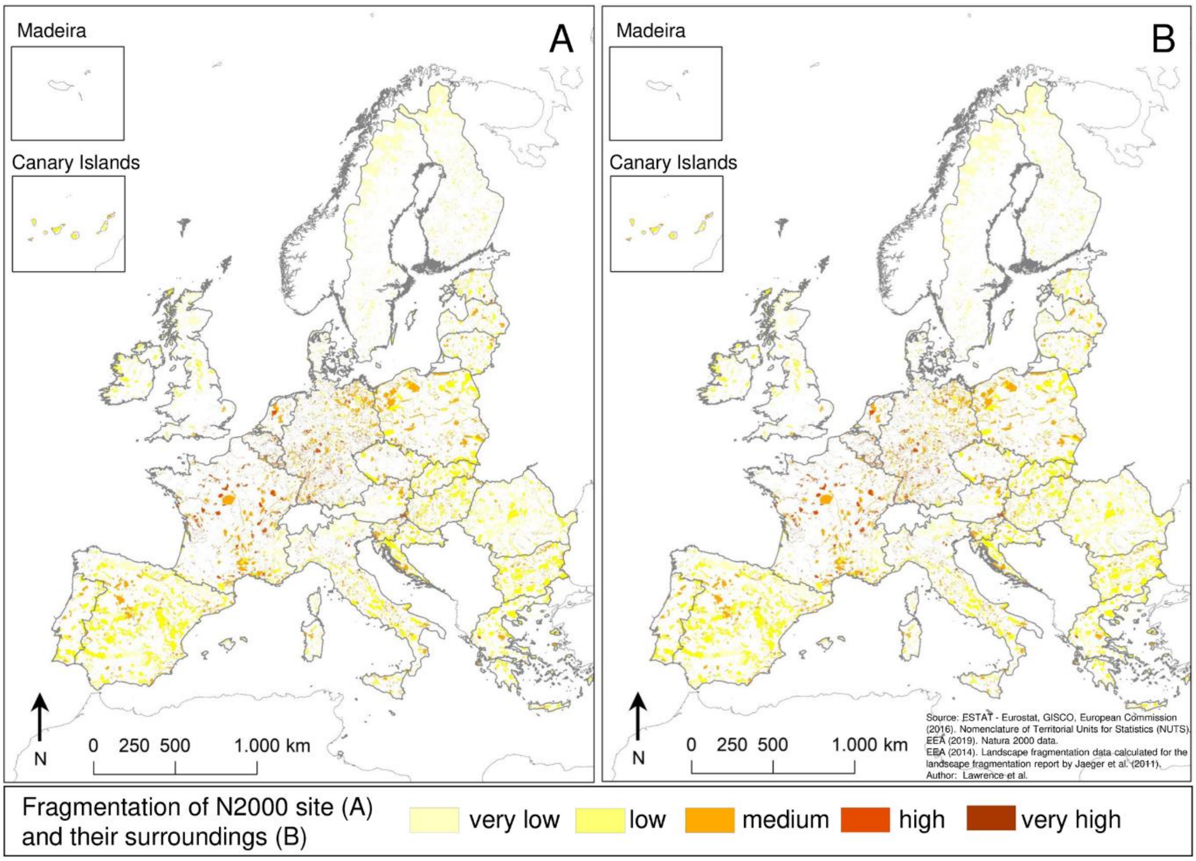
Supporting information



Source: ESTAT - Eurostat, GISCO, European Commission (2016). Nomenclature of Territorial Units for Statistics (NUTS).
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EEA (2014). Landscape fragmentation data calculated for the landscape fragmentation report by Jaeger et al. (2011).
Author: Lawrence et al.

S1 Fig. Fragmentation within N2k sites (A) and in their surroundings (B). We calculated $seff_{within}$ (A) and $seff_{surrounding}$ (B) for each N2k site. The coloration of N2k sites represents one of five fragmentation categories (Table 3). Map generated in ArcGIS 10.6.1 (http://www.esri.com/software/arcgis/ arcgis-for-desktop).

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9 Appendix

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

Conference	Location and Date	Title	Authors
International Biogeography Society	Vancouver, Canada June 2022	Landscape fragmentation of the Natura 2000 network and its surrounding areas	Lawrence, A., Friedrich, F., Beierkuhnlein, C.
AK Biogeografie	Bonn, Germany May 2018	Diversity of Ecosystem Services across European Protected Areas	Lawrence, A., Zennaro, B., Beierkuhnlein, C.
Horizon 2020 Ecopotential Workshop	Bayreuth, Germany March 2018	Diversity of Ecosystem Services across European Protected Areas	Lawrence, A., Zennaro, B., Beierkuhnlein, C.

Appendix 2. My conference contributions to other topics while working on my dissertation.

Conference	Location and Date	Title	Authors
Future with data. Models that simplify the world. National platform for zoonotic diseases and the academy for public health	Berlin, Germany December 2019	Cartographic modeling of zoonotic diseases using the R-based RISKTOOL	Thomas, S., Jaeschke, A., Tjaden, N., Lawrence, A. (presenter), Beierkuhnlein, C.
German-Central Asian Cooperation on Zoonotic diseases	Munich, Germany June 2019	Species distribution modelling of reservoir tick species for Crimean-Congo Hemorrhagic Fever in Central Asia	Lawrence, A., Thomas, S.
13th intern. Symposium on Tick and Tick-borne Diseases	Weimar, Germany March 2019	The factors that shape vector aggregation on small mammal hosts	Salomon, J., Lawrence, A. (presenter), Crews, A., Sambado, S., Swei, A.

Appendix 3. Peer-reviewed publications on other topics that I contributed to during the time that I wrote my dissertation.

- Salomon, J., **Lawrence, A.**, Crews, A., Sambado, S., & Swei, A. (2021). Host infection and community composition predict vector burden. *Oecologia*, 196(2), 305-316. https://doi.org/10.1007/s00442-021-04851-9
- **Lawrence, A.,** O'Connor, K.E., Haroutounian, V., & Swei, A. (2018). Patterns of diversity along a habitat size gradient in a biodiversity hotspot. *Ecosphere*, 9(4), e02183. https://doi.org/10.1002/ecs2.2183

Appendix 4. Bachelor and Master theses that I supervised while working on my dissertation.

Master theses supervised

- Hannah Pepe “Spatial distribution of wolves in Germany with respect to protected areas” (02/2022 – Present)
- Fabian Friedrich “Varying degrees of landscape fragmentation within and around the Natura 2000 network in the EU” (04//2019)

Bachelor theses supervised

- Leon Prucker “Factors associated with varying degrees of landscape fragmentation among Natura 2000 protected areas” (12/2021)
- Sophy Cley de Guimaraes “Using indicator values according to Ellenberg to investigate recovery of saplings in temperate forests in northern Bavaria” (03/2022)

Appendix 5. My teaching activities while working on my dissertation.

- Course instructor for concepts of **biogeographical modelling**, species distribution modelling

  Weekly graduate seminar classes on biogeographical modelling. Lecture on species distribution modelling, bioclim models, domain models, maxent models, correlative models, joint-species distribution models, process-based models, hybrid models, individual based models. Demonstrations implemented in R and ArcGIS.
- Course instructor for **spatial ecology/modelling of ecological processes**

  Weekly graduate seminar and exercise classes on ecological modelling in R.

  Design and teach R-programming on ecological models assessing metapopulation dynamics, spread of invasive species, water-soil-vegetation interactions, breeding synchrony, wildfire spread, species diversity patterns, reserve network design. Models include among others Cellular-Automaton-Model, Drossel-Schabel-Model, Incidence-Function-Model, Reaction-Diffusion-Model, etc.
- Course instructor for **biogeography**

  Weekly undergraduate seminar on biogeographical topics including theory, methods, and applications in various topics of terrestrial and marine biogeography.

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.

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Ort, Datum, Unterschrift