

**Extending the climate envelope:
Methodological approaches
to integrate ecological prerequisites
in species distribution models
at large spatial extents**

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Summary

The following thesis presents potential impacts of climate change on the distribution of protected animal species. Here, different influencing factors like uncertainty in the data basis, dispersal distances, and biotic interactions, as well as their influence on projections of distribution models are analysed. The aim is to amend established climate envelope models by ecological prerequisites and therewith to create a new basis for action for nature conservation.

The species considered in this work are protected throughout the European Union and their conservation is a main target, more than ever under the conditions of recent climate change. Distribution changes of animal and plant species, in situ changes of habitats as well as changes in communities and their biotic interactions have to be increasingly expected and can no longer be compensated or mitigated by established management concepts only.

There is an increasing amount of literature concerning climate change impacts on organisms and ecosystems. This literature was surveyed to get an impression of the derived knowledge patterns so far and to detect potential knowledge gaps. The analysis reveals large imbalances concerning the spatial distribution of study areas, the studied taxonomic groups and ecosystems as well as the applied methods.

Climatic changes are expected to have a relevant influence on the distribution of species. Changes in species' distributions are already observed and attributed to the recent climate change at least for some species. In order to assess the degree of the awaited distribution changes climate envelope models have been increasingly used in the recent past. They put the spatial distribution of a species in relation to different environmental factors, such as climatic conditions. With their help potential impacts of a changing climate on a species' distribution can be analysed. The present work uses these climate envelope models to estimate potential range changes of animal species.

Beside the pure availability of new climatically suitable areas the accessibility and in situ establishment are main influencing factors concerning the estimation of the future potential distribution of a species. Accessibility is on the one hand determined by the species-specific dispersal ability and on the other hand by the permeability of the landscape. The establishment depends also on biotic conditions. Climatic suitability and accessibility of an area are insufficient if the individual cannot discover its essential interaction partner.

Odonata are often recognized as good dispersers because of their flight ability. However, having a closer look, their dispersal ability may not be sufficient enough to keep up with the projected climatic changes. This is especially true for damselflies, for which potential suitable

areas could develop in the future, but may be not able to reach them on their own or within the next decades because of their small dispersal distance and/or because of the far distance between current and projected areas. Hence, the integration of observed dispersal distances in future projections needs to be given special attention to constrain overall assumptions like 'unlimited dispersal' and to receive more realistic projections regarding a species' dispersal potential.

Additionally, biotic interactions need to be increasingly considered in modelling. However, the implementation seems to be problematic. For this reason I developed different approaches to integrate specific interactions in the modelling process and compared these with a model which neglects the interaction. I could show that considering biotic interactions leads to less projected suitable areas and larger potential losses of the target species than a negligence of essential interaction partners and therewith to potentially more realistic results.

In the case of habitat types the question "How can we handle complex entities?" arises. To answer this question two principally different modelling approaches were developed: the indirect approach – modelling the distribution of a habitat type using the distribution of its characteristic plant species – and the direct approach – using the distribution of the habitat itself. Both approaches were tested by modelling five grassland habitat types defined by the EU Habitats Directive. Both approaches produce reasonable results, though the indirect approach is at least restricted by the required but actually lacking amount of plant distribution data.

Methodological improvements of species distribution models are an essential step to receive more realistic results. However, the knowledge of ecological conditions required by a certain species, i.e. the assumptions about the niche, provides the basis for all models. Ecological demands can differ across large (such as continental) spatial scales and the current knowledge is mainly restricted to a few well-studied species. Hence, also in times of progressing climate change it is worth to focus on monitoring programs and experiments to gain further knowledge on a species' niche.

The main focus of this thesis is on the estimation of potential distribution changes of protected animal species caused by climatic changes. It considers thereby not only the assumed relation between climatic conditions and the current distribution, but also integrates further distribution-determining aspects. For this purpose, different approaches were developed and compared. This work contributes to a more comprehensive understanding of the range influencing environmental factors in times of global climate change and therewith to an enhanced basis for actions for nature conservation measurements.

Zusammenfassung

Die vorliegende Arbeit stellt die potenziellen Auswirkungen des Klimawandels auf die Verbreitung von geschützten Tierarten dar. Dabei werden verschiedene Einflussfaktoren, hier Unsicherheiten in der Datengrundlage, Ausbreitungsdistanzen und biotische Interaktionen, sowie deren Einfluss auf die Projektionen von Verbreitungsmodellen analysiert. Ziel ist es, etablierte Klimahüllenmodelle um ökologische Grundvoraussetzungen zu ergänzen und damit neue Handlungsgrundlagen für den Naturschutz zu schaffen.

Die in dieser Arbeit berücksichtigten Arten stehen EU-weit unter Schutz und deren Erhalt ist ein zentrales Ziel, auch oder gerade unter den Bedingungen des rezenten Klimawandels. Verbreitungsänderungen von einzelnen Tier- und Pflanzenarten, in situ Veränderungen von Lebensräumen sowie eine Beeinflussung von Lebensgemeinschaften und deren Interaktionen sind in zunehmendem Maße zu erwarten und können nicht mehr nur mit bestehenden Managementkonzepten kompensiert oder abgemildert werden.

Es gibt zunehmend mehr wissenschaftliche Publikationen, die sich mit Auswirkungen des Klimawandels auf Organismen und Ökosysteme befassen. Diese Literatur wurde dahingehend untersucht, einen Eindruck vom bisher erzielten Wissen zu erlangen, aber auch potenzielle Wissenslücken aufzudecken. Die Analyse zeigt ein deutliches Ungleichgewicht bezüglich der räumlichen Verteilung der Untersuchungsgebiete, der untersuchten taxonomischen Gruppen und Ökosysteme sowie der angewandten Untersuchungsmethoden auf.

Es wird erwartet, dass klimatische Veränderungen die Verbreitung von Arten maßgeblich beeinflussen. Veränderungen in der Verbreitung von Arten können bereits beobachtet und auf den rezenten Klimawandel zurückgeführt werden. Zur Abschätzung des Ausmaßes zu erwartender Verbreitungsänderungen werden in jüngster Zeit verstärkt Klimahüllenmodelle verwendet, die die räumliche Verbreitung einer Art mit verschiedenen Einflussfaktoren, z.B. klimatischen Bedingungen, in Verbindung setzt. Mit deren Hilfe kann die Auswirkung eines sich ändernden Klimas auf die Verbreitung analysiert werden. Die vorliegende Arbeit nutzt diese Klimahüllenmodelle, um potentielle Verbreitungsänderungen von Tierarten zu ermitteln.

Neben dem reinen Vorliegen neuer klimatisch geeigneter Flächen sind die Erreichbarkeit und die Etablierung vor Ort wesentliche bestimmende Faktoren für die Ermittlung der zukünftigen Verbreitung. Die Erreichbarkeit bestimmt sich zum einen aus der artspezifischen Ausbreitungsfähigkeit und zum anderen aus der Durchlässigkeit der Landschaft. Die Etablierung hängt nicht zuletzt von den biotischen Gegebenheiten ab. Klimatische Eignung und Erreichbarkeit einer Fläche nützen einem Individuum wenig, wenn es nicht auch seinen

essentiellen Interaktionspartner vorfindet.

Bei Libellen erwartet man zunächst ein großes Ausbreitungspotential aufgrund ihrer guten Flugfähigkeit. Dennoch sind bei genauerer Betrachtung längst nicht alle Libellen ausbreitungsstark genug, um mit den projizierten klimatischen Veränderungen Schritt zu halten. Dies gilt z.B. für Kleinlibellen, für die durchaus zukünftig geeignete Flächen entstehen können, diese jedoch aufgrund ihrer geringen Ausbreitungsdistanz und der Entfernung zu bestehenden Vorkommen aus eigener Kraft nicht oder nicht in den nächsten Jahrzehnten erreichen können. Der Integration von beobachteten Ausbreitungsdistanzen in Zukunftsprojektionen sollte daher besondere Aufmerksamkeit geschenkt werden, um pauschale Erwartungen, wie sie auch in dem Ausbreitungsszenario ‚uneingeschränkte Ausbreitung‘ stecken, zu beschränken und realistischere Projektionen hinsichtlich des Potentials einer Art zu ermöglichen.

Zudem bedürfen biotische Interaktionen einer zunehmenden Berücksichtigung in der Modellierung. Die Umsetzung scheint jedoch problematisch. Aus diesem Grund entwickelte ich verschiedene Ansätze zur Berücksichtigung von spezifischen Interaktionen in der Modellierung und verglich diese mit einem Modell ohne Interaktionen. Ich konnte zeigen, dass bei Berücksichtigung von biotischen Interaktionen die projizierten geeigneten Flächen geringer und potentielle Verluste der Zielart größer sind als bei der Nichtberücksichtigung des essentiellen Interaktionspartners, und somit die Berücksichtigung von Interaktionspartnern ein vermutlich realistischeres Ergebnis liefert.

Im Fall von Lebensraumtypen stellt sich zudem die Frage: Wie kann man komplexe Gebilde in der Modellierung handhaben? Um diese Frage zu beantworten wurden zwei verschiedene Modellierungsansätze entwickelt: der indirekte Ansatz, der die Verbreitung des Lebensraumtyps auf Grundlage der Verbreitung der charakteristischen Pflanzenarten modelliert, und der direkte Ansatz, der die Verbreitung des Lebensraumtyps als Grundlage verwendet. Beide Ansätze wurden mit der Modellierung von fünf Grasland-Lebensraumtypen, definiert durch die Fauna-Flora-Habitat-Richtlinie der EU, getestet. Beide Ansätze liefern gute Ergebnisse, auch wenn der indirekte Ansatz zumindest durch die Abhängigkeit von verfügbaren Verbreitungsdaten von Pflanzen eingeschränkt wird.

Methodische Verbesserungen von Artverbreitungsmodellen sind ein essentieller Schritt, realistischere Modellierungsergebnisse zu erzielen. Nichtsdestotrotz stellt die Kenntnis der ökologischen Ansprüche einer Art, d.h. die Annahmen über die Nische, die Grundlage für alle Modelle dar. Die ökologischen Ansprüche können sich hierbei auf großen räumlichen Skalen (wie z.B. Kontinenten) unterscheiden und auch das aktuelle ökologische Wissen ist meist auf wenige gut-untersuchte Arten beschränkt. Daher ist es auch in Zeiten voranschreitenden

Klimawandels notwendig und angemessen, Monitoring-Programme und experimentelle Untersuchungen durchzuführen, um weitere Kenntnisse zur Nische einer Art zu erlangen.

Der Schwerpunkt dieser Arbeit liegt in der Abschätzung von potenziellen Verbreitungsänderungen von geschützten Tierarten aufgrund klimatischer Veränderungen. Sie berücksichtigt dabei nicht nur den vermuteten Zusammenhang zwischen klimatischen Gegebenheiten und der aktuellen Verbreitung, sondern integriert weitere verbreitungsbestimmende Aspekte. Dazu wurden verschiedene Ansätze entwickelt und verglichen. Sie leistet damit einen Beitrag zu einem umfassenderen Verständnis der verbreitungsbeeinflussenden Umweltvariablen im Zuge des Klimawandels und damit zu einer erweiterten Handlungsgrundlage für Naturschutzmaßnahmen.

Introduction

1. Motivation

Climate change is increasingly affecting organisms and ecosystems. These consequences of anthropogenic climate change have become a major topic of research (e.g. Loarie et al. 2009, Körner & Basler 2010, Cahill et al. 2013) and policy (e.g. IPCC 2012, 2013). However, despite observational, experimental and modelling studies are published in high frequency there is still uncertainty about the responses of plant and animal populations, of communities as well as of entire ecosystems (Peñuelas et al. 2013).

Hence, this thesis provides an estimation of the potential responses of protected species and habitats to climate change in Europe. To achieve this, existing and well-established statistical (correlative) modelling techniques were coupled with ecological constraints, such as dispersal distances and biotic interactions.

The model species and habitats considered in this thesis are protected throughout the European Union by the EU Habitats Directive (Council of the European Union 1992). It is important to know how climate change may influence these protective goods to contemporarily develop adaptation strategies and to install management measurements.

Modelling potential responses of organisms and ecosystems provides a useful tool for contemporary estimations and hence the development of adaptation strategies for nature conservation (e.g. Bush et al. 2014). However, statistical models are often criticised due to their lacking implementation of ecological constraints. Consequently, this thesis not only provides estimates of range shifts, but particularly emphasizes approaches for the integration of ecological prerequisites in species distribution modelling.

2. Structure of this thesis

My thesis starts with an introductory overview of the current knowledge on climate change and observed and expected ecological impacts on animals, especially on their distribution. This is followed by a summary of statistical climate envelope modelling - the most prominent methodology for estimating future impacts of climate change -, its potential and limitations. Based on the outlined limitations, the third part of the introduction highlights the need to combine a statistical modelling approach with species-specific ecological constraints. These three sections include and refer to findings from the four articles of this dissertation. They show how the single publications build up on each other. Furthermore, these chapters highlight the importance of my research findings for the state of knowledge in this field. Subsequently, a synopsis of all manuscripts contributing to this thesis is given, followed by a

summarizing conclusion and emerging research challenges. The introductory section closes with the declaration of my contribution to the articles.

My thesis highlights gaps in the current knowledge of ecological climate change impact research and discusses options to address these deficits. Further, I focus on the improvement of climate envelope models by considering ecological constraints like dispersal and biotic interactions and how these processes can be implemented in projective modelling approaches. Additionally, I have a closer look on the modelling of complex entities such as habitat types and develop two different approaches for their consideration in climate envelope modelling.

The thesis ends with a summary and an appendix, which lists further own manuscripts that were published during the PhD period but are not included in this dissertation. In addition, presentations at conferences as well as activities as scientific reviewer are documented.

3. Climate change and species ranges

On-going climate change is a driving factor for species range shifts (e.g. Parmesan et al. 1999, Hickling et al. 2006, Chen et al. 2011) and will pose a serious challenge for organisms and ecosystems (McCarty 2002). Beside distributional changes of single species, climate change is expected to alter biotic interactions. Positive changes, such as an escape from parasites or predators, are possible (Menéndez et al. 2008) as well as diverging influences on interacting species, hindering range expansions of the dependent species into new areas although climatic suitability is expected (e.g. Schweiger et al. 2008). Hence, potential risks for ecosystems and organisms must be detected as soon as possible.

An increasing amount of scientific literature mirrors the current discussion on ecological impacts of climate change and emphasizes the importance of a contemporary estimation of climate change impacts (for a review see **article 1**). However, it is difficult to gain an overview in the rapidly expanding field of scientific literature on ecological impacts of climate change. There is an increasing need for structuring the research approaches and findings in climate change research in order to direct future action in an efficient way towards research gaps and areas of uncertainty. **Article 1** analyses the published scientific literature on climate change impacts of the last decade (2003-2012) and provides an overview of geographical, taxonomical and methodological aspects in the field covered or ignored so far. I come to the conclusion that it is not only important to see differences between organisms and ecosystems in the expected intensity of impact and the speed and magnitude of response, but that it is also relevant to identify where knowledge is sufficient to decide upon proactive action and to direct management, and where this is not the case. To improve the strategies for the maintenance of functioning (and existence) of species, communities and ecosystems future

research priorities must be detected and knowledge gaps must be closed.

Nevertheless, as climate change is considered to be a driving factor for species range shifts (e.g. Walther et al. 2005, Hickling et al. 2006, Hitch & Leberg 2007, Ott 2009) contemporary estimations with the currently available information is just as important as the closing of knowledge gaps. Especially for nature conservation, range changes are of major concern, e.g. in case of reserve selection, immigration of invasive species or fulfilment of protection targets of existing reserves. Hence, adaptation strategies are immediately needed. To derive effective adaptation strategies, not only in nature conservation, it is important to assess potential influences of climate change on the distribution of species and habitats (**article 2, 3, 4**, Bush et al. 2014). Ecologically meaningful projections will require assessments of both future climatic suitability and species-specific ecological requirements and restrictions (**article 2, 3**).

One of the most important tools in ecological climate change impact research is the climate envelope modelling (**article 1**). Climate envelope models correlate species' occurrences with climatic variables that are expected to describe the observed distribution in a suitable way (Guisan & Thuiller 2005, Elith & Leathwick 2009). The resulting climate envelopes are used as a source for projections of climatically suitable future habitats of a species, which form the basis for the evaluation of potential range changes (Araújo & Guisan 2006). However, the model output depends on the choice of explanatory variables, climate model, emission scenario and modelling algorithm (Dormann et al. 2008). Nevertheless, climate envelopes are a useful first approach to estimate potential effects of climate change on species' distributions.

Suitable environmental conditions are characterized using either a statistical (i.e. correlative) or process-based (i.e. mechanistic) approach (Pearson 2007). Correlative models estimate environmental conditions that are suitable for a species by correlating known occurrences with reasonable environmental variables. Process-based models on the other hand incorporate physiologically limiting mechanisms such as phenology or reproductive success (e.g. Chuine & Beaubien 2001) even on a continental scale (Kearney & Porter 2009, Morin & Thuiller 2009). Correlative models are often criticized as they ignore important ecological processes such as demographic relationships or interspecific interactions that also limit geographic ranges (Cuddington et al. 2013). In contrast, process-based models are built on explicit assumptions based on causal mechanisms rather than correlation and are seen to be better suited to describe how a system works. However, process-based models require more resources (information, time as well as computational power) that are rarely available.

As "[...] spatially explicit occurrence records are available for a large number of species, the vast majority of species' distribution models are correlative" (Pearson 2007). However, the advantages of the single approaches (statistical vs. process-based) as well as their limitations

led to the development of hybrid models combining ecological processes and correlational components (e.g. Schurr et al. 2012, Ceia-Hasse et al. 2014). These models estimate both range dynamics and the response of demographic rates from observed species distribution data (Schurr et al. 2012), hence providing a promising “tool” for a more comprehensive estimation of climate change impacts.

4. Climate envelopes in species distribution modelling: potential and limitations

4.1 Nomenclature and definitions

Modelling approaches used to project current and future distributions of species and habitats are variously termed, e.g. “species distribution”, “ecological niche”, “environmental niche”, “habitat suitability” or “(bio)climate envelope” modelling (Pearson 2007). The term “species distribution modelling” is widespread. However, it should be considered that it is actually the distribution of suitable environmental conditions that is modelled, rather than the species’ distribution per se. Nevertheless, regardless of the name used, the basic modelling process as well as the central aim are essentially the same.

For a better understanding of the following paragraphs I here define how I understand and use the different terms throughout the thesis:

- Species distribution model (SDM): umbrella term for modelling the current and potential future or past distribution of species and habitat types
- Climate envelope model: one special approach within SDMs referring to the type of explanatory variables (i.e. climate) used for making projections
- Process-based (or mechanistic) model: incorporates physiologically limiting mechanisms in SDMs as explanatory variables (see chapter 3 for more details)
- Statistical (or correlative) model: correlates species’ distributions with environmental conditions (see chapter 3 for more details)

Generally, the occurrence of a species is seen in geographical space, i.e. plotted on a map. In case of species distribution modelling it is also important to see the occurrence of a species in environmental space. The environmental space is a conceptual space to which a species is expected to respond (Pearson 2007). The concept of environmental space is founded in ecological niche theory. Hutchinson (1957) defined the fundamental niche as an n-dimensional hypervolume that contains a set of environmental conditions allowing the species to survive and persist. The axes of this hypervolume define the environmental space (Pearson 2007). However, it has to be recognised that the environmental variables used in a species

distribution model cannot consider all possible dimensions of the environmental space - as proposed by Hutchinson (1957) – but rather represent a subset of possible environmental factors that influence a species' distribution.

All modelling examples in this thesis rely on statistical species distribution models using climate as main explanatory variable, i.e. I build climate envelopes for the considered species to estimate their potential future distribution. Hence, the term climate envelope is used synonymously with statistical species distribution modelling.

4.2 Potential of climate envelopes

The need for reliable projections is constantly increasing (Heikkinen et al. 2006, McMahon et al. 2011). Today, methods are becoming more and more sophisticated (Stankowski & Parker 2011), user-friendly algorithms are available and there is an increasing community of biogeographical modelling in the face of climate change (Hijmans & Graham 2006, Thomas 2010).

Climate envelope modelling provides several advantages for the analysis of present and potential future occurrences of species allowing different simulations and scenarios leading to a large span width of potential outcomes without harming any species. Models of the present situation are successfully applied in many ways, e.g. to guide field surveys to find new populations of known species (e.g. Bourg et al. 2005, Guisan et al. 2006) or to accelerate the discovery of unknown species (Raxworthy et al. 2003), to support conservation prioritization and reserve selection (e.g. Cabeza et al. 2010, Lessmann et al. 2014), or to guide the reintroduction of endangered species (e.g. Pearce & Lindenmayer 1998). These model results can be compared with observations and current knowledge, which means that they are verifiable.

Furthermore, they form the basis for future projections. The currently most prominent application is surely the projection of potential impacts of climate change on species distributions in general (e.g. **article 2, 3, 4**) assessing potential range changes from extinctions to stability and range gains. Further applications focus on impacts of land cover change (e.g. Wisz et al. 2008) as well as the spread of invasive species (e.g. Bradley et al. 2010, Stiels et al. 2011). Another currently very important approach is the assessment of disease risks (e.g. Rose & Wall 2011, Fischer et al. 2013, Porretta et al. 2013). In case of nature conservation, well-adapted models of future projections will further serve as a basis for decision-making (e.g. Summers et al. 2012, Faleiro et al. 2013, Guisan et al. 2013, Amorim et al. 2014).

4.3 Limitations of climate envelopes

Several methodological issues lead to uncertainties in model projections (Heikkinen et al.

2006). Such uncertainties arise for example from the choice of the modelling algorithm(s) and the type of model validation as well as from the choice of the climate model and emission scenario for future projections (Buisson et al. 2010). Uncertainties are also contained in the explanatory variables such as spatial autocorrelation (Legendre & Fortin 1989) and its impacts on model results (e.g. Crase et al. 2014). These methodological limitations are well acknowledged in current publications (Barry & Elith 2006, Elith & Leathwick 2009). However, further fundamental limitations occur concerning the data basis and will be discussed in the following sections.

4.3.1 Availability, timeliness and completeness of data on a continental scale

The feasibility and potential of climate envelope models has been enormously increased by the availability of large data sets. These comprise distribution and climate data as well as data on the ecological niche.

However, modelling results depend to some extent on the quality and quantity of species distribution data (e.g. Buisson et al. 2010). Still, the availability of distribution data, especially on a continental scale, is limited. For Europe, there are some comprehensive digital databases for animal and plant species distribution data available, such as the reporting of the EU Habitats Directive and the Atlas Florae Europaeae. However, timeliness, completeness and quality have to be questioned. For example, the maps with the “current” plant distribution within the Atlas Florae Europaeae were prepared between 1972 and 2004. The data thus integrate more than 30 years without any information if temporal changes during this period affect the data. In addition, the data are at least 10 years old. Further, it currently covers only 20% of the European flora (Bergmann et al. 2010). The Habitats Directive covers only species listed in its Annexes, though it comprises more than 1000 species. Currently, there are more than 12.000 plant species resident in Europe (Winter et al. 2009), and much more animal species (particularly insects, e.g. Fauna Europaea). So far underrepresented – if not neglected – are for example fungi, mosses, lichens and prokaryotes (incl. pathogens). These groups in most cases lack sufficient data regarding their distribution, their ecological requirements as well as their connection with climate and anthropogenic influences. Hence, they are difficult to model (e.g. Murray et al. 2011, Rohr et al. 2011).

Beside this, some species or species groups are overrepresented in data bases. For example, Cardoso (2012) highlighted that species of certain taxa (e.g. Lepidoptera) are favoured in the Annexes of the Habitats Directive as well as species that are widespread, of large size and attractive. In contrast, inconspicuous species are underrepresented – not only in data bases, but also in climate envelope modelling (e.g. Rubio-Salcedo et al. 2013). Obviously, species that are easily detectable and identifiable are better represented in databases than cryptic

species or species that are difficult to identify in the field. Further, the sampling method of the distribution data often leads to biased samples (Barry & Elith 2006). This means that the modelled relationships rather display the patterns at the sampled sites than the patterns across the entire study area, leading to spatial error. To sum up, suitable distribution data are available at least for some species (even on large spatial scales) providing the necessary information for (projective) species distribution modelling. However, most of the species are neglected or at least underrepresented.

The availability of climate data seems to be sufficient at first sight as there are a lot of weather stations all over the world collecting data for decades (National Climatic Data Center 1997). However, these weather stations are unevenly distributed concentrating in or near densely populated parts of the world, and in or near human settlements. Also the collected information differs. Predominantly, temperature and precipitation values are recorded (National Climatic Data Center 1997), whereas side effects such as wind are often missing. Additionally, as a matter of fact, rare climate or weather events disappear in long-term average values. However, effects of rare climatic events can be more important for species survival and even regeneration than long-term average conditions in climatic conditions (Jentsch & Beierkuhnlein 2008). Hence, there are some efforts to include information on climatic extremes. The inclusion of measures representing such climatic extremes lead to an improvement of model performance and a reduction of over- and under-prediction for tree species (Zimmermann et al. 2009).

Additionally, there are more than climatic variables determining the current distribution of a species that have to be considered for modelling. Depending on the spatial scale of climate envelope models, other factors become more important in the determination of the distribution (Pearson & Dawson 2003). Topography, land use, soil type and biotic interactions become even more important the finer the spatial scale. Topographic and soil type information is already available, even on a continental scale (e.g. European Soil Database, Digital Elevation Model). Land use information for Europe is provided by Corine land cover (EEA) and even land use scenarios are available (e.g. Prieler et al. 1998, Rounsevell et al. 2006). However, other data are less available or difficult to consider in the modelling process (e.g. dispersal distances (**article 2**) or biotic interactions (**article 3**)).

4.3.2 Integrating ecological knowledge (e.g. dispersal ability and biotic interactions) into species distribution models

The ecological niche of species is not only defined by abiotic settings, but to a large extent by biotic prerequisites. However, another limitation of climate envelopes is the restricted current knowledge and implementation of parameters defining the distribution of a species such as species' dispersal abilities and biotic interactions.

Up to now, most modelling studies apply two extreme (and unrealistic) dispersal scenarios: no dispersal and unlimited dispersal. In the very few studies that account for more specific dispersal traits in species distribution modelling, preferentially in plants (e.g. Dullinger et al. 2004, Brooker et al. 2007, Smolik et al. 2010), long-distance dispersal is one of the most widely considered processes. Long-distance dispersal is a rare event, but plays an important role in plant species dispersal (Nathan 2006). It is also relevant in animal dispersal, especially for small species that can be blown away by wind over large distances (Bonte et al. 2009). A recent study on *Leucorrhinia caudalis* by Keller et al. (2010) investigated the spread of this species over the last 20 years in Switzerland. The authors demonstrate long-distance colonisation at scales of 30 to 50 km.

The integration of realistic dispersal assumptions is difficult because of manifold factors. One problem is the limited availability of dispersal data. Only for some species these data are forthcoming, displaying in most cases single observations and only sometimes dispersal studies (e.g. on migratory birds). Second, climate change can influence dispersal in two directions - inhibition and facilitation - making the few available data additionally uncertain (see e.g. Massot et al. 2008 for inhibition). Third, dispersal rates are not constant in space. The dispersal distance follows a negative exponential curve meaning a high probability of low distance dispersal and a low probability of reaching far distances (Kot et al. 1996). Further studies even detected sigmoidal distributions of dispersal (Heinz et al. 2005). Fourth, landscape permeability influences dispersal in space and time. In-hospitable landscapes inhibit dispersal although a species is able to reach distant areas or they necessitate a circumvention of barriers leading to time lags compared to the direct way (Lawler et al. 2013). A further challenge in species distribution modelling is the integration of biotic interactions. Observations and experimental studies on biotic interactions in times of climate change are increasingly conducted (e.g. Jentsch et al. 2011, Liu et al. 2011). However, methods to integrate interactions in species distribution modelling are still rare (see Araújo & Luoto 2007 or Schweiger et al. 2008 for an example), and no comprehensive analysis on how to best represent biotic interactions in species distribution models has been conducted.

Climatic suitability of a site alone and the organismic potential to reach these habitats are not sufficient to project in a realistic way whether species might adapt to climate change by range shifts. Many species are influenced by other species, such as through competition. Or they even depend on interacting partners such as host plants for the offspring. Climate change is seen as a major threat for biotic interactions potentially leading to their disruption or de-synchronisation (Van der Putten et al. 2010). Such kind of reactions has a large impact on the future distribution of a species – such as making climatically suitable habitats inhospitable.

Hence, model projections neglecting specific biotic interactions lead to significant differences compared to models considering biotic interactions in their projections of future ranges (Araújo & Luoto 2007).

4.3.3 Modelling complex entities

The focus of practical and theoretical climate envelope research has been predominantly on single species. Communities and especially habitat types as a whole, are still rarely considered (Mücher et al. 2009). However, changes in climatic conditions lead to responses in species composition and community structure (Bruehlheide 2003, Kreyling et al. 2008).

Habitats, especially the habitat types of the EU Habitats Directive, are defined by their characteristic abiotic conditions and characteristic plant species communities (European Commission 2007). Hence, these habitat types form a complex entity which can be handled differentially in climate envelope modelling: 1) as one object (comparable to one species in case of an organism) whose distribution is described by correlative environmental conditions, and 2) as an object whose distribution is defined by correlative environmental conditions and the occurrence of characteristic plant species. We expect that the way these complexes are integrated into the modelling process influence the modelling results.

The consideration of such complexes refers to a further limitation: that habitat conditions in the potentially newly suitable areas have to be fulfilled. For example, Keller et al. (2010) trace the recently observed spread of *Leucorrhinia caudalis* in Switzerland back to the recreation and restoration of ponds. Beside climate, dispersal ability and potentially interacting partners, the habitat requirements are limiting for all species. For example, the non-availability of habitats at the new climatically suitable area or a time lag in their short-term development prevent successful breeding and colonization.

4.4 Climate envelopes in this thesis

Climate envelope models are powerful tools in ecological climate change impacts research and provide a first approximation of potential consequences of climate change. However, uncertainties constrain their explanatory power. Hence, further developments in species distribution models are needed to reduce these constraints as well as a responsible consideration of modelling results in environmental management.

This thesis elaborates three points of criticism regarding projective climate envelope modelling and introduces different methods of resolution: 1) the consideration of dispersal abilities, 2) the consideration of biotic interactions – both coping with the above mentioned limitations in the data availability –, and 3) the consideration of the complexity of the study object.

5. Extending the climate envelope: towards more ecology in species distribution modelling

5.1 Dispersal

One rather simple approach for considering animal dispersal abilities was applied by Buse & Griebeler (2011) who classified dispersal distances of grasshoppers and bush-crickets depending on the degree of wing development. With unlimited dispersal three of seven species exhibit a strong increase in suitable area. However, the unlimited dispersal strongly overestimated ranges in comparison to classified dispersal (i.e. by up to 200% in Rhineland-Palatinate and by up to 494% in southern Germany). Even the most mobile of these species were unable to completely fill future suitable areas assuming classified dispersal capacity. These findings of Buse & Griebeler (2011) illustrate that a more realistic assessment of species dispersal capacity strongly alters model results by constraining the extreme assumption of unrestricted dispersal.

I apply another approach by considering observed dispersal distances to restrict the maximum reachable distance (**article 2**). Comparing two common dispersal scenarios (no and unrestricted dispersal) with a species specific one for six Odonata leads to contrasting modelling results in three cases. I show that even rough estimates of dispersal distances provide more realistic results, reducing the overestimation of unlimited dispersal scenarios and providing a basis for nature conservation management options.

Further approaches to cope with this problem define cost distances for different landscape types (e.g. Foltête et al. 2008), calculate least-cost paths for species to reach a certain target (e.g. Fischer et al. 2011) or produce continuous maps of movement probabilities that cover all possible routes (Lawler et al. 2013).

5.2 Biotic interactions

There are already approaches to integrate biotic interactions into SDMs, such as implemented by Araújo & Luoto (2007) and Schweiger et al. (2008), coping with the influence of essential host plants on the current and future distributions of butterflies. In **article 3** I compare three different approaches to consider biotic interactions in projective species distribution modelling, and analyse the general results of these approaches, their modelling performance and the span width in their projections. The example of the dragonfly *Aeshna viridis* and its essential egg-laying plant *Stratiotes aloides* shows that spatial differences in future projections are small between the applied approaches. However, the modelling performance and similarity in the projected niches differ considerably within the approaches and partly contradict the results of Araújo & Luoto (2007) and Schweiger et al. (2008). Nevertheless, it

seems obvious that it is more important to consider biotic interactions at all than to neglect essential interaction partners.

Most of the currently applied approaches to integrate biotic interactions, including **article 3**, are unidirectional, i.e. one species depends on one or several other species (Kissling et al. 2012). Hence, reciprocal effects of interactions have been neglected so far. Recently, novel approaches are developed to model biotic interactions in multispecies assemblages at large spatial extents (Kissling et al. 2012). These approaches additionally consider linkages between species pairs, the strength of interaction as well as interactions mediated by resources or environmental conditions.

5.3. Complexity

Regarding the question on how to model complex entities such as habitat types, we apply two fundamental approaches: 1) the 'direct habitat approach' - treating the habitat type as a species, i.e. the occurrence of the habitat type (as reported by the member states of the EU) is used, and 2) the 'indirect species approach' where the habitat type is modelled on the basis of the joint occurrence of its characteristic plant species (**article 4**). Both approaches perform well, though the direct approach yields a better model performance. Under the no dispersal scenario both approaches project similar range losses. However, under unrestricted dispersal the indirect approach projects a much lower gain than the direct approach.

Article 4 illustrates two rather different approaches that technically perform well regarding the applied performance criteria, though the choice of modelling approach strongly affects the assessment of potential climate warming impacts. Furthermore, one has to bear in mind that habitat types are complex structures. They are not only characterized by specific species compositions and climatic demands, but depend on further abiotic conditions, such as soil type. Beyond that, the boundaries between different habitat types are fluent. Some of the characteristic plant species may lose and some may gain distribution area, which can lead to a more restricted expansion of the distribution. Additionally, the selected plant species cover only parts of the current distribution of the habitat type. Most plants are wider distributed than the habitat type, and some are even more restricted. In addition, throughout Europe, not all characteristic plants of one habitat type appear at all of its locations.

All this complicates the modelling of habitat types. However, with the current availability of data, potential impacts of climate change on European protected habitat types are identified.

6. Synopsis of the following manuscripts

In the following I briefly summarize the manuscripts of this thesis and show how they relate to the current state of knowledge and recent developments in species distribution modelling.

Article 1 reviews the current state of knowledge accumulated over the last ten years (2003-2012) about impacts of climate change on species and ecosystems. The amount of research and the number of articles in this field is overwhelming. Hence, there is an increasing need for structuring the research approaches and findings in climate change research in order to direct future action in an efficient way towards research gaps and areas of uncertainty. Almost 1200 articles of the scientific literature listed in the ISI Web of Science are analysed and explored regarding the geographical distribution of knowledge gain, the studied taxonomic groups, ecosystems and environmental parameters as well as the applied methods. In a rapidly evolving research landscape, this review provides an overview of the current patterns of knowledge distribution and research demands arising from knowledge gaps and biases.

The implementation of ecological data in climate envelope models is an increasing field of research requiring reliable data. In **article 2** observed species-specific dispersal distances of six dragon- and damselflies are integrated in the modelling process, and the results are compared to an 'unlimited dispersal scenario' and a 'no dispersal scenario'. Considering species-specific dispersal distances leads to contrasting results regarding the 'unlimited dispersal scenario', even for highly mobile species, if the projected future potential suitable climatic areas are far too distant from the current occurrences. The integration of observed dispersal distances enables an approximation to more realistic projections compared to the regularly applied two dispersal extremes. However, the data basis is scarce and observational data are associated with a high degree of uncertainty.

Beside the shift of species' ranges climate change is expected to alter biotic interactions, and may lead to temporal and spatial mismatches of interacting species. However, biotic interactions are still rarely incorporated in species distribution models. In **article 3** potential impacts of climate change on the obligate interaction between *Aeshna viridis* and its egg-laying plant *Stratiotes aloides* in Europe are assessed. Three different approaches for incorporating biotic interactions in species distribution models are compared: (1) 'overlap approach', (2) 'explanatory variable approach', and (3) 'reference area approach'. All approaches are compared to a single species model of *A. viridis* without interactions. This comparison emphasizes the importance of including obligate biotic interactions in projective species distribution modelling. The use of the 'reference area approach' is recommended as this method allows a separation of the effect of climate and occurrence of the host plant.

For the habitat of a species another question arises concerning climate envelope modelling: How to model such complex entities? Habitat types of the Habitats Directive are characterized by abiotic conditions and their plant species composition. Therefore, climate change impacts on habitats can be assessed by two complementary statistical approaches: either directly by modelling the climate envelope of the habitat, or indirectly by modelling the habitat in terms of its plant species. In **article 4** potential climate change impacts on the distribution of five natural and semi-natural grassland habitat types, defined by the EU Habitats Directive, are modelled. Both approaches yield reasonable results, though the indirect approach strongly depends on the availability of plant distribution data of the habitat types' characteristic plant species. However, the modelling of the future distribution of habitat types not exclusively based on their mapped distributions, but also based on their constituent elements, and in particular their characteristic plant species, is suggested.

7. Summarizing conclusions and emerging research challenges

Climate change effects on species and their distributions is one of the major topics of research today (Loarie et al. 2009, Körner & Basler 2010, Cahill et al. 2013, **article 1**). Assessing potential consequences is a contemporary requisite for the preservation of biodiversity. To achieve this, potential range changes are estimated using climate envelope modelling techniques (Elith & Leathwick 2009). Within the last years lots of techniques and tools were developed and improved providing the basis for future projections. However, all models have their pros and cons, are afflicted with uncertainties, and explain the current distribution of a species in a more or less suitable way (chapter 4).

Hence, handling uncertainties and improving models has become an important key aspect in climate change impacts research. Beside methodological improvements an enhancement of the data basis, especially on ecological – but also on reliable distributional - data, is urgently needed (e.g. Araújo & Guisan 2006). In most cases the ecological knowledge concerning a certain species is restricted or practically non-existent. However, improving models requires the collection and provision of suitable (ecological) data (Araújo & Guisan 2006, Jeltsch et al. 2008).

This requires on the one hand observational data. Global monitoring programs provide large datasets on species' distributions, ecology, and functional traits (e.g. GBIF, TRY). Further monitoring programs with emphasis on observable climate change impacts can promptly assess changes in distribution, abundance, and population structure, and thereby provide an observational-based data basis for modelling studies. Hence, models no longer rely on ecological assumptions concerning the potential reaction of a species, but known reactions

on climatic changes are projected into the future. However, the current monitoring status is scarce. Nevertheless, there is not the option to wait for better monitoring data for all species as reactions on changed climatic conditions may become obvious within a few years. Then, it may be too late for adaptation strategies. Anyhow, efficient long-term monitoring programs with high spatial and temporal resolutions and comparable data acquisition need to be installed as soon as possible (e.g. Jacquet et al. 2014).

On the other hand, the ecological knowledge is extended by experimental studies. These studies have the advantage that they experimentally modify the surrounding conditions in a way that is expected for the next years or decades. These experiments can also include the simulation of extreme events, which are another important component of global climate change (IPCC 2012). Although experiments rely on assumptions concerning the direction and degree of change, they provide first approximations of potential reactions and their direction (e.g. positive or negative effect of warming). They also allow focussing on key aspects of species, such as forage quality (Grant et al. 2014a), biotic interactions (Grant et al. 2014b) or genetic diversity (Avolio et al. 2013).

However, the main challenge for the next years is surely the need to extend climate envelope models with ecological constraints to achieve a more comprehensive assessment of the vulnerability and adaptive capacity of species. This leads directly to more process-oriented models that include for example biotic processes such as dispersal (**article 2**), biotic interactions (Kearney & Porter 2009, **article 3**) or population dynamics (Buckley 2008, Keith et al. 2008), but also population genetics (McCallum et al. 2014). The integration of processes in statistical models helps to enhance realism of modelling results even on large spatial scales (Schurr et al. 2012).

Data availability and their reasonable use in species distribution modelling provide the fundament for adaptation strategies in times of climate change. A contemporary assessment of potential impacts on species' ranges is vitally important to derive effective strategies. The improvement of the data basis and availability as well as the implementation of processes in climate envelope models have a direct effect on the future projections of species' distributions and therefore on the development of suitable management measures.

The present thesis highlights the above mentioned key aspects: performing model projections, considering model uncertainties and developing model improvements. The articles include the analysis of potential effects of climate change on the distribution of selected species and show options to improve species distribution models by implementing ecological knowledge such as dispersal distances and biotic interactions. This work provides a contribution to the current state of knowledge regarding climate envelope modelling by supplying ideas and

methods to improve modelling studies and therewith the basis for adaptation strategies.

Finally, I have *learned* two things during my thesis regarding climate envelope modelling: “Models don’t represent the truth (and it is neither their aim!)” and “Garbage in, garbage out (- model assumptions influence model results!)”

8. List of articles and declaration of own contribution

Article 1:

Authors: Anja Jaeschke , Torsten Bittner, Anke Jentsch, Carl Beierkuhnlein

Title: The last decade of ecological climate change impact research: Where are we now?

Journal and status: Naturwissenschaften 101: 1-9 (2014)

Authors’ contribution: The idea and concept of the manuscript were developed by Anja Jaeschke, Torsten Bittner and Anke Jentsch. The literature study as well as the preparation of tables and figures was done by Anja Jaeschke and Torsten Bittner. The manuscript was written and revised by Anja Jaeschke. The final editing was provided by Carl Beierkuhnlein and Anke Jentsch. Anja Jaeschke is the corresponding author.

Article 2:

Authors: Anja Jaeschke, Torsten Bittner, Björn Reineking, Carl Beierkuhnlein

Title: Can they keep up with climate change? - Integrating specific dispersal abilities of protected Odonata in species distribution modelling

Journal and status: Insect Conservation and Diversity 6: 93-103 (2013)

Authors’ contribution: Anja Jaeschke and Torsten Bittner had the idea and developed the concept for this article. Both authors also did the modelling, the data analysis and developed the R-Code. The article was written by Anja Jaeschke. Torsten Bittner provided the figures. Torsten Bittner, Björn Reineking and Carl Beierkuhnlein gave valuable comments and processed the final editing. The revision of the manuscript was performed by Anja Jaeschke. Anja Jaeschke is the corresponding author.

Awards: Best paper published 2012/2013 in Insect Conservation and Diversity (awarded by the Royal Entomological Society in March 2014)

Article 3:

Authors: Anja Jaeschke, Torsten Bittner, Anke Jentsch, Helmut Schlumprecht, Björn Reineking, Carl Beierkuhnlein

Title: Biotic interactions in the face of climate change: A comparison of three modelling approaches

Journal and status: PLoS ONE 7(12): e51472 (2012)

Authors` contribution: Carl Beierkuhnlein had the idea and Anja Jaeschke and Torsten Bittner developed the concept for this manuscript. Björn Reineking helped with the development of the R-Code and Anja Jaeschke did the modelling. The article was mainly written by Anja Jaeschke. Helmut Schlumprecht added valuable text passages in the discussion and literature. Figures and tables were prepared by Torsten Bittner and Anja Jaeschke. Carl Beierkuhnlein, Anke Jentsch and Björn Reineking finally edited the manuscript. The revision of the manuscript was done by Anja Jaeschke. Anja Jaeschke is the corresponding author.

Article 4:

Authors: Torsten Bittner, Anja Jaeschke, Björn Reineking, Carl Beierkuhnlein

Title: Comparing modelling approaches at two levels of biological organisation – Climate change impacts on selected Natura 2000 habitats

Journal and status: Journal of Vegetation Science 22: 699-710 (2011)

Authors` contribution: The idea and concept of the article were developed by Torsten Bittner, Anja Jaeschke and Björn Reineking. Björn Reineking helped with the development of the R-Code, Torsten Bittner analysed the data and Anja Jaeschke performed the modelling. The figures and tables were created by Torsten Bittner. Torsten Bittner and Anja Jaeschke contributed equally to the writing of the manuscript. Carl Beierkuhnlein did the final editing. The revision was done by Torsten Bittner and Anja Jaeschke.

9. References of Introduction

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Article 1

The last decade of ecological climate change impact research: Where are we now?

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The last decade in ecological climate change impact research:

Where are we now?

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Abstract

Climate change is increasingly affecting organisms and ecosystems. The amount of research and the number of articles in this field is overwhelming. However, single studies necessarily consider limited aspects. Hence, there is an increasing need for structuring the research approaches and findings in climate change research in order to direct future action in an efficient way towards research gaps and areas of uncertainty.

Here, we review the current state of knowledge accumulated over the last ten years (2003-2012) about impacts of climate change on species and ecosystems. Almost 1200 articles of the scientific literature listed in the ISI Web of Science are analysed. We explore the geographical distribution of knowledge gain, the studied taxonomic groups, ecosystems and environmental parameters as well as the applied methods.

Several knowledge gaps arise. Most of the first authors of the analysed articles are resident in North America, Australia or Europe. A similar pattern is found for the study areas. Vascular plants and therewith forests are the most studied taxonomic group and ecosystem. The use of models to estimate potential impacts of climate change is well established in climate change impact research and is continuously developing. However, there is a lack of empirical data derived from experimental climate change simulations.

In a rapidly evolving research landscape, this review aims at providing an overview of the current patterns of knowledge distribution and research demands arising from knowledge gaps and biases. Our results should help to identify future research needs and priorities.

Keywords

Global warming, knowledge gaps, research demands, scientific literature

Introduction

The consequences of anthropogenic climate change have become a major topic of research (e.g. Loarie et al. 2009; Körner and Basler 2010; Cahill et al. 2013) and policy (e.g. IPCC 2012, 2013). Observational, experimental and modelling studies are published in high frequency. It is especially the response of species and ecosystems that needs to be clarified because these deliver services to the human society or may contribute to novel qualities of risk. However, there is still uncertainty about the responses of plant and animal populations, of communities as well as of entire ecosystems.

An increasing amount of scientific literature mirrors the current discussion and emphasizes its importance (see Peñuelas et al. 2013). However, as ecological research projects must in general focus on specific case studies or single experiments, a generalization of the results is difficult. Findings may differ in dependence on the methodological approach. And finally, there is a wide array of mechanisms and biological units that can be addressed such as species range shifts, extinction risks or altered biotic interactions. Problems of temporal (e.g. speed of change, inertia, lagged response), spatial (e.g. grain, resolution, extent) and biological (e.g. demography, life cycles, levels of organisation) scales must be related to each other, which cannot be handled within the scope of one single study.

Unfortunately, knowledge gaps are also a consequence of an uneven distribution of research funding across countries and regions (Felton et al. 2009). Additionally, bias is reflecting self-accelerating processes in science such as the preference of a specific ecosystem due to its suitability for experiments or because stimulating results of single case studies were published in high-ranking journals, provoking anti-theses, alternative explanations, and a legacy of further studies in an emerging citation network.

The amount of studies varies considerably between taxonomic groups. Some groups are more intensively investigated because they are well known and easy to access (such as plants), exhibit short life cycles (such as insects) or are connected to an extensive data basis (such as migratory birds). Other taxonomic groups (such as protozoa or archaea) have received much less attention although they are crucial for the functioning of ecosystems. At the scale of ecosystems, most approaches are – by purpose – relatively simple according to the involved organisms and processes. Global vegetation models cannot cope with the total complexity of life and consider all individual species (which are moreover largely unknown). They must refer to a rough and simplifying classification of a small set of functional groups or on selected

plant traits (Lavorel et al. 2007 and references therein).

However, it is unquestioned that climate change will pose a serious challenge for organisms and ecosystems (McCarty 2002). Potential risks for ecosystems and organisms, especially for those where current proactive management activities are low, must be detected as soon as possible. As a matter of fact, it is difficult to gain an overview in this rapidly expanding field of scientific literature on impacts of climate change. There is an increasing need for structuring research approaches and findings in order to direct future action in an efficient way towards research gaps and areas of uncertainty. Additionally, practitioners and politicians are looking forward to an evaluation in which fields the knowledge basis is already rather sound and where information is scarce. It is not only important to know about specific differences between organisms and ecosystems in the expected intensity of impact and the speed and magnitude of response. It is also relevant to identify where knowledge is sufficient to decide upon proactive action and to direct adaptation management, and where this is honestly spoken not the case. To improve the strategies for the maintenance of functioning (and existence) of species, communities and ecosystems, future research priorities must be detected and knowledge gaps must be closed. Contributing to this ambitious task is the goal of this study.

Here, we present a review of the last ten years of scientific literature focusing on biological and ecological climate change impacts on organisms and ecosystems. First, we conduct a systematic literature survey using the ISI Web of Science (Thomson Reuters, 2013). The literature is scrutinized in terms of i) the location of the study area, ii) the first author's institutional address, iii) the studied taxonomic group(s), iv) the studied ecosystem, v) the studied climate change affected parameter, and vi) the applied study method. The obtained results are used to identify knowledge gaps and research challenges. We identify areas of particular uncertainty and suggest ways to address these gaps.

Methods

We use the ISI Web of Science database to search for articles on responses of fauna, flora and habitats to climate change impacts. Relevant alternative suffixes are included using the asterisk (e.g. "clima* envelop*"). The whole search string is given in Table S1.

Our search covers the last ten years (2003-2012): Thus it reflects the current state of knowledge for climate change impacts research. Articles on palaeontological and past climatic changes are excluded. The comprised research articles (excluding review articles) are analysed on the basis of title, keywords and abstract with a set of criteria: Geographic (location of the study area, first author's institutional address), taxonomic (studied taxonomic group), ecosystem (type of ecosystem) and methodological coverage (method, climatic aspects) are assessed.

For the geographic analysis we further correlate the number of studies per country with the gross domestic product (GDP) and the climate risk index (CRI). We then correlate the GDP with the CRI to estimate the influence of funding opportunities and climate change vulnerability on the amount of research. Correlation analyses were performed using Pearson's product-moment correlation. Additionally, we analyse the number of publications per taxonomic group and compare it to the number of species per taxon to estimate if certain taxonomic groups are over- or underrepresented in climate change research.

Results

Our search yielded 1189 research articles that are really focused on the biological responses to climate change at the ecologically relevant levels of organisation. The number of articles increased between 2003 and 2008, reaching the overall maximum of published articles in 2008 (184 articles) (Fig. 1).

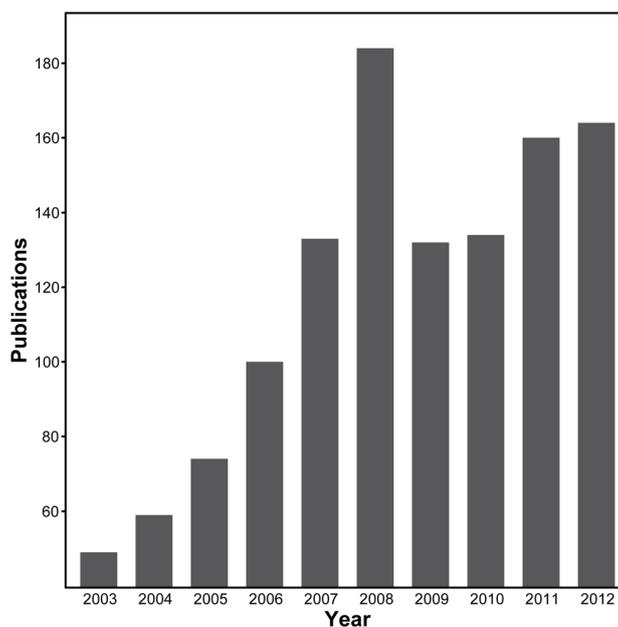


Fig. 1 Number of English-language scientific publications concerning climate change impacts on organisms and ecosystems between 2003 and 2012 derived from the ISI Web of Science

Study areas

Most of the studies on ecological climate change impacts were conducted in Europe and North America (Figs. 2 and 3). Africa is expected to be influenced most by climate change (IPCC 2007), but only very few climate change studies address the organisms and ecosystems on this continent. Within Africa, most studies were conducted in South Africa, within the Cape Floristic Region, whereas studies in Northern or in Central Africa are still rare.

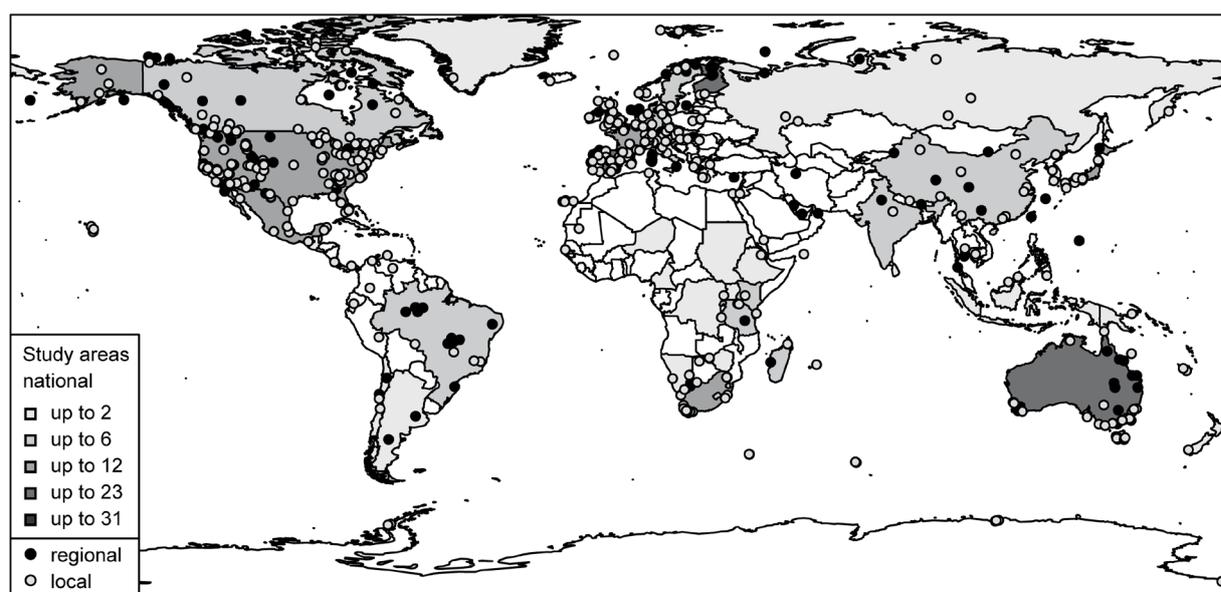


Fig. 2 Global distribution of study areas on the impacts of climate change on organisms and ecosystems. Information on study areas is taken from English-language publications in the ISI Web of Science between 2003 and 2012. Study areas are categorized into local, regional and national levels. National studies involve analyses of whole countries. Regional is defined as studies in regions within countries. Local studies are in local areas such as a National Park or a city. Publications on global processes or continents (except for Australia) are not displayed

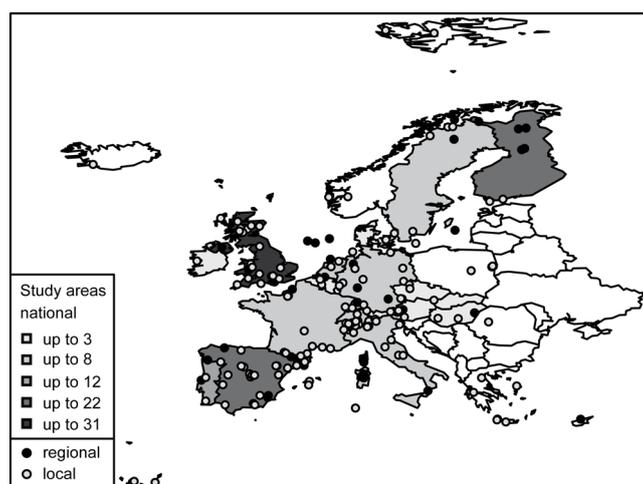


Fig. 3 Distribution of study areas on the impacts of climate change on organisms and ecosystems in Europe (except of the European part of Russia). Information on study areas is taken from English-language publications in the ISI Web of Science between 2003 and 2012. Study areas are categorized into local, regional and national levels. National studies involve analyses of whole countries. Regional is defined as studies in regions within countries. Local studies are in local areas such as a National Park or a city

Twenty-nine articles were global studies considering climate change impacts on organisms and ecosystems over all continents. Continental scale studies form a further proportion of articles (105 studies). Their geographical distribution is quite uneven, led by Europe (58), and followed by North America (17), Australia (17), Africa (8) and South America (5). An additional twenty-three studies considered individual federal states of the USA, while twelve studies were focused on federal states of Canada as study area.

Research institutions of first authors show a comparable distribution as detected for the study areas (Fig. 4). Most of the publications have a first author who is resident in the USA (29%), followed by the United Kingdom (10%), Australia (9%), Germany (7%) and Canada (7%). There are few first authors from developing countries.



Fig. 4 Number of publications in the ISI Web of Science per country between 2003 and 2012 about the impacts of climate change on fauna, flora and habitats, according to the first authors' institutional address

The global distribution of research and published findings concerning current and future climate change impacts on organisms and ecosystems partly reflects global patterns in the vulnerability of ecosystems (e.g. the arctic biome) and of their biodiversity (e.g. Central European hay meadows). But it also reveals a strong bias on the regions of scientific excellence and of economic power that is translated into research funding (see also Beier et al. 2012).

Studies concerning climate change are mainly conducted in countries with a high gross domestic product (GDP) (Fig. S2a) ($r: 0.76$, $p\text{-value}: < 0.001$; Pearson's product-moment correlation). However, parts of the world with high GDP are still underrepresented including some states in South America and Asia. With regard to the Climate Risk Index of 2011 (Harmeling and Eckstein 2012), which indicates the extent to which countries have been affected by extreme events (such as storms, floods or heat waves), there is a negative correlation between the number of studies and the ranking of the Climate Risk Index (Fig. S2b) ($r: -0.24$, $p\text{-value}: < 0.01$; Pearson's product-moment correlation), which might be explained by the high number of countries with the lowest risk (rank 131, 52 of 182 considered countries). These 52 countries contributed to only nine studies on climate change impacts. Comparing the Climate Risk Index with the GDP also a negative trend becomes obvious (Fig. S2c). The higher the GDP the more affected was a country by extreme weather events in 2011.

However, the high vulnerability of Asia for example is absolutely underrepresented in research and not sufficiently addressed in regional studies. In fact, six of the first ten countries that were most affected by extreme weather events in 2011 are countries in Asia with Thailand in

front (Harmeling and Eckstein 2012). Very recently, the Philippines were hit by the typhoon Haiyan.

Funding for climate change research increased during the last years. Nevertheless, there are large discrepancies between a country's GDP and the percentage gross expenditure on research and development (GERD) (Palmer 2011). The highest relative investment in research and development in 2009 is achieved by Israel (4.2% of GDP). In contrast, the United States and China, which are indeed leading the global GERD ranking regarding the monetary amount (absolute investment), provided just 2.7% and 1.4% of GDP, respectively, for research and development.

Investigated taxonomic groups and study parameters

Vascular plants are the primary taxonomic focus of the reviewed studies (40%). This can be understood, because plants are the most important functional group for primary production and the basis of terrestrial food chains. However, plants are also good study subjects as they are not mobile, of macroscopic scale, and well investigated. Birds and insects make up a further large proportion (13%, each). Other taxonomic groups such as reptiles, amphibians or lichens are underrepresented in current research (< 3%), although these are known to be very sensitive to and even already influenced by climate change (European Topic Centre on Biological Diversity 2008; D'Amen et al. 2011).

Compared to the number of known species, vascular plants, birds and mammals can be evaluated as well covered (Fig. 5). Although many studies exist on insects, as a consequence of their tremendous species richness, this group is still absolutely under-investigated (0.4%). This is also true for other groups such as crustaceans (0.07%), lichens (0.1%) and mosses (0.03%) which are highly underrepresented concerning the number of species per taxonomic group, too (Fig. 5).

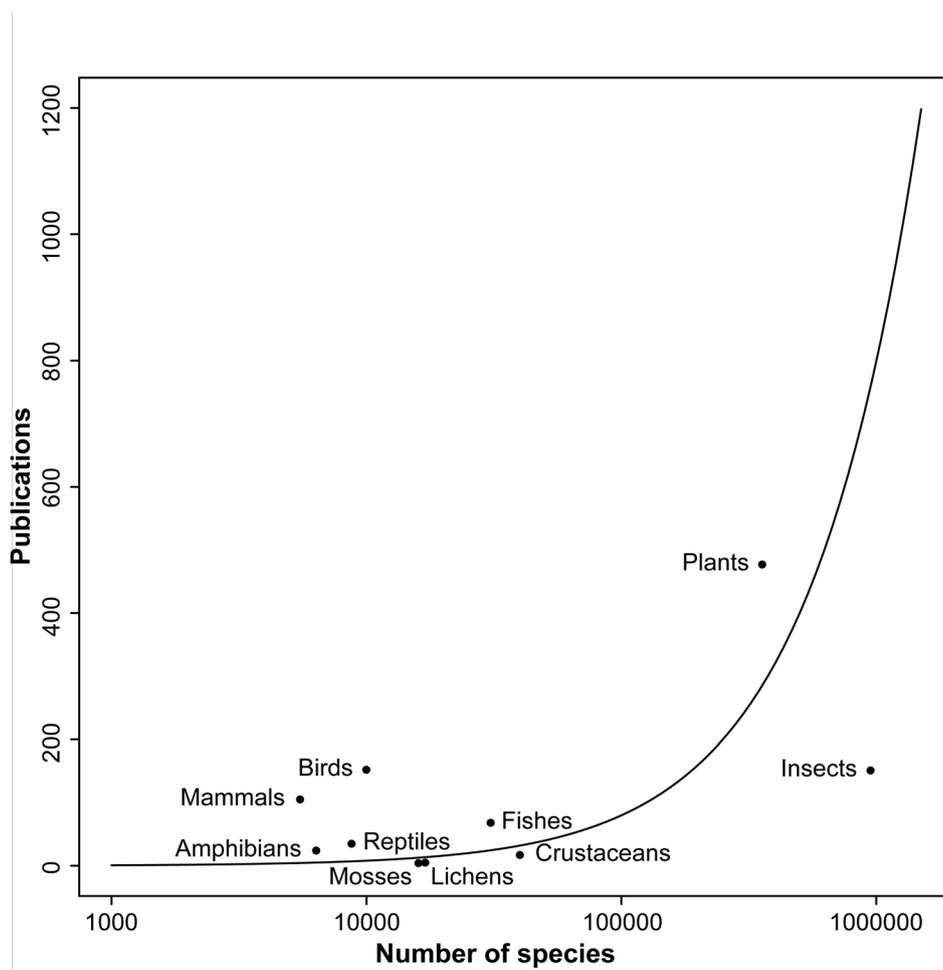


Fig. 5 Taxonomic coverage of the reviewed climate change literature between 2003 and 2012. The graph shows the number of publications against the number of known species for each taxonomic group. The curve represents the mean expected number of publications per taxonomic group. The numbers of species are taken from Vié et al. (2009)

Direct modifications in climatic parameters, such as changes in the temperature and precipitation regime, are predominant in our review (Tab. 1). However, it must be kept in mind that it is rather the modification of climatic variability, timing and extremeness of weather events that is important for most biota rather than a gradual change in average climatic conditions (Jentsch and Beierkuhnlein 2008). More indirect drivers of environmental change such as climate change induced modified land use, but also sea level rise, changes in snow cover or biogeochemical feedback loops affecting the soil carbon, nutrient availability and cycling, or changes in the salinity of limnic are not detected adequately by our search string or are investigated independently from climate change.

Table 1 Percentage of climate change related study parameters. The main focus lies on changes in temperature and precipitation. Parameters are only listed if they are studied in at least 1% (rounded) of the analysed articles (N = 1189)

Parameter	Number	Percentage (%)
Temperature	482	40
Precipitation	230	19
CO ₂	27	2
Moisture (soil, air)	14	1
Fire	12	1
Land use/ Land cover	10	1
Nutrients	7	1
N ₂	6	1
Hurricane	6	1
Snow/Ice cover	6	1
Flooding	6	1
Sea level rise	6	1
Salinity	6	1
Sea ice	6	1

This seems to be the case also with studies on the increase in atmospheric carbon dioxide content. Here many studies have been performed, but many of them are not found by our search string that is concentrated on climatic consequences of increased levels of greenhouse gases and not on the atmospheric chemistry in its background. However, environmental and biotic interactions between temperature, water supply and the partial pressure of carbon dioxide should not be ignored.

Type of ecosystem

More than two fifths of the articles, that clearly state an ecosystem in title, abstract or keywords, focus on aquatic ecosystems, such as freshwater, saltwater and coastal ones (44%, 233 out of 531 articles). A comparably high portion is related to forests (41%) (Fig. 6). With 7% grassland ecosystems are underrepresented in climate change research, although they are suitable model ecosystems for climate change experiments (Shaw et al. 2002; Jentsch et al. 2007). Raised bogs, fens and palsa mires are almost neglected (2%) in ecological climate change impact research, although they are considered to be extraordinarily sensitive to changes in climatic conditions, often harbour a rich diversity of species, and are undergoing a heavy degradation (Fronzek et al. 2006).

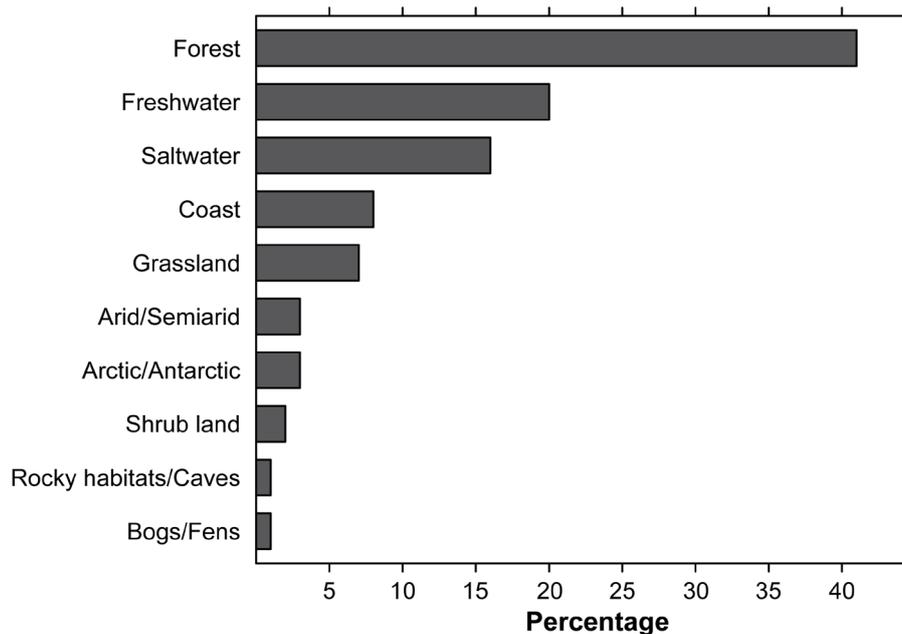


Fig. 6 Ecosystem coverage in published climate change literature in the ISI Web of Science between 2003 and 2012 (N = 536). Grassland ecosystems include savannahs, wetlands, prairies and tundra; coastal ecosystems include estuaries, intertidal zones, brackish water and marshland; raised bogs and fens include palsa mires. Arctic and antarctic sea life is double-coded as saltwater and arctic/antarctic

And there are more spatially and biologically important ecosystems that are almost neglected such as those in arid and semi-arid as well as arctic and antarctic regions. Arctic and antarctic sea life is double-entered as saltwater and arctic and antarctic ecosystem (10 cases).

Research method

Research methods that are applied predominantly in ecological climate change impact research include field observations, experiments (field and lab), modelling of future trends and meta-analyses or data mining, respectively. Half of the articles concentrate primarily on the modelling of future trends in ecological responses (50%). A substantial proportion of the literature is based on field observations (27%). Field and lab experiments are still underrepresented (12%), even if this field of research is strongly increasing (e.g. Beier et al. 2012). The limited contribution in the amount of experimental studies may reflect the higher requirements of cost-intensive instrumentation and experimental design as well as the need for technical staff in experiments. Factitiousness must be accepted as a trade of in controlled and replicated experiments. However, in contrast to observational and modelling studies, experiments are tools that allow testing hypotheses. Meta-analyses are also not common (10%), which is well to be understood as they unite the results of many single studies.

The application of modelling, field observations and experiments shows a peak in 2008 (Fig. S1), one year after the last IPCC report. In the following year, only modelling studies are exceeding this peak.

Discussion

Patterns and knowledge gaps

The detected geographical bias in the distribution of study areas and the first author's institutional addresses can be seen as the result of discrepancies in the scientific and technological research capacities of nations and illustrate the uneven availability of financial resources (Fazey et al. 2005). The amount of research that is reflected in the financial support for research on consequences of global warming is usually of national interest. Consequently, policy relevance demands for national analyses and products for decision makers and conservation managers. As a matter of fact, such studies are often published in national journals (and languages) with limited access for an international readership.

However, beside financial infrastructure and national interests major science questions drive climate change research. Impacts on species and their distributions especially of those protected by laws in nature conservation are one key aspect. The aim of ecological climate change impacts related research is to estimate potential reactions of species with the help of observational, experimental or modelling studies. To gain an overview in this large field of research a broad taxonomic coverage has to be integrated. Insects and birds are definitively suitable for studying climate change impacts and at the same time the most favoured animal species in research. Insects have relatively short life-cycles, so impacts of climate change as well as adaptation needs for the conservation of species can quickly become evident (e.g. Roy and Sparks 2000). Migratory birds may track climate change through range shifts (e.g. Tingley et al. 2009) due to their high mobility – at least in latitudinal direction (Chen et al. 2011). Birds' flight paths are well documented by scientific and amateur bird watchers. Changes in migration patterns can be well detected. Bird migration is also an important field of fundamental research according to the ethological and physiological mechanisms.

Beside the faunal part of nature plants make up the largest proportion of studied taxonomic groups. Many plant species are of economic relevance, for instance in timber and food production but also as renewable resources. Vedder et al. (2013) state that due to constraints in the ability of many plant species exhibit short-term range shifts, in-situ adaptations to a changing environment is unavoidable. As plants are often expected to lag behind a shifting climate (e.g. Chen et al. 2011 for a lag in elevational shifts) due to limits in dispersal distance, successful establishment and ecosystem inertia they will be exposed to climate change at their current growing sites.

The current taxonomic bias does not represent the species richness in taxonomic groups (Fig. 5). At the global scale, vascular plants and insects form the largest groups (Vié et al 2009). Nevertheless, vascular plants are comparably overemphasized as study organisms compared

to insects which are underrepresented regarding to the number of species per taxon. Similarly, crustaceans, lichens and mosses include a high number of species compared to well-investigated groups such as birds or mammals but are rarely studied. Here in particular, further research is required.

A second major research question is how entire ecosystems will be influenced by and respond to climate change. The question is whether and how changes in diversity, composition, or structure will impact key ecosystem functions. A comprehensive perspective of ecosystem dynamics and functioning must be achieved.

Among types of ecosystems, forests have been intensively studied. Evidently, this term includes not only forest of high nature value in conservation policy (such as tropical forests) but also to a large extent forest of economic value. Hence, the research focus on forest ecosystems that is reflected in the volume of publications is related to their economic importance, particularly in North America and in Europe.

Climate change is seen as major driver of biodiversity loss not only in forest dominated terrestrial biomes such as tropical or boreal forests, but also in savannahs, steppes, tundra, and Mediterranean ecosystems (Fischlin et al. 2007). In the aquatic environment, coral reefs are most highlighted but again certain other types of ecosystems such as mangroves, lakes or springs are evidently very sensitive to climate change but these research challenges have not been adequately addressed, yet.

The vulnerability of ecosystems is only partly considered in the analysed literature of the last decade. Ecosystems that exist under thermal (polar regions or hot deserts) or hygric extremes (semi-arid grasslands as well as peat bogs) are surprisingly underrepresented in ecological climate change impact research. Ecosystems that evolved under an extreme shortage or excess supply of water and temperature can be as well quite resilient but also very sensitive. The omission of strong climatic constraints for other species, for instance melting permafrost soils or increased precipitation in deserts, is likely to cause a plethora of invasion and extinction processes and novel legacies of successional trajectories.

The analysis of the applied methods in climate change impact research revealed a strong preference for modelling approaches. At the level of organisms, climate envelope models (or species distribution models) are found to be useful tools to estimate potential impacts of climate change on species distributions (Elith and Leathwick 2009). Modelling results provide information on potential future developments: where species might undergo extinction risk or gain newly suitable habitats. Such projections are an important guidance for decision makers for instance when management plans have to be adapted in nature conservation, forestry, or agriculture.

Today, we see a large family of modelling algorithms and approaches. Fundamental limitations for ecologically meaningful results are related to parameterization and validation via empirical data (Araújo et al. 2005). Model quality is evaluated based on statistical performance criteria or by their ability to project the current recorded distribution of a species. Yet, a lack of empirical data becomes apparent from our literature survey. This important shortcoming and restriction can be attributed to the high expenses for field research, long-term monitoring, and assessments.

Additionally, studies on observed or experimental climate change impacts provide a valuable source of information for decision makers. On the one hand these studies emphasise current adaptation needs as well as areas and species at risk. On the other hand they provide the data basis for climate envelope modelling. Hence, there is an urgent need to increase the monitoring, especially in areas that are expected to be most influenced by climate change, to provide a validation of modelling approaches.

Another limitation of climate envelope models refers to spatial scales and to the grain and extent of data sets. A large proportion of modelling studies is based on a coarse spatial resolution and focuses on large-scale changes in distributions. Processes that allow species survival in microhabitats are neglected in most modelling approaches. The use of coarse spatial resolutions in distribution modelling is suitable for assessing potential general and perhaps long-term trends at continental or national scales, but they pose the risk of misleading conservation planning (Seo et al. 2009). Adaptation measures have to take into account processes on micro-scales instead of focusing solely on macro-scale projections of distribution changes.

Where to go from here?

The focus of the current scientific literature on observed or expected impacts of current and future climatic changes on organisms and ecosystems covers an impressively broad spectrum regarding regions and continents, taxa, methods, climatic parameters and affected types of ecosystems. Nevertheless, regional biases, a lack of experiments as well as a narrow focus on specific taxonomic groups and ecosystems are still constraining the options for efficient adaptation strategies on regional, national and global levels.

When efficient adaptation strategies in face of projected climatic changes are discussed, the fundamental questions are which ecological responses are to be expected and if these can be counteracted. If knowledge is sufficient, management concepts can be implemented. Unfortunately, this is rarely the case. Target-oriented research is needed to improve the knowledge base for climate change impacts on organisms and ecosystems. Here we provide an overview on research gaps and challenges in this field.

Decision makers need updated results of scientific studies on certain species or ecosystems of societal value. Observational studies and experiments are indispensable, but they can hardly cover the entire diversity and space. In consequence, research activities have to concentrate on key taxa, ecosystems, and processes. Conceptual links to future modelling approaches would be helpful as only models can deliver rapid approximations of ecological climate change impacts and therewith the identification of adaptation needs. Combining modelling with remote sensing approaches is another promising direction of science.

Modelling results are supporting decision making processes (Guisan et al. 2013). For instance, species, habitats, and areas of conservation concern under climate change can be highlighted. Additionally, they can be used to identify current and prospective suitable areas, e.g. for translocations. However, Guisan et al. (2013) also point out that the results of modelling studies are susceptible to misclassifications which can cause costly consequences.

Funding is the basis of research. Today, funding structures in climate change impacts research depend strongly on GDP. Especially in this global field of research, economic power should go hand in hand with responsibility for progress. Still some prosperous countries are not adequately visible in research output. Additionally, funding of research must be enforced in and directed to less studied but high risk regions in the world, where GDP and financial resources for research funds are low (Amano and Sutherland 2013). It is to be hoped that the special responsibilities of industrial countries for the global consequences of anthropogenic greenhouse emissions will soon be translated into efficient research strategies.

The current choices of the studied species and – connected with this – the emphasis on certain taxonomic groups reflects besides economic aspects (agriculture, forestry) the availability of ecological data and the state of taxonomic knowledge. Global patterns and the reliability of research are directly related to the detectability and identification effort of species (Cardoso 2011). Monitoring programs with well-trained experts are needed to improve the taxonomic coverage. These should focus on groups and species that are overlooked to date but contribute to the functioning of ecosystems.

The maintenance of complex ecosystems is a great challenge in times of climate change. Some ecosystems are expected to be more vulnerable than others and will require more research and conservation effort.

Species turnover, inertia, stability, dispersal, and the capacity for natural adaptation must be addressed at the scale of ecosystems. It would clearly be difficult to address all these aspects at the ecosystem level. However, long-term field experiments are an appropriate approach (e.g. <http://www.neoninc.org/>). Identifying regions that will be especially at risk in a global perspective will contribute to reduce the bias in the geographic distribution of study areas.

Concerning the methodological approaches used to estimate and quantify impacts of climate change there is still need for improvement. The use of climate envelope models is popular and fast developing. Modelling approaches can be further improved by including ecological knowledge such as biotic interactions (e.g. Jaeschke et al. 2012; Kissling et al. 2012) or dispersal abilities (e.g. Buse and Griebeler 2011). First of all, the modelling of climate envelopes of species distributions requires a profound knowledge of a species' ecology, which differs between taxonomic groups and is incomplete (Botkin et al. 2007). The prerequisite for ecological meaningful species distribution models is to increase the empirical data basis by the use of experiments and field observations. This will not only promote the improvement of models but help to identify specific organisms and ecosystems at risk as well as to detect in-situ changes in conditions and distribution patterns.

For the protection of organisms and ecosystems future research priorities have to be detected and knowledge gaps must be closed. Unbalanced knowledge would lead to inadequate adaptation strategies. Decision makers must be aware of such biases and take them into account. Finally, based on the current data availability the most useful research in the field of ecological climate change impacts is being done at least in parts of the world. What we now need is to broaden our view on so far overlooked species, ecosystems and regions.

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Supplement

Table S1 Search string for the literature study in the ISI Web of Science. The search was restricted to publications between 2003 and 2012. Relevant alternative suffixes were included using the asterisk *

Category	Search term
"Topic"	"climat* chang*" or "changing climat*" or "global chang*" or "global warmin"
AND "Topic"	"bioclim* envelop*" or "envelop* model*" or "clima* envelop*" or "bioclim* model*" or "ecosys* manage*" or "species range" or "species distribution" or (habit* AND "Natura 2000") or endangered or "ecolog* model*" or "habitat directive" or "invasive species" or "community ecology" or "population* ecology" or sac or "Special area of conservation" or spa or "special protection area" or "conservation biology" or fragmentation or "habitat model" or "nature reserv*" or "range expansion" or "range extension" or "red list" or (biol* AND conservation) or "sites of community importance" or "national park" or "biosphere reserve"
NOT "Topic"	palaeo* or holocene or "bronze age" or archaeo*

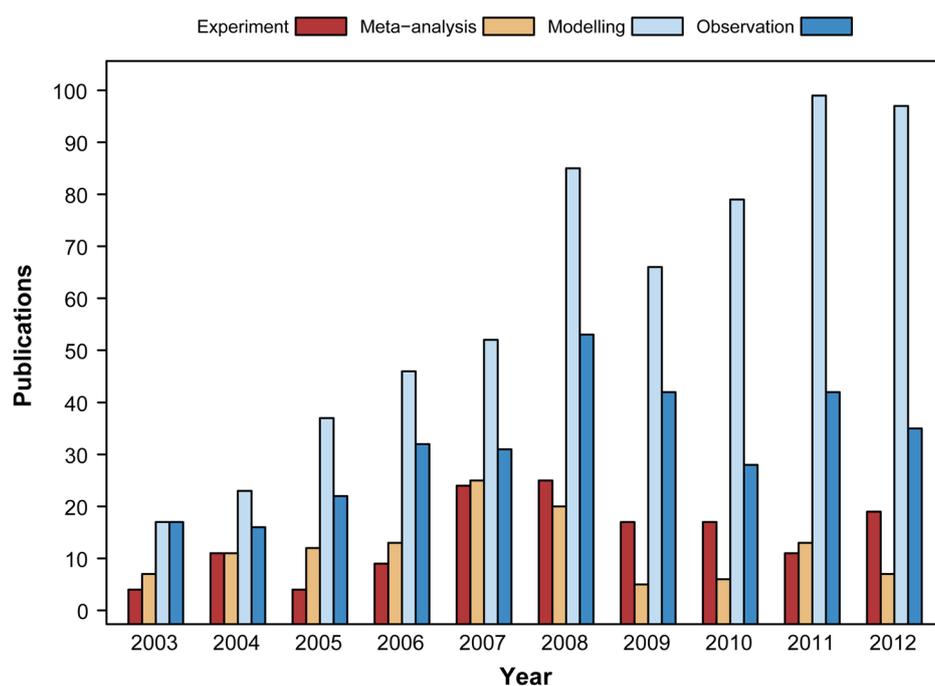


Fig. S1 Development of the applied methods in scientific climate change impacts research in the ISI Web of Science between 2003 and 2012

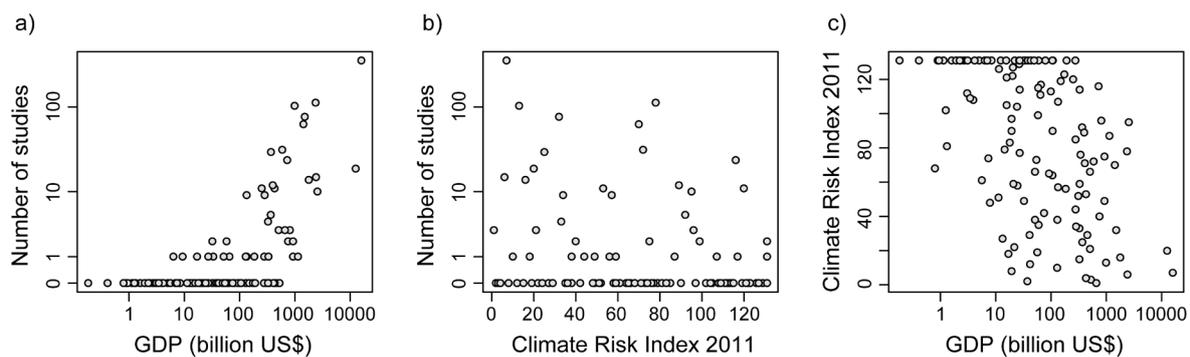


Fig. S2 Correlation of the number of studies with a) the gross domestic product (GDP) of a country, b) the Climate Risk Index (CRI) of a country in 2011, and a correlation of the CRI against the GDP. Sources: <https://www.cia.gov/library/publications/the-world-factbook/rankorder/2001rank.html> (GDP, last accessed 30.08.2013) and Harmeling and Eckstein (2012) (Climate Risk Index 2011)

Article 2

Can they keep up with climate change? - Integrating specific dispersal abilities of protected Odonata in species distribution modelling

Anja Jaeschke, Torsten Bittner, Björn Reineking, Carl Beierkuhnlein

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Can they keep up with climate change? - Integrating specific dispersal abilities of protected Odonata in species distribution modelling

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Abstract

1. The effects of climate change on the distribution of species are typically inferred using bioclimatic envelope models, assuming either no or unrestricted dispersal abilities. Information on species-specific dispersal abilities, especially of animals, is rarely incorporated.

2. We analysed European records of two damselflies and four dragonflies protected by the Habitats Directive of the European Union. In addition to no or unrestricted dispersal scenarios, we considered species-specific dispersal distances based on literature information to improve realism in assessing conservation implications of climate change. The climate model HadCM3 and the emission scenario A2 were applied to project potential changes in occurrence probabilities up to 2035. As modelling algorithms generalised linear models (GLM) and boosted regression trees (BRT) were used.

3. The species *Coenagrion ornatum*, *Coenagrion mercuriale* and *Ophiogomphus cecilia* are projected to lose range (up to -68%) when incorporating specific dispersal distances, while they are projected to extend their range (up to +23%) in the unrestricted dispersal scenario. Furthermore, suitable climatic conditions tend to decline for *Leucorrhinia albifrons* and *Leucorrhinia caudalis* (up to -73%), whereas *Leucorrhinia pectoralis* is projected to gain distribution area (up to +37%) assuming either species-specific or unrestricted dispersal and subsequently successful breeding. Cross-validated model performance (AUC values) ranges between 0.77 and 0.92.

4. The integration of species-specific knowledge about dispersal distances in species distribution models promises to improve estimates of potential range changes and their implications for conservation management. Contrasting model results under different dispersal scenarios highlight the importance of research on species' ecology including dispersal distances.

Keywords

Europe, global warming, Habitats Directive, insect conservation, species distribution model, SDM, species range, species-specific dispersal ability, range shift

Introduction

Climate change is a driving factor for species range shifts (Walther *et al.*, 2005; Hickling *et al.*, 2006; Hitch & Leberg, 2007; Ott, 2009). Such range changes are of major concern for nature conservation, especially since endangered and/or rare species are expected to be most vulnerable to changes in climatic conditions and may be most threatened by extinction (Schlumprecht *et al.*, 2010). To derive effective adaptation strategies in nature conservation it is important to assess potential influences of climate change on species ranges. Realistic projections will require assessments of both future habitat suitability and species-specific dispersal restrictions.

Climate envelope models correlate species' occurrences with environmental variables (Guisan & Thuiller, 2005; Elith & Leathwick, 2009). The resulting climate envelopes can be used as a basis for projections of suitable future habitats of a species, which form the basis for the evaluation of potential range changes (Araújo & Guisan, 2006).

The reliability of model output depends on the selection of explanatory variables, the choice of the climate model, emission scenario and modelling algorithm (Dormann *et al.*, 2008). Nevertheless, climate envelopes are a useful first approach to estimate potential effects of climate change on species' distributions.

Assuming the two extreme options of 'no dispersal' and 'full dispersal' is the state-of-the-art approach to model future occurrence probabilities of species (Coetzee *et al.*, 2009; Franklin, 2010; Fitzpatrick *et al.*, 2011). This provides lower and upper boundaries on expected future range sizes: A 'no dispersal' scenario will overestimate potential losses in range size, whereas a 'full dispersal' scenario neglects dispersal barriers and tends to overestimate species' dispersal and thus adaptation abilities. While both dispersal scenarios provide hints on where current suitable area might be lost and where future suitable area might be found, they give limited guidance on where species ranges may realistically shift. The integration of species-specific dispersal distances may contribute to overcome this limitation (Buse & Griebeler, 2011). However, fully integrating such biological traits into modelling requires an explicit knowledge on species-specific behaviour, stress tolerance, life cycles, vitality, activity periods, and dispersal capacity.

Odonata are prominent indicator species for the biological effects of climate change (Ott, 2010). They are influenced by climate change in many ways, covering aspects of life history,

thermoregulation, ecology, habitat and evolution (Hassall & Thompson, 2008). Hickling *et al.* (2005) provide evidence for northward range shifts of several British Anisoptera and Zygoptera species as a response to climate warming. Braune *et al.* (2008) analysed the voltinism flexibility along a thermal gradient for *Gomphus vulgatissimus*. They developed a population dynamic model allowing projections for future climate change. As their field results indicate a decreasing voltinism from warm (southern Europe) to cold (northern Europe) the model projected an increased development speed in the northern part, a range expansion at the northern range margin and an extended flight period under a warming scenario. Also, climate change induced shifts in community composition and species abundance could be observed (Flenner & Sahlén, 2008). Most of the considered Odonata included in this study have a lifespan of at least two years as larvae (Petersen *et al.*, 2003; Corbet *et al.*, 2006) and therefore highly depend on habitat conditions, e.g. water temperature, oxygen content, and the availability of freshwater pools (e.g. Sternberg & Buchwald, 1999; Sternberg & Buchwald, 2000). On the other hand, imagines of many species are highly mobile and thus respond rather directly to a shifting climate space. However, they are active only for a few months, which limits the temporal window for dispersal processes. Furthermore, especially the endangered dragonflies and damselflies tend to show restricted mobility. Such limitations in dispersal abilities can be related to various factors such as morphological constraints or close dependence on specific habitat conditions (Thompson *et al.*, 2003).

Here, we analysed six strictly protected odonate species in order to assess how climate change may influence their future distributions. We assumed that considering species-specific dispersal abilities can lead to contrasting results in projected future range changes with regard to no and full dispersal and that the integration of dispersal distances (beside climate) in species distribution modelling enhances realism of model results. Finally, we discuss potential management options for protecting these species under future climate conditions.

Methods

Species

We selected six Odonata (out of 16 odonate species listed in the EU Habitats Directive) for which observed dispersal distances are available in the literature. All these species are listed in Annex II and/or IV of the EU Habitats Directive and in the European Red List (Kalkman *et al.*, 2010) and are therefore under special protection. Two species belong to the Zygoptera: *Coenagrion mercuriale* (Charpentier, 1840) (Annex II) and *Coenagrion ornatum* (Sélys, 1850) (Annex II). For the Annex II species the member states have to designate 'Special Areas of Conservation'. Both species develop in lotic waters with a moderate or slow flow velocity

(Sternberg *et al.*, 1999, Sternberg 1999). The habitat requirements of both species are very similar. They can be found at sunny streams and springs rich in aquatic and riparian vegetation, often with a calcareous substrate. Flowing drainage ditches may also offer suitable habitats (Sternberg *et al.*, 1999, Sternberg 1999). *C. mercuriale* is distributed in South West Europe and partly in Central Europe. *C. ornatum* is common in South East Europe and very local in Central Europe.

The four other species are Anisoptera: *Leucorrhinia albifrons* (Burmeister, 1839) (Annex IV), *Leucorrhinia caudalis* (Charpentier, 1840) (Annex IV), *Leucorrhinia pectoralis* (Charpentier, 1825) (Annex II and IV) and *Ophiogomphus cecilia* (Geoffrey in Fourcroy, 1785) (Annex II and IV). For the species listed in Annex IV a strict protection is required. Except for *O. cecilia*, the larvae of all these Anisoptera species inhabit lentic waters (e.g. Corbet *et al.*, 2006). The three *Leucorrhinia* species prefer oligotrophic to mesotrophic lakes and shallow waters, often located in forests (Dijkstra & Lewington, 2006). Their distribution ranges over Eastern and Central Europe. *O. cecilia* is the only representative of this genus in Europe and widespread in most of Eastern Europe up to Germany, with isolated populations in France and Italy. Preferred habitats are large to mid lowland and small highland rivers with a sandy substrate (Sternberg *et al.*, 2000).

Species and climate data

Information on current species distributions was taken from the EIONET (European Environment Information and Observation Network) Central Data Repository server (EIONET, 2009). The data originate from the European reporting of the year 2007 pursuant to Article 17 of the Habitats Directive. They are available for 25 EU countries in different spatial resolutions. All of those member states are committed to report the current occurrences and the conservation status of the listed species in a six year interval. Data from non-EU countries (Switzerland, Balkan region, Norway) were added: For Switzerland we used the database of the Swiss Biological Records Center (<http://lepus.unine.ch/cartto/>; public access). Balkan data were taken from Boudot *et al.* (2009) and data for Norway from Olsvik & Dolmen (1992). These data were digitised and geo-referenced in ArcGIS 9.3.1.

Current and projected future European climate was quantified on a 10' (arcminutes) grid from interpolated observed and future simulated climate data (Mitchell *et al.*, 2004). Future projections were based on the intermediate BAMBU ("Business As Might Be Usual", A2) scenario (Spangenberg, 2007), developed for the European project ALARM (Settele *et al.*, 2005). The future projection is driven by the global HadCM3 climate model (Hadley Centre Coupled Model, version 3) and covers the period 2021-50 (2035). The emission scenario A2 assumes a temperature increase of 3.4°C up to 2100 based on a high global population growth, and a slow economic development and technological change (IPCC, 2007).

The following climatic variables were used in the modelling process, each with monthly, mean, minimum and maximum values: cloudiness (CLD, %), equilibrium evapotranspiration (EET, mm), precipitation (PRE, mm), temperature (TMP, °C), diurnal temperature range (DTR, °C), minimum temperature (TMN, °C), maximum temperature (TMX, °C) and growing degree days above 5°C (GDD, degree days).

In this study, we decided to exclusively use climatic variables, leaving out other potentially relevant factors such as elevation and land cover. Initially, we carried out an analysis (with hierarchical partitioning) testing which factor (climate, elevation, land cover) explains most of the current distribution for each of the six species. For all tested species, elevation plays only a minor role. For three of the six species climate is most important. For the other three species (*L. albifrons*, *L. caudalis* and *O. cecilia*) land cover (in these cases forest) is the most or the secondary important factor, followed by climate. However, the problem with land cover is its coarse resolution and its constraint predictability. On a European scale we cannot yet distinguish between e.g. types of forests and have to work with classifications like “urban”, “crop”, “grassland” and “forest”, which are difficult to interpret in the present context. Another problem is the future projection of land cover. Although some scenarios exist, the future development is not only influenced by climate but also by political developments, making these scenarios highly uncertain. For these reasons we left land cover out of the analysis.

Dispersal scenarios

Although species distribution models assume that species' range margins are in equilibrium with environmental variables current ranges are in a state of flux. To counter this problem a consideration of realistic dispersal abilities is required. We applied three dispersal scenarios: the conventional 'no dispersal' and 'full dispersal' scenarios to detect sources of potential extinction and to identify future climatically suitable areas, and a scenario which accounts for the species-specific dispersal distances.

To account for species-specific dispersal abilities, observed maximum dispersal distances of the six Odonata were used. Dispersal lags caused by larval development were considered by allowing dispersal only after the completion of the development cycle. The dispersal distances were taken from the literature (Table 1).

Table 1. Applied maximum dispersal distances until 2035 derived from literature information for each species. The maximum reachable distances take into account the duration of larval development by allowing dispersal every 2 or 3 years (after completion of the lifecycle). For species with time spans in larval development (e.g. 2-3 years) we used the more likely value given by the literature.

Species	Observed dispersal distances	Used dispersal distances	Used larval development	References	Maximum distance 2007 - 2035
<i>Coenagrion mercuriale</i>	Up to 1 km/a	1 km/a	2 years	Thompson <i>et al.</i> (2003), Corbet <i>et al.</i> (2006)	14 km
<i>Coenagrion ornatum</i>	200 m up to several km/a	1 km/a	2 years	Burbach <i>et al.</i> (1996)	14 km
<i>Leucorrhinia albifrons</i>	Up to 18 km/a	18 km/a	2 years	Mauersberger (2003a)	252 km
<i>Leucorrhinia caudalis</i>	Up to 7 km/a	7 km/a	2 years	Mauersberger (2003b), Corbet <i>et al.</i> (2006)	98 km
<i>Leucorrhinia pectoralis</i>	Up to 27 km/a	27 km/a	2 years	Wildermuth (1993), Corbet <i>et al.</i> (2006)	378 km
<i>Ophiogomphus cecilia</i>	Up to 10 km/a	10 km/a	3 years	Suhling <i>et al.</i> (2003), Corbet <i>et al.</i> (2006)	93 km

In order to take species-specific dispersal abilities throughout Europe into account we used the Euclidean Distance, calculated through the maximum dispersal distance divided by developmental time and multiplied by the number of considered years. Based on this, a buffer zone around each current occurrence point was calculated. This allows restricting the potential distance of movement in a given time frame. By clipping the projected future full dispersal distribution and the calculated buffer zone we got the projected suitable and accessible ranges for the six species. This was implemented with ArcGIS using the 'Euclidean Distance' function of the 'Spatial Analyst Tools'.

Species Distribution Modelling

We used two different modelling algorithms, namely generalised linear models (GLM) and boosted regression trees (BRT) (see Elith *et al.*, 2008 for details) to assess the uncertainty in these model decisions relative to other uncertainties in the modelling process (Dormann *et al.*, 2008). For both model algorithms, we first dealt with collinearity in the predictors by selecting a variable set where pairwise Pearson correlations are < 0.7 . In pairs of correlated variables, we retain that variable with higher univariate predictive ability (assessed by GLM with a quadratic term) of the species' distribution. Subsequently, a stepwise selection in the

GLM model of the retaining variables was based on BIC (Bayesian information criterion); no variable selection was performed for BRT models.

The results were validated with a 32-fold geographically stratified cross-validation, separating Europe in 32 equally sized parts. We used the AUC (area under the receiver operating characteristic curve) as model performance criterion to measure overall model discrimination (Swets, 1988), i.e. the model's ability to differentiate between locations where the species occurs from those where it is absent. In addition, we used the slope of the calibration curve to measure model calibration, i.e. the correspondence of predicted occurrence probabilities to observed occurrence frequencies (Reineking & Schröder, 2006). The cut-off point for occurrence and non-occurrence projections was selected such that the resulting prevalence (i.e. fraction of occupied sites) equalled the mean predicted occurrence probability.

All analyses were performed with R 2.10.0 (R Development Core Team, 2010). In addition to the standard R packages we used the PresenceAbsence package version 1.1.4 (Freeman, 2007). Model performance was quantified with `val.prob` from the Design package version 2.3-0 (Harrell, 2009). The `gbm` package version 1.6-3.1. (Ridgeway, 2010) was used for the boosted regression trees. Spatial climate and species distribution data were processed with ArcGIS 9.3.1.

Results

Climate change is projected to strongly affect the investigated Odonata. All modelled species are projected to lose more than 50% of their climatically suitable area with both modelling algorithms under the assumption of no dispersal (Table 2). *L. albifrons* and *L. caudalis* are also projected to lose at least 30% of their current distribution by 2035, both with the species-specific and the full dispersal scenario. In contrast, *L. pectoralis* is projected to gain distribution area independent of modelling algorithm and dispersal scenario (with the exception of no dispersal). The modelling results of the two *Coenagrion* species (Fig. 1), and *O. cecilia* (Fig. 3) differ considerably between the species-specific and full dispersal scenario. These three species are projected to gain distribution area under a full dispersal scenario, but to lose distribution area under a species-specific dispersal scenario.

Table 2. Projected change in the distribution of six odonate species in Europe for 2035, using boosted regression trees (BRT) and generalised linear models (GLM) as modelling algorithms. The percentage change until 2035 is given for the three dispersal scenarios: no, species-specific, and full dispersal.

Species	HadCM3, A2, 2035					
	No dispersal		Specific dispersal		Full dispersal	
	BRT	GLM	BRT	GLM	BRT	GLM
<i>Coenagrion mercuriale</i>	- 71%	- 65%	- 52%	- 48%	+ 7%	+ 5%
<i>Coenagrion ornatum</i>	- 73%	- 77%	- 65%	- 68%	+ 23%	+ 17%
<i>Leucorrhinia albifrons</i>	- 64%	- 65%	- 39%	- 38%	- 35%	- 30%
<i>Leucorrhinia caudalis</i>	- 73%	- 71%	- 59%	- 57%	- 35%	- 34%
<i>Leucorrhinia pectoralis</i>	- 67%	- 67%	+ 34%	+ 7%	+ 37%	+ 7%
<i>Ophiogomphus cecilia</i>	- 58%	- 60%	- 16%	- 31%	+ 8%	+ 9%

Species show geographically differentiated responses to projected climate change (Fig. 1-3). Both *Coenagrion* species are projected to lose most of their occurrences in Central Europe and in parts of Southern Europe, leading to a range contraction to France and Northern Spain (*C. mercuriale*) and to the Balkans and parts of Turkey (*C. ornatum*), probably caused by a higher temperature and lower precipitation in the current distribution areas. *Coenagrion mercuriale* is mainly distributed in the Atlantic biogeographical region with further occurrences in the Continental and Mediterranean biogeographical regions. The projected decline in the Continental and Mediterranean regions can be related to the projected increasing aridity in the future in these regions. For *C. mercuriale* the full dispersal scenario projects new climatically suitable area in the Czech Republic, Austria and the Balkans, causing a potential eastward shift in distribution. With the application of the specific dispersal scenario these projected new occurrences are excluded if they are not in reach within the considered time period and the given dispersal distance, leading to a smaller expansion in the surrounding of the current occurrence. In contrast, the full dispersal scenario for *C. ornatum* projects new climatically suitable area in Spain and Portugal provoking a westward shift in the potential future distribution.

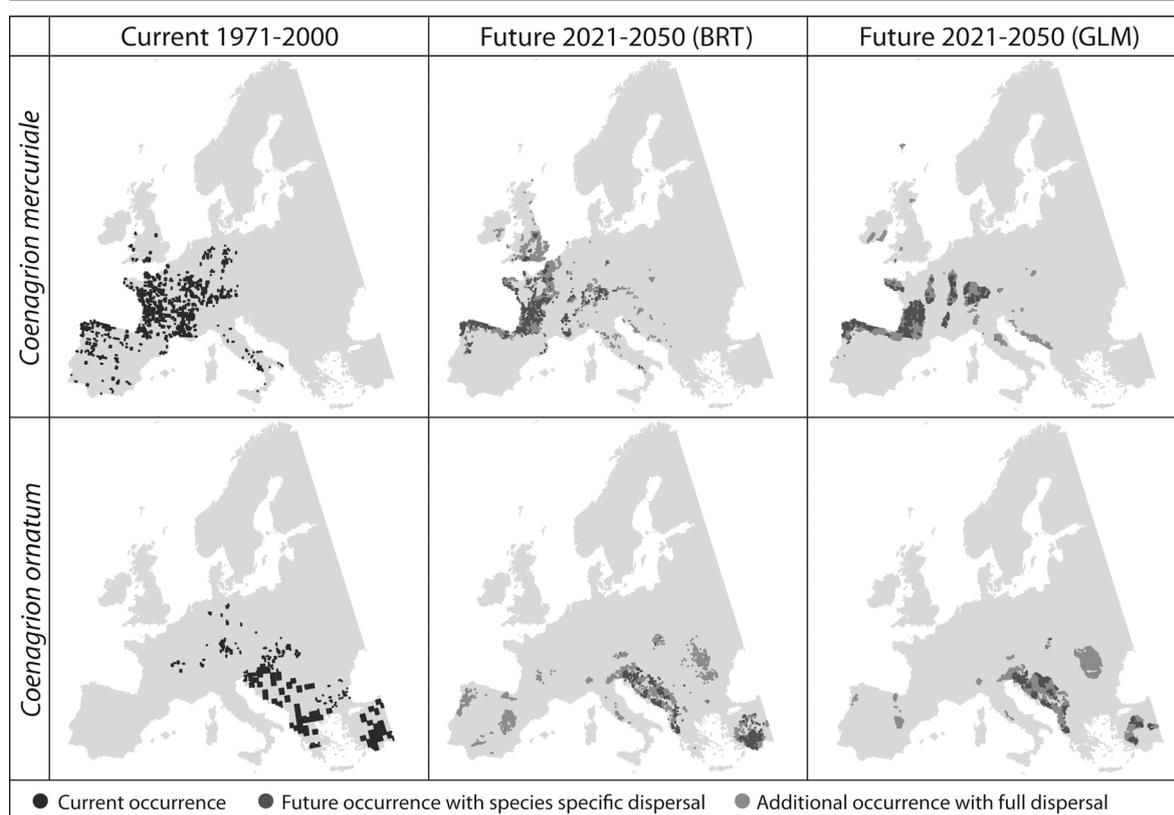


Fig. 1. Current and future projected distribution of *Coenagrion mercuriale* and *Coenagrion ornatum* in Europe. Both damselflies are projected to gain distribution area under the full dispersal scenario, but to lose distribution area under the species-specific dispersal scenario (1 km/a). Occurrence thresholds: BRT: 0.32 (*C. mercuriale*), 0.17 (*C. ornatum*), GLM: 0.27 (*C. mercuriale*), 0.24 (*C. ornatum*); modelling algorithms: BRT and GLM; climate model: HadCM3; scenario: A2; AUC (test data): BRT: 0.89 (*C. mercuriale*), 0.79 (*C. ornatum*), GLM: 0.88 (*C. mercuriale*), 0.77 (*C. ornatum*).

Two of the three *Leucorrhinia* species, *L. albifrons* and *L. caudalis*, are projected to lose almost all locations within their current distribution in Central Europe, Western France, and in the Baltic states. The full dispersal scenario projects new suitable area in Finland, Sweden and Norway, leading to a slight range shift towards the north-east. Though these two species may be good dispersers, the climatically suitable area is projected to be reduced to such a large extent that their dispersal ability has no influence on their potential future distribution. For *L. pectoralis* the full dispersal scenario projects a tendency to a range expansion towards the north-east, similar to the two other *Leucorrhinia* species. Projected range losses in the western (France) and southern (Turkey) parts of the current distribution could lead to a range shift. With the specific dispersal distances *L. pectoralis* is projected to reach almost all of the future suitable climate area.

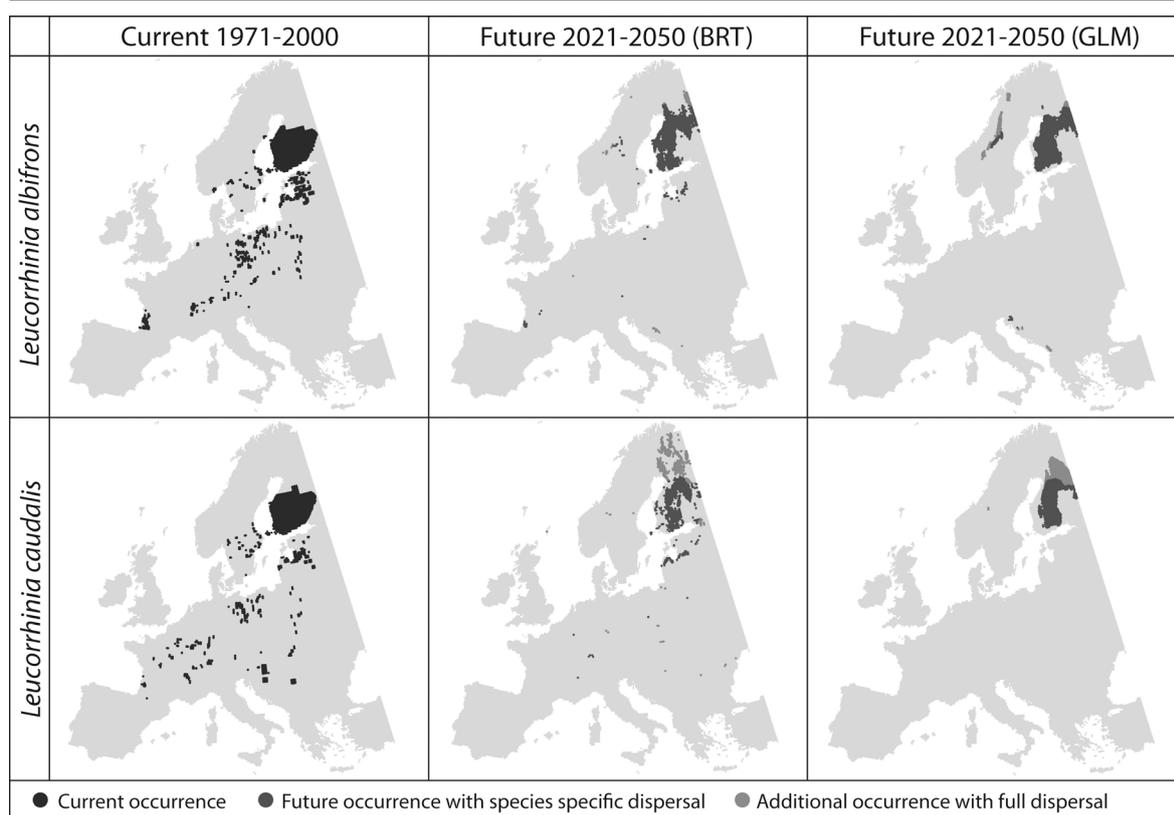


Fig. 2. Current and future projected distribution of *Leucorrhinia albifrons* and *Leucorrhinia caudalis* in Europe. Both dragonflies are projected to lose distribution area with all dispersal scenarios. Occurrence thresholds: BRT: 0.33 (*L. albifrons*), 0.27 (*L. caudalis*), GLM: 0.40 (*L. albifrons*), 0.37 (*L. caudalis*); modelling algorithms: BRT and GLM; climate model: HadCM3; scenario: A2; AUC (test data): BRT: 0.92 (*L. albifrons*), 0.84 (*L. caudalis*), GLM: 0.92 (*L. albifrons*), 0.88 (*L. caudalis*).

The fourth dragonfly, *O. cecilia*, is as well projected to lose range in the western parts (France) but additionally also in Denmark. The full dispersal scenario projects a range shift towards the north-east, especially to Belarus. With the application of the specific dispersal distances a great part of these projected new occurrences would be in reach because of the species' high dispersal ability. However, for the most northerly projected suitable areas the species dispersal ability is insufficient.

The statistically selected climatic variables differ between the species as the applied method incorporates the current occurrence in the decision process (Fig. S1-S6). Therefore, all selected variables describe the current distribution best considering a correlation of the remaining variables of less than 0.7. For all modelled species precipitation is an important factor (Table 3). In the models, precipitation amounts in spring and summer as well as minimum and maximum values were selected, reflecting the dependence on water availability for reproduction. All other selected climatic variables, i.e. minimum temperature, growing degree days, diurnal temperature range and cloudiness, are related to temperature. Diurnal temperature range and cloudiness are important for five of the six species. All these temperature-related variables consider the cold period of the year and therefore the diapause, which is especially relevant

for the survival of the larvae.

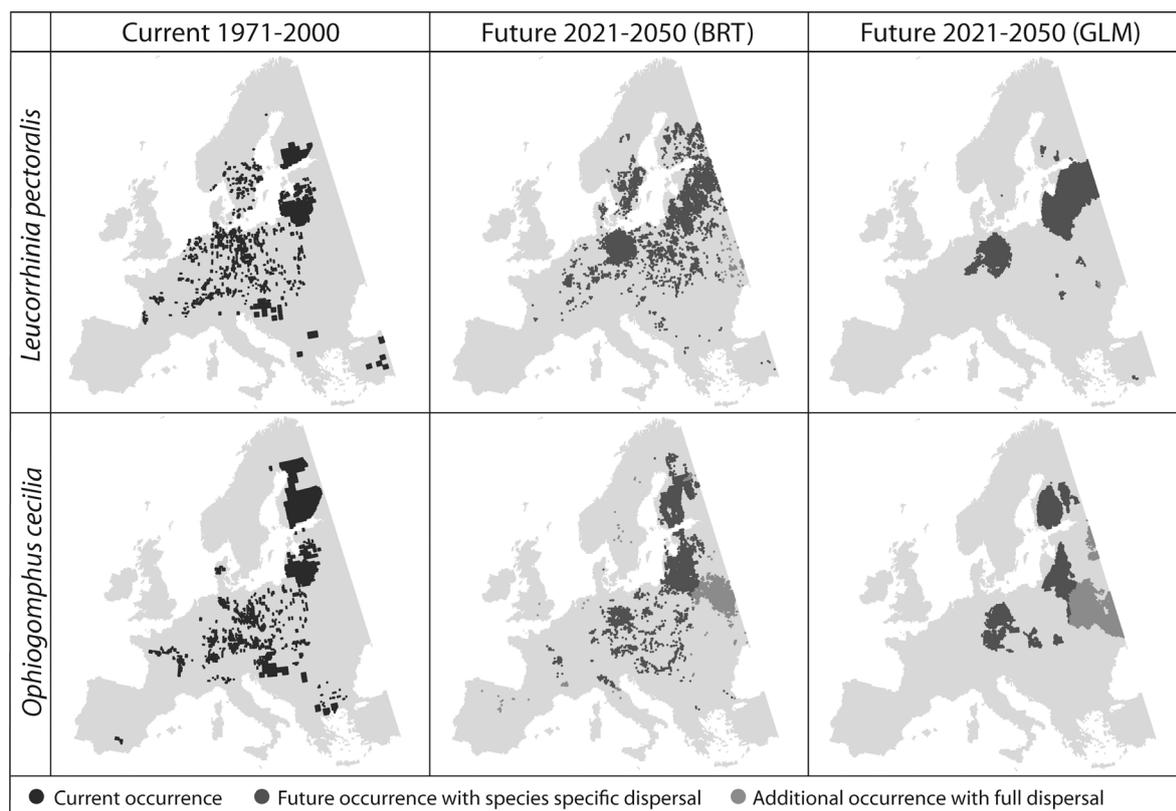


Fig. 3. Current and future projected distribution of *Leucorrhinia pectoralis* and *Ophiogomphus cecilia* in Europe. Both dragonflies are projected to gain distribution area under the full dispersal scenario, but *O. cecilia* is projected to lose distribution area with the species-specific dispersal scenario. Occurrence thresholds: BRT: 0.42 (*L. pectoralis*), 0.30 (*O. cecilia*), GLM: 0.19 (*L. pectoralis*), 0.31 (*O. cecilia*); modelling algorithms: BRT and GLM; climate model: HadCM3; scenario: A2; AUC (test data): BRT: 0.83 (*L. pectoralis*), 0.81 (*O. cecilia*), GLM: 0.80 (*L. pectoralis*), 0.77 (*O. cecilia*).

Both modelling algorithms, GLM and BRT, perform well in predicting the current distribution of all six species (Table 3). All cross-validated AUC values are between 0.77 and 0.92, with BRT showing slightly better discriminatory performance (mean AUC values: 0.85 BRT, 0.84 GLM). Both algorithms tend to be overconfident in modelling the current occurrence (BRT more so than GLM), as indicated by the slope of the calibration curve (mean values: 0.57 BRT, 0.68 GLM; values of 1 correspond to well-calibrated models).

Table 3. Model performance of the two modelling algorithms (GLM, BRT) showing the AUC and slope of the calibration curve for the test data (32-fold cross-validation), and importance of the climatic variables selected by the model. TMN: minimum temperature (°C), PRE: precipitation (mm), CLD: cloudiness (%), DTR: diurnal temperature range (°C), GDD: growing degree days (°C).

Species	Calibration		AUC	Variable importance					
	BRT	GLM		BRT	GLM	TMN minimum	PRE minimum	PRE in May	CLD in January
<i>Coenagrion mercuriale</i>	0.66	0.64	0.89	0.88	26.6%	22.4%	22%	17%	12%
<i>Coenagrion ornatum</i>	0.59	0.55	0.79	0.77	DTR in October	PRE in April			
<i>Leucorrhinia albifrons</i>	0.60	0.81	0.92	0.92	64.2%	35.8%			
<i>Leucorrhinia caudalis</i>	0.48	0.82	0.84	0.88	36.5%	24.4%	19.7%	19.4%	
<i>Leucorrhinia pectoralis</i>	0.54	0.73	0.83	0.80	43.5%	29.4%	27.1%		
					CLD in January	DTR in January	GDD in December	DTR in May	PRE in February
					26.2%	20.6%	20.1%	16.7%	16.3%
<i>Ophiogomphus cecilia</i>	0.50	0.53	0.82	0.77	32.8%	18%	17.3%	16.5%	15.4%
					CLD in November	PRE in February	DTR in November	PRE maximum	DTR in May

Discussion

Dispersal scenarios

Most recent modelling studies only apply two dispersal scenarios: no dispersal and unlimited dispersal (e.g. Schweiger *et al.*, 2008; Lawler *et al.*, 2009; Carvalho *et al.*, 2010). In the case of nature conservation and its adaptation needs in times of climate change, these projected extremes in dispersal are informative but insufficient.

The species *C. ornatum*, *C. mercuriale* and *O. cecilia* illustrate the limitations of the full dispersal approach. Both modelling algorithms project more suitable space in the near future considering unrestricted dispersal ability. In contrast, when considering species-specific dispersal distances the model projects a large loss of suitable climate space. This is due to the species' limited dispersal ability relative to the distance to the projected future suitable climate space. For *C. mercuriale* it seems that the no dispersal scenario is more likely at least for parts of Europe. For Great Britain the applied distance of one kilometre per generation might be rather optimistic. However, maximum dispersal distances of one kilometre can be also observed there (Purse *et al.*, 2003).

We have shown that available ecological knowledge such as observed dispersal distances can be integrated into the modelling process for animal species. We believe that this gives a more realistic projection of the potential future distribution of the studied species. A particular challenge of this approach lies in the definition of suitable dispersal scenarios.

In the few studies that account for specific dispersal in species distribution modelling, especially in plants (e.g. Dullinger *et al.*, 2004; Brooker *et al.*, 2007; Smolik *et al.*, 2010), long-distance dispersal is one of the most widely considered processes. Long-distance dispersal is a rare event, but plays an important role in plant species dispersal (Nathan, 2006). It is also relevant in animal dispersal, especially for small species that can be blown away by wind over large distances (Bonte *et al.*, 2009). A recent study on *L. caudalis* by Keller *et al.* (2010) investigated the spread of this species over the last 20 years in Switzerland. They could demonstrate long-distance colonisation at distances of 30 to 50 km. Such long-distance dispersal is also conceivable for all other species in our study, adding uncertainty to the observed dispersal distances and their application in species distribution modelling. However, we did not include long-distance dispersal in order to represent a realistic conservative instead of a realistic optimistic scenario.

Climatic suitability of a site alone and the organismic potential to reach these novel habitats are not sufficient to project in a realistic way whether species might adapt to climate change by range shifts. Keller *et al.* (2010) trace the observed spread of *L. caudalis* in Switzerland

back to the recreation and restoration of ponds. *C. mercuriale* is also highly dependent on the habitat (Rouquette & Thompson, 2007). Beside climate and dispersal ability the habitat requirements are limiting for all investigated species. Habitats may not be available at the new climatically suitable area and may not develop in the short-term thus preventing successful breeding and colonization. Furthermore, colonization success depends on propagule size (e.g. Ahlroth *et al.*, 2003). Nevertheless, for all the studied species climate change effects are reported regarding trends in range, area and/or population (European Topic Centre on Biological Diversity (ETC/BD), 2008) pointing to a sensitivity of these to climate change. The relative importance of habitat versus climate has not been investigated yet for these species. However, indirect effects of climate change, such as desiccation of water bodies or reduced prey abundance combining habitat characteristics and climate change, play also a major role in assessing the impacts of environmental change on Odonata.

Further, other abiotic factors like elevation and land cover determine the current distribution and the future spreading potential. For example, the size of fragmented patches of suitable habitats can influence the dispersal distance of a species (Ahlroth *et al.*, 2010). However, the problem with land cover is its presently coarse classification, especially on a continental scale, and its constrained predictability.

Research gaps and uncertainties

The estimation of dispersal distances contains several uncertainties. First, observed maximum distances can be highly unrepresentative. In addition, observed dispersal distances of populations (e.g. assessed by mark-release-recapture studies) do not necessarily represent the dispersal ability of the species, but may reflect regional characteristics or methodological constraints, and therefore underestimate the real dispersal ability. Next, dispersal abilities and dispersal distances may change over time due to climate change. Alterations in environmental conditions can force adaptation processes leading directly to higher mobility (Hill *et al.*, 1999) and increased dispersal distances (Hill *et al.*, 2011), or indirectly by improving a species' fitness and thereby its ability to spread. Hill *et al.* (1999) studied morphological traits of a butterfly from newly colonised sites. They observed individuals with larger adult live mass, larger thoraxes and lower wing aspect ratios compared to reference sites with established populations. Similarly, morphological changes over short periods have been observed for Odonata, in the form of changes in wing-abdomen length ratio and aspect ratio (Hassall *et al.*, 2009). Alternatively, range expansions can decrease the predator or parasite pressure (Menéndez *et al.*, 2008) and thereby increase realised dispersal distances. However, there is some evidence that infection by e.g. parasites may increase dispersal distance in damselflies (see Suhonen *et al.*, 2010), so that release of parasite pressure can have differential effects.

Finally, climate change can also lead to dispersal inhibition, as shown for the common lizard (Massot *et al.*, 2008).

Similar problems can be suggested for the larval development time. Depending on latitude the larval development can be longer or shorter. This is hardly to cover in species distribution models as the climatic information on large scales often provides only monthly values even though daily values are needed. It can be further suggested that climate change will influence the larval development time (Richter *et al.*, 2008).

Another source of uncertainty relates to effects of winter warming on the diapause. Winter warming passing certain diapause-inducing temperature thresholds can prevent the beginning of the diapause (Hassall & Thompson, 2008) or increase the metabolic rate during this stage (Irwin & Lee, 2000). This and the fact that there are not enough food resources to compensate the energy deficit can lead to higher winter mortality and an increased extinction risk.

Though observations on dispersal distances already exist for some species, for most species the real dispersal ability is unknown, limiting the applicability of species-specific dispersal approaches. Allouche *et al.* (2008) provide alternative methods to incorporate distance constraints in species distribution models beside observed dispersal distances. These methods calculate the occurrence likelihood at a site based on the geographical locations of known occurrences. However, this approach is just another estimation of dispersal distance with its corresponding uncertainties. Hence, the improvement of existing and the development of new methods to estimate dispersal distances is required. Testing for correlations combining geographic range sizes with species-specific traits such as morphology and dispersal abilities is one option (Boehning-Gaese *et al.*, 2006). Field studies, like mark-release-recapture, can also provide information on dispersal distances. Further, other factors like Allee effects should be considered as these can influence the dispersal ability of a species (e.g. Veit & Lewis, 1996). In addition, modelling studies can be helpful tools to estimate dispersal distances. Recent work by Cabral & Schurr (2010) applies process-based modelling approaches to estimate plant species wind dispersal. While estimates of dispersal abilities will remain uncertain, the more we know about a species' ecology the better we can interpret model estimates of potential range changes. Such models with integrated species-specific dispersal abilities can help identifying species that may not keep up with rapid climate change. A further step to take species-specific dispersal abilities into account is to apply a cost grid (e.g. Foltête *et al.*, 2008). Such kind of ecological filters are enabling to consider a more realistic measure of the accessibility of suitable area than merely geographic distances, based on resistance values that are assigned to specific spatial parameters, such as landscape units.

All species distribution modelling approaches are influenced by the quantity and quality of occurrence data (Bittner *et al.*, 2011). The spatial resolution of the distribution data of the 25 EU states (Article 17 Habitats Directive) differs between countries and provides only data for EU member states at the time of the reporting obligation in 2007. Non-EU countries, such as Switzerland, Norway and the Balkan States, are not represented in the Habitats Directive but hold a certain part of the European distribution of listed species (especially the Balkan States). Leaving these occurrences out of consideration may distort the species distribution model, but the availability of such data (if they exist at all) is often limited. Therefore, the database of the species listed in the Habitats Directive, covering the European Union, provides a substantial and valuable source of distribution data in Europe. Nevertheless, a higher resolution of occurrence and distribution data (Seo *et al.*, 2009) as well as homogenous reporting of all countries in the next reporting obligation in 2013 would improve the basis for estimating effects of environmental change on species distributions.

Implications for nature conservation

An analysis of species and their habitats concerning their vulnerability to climate change is a first step. Such an assessment gives insights into potential future threats and highlights future conservation needs. In spite of model uncertainties, nature conservation practice needs more specific information on expected impacts of climate change on protected species and habitats for developing adaptation strategies. More 'realistic' model projections of future occurrences integrating species-specific traits, like dispersal abilities, can provide decision support for nature conservation (Franklin, 2010). These projections can be used to derive targeted management measures.

For species that cannot keep up with climate change, management measures have to be initiated. One opportunity would be the much-criticised assisted migration (Davidson & Simkanin, 2008; Hoegh-Guldberg *et al.*, 2008; Ricciardi & Simberloff, 2009). Kreyling *et al.* (2011) are discussing the pros and cons of this technique. The pros of this concept are a reduced risk of extinction for the focal unit, a conservation of genetic diversity and its pragmatic and cost-effective implementation. On the other hand there is a high risk of adverse effects on native species compositions; it can lead to biological homogenisation or a biased fauna and flora and poses the problem of identifying recipient localities with imperfect knowledge on ecology and climate change. For these reasons, assisted migration cannot be proposed as a suitable method without restrictions. It is an option in times of climate change, worth of consideration, needing a carefully weighting of pros and cons and the expected effectiveness.

However, not only such novel methods may be considered in times of climate change. Well established nature conservation approaches, such as monitoring, habitat preservation,

creation / extension of protected areas, retaining viable population sizes and the increase of landscape permeability (Opdam *et al.*, 2006; Bissonette & Adair, 2008) are important instruments to support species range changes and to improve the vitality of populations. Ott (2010) emphasises the increasing need for monitoring programs that allow the detection and contemporary quantification of changes in distribution and population size.

Concluding remarks

The present study highlights the need of explicit knowledge on species dispersal ability for the purpose of modelling potential impacts of climate change. Simple modelling approaches under the assumption of no and full dispersal may indicate where to find future suitable space and where it may potentially be lost. However, the integration of specific dispersal distances in the modelling process may substantially improve assessments of expected range shifts. This is needed for the development of targeted and efficient adaptation strategies for the conservation of endangered species.

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Supplemental figures

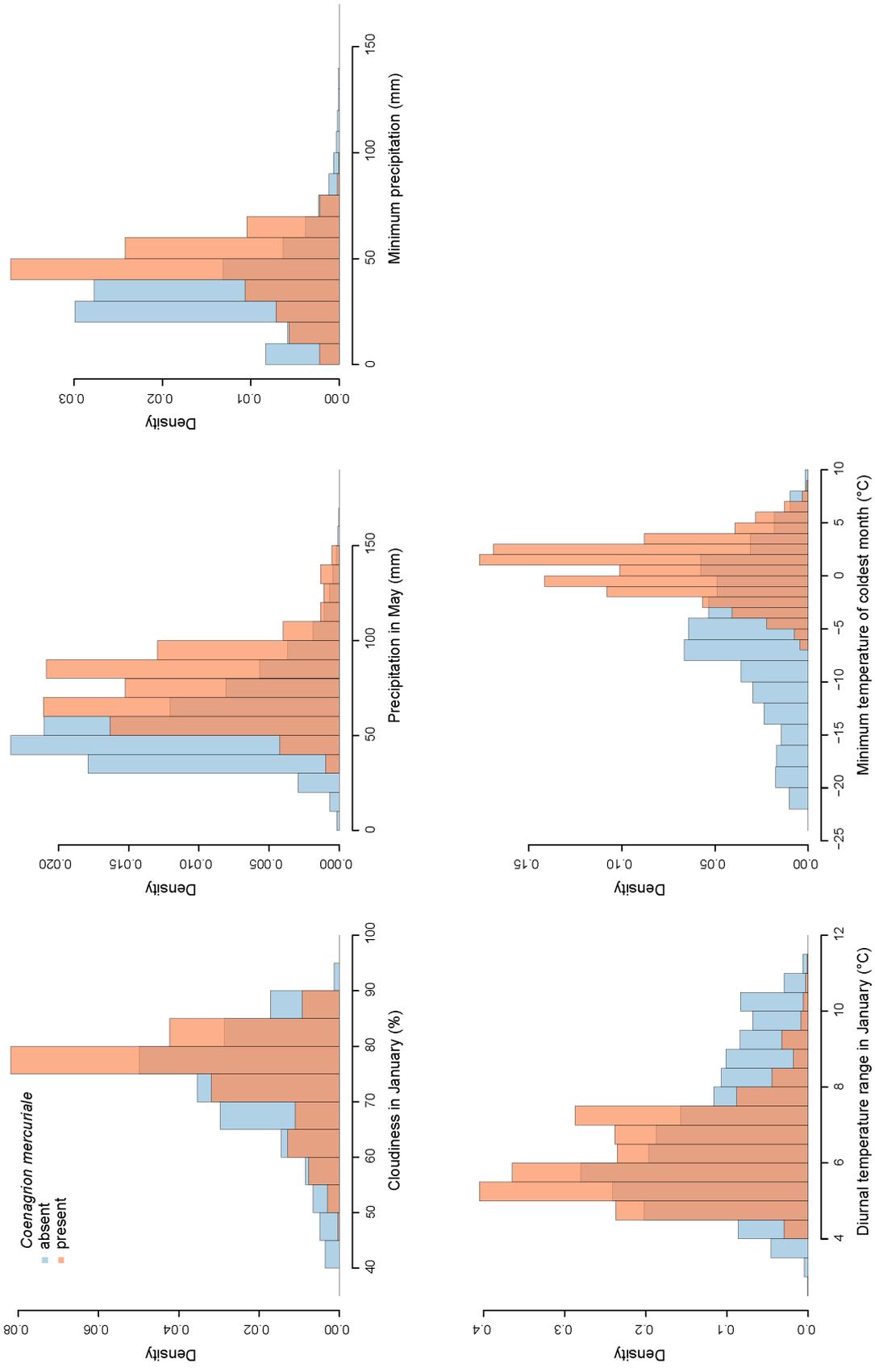


Fig. S1. Histograms of selected climatic variables for *Coenagrion mercuriale* at occurrence and absence locations in Europe. Of variable pairs that correlated more than 0.7, the one showing higher explanatory power in a single variable GLM was retained.

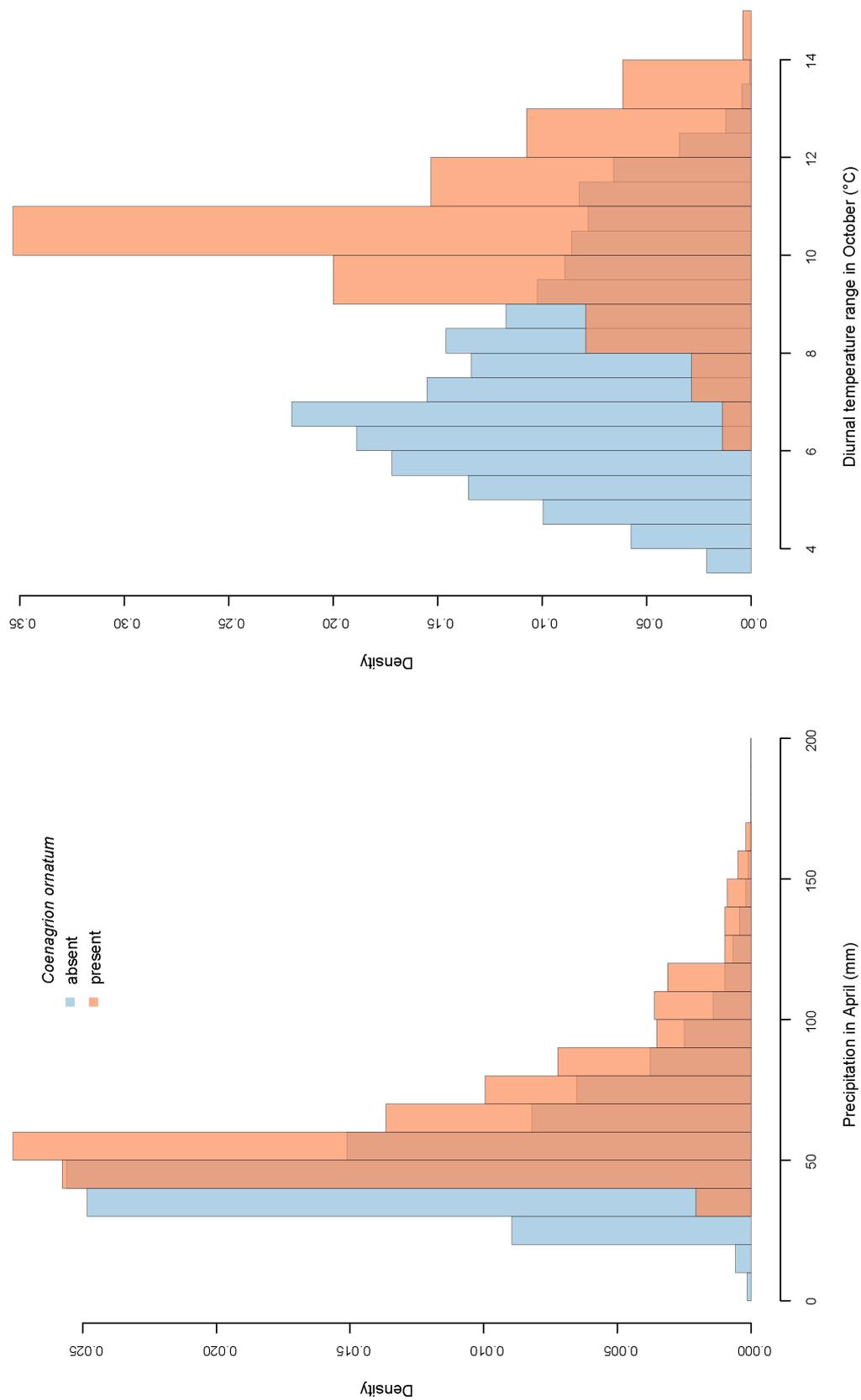


Fig. S2. Histograms of selected climatic variables for *Coenagrion ornatum* at occurrence and absence locations in Europe. Of variable pairs that correlated more than 0.7, the one showing higher explanatory power in a single variable GLM was retained.

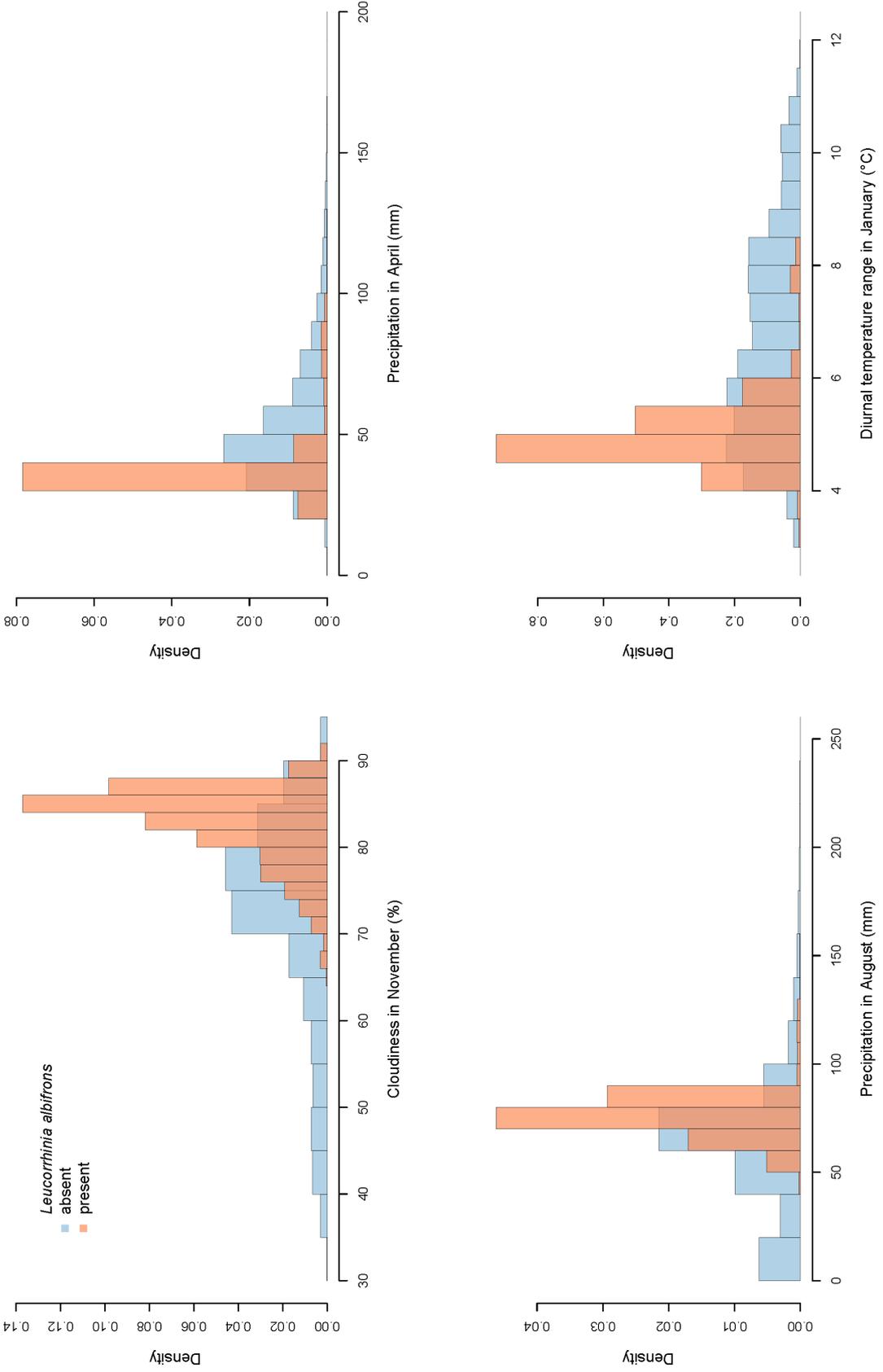


Fig. S3. Histograms of selected climatic variables for *Leucorrhinia albifrons* at occurrence and absence locations in Europe. Of variable pairs that correlated more than 0.7, the one showing higher explanatory power in a single variable GLM was retained.

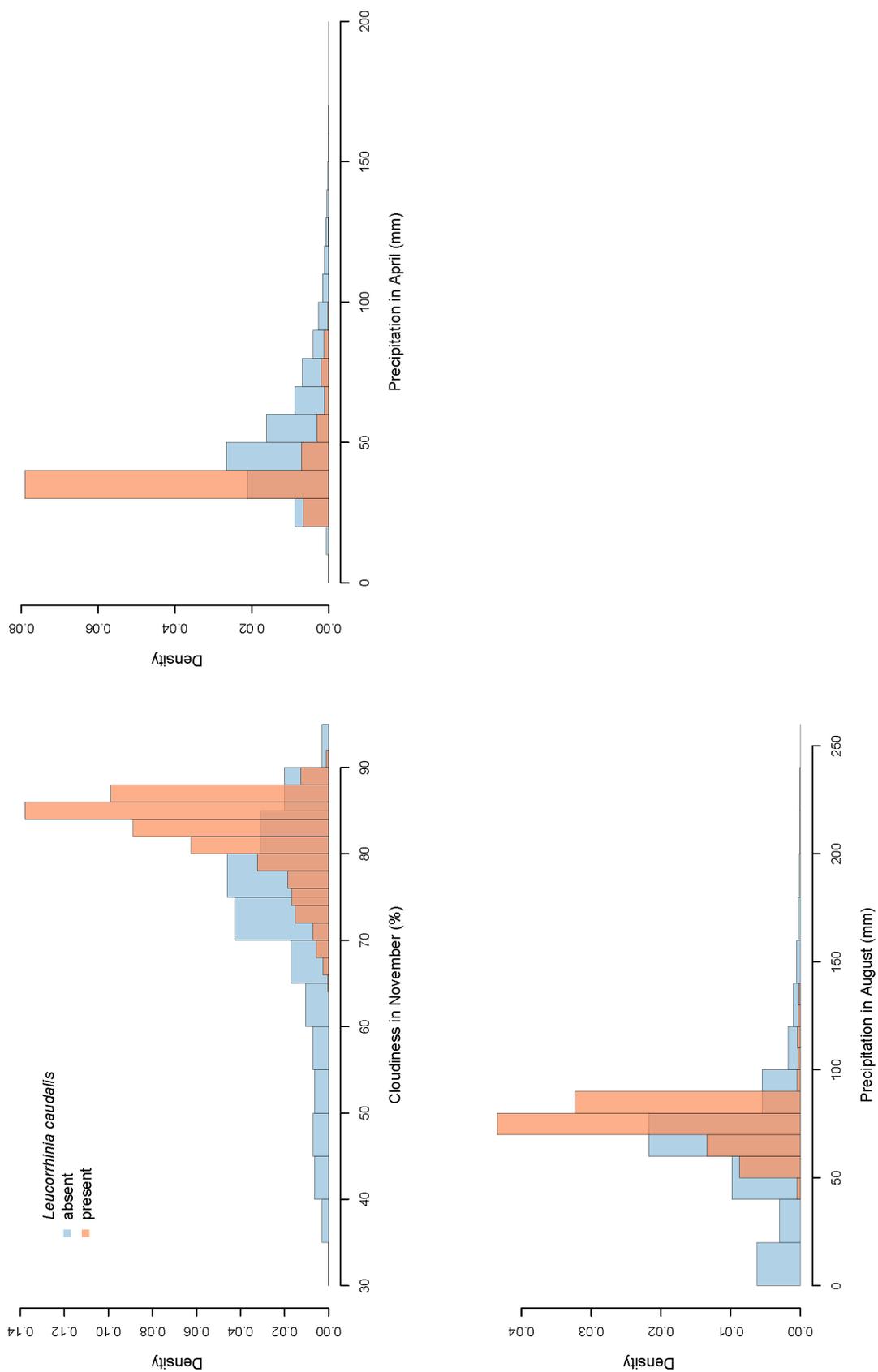


Fig. S4. Histograms of selected climatic variables for *Leucorrhinia caudalis* at occurrence and absence locations in Europe. Of variable pairs that correlated more than 0.7, the one showing higher explanatory power in a single variable GLM was retained.

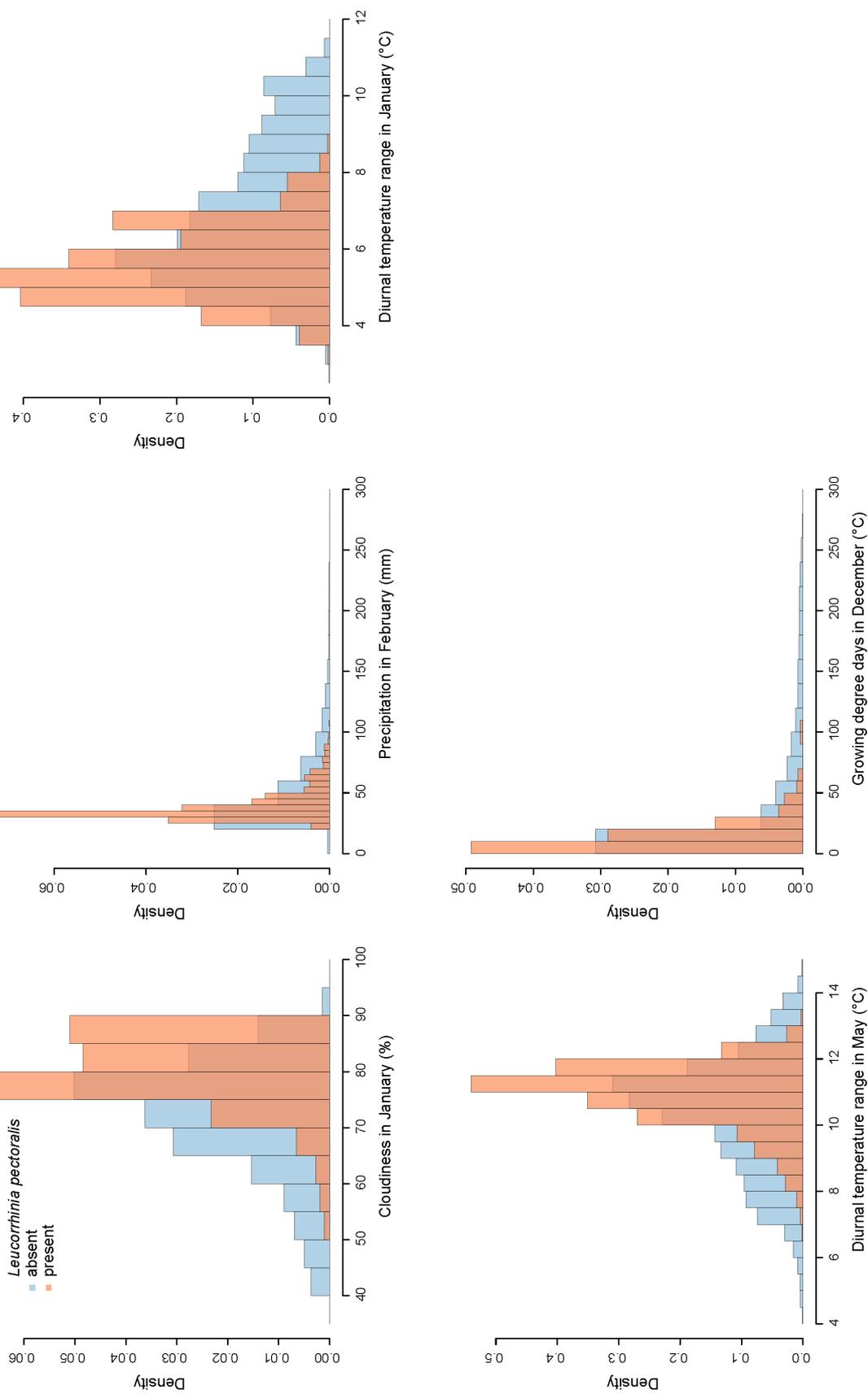


Fig. S5. Histograms of selected climatic variables for *Leucorrhinia pectoralis* at occurrence and absence locations in Europe. Of variable pairs that correlated more than 0.7, the one showing higher explanatory power in a single variable GLM was retained.

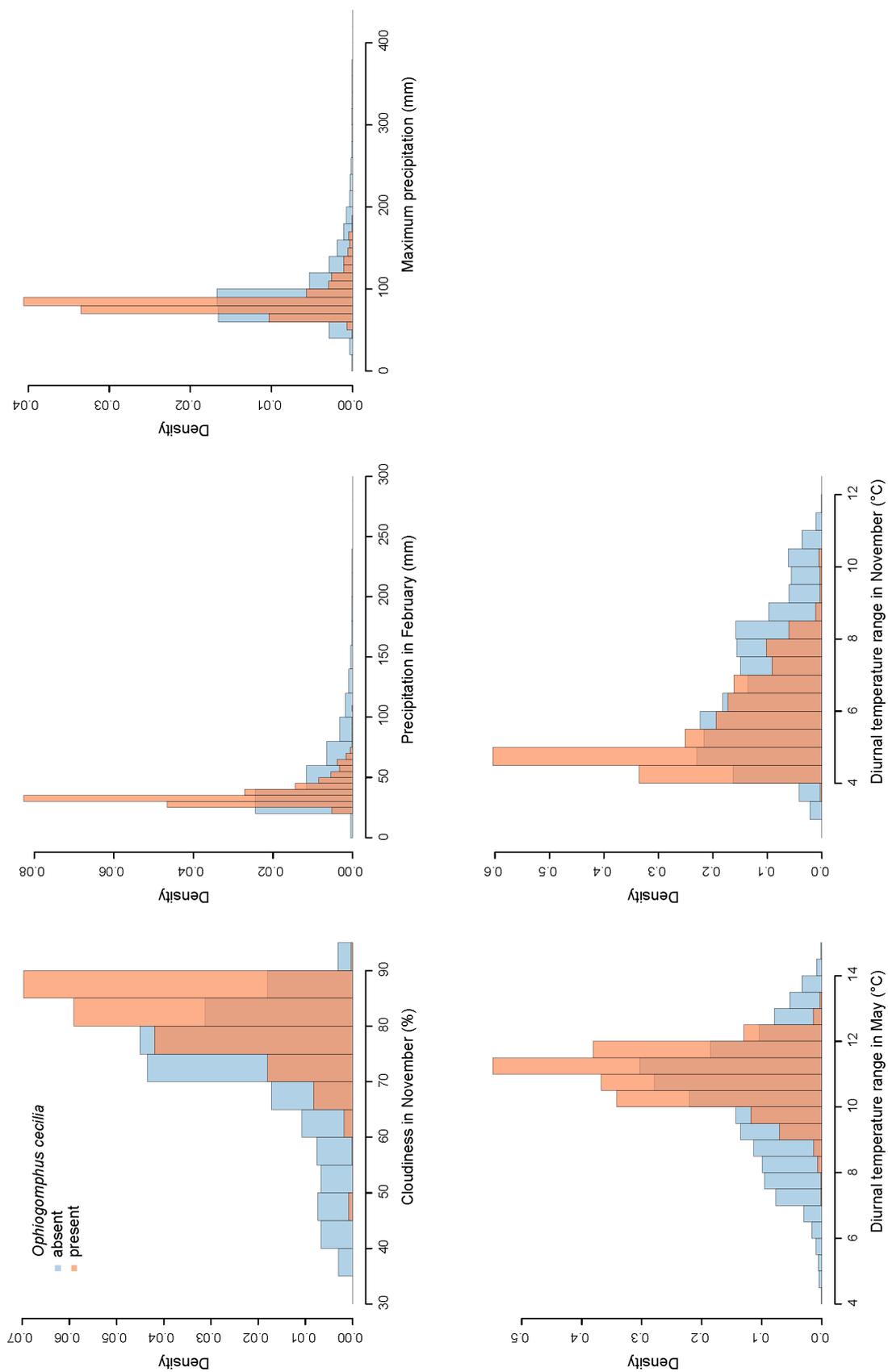


Fig. S6. Histograms of selected climatic variables for *Ophiogomphus cecilia* at occurrence and absence locations in Europe. Of variable pairs that correlated more than 0.7, the one showing higher explanatory power in a single variable GLM was retained.

Article 3

Biotic interactions in the face of climate change: a comparison of three modelling approaches

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Biotic interactions in the face of climate change: a comparison of three modelling approaches

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Abstract

Climate change is expected to alter biotic interactions, and may lead to temporal and spatial mismatches of interacting species. Although the importance of interactions for climate change risk assessments is increasingly acknowledged in observational and experimental studies, biotic interactions are still rarely incorporated in species distribution models.

We assessed the potential impacts of climate change on the obligate interaction between *Aeshna viridis* and its egg-laying plant *Stratiotes aloides* in Europe, based on an ensemble modelling technique. We compared three different approaches for incorporating biotic interactions in distribution models: (1) We separately modelled each species based on climatic information, and intersected the future range overlap ('overlap approach'). (2) We modelled the potential future distribution of *A. viridis* with the projected occurrence probability of *S. aloides* as further predictor in addition to climate ('explanatory variable approach'). (3) We calibrated the model of *A. viridis* in the current range of *S. aloides* and multiplied the future occurrence probabilities of both species ('reference area approach'). Subsequently, all approaches were compared to a single species model of *A. viridis* without interactions.

All approaches projected a range expansion for *A. viridis*. Model performance on test data and amount of range gain differed depending on the biotic interaction approach. All interaction approaches yielded lower range gains (up to 667% lower) than the model without interaction. Regarding the contribution of algorithm and approach to the overall uncertainty, the main part of explained variation stems from the modelling algorithm, and only a small part is

attributed to the modelling approach.

The comparison of the no-interaction model with the three interaction approaches emphasizes the importance of including obligate biotic interactions in projective species distribution modelling. We recommend the use of the 'reference area approach' as this method allows a separation of the effect of climate and occurrence of host plant.

Introduction

On-going climate change is a driving factor for species range shifts (e.g. [1-3]). Expected range changes are often assessed by climate envelope models, which relate species' occurrences to environmental variables [4,5]. Such models can be projected into the future and used to detect suitable future habitats of a species and indicate potential range changes [6]. However, the restriction to climatic variables has been criticized [7,8] and calls for the consideration of other factors determining species distributions such as biotic interactions [9].

Climate change is expected to alter biotic interactions and thereby to influence species range shifts both directly and indirectly. Positive changes, such as an escape from parasites or predators are possible [10] allowing some species to exploit a wider range of environments providing the opportunity to spread faster and in larger numbers into new areas. On the other hand, diverging influences on interacting species, such as a range contraction of the essential species, can hinder range expansions of the dependent species into new suitable areas although climatic suitability is expected (e.g. [11]). Observations and experimental studies on interactions in times of climate change are increasingly conducted (e.g. [12,13]). However, methods to integrate interactions in species distribution modelling are still rarely implemented so far (but see [9,11]), and no comprehensive analysis on how to best represent biotic interactions in species distribution models has been conducted.

Here, we analysed the interaction between a dragonfly, the green hawker (*Aeshna viridis* Eversmann, 1836), which is protected in the European Union under the EU Habitats Directive, Annex IV, and its egg-laying plant water soldier (*Stratiotes aloides* L.). In Europe, water soldier is nearly the only egg-laying plant of *A. viridis*, whereas this plant plays no role for reproduction in the Asian populations of the dragonfly. The restriction to *S. aloides* in Europe is advantageous for the dragonfly larvae as the spiny leaves of the plant provide shelter against fish predation [14]. Additionally, intra-guild predation and interference competition against other dragonfly larvae is reduced [15]. *S. aloides* has declined during the last decades in Europe, mainly as a consequence of eutrophication, light competition, and multiple environmental stressors resulting from water pollution [16]. With the decrease of the egg-laying plant, the dragonfly has disappeared from large parts of its European distribution and is at present highly

endangered in Europe and listed in the Red Data Books of e.g. The Netherlands, Germany and Finland.

Based on the current European distribution of both species bioclimatic envelope models were developed. We applied three different approaches to consider the species' obligate biotic interaction. First, we applied an approach that intersects the projected future distributions of both species ('overlap approach'). Second, we used the current and future projected occurrence probabilities of *S. aloides* as additional explanatory variable for the occurrence of *A. viridis* ('explanatory variable approach') (similar to [9]). As third approach we restricted the climatic reference area for *A. viridis* to where the egg-laying plant is currently present ('reference area approach') (similar to [11]). We hypothesized that these three approaches differ considerably in their performance and in the projected extent of range change from the model without interaction and among each other. In particular, we expected a higher model performance and a lesser range change with the consideration of biotic interactions. In addition, our a priori expectation was that spatial mismatches between the dragonfly and its egg-laying plant might occur in the future.

Materials and Methods

Species

The dragonfly *A. viridis* inhabits marshlands, ditches and lakes with sizeable masses of *S. aloides* in the Continental, Atlantic and Boreal biogeographical region of Europe (Figure 1A). Due to its habitat specialisation, this species is scarce and under threat in much of its European range. *A. viridis* is listed in Annex IV of the European Union Habitats Directive and therefore EU-wide protected, but is also protected by national law or under special conservation concern. Flight season is from late June onwards to early October. The species is most abundant in August [17].

The water plant *S. aloides* inhabits standing or slow-flowing, meso-eutrophic waters [18] in the same biogeographical regions as *A. viridis*, with small outposts in the Mediterranean region (Figure 1B). It exists in the shallow parts of the littoral zone as an emerged form and in deeper parts as a submerged form. During the vegetation cycle translocations of individuals between water bottom and surface occurs [14]. *S. aloides* can be used as an indicator of valuable habitat in terms of high macro-arthropod diversity and species richness [19,20], and the occurrence of *A. viridis* further increases the conservation value of these plant populations [19].

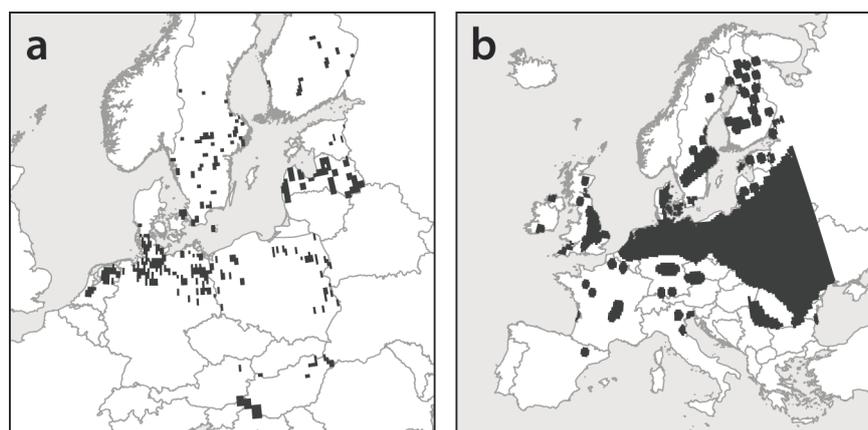


Figure 1. Current distribution of A) *Aeshna viridis* and B) *Stratiotes aloides* in Europe [21,22].

Species and climate data

Information on the current distribution of *A. viridis* was retrieved from the EIONET (European Environment Information and Observation Network) Central Data Repository server [21]. The data stem from the European reporting due in 2007 pursuant to Article 17 of the Habitats Directive. They are available for 25 EU countries in different spatial resolutions. The distribution of *S. aloides* was scanned from a map in the Atlas of North European vascular plants: north of the tropic of cancer [22] and geo-referenced in a Geographic Information System (ArcGIS 9.3.1) integrating the distribution data in our 10' (arcminutes) grid. Distribution data of both species were provided as presence-absence data with 9932 presence points for *S. aloides* and 658 presence points for *A. viridis*. These distribution data were reported by the member states of the European Union Habitats Directive in 2007 (25 EU members). Each member has an obligation to report the distribution and state of species and habitat types protected by the Habitats Directive every six years.

Current and potential future European climate was quantified on a 10' (arcminutes) grid from interpolated observed and future simulated climate data [23]. Future projections were based on the intermediate BAMBU (Business As Might Be Usual, A2) scenario [24], developed for the European project ALARM [25]. The future projection is driven by the HadCM3 climate model for the time period 2021-50. The observed climate data for model calibration cover the time period 1971-2000 and were taken from the ALARM dataset. Only one climate model and one emission scenario were chosen to exemplarily illustrate the application of biotic interaction approaches, although we are aware that climate models and scenarios differ among each other and therefore influence modelling results [26,27].

The following climatic variables were used in species distribution modelling both for the dragonfly and the egg-laying plant covering the necessary ecological conditions for survival and reproduction during the activity period of the dragonfly and the vegetation period of

the plant: mean monthly precipitation during the activity period of the adult dragonfly (May-August, mm), mean monthly temperature during the activity period of the adult dragonfly (May-August, °C), precipitation sum in the vegetation period (March-September, mm), sum of equilibrium evapotranspiration in the vegetation period (March-September, mm), maximum temperature of the warmest month of the year (°C), minimum temperature of the coldest month of the year (°C). Additionally, the projected current and potential future occurrence probabilities of *S. aloides* in Europe were used as explanatory variable. The average value of the projected current occurrence probability amounts to 0.35. On a local scale the existence of suitable water bodies would be additionally relevant for the occurrence of *A. viridis*. However, on the applied spatial scale (ca. 20 x 20km) together with the preference of *S. aloides* for small, nutrient-rich water bodies, such as drainage ditches [18] it can be assumed that a neglect of this would be less problematic in future projections.

Species distribution modelling

We used the ensemble modelling approach of BIOMOD [28,29] with nine different modelling algorithms (generalised linear models (GLM), generalised additive models (GAM), multivariate adaptive regression splines (MARS), classification tree analysis (CTA), flexible discriminant analysis (FDA), artificial neural networks (ANN), generalised boosted models (GBM), random forests (RF), and surface range envelope (SRE)). BIOMOD allows the calculation of an ensemble prediction of all algorithms, reducing the uncertainties arising from using only a single algorithm. It provides several methods to calculate the ensemble, such as probability mean and weighted mean. We here used the probability mean, which has been reported to provide more robust predictions than other consensus methods [30]. Additionally, BIOMOD provides an assessment of variable importance based on the extent to which model predictions change when a given variable is randomized [31].

The models were trained using observed current species distribution data and observed climate data (reference period 1971-2000). The results were internally validated with a one-time data splitting method [32], randomly partitioning the data set in 70% training and 30% test data. We used the AUC (area under the receiver operating characteristic curve) as model performance criterion to measure the overall model discrimination [33]. While the AUC has been recently criticised (e.g. [34]) it still provides an informative measure of model discriminatory performance [35]. Additionally, we provide omission (fraction of observed presences projected as absences) and commission (fraction of observed absences projected as presences) rates. The threshold for occurrence and non-occurrence projections corresponds to the prevalence of model-building data [36]. A certain threshold was selected to delineate potential future range borders for calculating the projected proportion of percentage gain

and loss (e.g. [37]).

All analyses were performed with R 2.12.0 [38]. In addition to the provided R packages we used the BIOMOD package version 1.1-5 [39] and the package hier.part version 1.0-3 [40]. Spatial data were processed with ArcGIS 9.3.1.

Biotic interaction approaches

For modelling the distribution of *A. viridis*, the following three approaches were applied: (1) 'overlap approach', (2) 'explanatory variable approach', and (3) 'reference area approach' (Figure 2). For the 'overlap approach', the current and potential future distributions of *A. viridis* and *S. aloides* were modelled individually with climatic variables. The projected future occurrences of both species were intersected, retaining only those areas where both species are projected to occur mutually in the future assuming unlimited dispersal (Figure 2A). The 'explanatory variable approach' includes for the modelling of the dragonfly, beside the climatic variables, the modelled current and projected future occurrence probability of the egg-laying plant in Europe (Figure 2B). For the 'reference area approach' the distribution model of *A. viridis* was calibrated on the current occurrence of *S. aloides* and then projected on Europe. This model thus describes the conditional probability of finding *A. viridis* under particular climate conditions, given that *S. aloides* is present. To yield the unconditional occurrence probability for *A. viridis*, this conditional occurrence probability was multiplied with the modelled occurrence probability of *S. aloides* (Figure 2C).

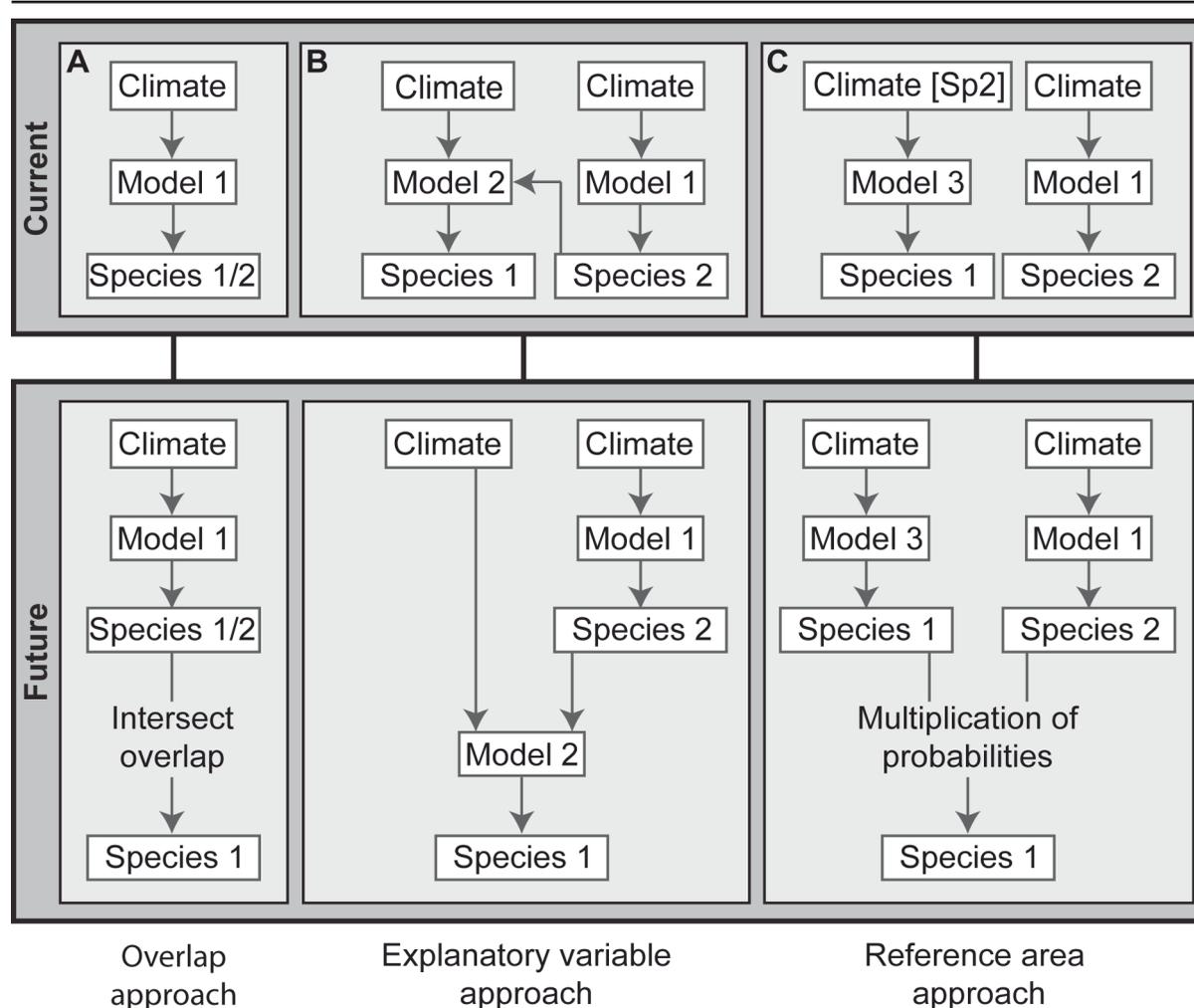


Figure 2. Conceptual framework of the three applied approaches for modelling biotic interactions. A) 'Overlap approach': modelling both species separately and intersecting the future range overlap. B) 'Explanatory variable approach': modelling the dependent species with the essential species as additional explanatory variable. C) 'Reference area approach': modelling the dependent species in the range of the essential species and multiplication of the occurrence probabilities of both species. Species 1: dependent species (here: *Aeshna viridis*), Species 2: essential species (here: *Stratiotes aloides*), Climate [Sp2]: restriction of climatic reference area of species 1 to the current distribution of species 2.

Comparison of interaction approaches

We compared the results of the three approaches according to four criteria: First, we evaluated the modelling performance with the criterion AUC on test data. Second, we analysed the spatial projections. For this purpose, we identified the two most important climatic variables determining the current distribution of *A. viridis* in Europe using the variable importance function in BIOMOD. We then plotted the projected future losses and gains of all three approaches within the range of these two variables to assess where (in terms of the variable range) the projections differ.

Third, potential non-analogue climatic conditions between current conditions and future projections in time were calculated for the 'reference area approach', which is particular susceptible to this phenomenon as it restricts the climate space used for model fitting of

the dragonfly species to that space occupied by the egg-laying plant. Non-analogue climate demands caution in the interpretation of the results [41]. Potential non-analogue climate was determined by the Multivariate Environmental Similarity Surface (MESS) analysis [42]. The MESS analysis measures the similarity between the current observed climate used to train the model and the future projected climate for any grid cell. Negative values imply non-analogue climatic conditions.

Finally, we analysed the main source of variation in modelling results, i.e. either modelling algorithm or biotic interaction approach, using hierarchical partitioning. This method measures the contribution of each applied variable, independently and in conjunction with the other variables, to the total variance of a regression model and provides its relative importance. The nine modelling algorithms and three biotic interaction approaches resulted in 27 different future projections. These were analysed by calculating the difference between the amount of gained sites (number of projected future suitable grid cells where the species is currently absent) and the amount of lost sites (number of projected future unsuitable sites where the species is currently present) relative to the number of currently occupied sites [43]. These values were related to uncertainty factors (modelling algorithm, biotic interaction approach) using a linear model with a Gaussian error distribution.

Results

Projected geographical changes

Modelling the future European distribution of *A. viridis* solely with climatic information leads to a projected northward range expansion of this species (Figure 3A). Overall, a substantial range gain is projected for *A. viridis* (+ 1069%) assuming unlimited dispersal ability.

Including the biotic interaction with *S. aloides* leads to a smaller projected range expansion, irrespective of the particular biotic interaction approach. With the 'overlap approach', the overlapping area of both species is projected to increase. The projected overlapping region concentrates around the Baltic Sea in the future with core areas in North Germany/Denmark, Poland, Southeast Sweden, and Estonia/Latvia/South Finland (Figure 3B). The projected gain of area amounts to 860% compared to the current range of *A. viridis* assuming unlimited dispersal.

With the 'explanatory variable approach', the dragonfly is projected to gain, similar to the 'overlap approach'. The overall projected gain is, however, larger than with the 'overlap approach' (+ 984%, unlimited dispersal). The potential climatically suitable area of the dragonfly is mostly distributed around the Baltic Sea with core areas in North Germany/Denmark, Southeast Sweden and Estonia/Latvia/South Finland (Figure 3C). Some more

potentially suitable areas are projected in Finland, Sweden and Poland than in the overlap approach.

The 'reference area approach' projected the smallest gain of suitable area in the future: The amount of the projected gain accounts for 402% with unlimited dispersal. The projected area is more fragmented and contracted around the Baltic Sea than with the other approaches (Figure 3D).

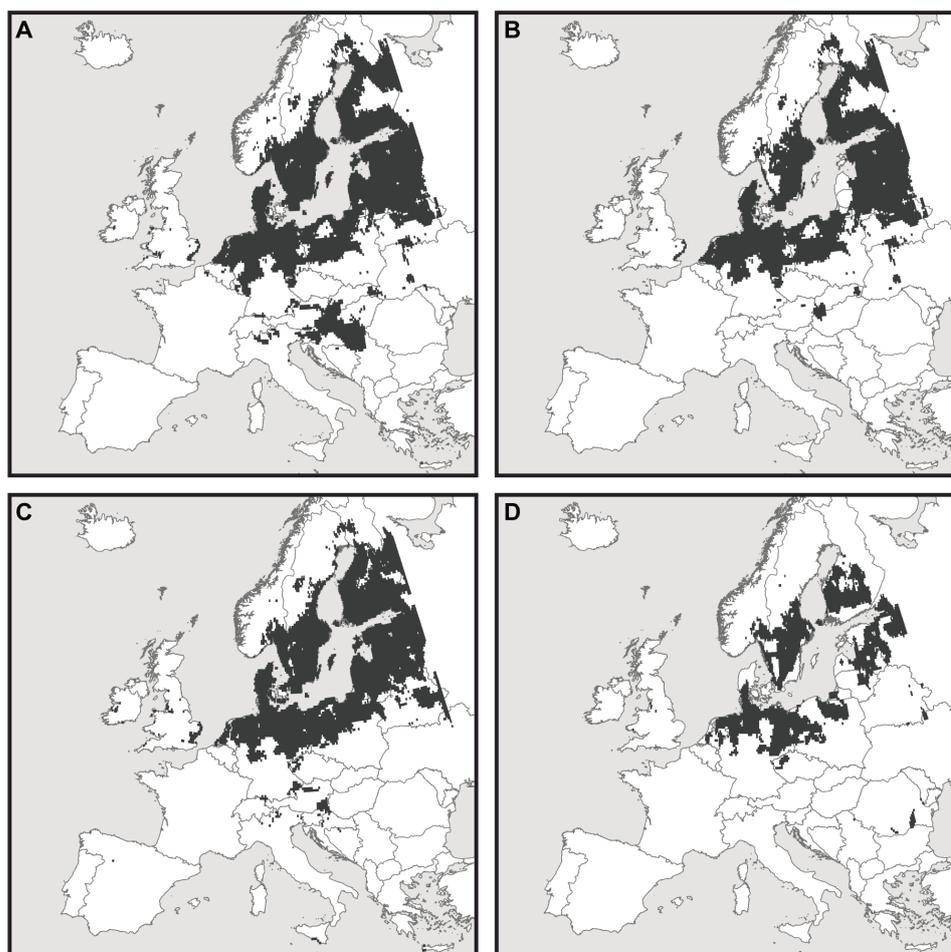


Figure 3: Projected potential future distributions of *Aeshna viridis* in Europe assuming unlimited dispersal. A) *A. viridis* without interaction, occurrence threshold: 0.02, AUC: 0.93. B) Overlapping area of the potential future distributions of *A. viridis* and *S. aloides*, occurrence threshold: 0.02 (*A. viridis*), 0.35 (*S. aloides*). AUC: 0.93 (*A. viridis*), 0.94 (*S. aloides*). C) Considering the modelled occurrence probability of *S. aloides* in Europe as additional explanatory variable beside climate. Occurrence threshold: 0.02. AUC: 0.92; D) Potential future distribution of *A. viridis* in Europe applying the 'reference area approach'. The model for *A. viridis* was calibrated within the distribution area of *S. aloides*. The modelled future occurrence probabilities of both species were multiplied. Occurrence threshold: 0.05. AUC: 0.88. All modelling results are based on an ensemble modelling with nine model algorithms with the climate model HadCM3 and the emission scenario A2 for the time period 2021-50.

For the 'reference area approach', climatic similarity between calibration and projection region was determined by MESS analysis. Non-analogue climate can be identified along the Mediterranean coast, in the Alps and in the alpine parts of Northern Scandinavia (Figure S1). Projections of the species' climatic suitability into these regions must be interpreted with

particular caution.

Comparison of interaction approaches

All approaches showed high discriminatory model performance according to AUC, ranging from 0.88 to 0.94 (Table 1). Nevertheless, AUC values differ considerably between the approaches, especially between the 'reference area approach', which yielded the lowest AUC value of 0.88, and the others. The other approaches yielded higher and more similar values. Concerning omission and commission rates the 'explanatory variable approach' showed the lowest omission error, but the highest commission error compared to all other approaches (Table 1).

Table 1. Model performance and occurrence thresholds of the applied approaches. The occurrence threshold is equivalent to the prevalence of the model-building data.

Approach	AUC	Omission rate (%)	Commission rate (%)	Occurrence threshold
<i>Aeshna viridis</i> only	0.93	0.84	5.90	0.02
<i>Stratiotes aloides</i> only	0.94	6.05	5.81	0.35
Overlap	/	0.67	4.40	/
Explanatory variable	0.92	0.58	12.02	0.02
Reference area	0.88	1.20	1.88	0.05

As the 'overlap approach' represents the intersection of both species' projected occurrences the AUC, threshold values, omission and commission rates of the single species modelling without interaction are shown.

Similarly, the differences in spatial patterns between the approaches are small but not negligible. The variable importance function in BIOMOD revealed the variables sum of equilibrium evapotranspiration in the vegetation period (March-September) and mean precipitation in July as the most important variables explaining the current distribution of *A. viridis* in Europe. For the 'overlap approach' most of the projected gaining points cover the range between 40 and 90 mm precipitation in July and 300 and 600 mm equilibrium evapotranspiration sum in the vegetation period (Figure 4). Losses are mainly projected between 600 and 700 mm equilibrium evapotranspiration sum in the vegetation period. The 'explanatory variable approach' shows a similar pattern. But in contrast to the 'overlap approach' additional gains are projected in the range of 600 and 700 mm evapotranspiration sum in the vegetation period and 90 till 140 mm precipitation in July. For the 'reference area approach' projected gains and losses cover similar ranges with precipitation in July mainly between 50 and 90 mm and equilibrium evapotranspiration sum in vegetation period between 450 and 550 mm representing a narrower range than the two other approaches. Compared to the current distribution (Figure S2) all biotic interaction approaches project gains in grid cells with climatic conditions that are currently not populated by *A. viridis*.

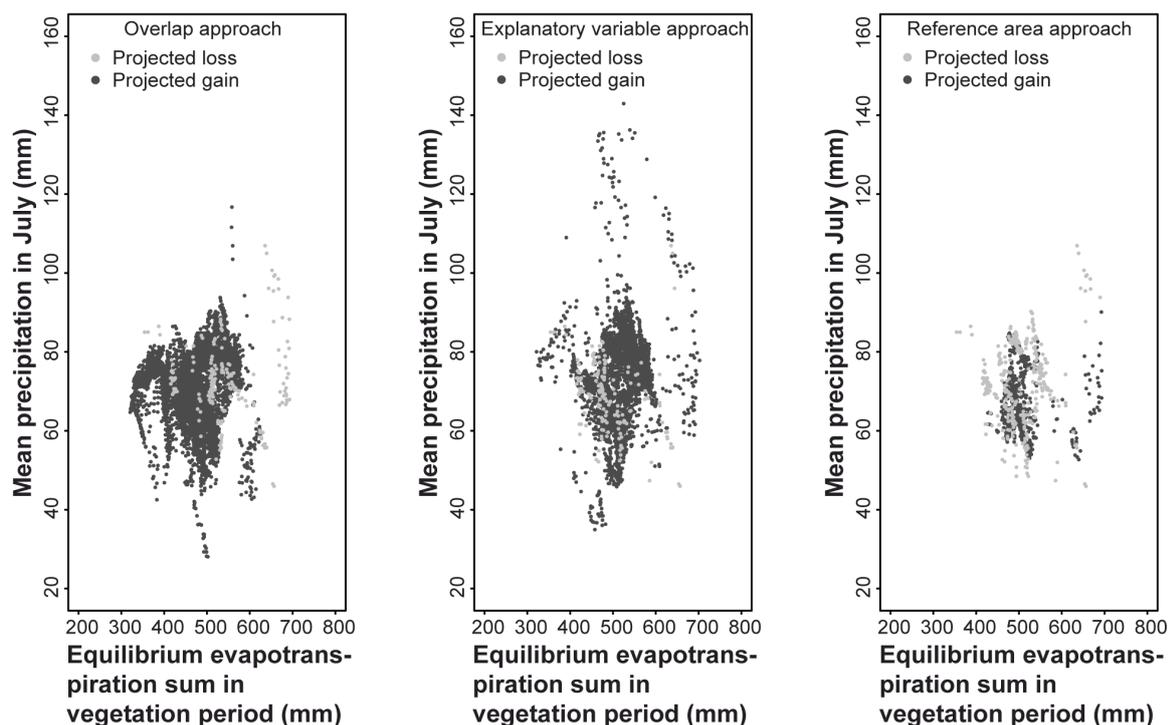


Figure 4. Projected future losses and gains of the current distribution of *Aeshna viridis* in Europe. Losses and gains are shown for the three applied biotic interaction approaches depending on the two most range-influencing climatic variables (out of six variables; variable importance measured by BIOMOD). Climate model: HadCM3, emission scenario: A2, time period: 2021-50. The vegetation period ranges from March until September.

Regarding the contribution of algorithm and approach to the overall uncertainty, the main part of explained variation stems from the modelling algorithm (99.3 %), and only a small part is attributed to the modelling approach (0.7 %).

Discussion

Projected changes in spatial distribution patterns

The projected range changes for *A. viridis* up to 2021-50 were similar independent of the applied method for incorporating biotic interactions – namely ‘overlap’, ‘explanatory variable’ and ‘reference area approach’ – and of the modelling result for the target species *A. viridis* only. All model results projected a range expansion. However, smaller percentage gains were projected when biotic interactions were included. Similar results were found in a study where biotic variables were included in niche models for a butterfly and a bird species [44]. There, habitat availability was also reduced compared to a climate-only model although the species’ ranges generally declined. In our case, the essential egg-laying plant is projected to increase its range northwards, which could favour the spread of *A. viridis*.

The populations at the tail end of the distribution are regarded to be crucially important for the survival of a species due to high levels of regional genetic diversity and local adaptations

[45]. The loss of genetic diversity, as expected through climate change, could mean the loss of potentially adaptive alleles leading to a lower adaptation potential and therefore to a higher extinction probability [46]. Here, *A. viridis* seems not to be affected by a loss of genetic diversity as range losses at the southern range margin are rarely projected. In this case, the projected range concentration around the Baltic Sea and its potential as leading edge for northward-directed range expansions might be a primary focus of nature conservation. However, a secondary focus on regions where a distribution loss might occur may be beneficial to maintain genetic diversity and local adaptation possibilities.

Another study showed that the incorporation of biotic interactions into species distribution modelling has an effect on the projections of the potential future distribution of a species [9]. They tested a modelling approach similar to our 'explanatory variable approach' with the result that the consideration of the host plant of *Parnassius mnemosyne* affected the projection of the species' future potential distribution and significantly improved model performance. In our study, we could partly confirm this finding for a dragonfly and its specific egg-laying plant. The incorporation of the interaction affected the future spatial projections, although the performance criterion AUC did not improve. Other authors could also demonstrate an improvement of model performance with the inclusion of biotic interactions [47]. In addition, they suggest that species interactions may significantly affect distributions on macro-ecological scales at least for boreal birds.

Our expectation that a strong spatial mismatch between *A. viridis* and *S. aloides* might occur in the future is not supported by the modelling results. All applied modelling approaches resulted in remaining overlapping areas and showed similar tendencies in projected range losses and gains. Beside this spatial congruence a temporal mismatch could occur, which is not considered so far. Field studies could already prove temporal mismatches caused by climate change for different species with both positive (i.e. range expanding) (e.g. [10]) and negative (i.e. range declining) (e.g. [48]) effects on the studied populations. However, we suggest for our case that such a temporal mismatch is unlikely as *A. viridis* is not dependent on a specific stage of *S. aloides* (such as flowering), which is only available for a short time, but is rather dependent on the occurrence of the plant in general.

A host plant change as currently observed for the butterfly *Aricia agestis* in Great Britain and therewith a facilitation of range expansion [49] could be imaginable. However, a change of the egg-laying plant of *A. viridis* seems unlikely. Though *A. viridis* occasionally uses other plants, such as *Typha* spp. and *Sparganium* spp., only *S. aloides* provides shelter for the larvae against fish predation [14]. In a predation experiment they revealed a significant higher survival of larvae in tanks with *S. aloides* than in tanks without this plant.

Interaction approaches

The hypothesis that the three biotic interaction approaches differ considerably in their performance and their projected extent of range change is only partly supported by our results. The AUC values differed between the approaches to a varying extent, but all approaches exhibited high model performance. However, the value of the performance criterion did not improve with the inclusion of the host plant as additional predictive variable. Omission and commission rates were relatively small to moderate but nevertheless differed between approaches. The climate-only model of *A. viridis* yielded both a low omission and commission rate whereas the other approaches differed more in these rates. As an extreme example, the 'explanatory variable approach' had the lowest omission but the highest commission rate.

The projected geographical range changes were similar, concentrating the future potential suitable habitat around the Baltic Sea. All approaches projected range expansions in the north of the current distribution approving the recent findings of poleward range expansion of Odonata (e.g. [50,51]). Additionally, the current distribution gaps of *A. viridis* in Central and Northern Europe could be closed provided that suitable habitat is available. Nevertheless, there were some geographical differences distinguishing the outcomes of the three biotic interaction approaches. The question is how important these differences are on the applied spatial scale. At a finer scale, other factors than climate, such as land use and habitat fragmentation, play a more important role for species performance [8] overruling the projected range changes and necessitating a more detailed look at the projected regions.

The projected losses and gains depending on the two most important variables and biotic interaction approach differ considerably. These differences may be caused by the different ways *S. aloides* affects the distribution of *A. viridis* in the approaches. Projected range gains in grid cells with currently unoccupied climatic conditions by *A. viridis* can be attributed to *S. aloides*. The egg-laying plant currently occurs in habitats with an equilibrium evaporation sum in the vegetation period up to approximately 800 mm and a mean precipitation in July between approximately 10 and 160 mm.

Limitations

Absence data can be ambivalent, i.e. indicating unsuitable habitat or habitat that is suitable but unoccupied [5]. Further, for cryptic species or species that are difficult to detect in the field recorded absences might not be 'real' absences since the chance that the species occurs in a grid cell but is not detected is very high. Otherwise, presence-only data (such as museum data) often have strong sampling biases. Additionally, presence-only distribution modelling requires background (or pseudo-absence) data. The selection of such background data can influence model parameterization and therewith the accuracy of model projections [52]. Still,

more detailed data is rarely available at continental scales.

Biotic interactions may play a minor role on a continental scale and climate seems to be the most important factor determining the distribution of species [8]. However, in Europe the spatial distribution of *A. viridis* is controlled by the occurrence of *S. aloides*, and is thus crucial at this spatial scale. In another study the incorporation of biotic interactions at macro-scales significantly improved projections of species distributions [47] and therewith partly disproved the minor importance of biotic interactions on larger macro-scales. Hence, it seems appropriate to include the biotic interaction between *A. viridis* and *S. aloides* in species distribution modelling even at a continental scale.

A study about uncertainty in the model-building process determined model algorithm and data quality as the most influential factors [53]. Similar to these results, here the main source of uncertainty is the modelling algorithm. We dealt with this uncertainty by using an ensemble modelling approach giving mean values of the projections over all modelling algorithms. The variation explained by the approach to incorporate biotic interactions is minimal, suggesting that the choice of a particular approach is not a significant source of prediction uncertainty. However, the incorporation of biotic interactions improves the model ability to explain the data variance.

The MESS analysis [42], comparing the novelty of climate between projected and calibrated space, revealed a large extent of non-analogue climate. While the 'reference area' approach is conceptually appealing, as it allows separating the effect of climate and occurrence of the host plant, the restriction of the model calibration area to the current occurrence of the host plant increases the extent of novel climate. The ensemble modelling and the threshold method for calculating presence-absence points from occurrence probabilities applied in this study reduced the effect of extreme projections. Nevertheless, the issue of non-analogue climate has to be kept in mind, especially when applying other modelling techniques that are more prone to make extreme predictions. We recommend a visualization of the different projections of the single algorithms to detect such projections into regions with non-analogue climate conditions.

All species distribution modelling approaches depend on the availability, quality and timeliness of distribution data [54]. The spatial resolution of distribution data provided by the EU 25 member states (report obligation of the Habitats Directive 2007) differs between countries. Non-EU countries, such as Switzerland, Norway, Ukraine or the Balkan States, are not listed in the Habitats Directive. Leaving occurrences in these countries out of consideration may distort the species distribution model. However, the availability of such data is often limited. European distribution data of plants, not listed in the Habitats Directive and not

yet covered by the Atlas Florae Europaeae, can be most often only found in 'old' maps of distribution atlases, not necessarily representing the current distribution and mostly afflicted with sampling biases. The distribution data of *S. aloides* are from 1986 and may over- or underestimate the current distribution in Europe and therewith influence modelling results. Especially, the 'reference area approach' might be susceptible to incomplete occurrence data because of its model calibration on the range of the plant. Comparing the current distributions of both species *A. viridis* seems to occur where *S. aloides* does not exist. Two reasons for this are imaginable: Observed individuals of *A. viridis* are vagrants and do not breed there or the distribution map of *S. aloides* is incomplete at these places. Nevertheless, these databases provide a substantial and valuable source of distribution data in Europe.

Beside the well-studied uncertainties in forecasting species distribution modelling, such as the choice of model algorithm, climate model, emission scenario and so on, the selection of a certain threshold to convert occurrence probabilities into presence-absence points has remained a topic of debate. Several studies compared the performance of different thresholds (e.g. [36,55,56]) leading to different and even contrasting results in which threshold method performs best. We decided to use a threshold that equals the observed prevalence of the species in Europe. This has been shown to perform well with comparable high values for sensitivity, specificity and kappa [36]. However, this threshold resulted in low kappa values in another study [56]. Moreover, a recently published article documents that the choice of threshold is the second highest source of uncertainty following the modelling method [57]. Consequently, the choice of threshold can alter future range projections. In an extreme case, future projections may be reversed leading to projected range contractions (Figure S3) where with another threshold the range is projected to increase (Figure 3). Hence, it is important to evaluate the ecological plausibility of modelling results after deciding for a certain threshold.

All three here evaluated approaches for incorporating biotic interactions are static, i.e. they do not explicitly model range dynamics. Range dynamics of interacting species may lead to temporal mismatches, i.e. even if climatic conditions were suitable for both species, a lower range filling capacity of the host plant would limit the range expansion of the dependent species. Several approaches have been developed towards dynamic species distribution models, e.g. by coupling stochastic (meta-)population models with temporally varying species distribution models [58,59] or dynamic range models [60]. To our knowledge, these approaches have not yet been expanded to take biotic interactions into account.

Implications for future modelling of biotic interactions

Many species, for example insect species of the EU Habitats Directive such as *A. viridis*, have highly specialised habitat requirements and fragmented distributions. Therefore, it is unlikely

that they can colonise regions that become climatically favourable under climate change in the future. Hence, projections of the future distribution considering dispersal limitations and explicitly incorporating range dynamics may be more realistic for such species.

However, here we showed smaller range expansions to occur under a full dispersal scenario, only by including biotic interactions. Therefore, we conclude that for specialised species it is relevant to include biotic interactions in distribution modelling. Previous species distribution models without considering biotic interactions may have overestimated range gains and are over-optimistic in assessing future distributions.

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Supporting Information

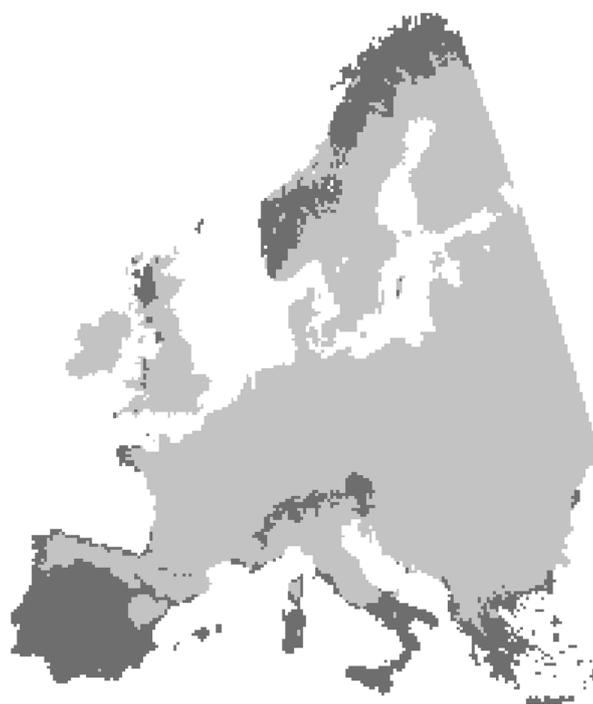


Figure S1. Results of the MESS-analysis for the 'reference area approach'. Light grey indicates a climatic similarity (values between 0 and 100) between calibrated (restricted to the current occurrence of *Stratiotes aloides*) and projected area (Europe). Dark grey areas (values < 0) indicate novel climate conditions in the projected area.

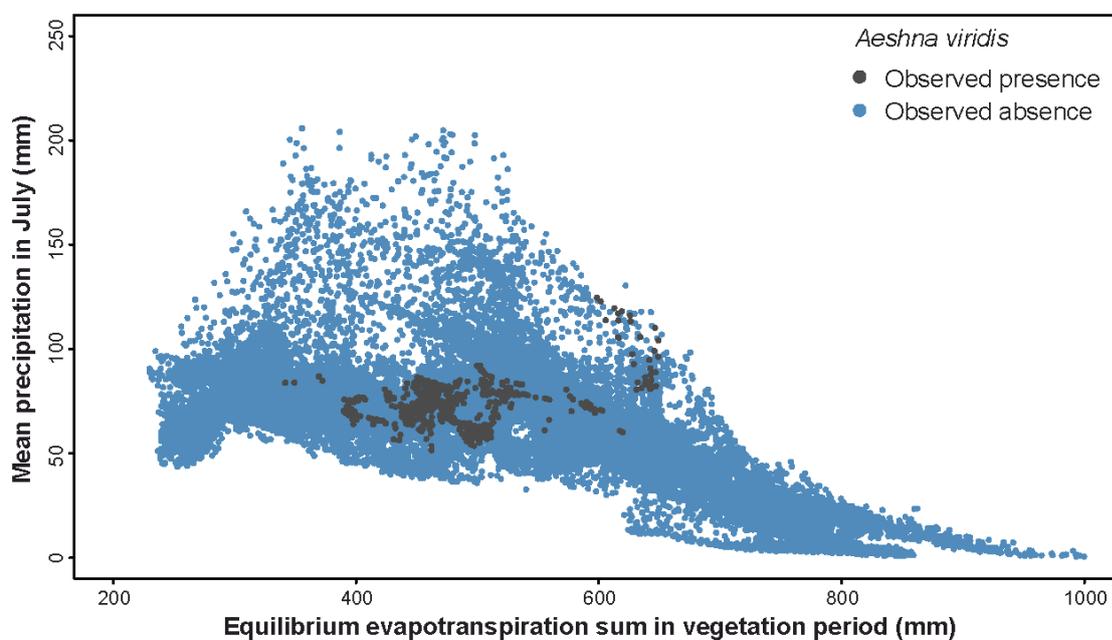


Figure S2. Distribution of *Aeshna viridis* depending on the two most range-influencing climatic variables. The current distribution in Europe comprises 658 observed presence points. The vegetation period ranges from March until September.

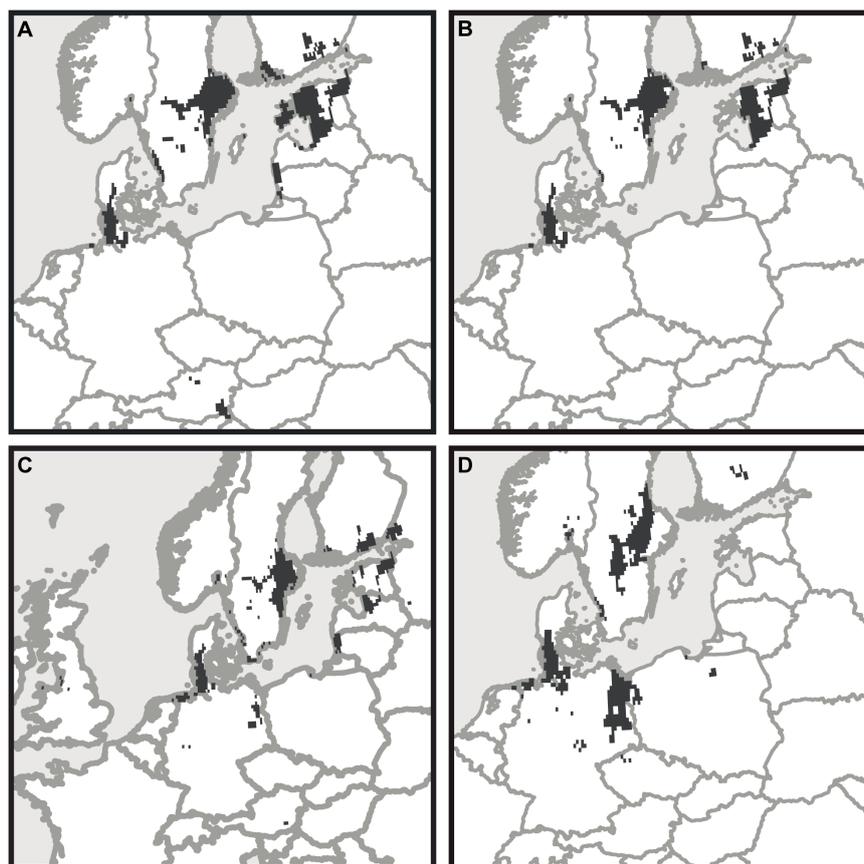


Figure S3. Projected potential future distributions of *Aeshna viridis* in Europe assuming unlimited dispersal. The threshold for occurrence and non-occurrence projections was selected such that the resulting prevalence (i.e. fraction of occupied sites) equalled the mean predicted occurrence probability. A) *A. viridis* without interaction, occurrence threshold: 0.12, AUC: 0.93. B) Overlapping area of the potential future distributions of *A. viridis* and *S. aloides*, occurrence threshold: 0.12 (*A. viridis*), 0.44 (*S. aloides*), AUC: 0.93 (*A. viridis*), 0.94 (*S. aloides*). C) Considering the modelled occurrence probability of *S. aloides* in Europe as additional explanatory variable beside climate. Occurrence threshold: 0.10, AUC: 0.92. D) Potential future distribution of *A. viridis* in Europe applying the 'reference area approach'. The model for *A. viridis* was calibrated within the distribution area of *S. aloides*. The modelled future occurrence probabilities of both species were multiplied. Occurrence threshold: 0.10, AUC: 0.88. All modelling results are based on an ensemble modelling with nine model algorithms with the climate model HadCM3 and the emission scenario A2 for the time period 2021-50.

Article 4

Comparing modelling approaches at two levels of biological organization – Climate change impacts on selected Natura 2000 habitats

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Comparing modelling approaches at two levels of biological organisation – Climate change impacts on selected Natura 2000 habitats

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Abstract

Question: Habitats are characterized by their plant species composition. Therefore, climate change impacts on habitats can be assessed by two complementary statistical approaches: either directly by modelling the climate envelope of the habitat, or indirectly by modelling the habitat in terms of its plant species. How do these approaches differ in their projected habitat distribution? What are the consequences for nature conservation?

Location: Europe.

Methods: Potential climate change impacts on the distribution of European protected Natura 2000 sites were modelled for five natural and semi-natural grassland habitat types, defined by the EU Habitats Directive, using data from the Atlas Florae Europaeae and reports on Natura 2000 sites. We used random forests (RF) and logistic regression (GLM) to model current and potential future distributions for 2050.

Results: All habitats are projected to lose between 22% and 93% of their range in the ‘no dispersal’ scenario. In the ‘unrestricted dispersal’ scenario, almost all habitats gain suitable climate space, between 5% and 100% of their current range. In the direct habitat approach, both model algorithms have high discriminatory performance on test data and are well calibrated. In the indirect species approach, only GLM shows high model performance; RF models are overfitted. Projections of occurrence probabilities differ more strongly between model approaches (‘direct’ versus ‘indirect’) than between model algorithms (GLM versus RF).

Conclusions: Habitats are complex entities. Because of their dynamic nature, particularly in the face of climate change, we suggest modelling the future distribution of habitat types not exclusively based on their current definitions and mapped distributions, but also based on their constituent elements, and in particular their characteristic plant species.

Keywords

Ecoinformatics; Ecosystem; GLM; Grasslands; Multi-species approach; Natural habitat type of community interest; Random forest; Species distribution model; Vegetation database

Introduction

Despite intense research efforts, large uncertainties remain about the effects of rapid climate change on plant and animal populations, as well as on entire ecosystems. Changes in habitats due to climate change pose a great challenge for nature conservation. In experiments, changes in climatic conditions lead to changes in species composition and community structure (Bruehlheide 2003; Kreyling et al. 2008). Furthermore, an increase of extreme weather events is expected to strongly affect plant communities (Jentsch et al. 2007; Jentsch & Beierkuhnlein 2008). The focus of research has been predominantly on individual species, and habitats as a whole are still rarely considered (Mücher et al. 2009). However, current concepts of nature protection are aimed at habitats in their entirety, such as in the European Natura 2000 system of the EU Habitats Directive.

Species and habitat types are entities of different kinds. In comparison, species are much better delineated, whereas there are substantial disparities in the definition of habitat types in ecology. In Article 1 of its Habitats Directive (92/43/EEC), the Council of the European Communities gives the following definition: “natural habitats means terrestrial or aquatic areas distinguished by geographic, abiotic and biotic features, whether entirely natural or semi-natural.” Here, we use the term habitat to indicate types of sites that are characterized by the occurrence of certain locally recorded plants. While this interpretation does not entail the full complexity of the EEC definition, it captures the key components of how habitats are interpreted in conservation practice (e.g. European Commission 2007).

We note that the concept of continuity in community composition and of potentially ‘natural’ assemblages has recently been questioned (Chiarucci et al. 2010). Species may react differently to environmental changes. Ultimately, this may result in altered community composition, the disruption of important biotic interactions and the loss of species. Nevertheless, a community-oriented approach is needed when ecological questions and nature conservation are addressed.

Ecoinformatics and vegetation databases provide important tools to analyse and project current and future potential implications of global climate change on habitats. In particular, species distribution models (SDMs) allow projections of possible range shifts (Elith & Leathwick 2009; Seo et al. 2009). Modelling distributions at a community or species assemblage level can help to address this challenge, as well as to overcome problems posed by biased and

incomplete data sets, and yield more complete information on the potential future suitability of habitats compared to individual species modelling (Riordan & Rundel 2009). There are several approaches dealing with spatial community-level data (e.g. Guisan & Zimmermann 2000; Ferrier et al. 2002; Ferrier & Guisan 2006; Riordan & Rundel 2009). In the case of habitats, species distribution modelling is conceivable in two ways: either directly by modelling the climate envelope of the habitat using the distribution data of the habitat itself, or indirectly by first modelling the habitat in terms of its plant species, and then modelling the climate envelope of these species in combination.

Here, we modelled selected habitats that are specified in the European Natura 2000 Directive and are therefore similarly or identically defined in the entire European Union (European Commission 2009). We compared two complementary modelling approaches working at two different levels of biological organisation. First, in the direct ‘habitat’ approach we focused at the ‘community’ level. Second, we looked at the single species level using the indirect ‘species’ approach. We analysed how these approaches differ in their projections and what practical implications this has. As example habitat types, we used five ‘natural and semi-natural grassland formations’. All these habitats are open, nutrient-poor and species-rich, and are well characterized by a set of specific plant species. According to Petermann et al. (2007), all these habitat types are affected by climate change to a medium high or high degree. The reaction of grasslands to changing environments is nevertheless an open question (Soussana & Lüscher 2007). Furthermore, we selected natural and semi-natural grassland formations, because their characteristic species are well represented in the Atlas Florae Europaeae (Jalas & Suominen 1972–1994; Jalas et al. 1996, 1999; Kurtto et al. 2004).

Our aim is to identify generality in expected habitat responses to climate change by comparing two modelling techniques. In addition, this allows us to evaluate the methodology. While we expect the direct ‘habitat’ approach to exhibit higher model performance as it ‘sees’ more of the climate–habitat relationship, we are interested in the way that the two approaches differ and in their consequences for nature conservation.

Methods

Habitat types

This study focuses on five ‘natural habitat types of community interest’, defined in Annex I of the EU Habitats Directive. Habitats of type 6110 are open, xerothermophile pioneer communities on superficial calcareous or base-rich soils (basic volcanic substrates), dominated by annuals and succulents of the *Alyssa alyssoides*–*Sedion albi* (European Commission 2007). Habitats of type 6120 are characterized by dry, frequently open grasslands on more-or-less calciferous

sand with a sub-continental centre of distribution (European Commission 2007). Habitats of type 6210 are described by dry to semi-dry calcareous grasslands of the *Festuco-Brometea*. This habitat is formed on the one hand by steppe or sub-continental grasslands (*Festucetalia valesiaca*) and, on the other by grasslands of more oceanic and sub-mediterranean regions (*Brometalia erecti*). In the latter case, a distinction is made between primary *Xerobromion* grasslands and secondary (seminatural) *Mesobromion* grasslands with *Bromus erectus*; the latter are characterized by their rich orchid flora (European Commission 2007). Habitats of type 6410 are *Molinia* meadows of plain to montane levels, on more-or-less wet nutrient-poor soils. They stem from extensive management, sometimes with a mowing late in the year, or correspond to a deteriorated stage of drained peat bogs (European Commission 2007). Habitats of type 6520 are species-rich mesophile hay meadows of the montane and sub-alpine levels (mostly above 600 m), usually dominated by *Trisetum flavescens* (European Commission 2007).

Information on the current distribution data of the habitat types was received from the EIONET (European Environment Information and Observation Network) Central Data Repository server (EIONET 2009). The data stem from the European reporting for the year 2007 pursuant to Article 17 of the Habitats Directive. They are available for 25 EU countries at different spatial resolutions (Fig. 1).

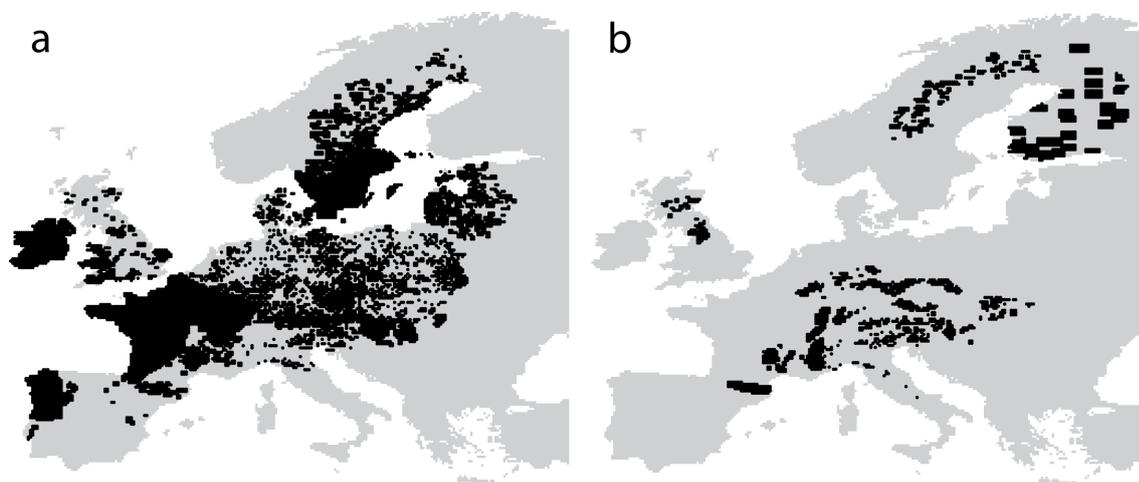


Fig. 1. Examples of distribution data within the EU (EU25) from the Article 17 Report (Source): (a) Distribution of 6410 *Molinia* meadows on calcareous, peaty or clayey-silt-laden soils (*Molinia caerulea*) and (b) 6520 Mountain hay meadows.

Species data

Data on the current distribution of characteristic plant species were taken from the Atlas Florae Europaeae (Jalas & Suominen 1972–1994; Jalas et al. 1996, 1999; Kurtto et al. 2004), the most comprehensive plant distribution data at the European continental scale (Bergmann et al. 2010). The Atlas Florae Europaeae (AFE) data are collected according to a grid map with

squares of 50km x 50 km. Due to the limited species coverage (20% of the European flora, Bergmann et al. 2010), many of the characteristic species of the habitat types, e.g. Poaceae, are not represented in the database. One important criterion for the selection of habitat types was, therefore, the representation of characteristic species in the AFE. First, we selected species that are specified as characteristic species of a habitat type by the European Commission (2007) and Ssymank et al. (1998) and that are available in the AFE (Table 1). These species have a high indicator value for the particular habitat. Starting from these expert knowledge-based, habitat-specific species sets, we used variable selection to identify the most suitable species to depict the respective habitat (see Modelling Design below).

Table 1. Characteristic plant species for the five selected habitat types, as defined by the European Commission (2007) and Ssymank et al. (1998) and represented in the Atlas Florae Europaeae. The asterisk '*' indicates priority habitat types.

Habitat type	Characteristic plant species
6110 * Rupicolous calcareous or basophilic grasslands of the <i>Alyso-Sedion albi</i>	<i>Alyssum montanum</i> , <i>Alyssum alyssoides</i> , <i>Dianthus gratianopolitanus</i> , <i>Holosteum umbellatum</i> , <i>Jovibarba globifera</i> , <i>Petrorhagia prolifera</i> , <i>Potentilla heptaphylla</i> , <i>Sanguisorba minor</i> , <i>Saxifraga tridactylites</i> , <i>Sedum album</i> , <i>Sedum sexangulare</i> , <i>Sedum acre</i>
6120 * Xeric sand calcareous grasslands	<i>Alyssum montanum</i> , <i>Cardaminopsis arenosa</i> , <i>Cerastium arvense</i> , <i>Dianthus arenarius</i> , <i>Dianthus deltoides</i> , <i>Gypsophila fastigiata</i> , <i>Herniaria glabra</i> , <i>Petrorhagia prolifera</i> , <i>Potentilla argentea</i> , <i>Sedum reflexum</i> , <i>Silene chlorantha</i> , <i>Silene otites</i>
6210 Semi-natural dry grasslands and scrubland facies on calcareous substrates (<i>Festuco-Brometalia</i>)	<i>Agrimonia eupatoria</i> , <i>Arenaria serpyllifolia</i> , <i>Arabis hirsuta</i> agg., <i>Cerastium brachypetalum</i> , <i>Cerastium glutinosum</i> , <i>Cerastium pumilum</i> , <i>Dianthus armeria</i> , <i>Dianthus carthusianorum</i> , <i>Dianthus deltoides</i> , <i>Erophila verna</i> , <i>Filipendula vulgaris</i> , <i>Fragaria viridis</i> , <i>Petrorhagia prolifera</i> , <i>Potentilla inclinata</i> , <i>Potentilla rupestris</i> , <i>Potentilla argentea</i> agg., <i>Potentilla heptaphylla</i> , <i>Potentilla tabernaemontani</i> , <i>Pulsatilla pratensis</i> , <i>Pulsatilla vulgaris</i> , <i>Ranunculus bulbosus</i> , <i>Sanguisorba minor</i> ssp. <i>minor</i> , <i>Silene vulgaris</i> , <i>Thalictrum minus</i> , <i>Thlaspi perfoliatum</i>
6410 <i>Molinia</i> meadows on calcareous, peaty or clayey-silt-laden soils (<i>Molinion caeruleae</i>)	<i>Cardamine pratensis</i> , <i>Dianthus superbus</i> , <i>Equisetum palustre</i> , <i>Geum rivale</i> , <i>Ophioglossum vulgatum</i> , <i>Parnassia palustris</i> , <i>Potentilla alba</i> , <i>Potentilla erecta</i> , <i>Ranunculus nemorosus</i> , <i>Ranunculus polyanthemus</i> , <i>Salix repens</i> , <i>Sanguisorba officinalis</i> , <i>Silene flos-cuculi</i> , <i>Thalictrum flavum</i> , <i>Trollius europaeus</i>
6520 Mountain hay meadows	<i>Anemone nemorosa</i> , <i>Dianthus deltoides</i> , <i>Potentilla erecta</i> , <i>Ranunculus nemorosus</i> , <i>Saxifraga granulata</i> , <i>Silene dioica</i> , <i>Silene flos-cuculi</i> , <i>Thlaspi caerulescens</i> , <i>Trollius europaeus</i>

Climate data

Current and potential future European climate was quantified on a 100 (arcminutes) grid from interpolated observed and future simulated climate data (Mitchell et al. 2004). Future projections were based on the intermediate BAMBU (Business As Might Be Usual, A2) scenario (Spangenberg 2007), developed for the European project ALARM (Settele et al. 2005). The future projection is driven by the HadCM3 climate model.

Modelling design

We compare two complementary modelling approaches, the direct 'habitat' and the indirect 'species' approach (Fig. 2). In the direct 'habitat' approach, we used the distribution of the habitat itself and modelled its climate envelope based on environmental factors of the habitat's current distribution. In other words, the habitat was treated like a species in regular species distribution modelling.

In the indirect 'species' approach, we modelled the habitat in terms of its characteristic species. This comprised two steps. First, a model for the occurrence of the habitat was developed, where we used as explanatory variables the presence or absence of the characteristic species instead of climatic variables. Second, we modeled the climatic envelope for each species. In order to project the distribution of the habitat as a function of the climate, we first projected the future occurrence probabilities of the species based on their climatic envelopes, and used these as input for the model of habitat distribution that uses species presence as explanatory variable.

In addition, we used two different modelling algorithms, the parametric generalized linear model (GLM) and the quasi non-parametric random forest (RF), to assess the uncertainty in model decisions (Dormann et al. 2008). For both approaches and model algorithms, we first dealt with collinearity in the predictors by selecting a variable set with pair-wise Pearson correlations < 0.7 . In pairs of correlated variables, we retain that variable with higher univariate predictive ability of the distribution of the species or habitat. Subsequently, a step-wise selection in the GLM model of the retained variables was based on BIC (Bayesian information criterion). Using the OOB error (ot uf bag error rate) as minimization criterion, variable elimination was carried out for the random forest model. The cut-off point for occurrence and non-occurrence projections was selected such that the resulting prevalence (i.e. fraction of occupied sites) equalled the mean predicted occurrence probability.

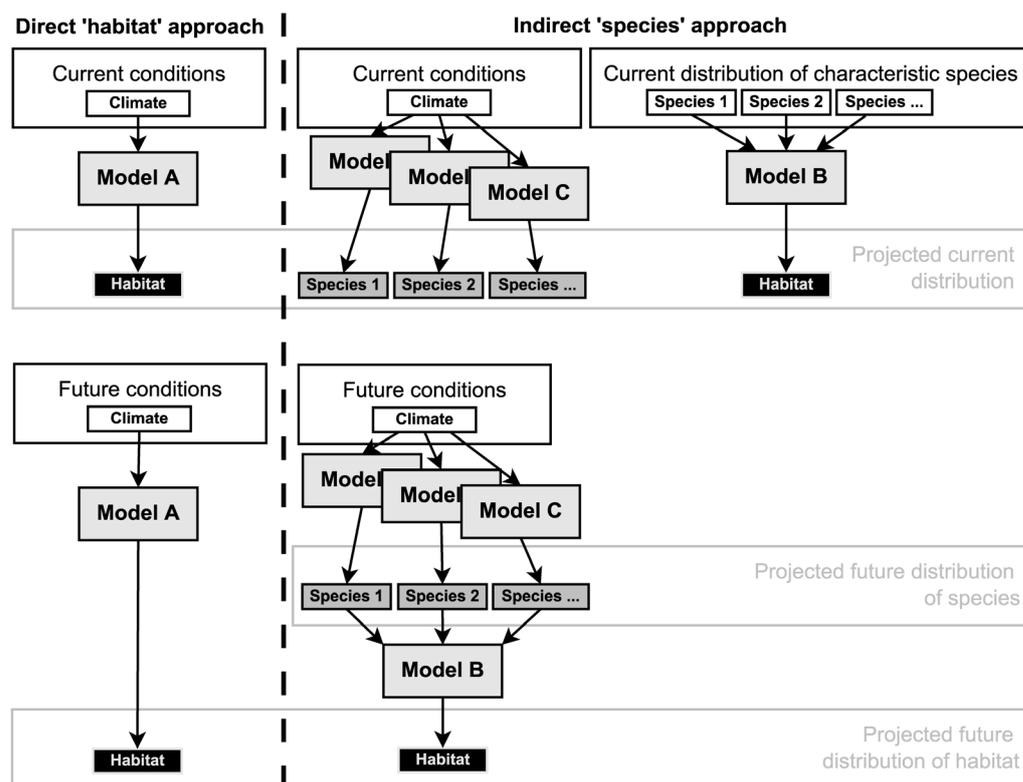


Fig. 2. Modelling framework illustrating the direct 'habitat' and indirect 'species' approaches. In both cases, the habitat is projected in its current and in a potential future distribution. Black boxes indicate results, white boxes are the input data, light grey are the model and dark grey are intermediate results.

For model validation we used a one-time random split approach with 70% training data and 30% test data. We used four model performance criteria: first, the AUC (area under the receiver operating characteristic curve) as a measure of overall model discrimination (Swets 1988); second, the slope of the calibration curve as a measure of overfitting – values below one indicate models that have been fitted too closely to the training data (the predicted probabilities are systematically too extreme; Reineking & Schröder 2006); third, the intercept of the calibration curve as a measure of bias (i.e. indicating whether the predicted probabilities are systematically too high or too low; Reineking & Schröder 2006); and fourth, the coefficient of determination, Nagelkerke R^2 , as a measure of explained variation.

While we are aware that entire habitats are not able to disperse, we applied two scenarios for the ability of habitats to keep up with climate change that, for simplicity, we call 'dispersal' scenarios: a no dispersal scenario, assuming that no range expansion is possible, and a full dispersal scenario, assuming the possibility of unrestricted dispersal processes for the characteristic plant species. A full dispersal scenario can provide hints on the potential future distribution of suitable space and therefore where to apply management measures. We expect that the no dispersal scenario is more realistic as habitats consist of different species with different dispersal abilities, which may react in different ways to a changing climate. It seems likely that habitats will rather develop into something new than shift their range.

All analyses were performed with R 2.10.1 (R Development Core Team, Vienna, AT, <http://www.R-project.org>). We used the randomForest package version 4.5–34 (Liaw & Wiener 2002); model performance was quantified with val.prob from the Design package version 2.3-0 (<http://CRAN.R-project.org/package=Design>). Variable selection in the RFModel was implemented with the varSelRF package version 0.7-1 (<http://ligarto.org/rdiaz/Software/Software.html>). Spatial data were processed with ArcMap 9.3.1.

Results

Habitat types

Almost all of the modelled habitats are projected to lose in every model (under the assumption of missing dispersion) more than 50% of their suitable area (Table 2). The Xeric sand calcareous grasslands (6120) lose least area with 22%, in the direct ‘habitat’ approach. Assuming that there is an unrestricted dispersion possibility, most habitat types gain distribution area; more in the direct ‘habitat’ approach than in the indirect ‘species’ one. The Mountain hay meadows (6520) habitat loses more than any other, even under the unrestricted dispersal scenario (Table 2, Fig. 4; Fig. S10–S11). Habitat type 6410 (*Molinia* meadows on chalk and clay) is projected to lose about 60% of its current distribution area with the GLM model, independent of the modelling approach (Fig. 3, Fig. S8–S9). Maps for the other habitat types are provided in the Supplementary data (Fig. S2–S11).

Table 2. Changes in habitat distribution, assuming no dispersal and unrestricted dispersal (‘full dispersal’) for the direct ‘habitat’ approach and the indirect ‘species’ approach and two modelling algorithms (GLM, RF). The future climate scenario is A2 based on the HadCM3 climate model.

Habitat type	Current distribution (km ²)	Direct ‘habitat’ approach				Indirect ‘species’ approach			
		GLM		Random Forest		GLM		Random Forest	
		No dispersal scenario (%)	Full dispersal scenario (%)	No dispersal scenario (%)	Full dispersal scenario (%)	No dispersal scenario (%)	Full dispersal scenario (%)	No dispersal scenario (%)	Full dispersal scenario (%)
6110	382 332	- 89	+ 89	- 70	+ 52	- 91	+ 5	-	-
6120	475 805	- 22	+ 98	- 22	+ 100	- 57	+ 33	- 32	+ 20
6210	1 500 421	- 71	+ 79	- 66	+ 63	- 68	+ 2	- 74	+ 21
6410	1 724 925	- 64	+ 26	- 57	+ 46	- 51	+ 22	- 72	+ 11
6520	444 155	- 89	+ 15	- 92	+ 33	- 93	- 5	-	-

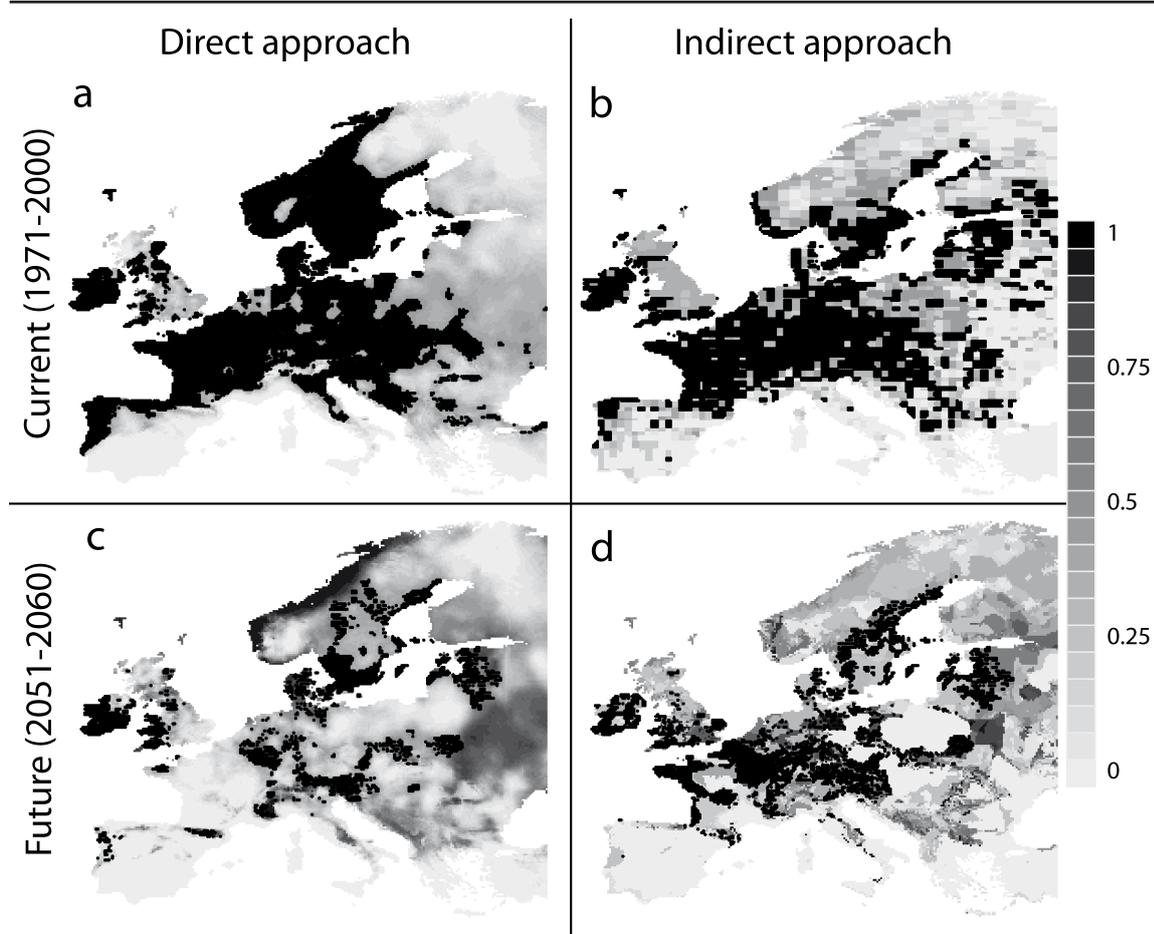


Fig. 3. Modelled occurrence probabilities of Molina meadows on chalk and clay (6410), based on GLM. The coarse-grained pattern in (b) results from the 50 km x 50 km resolution of species distributions in the Atlas Florae Europaeae. The future climate scenario is A2 based on the HadCM3 climate model. Future scenario maps show no dispersal ability. Black dots indicate the modelled occurrence, with thresholds: (a) 0.49, (b) 0.49, (c) 0.46 and (d) 0.42.

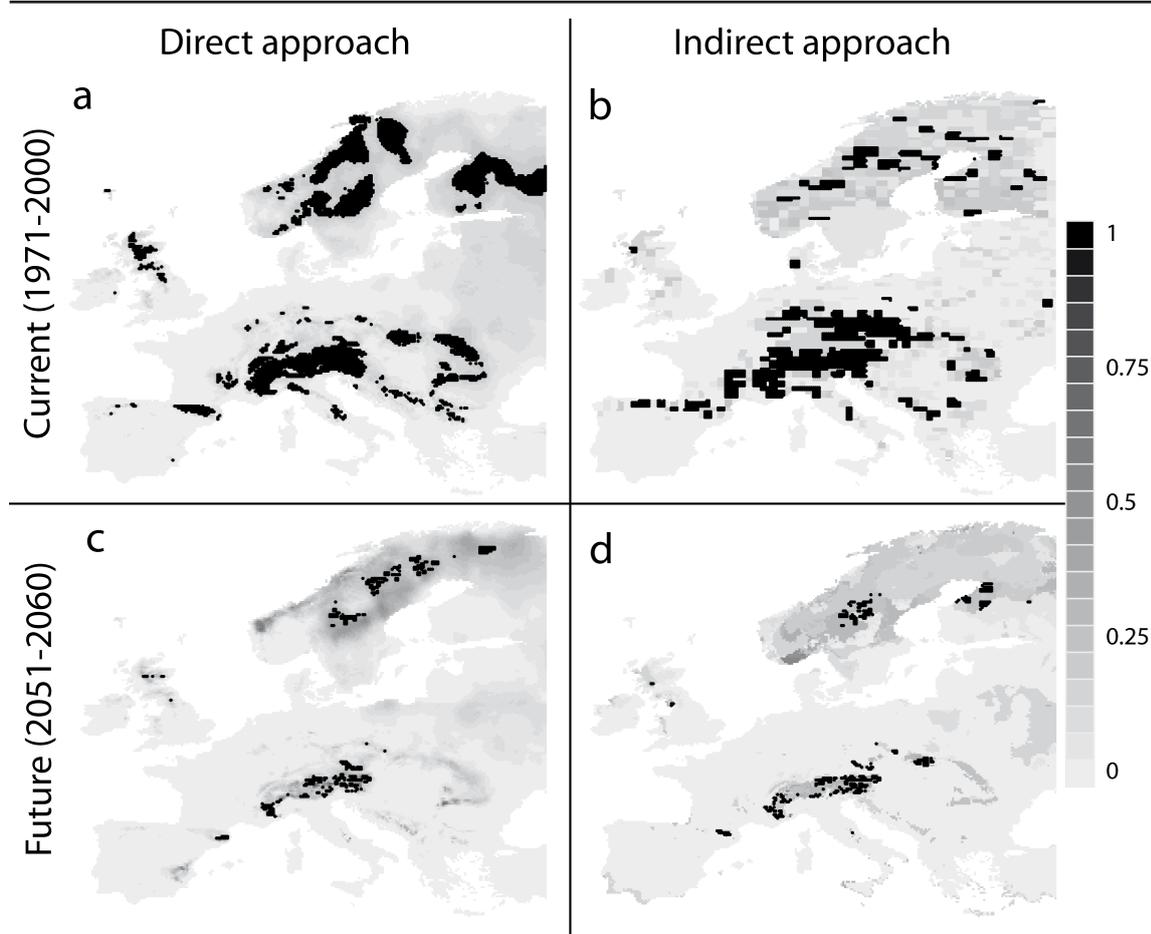


Fig. 4. Modelled occurrence probabilities of Mountain hay meadows (6520), based on GLM. The coarse-grained pattern in (b) results from the 50 km x 50 km resolution of species distributions in the Atlas Florae Europaeae. The future climate scenario is A2 based on the HadCM3 climate model. Future scenario maps show no dispersal ability. Black dots indicate the modelled occurrence, with thresholds: (a) 0.25, (b) 0.28, (c) 0.28 and (d) 0.27.

Modelling

Overall, the direct ‘habitat’ approach results in models with higher performance as measured by three out of four criteria (Table 3): models of the direct ‘habitat’ approach have a mean AUC of 0.90 with a standard deviation of ± 0.06 , versus 0.84 ± 0.07 in the indirect ‘species’ approach. Direct ‘habitat’ approach models have a mean calibration slope of 1.10 ± 0.10 , and a mean R^2 of 0.53 ± 0.18 , in the indirect ‘species’ approach a mean slope of 0.78 ± 0.28 , indicating overfitting, and a lower mean R^2 (0.40 ± 0.16).

Table 3. Model performance of the direct ‘habitat’ and indirect ‘species’ approach for two modelling algorithms (GLM, RF), showing AUC, slope (SL) and intercept (I) of the calibration curve and Nagelkerke R² for the test data (30% random selection). For the habitat types 6110 and 6520, the RF model yielded no results due to the limited number of plant species chosen in the variable selection step.

Habitat type	Direct ‘habitat’ approach								Indirect ‘species’ approach							
	GLM				Random Forest				GLM				Random Forest			
	AUC	SL	I	R ²	AUC	SL	I	R ²	AUC	SL	I	R ²	AUC	SL	I	R ²
6110	0.85	1.07	0.06	0.29	0.90	1.16	0.18	0.48	0.85	1.03	-0.03	0.28	-	-	-	-
6120	0.98	1.03	0.01	0.75	0.97	1.19	0.23	0.78	0.96	0.97	-0.03	0.68	0.81	0.44	0.18	0.38
6210	0.85	1.01	-0.01	0.45	0.94	1.26	0.00	0.71	0.90	0.98	-0.03	0.56	0.86	0.52	-0.14	0.48
6410	0.84	0.95	0.06	0.43	0.92	1.09	0.13	0.65	0.79	0.90	0.04	0.35	0.74	0.36	-0.06	0.21
6520	0.83	1.02	0.00	0.27	0.92	1.17	0.20	0.53	0.83	1.01	-0.02	0.27	-	-	-	-

The direct ‘habitat’ approach projects a large range loss ($-64 \pm 25\%$) under the assumption of no dispersal possibilities. With unrestricted dispersal, this approach projects a gain in distribution area of about $60 \pm 31\%$. The indirect ‘species’ approach results in a similar projected loss of distribution area ($-67 \pm 20\%$) under the no dispersal scenario. In contrast, it projects a lower gain in distribution area ($14 \pm 13\%$) than the direct ‘habitat’ approach with unrestricted dispersal (Table 2).

In the direct ‘habitat’ approach, the two modelling algorithms GLM and RF generate different but not dissimilar results (Table 2). The current distribution of all habitats is captured well by both algorithms: the RF model delivered a mean AUC of 0.93 ± 0.03 and a mean slope of 1.17 ± 0.06 for all habitats; the GLM results in a mean AUC of 0.87 ± 0.06 and a mean calibration slope of 1.02 ± 0.04 . Furthermore, when comparing maps of the projected current distribution, those based on RF are more spatially differentiated than those based on GLM (Figs 3a and 4a; Fig. S2a–S11a). The same situation holds for the projected potential future distribution: RF generally provides more extreme predictions (Fig. 3c and 4c; Fig. S2c–S11c).

In the species-based (indirect) approach, the two modelling algorithms differ more than in the direct ‘habitat’ approach. In particular the quality measures distinguish the two algorithms from each other: the average AUC of the GLM model is 0.87 ± 0.07 and the average slope

is 0.98 ± 0.05 ; in the RF model the average AUC is 0.80 ± 0.06 and the average calibration slope is 0.44 ± 0.08 . This means a substantial over-prediction by the RF model. Nevertheless, the maps of the modeled current distribution for the habitat types 6210 (dry to semi-dry calcareous grasslands of the *Festuco-Brometea*), 6120 (Xeric sand calcareous grasslands) and 6410 (*Molina* meadows on chalk and clay), look quite similar for both modelling algorithms. The same holds for the potential future distribution. For the habitat types 6110 (Rupicolous calcareous or basophilic grasslands of the *Alyso-Sedion albi*) and 6520 (Mountain hay meadows) the random forest model predicts constant probabilities, i.e. does not differentiate between different locations.

The mean correlation of the predictions of the current habitat type distributions is higher between the two modelling algorithms (0.75 ± 0.17) than between the two modelling approaches (0.64 ± 0.07). The same applies to the predictions of the future habitat type distributions, with a mean correlation of 0.55 ± 0.06 between the algorithms and 0.49 ± 0.14 between the approaches (Table 4).

Table 4. Pearson correlation of predicted probabilities of occurrence for habitat types between the two approaches (direct versus indirect) and the two algorithms (GLM versus RF).

Habitat type	GLM direct vs RF indirect current	RF direct vs RF indirect current	GLM direct vs RF direct current	GLM indirect vs RF indirect current	GLM direct vs GLM indirect future	RF direct vs RF indirect future	GLM direct vs RF direct future	GLM indirect vs RF indirect future
6110	0.59	-	0.51	-	0.50	-	0.58	-
6120	0.74	0.74	0.86	0.92	0.44	0.68	0.77	0.57
6210	0.50	0.75	0.62	0.87	0.02	0.56	0.39	0.40
6410	0.56	0.58	0.65	0.83	0.40	0.53	0.59	0.52
6520	0.64	-	0.52	-	0.60	-	0.60	-
Mean \pm SD	0.59 ± 0.09	0.69 ± 0.09	0.63 ± 0.14	0.87 ± 0.05	0.39 ± 0.22	0.59 ± 0.08	0.59 ± 0.14	0.50 ± 0.09

Discussion

Habitat types

All modelled habitats, with the exception of Mountain hay meadows (6520), gain distribution area until 2051–2060 under an A2 climate scenario and unrestricted dispersal, independent of modelling approach and modelling algorithm. Habitat type 6520 seems to be a loser in climate change even with unrestricted dispersal, likely because of its montane distribution. The projected range losses of habitat type 6110 (Rupicolous calcareous or basophilic grasslands

of the *Alyso-Sedion albi*) and 6520 (Mountain hay meadows) under the no dispersal scenario could result in complete disappearance of these habitats.

The no dispersal scenario is more conservative but seems more realistic than the full dispersal scenario. Habitats consist of a composition of species, where each species has its own dispersal ability and velocity. Additionally, different plant species may react differently to changing conditions. Beside dispersal, other factors like seed production, competition, land use and soil type influence the successful establishment (Jones & del Moral 2009; Allred et al. 2010). All these factors contribute to a deceleration in the shifts of whole habitats. However, modelling under the assumption of unrestricted dispersal can provide hints on where to find future climatic suitable space.

Habitats are human constructs and, due to their multifactorial nature, difficult to adequately capture in modelling approaches. Here, we apply the concept of habitats typically used in the European Union for political and practical conservation. Novel habitats with so far unknown species compositions (le Roux & McGeoch 2008) seem possible and likely. The Natura 2000 concept protects defined habitat types with characteristic plant species compositions. Due to range shifts in plants, some of these characteristic species may go extinct in a certain habitat. Further, new species may arrive and establish under future suitable climatic conditions. The loss of a characteristic species or the arrival of another species may overrule the specific habitat type definition and the protection status of this 'new' habitat. Hence, a dynamic adaptation of protection concepts and habitat type definitions in the European Union seems necessary.

Modelling

In general, both modelling approaches perform well in capturing the current distribution of the habitat types. Nevertheless, some differences can clearly be distinguished. The indirect 'species' approach is less extreme in its projection of the potential future distribution under unrestricted dispersal than the direct 'habitat' approach. The variable selection chose different climatic variables for each species. Under the expected future climate conditions some of the characteristic plant species may lose and some may gain distribution area, which can lead to a more restricted expansion of the distribution.

The selected plant species cover the current distribution of the habitat type only in parts. Most plants are wider distributed than the habitat type, and some are even more restricted. Throughout Europe, not all characteristic plants of one habitat type appear at all of its locations. However, the indirect 'species' approach performs comparably to the direct 'habitat' approach in projecting the current distribution, at least with the GLM. In contrast, the RF model performs worse in the indirect 'species' approach and even produced no results for two of the habitat types. Habitat type 6520 (Mountain hay meadows) has a very restricted distribution,

although its characteristic plant species are distributed widely in Europe. The variable selection chose only two of the nine characteristic plant species, which was obviously too few for further calculations. It could be suggested that these plants are not sufficiently suitable to represent this habitat type, at least for the RF model. The same applies to habitat type 6110 (Rupicolous calcareous or basophilic grasslands of the *Alyso-Sedion albi*). In addition, RF tends to overpredict the current distribution for the three remaining habitat types within the indirect 'species' approach. This leads to more predicted presences than currently observed, which in turn influences the outcome of the projected future distribution.

Overall, GLM copes better with the two modelling approaches (similar modelling performance) than RF. However, the best results originate from RF and the direct 'habitat' approach, as measured by AUC and Nagelkerke R^2 . In our application, GLM yielded more robust and universal results. The choice of the modelling algorithm seems to cause some differences, but mostly performs well in both cases. The disparity between the two modelling approaches is much bigger than between the two modelling algorithms. However, using more than one approach can help reducing the uncertainty of only one approach.

Limitations

Habitat types are complex structures. They are not only characterized by specific species compositions and climatic demands, but depend on further abiotic conditions, such as soil type. Furthermore, the current distribution of habitats as well as species reflects historical and actual traditions, management, cultural and political circumstances. Finally, the boundaries between different habitat types are fluent. All this complicates the modelling of habitat types. However, with the current availability of data, potential impacts of climate change on European protected habitat types can be identified and adaptation possibilities can be derived.

All modelling approaches are limited by the quantity and quality of occurrence data. The Natura 2000 natural habitat types of community interest are only defined and reported for member states of the European Union. However, this does not exclude the occurrence of similar or identical habitats in non-member states. In addition, the spatial resolution of the reported distribution data (Article 17 Habitats Directive) differs between countries. Higher resolution information about occurrence and distribution would lead to better modelling results.

The indirect modelling approach depends on the habitat type characteristic plant species. As the Natura 2000 habitat types are distributed over a large scale, we need a European focus to cover the 'whole' climatic niche. More complete and enlarged vegetation databases, as well as further field mapping, will help to improve the scientific basis for modelling, not only with

respect to the consequences of climate change. This scientific desideratum underlines the importance of projects that merge regional and national occurrence data in international databases, as does, for instance, the information accumulation platform of the newly developed information system SynBioSys Europe (Schaminée et al. 2007), an initiative of the European Vegetation Survey (EVS).

Implications for management

In general, natural and semi-natural grassland formations highly depend on management. All considered habitat types only exist in anthropogenically influenced areas. Without appropriate management, these habitats are expected to disappear (Plassmann et al. 2010). However, over their present ranges they are also likely to be strongly affected by future climate change, putting additional pressure on management. On the other hand, both approaches to modelling the distribution of habitats used here indicate future climatically suitable areas, and these may be further developed through appropriate management.

An analysis of protected areas concerning their vulnerability to climate change seems necessary. By assessing the impact factors, such as climatic, physical and biological variables, the sensitivity of an ecosystem and its adaptive capacity, risks and opportunities over a certain area can be derived (Lindner et al. 2010). Together with the modelling of potential impacts on habitats, such an assessment supplies initial insights into future threats and highlights future conservation needs. Furthermore, important to forest management planning is the transferability of modelling results in the face of climate change (Falk & Mellert 2011). Modelling results could also be integrated into valuation methods such as a Red List of habitat types, as suggested by Kontula & Raunio (2009).

Conclusion

Habitats are complex entities. Because of their dynamic nature, particularly in the face of climate change, we suggest modelling of the future distribution of habitat types not exclusively based on their current definitions and mapped distributions, but also based on their constituent elements, e.g. their characteristic plant species. We demonstrate that the choice of modelling approach can strongly affect the assessment of potential climate warming impacts and therefore the planning of adaptation strategies. The application of modelling at different levels of ecosystem organisation is a promising area for future research.

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Supplemental figures

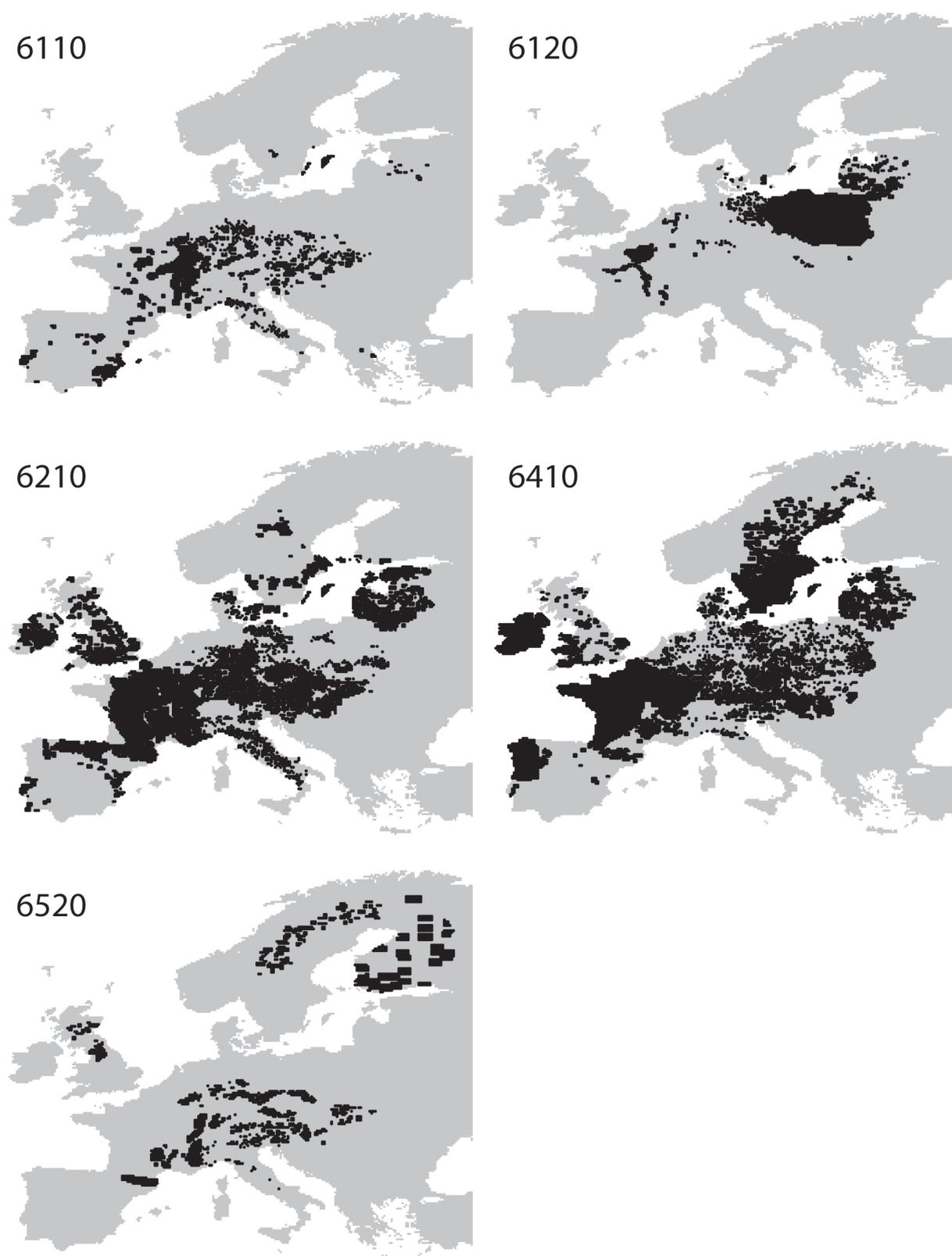


Fig. S1. Distribution data within the EU (EU25) from the Article 17 Report (Source): 6110 Rupicolous calcareous or basophilic grasslands of the *Alyso-Sedion albi*, 6120 Xeric sand calcareous grasslands, 6210 Semi-natural dry grasslands and scrubland facies on calcareous substrates (*Festuco-Brometalia*), 6410 *Molinia* meadows on calcareous, peaty or clayey-silt-laden soils (*Molinion caeruleae*) and 6520 Mountain hay meadows.

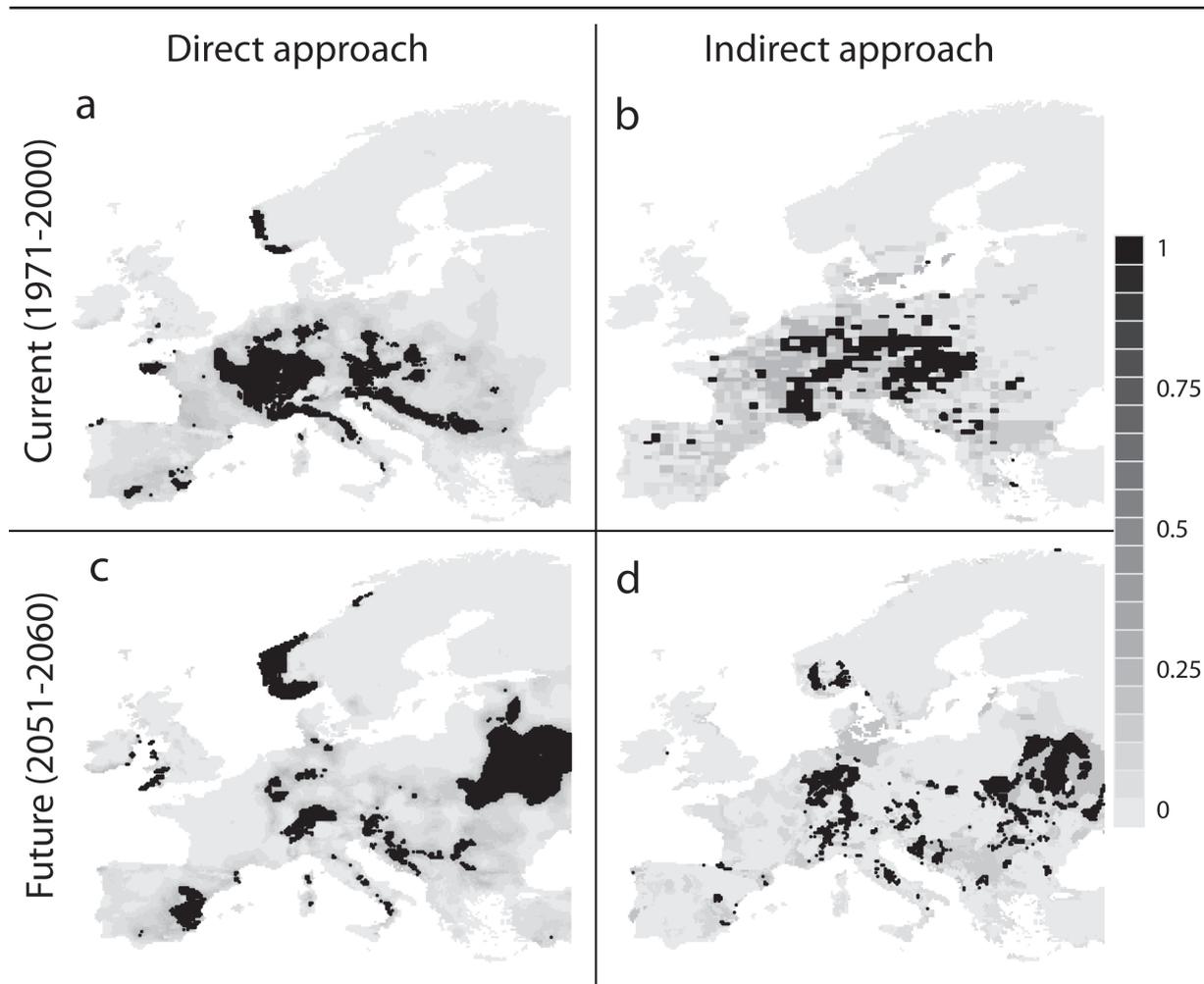


Fig. S2. Modelled occurrence probabilities of Rupicolous calcareous grasslands (6110), based on GLM. The coarse grained pattern in (b) results from the 50km x 50km resolution of species distributions in the Atlas Florae Europaeae. The future climate scenario is A2 based on the HadCM3 climate model. Future scenario maps show full dispersal ability. Black dots indicate the modelled occurrence, with thresholds: (a) 0.23, (b) 0.27, (c) 0.27 and (d) 0.24.

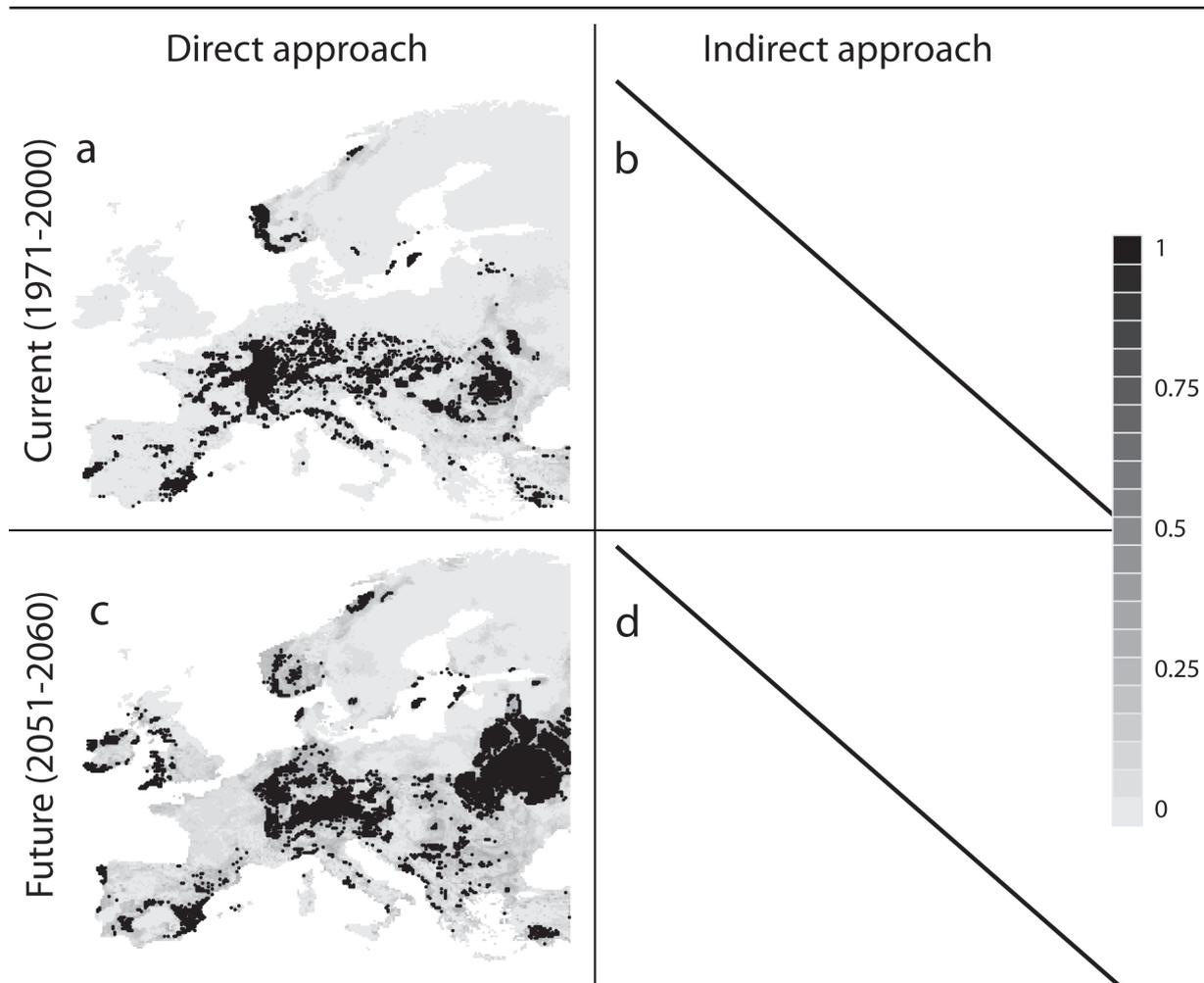


Fig. S3. Modelled occurrence probabilities of Rupicolous calcareous grasslands (6110), based on RF. The future climate scenario is A2 based on the HadCM3 climate model. Future scenario maps show full dispersal ability. Black dots indicate the modelled occurrence, with thresholds: (a) 0.27, (b) /, (c) 0.32 and (d) /.

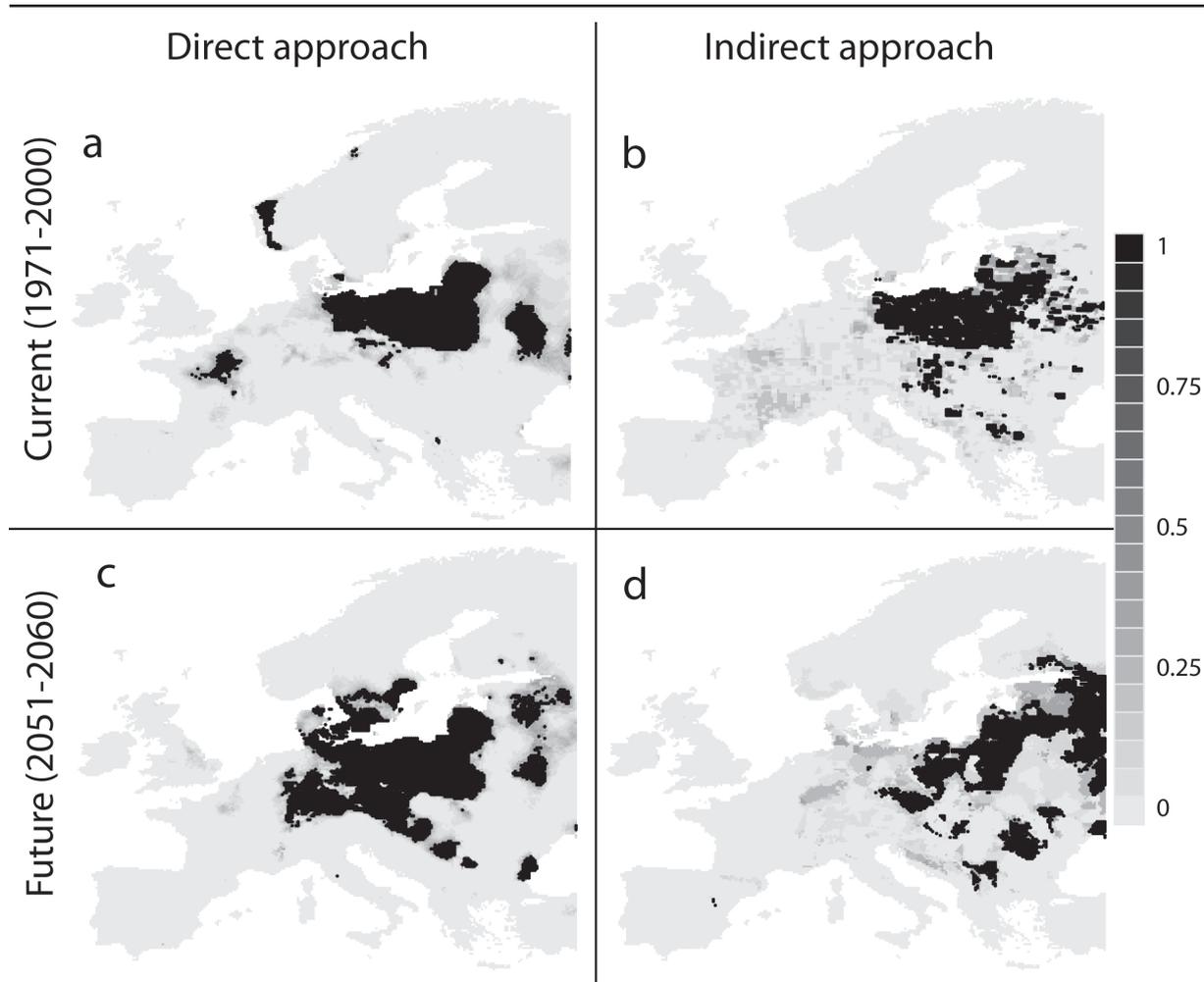


Fig. S4. Modelled occurrence probabilities of Xeric sand calcareous grasslands (6120), based on GLM. The coarse-grained pattern in (b) results from the 50km x 50km resolution of species distributions in the Atlas Florae Europaeae. The future climate scenario is A2 based on the HadCM3 climate model. Future scenario maps show full dispersal ability. Black dots indicate the modelled occurrence with thresholds: (a) 0.36, (b) 0.36, (c) 0.42 and (d) 0.38.

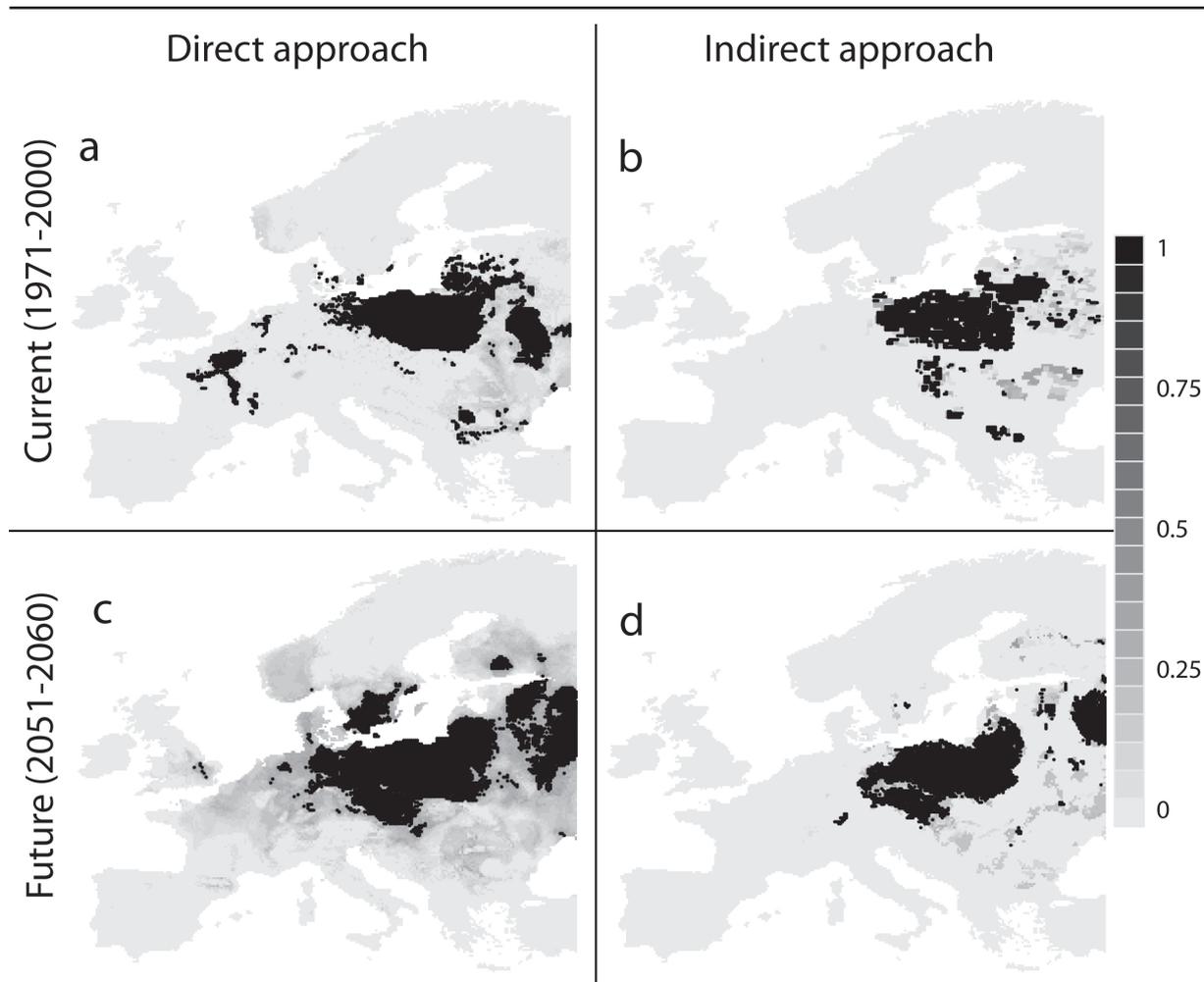


Fig. S5. Modelled occurrence probabilities of Xeric sand calcareous grasslands (6120), based on RF. The coarse-grained pattern in (b) results from the 50km x 50km resolution of species distributions in the Atlas Florae Europaeae. The future climate scenario is A2 based on the HadCM3 climate model. Future scenario maps show full dispersal ability. Black dots indicate the modelled occurrence, with thresholds: (a) 0.29, (b) 0.40, (c) 0.38 and 0.41.

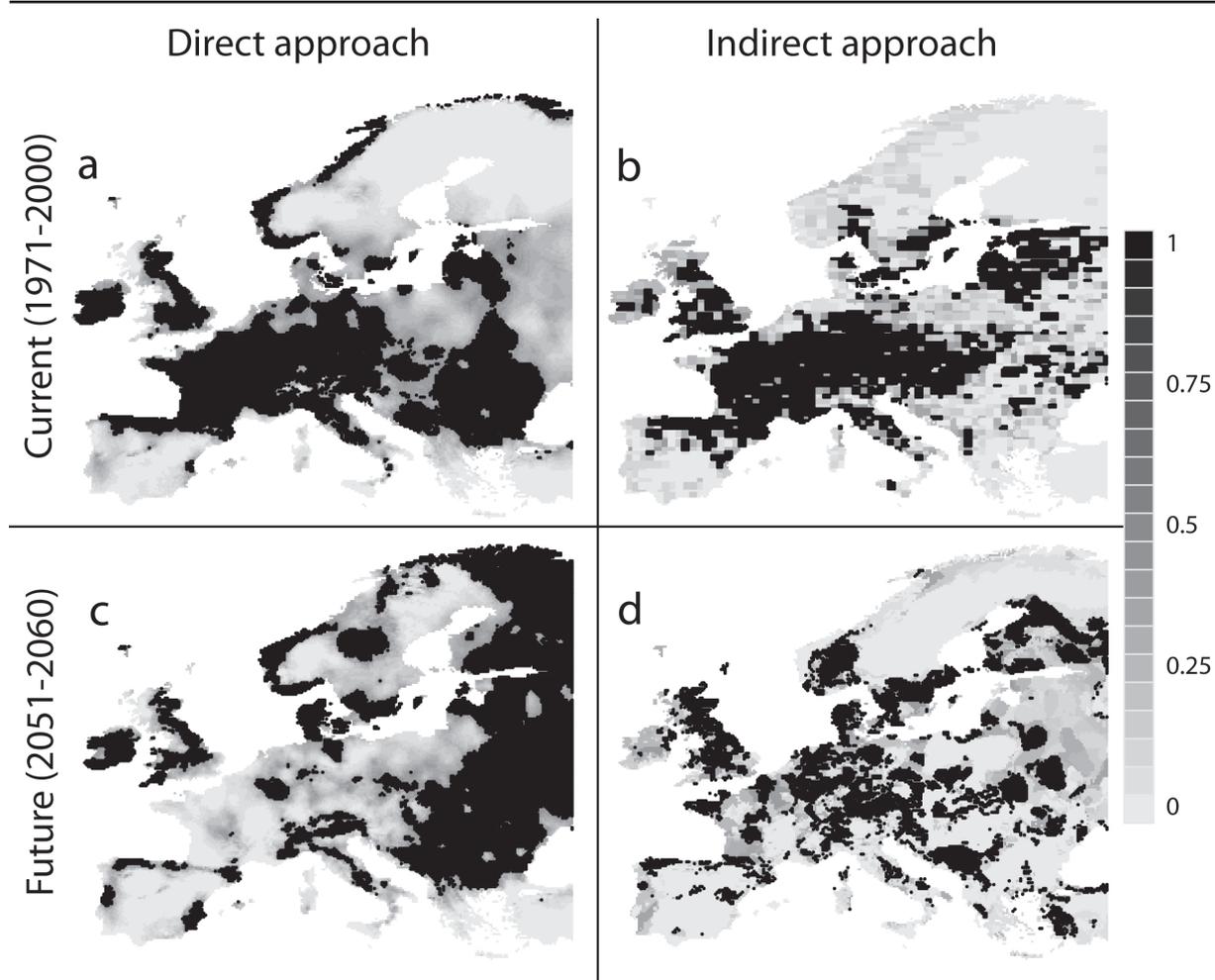


Fig. S6. Modelled occurrence probabilities of Seminal dry grasslands and scrubland facies on calcareous substrates (*Festuco-Brometalia*) (6210), based on GLM. The coarse-grained pattern in (b) results from the 50km x 50km resolution of species distributions in the Atlas Florae Europaeae. The future climate scenario is A2 based on the HadCM3 climate model. Future scenario maps show full dispersal ability. Black dots indicate the modelled occurrence, with thresholds: (a) 0.48, (b) 0.47, (c) 0.48 and (d) 0.42.

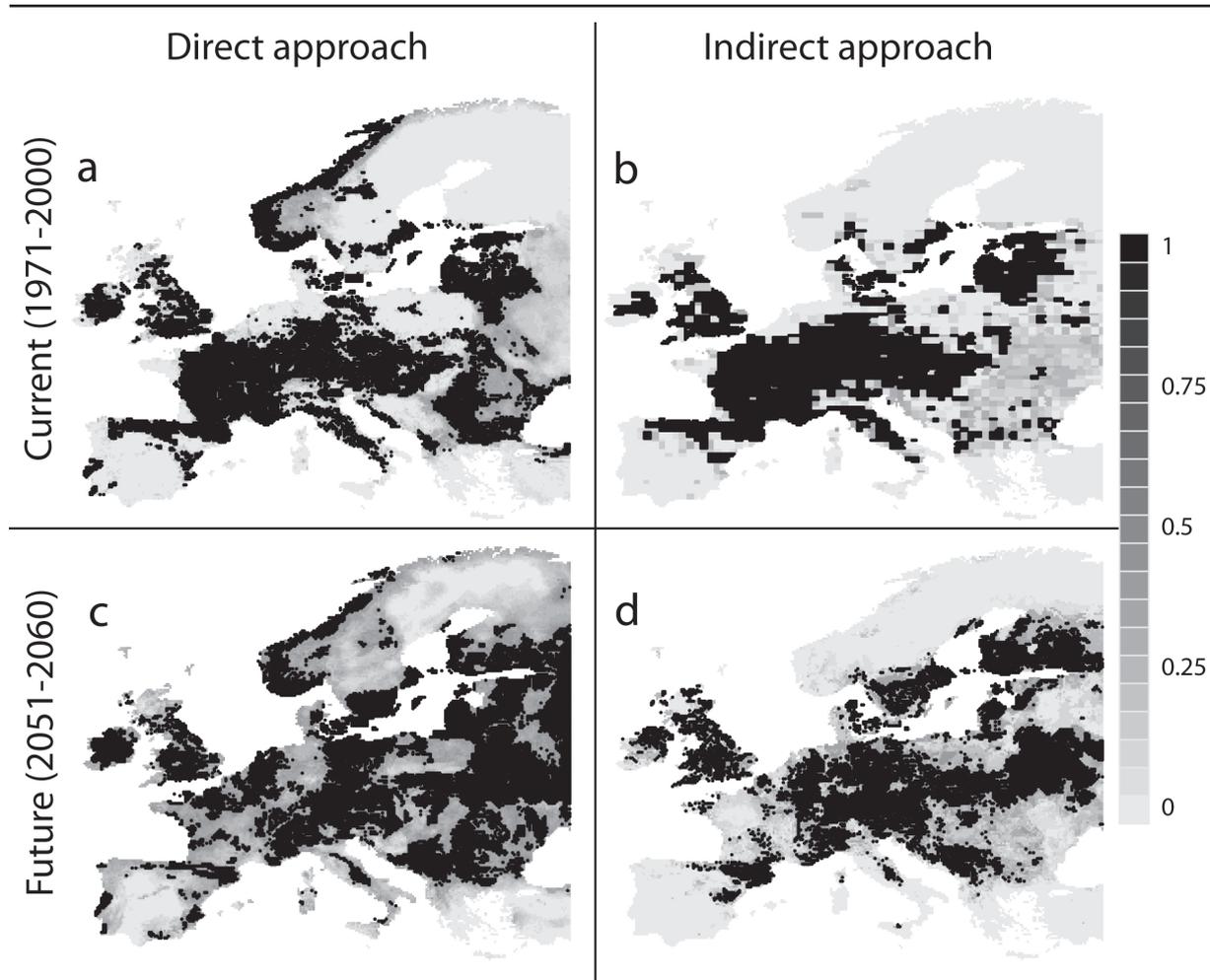


Fig. S7. Modelled occurrence probabilities of Semi-natural dry grasslands and scrubland facies on calcareous substrates (*Festuco-Brometalia*) (6210), based on RF. The coarse-grained pattern in (b) results from the 50km x 50km resolution of species distributions in the Atlas Florae Europaeae. The future climate scenario is A2 based on the HadCM3 climate model. Future scenario maps show full dispersal ability. Black dots indicate the modelled occurrence, with thresholds: (a) 0.43, (b) 0.39, (c) 0.46 and (d) 0.44.

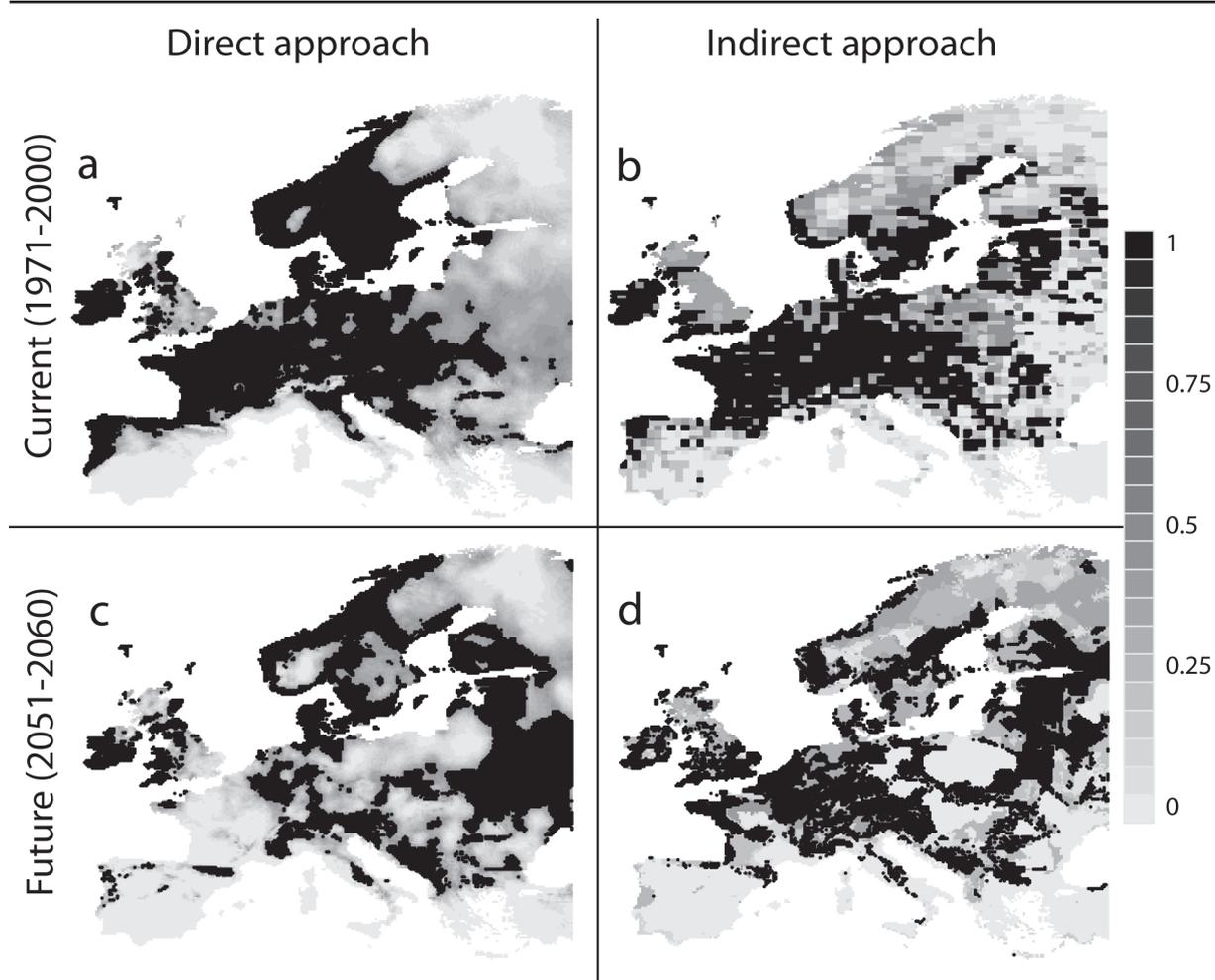


Fig. S8. Modelled occurrence probabilities of *Molinia* meadows on chalk and clay (6410), based on GLM. The coarse-grained pattern in (b) results from the 50km x 50km resolution of species distributions in the Atlas Florae Europaeae. The future climate scenario is A2 based on the HadCM3 climate model. Future scenario maps show full dispersal ability. Black dots indicate the modeled occurrence, with thresholds: (a) 0.49, (b) 0.49, (c) 0.46 and (d) 0.42.

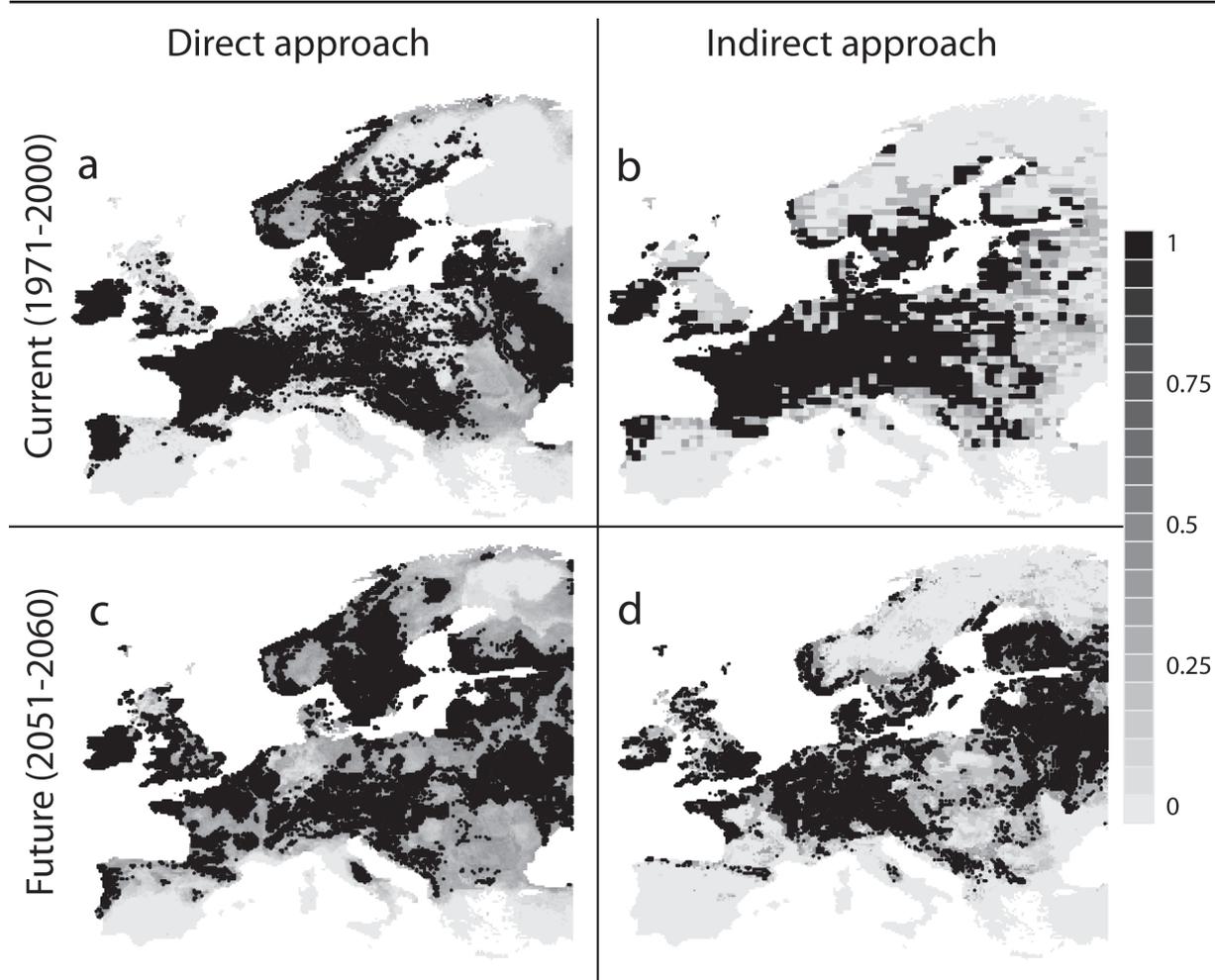


Fig. S9. Modelled occurrence probabilities of *Molinia* meadows on chalk and clay (6410), based on RF. The coarse-grained pattern in (b) results from the 50km x 50km resolution of species distributions in the Atlas Florae Europaeae. The future climate scenario is A2 based on the HadCM3 climate model. Future scenario maps show full dispersal ability. Black dots indicate the modelled occurrence, with thresholds: (a) 0.45, (b) 0.46, (c) 0.47 and (d) 0.48.

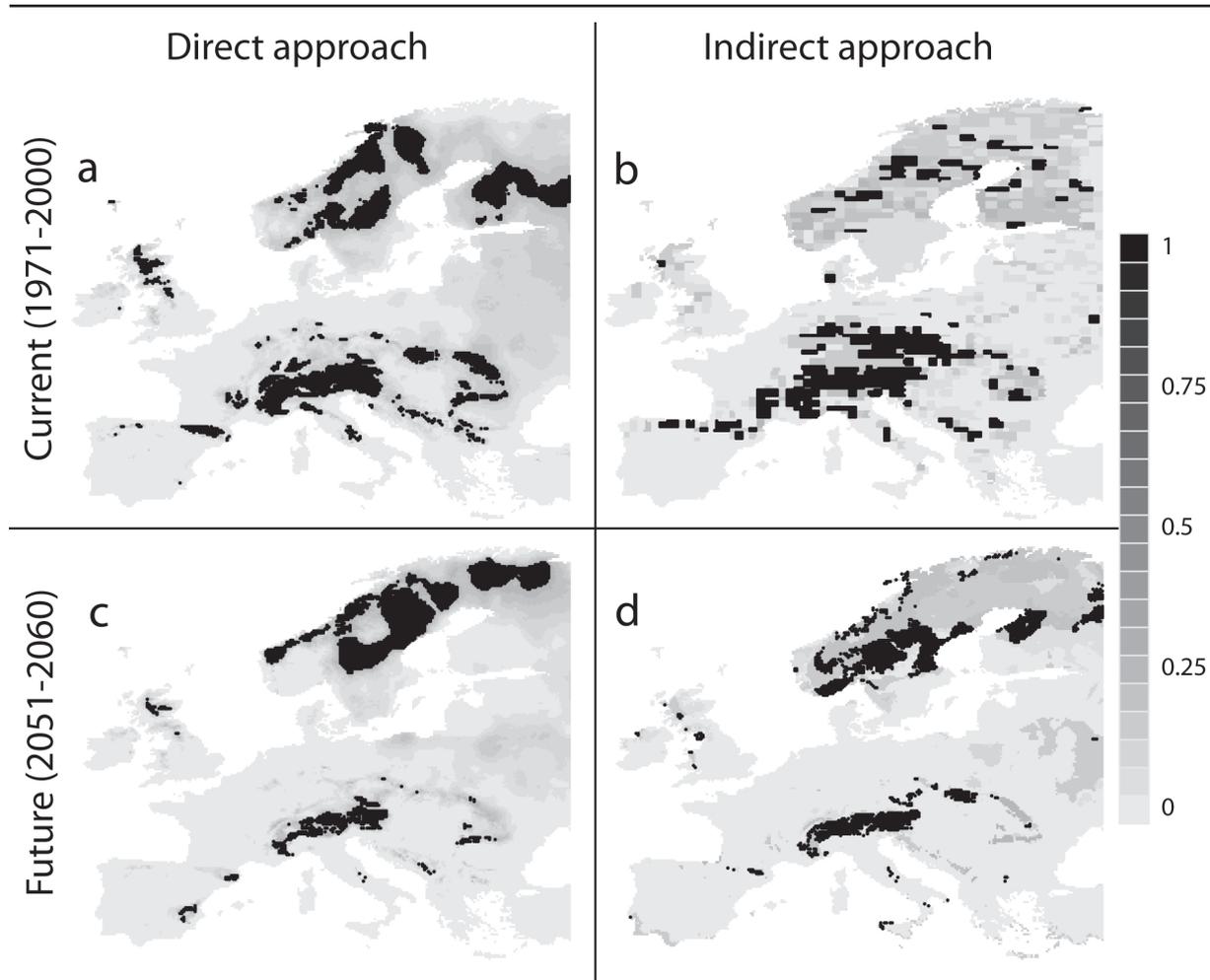


Fig. S10. Modelled occurrence probabilities of Mountain hay meadows (6520), based on GLM. The coarsegrained pattern in (b) results from the 50km x 50km resolution of species distributions in the Atlas Florae Europaeae. The future climate scenario is A2 based on the HadCM3 climate model. Future scenario maps show full dispersal ability. Black dots indicate the modelled occurrence, with thresholds: (a) 0.25, (b) 0.28, (c) 0.28 and (d) 0.27.

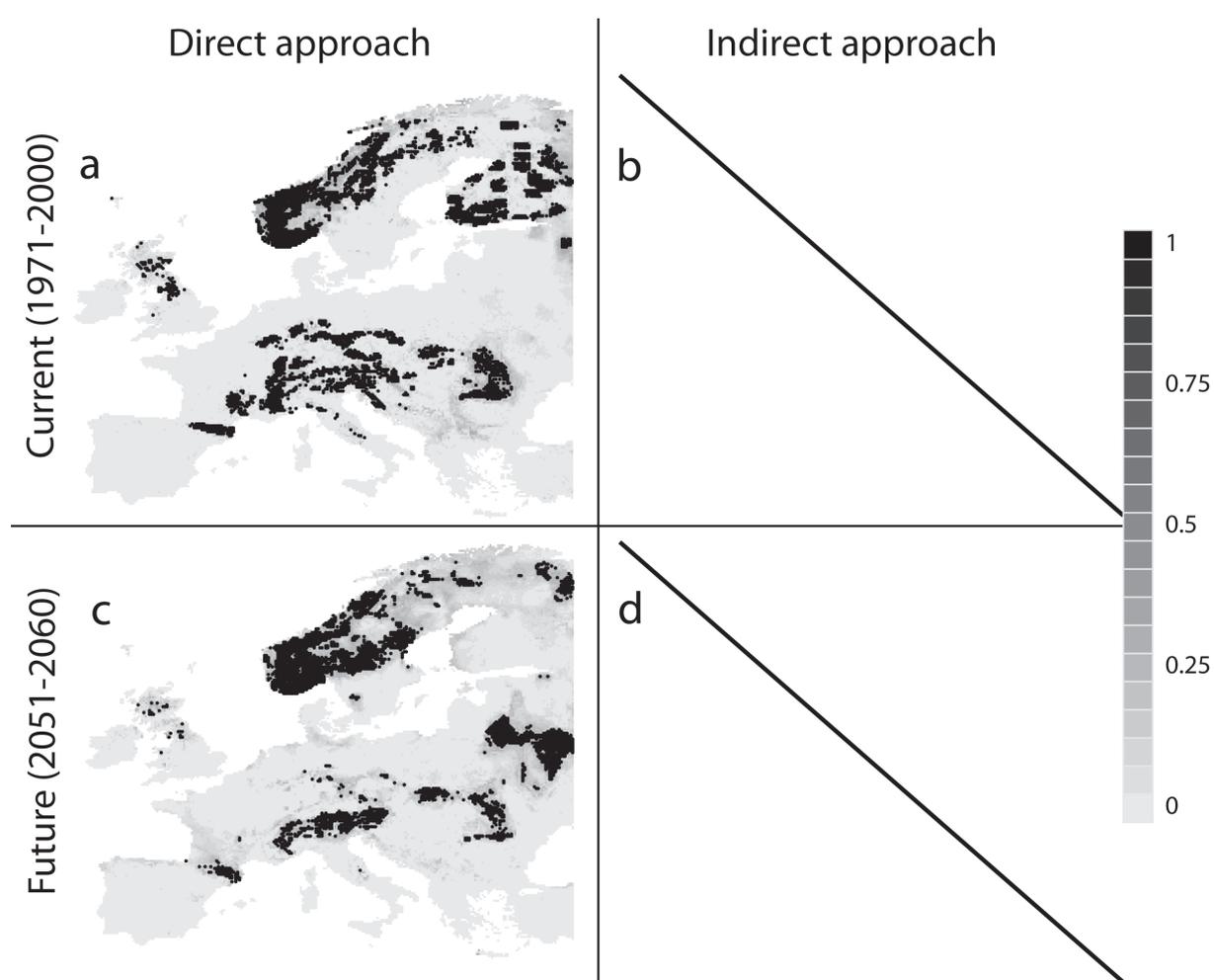


Fig. S11. Modelled occurrence probabilities of Mountain hay meadows (6520), based on RF. The future climate scenario is A2 based on the HadCM3 climate model. Future scenario maps show full dispersal ability. Black dots indicate the modelled occurrence, with thresholds: (a) 0.35, (b) /, (c) 0.31 and (d) /.

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List of Publications not included in this thesis

Peer-reviewed journals

- Gellesch, E., Hein, R., Jaeschke, A., Beierkuhnlein, C., Jentsch, A. (2012) Biotic Interactions in the Face of Climate Change. *Progress in Botany* 74 (4): 321-349.
- Dempe, H., Jaeschke, A., Bittner, T., Beierkuhnlein, C. (2012) Zukunft von Eichen-Hainbuchenwäldern und Heiden angesichts des Klimawandels - Potenzielle Entwicklung der Kohärenz von Lebensräumen im Natura-2000-Netzwerk. *Naturschutz und Landschaftsplanung* 44 (5): 149-153.
- Dempe, H., Bittner, T., Jaeschke, A., Beierkuhnlein, C. (2012) Potenzielle Auswirkungen des Klimawandels auf die Kohärenz von Schutzgebiets-Netzwerken - Ein Konzept für das Natura-2000-Netzwerk in Deutschland. *Naturschutz und Landschaftsplanung* 44 (4): 101-107.
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Book chapters and non-refereed periodicals

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- Trautmann, S., Lötters, S., Ott, J., Buse, J., Filz, K., Rödder, D., Wagner, N., Jaeschke, A., Schulte, U., Veith, M., Griebeler, E.-M., Böhning-Gaese, K. (2012) Auswirkungen auf geschützte und schutzwürdige Arten. In: Mosbrugger, V., Basseur, G. P., Schaller, M., Stribny, B. (eds.) Klimawandel und Biodiversität - Folgen für Deutschland. WBG, Darmstadt: 260-289.
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- Schlumprecht, H., Bittner, T., Gellesch, E., Gohlke, A., Jaeschke, A., Nadler, S., Beierkuhnlein, C., Ellwanger, G., Schröder, E. (2011) Climate change and Natura 2000. Bundesamt für Naturschutz. 80 pp.

List of presentations with content of this thesis

The contents of this thesis were presented at various conferences. Only presentations where I was the presenting author are listed. As part of my scientific work, I was involved in peer review activities for several journals.

a) Conference contributions

Title	Conference	Location	Type	Year
Areas at risk of zoonoses – Considering ecological knowledge of both pathogen and vector in modelling vector-borne diseases	Joint Conference: German Symposium on Zoonoses Research 2014 and 7th International Conference on Emerging Zoonoses	Berlin	poster	2014
Extending the climate envelope: Methodological approaches to integrate ecological prerequisites in species distribution models at large spatial extents	BayCEER Workshop 2013: Tracing the Life of Research Ideas	Bayreuth	oral	2013
Climate change impacts on terrestrial Natura 2000 habitats: Distribution, diversity and conservation options	43rd Annual Meeting of the GfÖ	Potsdam	oral	2013
Potential climate driven distribution changes of two closely related European toads	42nd Annual Meeting of the GfÖ	Lüneburg	poster	2012
Does climate change necessarily disrupt biotic interactions?	41st Annual Meeting of the GfÖ	Oldenburg	oral	2011
Modelling biotic interactions facing climate change: a comparative study of three different approaches	Jahrestreffen des AK Biogeographie	Hamburg	oral	2011
Model uncertainty in species distribution modelling considering a range of dispersal scenarios	Jahrestreffen des AK Biogeographie	Hamburg	poster	2011
Europe's Dragonflies on the Move	40th Annual Meeting of the GfÖ	Giessen	oral	2010
Climate Change and Lizards: Quo vadis <i>Lacerta</i> ?	Jahrestreffen des AK Biogeographie	Trier	oral	2010

Modellierung der Auswirkungen des Klimawandels auf NATURA 2000 Lebensraumtypen am Beispiel von Mooren	Fachtagung Schutz der Pflanzenvielfalt	Bayreuth	oral	2010
Modelling impacts of climate change on Natura 2000 habitats – an approach for nature conservation	9th Workshop on Vegetation Databases	Hamburg	oral	2010
Impacts of Climate Change on Fauna, Flora and Habitats – Adaptation Strategies of Nature Conservation	39th Annual Meeting of the GfÖ	Bayreuth	poster	2009
Species Distribution Models – Research Frontiers and Methodological Challenges	39th Annual Meeting of the GfÖ	Bayreuth	poster	2009
Impacts of Climate Change on Fauna, Flora and Habitats - Adaptation Strategies for Nature Conservation	Jahrestreffen des AK Biogeographie	Bayreuth	poster	2009

b) Reviewer activity

Peer review activity for: Insect Conservation and Diversity, Ecology and Evolution, Basic and Applied Ecology.

(Eidesstattliche) Versicherungen und Erklärungen

(§ 5 Nr. 4 PromO)

Hiermit erkläre ich, dass keine Tatsachen vorliegen, die mich nach den gesetzlichen Bestimmungen über die Führung akademischer Grade zur Führung eines Doktorgrades unwürdig erscheinen lassen.

(§ 8 S. 2 Nr. 5 PromO)

Hiermit erkläre ich mich damit einverstanden, dass die elektronische Fassung meiner Dissertation unter Wahrung meiner Urheberrechte und des Datenschutzes einer gesonderten Überprüfung hinsichtlich der eigenständigen Anfertigung der Dissertation unterzogen werden kann.

(§ 8 S. 2 Nr. 7 PromO)

Hiermit erkläre ich eidesstattlich, dass ich die Dissertation selbständig verfasst und keine anderen als die von mir angegebenen Quellen und Hilfsmittel benutzt habe.

(§ 8 S. 2 Nr. 8 PromO)

Ich habe die Dissertation nicht bereits zur Erlangung eines akademischen Grades anderweitig eingereicht und habe auch nicht bereits diese oder eine gleichartige Doktorprüfung endgültig nicht bestanden.

(§ 8 S. 2 Nr. 9 PromO)

Hiermit erkläre ich, dass ich keine Hilfe von gewerblichen Promotionsberatern bzw. -vermittlern in Anspruch genommen habe und auch künftig nicht nehmen werde.

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