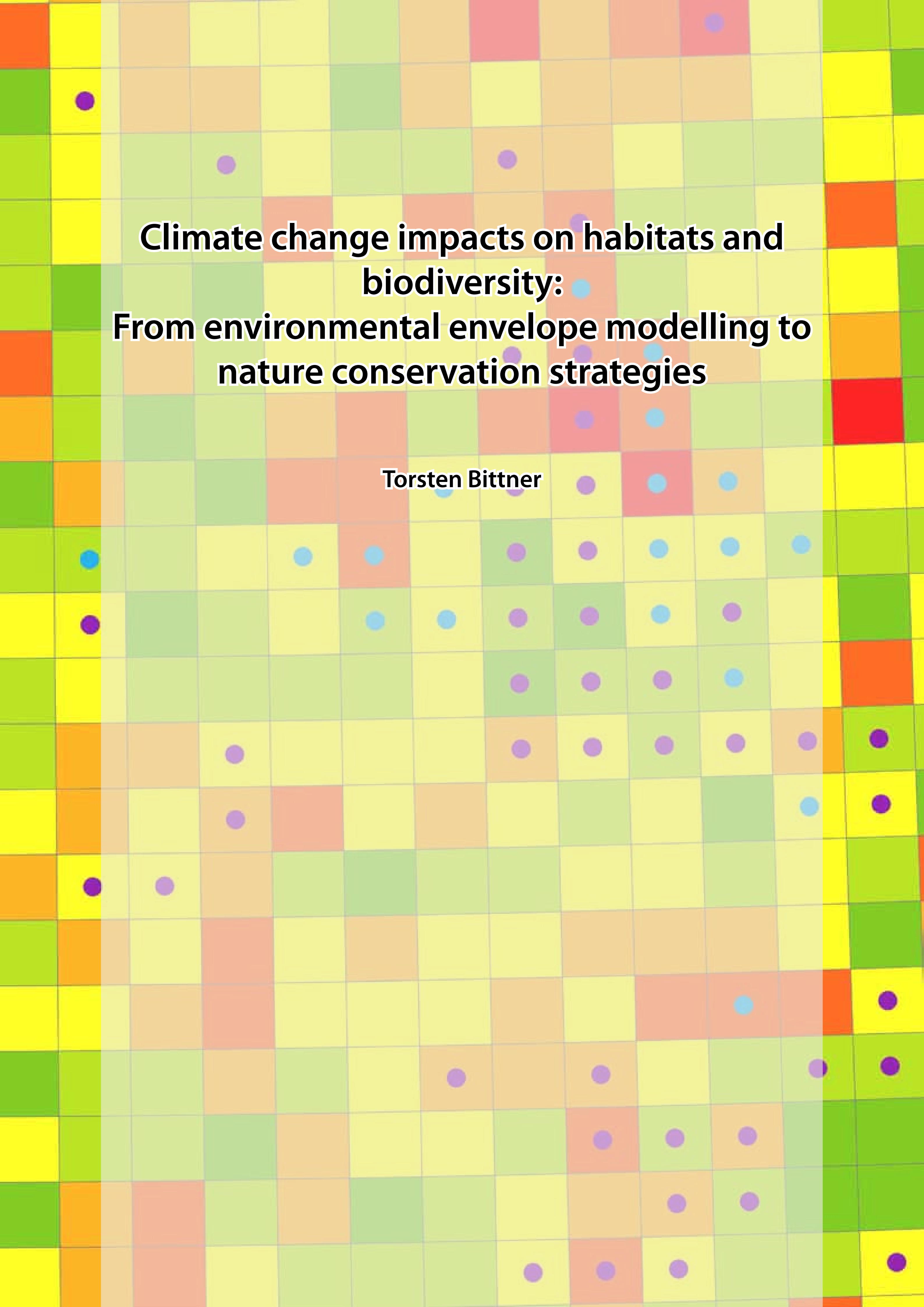


Climate change impacts on habitats and biodiversity:
From environmental envelope modelling to nature conservation strategies

Torsten Bittner

Climate change impacts on habitats and biodiversity: From environmental envelope modelling to nature conservation strategies

Dissertation

zur Erlangung des akademischen Grades

Dr. rer. nat.

Vorgelegt der Fakultät für Biologie, Chemie und
Geowissenschaften der Universität Bayreuth

Vorgelegt von

Herrn Dipl.-Biol. Univ. Torsten Bittner

geb. 18.08.1980 in Görlitz

Bayreuth, im September 2011

Die vorliegende Arbeit von Herrn Dipl.-Biol. Univ. Torsten Bittner, geb. am 18.08.1980 in Görlitz, wurde in der Zeit von Februar 2009 bis September 2011 unter der Betreuung von Herrn Prof. Dr. Carl Beierkuhnlein am Lehrstuhl für Biogeografie der Universität Bayreuth angefertigt.

Vollständiger Abdruck der von der Fakultät für Biologie, Chemie und Geowissenschaften der Universität Bayreuth genehmigten Dissertation zur Erlangung des akademischen Grades Doktor der Naturwissenschaften (Dr. rer. nat).

Dissertation eingereicht am:	28.09.2011
Datum des Wissenschaftlichen Kolloquiums:	10.02.2011
Amtierender Dekan der Fakultät II:	Prof. Dr. Beate Lohnert

Prüfungsausschuss:

1. Prof. Dr. Carl Beierkuhnlein	(Erstgutachter)
2. Prof. Dr. Michael Hauhs	(Zweitgutachter)
3. Prof. Dr. Thomas Köllner	(Vorsitz)
4. Prof. Dr. Bettina Engelbrecht	
5. Prof. Dr. Heike Feldhaar	

“You can never plan the future by the past.”
Edmund Burke (1729-1797)

“It’s hard to make predictions, especially about the future”
Niels Bohr (1885-1962)

„Jede Erkenntnis ist ein vorläufiger Blickwinkel,
der mich bis zum nächsten vorläufigen Blickwinkel begleitet.“
Romana Prinoth Fornwagner (*1960)

Contents

Summary

The present dissertation thesis depicts various aspects of impacts on the environment due to expected climate change, reveals new scientific and methodological approaches and formulates policy options for nature conservation.

Climate change will pose entirely new challenges for nature conservation. A literature study of 852 publications (between 2003 and 2010) illuminates this topic, examines driving research forces as well as focal points and shows recent research gaps. Here could be shown that changes in species distribution, diverse consequences for habitats, changing communities as well as biotic interactions and general aspects of diversity are the major challenges. Therefore, further developments of nature conservation strategies are needed. However, these aspects also offer new perspectives, options for preservation and development of biodiversity.

The potential climatic modifications can alter deeply the distribution of animals and plants. Range changes due to recent climate change already exist and are traceable for many animal and plant groups. In the near future, further distribution changes are expected. In order to quantify such changes, environmental envelope modelling can be used. In addition to individual species, changes in distribution of more complex units are also conceivable. The present work mainly focuses on habitat types listed in the Annex I of the European Habitats Directive.

To reveal the potential range changes of habitat types, two principally different modelling approaches have been developed. An indirect approach modelling the distribution of a habitat type using the distribution of its characteristic plant species and a direct approach, using the distribution of the habitat type itself. These two approaches were tested by modelling five grassland habitat types. Looking at the modelled 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. Both approaches produce reasonable results. However, modelling an extensive set of habitat types using the indirect approach is currently not possible, because of the required but actually lacking amount of plant distribution data.

Therefore, the direct approach is an appropriate instrument for modelling habitat types. Here, all 127 widespread terrestrial habitat types defined in the Annex I of the Habitats Directive were modelled and, resulting from this, a map of terrestrial habitat type diversity was calculated. Several habitat types are projected to lose many of their actually suitable areas, in particular bogs (up to a median of 43%), rocky habitats (up to a median of 49.5%), grassland (up to a median of 50.5%) and in part forests (up to a median of 48%). Due to their developmental time or rather due to their special abiotic requirements, bogs and rocky habitats even lose under the assumption of a full dispersal scenario. However, most heath and grassland habitats are also projected to lose in the full dispersal scenario. A couple of habitats, in particular scrublands and in part forests, are projected to win appropriate areas and some are remarkably stable. Pooling all modelled results together, terrestrial habitat type diversity is shifting partly to mountain regions and the atlantic biogeographical region is projected to decrease in habitat type diversity.

According to the Habitats Directive habitat types listed in Annex I are protected in 'sites of community interest' aiming to maintain or restore them at a favourable conservation status. Due to the projected changes a static nature conservation concept could face problems which particularly concern the coherence of the protected area network. This could lead to a loss of protective goods in spite of protected areas. To illustrate the potential problems and difficulties emerging with respect to spatial coherence of habitat types between protected areas, an analysis of spatial coherence under future conditions for a variety of habitat types in Germany was conducted. Here, a combination of environmental envelope modelling and graph theory is presented to assess the coherence of nature conservation networks.

The possible incapacity of species to reach all climatically suitable areas is currently debated. Therefore, spatial scales are not only crucial for the coherence of protected areas but also for the question if future projected suitable areas could be colonized. Biological restrictions such as ecology and morphology are limiting the dispersal capacity of most species. Moreover, dispersal movements of species are only infrequently possible in our highly fragmented landscape. To answer this raising question, Odonata listed in the Habitats Directive with known dispersal distances were contemplated. 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 *Leucorrhina caudalis* (up to -73%), whereas *Leucorrhinia pectoralis* is projected to gain distribution area (up to +37%) assuming either species-specific or unrestricted dispersal. Therefore, integration of realistic dispersal distances yielded new insights regarding the interpretation of environmental envelope model results. None of the considered species reached all projected climatically suitable areas.

The nature conservation measure of translocation is an at least 100 years old methodology with pros and cons. The importance and application of the methodology under current and projected changes will gain new dimensions. First anthropogenic translocations of insects in a climate change context have already been effected. In this thesis, the emerging problems and opportunities of this species preservation strategy are presented. Further, a new question about the 'focal unit' is pointed out as well as the problem of genetic variability and the aspect of pre-adopted subspecies. Moreover, a selective assisted colonisation not by moving species but ecotypes is referred.

The present thesis is not an exhaustive discussion of nature conservation in climate change. However, some relevant topics are highlighted and reveal new perspectives. This thesis improves the current state of research, demonstrates innovative approaches, provides ideas and creates new scientific links.

Zusammenfassung

In der vorliegenden Arbeit werden verschiedene Aspekte des erwarteten Klimawandels auf die Umwelt dargestellt, neue wissenschaftliche und methodische Ansätze präsentiert und Handlungsoptionen für den Naturschutz formuliert.

Durch den Klimawandel werden völlig neue Herausforderungen auf den Naturschutz zukommen. Eine Literaturrecherche basierend auf 852 Veröffentlichungen (aus den Jahren 2003 bis 2010) beleuchtet die Thematik, stellt die treibenden wissenschaftlichen Kräfte sowie Schwerpunkte und aktuelle Forschungslücken dar. Verbreitungsänderungen von Arten, verschiedene Entwicklungen der Lebensräumen, Änderung von Lebensgemeinschaften und biotischen Interaktionen sowie die allgemeinen Aspekte der Diversität verlangen in einer Zeit der Veränderung eine Weiterentwicklung des Naturschutzes, allerdings bieten sich auch neue Perspektiven.

Die potentiellen klimatischen Veränderungen können die Verbreitungen von Tieren und Pflanzen maßgeblich verändern. Räumliche Verbreitungsänderungen durch den rezenten Klimawandel existieren bereits und sind bei vielen Tier- und Pflanzengruppen eindeutig nachgewiesen. Weitere Verbreitungsänderungen sind in der nahen Zukunft vorstellbar. Um solche Veränderungen quantifizieren zu können, werden Tendenzen der Änderungen durch Umwelthüllen-Modellierungen dargestellt. Neben einzelnen Arten sind auch räumliche Veränderungen bei komplexeren Einheiten denkbar. Diese Arbeit fokussiert daher zu einem großen Teil auf die Lebensraumtypen des Anhangs I der europäischen Fauna-Flora-Habitat-Richtlinie (FFH-Richtlinie).

Um räumliche Änderungen darzustellen wurden zwei unterschiedliche Ansätze zur Modellierung der Lebensraumtypen entwickelt. Ein indirekter Ansatz, welcher über die Verbreitung der charakteristischen Arten die Lebensraumtypen modelliert und einen direkten, welcher die Verbreitung der Lebensraumtypen selbst benutzt. Diese Ansätze wurden mit fünf Grasland Lebensraumtypen getestet. Bei den hieraus resultierenden Projektionen (von fünf ausgewählten Grasländern) verlieren, unter der Annahme einer fehlenden Ausbreitung, alle fünf Lebensraumtypen zwischen 22% und 93% ihrer aktuellen Verbreitung. In einem uneingeschränkten Ausbreitungsszenario gewinnen alle modellierten Lebensraumtypen zwischen 5% und 100% an klimatisch geeignetem Raum. Beide Ansätze produzieren dabei gute Ergebnisse, jedoch sind für den indirekten Ansatz Datenquellen von Pflanzen-Verbreitungsdaten notwendig von denen momentan nur etwa 20% für ganz Europa existieren.

Der direkte Ansatz stellt daher ein probates Mittel dar Lebensraumtypen zu modellieren. Weiterhin wurden alle 127 weiterverbreiteten terrestrischen Lebensraumtypen des Anhangs I der FFH-Richtlinie modelliert und hiermit die Lebensraumtypen-Diversität analysiert. Verschiedene Lebensraumtypen, besonders Moore (Median bis zu 43%), Felslebensräume (Median bis zu 49,5%), Grasland (Median bis zu 50,5%) und teilweise Wälder (Median bis zu 48%), könnten einen Großteil ihres aktuell geeigneten Umweltraums verlieren. Wie vermutet werden kann, verlieren Moore und Felslebensräume auch unter der Annahme der uneingeschränkten Ausbreitung an Fläche. Unter anderem auf Grund ihrer langen Entwicklungszeit und ihrer hoch spezifischen abiotischen Standort Anforderungen. Es gibt klare Gewinner, wie die thermophilen Gebüschformationen sowie einige Wälder und Grasländer welche durch die zukünftigen Klimabedingungen sehr profitieren könnten. Die modellierte Lebensraumtypen-Diversität steigt besonders in den höheren und Gebirgslagen an und insbesondere in der atlantischen biogeografischen Region könnte es zu einem Rückgang kommen.

Gemäß der FFH-Richtlinie werden die Lebensraumtypen nach Anhang I in Schutzgebieten erhalten und in einem guten Erhaltungszustand gehalten bzw. soll dieser wiederhergestellt werden. Durch die projizierten Veränderungen könnte das eher statische Schutzgebietskonzept mit einigen Problemen konfrontiert werden, welche insbesondere die Kohärenz des Schutzgebietsnetzes betreffen. Trotz der Schutzgebiete könnte es zu einem Verlust der Schutzgüter kommen. Um die möglichen Probleme und aufkommenden Schwierigkeiten bzgl. der räumlichen Kohärenz von Lebensraumtypen zwischen den Schutzgebieten darzustellen, wurde eine Analyse der räumlichen Kohärenz unter zukünftigen Bedingungen für eine Auswahl von Lebensraumtypen in Deutschland durchgeführt. Eine Kombination aus Umwelthüllen-Modellierung und Methoden der Graphen-Theorie wurden dazu verwendet um die Kohärenz des Schutzgebietsnetzes unter zukünftigen Bedingungen zu bewerten.

Das Unvermögen von Arten klimatisch geeigneten Flächen zu erreichen, ist ein aktuell diskutiertes Thema. Der räumliche Maßstab ist daher nicht nur bei der Kohärenz von Schutzgebieten entscheidend sondern auch bei der Frage wie realistisch Modelle in der Vorhersage von neu zu besiedelnden Flächen sind. Die allermeisten Arten besitzen durch ihre Ökologie und Morphologie eine begrenzte Ausbreitungskapazität, weiterhin lässt unsere stark fragmentierte Kulturlandschaft Ausbreitungsbewegungen von Arten nur in einem geringen Maße zu. Um dieser Fragestellung nachzugehen, wurden FFH-Libellenarten, von denen Ausbreitungsdaten bekannt sind, betrachtet. Die Arten

Coenagrion ornatum, *Coenagrion mercuriale* und *Ophiogomphus cecilia* könnten bis zu 68% ihres geeigneten Umweltraumes verlieren, wenn man die artspezifischen Ausbreitungsdistanzen berücksichtigt. Wobei diese Libellen in einem uneingeschränkten Ausbreitungsszenario bis zu 23% an geeignetem Umweltraum dazu gewinnen würden. Weiterhin scheinen unter der Berücksichtigung einer artspezifischen Ausbreitungsdistanz sowohl für *Leucorrhinia albifrons* und *Leucorrhinia caudalis* klimatisch geeigneten Raum zu verlieren (bis zu 73%). Im Gegensatz dazu könnte *Leucorrhinia pectoralis* 37% an geeigneter Fläche dazugewinnen. Die Integration von realistischen Ausbreitungsdistanzen erbrachte neue Erkenntnisse zur Interpretation von Umwelthüllen-Model Ergebnissen. Trotz klimatischer Eignung erreichte keine Art alle potentiell besiedelbaren Flächen. Gerade die ausbreitungsschwachen Arten, die klimatisch profitieren würden, verlieren mit realistischen Ausbreitungsdistanzen stark.

Die Naturschutzmaßnahme der Translokation stellt seit mindestens 100 Jahren eine Methodik mit Für und Wieder dar. Der Stellenwert und die Anwendung der Methodik, Arten in Gebieten auszusetzen wo ihre Lebensgrundlagen vorhanden sind, diese jedoch dort noch nicht oder nicht mehr vorkommen, könnten unter den aktuellen und projizierten Veränderungen völlig neue Dimensionen erlangen. Erste anthropogene Umsiedlungen von Insekten im Klimawandel-Kontext wurden bereits durchgeführt. Die damit entstehenden Probleme und Chancen werden dargestellt. Weiterhin werden neue Fragen zu dem Thema der ‚Zieleinheit', genetische Variabilität und Aspekte zu pre-adaptierten Unterarten diskutiert. Des Weiteren wird auf ein selektives Translokations-Verfahren hingewiesen, bei dem auf Ökotypen fokussiert werden sollte.

Die vorliegende Arbeit stellt gewiss keine erschöpfende Auseinandersetzung des Naturschutzes im Klimawandel dar. Jedoch werden hier einige relevante Thematiken beleuchtet und neuartige Perspektiven aufgezeigt, welche den aktuellen Forschungstand verbessern, innovative Ansätze aufzeigen, Ideen liefern und neue wissenschaftliche Anknüpfungspunkte generieren.

Introduction

On this thesis

The topic of this dissertation thesis is the climate change impact on habitats and biodiversity in Europe. To quantify this, statistical modelling techniques were applied in order to yield quantifiable and spatially explicit projections of biological trends into the future. The results were coupled with questions of nature conservation and discussed in latest methodological and practical contexts. Primary conservation scope was the EU-wide Habitats Directive nature conservation network with a special focus on habitat types. Habitat types are protected units of communities on specific abiotic conditions and host large amounts of biodiversity. These entities are only protected in 'sites of community interest' and therefore it is import to know how climate change may influence these. Furthermore, the Habitats Directive protects more than 1000 plant and animal species in the EU. For these it is also crucial to develop adaptation strategies.

The following paragraphs provide a brief research overview about the main topics of this thesis. The first part will cover climate change and the associated distribution changes of species and habitats. Secondly, a summary of current knowledge on modelling species' distribution will be given. Thirdly, implications for nature conservation and future threats to the environment are condensed. Subsequently, a synopsis of all articles flowing into this thesis is depicted. Finally, a summarizing conclusion and emerging research challenges will be highlighted and close this chapter.

Climate change, range shifts and habitats

An intensive climate change debate has emerged since the last third of the 20th century (Mitchell 1961, 1972; Salinger & Gunn 1975) and associated with it the assessment of this changes to the environment (Bradley & Miller 1972) and ecological processes (Clark 1988; Parmesan 1996). The Number of studies reporting species' responses to climate change increased drastically during the last decade (e.g. Parmesan & Yohe 2003; Julliard et al. 2004; Walther et al. 2005; Cleland et al. 2007; Walther et al. 2009; Ott 2010). Observed and proven range shifts are known from various taxa from almost all regions of the world (Hill et al. 2011). There is a substantial amount of literature documenting the expansion of species to higher latitudes and elevations (Parmesan et al. 1999; Warren et al. 2001; Parmesan & Yohe; 2003; Hickling et al. 2005; Walther et al. 2005; Hickling et al. 2006; Hitch & Leberg 2007). Otherwise, a retraction of ranges from lower latitudes and elevations is also considered (Parmesan 1996; Wilson et al. 2005; Franco et al. 2006). Hence, a spatial shift of biodiversity and the evolution of new competing species, communities and biocoenoses can be inferred (Menéndez et al. 2006; Williams & Jackson 2007; Engelkes et al. 2008; Menéndez et al. 2008).

Moreover, responding to climate is not a new phenomenon. Changes in distribution over the last two centuries are observed for some animals (Hill et al. 1999; Asher et al. 2001) and plants (Kelly & Goulden 2008). Several changes can be explained by a changing climate. The most impressive example for the capacity of species to respond to climate change is the postglacial expansion induced by climate (Atkinson et al. 1987; Elias 1991; Huntley 1991; Coope 1995; Elias 2006). Recapped, species can respond to climate change by adapting to climate in situ, by evasion to suitable areas or by extinction (Hill et al. 2011).

The focus of practical and theoretical research has been predominantly on single species. Communities, especially habitats as a whole, are still rarely considered (Mücher et al. 2009, **article 2 and 3**). However, changes in climatic conditions lead to responses in species composition and community structure (Bruelheide 2003; Kreyling et al. 2008) at least evidenced by experiments. Nevertheless, current concepts of nature conservation are aimed particularly at habitats in their entirety, such as in the European Habitats Directive. In Article I of the Habitats Directive (Council Directive 92/43/EEC 1992), 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". This means that habitat types are reservoirs of biodiversity and inhabit many rare and valuable species. Therefore, the protection of habitat types protects biodiversity.

However, there are substantial disparities in the definitions of habitat types across Europe. Not only a reinterpretation of the habitat types concept (Chiarucci et al. 2010) but also a more robust reclassification to climate-induced changes in the Habitats Directive is clearly needed (Hossell et al. 2003; Normand et al. 2007). Nonetheless, habitat types are one huge group of protection goods, so the focus of climate impact research should relate stronger to practical conservation goals. Therefore, attempts to transpose projections on the consequences of climate change on habitats should be conducted (Hossell et al. 2003, **article 2, 3, 4**). Such assessments are likely to yield insights on potential problems but also on opportunities for management.

In this thesis two fundamental approaches to model habitat types are depicted. In **article 2**, a comparison of these approaches was published for the first time. The basis of these approaches is the environmental envelope modelling technique, which will be presented in the following chapter.

Environmental Envelope Modelling

Using environmental envelope models (or species distribution models, bioclimatic models, ecological niche models, envelope modelling, etc.) provides understanding and / or predicting species' distribution across a landscape (Elith & Leathwick 2009). These models can help to get an impression if range shifts are possible, can provide useful ecological insight, have strong predictive capabilities and can hint on which species may be threatened by climate change. Environmental Envelope Models (EEM) combine ecological, environmental and distributional data with modern statistical methods. The idea of the relationship between biological patterns and geographical and/or environmental gradients goes back to the early years of the last century and even the century before (Elith & Leathwick 2009). One prominent example is Joseph Grinnell (1904), who described in 1904 the spread of the Chestnut-backed Chickadee (*Poecile rufescens*) by geographical and environmental gradients. A basic understanding of ecology, biogeography and the distribution is necessary for environmental envelope modelling. Anyhow, the correlation of diverse environmental data with distributional data requires a lot of calculation performance. This means that higher model complexity has not become possible until recently.

First environmental envelopes were done, among others, by Austin (1985) in the 70s and 80s by Ferrier (2002) in 1984. Generalised linear models (GLM) produced more sophisticated and realistic results than ever before (Elith & Leathwick 2009). Furthermore, spatial data processing (Geographical Information Systems, GIS) and comprehensive mapping established databases for use in EEM.

Usually, the extent of the modelling reflects the scope of the analysis. Macroecological and global change studies are mostly on a continental up to global scale (e.g. Nenzén & Araújo 2011) and studies with a more ecological or conservational focus are mostly on a local up to regional scale (e.g. Ferrier et al. 2002). Despite the scope, the resolution of available data partly determines the course of modelling. In addition, depending on the applied scale different environmental variables are crucial for the modelling of distributions. At a global or continental scale climate is the most important predictor. Coming to finer scales other factors like topography, nutrient availability up to biotic interactions on a micro scale play a more important role (Pearson & Dawson 2003).

Many other adjusting screws exist in EEM based analysis (Figure 1), beside those mentioned above. The decision of where the predicted species occurs, for instance, is one of the most unexplored (Nenzén & Araújo 2011). Moreover, many methods are used to fit EEM (Franklin & Miller 2010). A variety of different algorithms can be applied. For example artificial neural networks (ANN, Olden et al. 2008, **article 3**), classification and regression trees (random forest: Prasad et al. 2006, **article 2**; boosted regression trees: Elith et al. 2008, **article 3**), genetic algorithms (Stockwell & Peters 1999) and maximum entropy models (Phillips et al. 2006; Fischer et al. 2011) are a small selection of available algorithms. However, choosing a specific algorithm induces uncertainty (Dormann et al. 2008). On this account, **article 2 and 5** are comparing two different algorithms and **article 3 and 4** use an ensemble approach of nine different algorithms. For implementing an ensemble modelling approach BIOMOD (Thuiller 2003; Thuiller et al. 2009) was used. It allows to model with nine different 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 enables an ensemble calculation of all algorithms and therefore a reduction of the uncertainty of applying one algorithm.

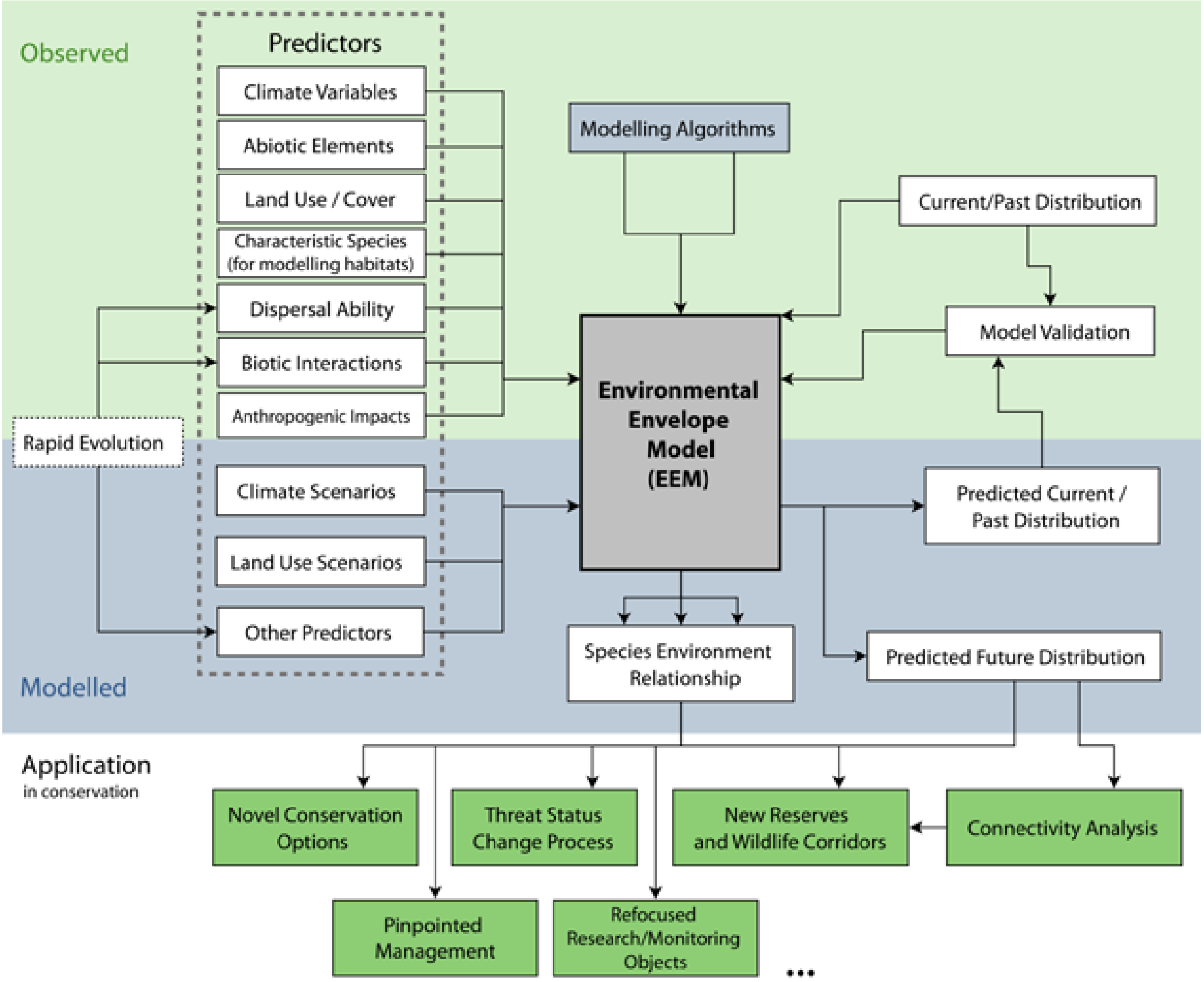


Fig.1: Conceptual framework on environmental envelope modelling. The framework shows a variety of possible predictors, yet the integration of rapid evolution, biotic interactions and anthropogenic impacts are not realised in this thesis. Furthermore, using the past species/habitat type distributions was not done here. The 'application in nature conservation'-part in the framework is showing examples for the application of such modelling results.

These EEM can be projected into the future and can be used to discover potential future suitable areas and potential range changes (Araújo & Guisan 2006). This is possible by using future projected predictor data, like climate models and land use scenarios. Current environmental envelope modelling studies project range shifts for a variety of taxa, e.g. amphibians and reptiles (Araújo et al. 2006), plants (Normand et al. 2007), birds (Green et al. 2008), butterflies (Schweiger et al. 2008); beetles (Thomaes et al. 2008), bats (Rebelo et al. 2010) and dragonflies (**article 5**). The number of these papers indicates the importance and flexibility of this methodology.

This thesis presents the implementation of environmental envelope models beside single species (**article 5**), with different approaches and scopes for habitat types (**article 2, 3 and 4**).

However, results calculated with EEM cannot be taken as accurate forecasts due to existing uncertainties in climate change scenarios (Thuiller et al. 2005; Heikkinen et al. 2006), spatial resolution (Weaver & Zwiers 2000), uncertainties in the modelling techniques (Guisan & Zimmermann 2000; Pearson & Dawson 2003; Dormann et al. 2008; Elith & Leathwick 2009), in the choice of occurrence threshold and basically in data quality (Heikkinen et al. 2006, **article 2**). Thus, these results can only give important hints on threats, future distributions and therefore an idea on the direction of nature conservation strategies (e.g. Gaston et al. 2008; Elith & Leathwick 2009, **article 2, 3, 4 and 5**).

Threats, challenges and possibilities: nature conservation facing climate change

Climate change is predicted to become one of the major threats to biodiversity in the 21st century. Associated with the loss of biodiversity is the termination of evolutionary potential and disruption of ecosystem services (Dawson et al. 2011). Both, species (e.g. Huntley 1991; Parmesan & Yohe 2003; Walther et al. 2005; Ott 2010, **article 5**) and habitats (Hannah et al. 2002; Petermann et al. 2007; European Topic Centre on Biological Diversity (ETC/BD) 2008, **article 2,3 and 4**) will experience modifications in distribution, population and community structure that are correlated with new risks during the coming years. This leads to challenges for nature conservation (Normand et al. 2007) and climate-proof protection concepts (Vos et al. 2008, **article 4**). The EU-wide Natura 2000-Concept (consisting of Birds and Habitats Directive) is the biggest and most precious nature conservation concept in Europe but some revisions should be expedited by facing climate change (Normand et al. 2007; Gaston et al. 2008, **article 3 and 4**).

While looking on natural and semi-natural habitat types in Europe, listed in the Annex I of the Habitats Directive, one realises that the majority of these habitat types are dependent on management (Ssymank et al. 1998). In particular, extensive agriculture and forestry in the past resulted in valuable cultural landscapes with high biodiversity. Several habitat types like grasslands, heaths and forests were directly anthropogenic influenced in their shaping, others only indirectly. Without continuing suitable management, for instance grazing, most habitat types will disappear (Plassmann et al. 2010).

Our image of nature, species, communities and biocenosis is to a certain degree actualistic, so it is not surprising that our conception of nature conservation is quite static. Due to changing climate conditions distribution changes are conceivable, which leads to a disappearance of protective targets from protection areas (Hannah et al. 2002; Hannah et al. 2007). Projected range changes of species and habitat types indicate that more dynamic concepts of nature conservation should be conducted (Hannah & Hansen 2005). Moreover, well-established nature conservation approaches, such as habitat preservation, creation or rather extension of protected areas and retaining viable population sizes (Gaston et al. 2008; Lengyel et al. 2008) are important instruments to support range changes and therefore biodiversity. Furthermore, monitoring programs can help to determine how well the goals of protection areas are realised (Gaston et al. 2008) and to detect problems as early as possible.

In Central Europe, in particular, dispersal processes are strongly limited due to increasing urban sprawl and fragmentation of landscape. Especially epigaeic or less-mobile species are affected by this problem. Therefore, the permeability of the landscape should be fundamentally improved (Opdam et al. 2006; Bissonette & Adair 2008) to enhance the ecological coherence (von Haaren & Reich 2006; Gaston et al. 2008, **article 4**). This can be realised among others by a creation of dispersal corridors and stepping stone habitats. This could contribute to a redynamisation of species movements in our landscape, allowing a better genetic exchange of currently isolated populations and supporting dispersal processes of species to cope with climate change (Mawdsley et al. 2009, **article 3 and 5**). The potential loss of genetic variations is one of the most challenging issues especially on the trailing edge of distribution (Balint et al. 2011; Hill et al. 2011; Provan & Maggs 2011). Therefore, the connectivity between protection areas should be assisted (**article 5**).

Expected nitrogen deposition rates could enhance more competitive or invasive species and therefore lead to a change in communities (Thuiller et al. 2005) yielding transition of habitat types. Also for this case adequate monitoring programs are an important method.

Monitoring could detect transitions in community structure and support suitable management concepts at an early stage.

Assisted colonisation presents a ‘new’ buzz word in the nature conservation community. A ongoing discussion on this topic exists in the scientific community (e.g. Hoegh-Guldberg et al. 2008; Ricciardi & Simberloff 2009; Willis et al. 2009). The concept of this approach is older than 100 years but was formerly used in nature conservation concepts for locally extinct species (e.g. Eurasian Beaver). The concept mapped to the climate change debate intends an assisted colonisation to climatically suitable areas, which were never colonised before by the focused species. Assisted migration as a species-by-species approach furthermore contradicts the current conservation concepts. These concepts, such as the European Habitats Directive, focus on habitats and so called umbrella species, which are representatives of entire ecosystems. This approach is based on the notion that the conservation of suitable habitats is the only sustainable option to manage endangered species. Habitats, however, are changing due to climate change and their conservation or management should be our main concern (Davidson & Simkanin 2008). **Article 6** discusses the pros and cons of this conservation concept and provides a new component for this discussion, the question about the focal unit.

In a nutshell, large-scale nature conservation frameworks, such as Natura 2000 with all installed communication and executive periphery provide a great foundation for a climate-proof nature conservation concept in Europe. However, some fundamental issues, such as a sophisticated monitoring and defragmentation concepts, have to be implemented.

Synopsis of the following articles

Article 1 is based on a literature survey on the topic of climate change and different associated nature conservation relevant subjects. In the present review five major challenges for applied ecology and nature conservation in times of climate change were postulated and condensed by the found publications: (1) Coping with species range dynamics; (2) Assessing consequences for habitats; (3) Understanding alterations of communities; (4) Considering all facets of diversity; (5) Development (and rediscovery) of management techniques. Furthermore, 852 relevant papers were analysed regarding to several points such as study area, investigated taxonomic group, study parameters, research method and study duration. This assessment highlights research gaps and gives insights into scientific focus for climate impact research.

Among other things, the literature survey highlights a research gap for modelling habitats types, and additionally a lacking focus on Natura 2000-related topics. That is one of the reasons that the focus of **article 2, 3 and 4** is on habitat types listed in the Annex I of the Habitats Directive, which is part of the Natura 2000 network. **Article 2** deals with the question of how to model habitat types. Therefore, two different modelling techniques were developed, a ‘direct habitat approach’ and an ‘indirect species approach’. Both are based on Environmental Envelope Modelling (EEM). For this purpose, five different grassland habitat types were used to compare both techniques. The direct as well as the indirect approach lead mostly to reliable results with good to very good performance criteria. However, applying the indirect approach is strongly limited by the availability of distribution data of habitat type’s characteristic plants.

To explore the question of how habitat types could develop under future conditions on a continental scale, only the direct approach is currently usable. All widespread terrestrial habitat types listed in Annex I of the Habitats Directive were modelled in **Article 3**. All 127 habitat types were fitted under current conditions and projected into the future. Habitat types or - more precisely - the environmental envelopes of the modelled habitats react specifically to climate change. Furthermore, all observed habitats and in comparison all projected envelopes were accumulated together. Hereby it was possible to analyse the potential development of habitat type diversity.

Apart from diversity a favourable coherence of the Natura 2000-Network is one of the main objectives of European nature conservation. Habitat types listed in Annex I are protected in Sites of Community Interest (SCI). Driven by climate change a range change of habitat types could be a large problem and lead to an insufficient coherence. **Article 4** assessed the projected future coherence of six different habitat types in Germany by a connectivity analysis. Projection is done by using environmental envelope modelling. Subsequently, a dispersal model under consideration of a cost grid was applied for different dispersal scenarios to identify the potentially reachable areas. As a last step, habitat coherence was calculated by graph-theory.

As previously dispersal distances were considered in the connectivity analysis, this is also a crucial issue regarding species. Most species are limited in its dispersal abilities inter alia by ecological and morphological characteristics. The integration of this point in an environmental envelope model would lead to a more realistic model. **Article 5** integrates species specific dispersal distances for six odonates. The results demonstrate that unlimited dispersal scenarios are too optimistic even for highly mobile species. In particular, less mobile species with many projected climatically suitable areas under an unlimited dispersal scenario reveal a fundamentally different trend when considering a species specific dispersal distance.

As mentioned above, especially less mobile species have a higher risk to become extinct due to shifting of their suitable range by climate change. In these cases, nature conservation management could help to save species from extinction. **Article 6** picks up the currently debated assisted colonisation/migration debate and highlights advantages and disadvantages of this interfering nature conservation method. Further, a new question about the 'focal unit' is pointed out. The opinion article presents, inter alia, the problem of genetic variability and of pre-adopted subspecies. Moreover, a selective assisted colonisation not by moving species but ecotypes is referred.

Summarizing conclusions and emerging research challenges

Climate change impact research is strongly associated with models and assumptions. Understanding how species, habitats and ecosystems respond to climate change has become a major focus of research in ecology, biogeography and conservation biology. Several modelling approaches provide important tools for projections of future changes. Nevertheless, many uncertainties, simplicities and potential improvements remain to optimize statements based on models (McMahon et al. 2011).

Thus, handling uncertainties should be considered, for instance the assumptions of currently accepted emission scenarios, which are an important adjusting screw for climate models. Recently, however, there has been increasing criticism against latest climate models (e.g. Stainforth et al. 2005; Polasky et al. 2011), IPCC emission scenarios (e.g. Kintisch 2008) and different future conditions (e.g. sea-level rise Solomon et al. 2008). Further, the integration of past atmospheric variability (Beerling & Royer 2011; Valdes 2011; Zeebe 2011) could help to achieve projections of future change. Stainforth et al. (2005) show, that a range of 2°C-11°C of change seems to be more likely than the 2.1°C-4.4°C range supposed by the IPCC, under assuming a doubling of CO_2-concentration. Next generation global and regional climate models that are capable of recreating the climate dynamics and conditions of past warm and glacial periods, as well as the more stable twentieth-century conditions, would be a valuable development. This would lead associated climate change research to more reliable results.

Beside improvements of global as well as regional climate models several potential innovations, amendments, refinements and updates of EEMs are conceivable. On the one hand data sources could be optimised, generated or made available. On the other hand modelling techniques has to be improved. One enhancement should be the integration and combination of different sources of ecological, palaeohistorical and evolutionary data to assess the adaptive capacity of species or habitats to climate change (Dawson et al. 2011). A further directive development of envelope modelling could be the integration of process-based, perhaps also individual-based, models and data (Pagel & Schurr 2011). The consideration of dynamic processes into usually statistical models could improve the relation of results to reality (Pagel & Schurr 2011). By dynamism of envelope models a direct integration of biotic interactions could be a possible option. Also some 'new' statistical conceptions like Bayesian approaches or machine learning methods can help to improve the envelope modelling technique in the coming years (Latimer et al. 2006, Hooten et al. 2007, Elith & Graham 2009, Aguilera et al. 2010).

Bierman et al. (2010) for example present a Bayesian model which deals with an omnipresent problem of envelope modelling, the spatial heterogeneity of distribution data.

In addition, genetic variability is a focal point when talking about species resilience to climatic changes (Habel et al. 2005). Due to range shifts, species (Hill et al. 2006) and therefore habitats are confronted with losses of species' genetic potency (likely on the trailing edge), but also evolutionary adaptation processes are possible (likely on the leading edge) (Balint et al. 2011; Hill et al. 2011). Up to now, these important facts are not integrated in envelope modelling approaches. Thus, intraspecific patterns of genetic diversity should be detected and considered when modelling impacts of climate change on biodiversity (Balint et al. 2011; Hill et al. 2011; Provan & Maggs 2011).

Improvements in modelled results could be realised by using data with optimal quality (Heikkinen et al. 2006). Comprehensive global monitoring programs which could complete distributional datasets would not only provide good modelling fundaments. In addition, due to observing biodiversity an early-warning system could timely document changes in abundance, community-structure and distribution (McMahon et al. 2011). This, in turn, supports more focused, adapted and pinpointed nature conservation strategies in face of climate change. Efficient Monitoring programs with high spatial and temporal resolution regarding the key species and habiat types under consideration have to be installed as soon as possible. These standardised programs should be designed and conceptualised for the detection of long-term trends.

Nonetheless, it should not be forgotten that many collected and valuable data are sleeping in rare or forgotten books, museums and in old and unpublished collections. These sources should no longer be ignored, especially for compiling datasets from the near past.

On the contrary to the other outlined points much basic research is needed to improve the basis for decision making and for quantifying the main determinants of sensitivity of species to climate change (McMahon et al. 2011). Therefore experiments could provide new insights and deliver basic understandings of species response to climate change (Jentsch et al. 2007; Beierkuhnlein et al. 2011). Using this knowledge on biotic interactions, substance flows, species responses, etc. a transfer to models or estimations of species' or habitats' response on larger scales or into the future is possible.

Even if such a thesis can not tackle all aspects related to nature conservation, species and habitats in times of climate change, a selection of relevant topics is highlighted and new perspectives are revealed. The articles include innovative approaches that are firstly published. The main focus of this work, namely habitat types, currently poses huge research gaps. With this work some parts of these gaps are closed but also opened new questions and research capabilities. Hence, this thesis improves the current state of scientific research, provides ideas and creates new scientific links.

References

Aguilera, P.A., Fernández, A., Reche, F. & Rumi, R. 2010. Hybrid Bayesian network classifiers: Application to species distribution models. *Environmental Modelling & Software* 25: 1630-1639.

Araújo, M.B. & Guisan, A. 2006. Five (or so) challenges for species distribution modelling. *Journal of Biogeography* 33: 1677-1688.

Araújo, M.B., Thuiller, W. & Pearson, R.G. 2006. Climate warming and the decline of amphibians and reptiles in Europe. *Journal of Biogeography* 33: 1712-1728.

Asher, J., Warren, M., Fox, R., Harding, P., Jeffcoate, G. & Jeffcoate, S. 2001. *The Millenium Atlas of Butterflies in Britain and Ireland*. Oxford Univ. Press. 433 pp., Oxford.

Atkinson, T.C., Briffa, K.R. & Coope, G.R. 1987. Seasonal temperatures in Britain during the past 22,000 years, reconstructed using beetle remains. *Nature* 325: 587-592.

Austin, M.P. 1985. Continuum Concept Ordination Methods and Niche Theory. *Annual Review of Ecology and Systematics* 16: 39-61.

Balint, M., Domisch, S., Engelhardt, C.H.M., Haase, P., Lehrian, S., Sauer, J., Theissinger, K., Pauls, S.U. & Nowak, C. 2011. Cryptic biodiversity loss linked to global climate change. *Nature Climate Change* 1: 313-318.

Beerling, D.J. & Royer, D.L. 2011. Convergent Cenozoic CO2 history. *Nature Geoscience* 4: 418-420.

Beierkuhnlein, C., Thiel, D., Jentsch, A., Willner, E. & Kreyling, J. 2011. Ecotypes of European grass species respond differently to warming and extreme drought. *Journal of Ecology* 99: 703-713.

Bierman, S.M., Butler, A., Marion, G. & Kühn, I. 2010. Bayesian image restoration models for combining expert knowledge on recording activity with species distribution data. *Ecography* 33: 451-460.

Bissonette, J.A. & Adair, W. 2008. Restoring habitat permeability to roaded landscapes with isometrically-scaled wildlife crossings. *Biological Conservation* 141: 482-488.

Bradley, R.S. & Miller, G.H. 1972. Recent Climatic Change and Increased Glacierization in the Eastern Canadian Arctic. *Nature* 237*:* 385-387.

Bruelheide, H. 2003. Translocation of a montane meadow to simulate the potential impact of climate change. *Applied Vegetation Science* 6: 23-34.

Chiarucci, A., Araújo, M.B., Decocq, G., Beierkuhnlein, C. & Fernández-Palacios, J.M. 2010. The concept of potential natural vegetation: an epitaph? *Journal of Vegetation Science* 21: 1172-1178.

Clark, J.S. 1988. Effect of climate change on fire regimes in northwestern Minnesota. *Nature* 334*:* 233-235.

Cleland, E.E., Chuine, I., Menzel, A., Mooney, H.A. & Schwartz, M.D. 2007. Shifting plant phenology in response to global change. *Trends in Ecology & Evolution* 22: 357-365.

Coope, G.R. 1995. The effects of Quarternary climatic changes on insect populations: lessons from the past. In: Harrington, R. & Stork, N.E. (eds.) *Insects in a changing environment. 17th symposium of the Royal Entomological Society, 7-10 September 1993 at Rothamsted Experimental Station, Harpenden.* Academic Press, 535 pp, London.

Council Directive 92/43/EEC (1992). Council Directive 92/43/EEC of 21 May 1992 on the conservation of natural habitats and of wild fauna and flora.

Davidson, I. & Simkanin, C. 2008. Skeptical of Assisted Colonization. *Science* 322: 1048-1049.

Dawson, T.P., Jackson, S.T., House, J.I., Prentice, I.C. & Mace, G.M. 2011. Beyond Predictions: Biodiversity Conservation in a Changing Climate. *Science* 332: 53-58.

Dormann, C.F., Purschke, O., Márquez, J.R.G., Lautenbach, S. & Schröder, B. 2008. Components of uncertainty in species distribution analysis: a case study of the Great Grey Shrike. *Ecology* 89: 3371-3386.

Elias, S.A. 1991. Insects and climate change. *Bioscience* 41: 552-559.

Elias, S.A. 2006. Quaternary beetle research: the state of the art. *Quaternary Science Reviews* 25: 1731-1737.

Elith, J., Leathwick, J.R. & Hastie, T. 2008. A working guide to boosted regression trees. *Journal of Animal Ecology* 77: 802-813.

Elith, J. & Graham, C.H. 2009. Do they? How do they? WHY do they differ? On finding reasons for differing performances of species distribution models. *Ecography* 32: 66-77.

Elith, J. & Leathwick, J.R. 2009. Species Distribution Models: Ecological Explanation and Prediction Across Space and Time. *Annual Review of Ecology Evolution and Systematics* 40: 677-697.

Engelkes, T., Morrien, E., Verhoeven, K.J.F., Bezemer, T.M., Biere, A., Harvey, J.A., McIntyre, L.M., Tamis, W.L.M. & van der Putten, W.H. 2008. Successful range-expanding plants experience less above-ground and below-ground enemy impact. *Nature* 456: 946-948.

European Topic Centre on Biological Diversity (ETC/BD) (2008). Article 17 Technical Report (2001-2006).

Ferrier, S., Drielsma, M., Manion, G. & Watson, G. 2002. Extended statistical approaches to modelling spatial pattern in biodiversity in northeast New South Wales. II. *Biodiversity & Conservation* 11: 2309-2338.

Fischer, D., Thomas, S.M., Niemitz, F., Reineking, B. & Beierkuhnlein, C. 2011. Projection of climatic suitability for Aedes albopictus Skuse (Culicidae) in Europe under climate change conditions. *Global and Planetary Change* 78: 54-64.

Franco, A.M.A., Hill, J.K., Kitschke, C., Collingham, Y.C., Roy, D.B., FOX, R., Huntley, B. & Thomas, C.D. 2006. Impacts of climate warming and habitat loss on extinctions at species' low-latitude range boundaries. *Global Change Biology* 12: 1545-1553.

Franklin, J., and J. A. Miller (eds.) 2010, *Mapping species distributions. Spatial inference and prediction*. Cambridge University Press, 338 pp,Cambridge.

Gaston, K.J., Jackson, S.F., Nagy, A., Cantú-Salazar, L. & Johnson, M. 2008. Protected Areas in Europe. *Annals of the New York Academy of Sciences* 1134: 97-119.

Green, R.E., Collingham, Y.C., Willis, S.G., Gregory, R.D., Smith, K.W. & Huntley, B. 2008. Performance of climate envelope models in retrodicting recent changes in bird population size from observed climatic change. *Biology Letters* 4: 599-602.

Grinnell, J. 1904. The Origin and Distribution of the Chest-Nut-Backed Chickadee. *The Auk* 21: 364-382.

Guisan, A. & Zimmermann, N.E. 2000. Predictive habitat distribution models in ecology. *Ecological Modelling* 135: 146-186.

Haaren, C. von & Reich, M. 2006. The German way to greenways and habitat networks. *Landscape and Urban Planning* 76: 7-22.

Habel, J.C., Schmitt, T. & Muller, P. 2005. The fourth paradigm pattern of post-glacial range expansion of European terrestrial species: the phylogeography of the Marbled White butterfly (Satyrinae Lepidoptera). *Journal of Biogeography* 32: 1489-1497.

Hannah, L. & Hansen, L. 2005. Designing landscapes and seascapes for change. In: Lovejoy, T.E. & Hannah, L. (eds.) *Climate Change and Biodiversity*, Yale University Press, pp. 329–341.

Hannah, L., Midgley, G., Andelman, S., Araújo, M., Hughes, G., Martinez-Meyer, E., Pearson, R. & Williams, P. 2007. Protected area needs in a changing climate. *Frontiers in Ecology and the Environment* 5: 131-138.

Hannah, L., Midgley, G.F. & Millar, D. 2002. Climate change-integrated conservation strategies. *Global Ecology and Biogeography* 11: 485-495.

Heikkinen, R.K., Luoto, M., Araujo, M.B., Virkkala, R., Thuiller, W. & Sykes, M.T. 2006. Methods and uncertainties in bioclimatic envelope modelling under climate change. *Progress in Physical Geography* 30: 751-777.

Hickling, R., Roy, D.B., Hill, J.K. & Thomas, C.D. 2005. A northward shift of range margins in British Odonata. *Global Change Biology* 11: 502-506.

Hickling, R., Roy, D.B., Hill, J.K., Fox, R. & Thomas, C.D. 2006. The distributions of a wide range of taxonomic groups are expanding polewards. *Global Change Biology* 12: 450-455.

Hill, J.K., Griffiths, H.M. & Thomas, C.D. 2011. Climate Change and Evolutionary Adaptations at Species' Range Margins. *Annual Review of Entomology* 56: 143-159.

Hill, J.K., Hughes, C.L., Dytham, C. & Searle, J.B. 2006. Genetic diversity in butterflies: interactive effects of habitat fragmentation and climate-driven range expansion. *Biology Letters* 2: 152-154.

Hill, J.K., Thomas, C.D. & Huntley, B. 1999. Climate and habitat availability determine 20th century changes in a butterfly's range margin. *Proceedings of the Royal Society of London. Series B: Biological Sciences* 266: 1197-1206.

Hitch, A.T. & Leberg, P.L. 2007. Breeding Distributions of North American Bird Species Moving North as a Result of Climate Change. Distribución Reproductiva de Especies de Aves Norte Americanas en Movimiento Hacia el Norte como Resultado del Cambio Climático. *Conservation Biology* 21: 534-539.

Hoegh-Guldberg, O., Hughes, L., McIntyre, S., Lindenmayer, D.B., Parmesan, C., Possingham, H.P. & Thomas, C.D. 2008. Ecology. Assisted colonization and rapid climate change. *Science* 321: 345-346.

Hooten, M.B., Wikle, C.K., Dorazio, R.M. & Royle, J.A. 2007. Hierarchical Spatiotemporal Matrix Models for Characterizing Invasions. *Biometrics* 63: 558-567.

Hossell, J.E., Ellis, N.E., Harley, M.J. & Hepburn, I.R. 2003. Climate change and nature conservation: Implications for policy and practice in Britain and Ireland. *Journal for Nature Conservation* 11: 67-73.

Huntley, B. 1991. How Plants Respond to Climate Change: Migration Rates, Individualism and the Consequences for Plant Communities. *Annals of Botany* 67: 15-22.

Jentsch, A., Kreyling, J. & Beierkuhnlein, C. 2007. A new generation of climate-change experiments: events, not trends. *Frontiers in Ecology and the Environment* 5: 365-374.

Julliard, R., Jiguet, F. & Couvet, D. 2004. Common birds facing global changes: what makes a species at risk? *Global Change Biology* 10: 148-154.

Kelly, A.E. & Goulden, M.L. 2008. Rapid shifts in plant distribution with recent climate change. *Proceedings of the National Academy of Sciences* 105: 11823-11826.

Kintisch, E. 2008. IPCC Tunes Up for Its Next Report Aiming for Better, Timely Results. *Science* 320: 300.

Kreyling, J., Beierkuhnlein, C., Ellis, L. & Jentsch, J. 2008. Invasibility of grassland and heath communities exposed to extreme weather events &x2013; additive effects of diversity resistance and fluctuating physical environment. *Oikos* 117: 1542-1554.

Latimer, A.M., Wu, S., Gelfand, A.E. & Silander, J.A., JR. 2006. Building Statistical Models To Analyze Species Distributions. Ecological Applications. *Ecological Applications* 16: 33-50.

Lengyel, S., Kobler, A., Kutnar, L., Framstad, E., Henry, P.-Y., Babij, V., Gruber, B., Schmeller, D. & Henle, K. 2008. A review and a framework for the integration of biodiversity monitoring at the habitat level. *Biodiversity and Conservation* 17: 3341-3356.

Mawdsley, J.R., O'Malley, R. & Ojima, D.S. 2009. A review of climate-change adaptation strategies for wildlife management and biodiversity conservation. *Conservation Biology* 23: 1080-1089.

McMahon, S.M., Harrison, S.P., Armbruster, W., Bartlein, P.J., Beale, C.M., Edwards, M.E., Kattge, J., Midgley, G., Morin, X. & Prentice, I. 2011. Improving assessment and modelling of climate change impacts on global terrestrial biodiversity. *Trends in Ecology & Evolution* 26: 249-259.

Menéndez, R., González-Megías, A., Lewis, O., Shaw, M.R. & Thomas, C.D. 2008. Escape from natural enemies during climate-driven range expansion: a case study. *Ecological Entomology* 33: 413-421.

Menéndez, R., Megias, A.G., Hill, J.K., Braschler, B., Willis, S.G., Collingham, Y., Fox, R., Roy, D.B. & Thomas, C.D. 2006. Species richness changes lag behind climate change. *Proceedings of the Royal Society B: Biological Sciences* 273: 1465-1470.

Mitchell, J.M. 1961. Recent secular changes of global temperature. *Annals New York Academy of Sciences* 95: 235-250.

Mitchell, J.M. 1972. The natural breakdown of the present interglacial and its possible intervention by human activities. *Quaternary Research* 2: 436-445.

Mücher, C.A., Hennekens, S.M., Bunce, R.G.H., Schaminée, J.H.J. & Schaepman, M.E. 2009. Modelling the spatial distribution of Natura 2000 habitats across Europe. *Landscape and Urban Planning* 92: 148-159.

Nenzén, H.K. & Araújo, M.B. 2011. Choice of threshold alters projections of species range shifts under climate change. *Ecological Modelling* 222: 3346-3354.

Normand, S., Svenning, J.-C. & Skov, F. 2007. National and European perspectives on climate change sensitivity of the habitats directive characteristic plant species. *Journal for Nature Conservation* 15: 41-53.

Olden, J.D., Lawler, J.J. & Poff, N.L. 2008. Machine Learning Methods Without Tears. A Primer for Ecologists. *The Quarterly Review of Biology* 83: 171-193

Opdam, P., Steingröver, E. & van Rooij, S. 2006. Ecological networks: A spatial concept for multi-actor planning of sustainable landscapes. *Landscape and Urban Planning* 75: 322-332.

Ott, J. 2010. Dragonflies and climatic change - recent trends in Germany and Europe. *BioRisk* 5: 253-286.

Pagel, J. & Schurr, F.M. 2011. Forecasting species ranges by statistical estimation of ecological niches and spatial population dynamics. *Global Ecology and Biogeography.* doi: 10.1111/j.1466-8238.2011.00663.x.

Parmesan, C. 1996. Climate and species' range. *Nature* 382: 765-766.

Parmesan, C. & Yohe, G. 2003. A globally coherent fingerprint of climate change impacts across natural systems. *Nature* 421: 37-42.

Parmesan, C., Ryrholm, N., Stefanescu, C., Hill, J.K., Thomas, C.D., Descimon, H., Huntley, B., Kaila, L., Kullberg, J., Tammaru, T., Tennent, W.J., Thomas, J.A. & Warren, M. 1999. Poleward shifts in geographical ranges of butterfly species associated with regional warming. *Nature* 399: 579-583.

Pearson, R.G. & Dawson, T.P. 2003. Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? *Global Ecology and Biogeography* 12: 361-371.

Petermann, J., Balzer, S., Ellwanger, G., Schröder, E. & Ssymank, A. 2007. Klimawandel - Herausforderung für das europaweite Schutzgebietssystem Natura 2000. *Naturschutz und Biologische Vielfalt* 46*:* 127-148.

Phillips, S.J., Anderson, R.P. & Schapire, R.E. 2006. Maximum entropy modeling of species geographic distributions. *Ecological Modelling* 190: 231-259.

Plassmann, K., Jones, M.L.M. & Edwards-Jones, G. 2010. Effects of long-term grazing management on sand dune vegetation of high conservation interest. *Applied Vegetation Science* 13: 100-112.

Polasky, S., Carpenter, S.R., Folke, C. & Keeler, B. 2011. Decision-making under great uncertainty: environmental management in an era of global change. *Trends in Ecology & Evolution* 26: 398-404.

Prasad, A., Iverson, L. & Liaw, A. 2006. Newer Classification and Regression Tree Techniques: Bagging and Random Forests for Ecological Prediction. *Ecosystems* 9: 181-199.

Provan, J. & Maggs, C.A. 2011. Unique genetic variation at a species's rear edge is under threat from global climate change. *Proceedings of the Royal Society B: Biological Sciences.* doi: 10.1098/rspb.2011.0536 .

Rebelo, H., Tarroso, P. & Jones, G. 2010. Predicted impact of climate change on European bats in relation to their biogeographic patterns. *Global Change Biology* 16: 561-576.

Ricciardi, A. & Simberloff, D. 2009. Assisted colonization is not a viable conservation strategy. *Trends in Ecology & Evolution* 24: 248-253.

Salinger, M.J. & Gunn, J.M. 1975. Recent climatic warming around New Zealand. *Nature* 256*:* 396-398.

Schweiger, O., Settele, J., Kudrna, O., Klotz, S. & Kühn, I. 2008. Climate change can cause spatial mismatch of trophically interacting species. *Ecology* 89: 3472-3479.

Solomon, S., Alley, R., Gregory, J., Lemke, P. & Manning, M. 2008. A Closer Look at the IPCC Report. *Science* 319: 409-410.

Ssymank, A., U. Hauke, C. Rückriem, and E. Schröder (eds.) 1998, *Das europäische Schutzgebietssystem NATURA 2000. BfN-Handbuch zur Umsetzung der Fauna-Flora-Habitat-Richtlinie (92/43/EWG) und der Vogelschutzrichtlinie (79/409/EWG).* Schriftenreihe für Landschaftspflege und Naturschutz 53. BfN-Schr.-Vertrieb im Landwirtschaftsverl., 558 pp, Münster.

Stainforth, D.A., Aina, T., Christensen, C., Collins, M., Faull, N., Frame, D.J., Kettleborough, J.A., Knight, S., Martin, A., Murphy, J.M., Piani, C., Sexton, D., Smith, L.A., Spicer, R.A., Thorpe, A.J. & Allen, M.R. 2005. Uncertainty in predictions of the climate response to rising levels of greenhouse gases. *Nature* 433: 403-406.

Stockwell, D. & Peters, D. 1999. The GARP modelling system: problems and solutions to automated spatial prediction. *International Journal of Geographical Information Science* 12: 143-158.

Thomaes, A., Kervyn, T. & Maes, D. 2008. Applying species distribution modelling for the conservation of the threatened saproxylic Stag Beetle (Lucanus cervus). *Biological Conservation* 141: 1400-1410.

Thuiller, W. 2003. BIOMOD - optimizing predicitions of species distributions and projecting potential future shifts under global change. *Global Change Biology* 9: 1353-1362.

Thuiller, W., Lafourcade, B., Engler, R. & Araújo, M.B. 2009. BIOMOD – a platform for ensemble forecasting of species distributions. *Ecography* 32: 369-373.

Thuiller, W., Lavorel, S., Araújo, M.B., Sykes, M.T. & Prentice, C.I. 2005. Climate change threats to plant diversity in Europe. *Proceedings of the National Academy of Sciences* 102: 8245-8250.

Valdes, P. 2011. Built for stability. *Nature Geoscience* 4: 414-416.

Vos, C.C., Berry, P., Opdam, P., Baveco, H., Nijhof, B., O'Hanley, J., Bell, C. & Kuipers, H. 2008. Adapting landscapes to climate change: examples of climate-proof ecosystem networks and priority adaptation zones. *Journal of Applied Ecology* 45: 1722-1731.

Walther, G.-R., Beißner, S. & Burga, C.A. 2005. Trends in the upward shift of alpine plants. *Journal of Vegetation Science* 16: 541-548.

Walther, G.R., Roques, A., Hulme, P., Sykes, M.T., Pyšek, P., Kühn, I., Zobel, M., Bacher, S., Botta-Dukát, Z., Bugmann, H., Czúcz, B., Dauber, J., Hickler, T., Jarošík, V., Kenis, M., Klotz, S., Minchin, D., Moora, M., Nentwig, W., Ott, J., Panov, V.E., Reineking, B., Robinet, C., Semenchenko, V., Solarz, W., Thuiller, W., Vilá, M., Vohland, K. & Settele, J. 2009. Alien species in a warmer world: risks and opportunities. *Trends in Ecology and Evolution* 24: 686-693.

Warren, M.S., Hill, J.K., Thomas, J.A., Asher, J., Fox, R., Huntley, B., Roy, D.B., Telfer, M.G., Jeffcoate, S., Harding, P., Jeffcoate, G., Willis, S.G., Greatorex-Davies, J.N., Moss, D. & Thomas, C.D. 2001. Rapid responses of British butterflies to opposing forces of climate and habitat change. *Nature* 414: 65-69.

Weaver, A.J. & Zwiers, F.W. 2000. Uncertainty in climate change. *Nature* 407: 571-572.

Williams, J.W. & Jackson, S.T. 2007. Novel climates, no-analog communities, and ecological surprises. Frontiers in Ecology and the Environment. *Frontiers in Ecology and the Environment* 5: 475-482.

Willis, S.G., Hill, J.K., Thomas, C.D., Roy, D.B., Fox, R., Blakeley, D.S. & Huntley, B. 2009. Assisted colonization in a changing climate: a test-study using two U.K. butterflies. *Conservation Letters* 2: 46-52.

Wilson, R.J., Gutiérrez, D., Gutiérrez, J., Martínez, D., Agudo, R. & Monserrat, V.J. 2005. Changes to the elevational limits and extent of species ranges associated with climate change. *Ecology Letters* 8: 1138-1146.

Zeebe, R.E. 2011. Where are you heading Earth? *Nature Geoscience* 4: 416-417.

List of manuscripts and specification of own contribution

"Writing" is understood as the actual formulation of sentences and paragraphs. Comments and inputs from discussions with the co-authors as well as corrections are covered under "discussion, editing & revisions". Proof-reading and grammar editing was done by professionals or by native speakers for each manuscript.

Article 1

Authors	Anja Jaeschke, Torsten Bittner, Anke Jentsch, Björn Reineking, Carl Beierkuhnlein
Title	Challenges for applied ecology and nature conservation in the face of climate change
Status	under review; invited for submission; submitted on 2011-01-20
Journal	Climatic Change
Own contributions	first draft and concept 35%; data anlysis, literature study & figures 50%; writing 20%; discussion, editing & revisions 30%
In this thesis	from page 29

Update:
major revisions

Article 2

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
Status	printed; submitted 2010-06-15; accepted 2011-01-30
Journal	Journal of Vegetation Science 2011 22(4) 699–710
Own contributions	first draft and concept 40%; modelling, data anlysis & figures 60%; writing 50%; discussion, editing & revisions 40%; corresponding author
In this thesis	from page 47

Article 3

Authors	Torsten Bittner, Anja Jaeschke, Björn Reineking, Carl Beierkuhnlein
Title	Climate change impacts on terrestrial Natura 2000 habitats: distribution, projected environmental space, threats and potential management
Status	under review submitted 2011-09-06
Journal	Biodiversity and Conservation
Own contributions	first draft and concept 90%; modelling, data anlysis & figures 90%; writing 90%; discussion & editing 75%; corresponding author
In this thesis	from page 77

Update:
major revisions

Article 4

Authors	Holger Dempe, Torsten Bittner, Anja Jaeschke, Carl Beierkuhnlein
Title	Habitat coherence and climate change: an analysis application for the Natura 2000 network in Germany
Status	submitted 2011-09-21
Journal	Ecological Applications
Own contributions	first draft and concept 33%; modelling, data anlysis & figures 10%; writing 10%; discussion & editing 33%
In this thesis	from page 101

Article 5

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
Status	revision submited 2011-09-16 submitted 2011-04-14
Journal	Insect Conservation and Diversity
Own contributions	first draft and concept 50%; modelling, data anlysis & figures 50%; writing 25%; discussion & editing 20%
In this thesis	from page 137

Update:
revised manuscript in press

Article 6

Authors	Juergen Kreyling, Torsten Bittner, Anja Jaeschke, Anke Jentsch, Manuel Jonas Steinbauer, Daniel Thiel, Carl Beierkuhnlein
Title	Assisted Colonization: A Question of Focal Units and Recipient Localities
Status	printed; submitted 2010-01-18; accepted 2010-12-21
Journal	Restoration Ecology 2011 19(4), 433–440
Own contributions	first draft and concept 20%; data anlysis & figures 0%; writing 20%; discussion, editing & revisions 30%
In this thesis	from page 159

Article 1

Challenges for applied ecology and nature conservation in the face of climate change

Anja Jaeschke, Torsten Bittner, Anke Jentsch, Björn Reineking, Carl Beierkuhnlein

invited for submission to Climatic Change, under review
submitted on 2011-01-20

Abstract

Climate change is increasingly affecting organisms and habitats. The knowledge about the potential responses of ecological units to gradual warming, altered precipitation patterns and extreme weather events is crucial for the conservation and management of ecosystems all over the world. However, various forms of uncertainty have to be considered: a) uncertainty in climate change models, b) uncertainty in model predictions, and c) knowledge gaps concerning a species' ecology. Here, we review the current state of first knowledge about the impacts of climate change on species and habitats. Further, we identify five challenges for nature conservation that arise from rapid climate change; coping with range dynamics, assessing consequences for habitats, understanding alterations of communities, considering all facets of diversity and the development of management techniques. In a rapidly evolving research landscape, this review aims at providing biodiversity driven perspectives for applied climate change research as well as for nature conservation practice.

Keywords

Global warming, Biodiversity, Knowledge gaps, Conservation planning

Challenges for applied ecology and nature conservation in the face of climate change

Anja Jaeschke[1,2,3], Torsten Bittner[1,2,3], Anke Jentsch[2], Björn Reineking[3], Carl Beierkuhnlein[1]

[1]Biogeography, BayCEER, University of Bayreuth, D-95440 Bayreuth, Germany
[2]Geoecology and Physical Geography, University of Koblenz-Landau, D-76829 Landau, Germany
[3]Biogeographical Modelling, BayCEER, University of Bayreuth, D-95440 Bayreuth, Germany

Introduction

Even though rapid climate change is a major topic of research today (Loarie et al. 2009; Körner and Basler 2010; Moss et al. 2010), the responses of plant and animal populations, of biocoenoses as well as of entire ecosystems to warming and to altered precipitation patterns are largely unclear. In particular, there is hardly any knowledge on the consequences of the amplification of the hydrological cycle and a higher frequency of extreme weather events (Jentsch et al. 2007; Jentsch and Beierkuhnlein 2010). Understanding the speed and form of potential alterations, e.g. in species distribution and biotic interactions, is fundamentally relevant for decision-making processes in nature conservation such as reserve site selection and conservation techniques. Extreme weather events in particular, are generating global concerns about the most effective strategies for conserving biological diversity (Sutherland et al. 2009). Considering turnover rates, life cycles and longevity of organisms, communities and ecosystems, such strategies have to be designed taking into account projected future conditions.

However, with climate change projections, two particular challenges become apparent here. First, mainly historical reference periods have been considered in process-orientated nature conservation so far. Secondly, knowledge gaps arise among practitioners and scientists publishing in international journals, because committed conservation managers often only access research literature if published in their native language. Thus, an interface between practitioners and scientists is essential and urgently needed (Mastrandrea et al. 2010).

Here, we present a contemporary review of the current ecology and conservation science literature on the impacts of climate change on species, communities and habitats. Our goal is to identify knowledge deficits and the arising challenging issues in nature conservation. We conducted a systematic literature research using the ISI Web of Science taking into account 852 peer-reviewed publications on climate change impacts on biodiversity and ecosystems. Specifically, we assessed how current knowledge covers the global geographical, taxonomic and ecosystem type diversity as well as methodological practices. The analysed results were used to identify five fundamental challenges for future nature conservation in the face of climate change.

Challenges for applied ecology and nature conservation

From the literature review we derived five major challenging issues for nature conservation, with each of these containing multiple sub items (Figure 1).

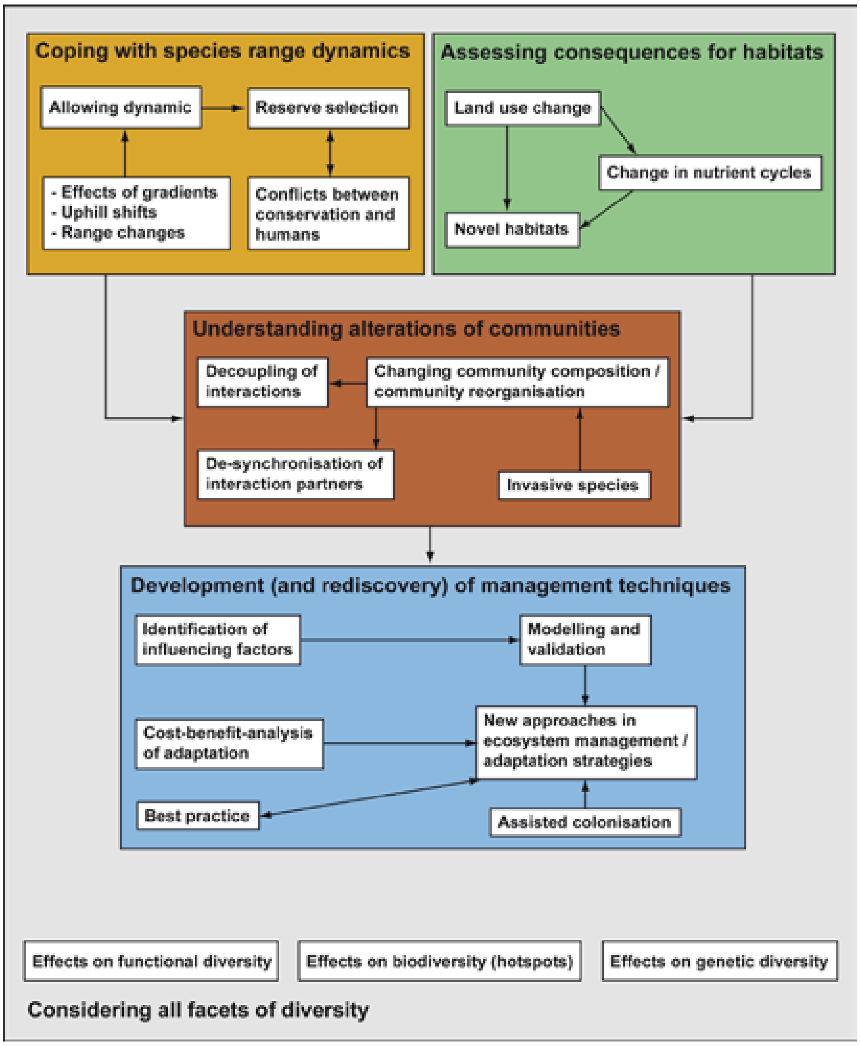


Figure 1: Five arising challenging issues for nature conservation in times of global climate change and their complex interactions.

Coping with species range dynamics

The expected range dynamics of plants and animals vary according to the species and are therefore one of the most important challenges for nature conservation and protected areas.

Climate change may influence large, ecotone-crossing populations of a species in different ways causing range benefits at one margin, but range losses at the other margin, leading to range movements (Gaston et al. 2005; Jiguet et al. in press). Also, uphill shifts of mountainous species have been documented and projected (Jentsch and Beierkuhnlein 2003; Popy et al. 2010). Hence, existing reserves may face two-fold dynamics: The range of protected species can increase and species may expand over reserve borders, or the range either decreases or remains stable within them. The question is, how can and how should reserves be adapted to these dynamics?

Flexibility in reserve sites, which allows for population dynamics and range shifts, is often proposed (Williams et al. 2005; Vos et al. 2008). Lawler (2009) mentioned three options for coping with range shifts: increasing existing reserves, adding new areas to allow directional movement, and adding new areas as stepping stones between existing reserves. The future selection of protected areas requires methods of reserve-selection, which will include the full, i.e. both current and future, environmental range of the target species (Pyke and Fischer 2005; McClean et al. 2006; Branquart et al. 2008). Further, political challenges in reserve selection have to be more and more considered. Conflicts between conservation goals and human interests, especially in poorer countries, have been widely documented. In South Africa, most conservation priority areas are exposed to high human population pressure, which is most likely to increase due to changes in the relationship between species richness, human density and rainfall (van Rensburg et al. 2004).

Assessing consequences for habitats

Increased nutrient deposition is one of the most important future threats, especially to nutrient-poor habitats such as bogs and dry acidic grasslands (Jentsch and Beyschlag 2003) but also to other habitats (Benítez-Gilabert et al. 2010; Marshall and Randhir 2008). Field experiments in an alpine ecosystem showed that experimental warming together with nutrient addition can substantially alter community structure and lead to shifts in dominance hierarchies (Klanderud and Totland 2005). These effects were associated with a decrease in diversity. Feuchtmayr et al. (2009) made similar experiments in microcosms, simulating shallow lakes. Nutrient additions were found to decrease plant biomass and in combination with warming there was a decrease in plant species richness. The alteration of nutrient uptake in nutrient-poor habitats is another effect of climate change. A study in tropical forests revealed that the examined plant species changed their dominant nitrogen source due to changes in the precipitation regime (Houlton et al. 2007).

It is expected that changes in the climate also affect land productivity, which in turn could lead to land use changes (Mendelsohn and Dinar 2009). Otherwise, changes in land use often depend on subsidies from governments and are therefore difficult to predict.

Changes in the composition of habitats can lead to a loss of defined habitats (Fronzek et al. 2006) e.g. those defined in Annex I of the EU Habitats Directive (Council Directive 92/43/EEC 1992). However, this could also result in the emergence of novel habitats i.e. plant communities that have never been observed before in a certain region (le Roux and McGeoch 2008), which may in turn be relevant for nature conservation. These novel habitats could also offer the same ecosystem functions and therefore be adequate alternatives to the original habitats.

Understanding alterations of communities

Climate change not only acts on the species level, but also has impacts on communities and their structure. Impacts on specific interactions within communities can be manifold: changes in community composition, de-synchronisation of interactions, spread of invasive species or decoupling of interactions.

The dispersal rates of species vary greatly, depending on specific niche requirements to a certain extent. As a result of these different rates, patterns of community composition can change and form new or even non-analogue communities. Le Roux and McGeoch (2008) conducted a field study on the flora of sub-Antarctic Marion Island concerning altitudinal range shifts. They could demonstrate that the range of variation in species responses to climate change caused great changes in community composition, especially at mid- and high altitudes.

A de-synchronisation of previously synchronised life cycles and a disruption of mutually beneficial interactions due to climate change appear possible (e.g. Harrison 2000; Parmesan 2007). Population declines can be a consequence, as shown for migratory birds and butterflies (Both et al. 2006; Schweiger et al. 2008). A temporal mismatch between bird breeding time and maximal abundance of food led to population declines of about 90%, whereas a spatial mismatch between the future niche spaces of butterflies and their larval host plants disrupted trophic interactions. Jentsch et al. (2009) refer to a potentially more powerful influence of extreme weather events on disturbing the synchronisation between organisms and community organisation, especially on short-term time scales.

The facilitation of invasive species can indirectly affect species and biocoenoses. This advancement can be induced by making colonisation possible, enhancing predator impacts, shifting competitive balances, enhancing diseases and increasing habitat alterations (Rahel et al. 2008). Rahel and Olden (2008) notice that temperature gradients may act as filters that prevent warm-adapted species from establishing populations in colder regions. As temperatures increase with climate change, the effectiveness of these filters may be reduced and species adapted to the heat could spread to new areas. These species with expanding ranges could be harmful to other native species and communities. However, we have to take into account that the invasive species of today might become acceptable or even desirable species of tomorrow to ensure the long-term functions of ecosystems. Therefore, management practices will have to carry out an extensive evaluation of changing habitat conditions and invasive species (Walther et al. 2009).

A decoupling of interactions can have both negative as well as positive effects. Some scientists are concerned that plants, which are successfully able to shift their range, may experience less control of natural enemies than native species and could therefore be potential invaders (van Grunsven et al. 2007; Engelkes et al. 2008). Otherwise, a study of Menéndez et al. (2008) on parasitoid-host interactions suggests that the decoupling of interactions may allow some species to exploit a wider range of environments and thus provide them with the opportunity to spread greater and faster into new suitable areas. Braschler and Hill (2007) demonstrate how polyphagy may enhance the ability of a species to track climate change. They were able to show that the current range expansion of a butterfly is associated with the exploitation of more widespread host plants.

Considering all facets of diversity

In the face of climate change, there must be a change from pure biodiversity conservation to the conservation of ecosystem functional diversity and genetic diversity. The effects of a changing climate on functional diversity and on ecosystem properties and functions such as productivity, carbon fixation, phenology, decomposition, resistance to invasion, gas regulation and nutrient cycling are substantial and increasingly being considered (Kreyling et al. 2008a; Kreyling et al. 2008b; Braschler and Hill 2007; Riutta et al. 2007; Mirzae et al. 2008; Jentsch et al. 2009). Implications for ecosystem structure and function increasingly are taken into account. Further attention should be given to the loss of genetic diversity and its consequences for potential adaptations to climate change. The loss of genetic diversity results, in the worst case, in a loss of ability to adapt to climate change (Hill et al. 2006; Ehlers et al. 2008; Jump et al. 2009; Sork et al. 2010).

Biodiversity hotspots are still the focus of international nature conservation strategies (Myers et al. 2000; Sutherland et al. 2009). Negative impacts here, are driven not only and in most cases to a negligible degree by local ethnic groups but rather by global trade and commerce. Thus, there is also an international responsibility for the maintenance of these extraordinary regions, where damages can have outstanding global repercussions.

Development (and rediscovery) of management techniques

Climate change and its expected impacts on species, biotopes and communities require a reconsideration and amendment of conservation techniques (Sutherland et al. 2009). This includes theoretical considerations such as factors influencing the impacts of climate change on the species level, modelling potential future distributions or analysing which locations are most vulnerable. Also practical approaches such as the implementation of adaptation strategies, modifying management practices or specific activities such as assisted migration are necessary.

The first and most important step is the identification of crucial factors influencing climate change impacts at the species level, mainly dispersal abilities, biotic interactions, resistance, rapid evolution and land cover (Dullinger et al. 2004; Bradshaw and Holzapfel 2006; Araújo and Luoto 2007; Brooker et al. 2007).

Another currently very popular technique is the modelling of potential impacts and the derivation of adaptation strategies. To deal with uncertainties in predictions, a validation of models with past and/or current conditions is necessary (Araújo et al. 2005) and should be included in conservation planning. Furthermore, the choice of models and scenarios has to be considered as no single best model exists (Beaumont et al. 2008; Platts et al. 2008). Beaumont et al. (2008) suggest not to undertake the selection of climate scenarios arbitrarily and to note the strengths and weakness of different climate models because they are complex tools with variability among alternate simulations.

These two procedures help us to estimate the impacts of climate change on species and habitats. Furthermore, the realisation and the costs and benefits of adaptation strategies are included in conservation planning. Early action in times of climate change seems to be more cost efficient than delayed action or inaction (Hannah et al. 2007; Hannah 2008).

A practical and vividly discussed approach is the so-called assisted colonization (also assisted migration, translocation, managed relocation) as an option for poor dispersers that are not able to track shifts of suitable climate space (McLachlan et al. 2007; Hoegh-Guldberg et al. 2008; Willis et al. 2009). To move species of conservation concern seems, at first sight, a viable method to overcome dispersal limitations and to allow species to reach future climatic suitable habitats (Willis et al. 2009). Nevertheless, we have to take into account the large uncertainty in our ecological understanding of what controls the distribution and abundance of species and the arising difficulties and problems of predicting suitable target regions (McLachlan et al. 2007).

Overall, we need more flexible, reversible and particularly mixed approaches for ecosystem management (Millar et al. 2007). Branquart et al. (2008) suggest a dynamic concept of nature conservation that enhances resilience, resistance and site restoration, and the development of permeable landscapes that provide "stepping stones" for species migration. Lawler (2009) declares that the available tools for conservation planning need a new perspective, i.e. restoring ecosystem functions and managing ecosystem services instead of species compositions.

Climate change impact research in scientific literature

We used the ISI Web of Science database (Thomson Reuters, 2010) to search for articles that focused on climate change impacts on fauna, flora and habitats. We limited our search to articles with "climate change" and related terms (i.e. "changing climate", "global warming", "global change") in the topic (including title, keywords and abstract). We narrowed our focus on a subset of these articles that contained terms of "conservation", "species range", "modelling", "ecology" or "protected habitats". Relevant alternative suffixes were included using the asterisk (e.g. "clima* envelop*"). The whole search string is given in Table 1.

Table 1: Search string for the literature study in ISI Web of Science. The search was restricted to publications between 2003 and 2010 (15.11.2010).

Category	Search term
„Topic“	“climat* chang*” or “changing climat*” or “global chang*” or “global warming”
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*

Our search was restricted to publications between 2003 and 2010 (15.11.2010) to analyse the current state of knowledge, and also excluded articles on paleontological climate change. Our search yielded 2373 articles. From this initial set, we excluded 1521 articles, which were non-climate change-related or which contained only the short topical statement that their results may change under climate change. Each of the remaining 852 articles was analysed on the basis of its title, keywords and abstract with a set of criteria. We assessed the geographic, taxonomic, ecosystem and methodological coverage.

Study area

Approximately one third of all studies on climate change impacts were conducted in North America and Europe, respectively (Figure 2). Research in tropical, sub-tropical and arctic biomes is highly underrepresented. Africa is expected to be influenced most by climate change (IPCC, 2007), but only 7% of the literature analysed is concerned with this continent. Most of those studies were conducted in South Africa, within the Cape Floristic Region, whereas studies in North or in Central Africa are missing. The research institutions of the first authors are similar distributed as the study areas (Figure 3). Most of the publications have a first author who is resident in North America, followed by Western Europe (in particular the United Kingdom), Central Europe and Australia.

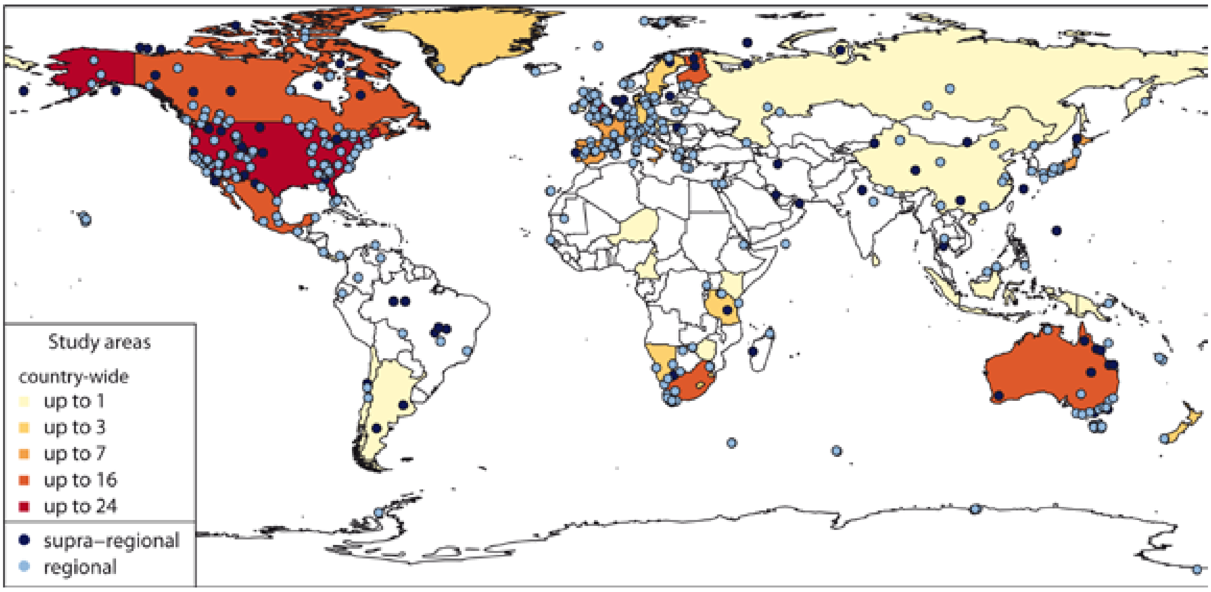


Figure 2: Study areas (regional: local, e.g. one National Park; supra-regional: within national boundaries, country-wide: considering the whole country), taken from publications in the ISI Web of Science about the impacts of climate change on fauna, flora and habitats between 2003 and 2010 (15.11.2010). Publications on global processes or continents (except for Australia) are not displayed.

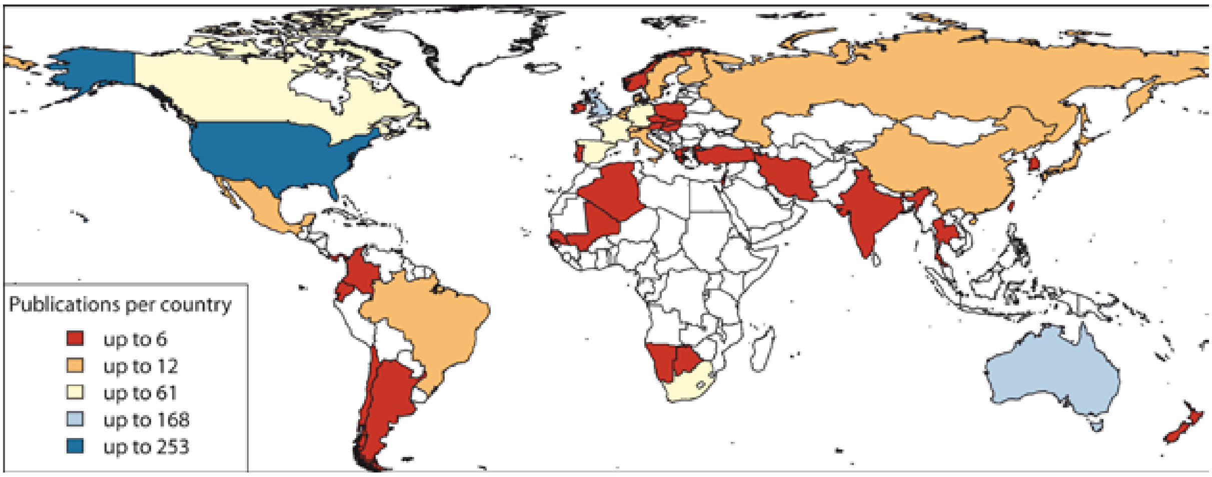


Figure 3: Number of publications in the ISI Web of Science per country between 2003 and 2010 (15.11.2010) about the impacts of climate change on fauna, flora and habitats, according to the first authors' institutional address.

The geographical bias in the distribution of study areas and the first author's institutional address may be the result of discrepancies in the scientific and technological research capabilities of nations and an uneven distribution of financial resources (Fazey et al. 2005). The amount of research and the financial support for research on consequences of global warming is usually of national interest. Consequently, such policy relevance demands a national analysis and a product for national decision makers and conservation managers. Often, such studies are published on national platforms and not accessible for an international readership.

Investigated taxonomic groups and study parameters

Vascular plants are the primary taxonomic focus of almost half of the studies (Figure 4). Insects and birds make up a further large proportion of analyses. Several other taxonomic groups such as reptiles, amphibians or lichen are underrepresented in current research, although these are sensitive to and even already influenced by climate change (European Topic Centre on Biological Diversity (ETC/BD) 2008).

Changes in temperature (55%) and precipitation regime (27%) are the main climatic parameters studied (Figure 4). Other parameters such as land use and carbon dioxide, but also salinity, snow cover and nitrogen deposition have rarely been considered so far.

Insects and birds seem to be suitable taxonomic groups for studying climate change impacts. Insects have relatively short life-cycles, so impacts of climate change as well as any adaptation possibilities can quickly become evident. Birds may track climate change through range shifts due to their high mobility. Birds' flight paths are also well documented by scientific and amateur bird watchers, so changes in migration patterns can be easily detected. Whereas plants are directly influenced by climate change at their location, enabling research to be conducted on less mobile species and species with longer life-cycles, especially trees. Here in particular, further research is required.

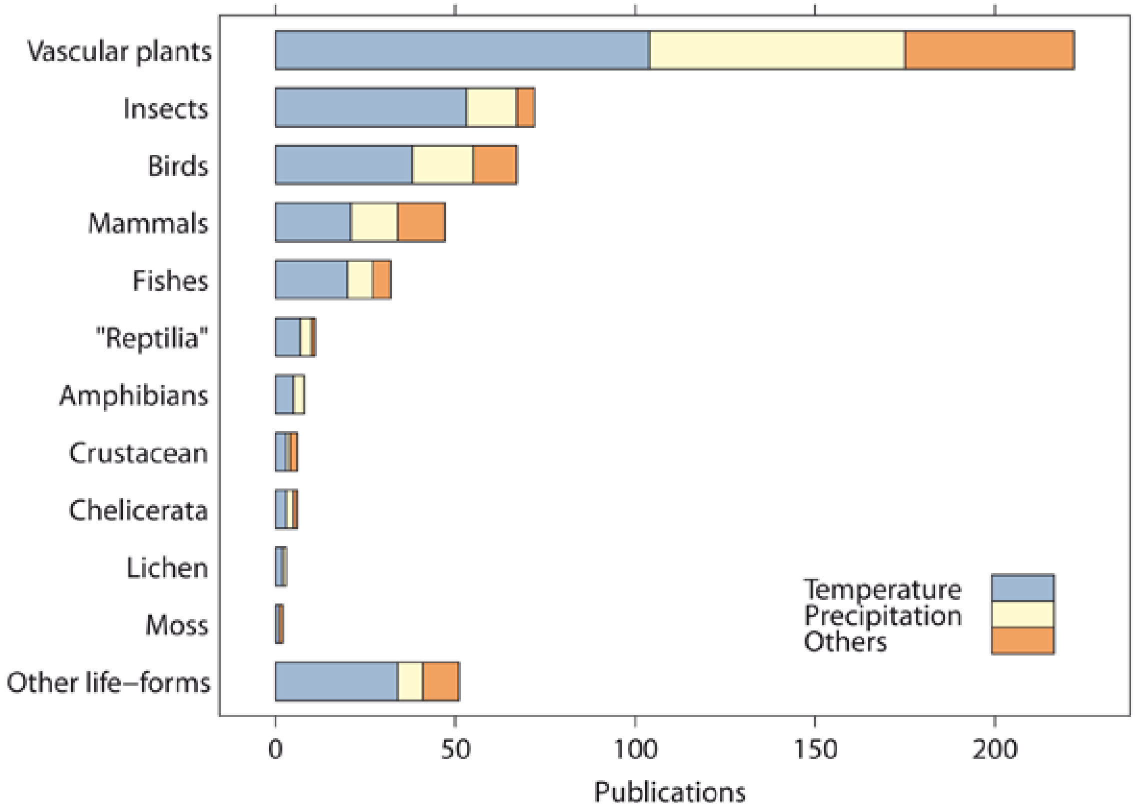


Figure 4: Taxonomic coverage and studied parameters of reviewed climate change literature between 2003 and 2010 (15.11.2010). Parts of the bars show the percentage of studied parameters. Multiple entries were possible.

Type of ecosystem

More than one third (40%) of climate change related ecosystem research focuses on forests (Figure 5). Almost another third of the studied ecosystems is non-terrestrial (31%) such as saltwater and freshwater ecosystems. Grassland ecosystems are with 10% less considered in climate change research.

Raised bogs, fens and palsa mires are rarely studied in conjunction with climate change impacts, although they often harbour a rich diversity of species and are currently being degraded (Fronzek et al. 2006). The same applies to shrub land, arid and semi-arid ecosystems, arctic and antarctic ecosystems and coastal ecosystems.

Probably, the research focus on forest ecosystems is due to their economic importance, particularly in North America and Europe. However, Cardoso et al. (2008) expressed concern that climate change together with other stressors may also have profound ecological as well as social and economic implications on coastal ecosystems.

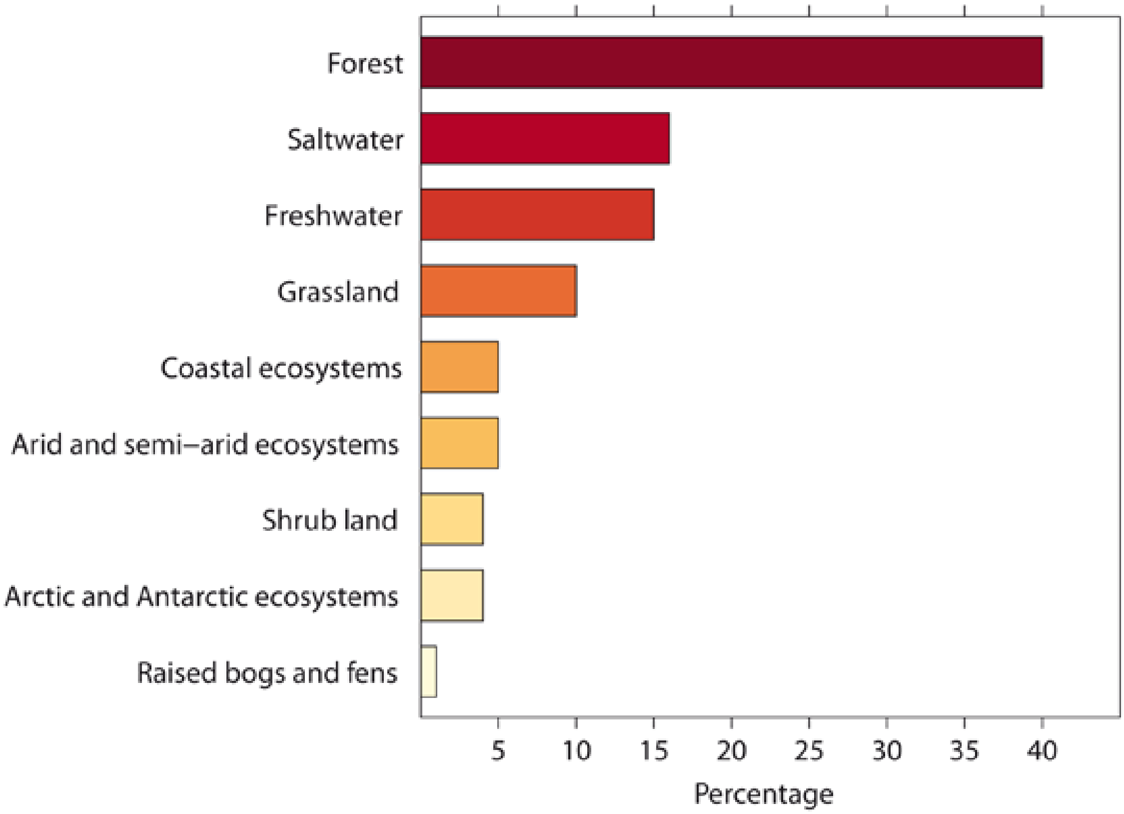


Figure 5: Ecosystem coverage in published climate change literature in the ISI Web of Science between 2003 and 2010 (15.11.2010). Grassland ecosystems include savannahs, wetlands, prairies and tundra; coastal ecosystems include estuaries, intertidal zones, brackish water and marshland; raised bogs and fens include palsa mires.

Research method and study duration

Research methods include field observations, field experiments, lab experiments and modelling of future trends. Almost half of the articles rely primarily on the modelling of future trends (47%) including empirical as well as artificial data. Also a substantial proportion of the literature is based on field observations (29%) only. However, there is a sincere lack of field and lab experiments (less than 10% respectively).

Due to the large amount of modelling studies, a large proportion of literature (68%) examines long-term processes for much more than ten years. Field observations or field experiments were mainly short-term, not exceeding three years (24%). Studies with a medium-term duration (more than three and less than ten years) make up the rest of the analysed articles (8%).

These methodological gaps demonstrate the need for long-term and usually very expensive field experimentation plans. A lack of empirical data becomes apparent here.

Conclusions

Climate change influences all parts of applied ecology and nature conservation. However, there are still lots of knowledge gaps concerning the impacts of global climate change on organisms, communities and biotopes. Geographic bias, a lack of long-term experiments and observations as well as a narrow focus on specific taxonomic groups and ecosystems constrain our possibilities to develop adaptation strategies on regional, national and global levels. Here, we provide an analysis of research demands and challenges for adapting nature conservation to the likely consequences of climatic changes, not only in temperature and precipitation regimes.

Acknowledgements

The authors thank the Federal Agency of Nature Conservation in Germany for funding this work (FKZ 3508 85 0600) and Sarah Gwillym for providing language help.

References

Araújo MB, Luoto M (2007) The importance of biotic interactions for modelling species distributions under climate change. Glob Ecol Biogeogr 16(6):743–753

Araújo MB, Pearson RG, Thuiller W, Erhard M (2005) Validation of species-climate impact models under climate change. Glob Change Biol 11(9):1504–1513

Beaumont LJ, Hughes L, Pitman AJ (2008) Why is the choice of future climate scenarios for species distribution modelling important? Ecol Lett 11(11):1135–1146

Benítez-Gilabert M, Alvarez-Cobelas M, Angeler DG (2010) Effects of climatic change on stream water quality in Spain. Clim Chang 103:339–352

Both C, Bouwhuis S, Lessels CM, Visser ME (2006) Climate change and population declines in a long-distance migratory bird. Nature 441:81–83

Bradshaw WE, Holzapfel CM (2006) Evolutionary Response to Rapid Climate Change. Science 312(5779):1477–1478

Branquart E, Verheyen K, Latham J (2008) Selection criteria of protected forest areas in Europe: The theory and the real world. Biol Conserv 141(11):2795–2806

Braschler B, Hill JK (2007) Role of larval host plants in the climate-driven range expansion of the butterfly Polygonia c-album. J Anim Ecol 76:415–423

Brooker RW, Travis JMJ, Clark EJ, Dytham C (2007) Modelling species' range shifts in a changing climate: The impacts of biotic interactions, dispersal distance and the rate of climate change. J Theor Biol 245(1):59–65

Cardoso PG, Raffaelli D, Lillebo AI, Verdelhos T, Pardal MA (2008) The impact of extreme flooding events and anthropogenic stressors on the macrobenthic communities' dynamics. Estuar Coast Shelf S 76(3):553–565

Council Directive 92/43/EEC (1992) Council Directive 92/43/EEC of 21 May 1992 on the conservation of natural habitats and of wild fauna and flora

Dullinger S, Dirnbock T, Grabherr G (2004) Modelling climate change-driven treeline shifts: relative effects of temperature increase, dispersal and invasibility. J Ecol 92(2):241–252

Ehlers A, Worm B, Reusch TBH (2008) Importance of genetic diversity in eelgrass Zostera marina for its resilience to global warming. Mar Ecol-Prog Ser 355:1–7

Engelkes T, Morriën E, Verhoeven KJF, Bezemer TM, Biere A, Harvey JA, McIntyre LM, Tamis WLM, van der Putten WH (2008) Successful range-expanding plants experience less above-ground and below-ground enemy impact. Nature 456(18):946–948

European Topic Centre on Biological Diversity (ETC/BD) (2008) Article 17 Technical Report (2001-2006). Annex J - Some specific analysis on conservation status

Fazey I, Fischer J, Lindenmayer DB (2005) Who does all the research in conservation biology? Biodivers Conserv 14:917–934

Feuchtmayr H, Moran R, Hatton K, Connor L, Heyes T, Moss B, Harvey I, Atkinson D (2009) Global warming and eutrophication: effects on water chemistry and autotrophic communities in experimental hypertrophic shallow lake mesocosms. J Appl Ecol 46(3):713–723

Fronzek S, Luoto M, Carter TR (2006) Potential effect of climate change on the distribution of palsa mires in subarctic Fennoscandia. Clim Res 32:1–12

Gaston AJ, Gilchrist HG, Hipfner JM (2005) Climate change, ice conditions and reproduction in an Arctic nesting marine bird: Brunnich's guillemot (Uria lomvia L.). J Anim Ecol 74(5):832–841

Hannah L (2008) Protected Areas and Climate Change. Ann NY Acad Sci 1134:201–212

Hannah L, Midgley G, Andelman S, Araujo M, Hughes G, Martinez-Meyer E, Pearson R, Williams P (2007) Protected area needs in a changing climate. Front Ecol Environ 5(3):131–138

Harrison RD (2000) Repercussions of El Niño: drought causes extinction and the breakdown of mutualism in Borneo. Proc R Soc Lond B 267(1446):911–915

Hill JK, Hughes CL, Dytham C, Searle JB (2006) Genetic diversity in butterflies: interactive effects of habitat fragmentation and climate-driven range expansion. Biol Lett 2(1):152–154

Hoegh-Guldberg O, Hughes L, McIntyre S, Lindenmayer DB, Parmesan C, Possingham HP, Thomas CD (2008) Assisted Colonization and Rapid Climate Change. Science 321(5887):345–346

Houlton BZ, Sigman DM, Schuur EAG, Hedin LO (2007) A climate-driven switch in plant nitrogen acquisition within tropical forest communities. Science 104(21):8902–8906

IPCC 2007. Summary for Policymakers. In: Parry ML, Canziani OF, Palutikof JP, van der Linden PJ and Hanson CE (Eds). Climate Change 2007: Impacts, Adaptation and Vulnerability. Contribution of Working Group II to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge, UK: Cambridge University Press.

Jentsch A, Beierkuhnlein C (2003) Global climate change and local distrubance regimes as interacting drivers for shifting altitudinal vegetation patterns. Erdkunde 57:216–231

Jentsch A, Beierkuhnlein C (2010) Simulating the future - Responses of ecosystems, key species and European provenances to expected climatic trends and events. Nova Acta Leopoldina 112:89–98

Jentsch A, Beyschlag W (2003) Vegetation ecology of dry acidic grasslands in the lowland area of Central europe. Flora 198(1):3–25

Jentsch A, Kreyling J, Beierkuhnlein C (2007) A new generation of climate-change experiments: events, not trends. Front Ecol Environ 5(7):365–374

Jentsch A, Kreyling J, Boettcher-Treschkow J, Beierkuhnlein C (2009) Beyond gradual warming: extreme weather events alter flower phenology of European grassland and heath species. Glob Chang Biol 15(4):837–849

Jiguet F, Devictor V, Ottvall R, van Turnhout C, van der Jeugd H, Lindström Å (2010) Bird population trends are linearly affected by climate change along species thermal ranges. Proc R Soc Lond B. doi:10.1098/rspb.2010.0796

Jump AS, Marchant R, Peñuelas J (2009) Environmental change and the option value of genetic diversity. Trends Plant Sci 14(1):51–58

Klanderud K, Totland Ø (2005) Simulated climate change altered dominance hierarchies and diversity of an alpine biodiversity hotspot. Ecology 86(8):2047–2054

Körner C, Basler D (2010) Phenology Under Global Warming. Science 327:1461–1462

Kreyling J, Beierkuhnlein C, Pritsch K, Radovski M, Schloter M, Wöllecke J, Jentsch A (2008a) Soil biotic processes remain surprisingly stable in face of 100-year extreme weather events in experimental grassland and heath. Plant Soil 308:175–188

Kreyling J, Ellis L, Beierkuhnlein C, Jentsch A (2008b) Biotic resistance and fluctuating resources are additive in determining invasibility of grassland and heath communities exposed to extreme weather events. Oikos 117:1524–1554

Lawler JJ (2009) Climate Change Adaptation Strategies for Resource Management and Conservation Planning. Ann NY Acad Sci 1162:79–98

le Roux PC, McGeoch MA (2008) Rapid range expansion and community reorganization in response to warming. Glob Chang Biol 14:2950–2962

Loarie SR, Duffy PB, Hamilton H, Asner GP, Field CB, Ackerly DD (2009) The velocity of climate change. Nature 462:1052–1055

Marshall E, Randhir T (2008) Effect of climate change on watershed system: a regional analysis. Clim Chang 89(3-4):263–280

Mastrandrea MD, Heller NE, Root TL, Schneider SH (2010) Bridging the gap: linking climate-impacts research with adaptation planning and management. Clim Chang 100:87–101

McClean CJ, Doswald N, Küper W, Sommer JH, Barnard P, Lovett JC (2006) Potential impacts of climate change on Sub-Saharan African plant priority area selection. Divers Distrib 12(6):645–655

McLachlan JS, Hellmann JJ, Schwartz MW (2007) A Framework for Debate of Assisted Migration in an Era of Climate Change. Conserv Biol 21(2):297–302

Mendelsohn R, Dinar A (2009) Land Use and Climate Change Interactions. Ann Rev Resour Econ 1:309–332

Menéndez R, González-Megías A, Lewis O, Shaw MR, Thomas CD (2008) Escape from natural enemies during climate-driven range expansion: a case study. Ecol Entomol 33(3):413–421

Millar CI, Stephenson NL, Stephens SL (2007) Climate change and forests of the future:managing in the face of uncertainty. Ecol Appl 17(8):2145–2151

Mirzae H, Kreyling J, Hussain Z, Li Y, Tenhunen J, Beierkuhnlein C, Jentsch A (2008) One extreme drought event enhances subsequent carbon uptake in experimental grassland communities. J Plant Nutr Soil Sci 171:681–689

Moss RH, Jae A. Edmonds JA, Hibbard KA, Manning MR, Rose SK, van Vuuren DP, Carter TR, Emori S, Kainuma M, Kram T, Meehl GA, Mitchell JFB, Nakicenovic N, Riahi K, Smith SJ, Stouffer RJ, Thomson AM, Weyant JP, Wilbanks TJ (2010) The next generation of scenarios for climate change research and assessment. Nature 463:747–756

Myers N, Mittermeier RA, Mittermeier CG, da Fonseca GAB, Kent J (2000) Biodiversity hotspots for conservation priorities. Nature 403:853–858

Parmesan C (2007) Influences of species, latitudes and methodologies on estimates of phenological response to global warming. Glob Chang Biol 13(9):1860–1872

Platts PJ, McClean CJ, Lovett JC, Marchant R (2008) Predicting tree distributions in an East African biodiversity hotspot: model selection, data bias and envelope uncertainty. Ecol Model 218(1-2):121–134

Popy S, Bordignon L, Prodon R (2010) A weak upward elevational shift in the distributions of breeding birds in the Italian Alps. J Biogeogr 37:57–67

Pyke CR, Fischer DT (2005) Selection of bioclimatically representative biological reserve systems under climate change. Biol Conserv 121(3):429–441

Rahel FJ, Bierwagen B, Taniguchi Y (2008) Managing Aquatic Species of Conservation Concern in the Face of Climate Change and Invasive Species. Conserv Biol 22(3):551–561

Rahel FJ, Olden JD (2008) Assessing the Effects of Climate Change on Aquatic Invasive Species. Conserv Biol 22(3):521–533

Riutta T, Laine J, Tuittila E- (2007) Sensitivity of CO2 Exchange of Fen Ecosystem Components to Water Level Variation. Ecosystems 10:718–733

Schweiger O, Settele J, Kudrna O, Klotz S, Kühn I (2008) Climate change can cause spatial mismatch of trophically interacting species. Ecology 89(12):3472–3479

Sork VL, Davis FW, Westfall R, Flint A, Ikegami M, Wang H, Grivet D (2010) Gene movement and genetic association with regional climate gradients in California valley oak (Quercus lobata Née) in the face of climate change. Mol Ecol 19:3806–3823

Sutherland WJ, Adams WM, Aronson RB, Aveling R, Blackburn TM, Broad S, Ceballos G, Côté IM, Cowling RM, da Fonseca GAB, Dinerstein E, Ferraro PJ, Fleishman E, Gascon C, Hunter Jr. M, Hutton J, Kareiva P, Kuria A, MacDonald DW, MacKinnon K, Madgwick FJ, Mascia MB, McNeely J, Milner-Gulland EJ, Moon S, Morley CG, Nelson S, Osborn D, Pai M, Parsons ECM, Peck LS, Possingham H, Prior SV, Pullin AS, Rands MRW, Ranganathan J, Redford KH, Rodriguez JP, Seymour F, Sobel J, Sodhi NS, Stott A, Vance-Borland K, Watkinson AR (2009) One Hundred Questions of Importance to the Conservation of Global Biological Diversity. Conserv Biol 23:557–567

van Grunsven RHA, van der Putten WH, Bezemer TM, Tamis WLM, Berendse F, Veenendaal EM (2007) Reduced plant–soil feedback of plant species expanding their range as compared to natives. J Ecol 95:1050–1057

van Rensburg BJ, Erasmus BF, van Jaarsveld AS, Gaston KJ, Chown SL (2004) Conservation during times of change: correlations between birds, climate and people in South Africa. S Afr J Sci 100(5-6):266–272

Vos CC, Berry P, Opdam P, Baveco H, Nijhof B, O'Hanley J, Bell C, Kuipers H (2008) Adapting landscapes to climate change: examples of climate-proof ecosystem networks and priority adaptation zones. J Appl Ecol 45:1722–1731

Walther GR, Roques A, Hulme P, Sykes MT, Pyšek P, Kühn I, Zobel M, Bacher S, Botta-Dukát Z, Bugmann H, Czúcz B, Dauber J, Hickler T, Jarošík V, Kenis M, Klotz S, Minchin D, Moora M, Nentwig W, Ott J, Panov VE, Reineking B, Robinet C, Semenchenko V, Solarz W, Thuiller W, Vilá M, Vohland K, Settele J (2009) Alien species in a warmer world: risks and opportunities. Trends Ecol Evol 24:686–693

Williams P, Hannah L, Andelman S, Midgley G, Araújo M, Hughes G, Manne L, Martinez-Meyer E, Pearson R (2005) Planning for Climate Change: Identifying Minimum-Dispersal Corridors for the Cape Proteaceae. Conserv Biol 19(4):1063–1074

Willis SG, Hill JK, Thomas CD, Roy DB, Fox R, Blakeley DS, Huntley B (2009) Assisted colonization in a changing climate: a test-study using two UK butterflies. Conserv Lett 2(1):46–52

Article 2

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

Torsten Bittner, Anja Jaeschke, Björn Reineking, Carl Beierkuhnlein

printed in Journal of Vegetation Science 2011 22(4) 699–710
submitted 2010-06-15
accepted 2011-01-30

Abstract

Question: Habitats are characterised by their plant species composition. Therefore, climate change impacts on habitats can be assessed by two complementary statistical approaches: Either directly, 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 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 the current and potential future distribution 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.

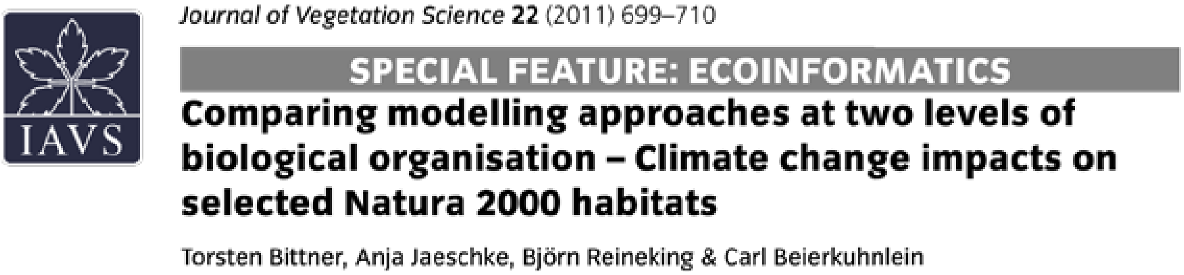
In the direct habitat approach, both model algorithms have high discriminatory performance on test data and are well calibrated. In the indirect species approach, only GLM shows high model performance; RF models are overfitted.

Projections of occurrence probabilities differ more strongly between model approaches ('direct' vs. 'indirect') than between model algorithms (GLM vs. RF).

Conclusions: Habitats are complex entities. Because of their dynamic nature, particularly in the face of climate change, we suggest to model 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



Journal of Vegetation Science 22 (2011) 699–710

SPECIAL FEATURE: ECOINFORMATICS

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

Torsten Bittner, Anja Jaeschke, Björn Reineking & Carl Beierkuhnlein

Torsten Bittner[1,2], Anja Jaeschke[1,2], Björn Reineking[2], Carl Beierkuhnlein[1]

[1]Biogeography, BayCEER, University of Bayreuth, 95440 Bayreuth, Germany
[2]Biogeographical Modelling, BayCEER, University of Bayreuth, 95440 Bayreuth, Germany

Introduction

Despite intensive research efforts, large uncertainties remain about the effects of rapid climate change on plant and animal populations, as well as 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 (Bruelheide 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 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 definitions 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 characterised 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. 2011). Species may react differentially to environmental changes (Janssen et al. 2011 in this special feature). 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 projection 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 datasets, 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 similar 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. Secondly, 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 characterised 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; Jalas et al. 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.

Material and 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 Alysso alyssoidis-Sedion albi (European Commission 2007). Habitats of type 6120 are characterised 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 valesiacae) 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 (semi-natural) Mesobromion grasslands with Bromus erectus; the latter are characterised 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 they correspond to a deteriorated stage of draining 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 metres) 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 of the year 2007 pursuant to Article 17 of the Habitats Directive. They are available for 25 EU countries in different spatial resolutions (Fig. 1).

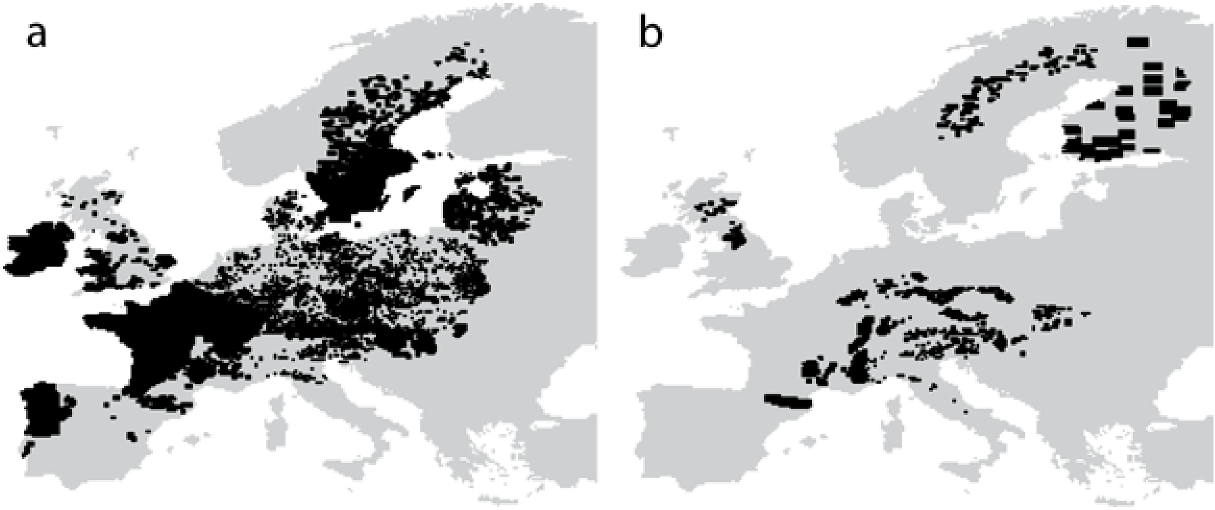


Fig. 1: Examples of distribution data within the EU (EU25) from the Article 17 Report (Source): (a) Distribution of 6410 Molinia meadows on calcareous, peaty or clayey-silt-laden soils (Molinion caeruleae) and (b) 6520 Mountain hay meadows.

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; Jalas et al. 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 50 km 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. Firstly, we selected species that are specified as characteristic species of a habitat type by the European Commission (2007) and Ssymank (1998) and that are available in the AFE (Tab. 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 (Modelling Design below).

Tab. 1: Characteristic plant species for the five selected habitat types defined by the European Commission (2007) and Ssymank (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 *Alysso-Sedion albi*	*Alyssum montanum*, *Alyssum alyssoides*, *Dianthus gratianopolitanus*, *Holosteum umbellatum*, *Jovibarba globifera*, *Petrorhagia prolifera*, *Potentilla heptaphylla*, *Sanguisorba minor, Saxifraga tridactylites*, *Sedum album*, *Sedum sexangulare*, *Sedum acre*
6120 * Xeric sand calcareous grasslands	*Alyssum montanum*, *Cardaminopsis arenosa*, *Cerastium arvense*, *Dianthus arenarius*, *Dianthus deltoides*, *Gypsophila fastigiata*, *Herniaria glabra*, *Petrorhagia prolifera*, *Potentilla argentea*, *Sedum reflexum*, *Silene chlorantha*, *Silene otites*
6210 Semi-natural dry grasslands and scrubland facies on calcareous substrates (*Festuco-Brometalia*)	*Agrimonia eupatoria*, *Arenaria serpyllifolia*, *Arabis hirsuta agg.*, *Cerastium brachypetalum*, *Cerastium glutinosum*, *Cerastium pumilum*, *Dianthus armeria, Dianthus carthusianorum*, *Dianthus deltoides*, *Erophila verna*, *Filipendula vulgaris*, *Fragaria viridis*, *Petrorhagia prolifera*, *Potentilla inclinata*, *Potentilla rupestris*, *Potentilla argentea agg.*, *Potentilla heptaphylla*, *Potentilla tabernaemontani*, *Pulsatilla pratensis*, *Pulsatilla vulgaris*, *Ranunculus bulbosus*, *Sanguisorba minor ssp. minor*, *Silene vulgaris*, *Thalictrum minus*, *Thlaspi perfoliatum*
6410 Molinia meadows on calcareous, peaty or clayey-silt-laden soils (*Molinion caeruleae*)	*Cardamine pratensis*, *Dianthus superbus*, *Equisetum palustre*, *Geum rivale*, *Ophioglossum vulgatum*, *Parnassia palustris*, *Potentilla alba*, *Potentilla erecta*, *Ranunculus nemorosus*, *Ranunculus polyanthemos*, *Salix repens*, *Sanguisorba officinalis*, *Silene flos-cuculi*, *Thalictrum flavum*, *Trollius europaeus*
6520 Mountain hay meadows	*Anemone nemorosa*, *Dianthus deltoides*, *Potentilla erecta*, *Ranunculus nemorosus*, *Saxifraga granulata*, *Silene dioica*, *Silene flos-cuculi*, *Thlaspi caerulescens*, *Trollius europaeus*

Climate data

Current and potential 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 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 characterising 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 characterising species instead of climatic variables. Secondly, we modelled 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 the habitat distribution that uses species presence as explanatory variable.

In addition, we used two different modelling algorithms, the parametric generalised 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 pairwise 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, respectively. Subsequently, a stepwise selection in the GLM model of the retaining variables was based on BIC (Bayesian information criterion). Using the OOB error (out of bag error rate) as minimisation 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.

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); secondly, 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); thirdly, 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 fourthly, 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 characterising plant species. A full dispersal scenario can give 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 ranges.

All analyses were performed with R 2.10.1 (R Development Core Team 2009). 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, Harrell 2009). Variable selection in the RF Model was implemented with the varSelRF package version 0.7-1 (Ramon Diaz-Uriarte 2009). Spatial data were processed with ArcMap 9.3.1.

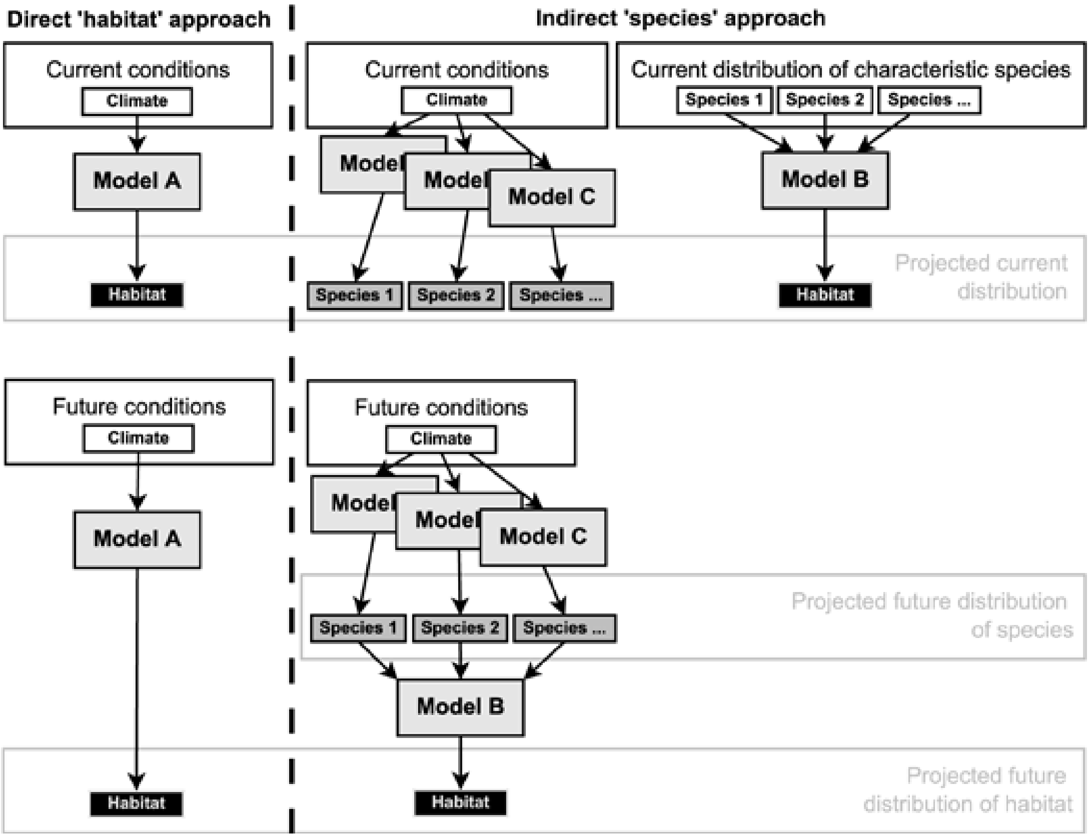


Fig. 2: Modelling framework illustrating the direct 'habitat' and indirect 'species' approach. In both cases, the habitat is projected in its current and in a potential future distribution. Black boxes indicate results, white boxes the input data, light grey the model and dark grey intermediate results.

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 (Tab. 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 (Tab. 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, S8-S9). Maps for the other habitat types are provided in the supplement (Fig. S2-S11).

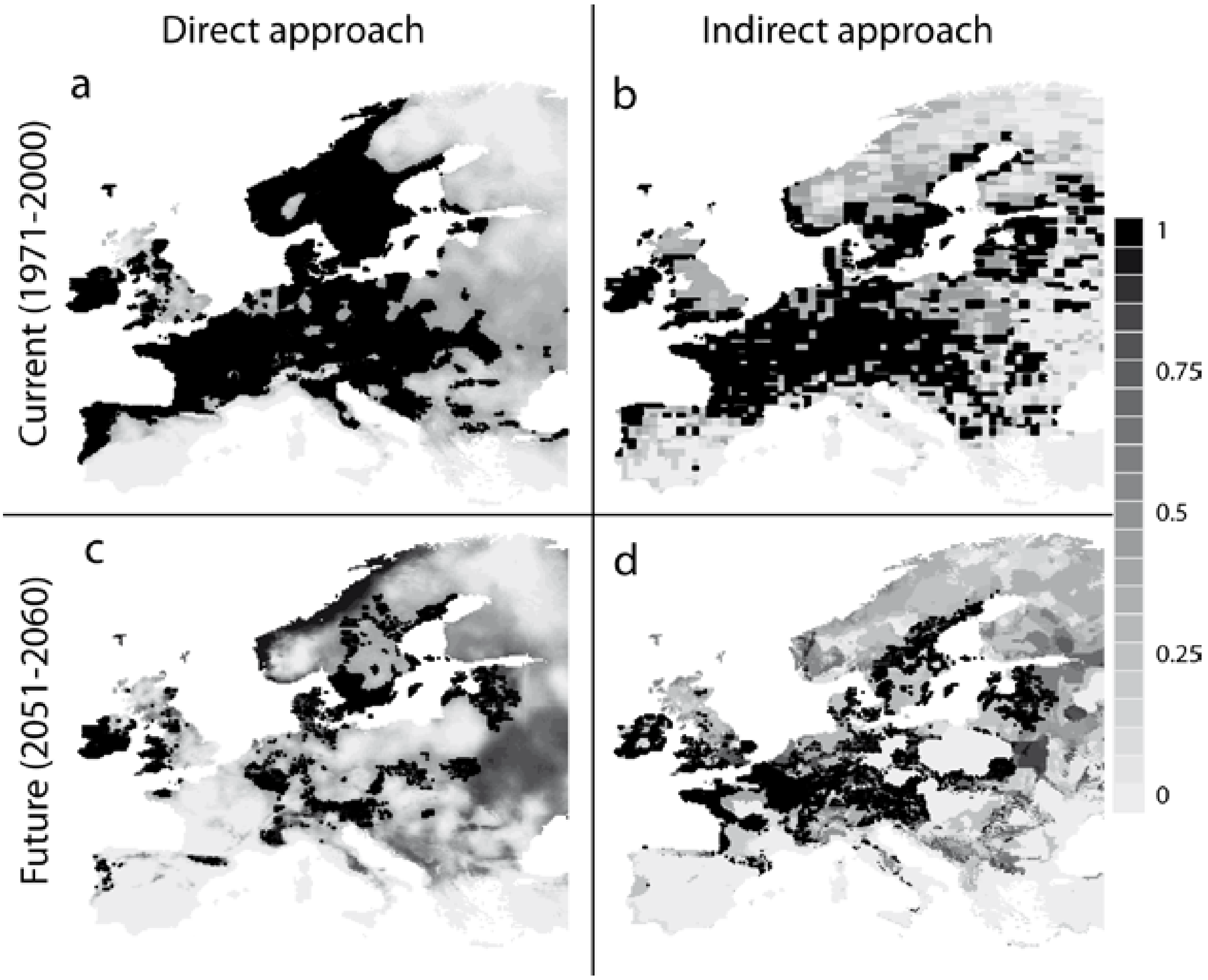


Fig. 3: Modelled occurrence probabilities of Molina meadows on chalk and clay (6410), based on GLM. The coarse grained pattern in b) results from the 50 km x 50 km resolution of species distributions in the Atlas Florae Europaeae. The future climate scenario is A2 based on the HadCM3 climate model. Future 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.

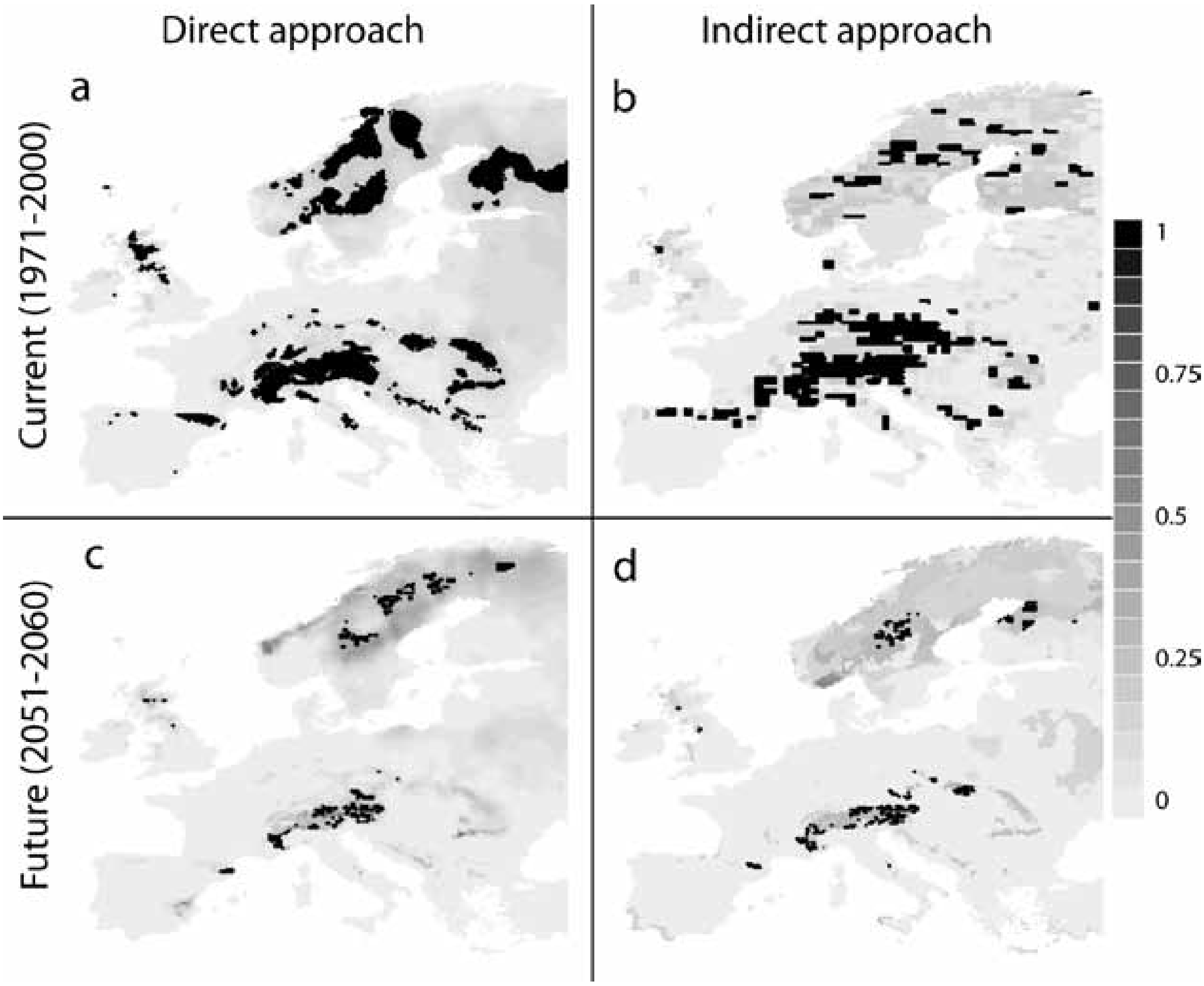


Fig. 4: Modelled occurrence probabilities of Mountain hay meadows (6520), based on GLM. The coarse grained pattern in b) results from the 50 km x 50 km resolution of species distributions in the Atlas Florae Europaeae. The future climate scenario is A2 based on the HadCM3 climate model. Future scenario 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.

Tab. 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, random forest). The future climate scenario is A2 based on the HadCM3 climate model.

		Direct 'habitat' approach				**Indirect 'species' approach**			
		GLM		**Random Forest**		**GLM**		**Random Forest**	
Habitat type	Current distribution (km^2)	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	/	/

Modelling

Overall, the direct 'habitat' approach results in models with higher performance as measured by three out of four criteria (Tab. 3): Models of the direct 'habitat' approach have a mean AUC of 0.90 with a standard deviation of ± 0.06, vs. 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, the indirect 'species' approach a mean slope of 0.78 ± 0.28, indicating overfitting, and a lower mean R^2 (0.40 ± 0.16).

Tab. 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 R^2 for the test data (30% random selection). For the habitat types 6110 and 6520, the random forest 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% ± 25) under the assumption of no dispersal possibilities. With unrestricted dispersal, this approach projects a gain in distribution area of about 60% ± 31. The indirect 'species' approach results in a similar projected loss of distribution area (-67% ± 20) under the no dispersal scenario. In contrast, it projects a lower gain in distribution area (14% ± 13) than the direct 'habitat' approach with unrestricted dispersal (Tab. 2).

In the direct 'habitat' approach the two modelling algorithms GLM and RF generate different but not dissimilar results (Tab. 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. (Fig. 3a, Fig. 4a, Fig. S2a-S11a). The same situation holds for the projected potential future distribution; RF provides generally more extreme predictions (Fig. 3c, Fig. 4c, Fig. S2c-S11c).

In the species based (indirect) approach, the two modelling algorithms differ more than in the direct 'habitat' approach. Especially the quality measures distinguish both 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 overprediction by the RF model. Apart from that, the maps of the modelled 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 Alysso-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).

Tab. 4: Pearson correlation of predicted probabilities of occurrence for habitat types, between the two approaches (direct vs. indirect) and the two algorithms (GLM vs. RF).

Habitat type	**GLM direct vs GLM 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	0.54	-	0.52	-	0.60	-	0.60	-
Mean ± 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 2051-60 under an A2 climate scenario and unrestricted dispersal, independent of modelling approach and modelling algorithm. Habitat type 6520 seems to be a loser of 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 *Alysso-Sedion albi*) and 6520 (Mountain hay meadows) under the no dispersal scenario could result in a 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 of the shifts of whole habitats. However, modelling under the assumption of unrestricted dispersal can give hints on where to find future climatic suitable space.

Habitats are human constructs and, due to their multi-factorial nature, difficult to adequately capture in modelling approaches. Here, we apply that 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 one may overrule the certain 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 conditions some of the characteristic plant species may lose and some may gain distribution area, which can lead in summary 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, some are even more restricted. Throughout Europe, not all characteristic plants of one habitat type appear at all 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 habitat types.

Habitat type 6520 (Mountain hay meadows) has a very restricted distribution, although its characterising plant species are distributed widely in Europe. The variable selection chose only two of the nine characteristic plant species, which were obviously too few for further calculations. It can be suggested that these plants are not suitable enough to represent this habitat type, at least for the random forest model. The same applies to habitat type 6110 (Rupicolous calcareous or basophilic grasslands of the *Alysso-Sedion albi*). In addition, random forest 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 performs mostly 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 characterised by specific species compositions and climatic demands, but depend on further abiotic conditions like 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 allow better modelling results.

The indirect modelling approach depends on 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 by appropriate management.

An analysis of protected areas concerning their vulnerability to climate change seems necessary. By assessing the impact factors, like climatic, physical and biological variables, the sensitivity of an ecosystem and its adaptive capacity, risks and opportunities of a certain area can be derived (Lindner et al. 2010). Together with the modelling of potential impacts on habitats, such an assessment supplies first 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 in this special feature). Modelling results could be also integrated in valuation methods like 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 to model 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 organisational levels is a promising area of future research.

Acknowledgements

The authors acknowledge funding by the Federal Agency for Nature Conservation Germany (FKZ 3508 85 0600). We would also like to thank Robert K. Peet and two anonymous reviewers for their comments on an earlier version of this work.

References

Allred, B.W., Fuhlendorf, S.D., Monaco, T.A. & Will, R.E. 2010. Morphological and physiological traits in the success of the invasive plant Lespedeza cuneata. Biological Invasions 12: 739–749.

Bergmann, J., Pompe, S., Ohlemüller, R., Freiberg, M., Klotz, S. & Kühn, I. 2010. The Iberian Peninsula as a potential source for the plant species pool in Germany under projected climate change. Plant Ecology 207: 191–201.

Bruelheide, H. 2003. Translocation of a montane meadow to simulate the potential impact of climate change. Applied Vegetation Science 6: 23–34.

Chiarucci, A., Araujo, M.B., Decocq, G., Beierkuhnlein, C., Fernandez-Palacios, J.M. 2011. The concept of Potential Natural Vegetation: an epitaph? Journal of Vegetation Science 22, in press.

Diaz-Uriarte, R. 2009. varSelRF: Variable selection using random forests. varSelRF: Variable selection using random forests. URL: http://ligarto.org/rdiaz/Software/Software.html.

Dormann, C.F., Purschke, O., Márquez, J.R.G., Lautenbach, S. & Schröder, B. 2008. Components of uncertainty in species distribution analysis: A case study of the Great Grey Shrike. Ecology 89: 3371–3386.

EIONET 2009. Central Data Repository(CDR). URL: http://cdr.eionet.europa.eu/.

Elith, J. & Leathwick, J.R. 2009. Species Distribution Models: Ecological Explanation and Prediction Across Space and Time. Annual Review of Ecology Evolution and Systematics 40: 677–697.

European Commission, D.E. 2007. Interpretation Manual of European Union Habitats. EUR 27, Brussels.

European Commission, D.E. 2009. Report from the Commission to the Council and the European Parliament Composite - Report on the Conservation Status of Habitat Types and Species as required under Article 17 of the Habitats Directive.

Falk, W. & Mellert, K.H. 2011. Species Distribution Models as a tool for forest managment planing under climate change. Journal of Vegetation Science (in this special feature).

Ferrier, S. & Guisan, A. 2006. Spatial modelling of biodiversity at the community level. Journal of Applied Ecology 43: 393–404.

Ferrier, S., Drielsma, M., Manion, G. & Watson, G. 2002. Extended statistical approaches to modelling spatial pattern in biodiversity in northeast New South Wales. II. Community-level modelling. Biodiversity and Conservation 11: 2309–2338.

Guisan, A. & Zimmermann, N.E. 2000. Predictive habitat distribution models in ecology. Ecological Modelling 135: 147–186.

Harrell, F.R. JR 2009. Design: Design Package. URL: http://CRAN.R-project.org/package=Design.

Jalas, J. & Suominen, J. (eds.) 1972-1994. Atlas Florae Europaeae. Distribution of vascular plants in Europe. vol 1-10. The Committee for Mapping the Flora of Europe and Societas Biologica Fennica Vanamo, Helsinki.

Jalas, J., Suominen, J. & Lampinen, R. (eds.) 1996. Atlas Florae Europaeae. Distribution of vascular plants in Europe. vol 11. The Committee for Mapping the Flora of Europe and Societas Biologica Fennica Vanamo, Helsinki.

Jalas, J., Suominen, J., Lampinen, R. & Kurtto, A. (eds.) 1999. Atlas Florae Europaeae. Distribution of vascular plants in Europe. vol 12. The Committee for Mapping the Flora of Europe and Societas Biologica Fennica Vanamo, Helsinki.

Janssen, J., Haveman, R., Hennekens, S.M., Ozinga, W.A. & Joop, H.J. 2011. Changes in the floristic composition of plant communities in relation to climate change. Journal of Vegetation Science (in this special feature).

Jentsch, A. & Beierkuhnlein, C. 2008. Research frontiers in climate change: effects of extreme meteorological events on ecosystems. CR Geoscience 340: 621-628.

Jones, C.C. & del Moral, R. 2009. Dispersal and establishment both limit colonization during primary succession on a glacier foreland. Plant Ecology 204: 217–230.

Kontula, T. & Raunio, A. 2009. New method and criteria for national assessments of threatened habitat types. Biodiversity and Conservation 18: 3861–3876.

Kreyling, J., Ellis, L., Beierkuhnlein, C. & Jentsch, A. 2008. Biotic resistance and fluctuating resources are additive in determining invasibility of grassland and heath communities exposed to extreme weather events. Oikos 117: 1524–1554.

Kurtto, A., Lampinen, R. & Junikka, L. (eds.) 2004. Atlas Florae Europaeae. Distribution of vascular plants in Europe. vol 13. The Committee for Mapping the Flora of Europe and Societas Biologica Fennica Vanamo, Helsinki.

le Roux, P.C. & McGeoch, M.A. 2008. Rapid range expansion and community reorganization in response to warming. Global Change Biology 14: 2950–2962.

Leathwick, J.R., Elith, J. & Hastie, T. 2006. Comparative performance of generalized additive models and multivariate adaptive regression splines for statistical modelling of species distributions. Predicting Species Distributions - Results from a Second Workshop on Advances in Predictive Species Distribution Models, held in Riederalp, Switzerland, 2004. Ecological Modelling 199: 188–196.

Liaw, A. & Wiener, M. 2002. Classification and Regression by randomForest. R News 2: 18–22.

Lindner, M., Maroschek, M., Netherer, S., Kremer, A., Barbati, A., Garcia-Gonzalo, J., Seidl, R., Delzon, S., Corona, P., Kolström, M., Lexer, M.J. & Marchetti, M. 2010. Climate change impacts, adaptive capacity, and vulnerability of European forest ecosystems. Forest Ecology and Management 259: 698–709.

Mitchell, T.D., Carter, T.R., Jones, P.D., Hulme, M. & New, M. 2004. A comprehensive set of high-resolution grids of monthly climate for Europe and the globe: the observed record (1901-2000) and 16 scenarios (2001-2100). Working Paper 55.

Mücher, C.A., Hennekens, S.M., Bunce, R.G.H., Schaminée, J.H.J. & Schaepman, M.E. 2009. Modelling the spatial distribution of Natura 2000 habitats across Europe. Landscape and Urban Planning 92: 148–159.

Petermann, J., Balzer, S., Ellwanger, G., Schröder, E. & Ssymank, A. 2007. Klimawandel - Herausforderung für das europaweite Schutzgebietssystem Natura 2000. Naturschutz und Biologische Vielfalt 46: 127–148.

Plassmann, K., Jones, M.L.M. & Edwards-Jones, G. 2010. Effects of long-term grazing management on sand dune vegetation of high conservation interest. Applied Vegetation Science 13: 100–112

R Development Core Team 2009. R: A Language and Environment for Statistical Computing. R: A Language and Environment for Statistical Computing. URL: http://www.R-project.org [R Foundation for Statistical Computing].

Reineking, B. & Schröder, B. 2006. Constrain to perform: Regularization of habitat models. Ecological Modelling 193: 675–690.

Riordan, E.C. & Rundel, P.W. 2009. Modelling the distribution of a threatened habitat: the California sage scrub. Journal of Biogeography 36: 2176–2188.

Seo, C., Thorne, J.H., Hannah, L. & Thuiller, W. 2009. Scale effects in species distribution models: implications for conservation planning under climate change. Biology Letters 5: 39–43.

Schaminée, J.H.J., Hennekens, S.M. & Ozinga, W.A. 2007. Use of the ecological information system SynBioSys for the analysis of large datasets. Journal of Vegetation Science 18: 463–470.

Settele, J., Hammen, V., Hulme, P., Karlson, U., Klotz, S., Kotarac, M., Kunin, W., Marion, G., O'Connor, M., Petanidou, T., Peterson, K., Potts, S., Pritchard, H., Pysek, P., Rounsevell, M., Spangenberg, J., Steffan-Dewenter, I., Sykes, M., Vighi, M., Zobel, M. & Kuhn, I. 2005. Alarm: Assessing Large-scale environmental Risks for biodiversity with tested Methods. GAIA - Ecological Perspectives for Science and Society 14: 69-72.

Soussana, J-F. & Lüscher, A. 2007. Temperate grasslands and global atmospheric change: a review. Grass and Forage Science 62: 127–134.

Spangenberg, J.H. 2007. Integrated scenarios for assessing biodiversity risks. Sustainable Development 15: 343–356.

Ssymank, A., Hauke, U., Rückriem, C. & Schröder, E. (eds.) 1998. Das europäische Schutzgebietssystem NATURA 2000. BfN-Handbuch zur Umsetzung der Fauna-Flora-Habitat-Richtlinie (92/43/EWG) und der Vogelschutzrichtlinie (79/409/EWG). BfN-Schr.-Vertrieb im Landwirtschaftsverl., Münster.

Swets, J.A. 1988. Measuring the accuracy of diagnostic systems. Science 240: 1285–1293.

Yee, T.W. & Mitchell, N.D. 1991. Generalized additive models in plant ecology. Journal of Vegetation Science 2: 587–602.

Supplemental figures

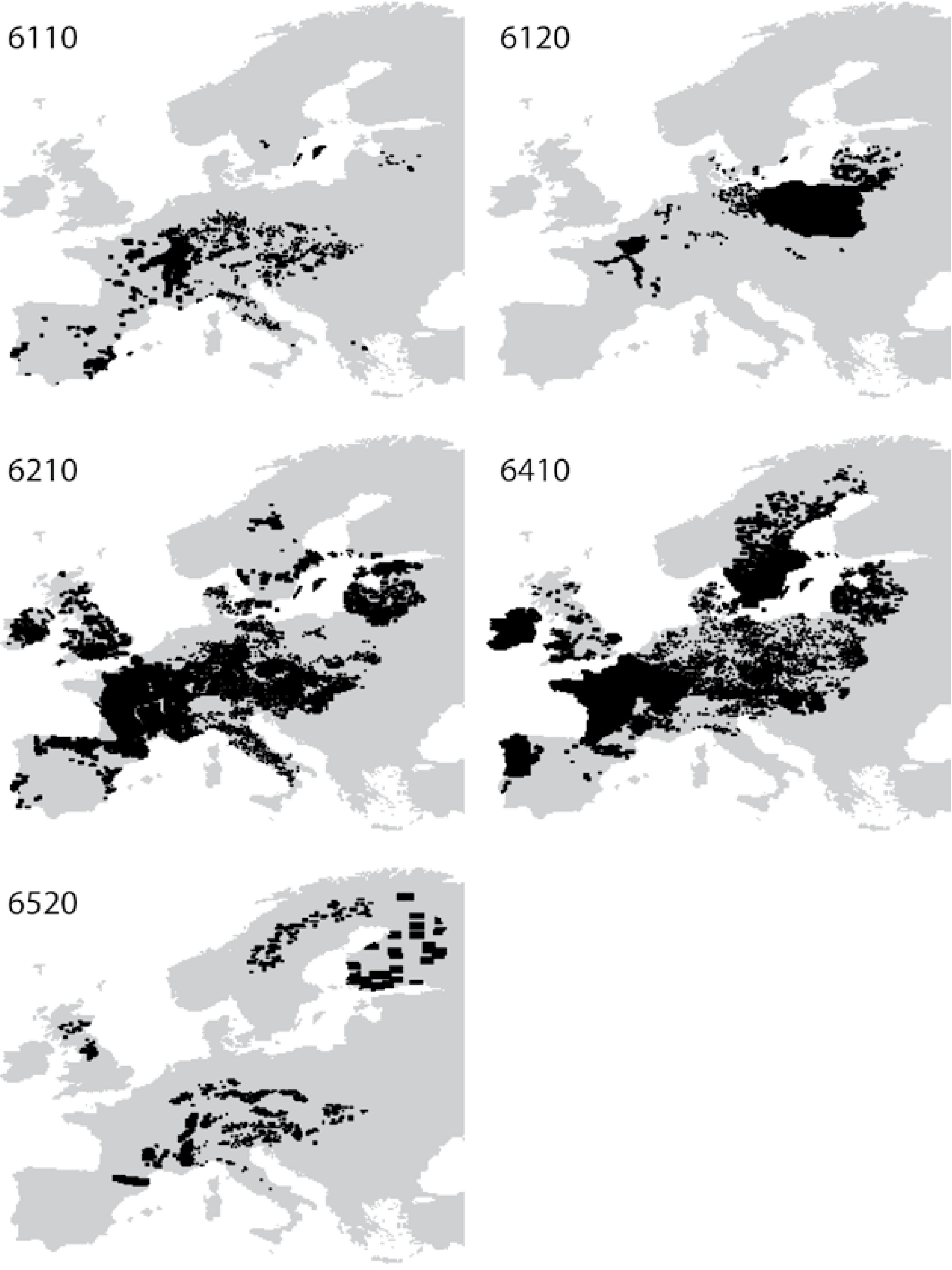


Fig. S1: Distribution data within the EU (EU25) from the Article 17 Report (Source): 6110 Rupicolous calcareous or basophilic grasslands of the Alysso-Sedion albi, 6120 Xeric sand calcareous grasslands, 6210 Semi-natural dry grasslands and scrubland facies on calcareous substrates (Festuco-Brometalia),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

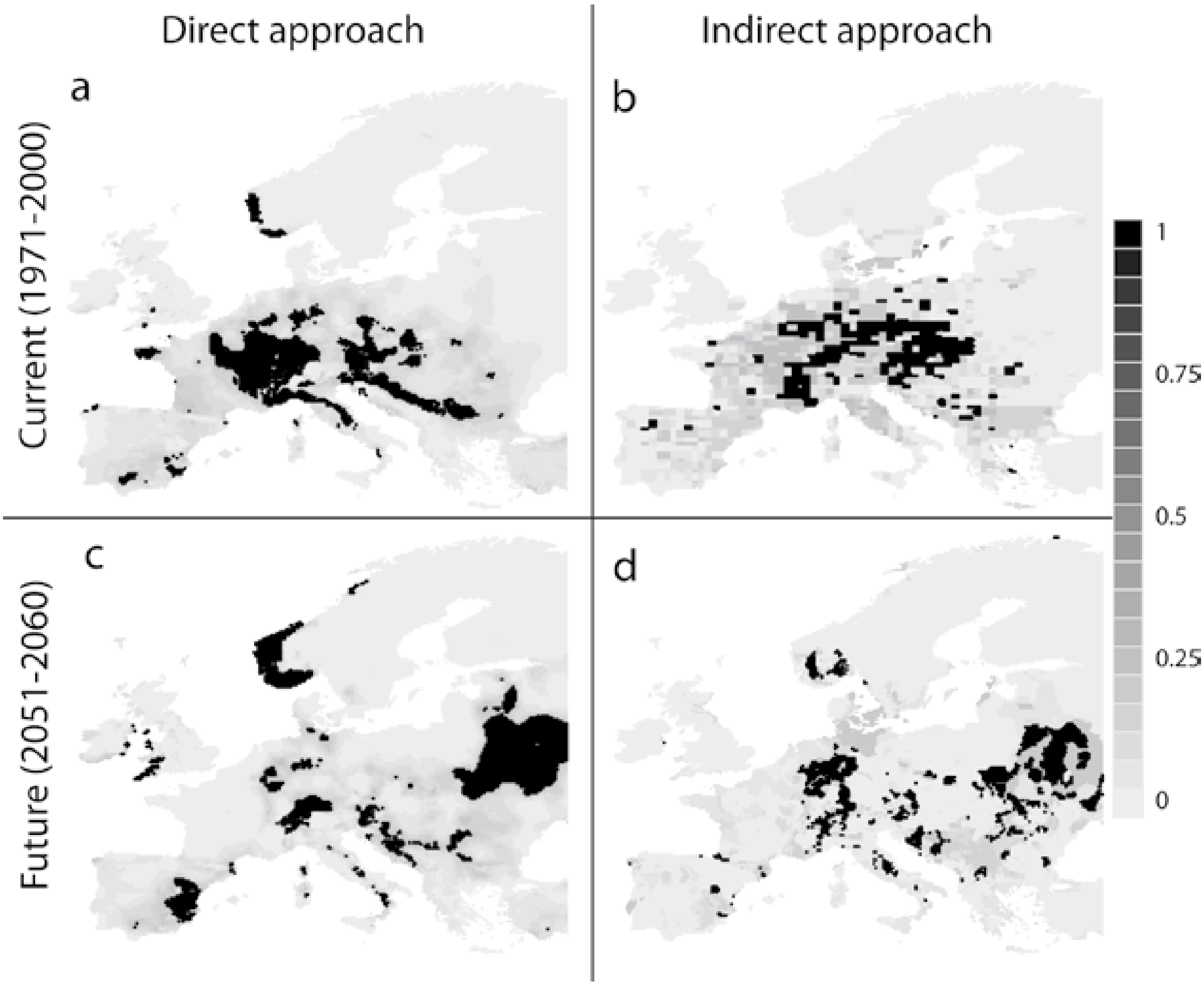


Fig. S2: Modelled occurrence probabilities of Rupicolous calcareous grasslands (6110), based on GLM. The coarse grained pattern in b) results from the 50 km x 50 km resolution of species distributions in the Atlas Florae Europaeae. The future climate scenario is A2 based on the HadCM3 climate model.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

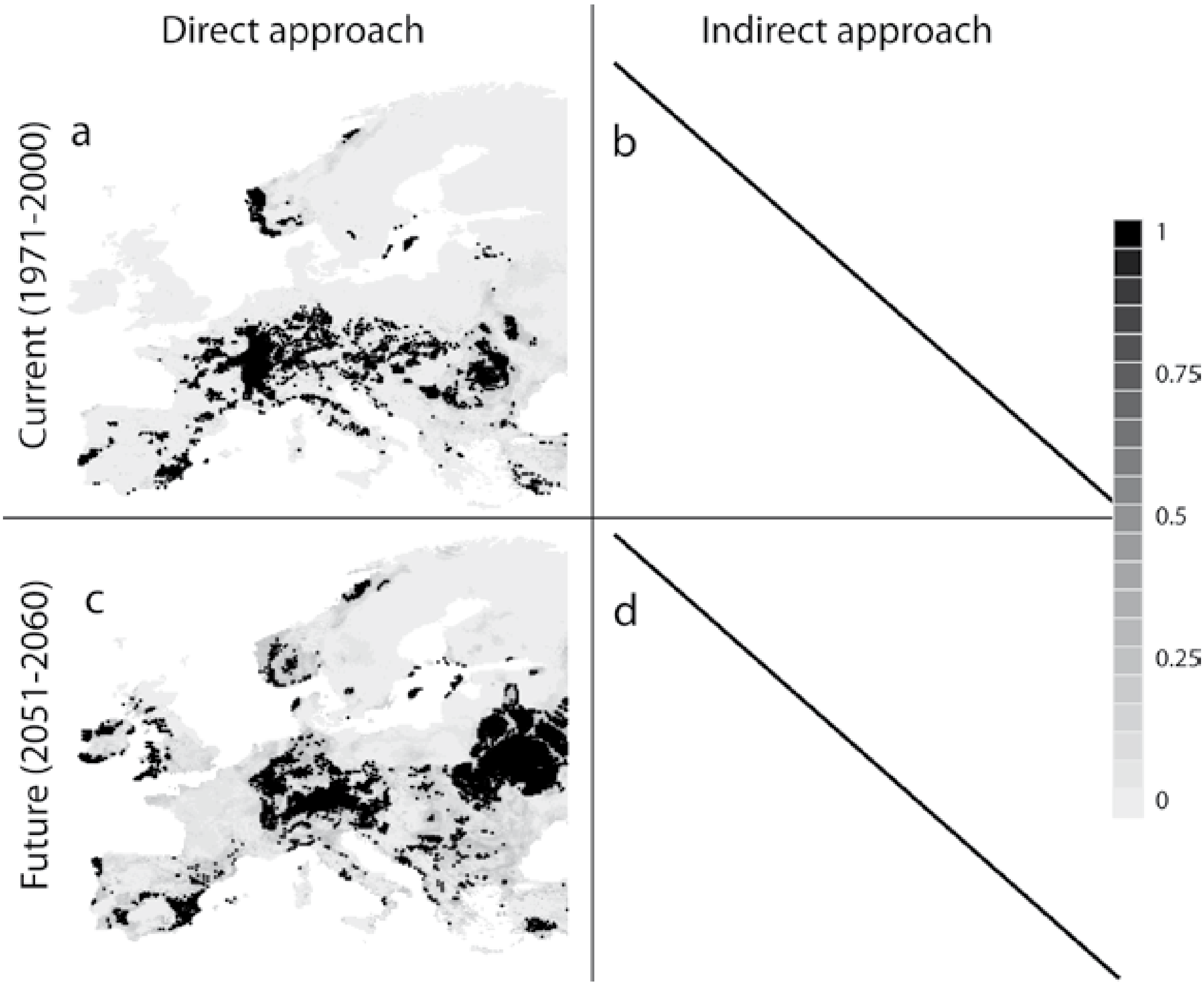


Fig. S3: Modelled occurrence probabilities of Rupicolous calcareous grasslands (6110), based on RF. The future climate scenario is A2 based on the HadCM3 climate model. Future scenario maps show full dispersal ability. Black dots indicate the modelled occurrence, with thresholds: a) 0.27, b) /, c) 0.32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

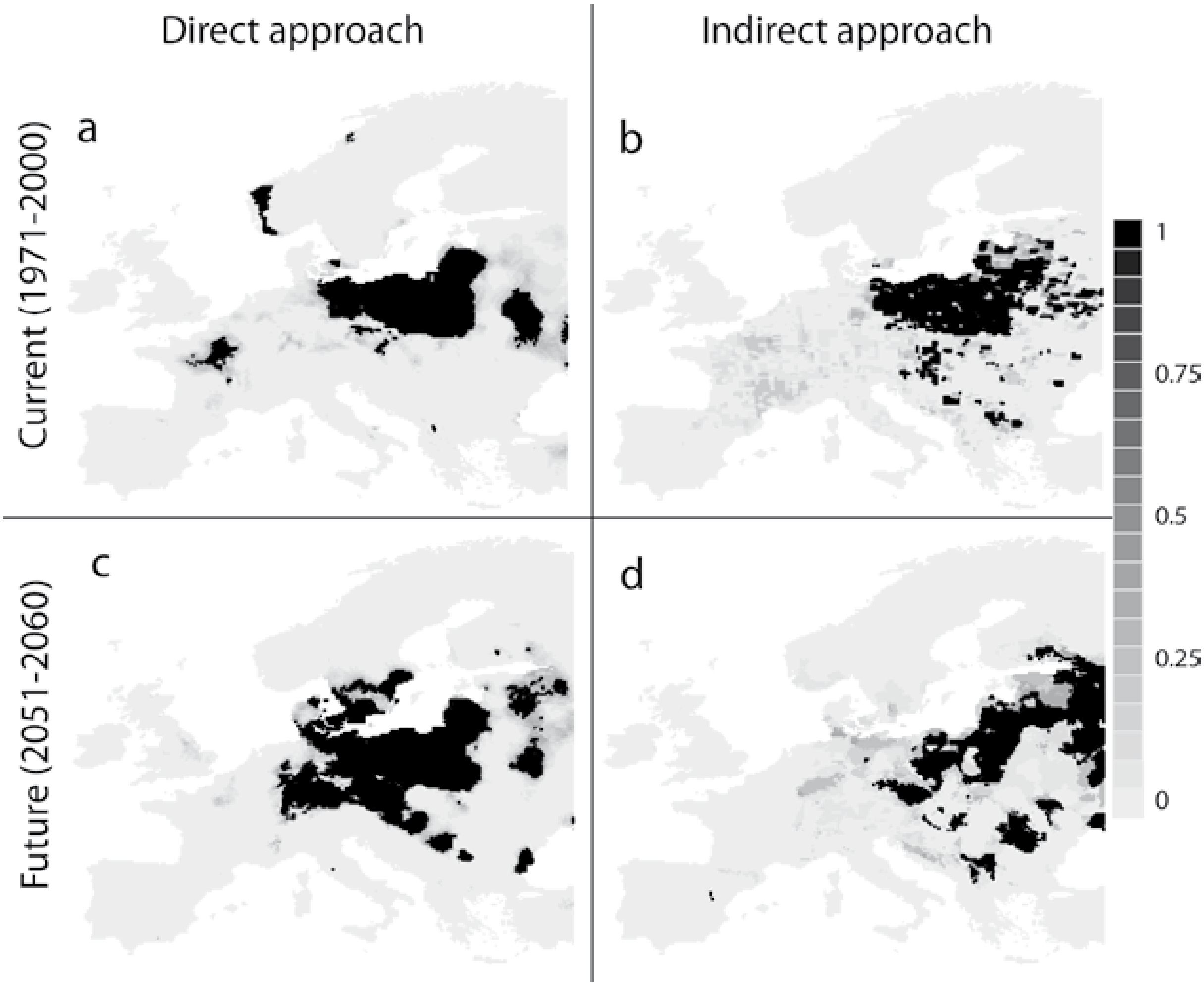


Fig. S4: Modelled occurrence probabilities of Xeric sand calcareous grasslands (6120), based on GLM. The coarse grained pattern in b) results from the 50 km x 50 km resolution of species distributions in the Atlas Florae Europaeae. The future climate scenario is A2 based on the HadCM3 climate model.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

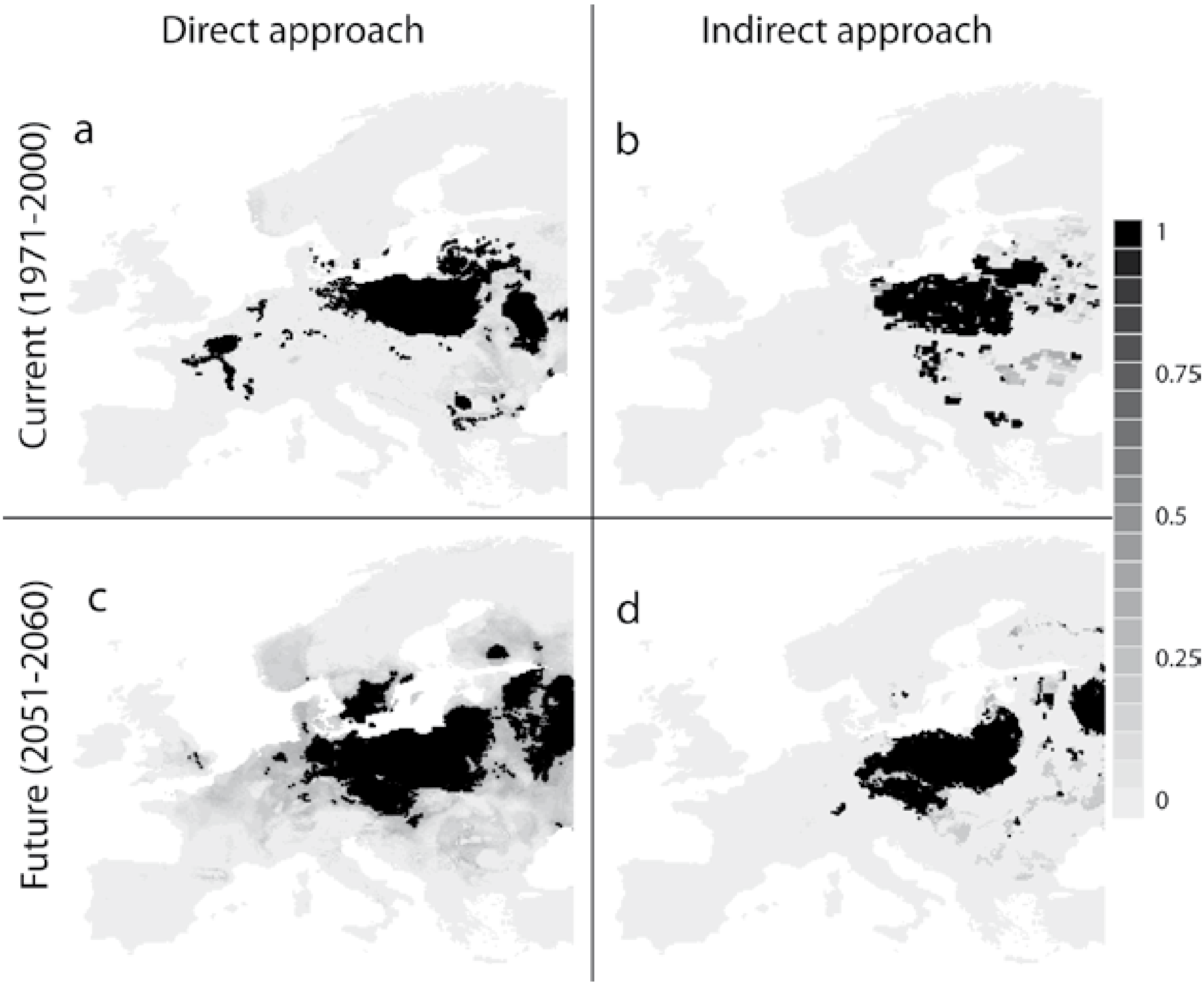


Fig. S5: Modelled occurrence probabilities of Xeric sand calcareous grasslands (6120), based on RF. The coarse grained pattern in b) results from the 50 km x 50 km resolution of species distributions in the Atlas Florae Europaeae. The future climate scenario is A2 based on the HadCM3 climate model. Future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

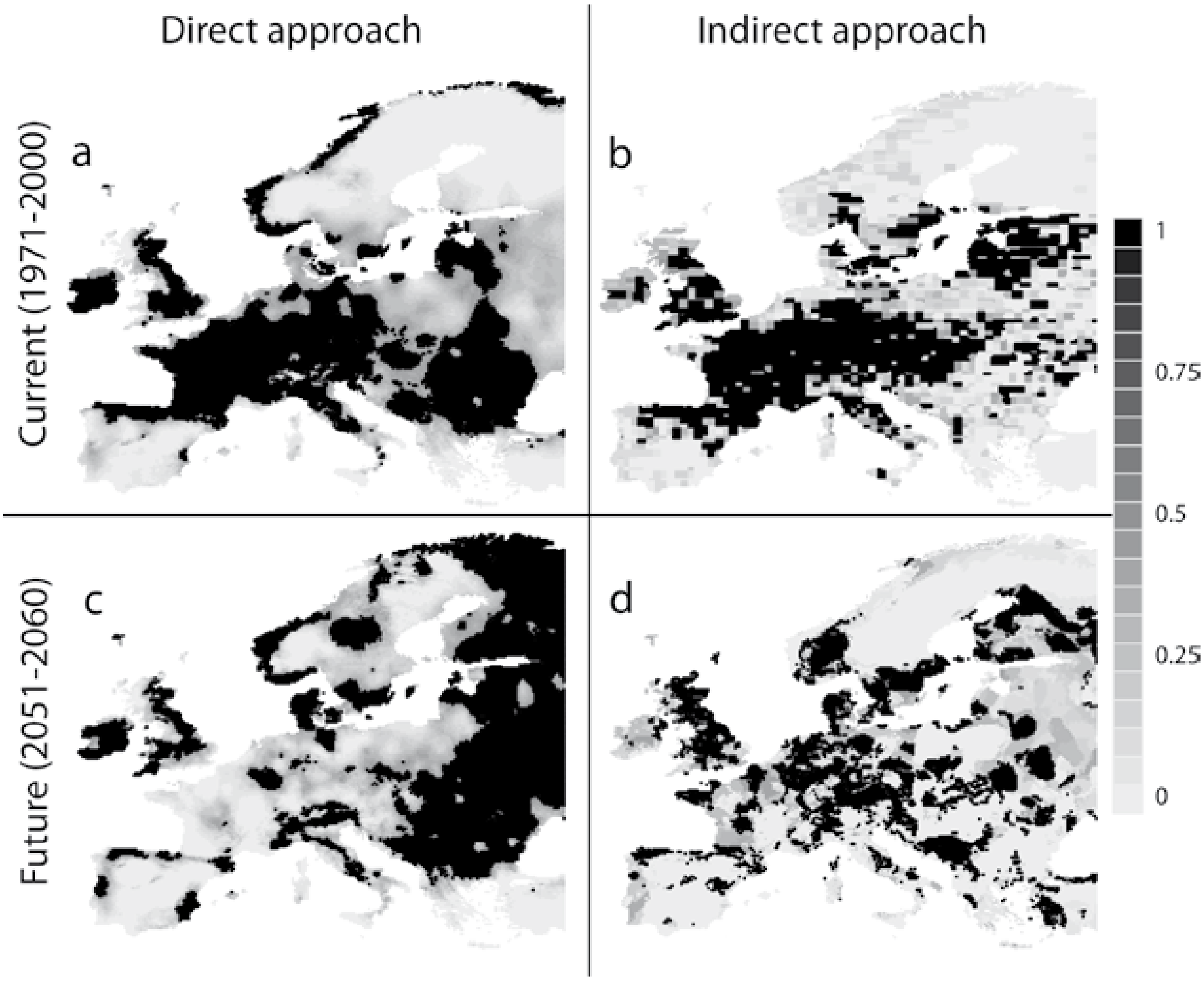


Fig. S6: Modelled occurrence probabilities of Semi-natural dry grasslands and scrubland facies on calcareous substrates (Festuco-Brometalia) (6210), based on GLM. The coarse grained pattern in b) results from the 50 km x 50 km resolution of species distributions in the Atlas Florae Europaeae. The future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

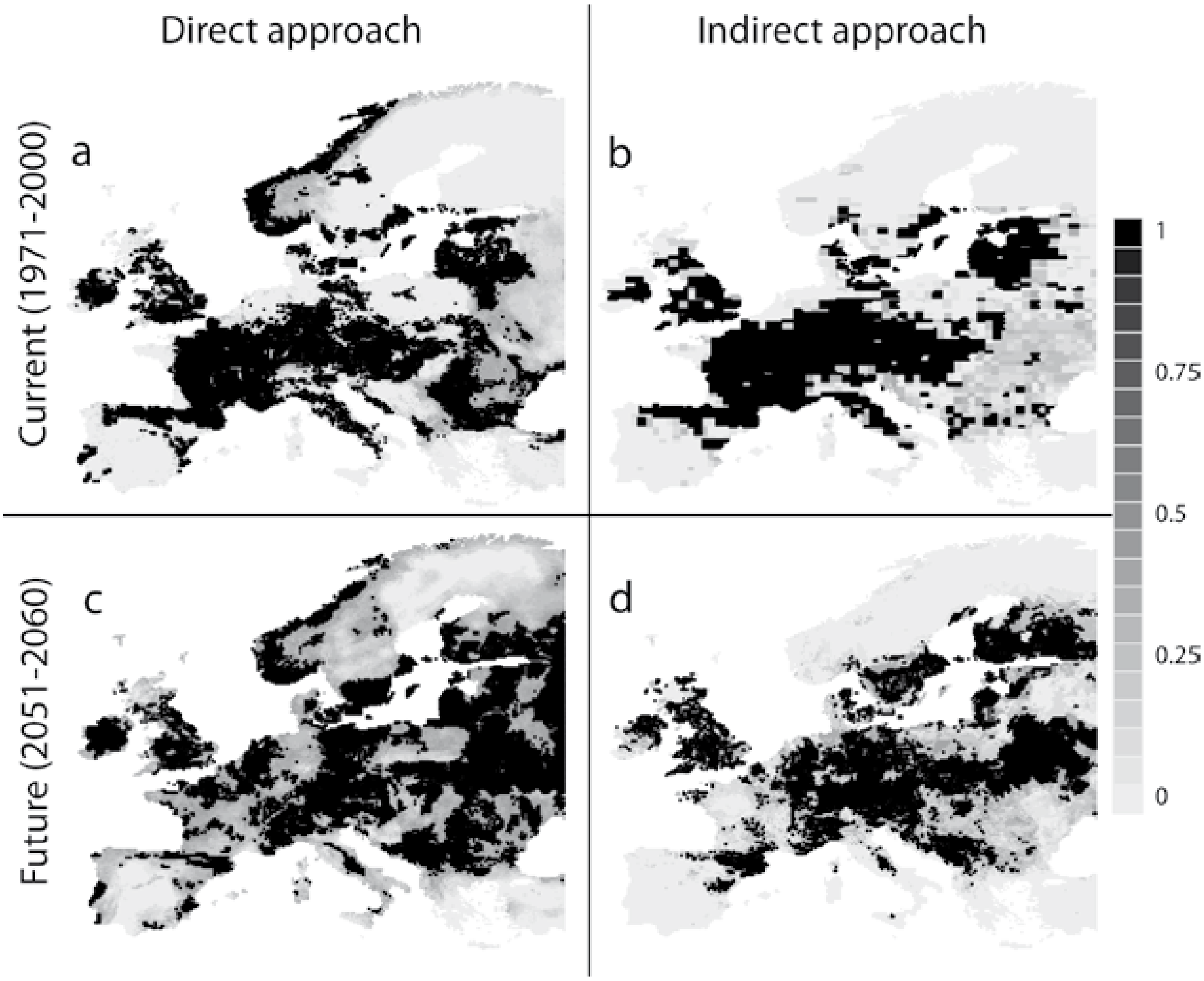


Fig. S7: Modelled occurrence probabilities of Semi-natural dry grasslands and scrubland facies on calcareous substrates (Festuco-Brometalia) (6210), based on RF. The coarse grained pattern in b) results from the 50 km x 50 km resolution of species distributions in the Atlas Florae Europaeae. The future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

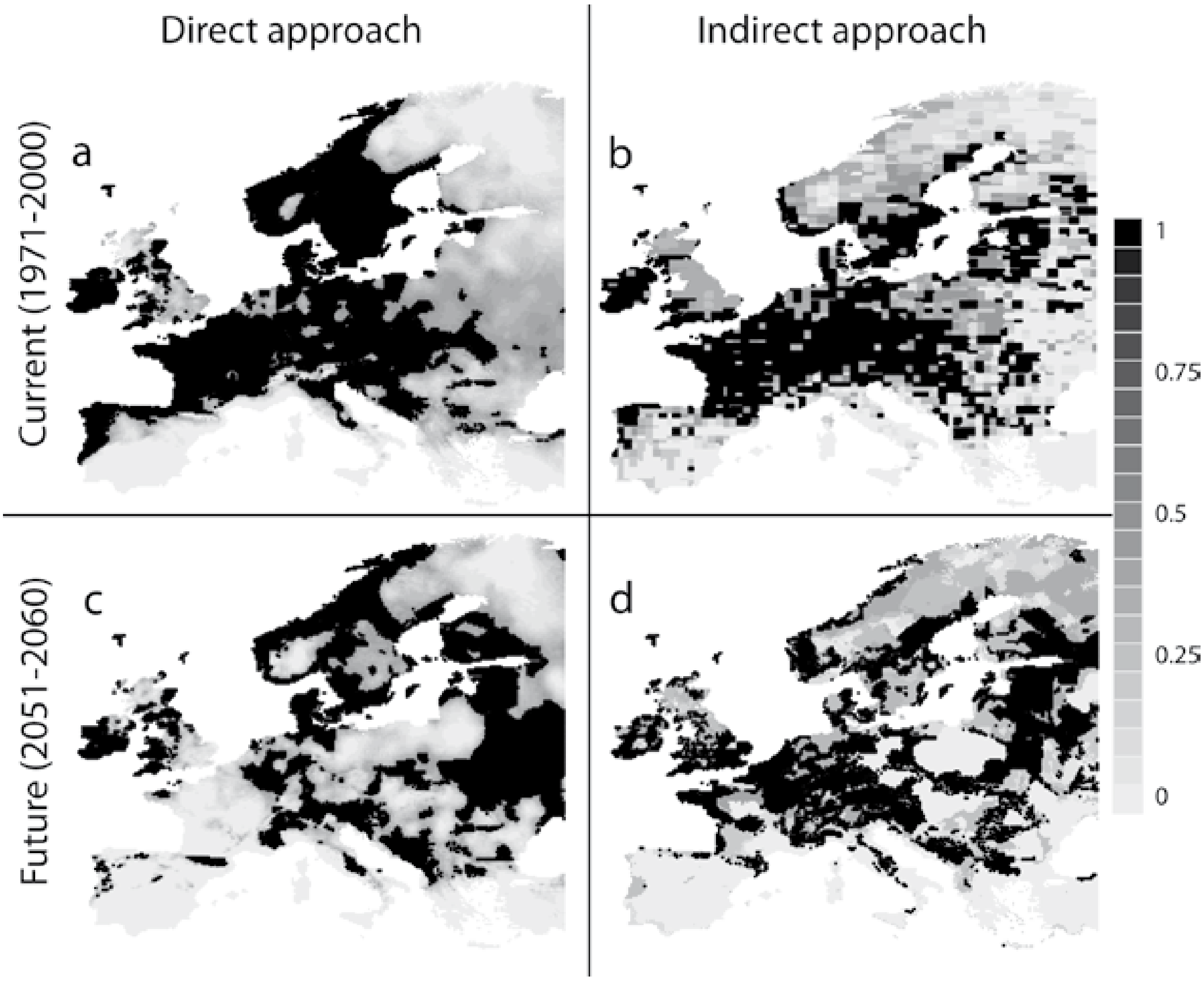


Fig. S8: Modelled occurrence probabilities of Molinia meadows on chalk and clay (6410), based on GLM. The coarse grained pattern in b) results from the 50 km x 50 km resolution of species distributions in the Atlas Florae Europaeae. The future climate scenario is A2 based on the HadCM3 climate model.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

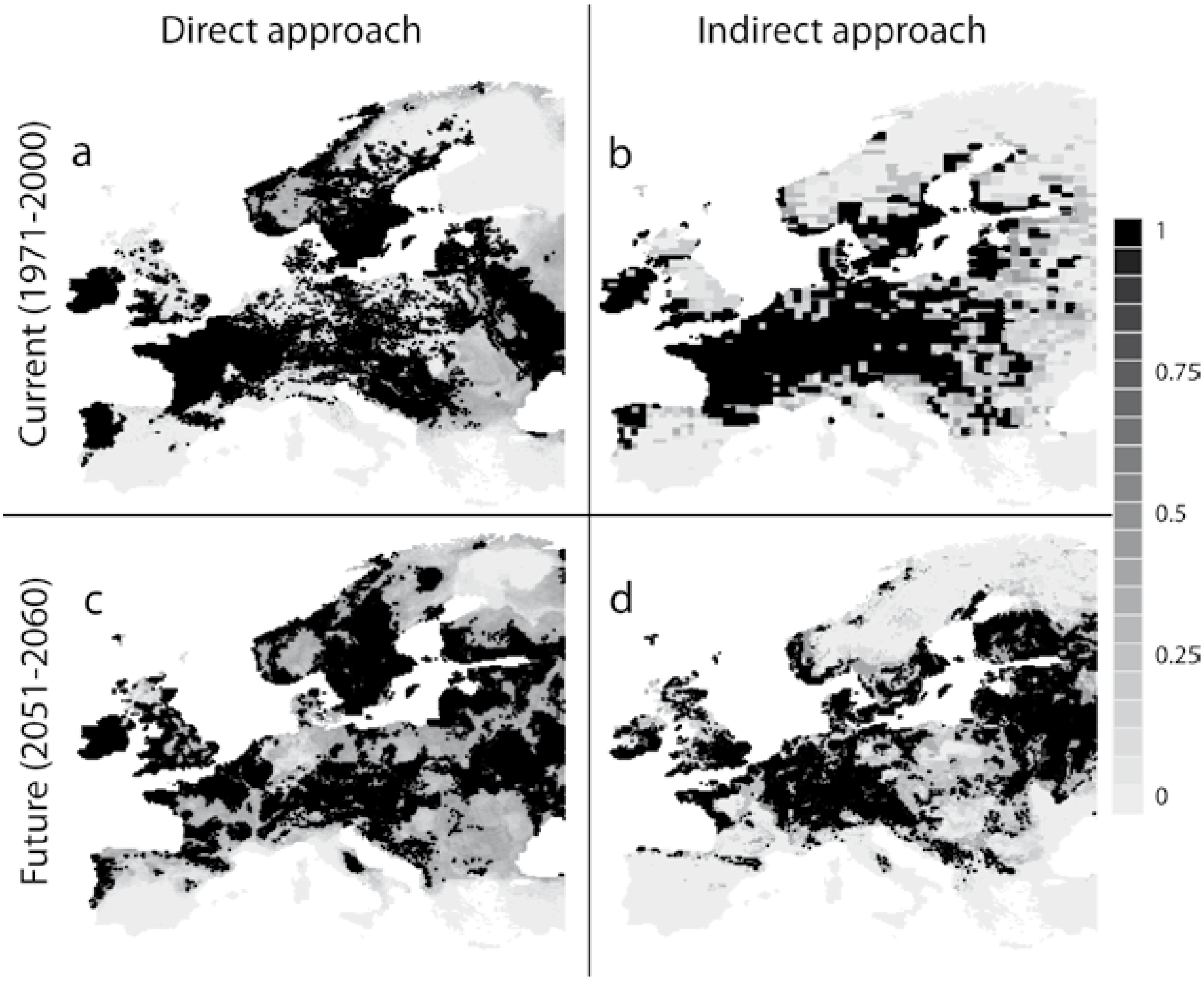


Fig. S9: Modelled occurrence probabilities of Molinia meadows on chalk and clay (6410), based on RF. The coarse grained pattern in b) results from the 50 km x 50 km resolution of species distributions in the Atlas Florae Europaeae. The future climate scenario is A2 based on the HadCM3 climate model.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

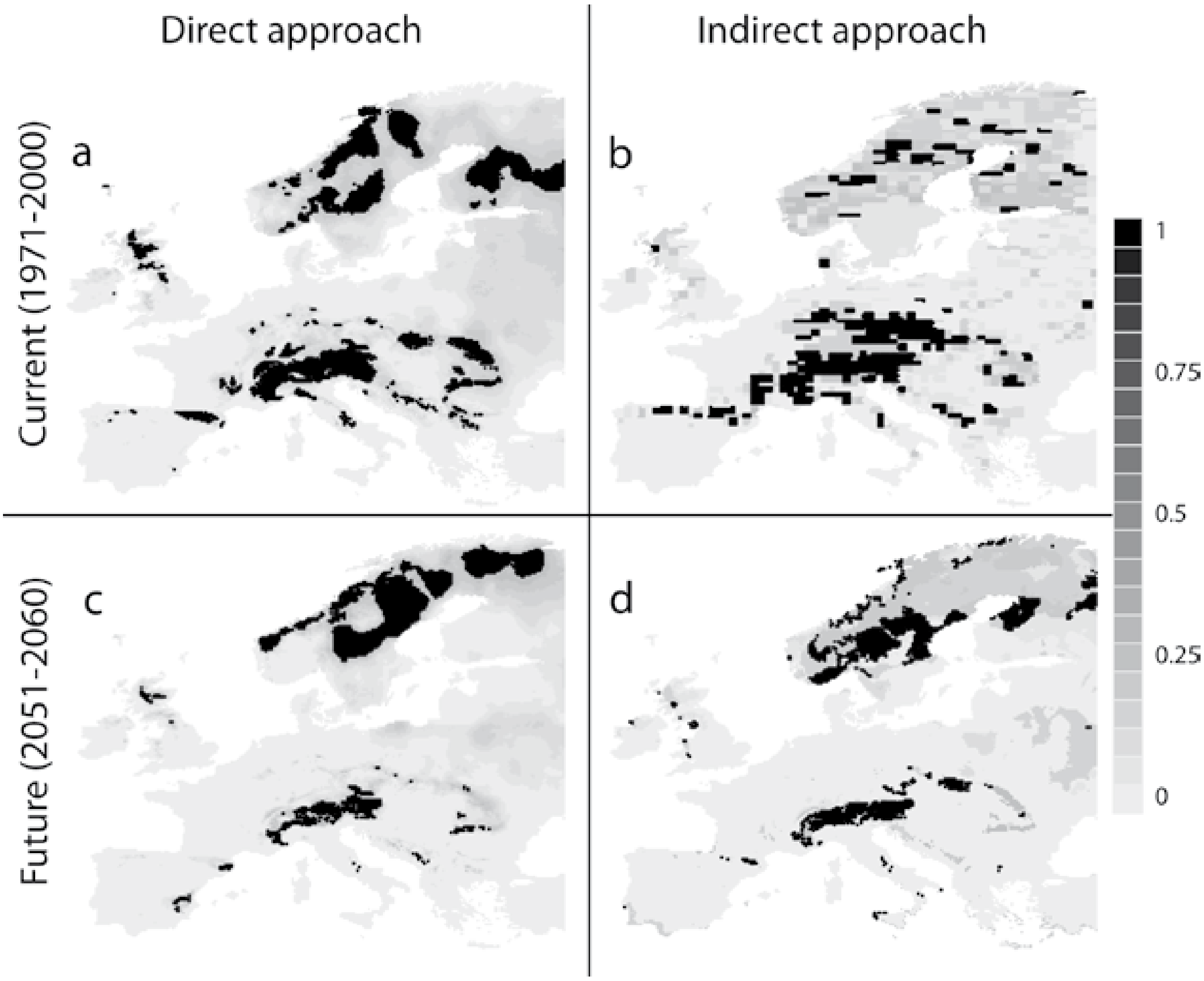


Fig. S10: Modelled occurrence probabilities of Mountain hay meadows (6520), based on GLM. The coarse grained pattern in b) results from the 50 km x 50 km resolution of species distributions in the Atlas Florae Europaeae. The future climate scenario is A2 based on the HadCM3 climate model. Future scenario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

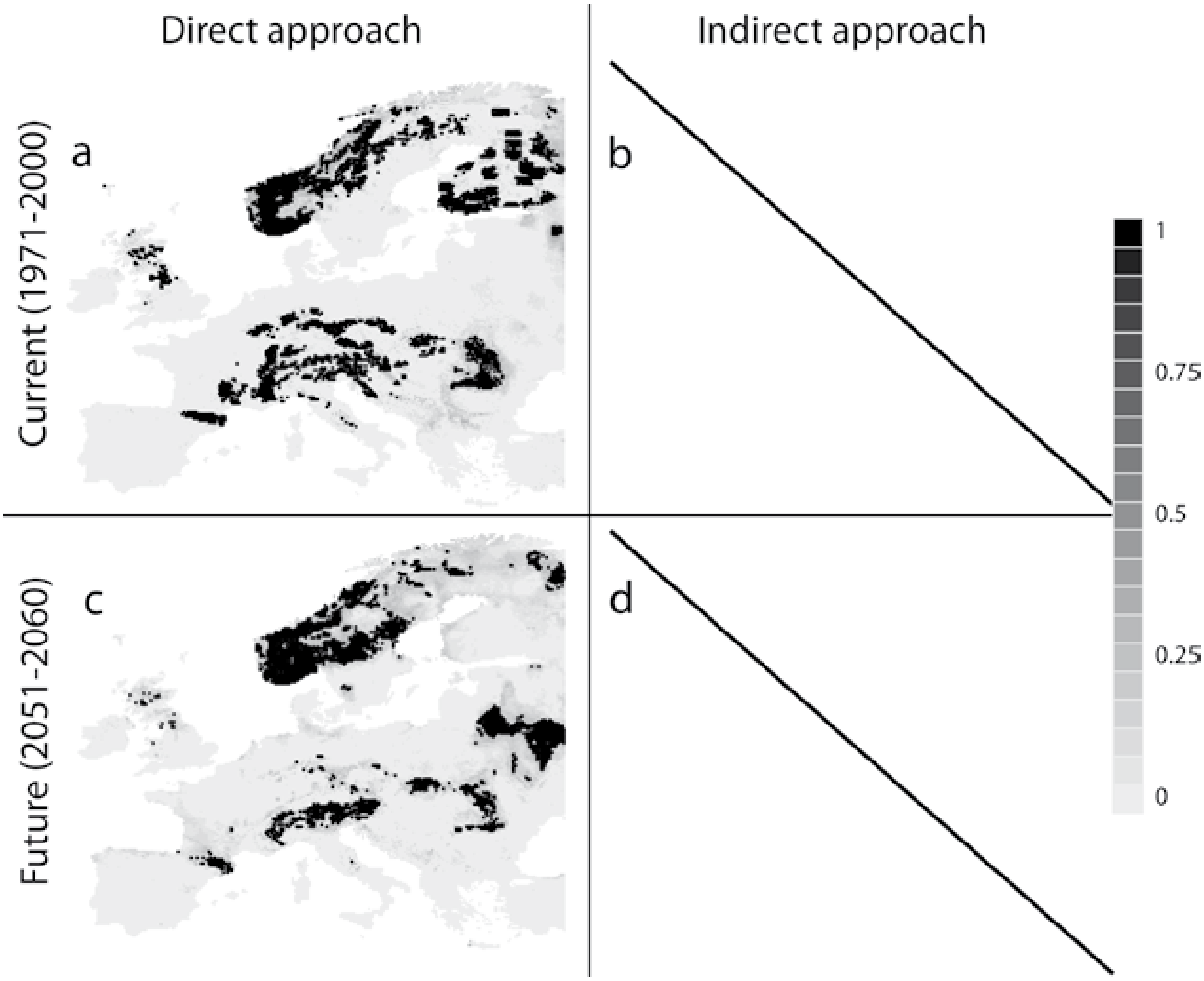


Fig. S11: Modelled occurrence probabilities of Mountain hay meadows (6520), based on RF. The future climate scenario is A2 based on the HadCM3 climate model. Future scenario maps show full dispersal ability. Black dots indicate the modelled occurrence, with thresholds: a) 0.35, b) /, c) 0.31 and d) /.

Article 3

Climate change impacts on terrestrial Natura 2000 habitats: Distribution, projected environmental space, threats and conservation options

Torsten Bittner, Anja Jaeschke, Björn Reineking, Carl Beierkuhnlein

under review
submitted to Biodiversity and Conservation on 2011-09-06

Abstract

The primary objective of the European Habitats Directive is to preserve a 'favourable' status of selected species and habitats. In the face of climatic changes this may become increasingly challenging.

Here, we assess the climate change sensitivity of 127 terrestrial habitats listed in Annex I of the Habitats Directive on a European scale, using environmental envelope modelling. Furthermore, the current and projected future spatial habitat diversity was evaluated. In addition to climatic variables, we integrated spatial information on land use and soil. We considered three time spans, three emission scenarios and nine modelling algorithms, respectively.

Habitats - or more precisely the environmental envelopes of the modelled habitats - react differentially to climate change. Bogs, rocky habitats, grasslands and some forest types (e.g. 9040, 91K0 and 9420) are projected to lose suitable area. Of these, bogs and rocky habitats are projected to even lose under the unrealistic assumption of full dispersal. Other habitats, in particular scrublands and some forest types (e.g. 91I0, 9260 and 9350), are projected to gain additional area, and some habitats appear remarkably inert. Terrestrial habitat type diversity is partly shifting towards mountain regions, and habitat type diversity is projected to decrease in the atlantic biogeographical region.

Modelling potential climate-driven threats to habitats can assist in detecting particularly affected areas and habitats. Adaptation strategies of the protection area networks are required, including measures at the network scale as well as pinpointed management for preserving or supporting specific habitats.

Keywords

SDM, Habitats Directive, range change, environmental envelope modelling, environmental change, biogeography, nature conservation, natural habitat types of community interest

Climate change impacts on terrestrial Natura 2000 habitats: Distribution, projected environmental space, threats and conservation options

Torsten Bittner[1,2]; Anja Jaeschke[1,2]; Björn Reineking[2]; Carl Beierkuhnlein[1]

[1]Biogeography, BayCEER, University of Bayreuth, Bayreuth, Germany
[2]Biogeographical Modelling, BayCEER, University of Bayreuth, Bayreuth, Germany

Introduction

The evidence of species' responses to climate change has been steadily increasing over the last decade (e.g. Parmesan and Yohe 2003; Julliard et al. 2004; Walther et al. 2005; Cleland et al. 2007; Walther et al. 2009; Ott 2010). Observed range shifts include various taxa from almost all regions of the world (Hill et al. 2011). Generally, species were detected to expand their ranges polewards or to higher elevations (Hickling et al. 2005; Walther et al. 2005; Hitch and Leberg 2007). Environmental envelope modelling has become established as a powerful tool for projecting range shifts for a variety of taxa under climate change (e.g. Araújo et al. 2006; Normand et al. 2007; Green et al. 2008; Thomaes et al. 2008; Rebelo et al. 2010).

An assessment of the likely impacts of climate change is required beyond the level of individual species. Within the European Habitats Directive, there is a unit that includes more than just individual species. It describes whole habitats that consist of species communities and specific abiotic conditions. Like species, habitats are projected to be affected by climate change as well (Bittner et al. 2011). It is important to note that these habitat types will experience modifications that are correlated with new risks during the coming years (Hannah et al. 2002; Petermann et al. 2007; European Topic Centre on Biological Diversity (ETC / BD) 2008).

Habitat types listed in the Annex I have been reported to designate protection areas throughout the EU (Council Directive 92/43/EEC 1992). It is important to understand upcoming threats to better assess future nature conservation and management of these habitats. For this, envelope models can be powerful tools (Hannah et al. 2002; Mawdsley et al. 2009).

A quick search in ISI Web of Knowledge (11/07/11) using ("climat* chang*" AND habitat*) AND ("habitats directive" OR "Natura 2000") as topic highlights 23 publications. After deleting duplicates and checking pertinence 12 publications remained, some of the search results write about habitats but focus on species. All articles were published in the past six years, with a rising number until 2010. Some of them deal with general aspects (Mueller et al. 2010; Raven et al. 2010; Zacharias & Zamparas 2010), others with restoration / management (Acreman et al. 2007; Feurdean & Willis 2008; Mayes & Codling 2009), land-use (Dimitriou & Zacharias 2005), diversity (Drakou et al. 2011), invasive species (Kleinbauer et al. 2010) and envelope modelling (Normand et al. 2007; Marage & Gégout 2009; Marage & Gégout 2010). This hints two aspects: (1) There are only few publications coping with Habitats Directive relevant habitats and climate change. (2) However, the increasing number of articles shows an interest in this topic. Both points highlight an indication for a research gap.

To tackle the question how climate change might impact habitats, we modelled terrestrial habitats listed in the Annex I of the Habitats Directive. In this work, we focused on the habitats, their projected range change and the associated threats. In addition, we investigated the potential change of whole habitat groups as defined in the Habitats Directive, namely heaths (habitat number beginning with 4), scrublands (5xxx), grasslands (6xxx), bogs (7xxx), rocky habitats (8xxx) and forests (9xxx). We analysed three time spans, three different IPCC emission scenarios, and nine different modelling algorithms to assess uncertainties from these sources.

We hypothesized that highly water-dependent habitat types will be particularly affected by climate change. Habitat types with their current range focus in the Mediterranean biogeographical region will strongly benefit in projected range expansion. Finally, habitat diversity in mountain regions will decrease similarly to previous modelled species diversity more than in other parts of the EU (e.g. Thuiller et al. 2005).

Methods

Habitats

We focused on terrestrial habitats defined in Annex I of the Habitats Directive (Council Directive 92/43/EEC 1992). We excluded aquatic habitats like 'coastal and halophytic habitats', 'coastal sand dunes' and 'freshwater habitats', because their future development is strongly related to projections of sea levels and hydrology, requiring different modelling approaches from terrestrial habitats. We reduced the list of terrestrial habitats according to the following criteria: (1) We removed all primary abiotic habitats (83xx, e.g. caves and fields of lava), because of their inability to shift in response to climate change. (2) Habitats with a small distribution were discarded to ensure sufficient occurrence points for reliable envelope modelling. As threshold, an occurrence of the habitat in at least 0.15% of grid cells was used, corresponding to a minimum of 30 grid cells out of 19.966 cells in our reference area. (3) Habitats that occur only in remote regions like the Canary Island were excluded due to our environmental reference area. A total of 127 habitats remained for analysis (Table 1). We thus modelled and analysed all wider distributed terrestrial habitats listed in the Annex I of the Habitats Directive including nine different heaths habitats (habitat number beginning with 4), 11 scrublands (5xxx), 24 grasslands (6xxx), 12 bogs (7xxx), 10 rocky habitats (8xxx) and 61 forests (9xxx).

Data

Information on the current distribution of all habitats are provided by the European reporting of the year 2007 pursuant to Article 17 of the Habitats Directive. We received the data from the EIONET (European Environment Information and Observation Network) Central Data Repository server (EIONET 2009). There, information for 25 EU countries in different spatial resolutions is available.

Current and potential 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 B1, A2 and the A1FI IPCC emission scenario (Spangenberg 2007), developed for the European project ALARM (Settele et al. 2005). The future climate projection is driven by the HadCM3 climate model for three different time periods (2021-50, 2051-80, 2071-2100).

Soil properties are an important component for the distribution and therefore of plants, but also for habitat types (Marage & Gégout 2009). Here, we used data from the European Soil Database. This database provides a comprehensive pH map for Europe (Reuter et al. 2008). Just as climate and soil, land use can be an important factor in the environmental envelope modelling. We used the future projections of European land use of the ECOCHANGE and ALARM projects in version 1.4 (Dendoncker et al. 2006; Spangenberg 2007).

Habitat occurrence and soil data were scaled to the same resolution as the climate and land use data, and all data were projected to the same geographical projection (LAEA ETRS89).

Modelling design

The occurrence of habitats was modelled by the direct 'habitat' approach as used by Bittner et al. (2011). This means that we directly used the distribution of the habitat type and modelled its environmental envelope based on climate, soil and in some cases land use factors, i.e. the habitat was treated like a species in traditional species distribution modelling.

We applied the ensemble modelling technique of BIOMOD (Thuiller 2003; Thuiller et al. 2009), using 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 of all algorithms, reducing the uncertainty of using one algorithm. For the calculation of the ensemble result, we used the unweighted probability mean which has shown favorable performance (Marmion et al. 2009). We dealt with collinearity in the predictors by selecting a variable set were all pairwise Pearson correlations were <0.7. In pairs of correlated variables, we retained the variable with higher univariate predictive ability of the distribution of the habitat, as assessed by a GLM and random forest (Bittner et al. 2011).

For model validation we used a one-time random split approach with 70% training data and 30% test data (Araújo et al. 2005). We used the AUC (area under the receiver operating characteristic curve) as a measure of overall model discrimination (Swets 1988). Furthermore, we calculated the sensitivity and specificity of our models. Specificity is calculated as the ratio of correctly predicted absences to the total number of absences. Sensitivity or proportion of true positives is the ratio of correctly predicted presences to all presence points (Jiménez-Valverde and Lobo 2007). Both reflect a model's ability of detecting true absences or presences, respectively (Moisen et al. 2006).

Although we are aware that entire habitats are not able to disperse, we applied two frequently used scenarios for the ability of habitats to keep up with climate change. For simplicity, we called these 'dispersal' scenarios: a 'no dispersal' scenario, hypothesizing that no range change is possible, and an 'unlimited dispersal' scenario. In the latter scenario we assumed a possibility of unrestricted dispersal processes for the characterising plant species. None of these scenarios is realistic, but a full dispersal scenario can indicate the potential future distribution of suitable space and therefore where to apply management measures (Bittner et al. 2011). We expect that the 'no dispersal' scenario is more realistic, because habitats consist of different species with different dispersal abilities, which may react in different ways to a changing climate.

In total, we modelled 127 different habitat types, considering three different time spans, three emission scenarios, two dispersal scenarios and nine modelling algorithms resulting in 20.574 different projections.

All analyses and calculations were performed with R 2.11.0 (R Development Core Team 2010), some GIS processing was carried out using GIS (ArcGIS 9.3) and its Python (2.5.5) script engine.

Results

Extent of range change

Habitats show a wide range of modelled responses to climate change (Table 1). Results depend on climate change and dispersal scenario, and, as expected, results become generally more extreme with more intensive scenarios and farther time periods. For the time period 2021-2050, range change values of all habitat envelopes vary in the B1 scenario between -74% and +385% (standard deviation (sd) 64.6) assuming unlimited dispersal. The variability of range change values between the habitat types increases until scenario A1FI and time period 2071-2100 to -100% and +1657% (unlimited dispersal, sd 310.78). This is an almost 5 times increase in standard deviation, indicating that variation increases with more intensive emission scenarios and even much more with temporally distant time spans. Differences between the results in the no dispersal scenario are not as strong, but show the same tendencies (for B1 and2021-2050 to A1FI and 2071-2100 a 1.6 times increase in standard deviation) (Table S1). However, results differ not only between different habitats, but also between different emission scenarios. This is exemplified by habitat type 9270. Here, the models differ from B1 to A1FI between +64% and +215% of projected range change (2021-2050). The results as a function of the three different emission scenarios over one exemplary time period (2051-2080) accumulated for all habitat types are shown in Figure 1.

Model performance was consistently high. Discriminatory ability as measured by AUC ranged for all habitats between 0.79 and 0.99, with a median of 0.95 and a mean of 0.94 (±0.045 standard deviation). Median sensitivity is 0.9, the mean is 0.89 (±0.061). Specificity has a median of 0.92 and a mean of 0.91 (±0.068).

Tab. 1: Modelling results and performance criterions of the 127 habitat types for the emission scenarios B1, A2 and A1FI and three different time spans 2021-2050 (2035); 2051-2080 (2065); 2071-2100 (2085) under the assumption of full dispersal. Results of the no dispersal scenario can be found in the supplement (Tab. S1). The asterisk * indicates priority habitat types.

Habitat type	**Modelling results in percentage range change**									**Performance criteria**		
	B1			**A2**			**A1FI**					
	2035	**2065**	**2085**	**2035**	**2065**	**2085**	**2035**	**2065**	**2085**	**AUC**	**Sensitivity**	**Specificity**
4010 Northern Atlantic wet heaths with *Erica tetralix*	-9	-20	-14	3	-12	-12	-5	-26	-23	0.96	0.9	0.9
4020 * Temperate Atlantic wet heaths with *Erica ciliaris* and *Erica tetralix*	24	57	43	44	100	141	57	151	167	0.97	0.92	0.93
4030 European dry heaths	7	-7	-1	17	19	35	20	23	25	0.86	0.79	0.79
4040 * Dry Atlantic coastal heaths with *Erica vagans*	29	31	174	8	-1	254	-7	28	243	0.98	0.96	0.97
4060 Alpine and Boreal heaths	-20	-28	-22	-27	-41	-36	-30	-35	-24	0.93	0.89	0.89
4070 * Bushes with *Pinus mugo* and *Rhododendron hirsutum* (*Mugo-Rhododendretum hirsuti*)	-40	-9	-42	-35	-10	-41	-44	-10	-23	0.97	0.94	0.97
4080 Sub-Arctic *Salix* spp. Scrub	-15	-12	-5	-20	-17	12	-14	23	77	0.96	0.93	0.95
4090 Endemic oro-Mediterranean heaths with gorse	35	52	69	29	65	114	30	100	155	0.97	0.92	0.92
40A0 * Subcontinental peri-Pannonic scrub	50	29	76	55	71	136	54	50	93	0.93	0.85	0.92
5110 Stable xerothermophilous formations with *Buxus sempervirens* on rock slopes (*Berberidion* p.p.)	-20	-43	-34	-18	-36	-37	-12	-36	-33	0.96	0.91	0.91
5120 Mountain *Cytisus purgans* formations	32	35	63	19	47	101	33	80	141	0.95	0.91	0.9
5130 *Juniperus communis* formations on heaths or calcareous grasslands	5	-4	-8	21	28	4	21	8	-19	0.93	0.85	0.85
5210 Arborescent matorral with *Juniperus* spp.	14	1	20	15	8	32	11	-4	11	0.96	0.91	0.91
5230 * Arborescent matorral with *Laurus nobilis*	-1	-2	-3	0	-1	-2	0	-3	-4	0.91	0.88	0.87
5310 *Laurus nobilis* thickets	18	159	83	50	350	331	65	125	294	0.94	0.88	0.96
5320 Low formations of Euphorbia close to cliffs	194	255	334	176	373	611	228	551	962	0.94	0.89	0.97
5330 Thermo-Mediterranean and pre-desert scrub	23	51	82	19	52	113	22	120	243	0.98	0.95	0.95
5410 West Mediterranean clifftop phryganas (*Astragalo-Plantaginetum subulatae*)	179	255	333	162	444	787	167	600	1301	0.97	0.94	0.96
5420 Sarcopoterium spinosum phryganas	331	633	649	270	816	1084	342	1026	1431	0.98	0.95	0.98
5430 Endemic phryganas of the *Euphorbio-Verbascion*	92	218	190	95	294	451	109	458	646	0.96	0.92	0.97
6110 * Rupicolous calcareous or basophilic grasslands of the *Alysso-Sedion albi*	-10	1	-6	-10	-7	-15	-15	-18	-26	0.87	0.8	0.8
6120 * Xeric sand calcareous grasslands	-23	-26	-11	-27	-51	-42	-36	-58	-57	0.95	0.89	0.9
6130 Calaminarian grasslands of the *Violetalia calaminariae*	-15	-17	-18	-10	-13	-14	-15	-19	-5	0.87	0.8	0.85
6140 Siliceous Pyrenean *Festuca eskia* grasslands	-24	-53	-42	-27	-63	-36	-28	-73	-47	0.98	0.96	0.99
6150 Siliceous alpine and boreal grasslands	-28	-17	-24	-33	-29	-22	-36	-9	37	0.98	0.95	0.95
6160 Oro-Iberian *Festuca indigesta* grasslands	100	161	247	25	155	355	54	329	434	0.98	0.94	0.95
6170 Alpine and subalpine calcareous grasslands	8	3	42	-3	-3	48	-3	31	30	0.94	0.88	0.88
6190 Rupicolous pannonic grasslands (*Stipo-Festucetalia pallentis*)	-16	-36	-20	9	-15	15	-14	-38	-32	0.93	0.88	0.89
6210 Semi-natural dry grasslands and scrubland facies on calcareous substrates (*Festuco-Brometalia*) (* important orchid sites)	-10	-12	-33	-1	-7	-47	-6	-22	-60	0.88	0.81	0.81
6220 * Pseudo-steppe with grasses and annuals of the *Thero-Brachypodietea*	15	14	28	15	22	53	15	34	60	0.97	0.93	0.93
6230 * Species-rich *Nardus* grasslands, on silicious substrates in mountain areas (and submountain areas in Continental Europe)	1	-19	-8	10	3	-7	7	-8	-20	0.84	0.76	0.76
6240 * Sub-Pannonic steppic grasslands	32	19	26	44	51	71	39	32	38	0.93	0.87	0.91
6250 * Pannonic loess steppic grasslands	104	70	158	112	128	292	118	151	239	0.98	0.96	0.97
6260 * Pannonic sand steppes	147	139	230	147	203	371	168	230	392	0.98	0.97	0.98
6270 * Fennoscandian lowland species-rich dry to mesic grasslands	-14	-35	-44	-8	-27	-60	-6	-30	-50	0.94	0.87	0.87
6280 * Nordic alvar and precambrian calcareous flatrocks	61	112	17	3	87	-30	37	67	13	0.92	0.85	0.9
6410 *Molinia* meadows on calcareous, peaty or clayey-silt-laden soils (*Molinion caeruleae*)	-4	-13	-3	4	-3	4	-2	-7	-11	0.82	0.75	0.75

6420 Mediterranean tall humid grasslands of the *Molinio-Holoschoenion*	13	15	23	12	18	34	14	23	40	0.96	0.91	0.91
6430 Hydrophilous tall herb fringe communities of plains and of the montane to alpine levels	-29	-34	-34	-29	-38	-48	-31	-47	-57	0.84	0.78	0.78
6440 Alluvial meadows of river valleys of the *Cnidion dubii*	39	29	39	45	65	105	45	39	57	0.96	0.92	0.92
6450 Northern boreal alluvial meadows	14	4	0	27	10	-4	22	-11	-26	0.96	0.91	0.91
6510 Lowland hay meadows (*Alopecurus pratensis, Sanguisorba officinalis*)	-3	-28	-18	9	-18	-25	1	-43	-55	0.87	0.8	0.8
6520 Mountain hay meadows	-47	-45	-62	-49	-62	-79	-49	-63	-82	0.89	0.82	0.82
6530 * Fennoscandian wooded meadows	128	116	79	117	114	31	112	83	15	0.94	0.88	0.87
7110 * Active raised bogs	-2	-2	0	-9	-15	-27	-10	-23	-39	0.85	0.78	0.78
7120 Degraded raised bogs still capable of natural regeneration	-18	-30	-40	-12	-24	-40	-12	-28	-42	0.83	0.76	0.76
7130 Blanket bogs (* if active bog)	13	5	21	20	24	53	22	44	39	0.99	0.96	0.97
7140 Transition mires and quaking bogs	-13	-22	-26	-9	-24	-37	-10	-32	-46	0.9	0.82	0.82
7150 Depressions on peat substrates of the *Rhynchosporion*	25	9	44	18	14	63	22	22	54	0.91	0.83	0.83
7160 Fennoscandian mineral-rich springs and springfens	-9	-17	-22	-13	-19	-28	-14	-27	-40	0.98	0.94	0.94
7210 * Calcareous fens with *Cladium mariscus* and species of the *Caricion davallianae*	19	-16	14	29	7	62	26	-3	33	0.87	0.8	0.8
7220 * Petrifying springs with tufa formation (*Cratoneurion*)	-17	-32	-26	-11	-29	-30	-17	-43	-49	0.79	0.73	0.73
7230 Alkaline fens	-9	-31	-28	5	-15	-29	-1	-37	-46	0.79	0.72	0.72
7240 * Alpine pioneer formations of the *Caricion bicoloris-atrofuscae*	-10	-7	-9	-14	-6	-9	-16	-14	-6	0.94	0.88	0.89
7310 * Aapa mires	-5	-9	-6	-2	-4	-5	-3	-4	-2	0.99	0.98	0.98
7320 * Palsa mires	-56	-70	-84	-44	-70	-86	-54	-72	-74	0.97	0.93	0.97
8110 Siliceous scree of the montane to snow levels (Androsacetalia alpinae and Galeopsietalia ladani)	-17	-20	-7	-24	-16	5	-24	7	42	0.94	0.9	0.89
8120 Calcareous and calcshist screes of the montane to alpine levels (Thlaspietea rotundifolii)	-25	-32	-36	-28	-40	-53	-32	-47	-53	0.95	0.91	0.91
8130 Western Mediterranean and thermophilous scree	-4	-28	-3	0	-15	29	-15	-47	-35	0.94	0.87	0.86
8140 Eastern Mediterranean screes	114	499	452	52	625	710	80	926	886	0.94	0.87	0.99
8150 Medio-European upland siliceous screes	11	58	23	12	60	37	7	33	10	0.93	0.86	0.85
8160 * Medio-European calcareous scree of hill and montane levels	-9	-2	-15	-9	-7	-40	-10	-22	-48	0.93	0.87	0.86
8210 Calcareous rocky slopes with chasmophytic vegetation	3	6	13	5	11	23	0	4	24	0.82	0.76	0.76
8220 Siliceous rocky slopes with chasmophytic vegetation	-5	-22	-25	-3	-20	-31	-3	-28	-47	0.81	0.75	0.75
8230 Siliceous rock with pioneer vegetation of the Sedo-Scleranthion or of the Sedo albi-Veronicion dillenii	-21	-32	-30	-22	-42	-41	-24	-43	-45	0.85	0.79	0.79
8240 * Limestone pavements	-22	-29	-25	-22	-31	-34	-26	-38	-41	0.93	0.87	0.87
9010 * Western Taïga	-3	-4	-7	-7	-12	-22	-9	-20	-36	0.97	0.91	0.91
9020 * Fennoscandian hemiboreal natural old broad-leaved deciduous forests (*Quercus, Tilia, Acer, Fraxinus or Ulmus*) rich in epiphytes	11	-7	-13	-6	-18	-31	-8	-26	-45	0.93	0.85	0.85
9030 * Natural forests of primary succession stages of landupheaval coast	-53	-45	-77	-47	-33	-91	-40	-36	-88	0.97	0.93	0.95
9040 Nordic subalpine/subarctic forests with *Betula pubescens* ssp. *czerepanovii*	-45	-70	-71	-50	-86	-93	-59	-95	-96	0.99	0.97	0.97
9050 Fennoscandian herb-rich forests with *Picea abies*	-19	-29	-42	-12	-24	-51	-10	-28	-53	0.98	0.94	0.93
9060 Coniferous forests on, or connected to, glaciofluvial eskers	-4	3	-14	-17	-25	-45	-26	-43	-70	0.95	0.9	0.9
9070 Fennoscandian wooded pastures	-10	-22	-31	-9	-22	-50	-9	-29	-54	0.96	0.9	0.9
9080 * Fennoscandian deciduous swamp woods	-8	-28	-33	-8	-30	-45	-12	-41	-61	0.96	0.9	0.9
9110 *Luzulo-Fagetum* beech forests	67	39	44	69	79	61	67	24	-22	0.95	0.89	0.89
9120 Atlantic acidophilous beech forests with *Ilex* and sometimes also *Taxus* in the shrublayer (*Quercion robori-petraeae or Ilici-Fagenion*)	24	17	29	29	12	37	35	22	41	0.95	0.89	0.89
9130 *Asperulo-Fagetum* beech forests	17	5	10	35	32	28	31	12	-18	0.94	0.88	0.88
9140 Medio-European subalpine beech woods with *Acer* and *Rumex arifolius*	-33	-18	-43	-27	-10	-24	-33	-28	-60	0.95	0.91	0.93
9150 Medio-European limestone beech forests of the *Cephalanthero-Fagion*	-9	-8	-14	-2	-2	-4	-12	-24	-28	0.94	0.88	0.88
9160 Sub-Atlantic and medio-European oak or oak-hornbeam forests of the *Carpinion betuli*	-21	-58	-52	8	-13	-10	-3	-35	-34	0.9	0.84	0.84
9170 *Galio-Carpinetum* oak-hornbeam forests	49	56	29	25	69	6	27	8	-23	0.97	0.92	0.92
9180 * *Tilio-Acerion* forests of slopes, screes and ravines	-9	-15	-26	-1	-6	-31	-3	-19	-42	0.87	0.79	0.8
9190 Old acidophilous oak woods with *Quercus robur* on sandy plains	52	66	75	48	70	98	52	81	97	0.93	0.87	0.87

91A0 Old sessile oak woods with *Ilex* and *Blechnum* in the British Isles	1	-3	0	5	4	11	4	2	25	0.98	0.96	0.97
91B0 Thermophilous *Fraxinus angustifolia* woods	75	157	286	63	224	510	87	411	635	0.96	0.91	0.92
91C0 * Caledonian forest	5	-34	2	-8	-26	-5	-5	-21	10	0.94	0.88	0.99
91D0 * Bog woodland	-15	-18	-22	-12	-19	-25	-18	-29	-33	0.91	0.84	0.84
91E0 * Alluvial forests with *Alnus glutinosa* and *Fraxinus excelsior* (*Alno-Padion, Alnion incanae, Salicion albae*)	7	8	14	5	8	15	3	1	7	0.87	0.79	0.79
91F0 Riparian mixed forests of *Quercus robur, Ulmus laevis* and *Ulmus minor, Fraxinus excelsior* or *Fraxinus angustifolia*, along the great rivers (*Ulmenion minoris*)	26	42	48	36	74	100	33	75	111	0.88	0.82	0.82
91G0 * Pannonic woods with *Quercus petraea* and *Carpinus betulus*	43	9	23	68	40	83	52	18	-7	0.97	0.93	0.94
91H0 * Pannonian woods with *Quercus pubescens*	16	3	39	41	28	89	22	27	65	0.92	0.85	0.89
91I0 * Euro-Siberian steppic woods with *Quercus* spp.	69	103	109	56	110	138	59	126	145	0.97	0.94	0.93
91J0 * *Taxus baccata* woods of the British Isles	55	71	126	50	57	111	56	72	203	0.96	0.93	0.94
91K0 Illyrian *Fagus sylvatica* forests (*Aremonio-Fagion*)	-41	-23	-56	-43	-27	-69	-50	-32	-70	0.9	0.8	0.93
91L0 Illyrian oak-hornbeam forests (*Erythronio-Carpinion*)	58	109	128	51	94	167	58	109	248	0.96	0.94	0.93
91M0 Pannonian-Balkanic turkey oak –sessile oak forests	89	137	142	124	214	301	133	265	355	0.95	0.9	0.91
91N0 * Pannonic inland sand dune thicket (*Junipero-Populetum albae*)	-74	-55	16	-77	-55	43	-61	27	355	0.98	0.97	0.99
91P0 Holy Cross fir forest (*Abietetum polonicum*)	-61	-48	-61	-91	-96	-99	-99	-100	-100	0.99	0.98	0.98
91Q0 Western Carpathian calcicolous *Pinus sylvestris* forests	-70	-77	-77	-53	-62	-48	-57	-55	-6	0.96	0.92	0.97
91R0 Dinaric dolomite Scots pine forests (*Genisto januensis-Pinetum*)	75	126	55	29	96	6	22	143	-56	0.99	0.99	1
91T0 Central European lichen Scots pine forests	75	60	74	13	-22	-36	-8	-69	-74	0.92	0.86	0.88
91U0 Sarmatic steppe pine forest	-8	52	18	-9	21	-6	13	38	27	0.88	0.82	0.89
9210 * Apeninne beech forests with *Taxus* and *Ilex*	53	73	163	58	132	373	61	216	607	0.97	0.94	0.94
9220 * Apennine beech forests with *Abies alba* and beech forests with *Abies nebrodensis*	65	68	236	69	196	685	58	402	1025	0.96	0.92	0.95
9230 Galicio-Portuguese oak woods with *Quercus robur* and *Quercus pyrenaica*	24	37	84	2	12	92	16	64	184	0.98	0.95	0.95
9240 *Quercus faginea* and *Quercus canariensis* Iberian woods	17	31	31	0	71	100	17	159	167	0.98	0.93	0.94
9250 *Quercus trojana* woods	50	136	181	60	210	501	50	317	668	0.95	0.9	0.97
9260 *Castanea sativa* woods	30	86	75	33	107	121	48	159	193	0.95	0.89	0.9
9270 Hellenic beech forests with *Abies borisii-regis*	64	205	222	126	623	795	215	782	1007	0.97	0.95	0.99
9280 *Quercus frainetto* woods	132	237	256	132	303	348	152	352	334	0.96	0.93	0.94
9290 *Cupressus* forests (*Acero-Cupression*)	19	86	62	11	132	78	24	249	176	0.99	0.98	1
92A0 *Salix alba* and *Populus alba* galleries	35	38	45	31	39	57	37	55	97	0.97	0.94	0.94
92C0 *Platanus orientalis* and *Liquidambar orientalis* woods (*Platanion orientalis*)	188	375	381	161	544	561	204	836	800	0.98	0.96	0.98
92D0 Southern riparian galleries and thickets (*Nerio-Tamaricetea* and *Securinegion tinctoriae*)	18	19	37	22	36	73	26	51	87	0.97	0.93	0.95
9320 *Olea* and *Ceratonia* forests	61	205	184	75	235	345	72	353	514	0.97	0.93	0.96
9330 *Quercus suber* forests	38	51	106	35	80	207	30	119	295	0.97	0.93	0.93
9340 *Quercus ilex* and *Quercus rotundifolia* forests	8	10	15	7	10	22	9	13	32	0.98	0.94	0.94
9350 *Quercus macrolepis* forests	385	743	789	337	961	1320	452	1285	1657	0.96	0.92	0.98
9380 Forests of *Ilex aquifolium*	37	44	129	16	25	186	9	64	252	0.96	0.9	0.93
9410 Acidophilous *Picea* forests of the montane to alpine levels (*Vaccinio-Piceetea*)	-39	-27	-42	-34	-26	-44	-44	-46	-64	0.96	0.91	0.92
9420 Alpine *Larix decidua* and/or *Pinus cembra* forests	-43	-35	-56	-42	-42	-67	-49	-53	-74	0.97	0.94	0.97
9430 Subalpine and montane *Pinus uncinata* forests (* if on gypsum or limestone)	-37	-55	-51	-31	-46	-41	-34	-52	-56	0.96	0.91	0.95
9510 * Southern Apennine *Abies alba* forests	69	5	126	50	16	162	29	-38	31	0.97	0.94	0.99
9530 * (Sub-) Mediterranean pine forests with endemic black pines	39	70	81	36	93	119	50	123	161	0.94	0.89	0.88
9540 Mediterranean pine forests with endemic Mesogean pines	57	83	131	47	96	170	56	148	227	0.96	0.92	0.92
9560 * Endemic forests with *Juniperus* spp.	33	43	62	22	66	134	31	103	138	0.95	0.9	0.9
9580 * Mediterranean *Taxus baccata* woods	3	-23	15	1	-10	46	-16	-18	53	0.95	0.92	0.9

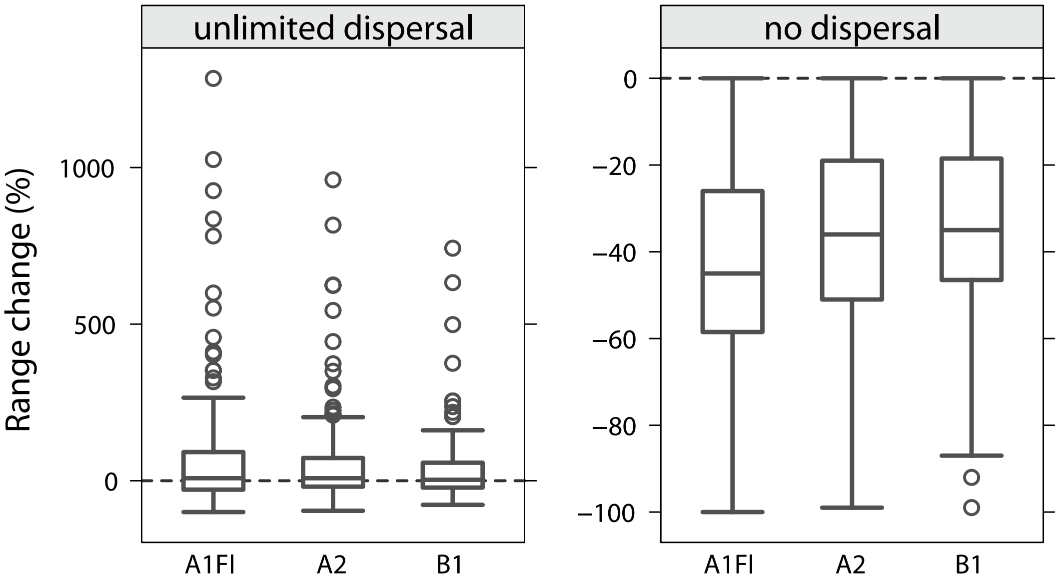


Fig. 1: Influence of three different emission scenarios on the range change of terrestrial habitat types. The graph shows the span of percentage range change accumulated over all habitat types, under the assumption of unlimited dispersal (left panel) or no dispersal (right panel). Range change values are calculated from the observed baseline (1971-2000 / Article 17 Habitats Directive reported data) and the modelled future scenario (2051-2080).

Major habitat types

The major groups of habitat types show differential responses to projected climate change (Figure 2). In the unlimited dispersal scenario, the median for percentage range change of scrublands and forests is above zero, which means that most habitats of these types are projected to gain in area. The median of percentage range change of heaths and grasslands are close to zero, which means that the number of winners and losers in these groups is about balanced. Two groups constitute losers of climate change: even under an unlimited dispersal scenario, bogs and rocky habitats are projected to lose suitable area.

The 'no dispersal' scenario shows similar trends with some slight differences. Forests and grasslands exhibit a wide range of range changes; some habitats are projected to lose large parts of their range while others are projected to remain stable. For the other habitats, the range of no dispersal results is not as large. With the exception of scrublands, the median of projected range change amounts to approximately -40% (-37.8% ± 23.53%). Scrublands show a lower degree of change with a median of -17.5% (± 20.3%).

Our results thus support the first two of our hypotheses: (1) Bogs are the most water-dependent habitat types of our focused habitats. Under the assumption of unlimited dispersal, bogs together with rocky habitats are the habitats with the lowest (even negative) average of range change. (2) The mainly Mediterranean-distributed scrublands are less affected than other habitat types and are projected to gain the largest area.

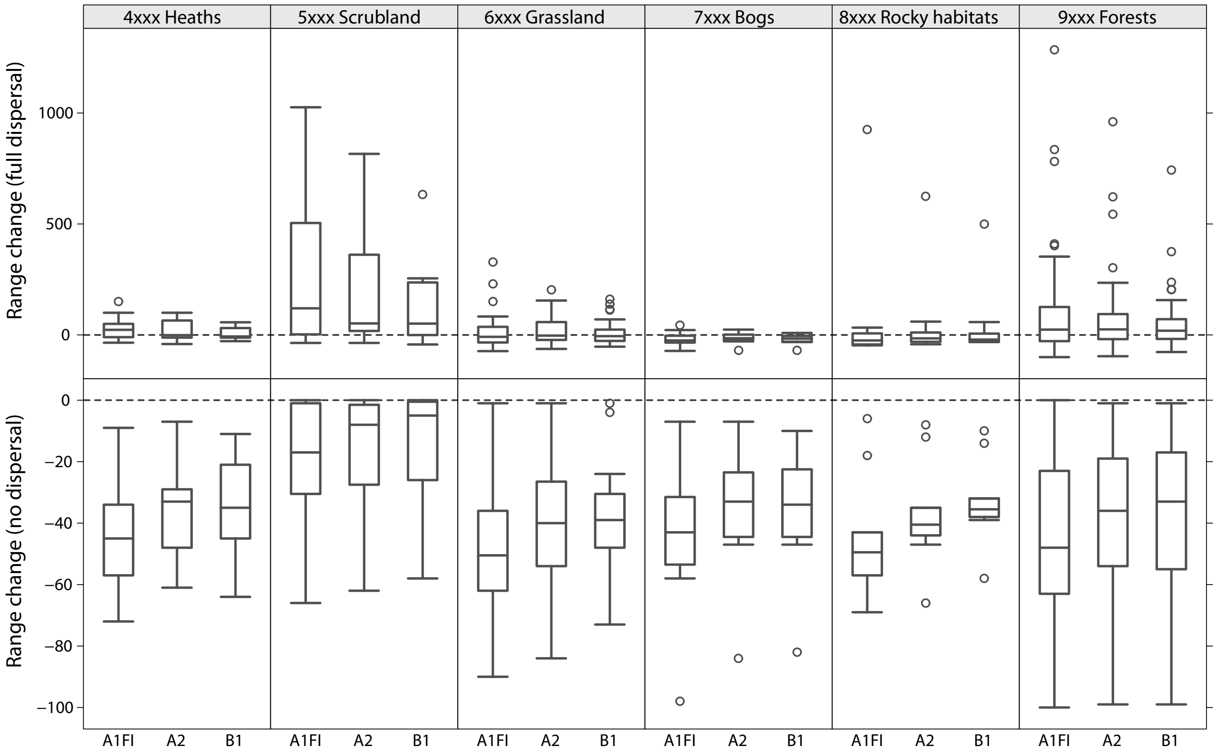


Fig. 2: Influence of different emission scenarios on the range change of habitat type groups under the assumption of unlimited dispersal (upper panel) or no dispersal (lower panel). Range change values are calculated from the observed baseline (1971-2000 / Article 17 Habitats Directive reported data) and the modelled future scenario (2051-2080).

Spatial context

The Alps, Pyrenees, Apennines, parts of France and Spain are the regions with highest observed current habitat diversity (Fig. 3a). The same spatial trends in the distribution of diversity are reflected in the modelled current habitat diversity (Fig. 3b).

There is a pronounced pattern in the spatial distribution of regions that might show the greatest loss of habitat types (Fig. 4a). In particlar, losses are most pronounced over large parts of France and in some Mediterranean regions. The regions with the largest projected gain of habitat types are, beside several smaller areas, Poland and the Baltic states (Fig. 4b). Pooling information on both projected loss and gain indicates overall change in terrestrial habitat diversity (Fig. 4c). Finally, absolute future habitat diversity was calculated by adding the gain to and subtract loses from current diversity (Fig. 4d). Especially regions in France are projected to decrease in habitat type diversity up to 29 habitats per grid cell. However, habitat diversity is projected to be stable or to increase in most areas. The highest increase in habitat diversity is calculated for the majority of the mountain regions in the EU including the Fatra-Tatra-Region. Based on these findings, we reject our third hypothesis: habitat diversity is projected to increase in mountain regions, in contrast to species diversity.

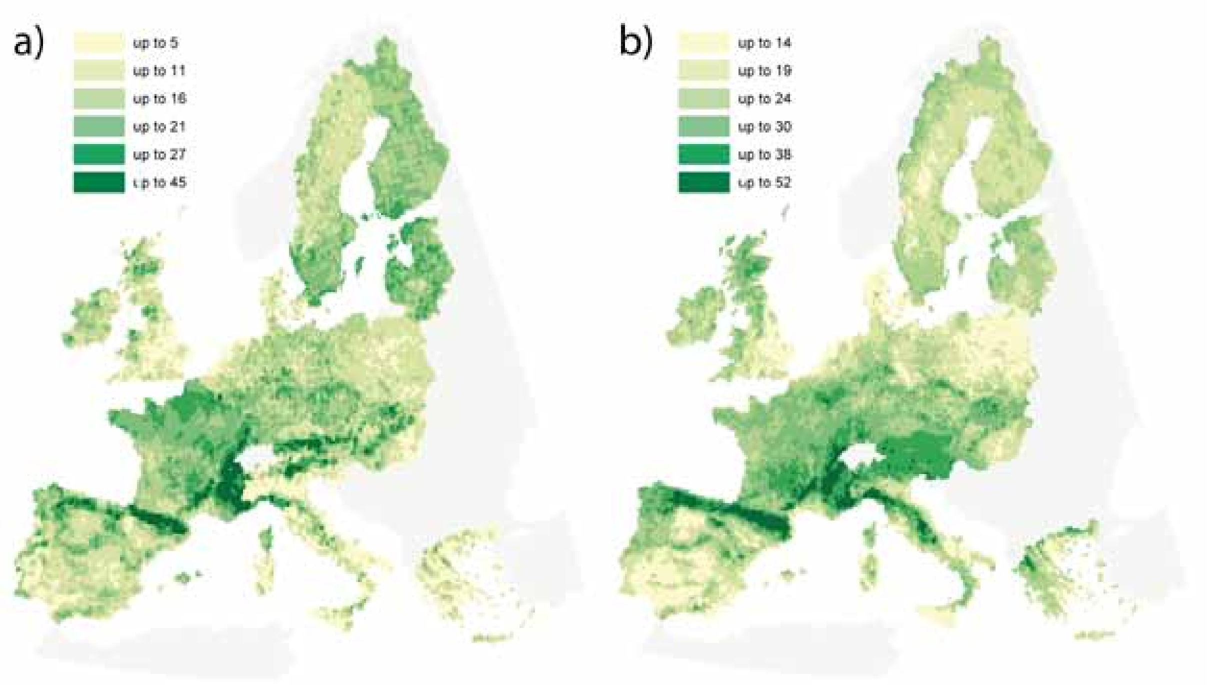


Fig. 3: Current distribution of habitat type diversity in the EU. a) Diversity of reported habitat types according to Annex I of the Habitats Directive. b) Modelled diversity of habitat types under current conditions (1971-2000).

Discussion

We find that habitat types behave differentially with respect to their modelled response to climate change. The results of our study are largely in agreement with the national risk assessment of habitat sensitivity done by Petermann et al. (2007). In their assessment, bogs were rated as the most sensitive habitat types concerning climate change as well as forests which were evaluated to be very sensitive. Furthermore, scrubland habitats emerged as winners. Bogs represent the group of habitat types that can hardly respond to climatic changes (Clark et al. 2010). Their occurrence depends on very specific climatic conditions and other abiotic factors and they take a long time even to develop. Similar aspects concern rocky habitats. They are not as reliant on very specific climatic conditions as bogs, but require very specific abiotic conditions for the occurrence, like the existence of scree slopes. The scrublands usually distributed in the Mediterranean benefit most from the projected changing environmental conditions. Most species of these habitat types are adapted to a warm and dry climate and thus will likely find more suitable environmental space in the future. The large group of forest habitat types has the widest span of decreasing and increasing suitable environmental space, corresponding to the large ecological differences between different forest habitats.

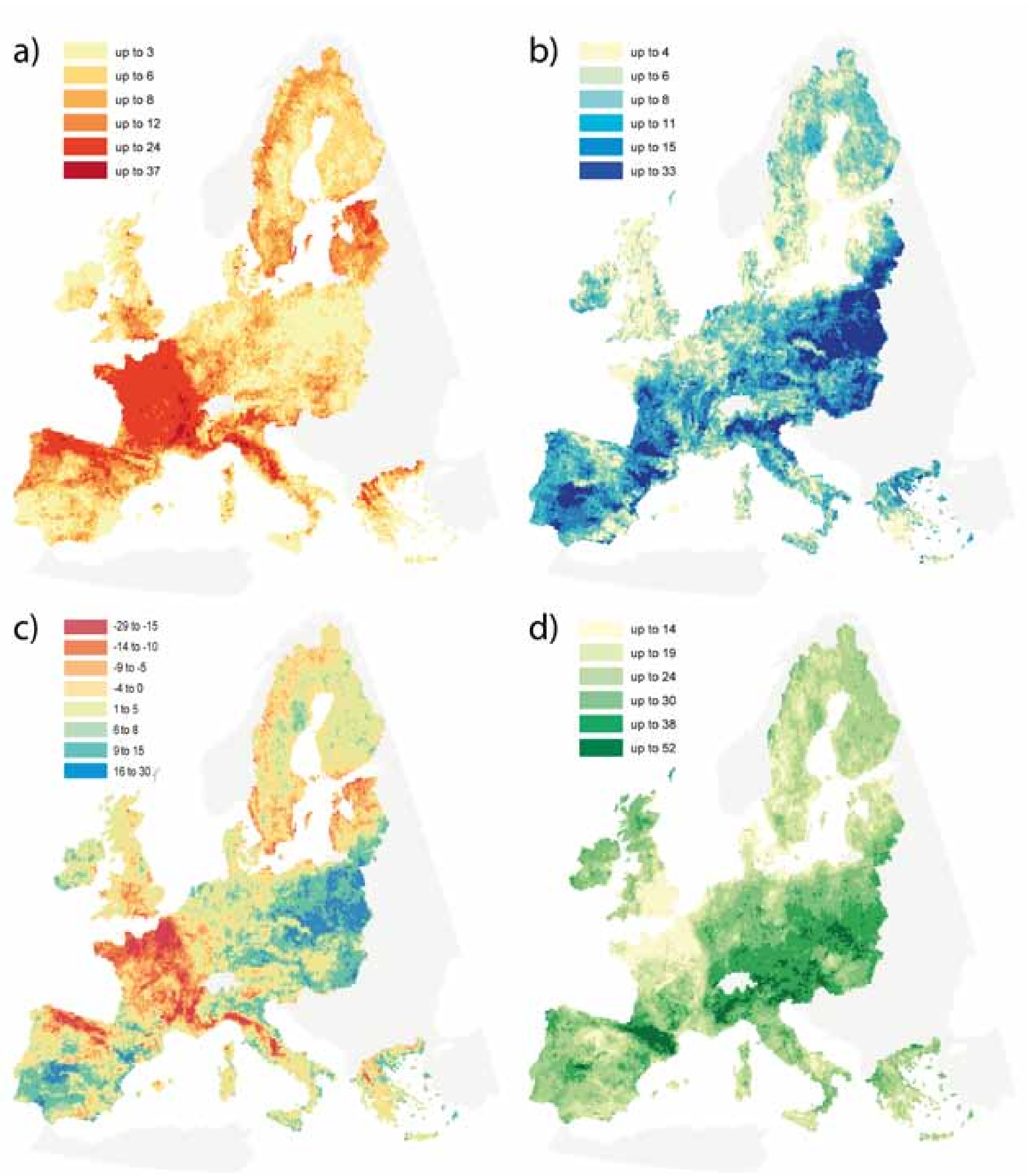


Fig. 4: Relative and absolute loss and gain of habitat types in the EU. a) Modelled absolute loss of habitat types (number of potentially lost habitat types). b) Modelled absolute gain of habitat types (number of potentially gained habitat types). c) Modelled relative diversity change of habitats under future conditions. d) Modelled diversity of habitats under future conditions. All maps are based on emission scenario A2 and climate model HadCM3 for the time period 2051-2080.

Based on our findings, we reject the third hypothesis: habitat diversity is projected to increase in mountain regions. This pattern contrasts with previous findings on projected changes in species diversity (e.g. Thuiller et al. 2005) and warrants discussion. Areas in or near mountains could represent refuges for many habitat types, because there will be climatic conditions which are currently found at lower elevations and larger areas (Jentsch and Beierkuhnlein 2003). Therefore it is possible that the higher regions could accumulate habitat types and increase habitat diversity.

Modelling, limitations and data quality

The projections presented here have to be interpreted with caution due to existing uncertainties in climate change scenarios (Thuiller et al. 2005; Heikkinen et al. 2006), spatial resolution (Weaver and Zwiers 2000), uncertainties in the modelling techniques (Guisan and Zimmermann 2000; Pearson and Dawson 2003; Dormann et al. 2008; Elith and Leathwick 2009) and underlying data quality (Heikkinen et al. 2006).

All modelling approaches are limited by the quantity and quality of occurrence data (Heikkinen et al. 2006; Bittner et al. 2011). One of the main problems of the natural habitat types of community interest is that they are only defined and reported by EU member states. Similar or identical habitats occur in non-member states (Bittner et al. 2011), meaning that the modelled envelope does not cover all occurrences of the habitat type in Europe. Although the habitat types can be projected to other regions of the continent is possible, the occurrence of habitats is strongly influenced historico-cultural and political circumstances and these differ widely between countries. It is likely that a projection of the habitat type to other regions leads to an increase of uncertainty. Furthermore, the spatial resolution of reported distribution data (Article 17 Habitats Directive) differs between countries. Summing up, information at higher and more consistent resolution on the distribution of habitat types in all EU states for the next data submission in 2013 would be beneficial and could lead to improved modelling results and reduced uncertainties.

Habitat types are complex in many ways. They are not only characterized by climatic demands or abiotic conditions, such as soil type, but depend on the occurrence of characteristic species (Normand et al. 2007). That is the reason why definitions of habitat types are somewhat arbitrary as the boundaries between different habitat types can be fluent. Definitions of one habitat type can also strongly differ between various regions. Hence, the concept of continuity in community composition and of potentially ‘natural’ assemblages can be questioned (Chiarucci et al. 2010). As mentioned above, habitat occurrence and distribution as with species reflects historico-cultural, political, traditional and management circumstances. All these factors complicate the modelling of habitat types (Bittner et al. 2011).

With regard to dispersal scenarios, our models projected under the no dispersal assumption a decrease of range size with a median of -37%, under a full dispersal scenario the median of range change is +5%. These results indicate the importance of dispersal processes for the capability of characteristic species of habitats to cope with climate change (Normand et al. 2007).

The modelled dimension of range loss could be overestimated due to the plasticity of species and habitats as well as the possibility of survival of species in favourable microhabitats (Thuiller et al. 2005). These factors are not considered in our models. Similarly, the scale of potential spread may be substantially underestimated: Many plant species outlive long time periods of adverse conditions in soil seed banks, waiting for suitable conditions to germinate. Consequently, many species may be currently farther distributed as indicated by distribution maps. A fast shift of habitat types to new areas therefore seem not to be impossible, but likewise a fast turnover of species composition and therefore possibly new formations of habitats or rather no-analogue communities is possible (Williams and Jackson 2007, Kleinbauer et al. 2010). Despite these uncertainties, our findings provide a point of reference for the potential importance and likely direction of climate change effects on habitat types in Europe.

Implications for nature conservation

The majority of natural and semi-natural habitat types of community interest listed in the Annex I of the Habitats Directive originate from management (Ssymank et al. 1998). In particular, extensive cultivation in the past resulted in a cultural landscape with high biodiversity in large parts of Europe. Many habitat types, such as grassland, heaths and forests were directly influenced in their shaping by humans, others such as bogs or rocky habitats only indirectly. Without appropriate extensive management, for instance grazing, many of habitats are expected to disappear (Plassmann et al. 2010).

Well-established nature conservation approaches, such as monitoring programs, habitat preservation, habitat creation or extension of protected areas, and retaining viable population sizes (Lengyel et al. 2008) are important instruments to support range changes and therefore biodiversity. Another method that is being increasingly applied over the last few years, is the improvement of landscape permeability (Opdam et al. 2006; Bissonette and Adair 2008). Improved landscape permeability allows a better genetic exchange of currently isolated populations and supports the dispersal of species to cope with climate change (Mawdsley et al. 2009).

Especially habitats with long-lived species are expected to be more affected than those with short-living species and will therefore become an important focal point in prospectively active nature conservation. Characteristic long-living species of habitat types that are weak in dispersal ability due to long time periods between germination and fructification, are primary candidates for species support programs, including potential assisted migration options with all its benefits and disadvantages (Kreyling et al. 2011).

In addition to climate change, the expected nitrogen deposition rate could affect habitats by favouring more competitive species and concomitant change communities (Thuiller et al. 2005) yielding in a transition of habitats. Sophisticated monitoring programs could detect such transitions, helping to apply suitable management at an early stage.

Our conception of nature, species, communities and the associated relationships is mostly actualistic and static. However, the objects of protection may, driven by climate change, disperse out of the protected areas and not be represented by the existing protected areas (Hannah et al. 2002; Hannah et al. 2007). Due to the forecasted climatic changes and the resulting projected spatial shifts of species and habitats, more dynamic concepts of nature conservation should gain prominence (Hannah and Hansen 2005). This includes an increased and early designation of protected areas (Hannah et al. 2007).

Conclusion

The distribution of habitats can effectively be captured by environmental envelope modelling techniques, showing different dependencies on abiotic factors. For most practical questions and problems, the habitat scale is of particular relevance. Habitat types differ in their potential response to climate change. However, regional habitat type diversity may increase in the EU overall in response to climate change, particularly in mountain regions.

In addition to an improved data quality, which can result from extensive monitoring programs (Lengyel et al. 2008; Conroy et al. 2011) more experimental studies are needed to enhance our understanding of ecological processes (Jentsch et al. 2007). With this improved knowledge could then be utilized for a further improvement of distribution models (Heikkinen et al. 2006).

Although the concept of the habitat types of the Habitats Directive is not without definitional weaknesses and a reclassification would have many benefits (Normand et al. 2007), this concept is prevailingly and currently the largest contiguous conservation concept in the EU. It should therefore be considered more intensively in climate change studies.

To limit the expected impacts of climate change on biodiversity, established as well as novel concepts of nature conservation are needed.

Acknowledgements

We thank the Federal Agency for Nature Conservation Germany for funding this work (FKZ 3508 85 0600).

References

Acreman MC, Fisher J, Stratford CJ, Mould DJ, Mountford JO (2007) Hydrological science and wetland restoration: some case studies from Europe. Hydrol Earth Syst Sci 11(1):158-169

Araújo MB, Pearson RG, Thuiller W, Erhard M (2005) Validation of species-climate impact models under climate change. Glob Change Biol 11(9):1504–1513

Araújo MB, Thuiller W, Pearson RG (2006) Climate warming and the decline of amphibians and reptiles in Europe. J Biogeogr 33:1712–1728

Bissonette JA, Adair W (2008) Restoring habitat permeability to roaded landscapes with isometrically-scaled wildlife crossings. Biol Conserv 141(2):482–488

Bittner T, Jaeschke A, Reineking B, Beierkuhnlein C (2011) Comparing modelling approaches at two levels of biological organisation – Climate change impacts on selected Natura 2000 habitats. J Veg Sci 22(4):699–710

Chiarucci A, Araújo MB, Decocq G, Beierkuhnlein C, Fernández-Palacios JM (2010) The concept of potential natural vegetation: an epitaph? J Veg Sci 21(6):1172-1178

Clark JM, Gallego-Sala AV, Allott TEH, Chapman SJ, Farewell T, Freeman C, House JI, Orr HG, Prentice IC, Smith P (2010) Assessing the vulnerability of blanket peat to climate change using an ensemble of statistical bioclimatic envelope models. Clim Res 45:131–150

Cleland EE, Chuine I, Menzel A, Mooney HA, Schwartz MD (2007) Shifting plant phenology in response to global change. Trends Ecol Evol 22(7):357–365

Conroy MJ, Runge MC, Nichols JD, Stodola KW, Cooper RJ (2011) Conservation in the face of climate change: The roles of alternative models, monitoring, and adaptation in confronting and reducing uncertainty. Biol Conserv 144(4):1204–1213

Council Directive 92/43/EEC (1992) Council Directive 92/43/EEC of 21 May 1992 on the conservation of natural habitats and of wild fauna and flora

Dendoncker N, Bogaert P, Rounsevell M (2006) A statistical method to downscale aggregated land use data and scenarios. J Land Use Sci 1(2):63–82

Dimitriou E, Zacharias I (2005) Assessing the impacts of hydrometeorologic and land use changes in a large freshwater body. Fresenius Environ Bull 14(11):1036–1045

Dormann CF, Purschke O, Márquez JRG, Lautenbach S, Schröder B (2008) Components of uncertainty in species distribution analysis: a case study of the Great Grey Shrike. Ecology 89(12):3371–3386

Drakou EG, Kallimanis AS, Mazaris AD, Apostolopoulou E, Pantis JD (2011) Habitat type richness associations with environmental variables: a case study in the Greek Natura 2000 aquatic ecosystems. Biodivers Conserv 20(5):929-943

EIONET (2009) Central Data Repository(CDR). http://cdr.eionet.europa.eu/

Elith J, Leathwick JR (2009) Species Distribution Models: Ecological Explanation and Prediction Across Space and Time. Annu Rev Ecol Evol Syst 40:677–697

European Topic Centre on Biological Diversity (ETC/BD) (2008) Article 17 Technical Report (2001-2006)

Feurdean A, Willis K (2008) The usefulness of a long-term perspective in assessing current forest conservation management in the Apuseni Natural Park Romania. For Ecol Manage 256(3):421-430

Green RE, Collingham YC, Willis SG, Gregory RD, Smith KW, Huntley B (2008) Performance of climate envelope models in retrodicting recent changes in bird population size from observed climatic change. Biol Lett 4(5):599–602

Guisan A, Zimmermann NE (2000) Predictive habitat distribution models in ecology. Ecol Model 135(2-3):147-186

Hannah L, Hansen L (2005) Designing landscapes and seascapes for change. In: Lovejoy TE, Hannah L (eds) Climate Change And Biodiversity Yale University Press, 329–341

Hannah L, Midgley G, Andelman S, Araújo MB, Hughes G, Martinez-Meyer E, Pearson R, Williams P (2007) Protected area needs in a changing climate. Front Ecol Environ 5(3):131-138

Hannah L, Midgley GF, Millar D (2002) Climate change-integrated conservation strategies. Glob Ecol Biogeogr 11(6):485-495

Heikkinen RK, Luoto M, Araujo MB, Virkkala R, Thuiller W, Sykes MT (2006) Methods and uncertainties in bioclimatic envelope modelling under climate change. Prog Phys Geogr 30(6):751–777

Hickling R, Roy DB, Hill JK, Fox R, Thomas CD (2005) A northward shift of range margins in British Odonata. Glob Change Biol 11(3):502–506

Hill JK, Griffiths HM, Thomas CD (2011) Climate Change and Evolutionary Adaptations at Species' Range Margins. Annu Rev Entomol 56(1):143–159

Hitch AT, Leberg PL (2007) Breeding Distributions of North American Bird Species Moving North as a Result of Climate Change. Conserv Biol 21(2):534–539

Jentsch A, Beierkuhnlein C (2003) Global climate change and local disturbance regimes as interacting drivers for shifting altitudinal vegetation patterns. Erdkunde 57(3):216–231

Jentsch A, Kreyling J, Beierkuhnlein C (2007) A new generation of climate-change experiments: events, not trends. Front Ecol Environ 5(7):365–374

Jiménez-Valverde A, Lobo JM (2007) Threshold criteria for conversion of probability of species presence to either-or presence-absence. Acta Oecol - Int J Ecol 31(3):361-369

Julliard R, Jiguet F, Couvet D (2004) Common birds facing global changes: what makes a species at risk? Glob Change Biol 10(1):148-154

Kleinbauer I, Dullinger S, Peterseil J, Essl F (2010) Climate change might drive the invasive tree Robinia pseudacacia into nature reserves and endangered habitats. Biol Conserv 143(2):382–390

Kreyling J, Bittner T, Jaeschke A, Jentsch A, Steinbauer MJ, Thiel D, Beierkuhnlein C (2011) Assisted Colonization: A Question of Focal Units and Recipient Localities. Restor Ecol 19(4):433-440

Lengyel S, Kobler A, Kutnar L, Framstad E, Henry PY, Babij V, Gruber B, Schmeller D, Henle K (2008) A review and a framework for the integration of biodiversity monitoring at the habitat level. Biodivers Conserv 17:3341–3356

Marage D, Gégout J (2009) Importance of soil nutrients in the distribution of forest communities on a large geographical scale. Glob Ecol Biogeogr 18(1):88–97

Marage D, Gegout J (2010) Response of a number of natural forest habitats and their typical species to climate change. Revue Forestiere Francaise (Nancy) 62(3-4):485–500

Marmion M, Parviainen M, Luoto M, Heikkinen RK, Thuiller W (2009) Evaluation of consensus methods in predictive species distribution modelling. Divers Distrib 15(1):59–69

Mawdsley JR, O'Malley R, Ojima DS (2009) A review of climate-change adaptation strategies for wildlife management and biodiversity conservation. Conserv Biol 23(5):1080-1089

Mayes E, Codling I (2009) Water Framework Directive and Related Monitoring Programmes. Biol Environ Proc Royal Irish Acad 109(3):321-344

Mitchell TD, Carter TR, Jones PD, Hulme M, New M (2004) A comprehensive set of high-resolution grids of monthly climate for Europe and the globe: the observed record (1901-2000) and 16 scenarios (2001-2100). Working Paper 55

Moisen GG, Freeman EA, Blackard JA, Frescino TS, Zimmermann NE; Edwards TC Jr (2006) Predicting tree species presence and basal area in Utah: A comparison of stochastic gradient boosting, generalized additive models, and tree-based methods. Ecol Model 199(2):176–187

Müller F, Baessler C, Frenzel M, Klotz S, Schubert H (2010) Long-Term Ecosystem Research Between Theory and Application - An Introduction. In: Müller F, Baessler C, Schubert H (ed) Long-term ecological research. Between theory and application Springer, Dordrecht, New York, 3–7

Normand S, Svenning J, Skov F (2007) National and European perspectives on climate change sensitivity of the habitats directive characteristic plant species. J Nat Conserv 15(1):41–53

Opdam P, Steingröver E, van Rooij S (2006) Ecological networks: A spatial concept for multi-actor planning of sustainable landscapes. Landsc Urban Plan 75(3-4):322–332

Ott J (2010) Dragonflies and climatic change - recent trends in Germany and Europe. BioRisk 5:253–286

Parmesan C, Yohe G (2003) A globally coherent fingerprint of climate change impacts across natural systems. Nature 421(6918):37–42

Pearson RG, Dawson TP (2003) Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? Glob Ecol Biogeogr 12(5):361-371

Petermann J, Balzer S, Ellwanger G, Schröder E, Ssymank A (2007) Klimawandel - Herausforderung für das europaweite Schutzgebietssystem Natura 2000. Naturschutz und Biologische Vielfalt 46:127–148

Plassmann K, Jones MLM, Edwards-Jones G (2010) Effects of long-term grazing management on sand dune vegetation of high conservation interest. Appl Veg Sci 13(1):100–112

R Development Core Team (2010) R: A Language and Environment for Statistical Computing, Vienna, Austria

Raven PJ, Holmes NTH, Vaughan IP, Dawson FH, Scarlett P (2010) Benchmarking habitat quality: observations using River Habitat Survey on near-natural streams and rivers in northern and western Europe. Aquat Conserv Mar Freshwat Ecosyst 20(S1):S13-S30

Rebelo H, Tarroso P, Jones G (2010) Predicted impact of climate change on European bats in relation to their biogeographic patterns. Glob Change Biol 16(2):561-576

Reuter HI, Lado LR, Hengl T, Montanarella L (2008) Continental-scale digital Soil Mapping using European Soil Profile Data: Soil pH. Hamburger Beiträge zur Physischen Geographie und Landschaftsökologie 19:91–102

Settele J, Hammen V, Hulme P, Karlson U, Klotz S, Kotarac M, Kunin W, Marion G, O'Connor M, Petanidou T, Peterson K, Potts S, Pritchard H, Pysek P, Rounsevell M, Spangenberg JH, Steffan-Dewenter I, Sykes M, Vighi M, Zobel M, Kühn I (2005) ALARM: Assessing Large-scale environmental Risks for biodiversity with tested Methods. GAIA 14(1):69–72

Spangenberg JH (2007) Integrated scenarios for assessing biodiversity risks. Sustainable Development 15(6):343–356

Ssymank A, Hauke U, Rückriem C, Schröder E (eds) (1998) Das europäische Schutzgebietssystem NATURA 2000. BfN-Handbuch zur Umsetzung der Fauna-Flora-Habitat-Richtlinie (92/43/EWG) und der Vogelschutzrichtlinie (79/409/EWG). BfN-Schr.-Vertrieb im Landwirtschaftsverl., Münster

Swets JA (1988) Measuring the accuracy of diagnostic systems. Science, 240:1285–1293

Thomaes A, Kervyn T, Maes D (2008) Applying species distribution modelling for the conservation of the threatened saproxylic Stag Beetle (Lucanus cervus). Biol Conserv 141(5):1400–1410

Thuiller W (2003) BIOMOD - optimizing predicitions of species distributions and projecting potential future shifts under global change. Glob Change Biol 9:1353–1362

Thuiller W, Lafourcade B, Engler R, Araújo MB (2009) BIOMOD – a platform for ensemble forecasting of species distributions. Ecography 32(3):369-373.

Thuiller W, Lavorel S, Araújo MB, Sykes MT, Prentice CI (2005) Climate change threats to plant diversity in Europe. Proc Natl Acad Sci U S A 102(23):8245–8250

Walther G, Beißner S, Burga CA (2005) Trends in the upward shift of alpine plants. J Veg Sci 16(5):541–548

Walther GR, Roques A, Hulme P, Sykes MT, Pyšek P, Kühn I, Zobel M, Bacher S, Botta-Dukát Z, Bugmann H, Czúcz B, Dauber J, Hickler T, Jarošík V, Kenis M, Klotz S, Minchin D, Moora M, Nentwig W, Ott J, Panov VE, Reineking B, Robinet C, Semenchenko V, Solarz W, Thuiller W, Vilá M, Vohland K, Settele J (2009) Alien species in a warmer world: risks and opportunities. Trends Ecol Evol 24:686–693

Weaver AJ, Zwiers FW (2000) Uncertainty in climate change. Nature 407(6804):571–572

Williams JW, Jackson ST (2007) Novel climates, no-analog communities, and ecological surprises. Front Ecol Environ 5(9):475–482

Zacharias I, Zamparas M (2010) Mediterranean temporary ponds. A disappearing ecosystem. Biodivers Conserv 19(14):3827–3834

Supplement:

Tab. S1: Modelling results of the 127 habitat types for the emission scenarios B1, A2 and A1FI and three different time spans 2021-2050 (2035); 2051-2080 (2065); 2071-2100 (2085) under the assumption of no dispersal.

Habitat type	Modelling results in percentage range change								
	B1			A2			A1FI		
	2035	2065	2085	2035	2065	2085	2035	2065	2085
4010	-24	-35	-42	-17	-33	-50	-26	-45	-63
4020	-11	-11	-19	-8	-7	-12	-8	-9	-13
4030	-10	-21	-21	-6	-18	-23	-8	-26	-32
4040	-50	-64	-61	-39	-61	-52	-48	-72	-71
4060	-21	-34	-34	-27	-48	-58	-31	-55	-63
4070	-49	-45	-65	-39	-44	-67	-49	-57	-78
4080	-24	-45	-46	-28	-61	-74	-30	-69	-78
4090	-11	-19	-19	-13	-29	-35	-14	-34	-43
40A0	-11	-37	-20	-8	-30	-15	-9	-44	-39
5110	-32	-58	-53	-33	-62	-68	-31	-66	-67
5120	-22	-35	-28	-26	-45	-35	-23	-31	-20
5130	-20	-35	-39	-14	-35	-58	-18	-48	-70
5210	-6	-14	-8	-4	-14	-11	-6	-21	-18
5230	-2	-4	-5	-2	-3	-4	-2	-5	-7
5310	-36	0	-17	-19	-20	-8	-35	-30	-47
5320	-3	-5	-3	-3	-2	-3	-3	-2	-3
5330	0	-1	0	-1	-1	0	0	0	0
5410	-13	-17	-18	-5	-8	-8	-12	-17	-19
5420	0	0	0	0	0	0	0	0	0
5430	-1	0	0	-2	0	0	-1	0	0
6110	-23	-36	-36	-21	-37	-48	-25	-46	-56
6120	-38	-48	-49	-38	-62	-64	-44	-66	-74
6130	-21	-24	-29	-20	-24	-29	-22	-31	-35
6140	-47	-73	-72	-46	-84	-82	-47	-90	-87
6150	-30	-31	-44	-35	-48	-74	-38	-57	-74
6160	-19	-40	-33	-31	-54	-56	-28	-53	-52
6170	-27	-45	-40	-29	-54	-56	-35	-63	-63
6190	-48	-72	-66	-26	-57	-45	-41	-71	-74
6210	-23	-30	-48	-16	-32	-66	-20	-48	-76
6220	0	-1	0	0	-1	0	-1	-1	0
6230	-19	-31	-31	-15	-26	-43	-17	-36	-50
6240	-27	-42	-42	-20	-33	-34	-24	-55	-61
6250	-15	-55	-56	-9	-53	-35	-12	-61	-50
6260	-15	-35	-24	-14	-27	-18	-14	-36	-35
6270	-26	-47	-53	-21	-39	-64	-21	-43	-58
6280	-34	-31	-52	-50	-41	-85	-41	-44	-72
6410	-30	-38	-38	-26	-36	-43	-29	-41	-56
6420	-3	-4	-2	-2	-4	-1	-2	-3	-1
6430	-36	-48	-46	-37	-54	-66	-38	-59	-69
6440	-8	-26	-23	-6	-18	-10	-8	-35	-44
6450	-15	-25	-31	-12	-21	-36	-14	-34	-48
6510	-24	-50	-46	-20	-48	-62	-25	-64	-82
6520	-50	-50	-62	-52	-64	-79	-53	-68	-82
6530	-44	-40	-54	-44	-45	-71	-47	-56	-78
7110	-19	-23	-25	-24	-34	-49	-27	-43	-60
7120	-31	-43	-51	-27	-42	-55	-27	-45	-60
7130	-7	-14	-10	-6	-14	-11	-7	-13	-16
7140	-17	-25	-29	-16	-26	-38	-17	-33	-47
7150	-14	-30	-26	-13	-32	-43	-16	-40	-51
7160	-12	-22	-25	-13	-21	-29	-15	-30	-41
7210	-15	-38	-30	-9	-30	-27	-13	-43	-47
7220	-31	-45	-47	-27	-47	-58	-33	-58	-67
7230	-27	-47	-45	-20	-39	-49	-24	-53	-60
7240	-32	-44	-43	-30	-47	-56	-34	-54	-58
7310	-5	-10	-7	-4	-7	-8	-5	-7	-6
7320	-58	-82	-94	-44	-84	-98	-55	-98	-99
8110	-24	-35	-35	-27	-41	-46	-30	-46	-50
8120	-28	-36	-39	-29	-44	-55	-33	-50	-62
8130	-16	-38	-24	-14	-35	-29	-21	-53	-52
8140	-13	-14	-12	-4	-8	-4	-3	-6	-2
8150	-29	-39	-48	-28	-42	-58	-37	-58	-74
8160	-28	-36	-47	-30	-47	-75	-32	-57	-80
8210	-8	-10	-9	-8	-12	-11	-9	-18	-17
8220	-18	-34	-37	-19	-40	-50	-21	-49	-62

8230	-38	-58	-55	-38	-66	-70	-39	-69	-70
8240	-24	-32	-31	-25	-36	-39	-30	-43	-47
9010	-12	-18	-18	-15	-22	-33	-16	-35	-48
9020	-23	-38	-39	-29	-46	-59	-31	-55	-69
9030	-56	-63	-80	-50	-61	-96	-44	-63	-95
9040	-45	-70	-71	-50	-86	-94	-59	-96	-99
9050	-21	-32	-45	-15	-26	-51	-13	-30	-53
9060	-15	-21	-25	-20	-29	-50	-27	-49	-78
9070	-16	-27	-35	-14	-26	-51	-14	-32	-57
9080	-14	-33	-37	-14	-32	-47	-17	-43	-63
9110	-26	-33	-46	-20	-27	-52	-25	-48	-70
9120	-24	-46	-49	-16	-50	-65	-23	-61	-79
9130	-17	-25	-32	-16	-24	-50	-16	-38	-71
9140	-39	-43	-54	-34	-42	-55	-40	-52	-72
9150	-23	-39	-41	-19	-39	-48	-24	-49	-59
9160	-30	-66	-61	-18	-44	-52	-28	-59	-64
9170	-21	-31	-39	-18	-25	-42	-24	-48	-56
9180	-22	-30	-40	-18	-32	-55	-19	-41	-62
9190	-8	-16	-25	-4	-11	-32	-8	-32	-57
91A0	-8	-15	-11	-6	-13	-10	-8	-15	-17
91B0	-5	-5	-4	-6	-4	-1	-6	-2	-1
91C0	-17	-55	-28	-20	-58	-49	-21	-65	-50
91D0	-18	-22	-25	-15	-23	-28	-20	-32	-36
91E0	-12	-16	-18	-13	-19	-24	-15	-26	-33
91F0	-13	-16	-16	-10	-12	-11	-13	-16	-14
91G0	-42	-76	-73	-26	-64	-54	-34	-84	-84
91H0	-30	-61	-43	-14	-49	-28	-24	-57	-48
91I0	-2	-2	-4	-6	-6	-3	-4	-3	0
91J0	-17	-17	-19	-18	-22	-25	-17	-26	-26
91K0	-53	-56	-68	-52	-58	-77	-57	-72	-82
91L0	-59	-65	-80	-48	-71	-76	-46	-61	-61
91M0	-25	-21	-19	-16	-11	-3	-16	-6	-6
91N0	-90	-92	-94	-88	-93	-94	-89	-94	-94
91P0	-96	-99	-97	-98	-99	-100	-99	-100	-100
91Q0	-76	-87	-94	-60	-84	-96	-68	-92	-96
91R0	-39	-40	-61	-35	-42	-64	-44	-74	-95
91T0	-27	-45	-46	-24	-65	-75	-35	-89	-95
91U0	-39	-31	-40	-38	-31	-27	-33	-22	-22
9210	-14	-20	-13	-13	-19	-11	-15	-23	-8
9220	-23	-47	-20	-22	-36	-10	-29	-24	-4
9230	-10	-37	-20	-19	-53	-55	-13	-56	-52
9240	-13	-25	-18	-29	-52	-51	-19	-38	-32
9250	-74	-74	-72	-71	-74	-75	-76	-75	-75
9260	-13	-9	-13	-11	-8	-11	-12	-6	-9
9270	-31	-66	-44	-14	-55	-41	-16	-57	-43
9280	-39	-53	-63	-30	-52	-70	-38	-64	-78
9290	0	-19	-5	0	-32	-22	0	-30	-24
92A0	-15	-30	-37	-14	-37	-54	-17	-52	-67
92C0	-1	-1	0	-2	-1	0	-1	0	0
92D0	-1	-2	-1	-1	-1	0	-1	0	0
9320	-6	-1	-2	-5	-1	-1	-6	-1	-1
9330	-6	-6	-4	-5	-5	-3	-5	-4	-3
9340	-1	-3	-2	-2	-4	-4	-2	-4	-4
9350	-1	-3	-1	0	-3	0	0	-1	-1
9380	-21	-39	-28	-21	-44	-33	-25	-53	-44
9410	-46	-46	-58	-40	-44	-59	-47	-58	-75
9420	-46	-49	-61	-45	-54	-73	-51	-64	-80
9430	-46	-66	-63	-44	-66	-69	-47	-72	-75
9510	-30	-74	-42	-35	-77	-55	-45	-84	-80
9530	-15	-15	-14	-15	-15	-14	-14	-17	-16
9540	-9	-10	-6	-8	-7	-3	-8	-6	-2
9560	-27	-39	-34	-24	-40	-42	-28	-50	-53
9580	-35	-57	-46	-34	-59	-54	-44	-70	-71

Article 4

Habitat coherence and climate change: an analysis application for the Natura 2000 network in Germany

Holger Dempe, Torsten Bittner, Anja Jaeschke, Carl Beierkuhnlein

submitted to Ecological Applications on 2011-09-21

Abstract

Climate change poses a sparsely researched threat to the Natura 2000 network of the Habitats Directive of the European Union. This study exemplary assesses in an integrative approach the impacts of climate change on habitat coherence in Germany for six different habitat types as defined by the Habitats Directive.

An ensemble of environmental envelope models (BIOMOD) was utilized to project future environmental space for three time steps (2020s, 2050s & 2080s). Subsequently, an omnidirectional dispersal model under consideration of costs was applied for realistic and optimistic dispersal distances to identify the potentially reachable areas. Finally, habitat coherence was calculated for two graph-based indices for a total of 108 cases split over 10 scenarios for the six habitat types.

The ensemble of environmental envelope models exhibits high performance for all six habitat types. Three out of six habitat types are not only projected to increase environmental space but also feature higher habitat coherence in the majority of scenarios. The remaining three habitat types show range contractions and lose coherence in nearly all scenarios. Inclusion of costs in the analysis triggers a lower coherence in comparison to the same scenarios without costs. Both graph based indices generally produce consistent results.

A feasible combination of environmental envelope models and graph theory to assess coherence of nature conservation networks is demonstrated in this study. Required information to guide decision makers can easily be inferred not only in form of raw numbers but also in a spatially explicit way by maps if desired.

Keywords

climate change, habitat types, coherence, Natura 2000, graph theory, environmental envelop models, Germany

Habitat coherence and climate change: an analysis application for the Natura 2000 network in Germany

Holger Dempe[1], Torsten Bittner[1,2], Anja Jaeschke[1,2], Carl Beierkuhnlein[1]

[1] Department of Biogeography, BayCEER, University of Bayreuth, Bayreuth, Germany
[2] Department of Biogeographical Modelling, BayCEER, University of Bayreuth, Bayreuth, Germany

Introduction

Today's knowledge on implications of rapid climate change for ecosystems and its constituting elements is still marked by high uncertainties and important aspects have not been covered yet or only to a small degree by science. Nevertheless, ecological effects related to climate change can already be observed. One aspect out of many concerns a wide range of taxonomic and functional groups, where strong evidence is given for responses to climate change in form of geographical range shifts (e.g. Parmesan and Yohe 2003, Lenoir et al. 2008).

Future projections of species distributions indicate even more drastic changes for habitats and ecosystems (e.g. Thuiller et al. 2011), representing a challenge for nature conservation (Hannah et al. 2007). This is especially true for large-scale conservation networks (Hole et al. 2009) like the Natura 2000 network of the European Union.

Habitat types, as defined in the Annex I of the Habitats Directive (Council Directive 92 43 EEC 1992), located within the Federal Republic of Germany are the focus of our study. Patches assigned to certain habitat types are classified and reported by the European Union member states and constitute the Sites of Community Importance (SCI). SCI together with Special Protection Areas (SPA), as defined in the Birds directive, form the Natura 2000 Network. This network represents one of the most extensive conservation networks in the world. It comprises 22,000 SCIs, accounting to 13.3% of the EU territory (European Commission 2009) respectively. Germany contributes a total of 4,627 SCIs, covering 9.3% of Germany's terrestrial surface (BfN and BMU 2008).

Starting point for a better understanding of possible future developments and for proactive management strategies are distribution models. Such models can help for example to identify the current potential geographical distribution of habitat types (Mücher et al. 2009) or enable an analysis of the effectiveness of networks under climate change by projecting into the future (e.g. Araújo et al. 2011).

One widely used group of tools to project the potential future distributions of species or habitats under climate change are environmental envelope models (EEM) that are based on the relationship between factors like climate or soil and the presence and/or absence of species or habitats (e.g. Araújo and Guisan 2006). During the past few years the concept has been extended by ensemble forecasting frameworks, like BIOMOD (Thuiller et al. 2009), combining the strengths of multiple EEMs into a single projection output with fewer uncertainties (Araújo and New 2007).

Knowledge of a potential future distribution alone is not sufficient for a sound assessment of the future conditions of a nature conservation network. A further important aspect is connectivity (e.g. Cabeza 2003), although the absolute importance is questioned (Hodgson et al. 2009, Doerr et al. 2011). Nevertheless, the general relevance of trade-offs between habitat-size, quality and connectivity is acknowledged (Hodgson et al. 2011). This is conform to the accepted rule, borrowed from island biogeography, that large, compact and better connected patches should be prioritized in order to achieve nature conservation targets (Diamond 1975). Including connectivity aspects in nature conservation planning is therefore recommended (e.g. Van Teeffelen et al. 2006).

One probate approach to analyze and model spatial relationships among patches in an ecological meaningful way comes from graph theory (e.g. Urban et al. 2009). Graphs can give insights in the functional response of habitat types (or other structural elements) to alterations of landscape pattern. Optionally, further aspects like impacts of climate change, land use scenarios or different management options can be evaluated.

Despite the importance of connectivity for nature conservation strategies, this field of application is just emerging in the context of climate change research. Although, there is indication that increased habitat fragmentation is likely to diminish species' capacity for range shifts under climate change (Opdam and Wascher 2004). Vos et al. (2008) were the first to employ EEM-techniques in combination with dispersal models to assess impacts of climate change on the spatial cohesion of the Natura 2000 network by considering a selection of species as representatives of different ecosystem types. In respect to the Natura 2000 network, only few studies have dealt explicitly with the proprietary entity of habitat types so far (Mücher et al. 2009, Zacharias and Zamparas 2010, Bittner et al. 2011), thus neglecting an important aspect of this conservation concept.

The aim of this study is to quantify the adaptation capacity of the Natura 2000 network to climate change in terms of functional properties of habitats by an integrative combination of environmental envelope models and graph theory. Habitat types potentially gaining space with suitable growing conditions both inside and outside existing Natura 2000 protection areas are expected to increase connectivity when all reachable patches are colonized under climate change. Vice versa, habitat types likely to loose suitable environmental space are expected to exhibit lower connectivity in the future. Furthermore, a coherence reducing effect by the inclusion of cost grids and land cover information in the analysis is anticipated, due to the implications for the effective dispersal distance of habitat types.

Material & methods

Habitat types

Six "natural habitat types of community interest" as defined in the Annex I of the EU Habitats Directive (Council Directive 92 43 EEC 1992) have been exemplary chosen. The selection (Tab. 1) represents the major Annex-I-groups of terrestrial habitat types and covers the complete territory of Germany. Coastal and halophytic habitats (group 1xxx), inland and coastal sand dunes (group 2xxx) as well as freshwater habitats (group 3xxx) have been excluded due to the necessity of a different modeling approach including data like for example sea level or water temperature dynamics (e.g. Boyd and Doney 2002).

Only habitat types with a medium abundance in Germany and a potential sensitivity to climate change (European Topic Centre on Biological Diversity ETC BD 2008) have been considered. A further selection criterion was to maximize the diversity of environmental requirements covered by the habitat types, especially in respect to substrate, moisture and temperature (Tab. 1). Further information on the six habitat types can be found in the Interpretation Manual of European Union Habitats (European Commission 2007).

Two representatives play a special role because they are limited to their presently known locations for future projections. In the case of "Raised bogs", the undifferentiated combination of "active raised bogs" (7110) and "degraded bogs" (7120), it is a matter of time as the formation of raised bogs takes place on time scales longer than the study period of 80 years. Similarly, habitat type 8160, belonging to the group of rocky habitats and caves, is restricted to places where calcareous or marly screes of the hill and montane levels occur (European Commission 2007).

For each of the six selected habitat types a hypothesis was formulated in respect to their expected response to climate change (Tab. 1).

Tab. 1: Selected habitat types. Expected response to climate change is marked by a plus sign '+' for habitat types gaining area with suitable growth conditions, while habitat types losing area are marked by a minus sign '-'. Symbols: s: siliceous, c: calcareous, o: organic, t: temperate, w: warm, c: cold, m: moist, sd: semidry, d: dry, * priority habitat types, $^{\#}$ no dispersal ability.

Habitat type		**Substrate**	**Temperature**	**Moisture**	**Response**
4030	European dry heaths	s	t	m-d	+
5130	*Juniperus communis* formations on heaths or calcareous grasslands	c/s	t	m	+
6210	Semi-natural dry grasslands and scrubland facies on calcareous substrates (*Festuco-Brometalia*) (* important orchid sites)	c	w	sd-d	+
71X0	Active raised bogs$^{\#*}$ (7110) and degraded raised bogs still capable of natural regeneration$^{\#}$ (7120)	o	c-w	m	-
8160	Medio-European calcareous screes of hill and montane levels$^{\#*}$	c	w	d	-
9170	*Galio-Carpinetum* oak-hornbeam forests	c/s	w	sd-d	+

Environmental and habitat type distribution data

Current European climate and elevation data was quantified on a 30″ (arc seconds) grid and originates from the WorldClim dataset version 1.4 as described in Hijmans et al. (2005). Future projections of the European climate are based on the intermediate BAMBU (Business As Might Be Usual, A2) scenario (Spangenberg 2007) driven by the HadCM3 climate model. Future datasets for the 2020s, 2050s and 2080s were obtained in a 30″ spatial-resolution from the International Centre for Tropical Agriculture (CIAT) climate change downscaled data website (CIAT 2010). Soil pH, as indicator for nutrient availability, was provided by the European Soil Data Center at the Joint Research Center of the European Commission and is depicted in Reuter et al. (2008). All environmental data were aggregated into a single vector grid with a spatial resolution of 2.5 km by 2.5 km, covering the EU25 countries except Cyprus and remote islands like the Canary Islands.

The Central Data Repository server of the European Environment Information and Observation Network (EIONET) delivered information on the current distribution of the selected habitat types for the EU25 countries in different spatial resolutions (EIONET 2009). The data originate from the European reporting of the year 2007 pursuant to Article 17 of the Habitats Directive. The distribution data were integrated in the same 2.5 km grid as the environmental data. In case of Germany, the presence data for habitat types were intersected with the exact borders of the SCIs and subsequently generalized to the 2.5 km resolution.

Environmental envelope modeling (EEM)

Prior to the actual modeling, a statistical variable selection for each habitat type was executed. Only those environmental variables with a correlation less than 0.7 were retained for the EEM runs (Appendix A).

Environmental envelope modeling was realized with the BIOMOD package version 1.1-6.7 (Thuiller et al. 2009) in addition to the provided packages within R 2.12.0 (R Development Core Team 2010). All nine in this version implemented modeling algorithms (generalized linear models (GLM), generalized additive models (GAM), multivariate adaptive regression splines (MARS), classification tree analysis (CTA), flexible discriminant analysis (FDA), artificial neural networks (ANN), generalized boosted models (GBM), random forests (RF), and surface range envelope (SRE)) were enabled for the ensemble forecasting with three evaluation runs. The results were validated with a one-time data splitting method (Araújo and Pearson 2005), randomly separating the data set in 70% calibration and 30% evaluation data. The area under the receiver operating characteristic curve (AUC) as projection performance criterion was applied to measure the overall model discrimination (Swets 1988). The threshold for occurrence and non-occurrence projections was selected by a maximizing Kappa approach (Pearson et al. 2002).

Dispersal distances and costs

The dispersal behavior of habitat types cannot be clearly defined for the reason that it is a heterogeneous mixture of different dispersal strategies of the constituting species (both flora and fauna). For each habitat type a realistic and an optimistic dispersal distance were defined (Appendix A) based on the dispersal traits (Rothmaler et al. 2005, Federal Agency for Nature Conservation Germany 2011) of the plant key species as listed in the Interpretation Manual of European Union Habitats (European Commission 2007).

A further important aspect for dispersal is the influence of landscape properties. These effects can for instance be incorporated in form of costs to cross a landscape (e.g. Foltête et al. 2008). In this study a 100 m by 100 m cost grid was generated by summing up the cost factors (Appendix A) based on the major classes of the Corine Land Cover 2006 100 m raster data (European Environment Agency 2010) and the classified WorldClim 30″ altitude data (CIAT 2010) for each raster cell. Possible cost factor sums range from one (natural areas below 500 m) to 18 (urban areas above 1500 m a.s.l.), where one represents the lowest costs and 18 the highest cost to cross the respective raster cell.

Under the assumption of an omnidirectional dispersal of habitat types, the reachable potential future suitable areas were identified with the tools “Cost distance” and “Extract Values by Points” within the Spatial Analyst extension of ArcGIS 10.0 SP2. Cost distances were calculated from the centroids of the 2.5 km grids cells representing the habitats of the preceding time step. Maximum dispersal distances for each of the three future time periods (2000-2020, 2020-2050, 2050-2080) were considered in the cost distance calculations as given in Appendix A. Preceding to the data preparation for the connectivity analysis with the help of the tool “Conefor Inputs for ArcGIS 10” revision 1.0.146 (Jenness 2011), the borders of directly adjacent 2.5 km habitat vector grid cells, depicting habitats, were dissolved into a single continuous habitat patch.

Connectivity analysis

In recent years many different (graph based) connectivity indices have been developed (e.g. Bunn et al. 2000, Urban and Keitt 2001, Saura and Rubio 2010). This study applies two recently introduced graph based indices the “integral index of connectivity” (IIC) (Pascual-Hortal and Saura 2006) and the “probability of connectivity” (PC) (Saura and Pascual-Hortal 2007). Both are included in the software package “Conefor Sensinode” version 2.5.8 (beta), described in Saura and Torne (2009).

In graph theory, a landscape is represented by habitat patches, the so-called nodes, and the possibility of dispersal between two habitat patches, the so-called links (Fig. 1). A set of nodes (or habitat patches) in which a path exists between every pair of nodes defines a component (Fig. 1). IIC belongs to the group of binary indices, where a connection between two patches simply either exists or not (Fig. 1). For probabilistic indices, like PC, interpatch connections are based on dispersal probabilities (Fig. 1). Here, the exponential decay function of interpatch distance included in Conefor Sensinode was used for this purpose (McCallum 2000, Saura and Pascual-Hortal 2007) with a probability of 0.05 assigned to the maximum connectivity distances. Both PC and IIC are sensitive to the loss of different types of landscape elements and help to identify the most critical SCIs for conservation (Saura and Torne 2009). Furthermore, they allow for the quantification of topological traits in combination with relevant ecological characteristics of habitat patches and links (Saura and Torne 2009).

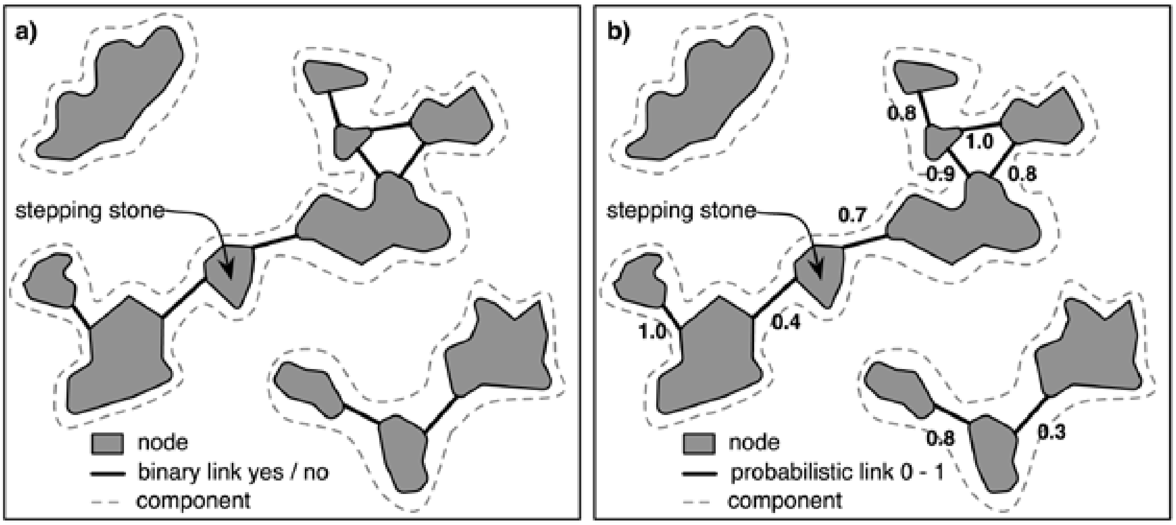


Fig. 1: Illustration of key terms in landscape graphs. Patches represent nodes that are connected by links from boundary to boundary. Components are a group of nodes connected by links. a) For binary connectivity indices a link either exists or not. b) Probabilistic indices assign a probability to each link, where a probability of zero denotes a non-existing link and a probability of one a strong link between two habitat patches.

A total of 108 connectivity cases for all habitat types were considered (Fig. 2). For each habitat type several connectivity cases for the four time steps current (2000s), 2020s, 2050s and 2080s were calculated. The patches within a specific distance range principally define connectivity, hereafter this range is termed "connectivity distance". Similar to the two dispersal distances (realistic and optimistic), the patches within reach were identified by calculating the Euclidean connectivity distance from the boundary of one patch to all other patches for a period of 30 years for each time step. A 30-year period was chosen to avoid biased connectivity measures due to the relationship between time, connectivity distance and overall connectivity values (the longer the time period, the bigger the connectivity distance, the higher the likelihood of a better connected landscape). Only those connections smaller than the maximum connectivity distances (realistic or optimistic) were kept and saved in a connection file by the "Conefor Inputs" tool.

The current situation of each habitat type was assessed for the two cases of a realistic and an optimistic connectivity distance (Appendix A). Future time steps were further differentiated for the case that habitat types cannot disperse and for the case that habitat types can disperse (based on the realistic and optimistic dispersal / connectivity distances). The dispersal case was further refined by two management options: the first option only considers the gain in new space within the existing boundaries of the current SCI network, while the second option allows for an additional gain of new space outside the SCI borders, namely the complete area of Germany, excluding urban areas.

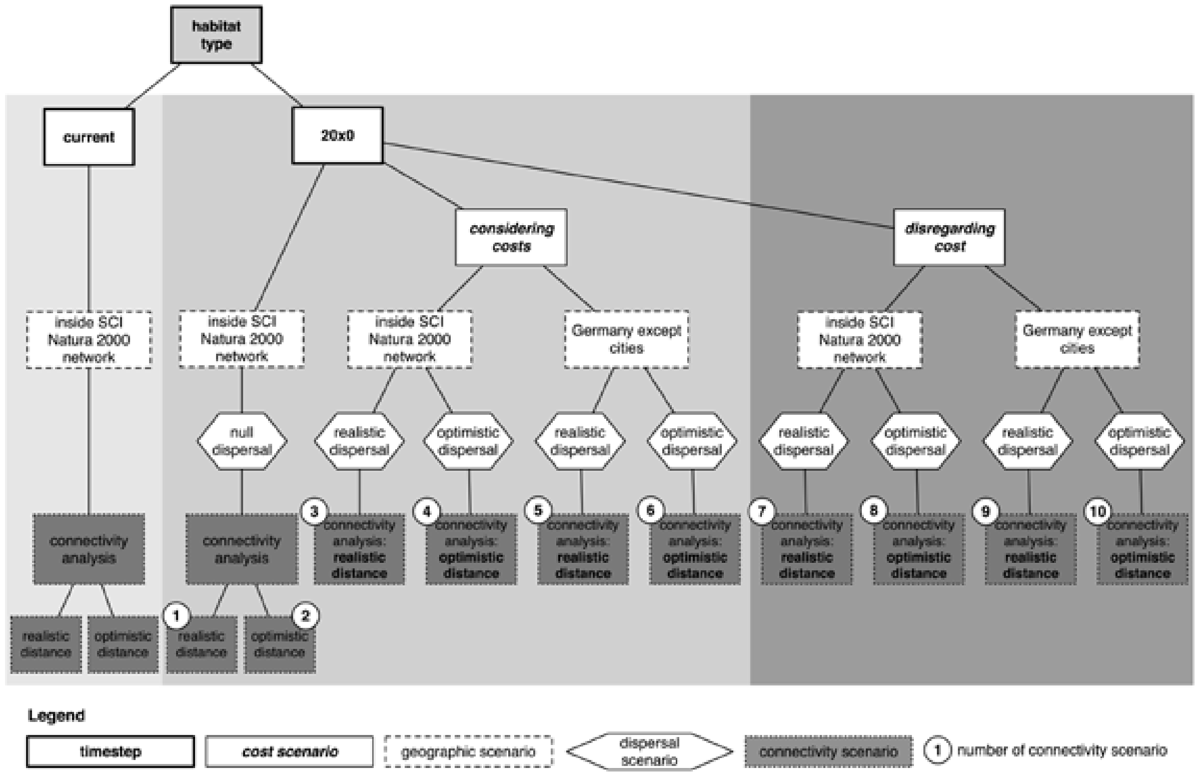


Fig. 2: Outline of the different connectivity scenarios accounted for in the modeling. The different scenarios are derived from a hierarchy of different boundary connections. Scenarios one and two apply to all habitat types. Scenarios three, four, five and six apply only to those habitat types capable of dispersal (4030, 5130, 6210, 9170). The branch of scenarios disregarding costs for dispersal (seven to ten) are exemplarily modeled for habitat type 4030.

The effects of cost exclusion in the analysis were exemplary assessed for habitat 4030, while for habitat types 5130, 6210 and 9170 the scenario of excluding costs was left out for the reason that no new findings were anticipated. As habitat types 71X0 and 8160 cannot disperse on the temporal scale of this study, only the two cases of realistic and optimistic connectivity distances were considered for all time steps.

Results

Potential future spatial developments

The EEM results are exemplarily depicted for three scenarios of "European dry heaths" (habitat type 4030) in Fig. 3 (for further details refer to Appendix A). "European dry heaths", "*Juniperus communis* formations on heaths or calcareous grasslands" (habitat type 5130) and "semi-natural dry grasslands and scrub-land facies on calcareous substrates (*Festuco-Brometalia*, habitat type 6210)" are projected to gain suitable new habitat for each time step in the majority of scenarios, while "raised bogs" (habitat type 71X0), "Medio-European calcareous screes of hill and montane levels" (habitat type 8160) and "*Galio-Carpinetum* oak-hornbeam forests" (habitat type 9170) lose suitable habitat space. "Raised bogs" (71X0) and

"Medio-European calcareous screes of hill and montane levels" (8160) exhibit an undirected range contraction, the forest habitat type 9170 a directed range contraction to the southeast. The remaining three habitat types do not exhibit distinct range shifts or range contractions.

Scenarios not restricted to the Natura 2000 network (scenarios 5, 6, 9 and 10) are clearly distinguishable from null dispersal and SCI limited scenarios as they form large, dense habitat patches (not shown here). The highest increase of suitable area is projected for dry heaths (4030), *Juniperus communis* formations (5130) and partly for "semi-natural dry grasslands and scrub-land facies on calcareous substrates" (6210) for the period of the 2050s.

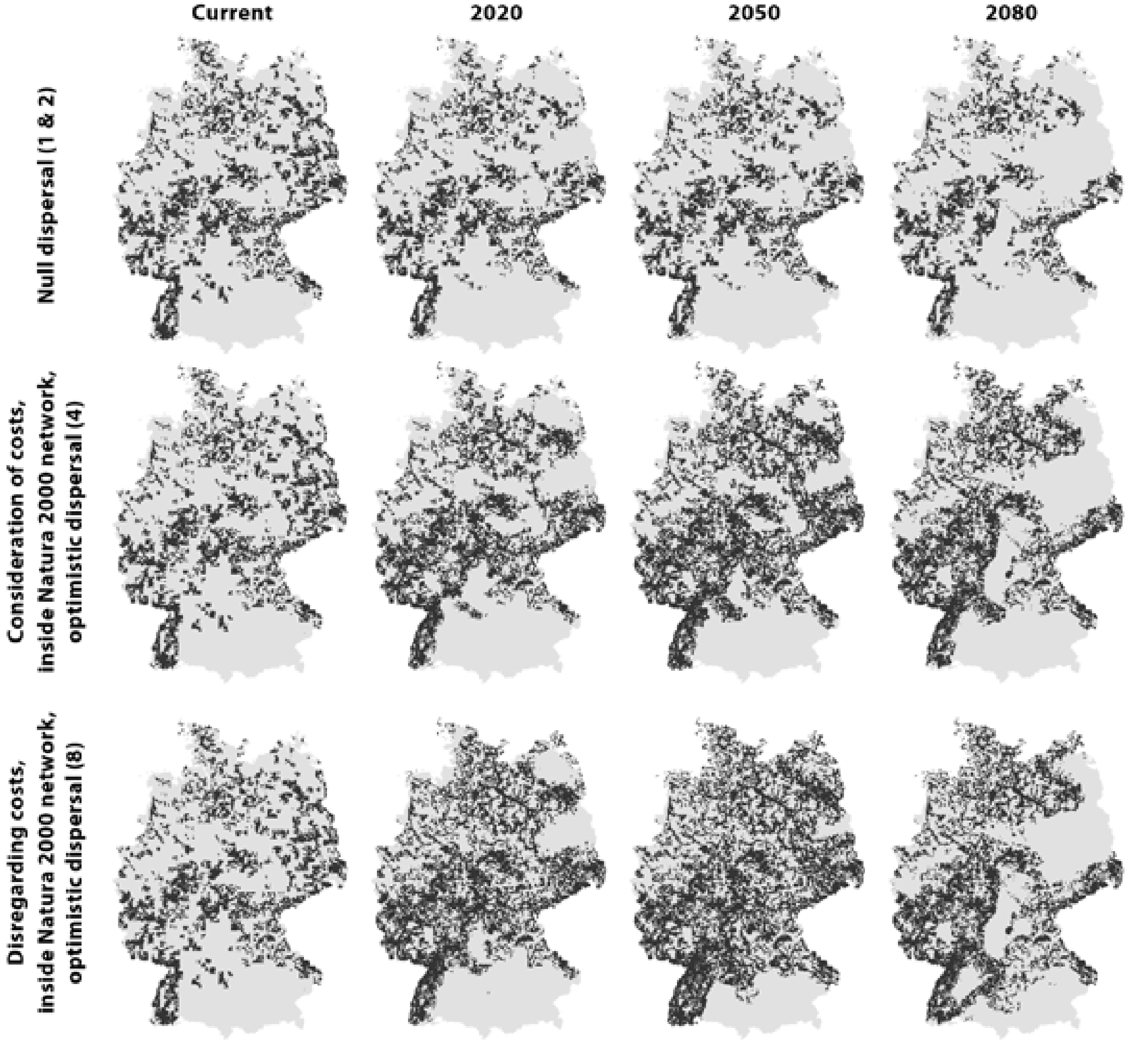


Fig. 3: Potential future development of the distribution of "European dry heaths" (4030) during the 21st century in Germany for the scenarios 1, 2, 4 and 8. Climate model HadCM3, IPCC emission scenario A2, AUC = 0.84.

All habitat types are projected to lose suitable environmental space for the null dispersal scenarios 1 and 2. The most severe losses in relation to the current situation particularly concern the habitat types restricted to their current occurrences, namely "raised bogs" (71X0) and "Medio-European calcareous screes of hill and montane levels" (8160). According to the EEM future projections "active raised bogs" might almost completely lose their current environmental space in Germany until 2080.

Not only the dispersal restricted habitat types exhibit losses, but also the suitable area of "*Galio-Carpinetum* oak-hornbeam forests" (9170) is drastically reduced to small remnants mainly in the southeast of Germany until 2080. Although the changes until 2020 are comparatively small, the changes from 2020 to 2050 and from 2050 to 2080 are considerably large for "*Galio-Carpinetum* oak-hornbeam forests".

Future trends in habitat coherence

The probability of connectivity index (PC) and the integral index of connectivity (IIC) are within the same value range and exhibit consistent trends (increase or decrease between two time steps) for most scenarios of all habitat types (Appendix A). Both indices calculate higher connectivity values for the optimistic scenarios of all habitat types. The optimistic scenarios not restricted to the SCI boundaries (scenarios 6 and 10) always feature the highest connectivity for all habitat types and time steps, while the corresponding realistic scenarios (scenarios 5 and 9) do so only in some cases. The omission of costs leads to higher connectivity values for both indices as exemplarily depicted for the "European dry heaths" (4030) in Fig. 4. The differences between the optimistic scenarios are smaller than between the realistic scenarios of habitat type 4030 (Fig. 4).

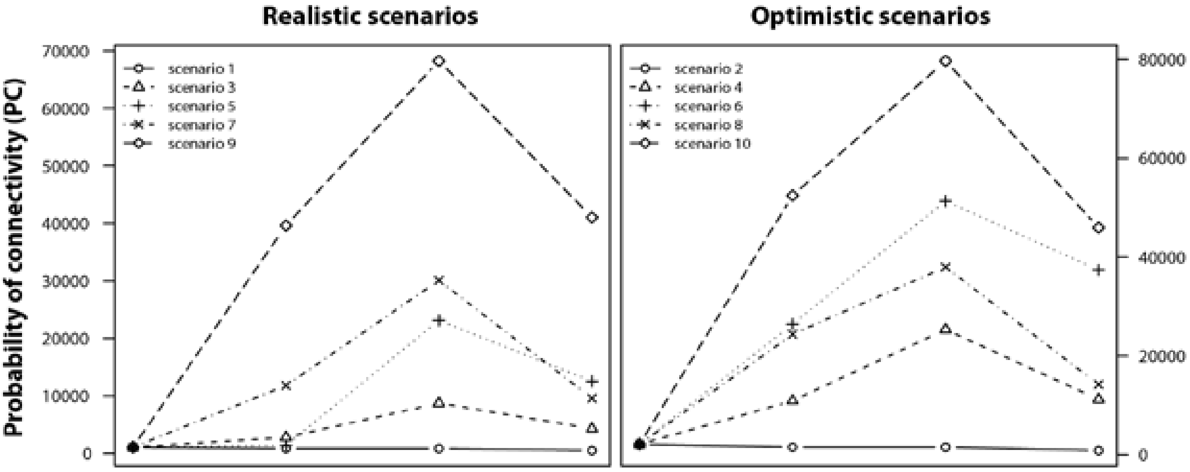


Fig. 4: Overall index values for "European dry heaths" (habitat type 4030) of the probability of connectivity index (PC) plotted separately for the realistic and the optimistic scenarios.

An evident tendency towards higher connectivity values for the unrestricted scenarios (5, 6, 9, 10) in comparison to the SCI boundary restricted pendants (3, 4, 7, 8) can be observed. The null dispersal scenarios (1 and 2) of all habitat types lose coherence in the future and exhibit the lowest connectivity values (both for PC and IIC) of all scenarios.

Apart from the null dispersal scenarios, a strong increase in connectivity can be observed in the 2050s for the dry heaths (4030), the *Juniperus communis* formations (5130) and the "semi-natural dry grasslands and scrubland facies on calcareous substrates" (6210). "*Galio-Carpinetum* oak-hornbeam forests" (9170) gain connectivity only in the 2020s for the optimistic geographic scenarios (4 and 6) (Appendix A).

Tab. 2 gives a summary of the potential response of the six modeled habitat types to climate change with respect to habitat coherence. Dry heaths (4030) and the *Juniperus communis* formations (5130) benefit in most cases under the influence of climate change. "Semi-natural dry grasslands and scrubland facies on calcareous substrates" (6210) draw an ambivalent picture as they profit mostly in the 2050s or for the complete scenario 6 (consideration of costs, SCI unlimited, optimistic dispersal). "*Galio-Carpinetum* oak-hornbeam forests" (9170) lose connectivity in nearly all scenarios except for the two optimistic geographic scenarios 4 and 6 in 2020. The two scenarios of the stationary habitat types "raised bogs" (71X0) and "Medio-European calcareous screes of hill and montane levels" (8160) lose coherence under climate change in all time steps.

Tab. 2: Summary of the potential response to climate change for the 2020s, 2050s and 2080s pertaining to habitat coherence of the six selected habitat types. Minus signs '-' indicate a loss of habitat coherence in respect to the current situation, while plus signs '+' denote a gain in coherence. Inconsistent results of the probability of connectivity index and the integral index of connectivity are marked with question marks. The different scenarios are depicted horizontally in italic numbers.

	4030										**5130**						**6210**						**71X0**		**8160**		**9170**					
	1	*2*	*3*	*4*	*5*	*6*	*7*	*8*	*9*	*10*	*1*	*2*	*3*	*4*	*5*	*6*	*1*	*2*	*3*	*4*	*5*	*6*	*1*	*2*	*1*	*2*	*1*	*2*	*3*	*4*	*5*	*6*
2020	-	-	+	+	?	+	+	+	+	+	-	-	+	+	-	+	-	-	-	-	-	+	-	-	-	-	-	-	-	+	-	+
2050	-	-	+	+	+	+	+	+	+	+	-	-	+	+	+	+	-	-	+	+	+	+	-	-	-	-	-	-	-	-	-	-
2080	-	-	+	+	+	+	+	+	+	+	-	-	?	+	?	+	-	-	-	-	?	+	-	-	-	-	-	-	-	-	-	-

Discussion

Trends and anomalies in habitat coherence

A gain in habitat space and habitat coherence was initially assumed for the prevailing thermophile habitat types "European dry heaths" (4030), "*Juniperus communis* formations on heaths or calcareous grasslands" (5130), "semi-natural dry grasslands and scrubland facies on calcareous substrates (*Festuco-Brometalia*)" (6210) and "*Galio-Carpinetum* oak-hornbeam forests" (9170). The increase in habitat space is confirmed for habitat types 4030, 5130 and partly for 6210 according to the environmental envelope model (EEM) projections in most of the applied dispersal scenarios. Although, the geographic restrictions of the different scenarios cause a reduction of the originally projected environmental space.

Like habitat space, also projected habitat coherence increases in the majority of scenarios for habitat types 4030 and 5130. Remarkably, habitat type 6210 particularly gains coherence for the scenarios of the 2050s only, which might be due to uncertainties related to the used climate projections produced by the HadCM3 model for the IPCC A2 emission scenario. Nevertheless, it shows the regeneration capacity of habitat type 6210 (for all dispersal and connectivity distances) because connectivity values for the 2020s are lower than the ones of the 2050s. Only when habitat type 6210 is not restricted to SCI borders and may disperse with the optimistic dispersal distance it is capable to reach higher connectivity values over time compared to the current situation.

For "*Galio-Carpinetum* oak-hornbeam forests" (9170) a positive response to climate change could not be confirmed by the EEMs. Even without any restrictions in dispersal (not shown here), "*Galio-Carpinetum* oak-hornbeam forests" exhibit a range contraction to the southeast, which is aggravated by the low dispersal rates of forests as successful dispersal for trees not only requires the establishment but also several subsequent years of favorable growing conditions to yield adult trees that may successfully reproduce. In the 2020s changes in the occurrence of environmentally suitable space for this habitat type are small. Nevertheless, only the optimistic dispersal / connectivity scenarios exhibit increases in habitat coherence, stressing the described connection.

On the time scale of this study, "raised bogs" (71X0) are limited to their presently known locations owing to their long development time. Similarly, "Medio-European calcareous screes of hill and montane levels" (8160) are restricted due to their habitat requirements. Both habitat types are projected to lose environmental space as well as habitat coherence. The initial hypothesis of a reduction of environmental space as well as habitat coherence due to their dispersal restraints is therefore confirmed. The results of the null dispersal scenarios 1 (realistic connectivity distance) & 2 (optimistic connectivity distance) lead to the questionable conclusion that the current environmental space is likely to become unsuitable in the future for all habitat types (not only 71X0 and 8160). However, the degree of this reduction varies for the different habitat types.

The anticipated coherence reducing effect could be exemplarily confirmed for "European dry heaths" (4030). Furthermore, the higher connectivity values for the optimistic scenarios as well as the highest connectivity values for the optimistic SCI unlimited scenarios are reasonable and comprehensible as the projections based on these scenarios lead to the largest increase in environmental space. The more extensive environmental space under the optimistic distance scenarios also accounts for the smaller differences between the optimistic scenarios than for the ones between the realistic distance scenarios.

Besides four exceptions (out of 108 cases), the integral index of connectivity (IIC) and the probability of connectivity index (PC) produced consistent results in respect to an increase or decrease in connectivity. Although, the exponential decay function used for the calculation of PC assigned a rather low value of 0.05 to the maximum connectivity distances.

Limitations and methodological issues

The complexity of the here presented integrative combination of environmental envelope models and graph theory comes along with some limitations and drawbacks, not only in respect to the interpretation of model outputs. One issue addresses the artificial construct of habitat types, existing only within the area of the European Union member states, although occurrences of such entities outside the borders of the European Union are likely. The application of a so far non-existing pan-European approach might yield more accurate modeling results as more information becomes available and in addition boundary effects (at least within the European Union) can be diminished. However, in the case of centers of distribution outside the European Union, edge effects may even increase and the transferability to the target area may be reduced due to deviating conditions.

A further problematic issue concerns the delimitation of the different habitat types, which is in some cases a gradual transition, e.g. "European dry heaths" (4030) and "*Juniperus communis* formations on heaths or calcareous grasslands" (5130) are closely related. Individual interpretations of the different reporting units (states, federal states, …) involved in the Habitats Directive reporting can deteriorate the results of EEMs by delivering either contradictory information or incomplete information on the realized niche of habitat types (although this is not necessarily only due to this reporting issue). In addition, the spatial resolution in data recording and the amount of reported data vary considerably between the member states.

The environmental data used for the EEMs in this study belong to the best available datasets for modeling on an European scale, especially in respect to spatial resolution. However, data on further ecological relevant variables / factors would be desirable (Pearson and Dawson 2003). In the ideal case a more detailed analysis of the impact factors acting on an ecosystem / habitat type would be possible and promote the performance of EEMs.

The non-standardized spatial resolutions of the raw data required a resampling, probably entailing artifacts and enforcing the propagation of uncertainty through the different data preparation steps in addition to the one occurring in the succeeding modeling steps. In general, a higher overall spatial resolution would allow for more accurate model projections in the context of the Natura 2000 network, as the real size of sites can be much smaller than 6.25 km^2. On the other hand, a spatial resolution of 2.5 km x 2.5 km for the complete European Union is far higher than the modeling resolution of 50 km x 50 km applied in many studies covering the area of Europe. In general, a mismatch of scales might cause problems when using EEMs (Pearson and Dawson 2003). While climatic processes act on global to regional scales (> 10 000 km to 200 km), the scale of interest for impacts on habitat coherence of the Natura 2000 network is a local one (10 km down to 10 m).

Problems arising from non-analogue climate (Fitzpatrick and Hargrove 2009) are covered in a first approach by incorporating the complete environmental space information of the European Union in the EEM ensemble projections for Germany. In addition a “Multivariate Environmental Similarity Surface” (MESS) analysis (Elith et al. 2010) can help to identify regions with non-analogue climate in a spatially explicit way.

Beside the prerequisite of analogue climate, the selection of the emission scenario influences model projections. The choice of the highly probable and strong IPCC A2 emission scenario (Le Quéré et al. 2009) helps to unveil potential problems for the Natura 2000 network and for the constituting habitat types under climate change.

The strength of EEM ensembles is to successfully project the direction of range alterations in a changing climate, but they are less effective in estimating the magnitude of the alterations (Araújo and Pearson 2005). An over- or underestimation of future environmental space can be caused by the underlying assumption of EEMs that the current distribution of species or habitat types reflects the completely realized niche. The applied maximizing Kappa approach of BIOMOD is regarded not to be the best solution for the determination of the threshold of occurrence and non-occurrence (Liu et al. 2005). Despite, the EEM ensemble performance, measured as AUC, is good for all modeled habitat types (Swets 1988) with a range of AUC values between 0.84 ("European dry heaths") and 0.97 ("*Galio-Carpinetum* oak-hornbeam forests").

A tradeoff between available data on the one hand and computational power on the other hand represents the applied omnidirectional dispersal model in dependence on a cost raster to cross the landscape. The general problem is to find data on factors reducing the dispersal of certain habitat types. The use of land cover information in combination with elevation data is a feasible and reasonable approach but leaves room for further ecological meaningful extensions. In this study, due to the lack of detailed data on habitat types or even on the constituting species, the same cost magnitude was assigned to all habitat types. Although, it is more likely that the assignment of costs varies from habitat type to habitat type. Beyond this, the cost magnitude in general might be too low or too high.

Costs are accounted for the dispersal of habitat types only and not for the connectivity analysis. In the best case all distances between single patches should be calculated as cost distances and not as basic Euclidean distances. Solutions like PATHMATRIX (Ray 2005) or the ArcGIS toolbox written by Etherington (2011) can achieve this, but in the current time the application of such methods is computationally not feasible for larger surfaces. On the other hand, "travel corridors", as implemented in the software package Circuitscape (theory described in McRae et al. 2008), are more realistic, but need an own methodology to be reflected in graph based approaches where links - independent of their strength - either exist or not.

Connectivity measures like the probability of connectivity index (PC) and the integral index of connectivity (IIC) strongly depend on the connectivity distance, thus the correct and realistic estimation of the distances is crucial for the validity of results (Saura and Pascual-Hortal 2007). In this study, the distance dependence is accounted for by the two distance values: realistic and optimistic. The great challenge is once again to find ecological data on this matter. For some habitat types connectivity distance values can be derived from the closely related dispersal distances. However, estimations for the species conglomerate of habitat types are difficult due to fragmentary information and potential interactions between species. Although, a common ecological function, the here applied exponential decay function for the probability of connectivity index only gives a rough estimation of the real, complex and unknown distance decay behavior of the selected habitat types - and their heterogeneous mixture of different plant (and animal) species.

Patch attributes can incorporate many different factors in one single measure, creating for example a composite quality measure. The inclusion of other patch attributes besides patch area could not only improve the performance of IIC- and PC-based model output in respect to ecological reality but also would allow for a more sound identification of priority patches for conservation.

Some disadvantages of the integral index of connectivity (IIC) suggest the preference of the probability of connectivity index (PC). First, owing to the binary connection model, IIC exhibits a higher sensitivity to uncertainties in the estimation of the threshold dispersal distance (Saura and Pascual-Hortal 2007). Second, the binary connection model is deterministic with no intermediate modulation of connectivity strength in dependence of relevant ecological processes (Saura and Pascual-Hortal 2007). Last but not least, Saura and Pascual-Hortal (2007) state the inability of IIC to adequately deal with adjacent patches. Nevertheless, as written above, IIC and PC produce consistent results, even if the absolute values slightly differ.

Context

The use of EEM techniques to assess species' potential geographic responses to climate change is an intensively researched topic of the recent past (e.g. Araújo et al. 2006, Green et al. 2008, Rebelo et al. 2010). Furthermore, conservation strategies to adapt to climate change or to mitigate the adverse effects in respect to nature conservation have been discussed (e.g. Araújo et al. 2004, Hannah et al. 2007). Not only in this context the importance of connectivity for nature conservation has been stressed and different methodological approaches, amongst these also graph theory, have been proposed (e.g. Briers 2002, Opdam and Wascher 2004, Galpern et al. 2011, Doerr et al. 2011). Only few very recent studies addressed the specific implications of climate change for the Natura 2000 network of the European Union (e.g. Araújo et al. 2011, Bittner et al. 2011, D'amen et al. 2011). Even less studies (not all in relation to climate change) took into account the specific constraints of the artificial construct of habitat types as defined in the Habitats Directive (Mücher et al. 2009, Zacharias and Zamparas 2010, Bittner et al. 2011).

The first approach to bring together so far unconnected methodologies with the aim to identify upcoming bottlenecks in the Natura 2000 network was published by Vos et al. (2008). They used an EEM to project future climate space of three ecosystems (forest, wetland and natural grassland), represented by three species each, in combination with a random walk dispersal model to assess the potential suitable habitat. Succeeding an analysis of projected shifts in suitable climate space and the distribution of habitat networks for each species, climate-proof and non-climate proof networks were identified with a "climate-based ecological network analysis" (Berry et al. 2007).

Although the methodology of this study shares some similarities with the work of Vos et al. (2008), there exist major differences. First of all, this study deals with the special concept of habitat types. Second, an ensemble of EEMs is employed in this study to yield more robust projection results and to reduce uncertainties (Dormann et al. 2008). Third, in consideration of costs an omnidirectional dispersal model is applied. Fourth, graph theory is used to assess habitat coherence under climate change. Last but not least, the focus here is not on the (important!) direct identification of bottlenecks in the Natura 2000 network but on general trends in habitat coherence of the network under climate change, although the identification of priority patches for nature conservation would be easily possible.

Implications for nature conservation

Habitat types are constituted by a complex interaction of different factors, like key species, climate and other abiotic properties such as soil type or nutrient availability. Furthermore, the cultural history and the current management of a landscape are essential factors influencing the formation of certain habitat types. In Germany, some grassland habitats have historically developed only due to the traditional forms of grazing. Therefore, a successful establishment of a habitat type not only requires an effective dispersal but all biotic, abiotic and anthropogenic requirements have to be fulfilled additionally (Plassmann et al. 2010). On the other hand, the different management options offer the opportunity to promote the selective establishment of a suitable habitat type.

The integration of landscape connectivity aspects in combination with future distribution projections of species and habitat types in nature conservation helps to identify bottlenecks in conservation networks in a changing environment and provides the necessary information to facilitate range changes triggered not only by climate change (Hannah et al. 2002). Further drivers that need to be considered besides climate change are mostly anthropogenic pressures like deforestation, ploughing up of grassland or urban sprawl strongly governed by politics and / or the economic situation.

The results of this study demonstrate the principal capability of the Natura 2000 network to adapt to climate change. Nevertheless, the changing climate requires a thorough rethinking of the current nature conservation philosophy by a shift away from the traditional concept of restoring or preserving the current situation to future oriented management options. This would allow, among other aspects, also the replacement of increasingly unadapted habitat types like "*Galio-Carpinetum* oak-hornbeam forests" in Germany by newly establishing habitat types. In the ideal case such a replacement maintains the same level of (functional) diversity or even increases it. Furthermore, the SCI unlimited scenarios of this study demonstrate at least for some of the habitat types, that their abundance can be increased by the creation of new protected areas in the future. Beyond this, it is advisable to keep in mind that, apart from living fossils, nature underlies constant changes and transformations and therefore always requires flexible and adapted nature conservation concepts.

Conclusion

Impacts of climate change are ubiquitous and pose a particular challenge to mankind and require an adequate respond to successfully mitigate as well as offset the adverse effects. Especially nature conservation is faced with a fundamental paradigm shift away from restoration and preservation only to additional flexible adaptation strategies. Integrative approaches bringing together so far independently used methods allow scientists to give guidance to decision makers in nature conservation living in a constantly changing world.

This study demonstrates a practicable and sound combination of environmental envelope models and graph theory to assess the coherence of nature conservation networks like the Natura 2000 network of the Habitats Directive of the European Union. Knowledge of the potential future developments of the conservation network pertaining to habitat coherence under different climate change scenarios does not only allow for a general assessment of the status but also concrete management options can be derived.

Acknowledgements

The authors acknowledge funding by the Federal Agency for Nature Conservation Germany (FKZ 3508 85 0600).

Literature cited

Araújo, M. B., M. Cabeza, W. Thuiller, L. Hannah, and P. H. Williams. 2004. Would climate change drive species out of reserves? An assessment of existing reserve-selection methods. Global Change Biology 10:1618–1626.

Araújo, M. B., W. Thuiller, and R. G. Pearson. 2006. Climate warming and the decline of amphibians and reptiles in Europe. Journal of Biogeography 33:1712–1728.

Araújo, M. B., D. Alagador, M. Cabeza, D. Nogués-Bravo, and W. Thuiller. 2011. Climate change threatens European conservation areas. Ecology Letters 14:484–492.

Araújo, M. B., and A. Guisan. 2006. Five (or so) challenges for species distribution modelling. Journal of Biogeography 33:1677–1688.

Araújo, M. B., and M. New. 2007. Ensemble forecasting of species distributions. Trends in Ecology & Evolution 22:42–47.

Araújo, M. B., and R. G. Pearson. 2005. Equilibrium of species' distributions with climate. Ecography 28:693–695.

Berry, P. M., A. P. Jones, R. J. Nicholls, and C. C. Vos. 2007. Assessment of the vulnerability of terrestrial and coastal habitats and species in Europe to climate change, Annex 2 of Planning for biodiversity in a changing climate. BRANCH project Final Report. Natural England, UK.

BfN, BMU. 2008. Natura 2000 in Germany: Nature's jewels. (A. Ssymank, S. Balzer, C. Ratte, M. Dieterich, C. Drebitz, B. Beinlich, and B. Hill, Eds.). Federal Agency for Nature Conservation (BfN), Federal Ministry for the Environment, Nature Conservation and Nuclear Safety (BMU), Bonn, Bad Godesberg, Germany.

Bittner, T., A. Jaeschke, B. Reineking, and C. Beierkuhnlein. 2011. Comparing modelling approaches at two levels of biological organisation - Climate change impacts on selected Natura 2000 habitats. Journal of Vegetation Science 22:699–710.

Boyd, P. W., and S. C. Doney. 2002. Modelling regional responses by marine pelagic ecosystems to global climate change. Geophysical Research Letters 29:53–1 – 53–4.

Briers, R. A. 2002. Incorporating connectivity into reserve selection procedures. Biological Conservation 103:77–83.

Bunn, A. G., D. L. Urban, and T. H. Keitt. 2000. Landscape connectivity: a conservation application of graph theory. Journal of Environmental Management 59:265–278.

Cabeza, M. 2003. Habitat loss and connectivity of reserve networks in probability approaches to reserve design. Ecology Letters 6:665–672.

CIAT. 2010. SRES A2 - Emission scenario. International Centre for Tropical Agriculture. Retrieved September 2011, from http://www.ccafs-climate.org/download_a2.html.

Council Directive 92 43 EEC. 1992. Council Directive 92/43/EEC of 21 May 1992 on the conservation of natural habitats and of wild fauna and flora.

D'amen, M., P. Bombi, P. B. Pearman, D. R. Schmatz, N. E. Zimmermann, and M. A. Bologna. 2011. Will climate change reduce the efficacy of protected areas for amphibian conservation in Italy? Biological Conservation 144:989–997.

Diamond, J. M. 1975. The island dilemma: lessons of modern biogeographic studies for the design of natural reserves. Biological Conservation 7:129–146.

Doerr, V. A. J., T. Barrett, and E. D. Doerr. 2011. Connectivity, dispersal behaviour and conservation under climate change: a response to Hodgson et al. Journal of Applied Ecology 48:143–147.

Dormann, C. F., O. Purschke, J. R. G. Márquez, S. Lautenbach, and B. Schroder. 2008. Components of uncertainty in species distribution analysis: a case study of the great grey shrike. Ecology 89:3371–3386.

EIONET. 2009. Central Data Repository (CDR). Retrieved September 6, 2011, from http://cdr.eionet.europa.eu/.

Elith, J., M. Kearney, and S. Phillips. 2010. The art of modelling range-shifting species. Methods in Ecology and Evolution 1:330–342.

Etherington, T. R. 2011. Python based GIS tools for landscape genetics: visualising genetic relatedness and measuring landscape connectivity. Methods in Ecology and Evolution 2:52–55.

European Commission. 2007. Interpretation Manual of European Union Habitats: EUR 27. Brussels.

European Commission. 2009. Report from the Commission to the Council and the European Parliament Composite - Report on the Conservation Status of Habitat Types and Species as required under Article 17 of the Habitats Directive.

European Environment Agency. 2010. Corine Land Cover 2006 raster data - version 13. Retrieved September 6, 2011, from http://www.eea.europa.eu/data-and-maps/data/corine-land-cover-2006-raster/.

European Topic Centre on Biological Diversity ETC BD. 2008. Article 17 Technical Report (2001-2006): Annex J - Some specific analysis on conservation status.

Federal Agency for Nature Conservation Germany. 2011. FloraWeb. Retrieved September 6, 2011, from http://www.floraweb.de/.

Fitzpatrick, M. C., and W. W. Hargrove. 2009. The projection of species distribution models and the problem of non-analog climate. Biodiversity and Conservation 18:2255–2261.

Foltête, J. C., K. Berthier, and J. F. Cosson. 2008. Cost distance defined by a topological function of landscape. Ecological Modelling 210:104–114.

Galpern, P., M. Manseau, and A. Fall. 2011. Patch-based graphs of landscape connectivity: a guide to construction, analysis and application for conservation. Biological Conservation 144:44–55.

Green, R. E., Y. C. Collingham, S. G. Willis, R. D. Gregory, K. W. Smith, and B. Huntley. 2008. Performance of climate envelope models in retrodicting recent changes in bird population size from observed climatic change. Biology Letters 4:599–602.

Hannah, L., G. F. Midgley, T. Lovejoy, W. J. Bond, M. Bush, J. C. Lovett, D. Scott, and F. I. Woodward. 2002. Conservation of biodiversity in a changing climate. Conservation Biology 16:264–268.

Hannah, L., G. Midgley, S. Andelman, M. Araújo, G. Hughes, E. Martinez-Meyer, R. Pearson, and P. Williams. 2007. Protected area needs in a changing climate. Frontiers in Ecology and the Environment 5:131–138.

Hijmans, R. J., S. E. Cameron, J. L. Parra, P. G. Jones, and A. Jarvis. 2005. Very high resolution interpolated climate surfaces for global land areas. International Journal of Climatology 25:1965–1978. John Wiley & Sons, Ltd.

Hodgson, J. A., C. D. Thomas, B. A. Wintle, and A. Moilanen. 2009. Climate change, connectivity and conservation decision making: back to basics. Journal of Applied Ecology 46:964–969.

Hodgson, J. A., A. Moilanen, B. A. Wintle, and C. D. Thomas. 2011. Habitat area, quality and connectivity: striking the balance for efficient conservation. Journal of Applied Ecology 48:148–152.

Hole, D. G., S. G. Willis, D. J. Pain, L. D. Fishpool, S. H. M. Butchart, Y. C. Collingham, C. Rahbek, and B. Huntley. 2009. Projected impacts of climate change on a continent-wide protected area network. Ecology Letters 12:420–431.

Jenness, J. 2011. Conefor Inputs for ArcGIS 10.

Le Quéré, C., M. R. Raupach, J. G. Canadell, G. Marland, L. Bopp, P. Ciais, T. J. Conway, S. C. Doney, R. A. Feely, P. Foster, P. Friedlingstein, K. Gurney, R. A. Houghton, J. I. House, C. Huntingford, P. E. Levy, M. R. Lomas, J. Majkut, N. Metzl, J. P. Ometto, G. P. Peters, I. C. Prentice, J. T. Randerson, S. W. Running, J. L. Sarmiento, U. Schuster, S. Sitch, T. Takahashi, N. Viovy, G. R. van der Werf, and F. I. Woodward. 2009. Trends in the sources and sinks of carbon dioxide. Nature Geoscience 2:831–836.

Lenoir, J., J. C. Gegout, P. A. Marquet, P. de Ruffray, and H. Brisse. 2008. A significant upward shift in plant species optimum elevation during the 20th century. Science 320:1768–1771.

Liu, C. R., P. M. Berry, T. P. Dawson, and R. G. Pearson. 2005. Selecting thresholds of occurrence in the prediction of species distributions. Ecography 28:385–393.

McCallum, H. 2000. Population parameters. Page 348. Wiley-Blackwell.

McRae, B. H., B. G. Dickson, T. H. Keitt, and V. B. Shah. 2008. Using circuit theory to model connectivity in ecology, evolution, and conservation. Ecology 89:2712–2724.

Mücher, C. A., S. M. Hennekens, R. G. H. Bunce, J. H. J. Schaminee, and M. E. Schaepman. 2009. Modelling the spatial distribution of Natura 2000 habitats across Europe. Landscape and Urban Planning 92:148–159.

Opdam, P., and D. Wascher. 2004. Climate change meets habitat fragmentation: linking landscape and biogeographical scale levels in research and conservation. Biological Conservation 117:285–297.

Parmesan, C., and G. Yohe. 2003. A globally coherent fingerprint of climate change impacts across natural systems. Nature 421:37–42.

Pascual-Hortal, L., and S. Saura. 2006. Comparison and development of new graph-based landscape connectivity indices: towards the priorization of habitat patches and corridors for conservation. Landscape Ecology 21:959–967.

Pearson, R. G., T. P. Dawson, P. M. Berry, and P. A. Harrison. 2002. SPECIES: A spatial evaluation of climate impact on the envelope of species. Ecological Modelling 154:289–300.

Pearson, R. G., and T. P. Dawson. 2003. Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? Global Ecology and Biogeography 12:361–371.

Plassmann, K., M. L. M. Jones, and G. Edwards-Jones. 2010. Effects of long-term grazing management on sand dune vegetation of high conservation interest. Applied Vegetation Science 13:100–112.

R Development Core Team. 2010. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Ray, N. 2005. PATHMATRIX: a geographical information system tool to compute effective distances among samples. Molecular Ecology Notes 5:177–180.

Rebelo, H., P. Tarroso, and G. Jones. 2010. Predicted impact of climate change on European bats in relation to their biogeographic patterns. Global Change Biology 16:561–576.

Reuter, H. I., L. R. Lasdo, T. Hengl, and L. Montanarella. 2008. Continental-scale digital Soil Mapping using European Soil Profile Data: Soil pH. Hamburger Beiträge zur Physischen Geographie und Landschaftsökologie 19:91–102.

Rothmaler, W., E. J. Jäger, and K. Werner. 2005. Exkursionsflora von Deutschland. Elsevier, Spektrum, Akad. Verl., München; Heidelberg.

Saura, S., and J. Torne. 2009. Conefor Sensinode 2.2: A software package for quantifying the importance of habitat patches for landscape connectivity. Environmental Modelling & Software 24:135–139.

Saura, S., and L. Pascual-Hortal. 2007. A new habitat availability index to integrate connectivity in landscape conservation planning: comparison with existing indices and application to a case study. Landscape and Urban Planning 83:91–103.

Saura, S., and L. Rubio. 2010. A common currency for the different ways in which patches and links can contribute to habitat availability and connectivity in the landscape. Ecography 33:523–537.

Spangenberg, J. H. 2007. Integrated scenarios for assessing biodiversity risks. Sustainable Development 15:343–356.

Swets, J. A. 1988. Measuring the accuracy of diagnostic systems. Science 240:1285–1293.

Thuiller, W., B. Lafourcade, R. Engler, and M. B. Araújo. 2009. BIOMOD - a platform for ensemble forecasting of species distributions. Ecography 32:369–373.

Thuiller, W., S. Lavergne, C. Roquet, I. Boulangeat, B. Lafourcade, and M. B. Araújo. 2011. Consequences of climate change on the tree of life in Europe. Nature 470:531–534.

Urban, D. L., E. S. Minor, E. A. Treml, and R. S. Schick. 2009. Graph models of habitat mosaics. Ecology Letters 12:260–273.

Urban, D., and T. Keitt. 2001. Landscape connectivity: a graph-theoretic perspective. Ecology 82:1205–1218.

Van Teeffelen, A. J. A., M. Cabeza, and A. Moilanen. 2006. Connectivity, probabilities and persistence: comparing reserve selection strategies. Biodiversity and Conservation 15:899–919.

Vos, C. C., P. Berry, P. Opdam, H. Baveco, B. Nijhof, J. O'Hanley, C. Bell, and H. Kuipers. 2008. Adapting landscapes to climate change: examples of climate-proof ecosystem networks and priority adaptation zones. Journal of Applied Ecology 45:1722–1731.

Zacharias, I., and M. Zamparas. 2010. Mediterranean temporary ponds. A disappearing ecosystem. Biodiversity and Conservation 19:3827–3834.

Appendix

Tab. A1: Variables used for environmental envelope modeling with a correlation less than 0.7. PREC: precipitation of the respective month, PRECMIN: minimum precipitation of the respective month, PREC SUM Mar - Sep: precipitation sum during the vegetation period, TMIN: minimum temperature of the respective month, TMAX; maximum temperature of the respective month, TMP SUM Mar - Sep: sum of the mean temperature during the vegetation period.

Habitat type	**Environmental envelope modelling variables**
4030	pH, PREC Jan, PREC May, TMIN Jan, PRECMIN, TMP SUM Mar – Sep, PREC SUM Mar - Sep
5130	pH, PREC May, TMAX Mar, PRECMIN, TMP SUM Mar - Sep, PREC SUM Mar - Sep
6210	pH, PREC May, TMIN Feb, PRECMIN, TMP SUM Mar - Sep, PREC SUM Mar - Sep
71X0	pH, PREC Aug, PREC Oct, TMAX Sep, TMP SUM Mar - Sep, PREC SUM Mar - Sep
8160	pH, PREC Jun, TMIN Jul, PRECMIN, TMP SUM Mar - Sep, PREC SUM Mar- Sep
9170	pH, PREC Jul, PREC Oct, TMP SUM Mar - Sep, PREC SUM Mar - Sep

Tab. A2: Dispersal and connectivity distances per year for the selected habitat types. #Habitat types 71X0 and 8160 cannot disperse on the temporal scale of this study. In this case, the given distances solely define the range in which a functional relation ship between patches exists.

Habitat type	**Realistic distance**	**Optimistic distance**
4030	0.5 km×a^{-1}	1.0 km×a^{-1}
5130	0.5 km×a^{-1}	1.0 km×a^{-1}
6210	1.0 km×a^{-1}	5.0 km×a^{-1}
71X0#	0.08 km×a^{-1}	0.2 km×a^{-1}
8160#	0.15 km×a^{-1}	0.5 km×a^{-1}
9170	0.15 km×a^{-1}	0.5 km×a^{-1}

Tab. A3: Cost factors for different land cover types and altitudes.

Description	**Cost factor**
Land use	
Urban areas (CLC classes 1xx)	10
Agricultural areas (CLC classes 2xx)	6
Natural areas (CLC classes 3xx)	1
Water dominated areas (CLC classes 4xx and 5xx)	4
Altitude	
Terrain altitude 0 – 500 m a.s.l.	0
Terrain altitude 501 – 1000 m a.s.l.	4
Terrain altitude 1001 – 1500 m a.s.l.	6
Terrain altitude > 1501 m a.s.l.	8

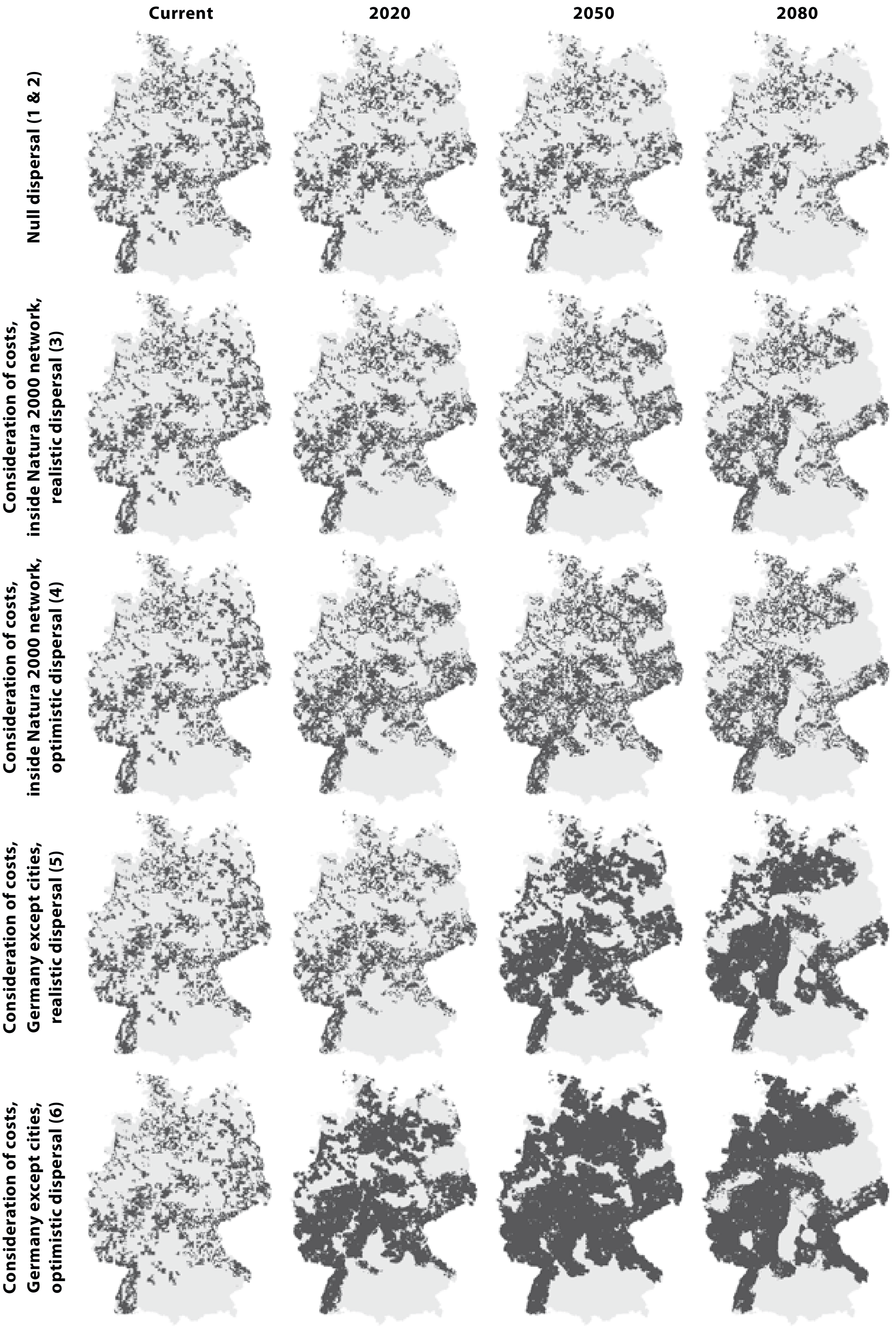


Fig. A1: Potential future development of the distribution of "European dry heaths" (4030) during the 21st century in Germany for the scenarios 1 to 6. Climate model HadCM3, IPCC emission scenario A2, AUC = 0.84.

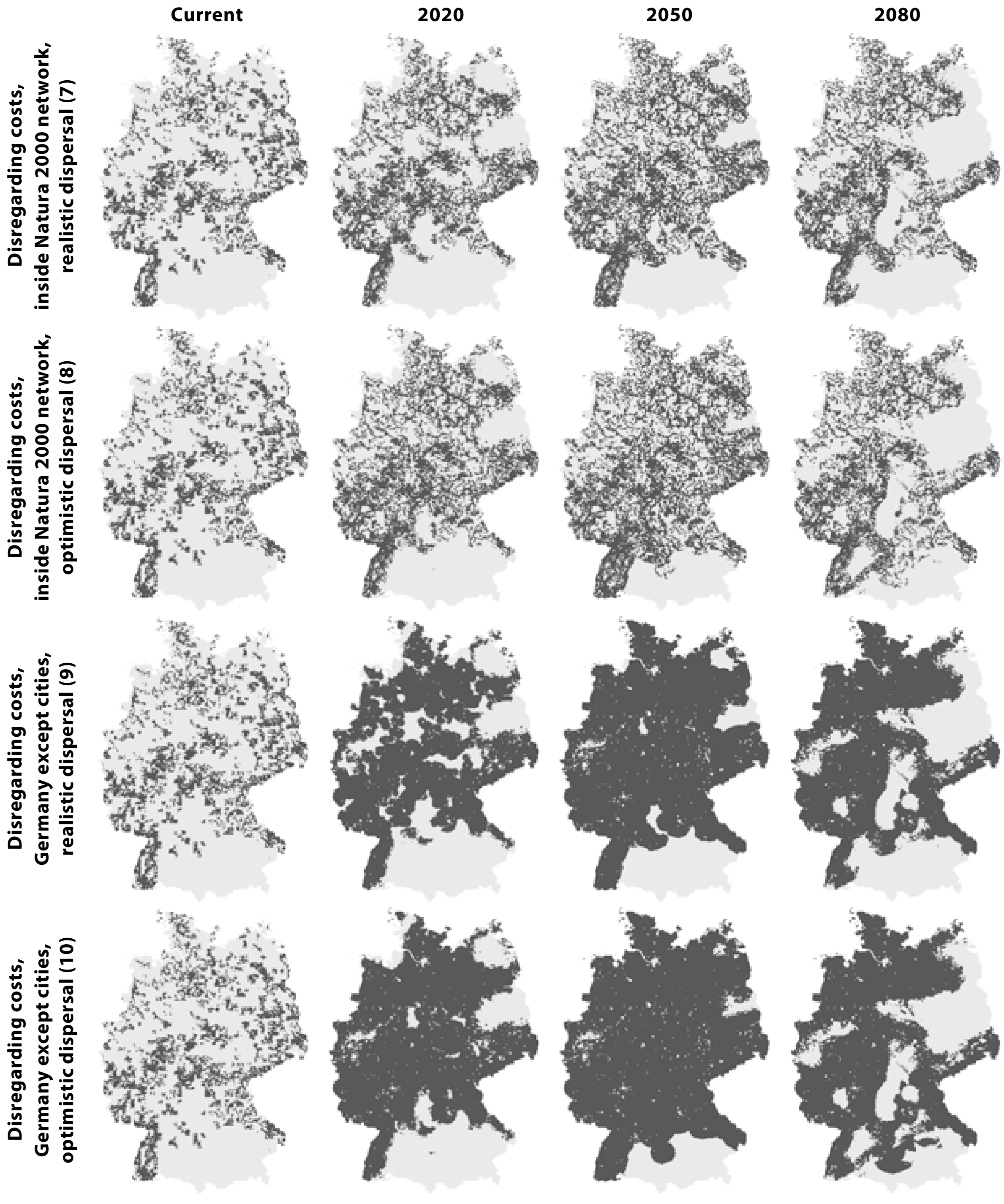


Fig. A2: Potential future development of the distribution of "European dry heaths" (4030) during the 21st century in Germany for the scenarios 7 to 10. Climate model HadCM3, IPCC emission scenario A2, AUC = 0.84.

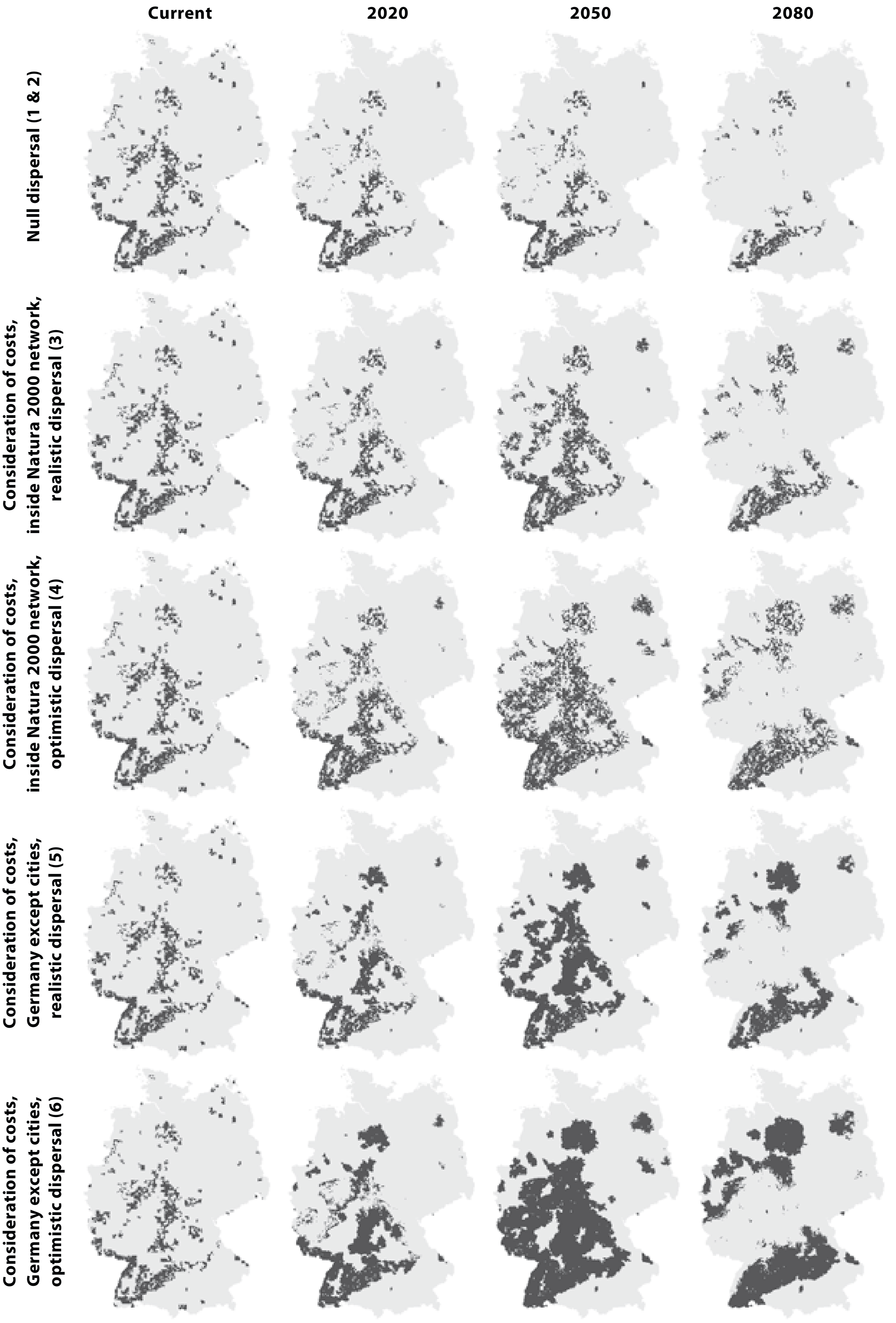


Fig. A3: Potential future development of the distribution of "*Juniperus communis* formations on heaths or calcareous grasslands" (5130) during the 21st century in Germany for the scenarios 1 to 6. Climate model HadCM3, IPCC emission scenario A2, AUC = 0.90.

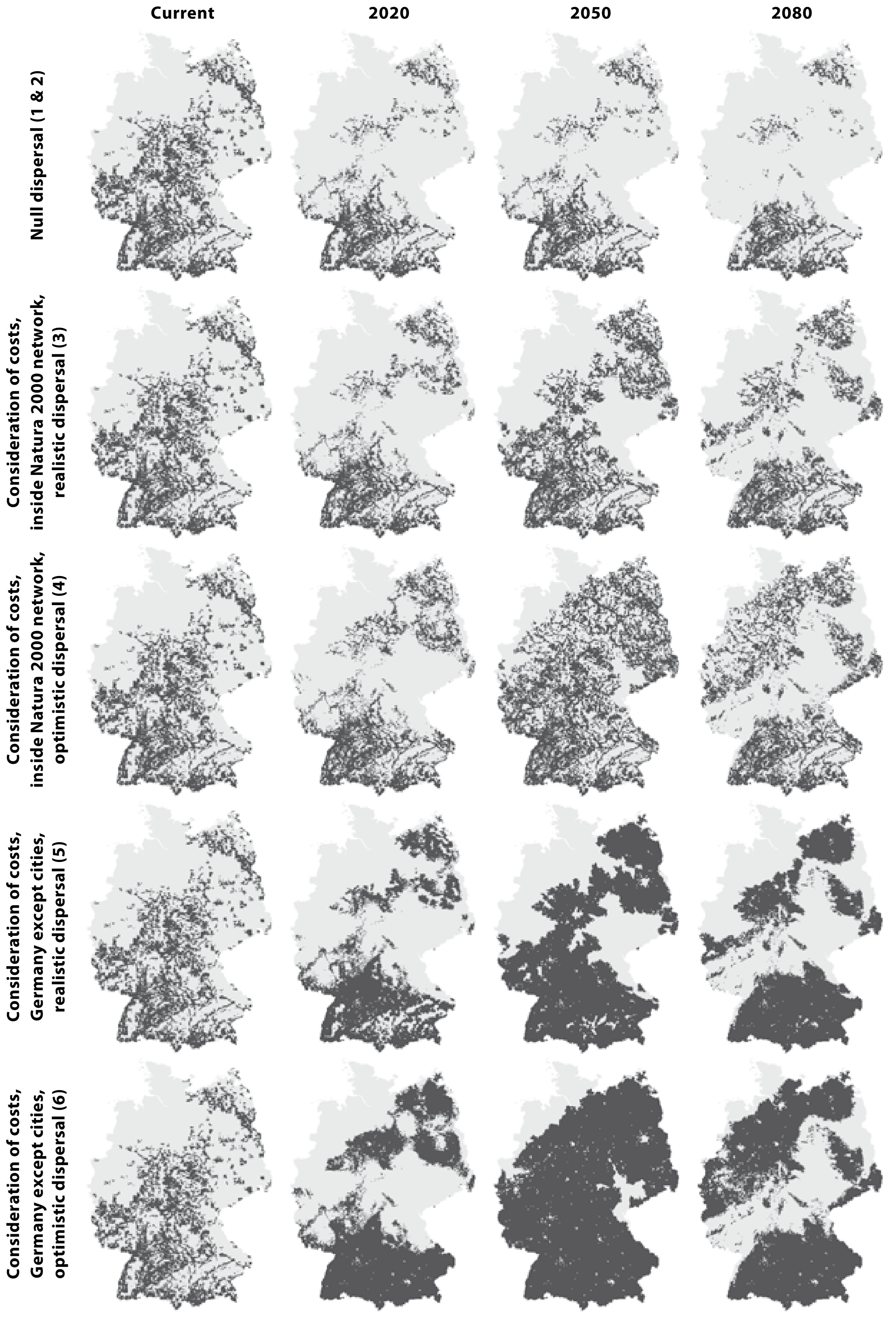


Fig. A4: Potential future development of the distribution of “semi-natural dry grasslands and scrub-land facies on calcareous substrates (*Festuco-Brometalia*)” (6210) during the 21st century in Germany for the scenarios 1 to 6. Climate model HadCM3, IPCC emission scenario A2, AUC = 0.85.

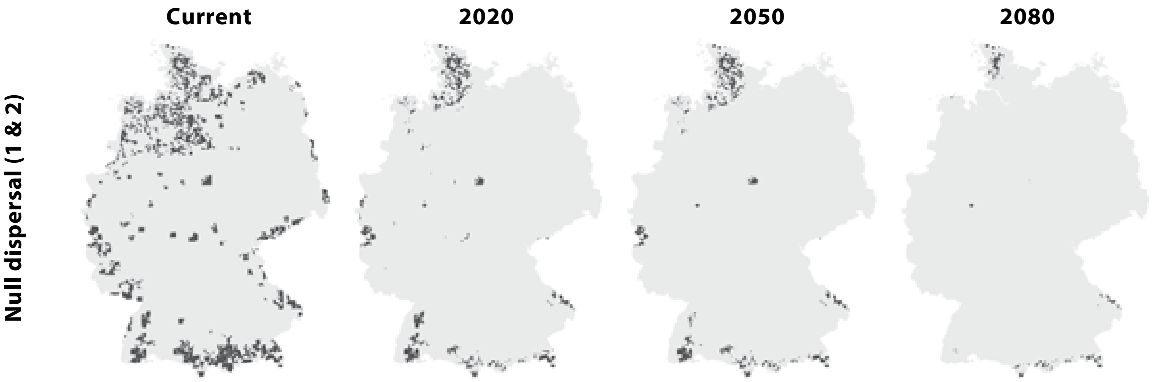


Fig. A5: Potential future development of the distribution of "raised bogs" (71X0) during the 21st century in Germany. Only scenarios 1 and 2 are depicted due to the null dispersal of the habitat type. Therefore, scenario 1 and 2 are differentiated for the connectivity analysis but not for the dispersal scenarios as depicted in the maps. Climate model HadCM3, IPCC emission scenario A2, AUC = 0.85.

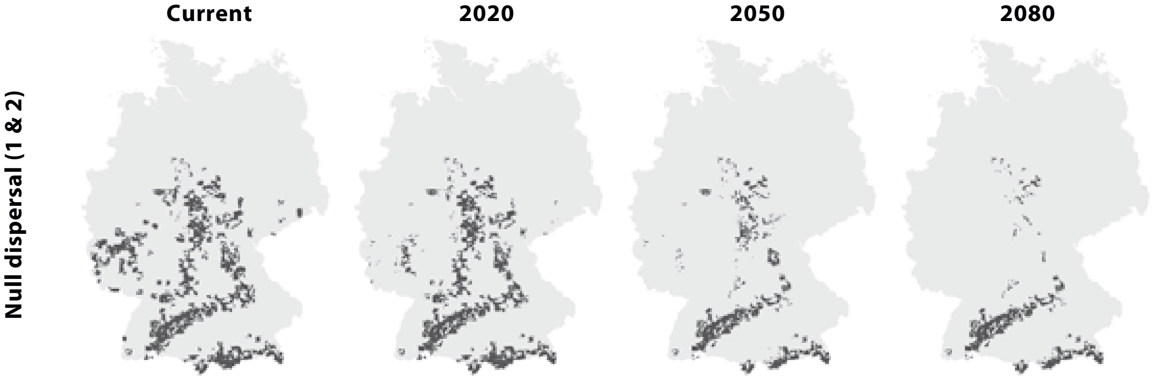


Fig. A6: Potential future development of the distribution of "Medio-European calcareous screes of hill and montane levels" (8160) during the 21st century in Germany. Only scenarios 1 and 2 are depicted due to the null dispersal of the habitat type. Therefore, scenario 1 and 2 are differentiated for the connectivity analysis but not for the dispersal scenarios as depicted in the maps. Climate model HadCM3, IPCC emission scenario A2, AUC = 0.91.

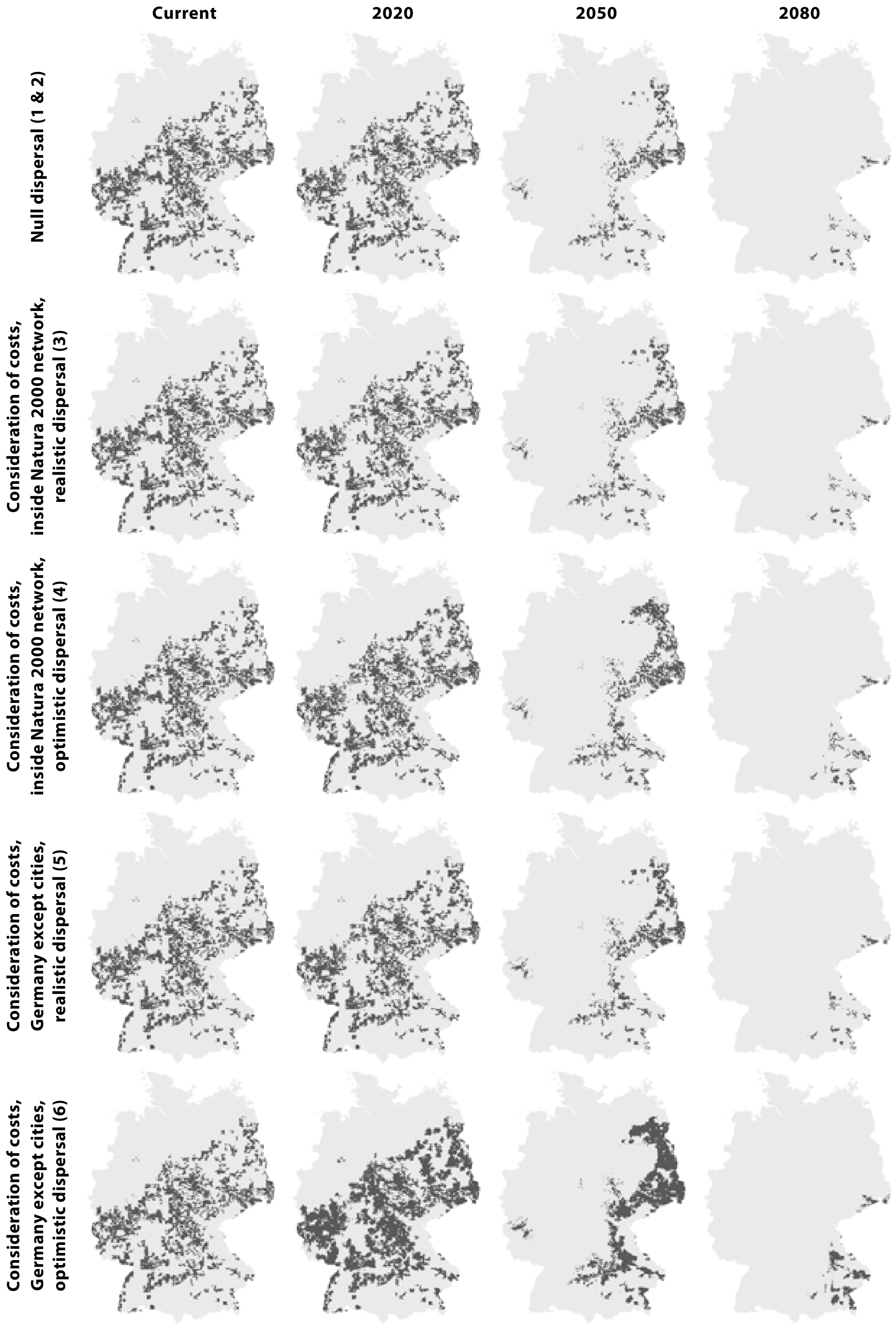


Fig. A7: Potential future development of the distribution of "*Galio-Carpinetum* oak-hornbeam forests" (9170) during the 21st century in Germany for the scenarios 1 and 2. Climate model HadCM3, IPCC emission scenario A2, AUC = 0.97.

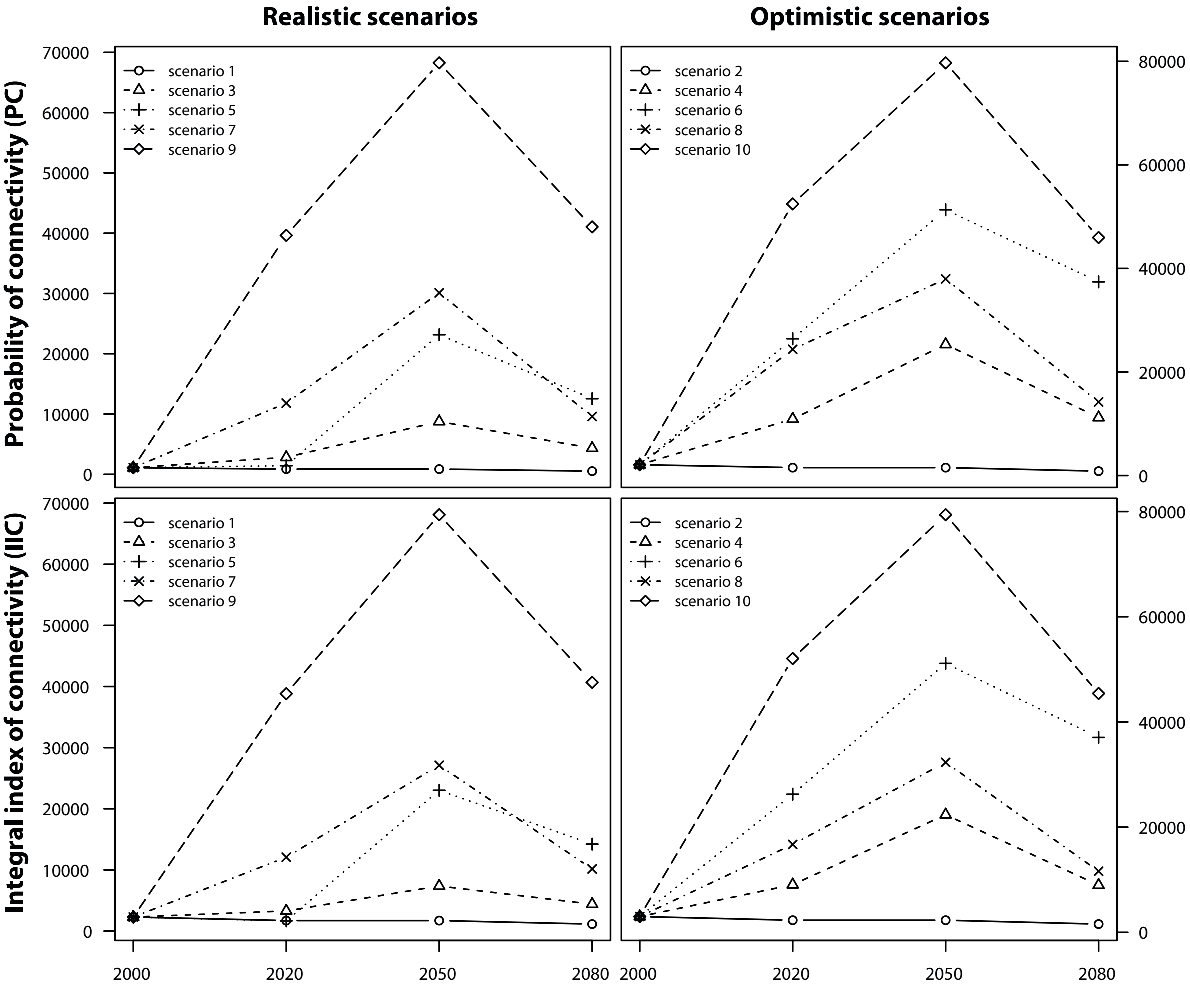


Fig. A8: Overall index values for "European dry heaths" (habitat type 4030) of the probability of connectivity index (PC) versus the integral index of connectivity (IIC) plotted separately for the realistic and the optimistic scenarios. Scenarios 1 & 2: null dispersal. Scenarios 3 & 4: realistic and optimistic dispersal / connectivity distance inside SCI Natura 2000 network under consideration of costs. Scenarios 5 & 6: realistic and optimistic dispersal / connectivity distance within Germany (except cities) under consideration of costs. Scenarios 7 & 8: realistic and optimistic dispersal / connectivity distance inside SCI Natura 2000 network neglecting costs. Scenarios 9 & 10: realistic and optimistic dispersal / connectivity distance within Germany (except cities) neglecting costs.

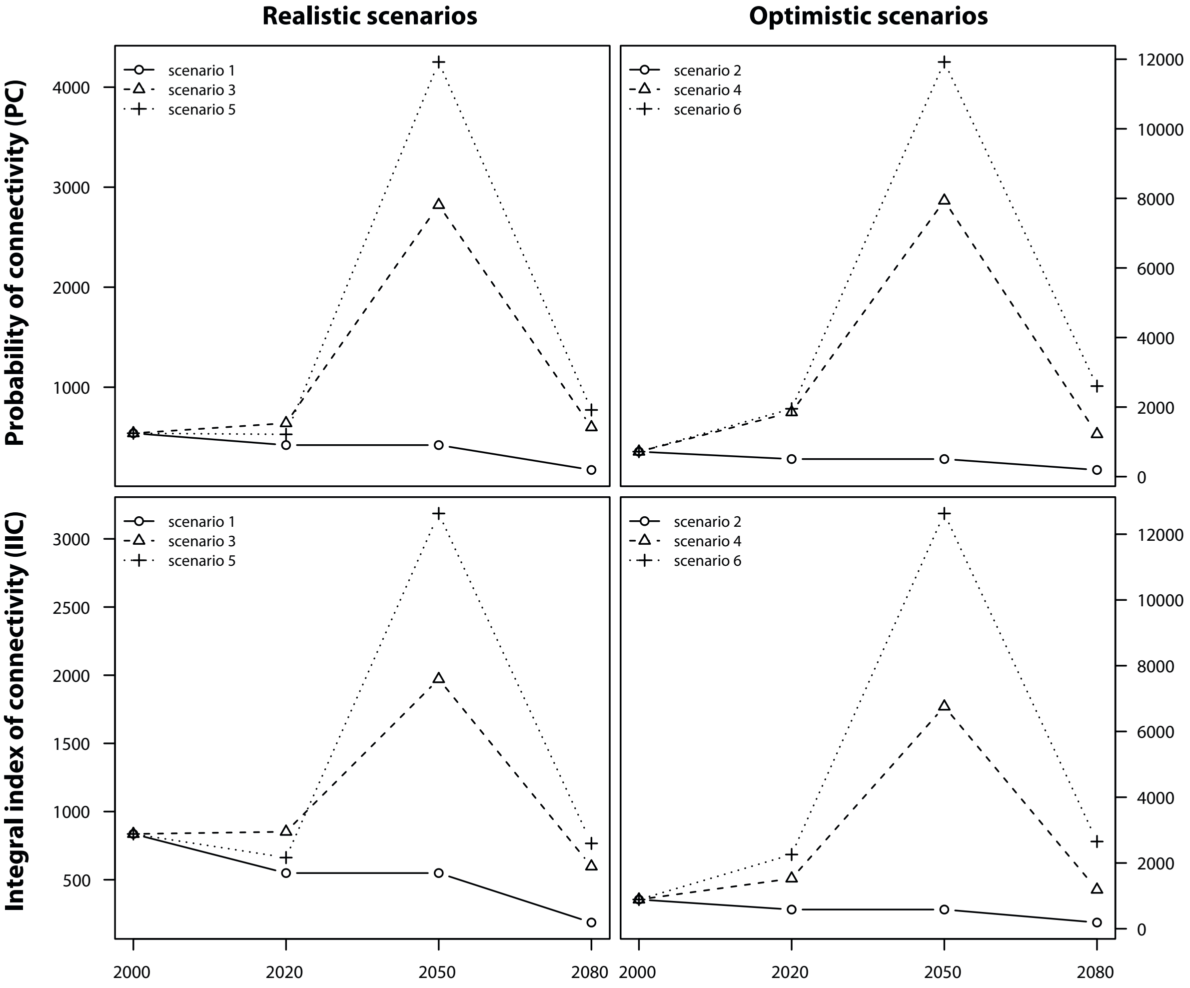


Fig. A9: Overall index values for "*Juniperus communis* formations on heaths or calcareous grasslands" (habitat type 5130) of the probability of connectivity index (PC) versus the integral index of connectivity (IIC) plotted separately for the realistic and the optimistic scenarios. Scenarios 1 & 2: null dispersal. Scenarios 3 & 4: realistic and optimistic dispersal / connectivity distance inside SCI Natura 2000 network under consideration of costs. Scenarios 5 & 6: realistic and optimistic dispersal / connectivity distance within Germany (except cities) under consideration of costs.

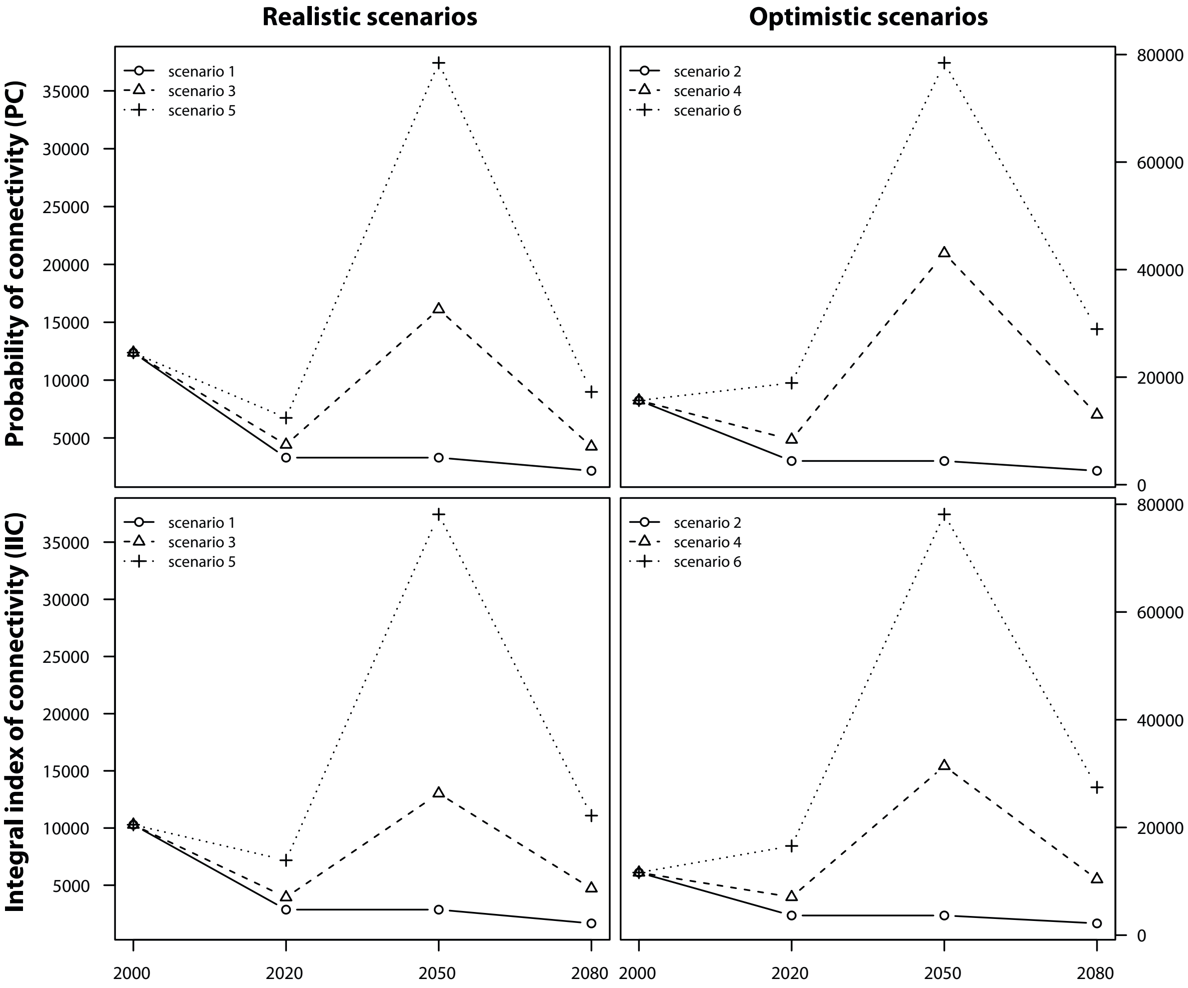


Fig. A10: Overall index values for "semi-natural dry grasslands and scrub-land facies on calcareous substrates (*Festuco-Brometalia*)" (habitat type 6210) of the probability of connectivity index (PC) versus the integral index of connectivity (IIC) plotted separately for the realistic and the optimistic scenarios. Scenarios 1 & 2: null dispersal. Scenarios 3 & 4: realistic and optimistic dispersal / connectivity distance inside SCI Natura 2000 network under consideration of costs. Scenarios 5 & 6: realistic and optimistic dispersal / connectivity distance within Germany (except cities) under consideration of costs.

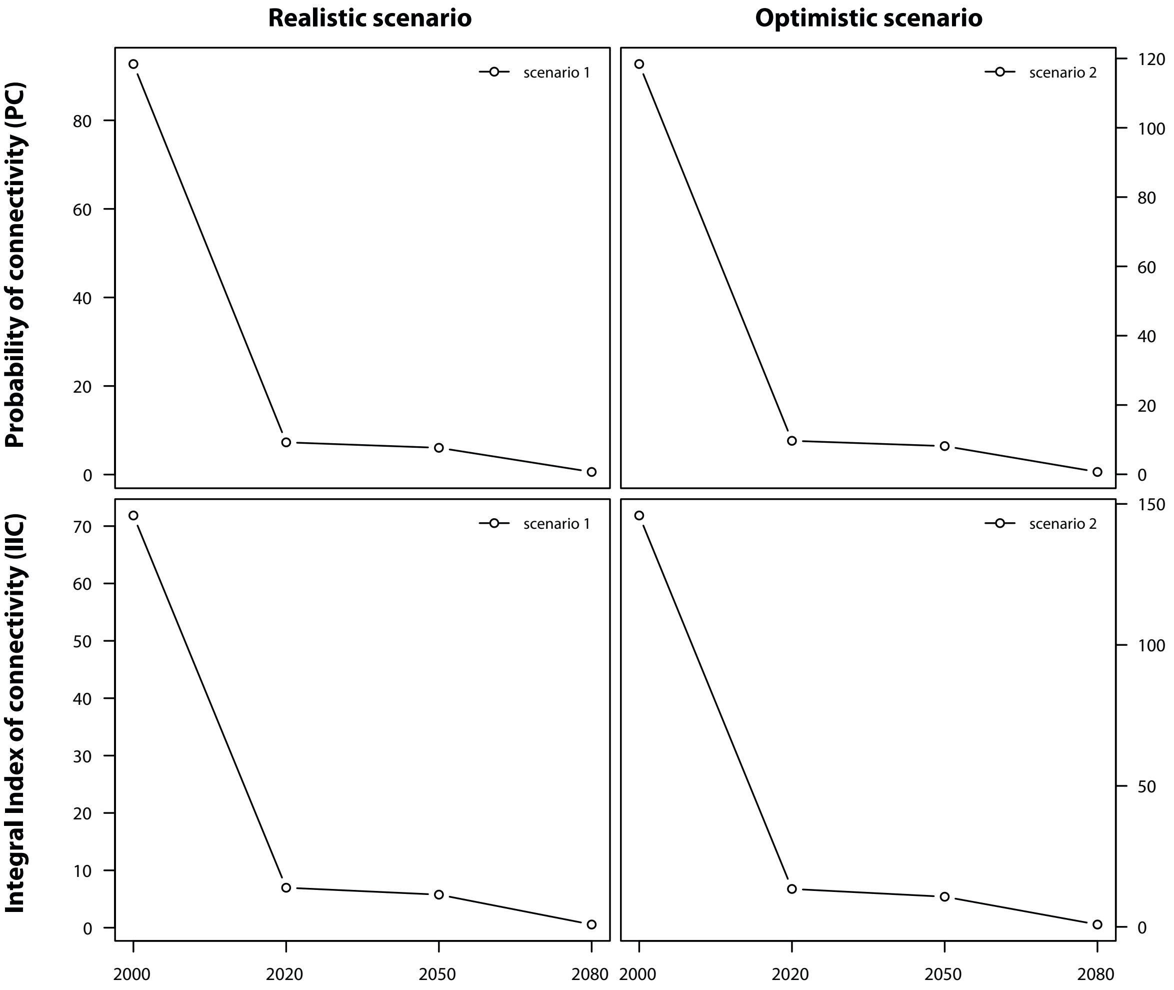


Fig. A11: Overall index values for "raised bogs" (habitat type 71X0) of the probability of connectivity index (PC) versus the integral index of connectivity (IIC) plotted separately for the realistic and the optimistic null dispersal scenarios.

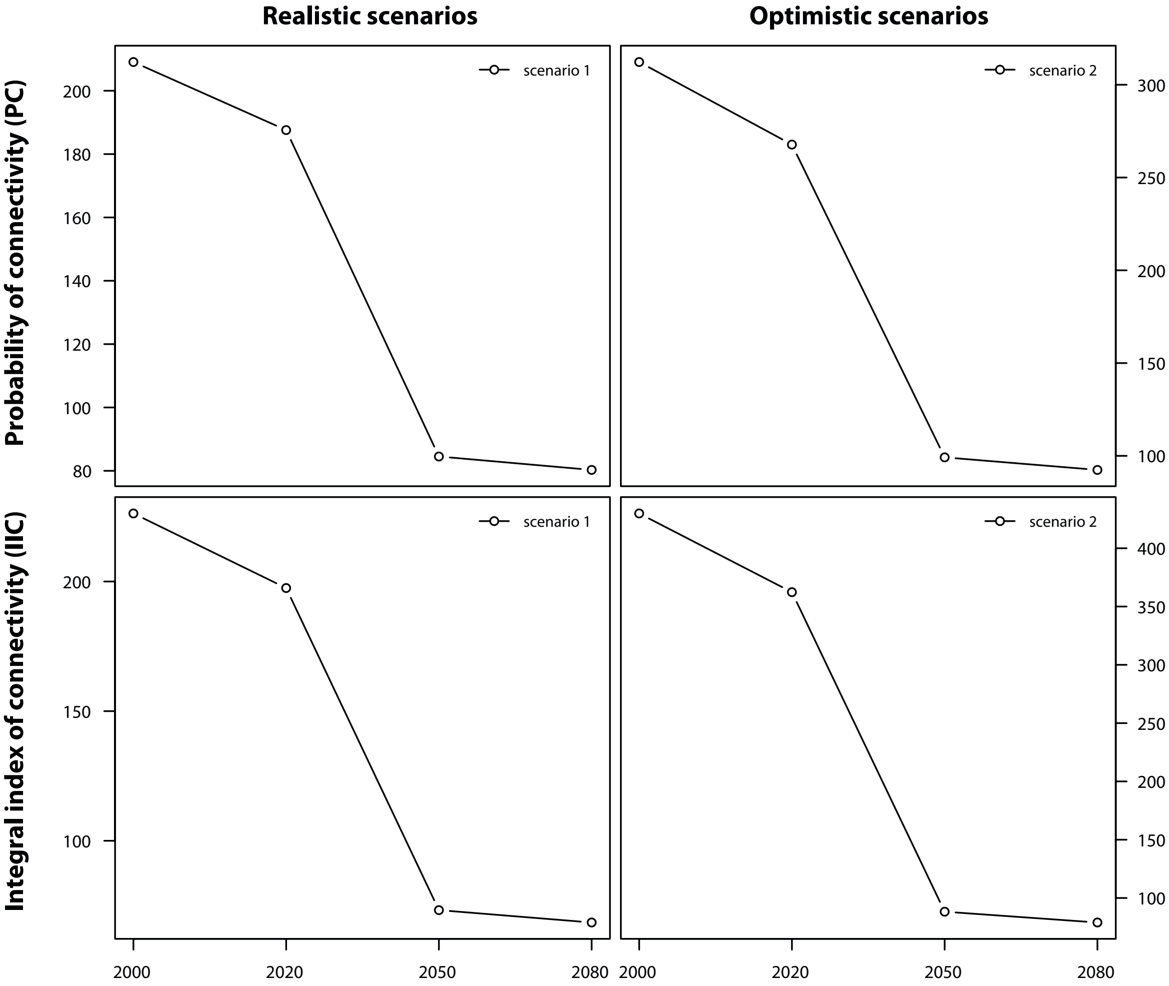


Fig. A12: Overall index values for "Medio-European calcareous screes of hill and montane levels" (habitat type 8160) of the probability of connectivity index (PC) versus the integral index of connectivity (IIC) plotted separately for the realistic and the optimistic null dispersal scenarios.

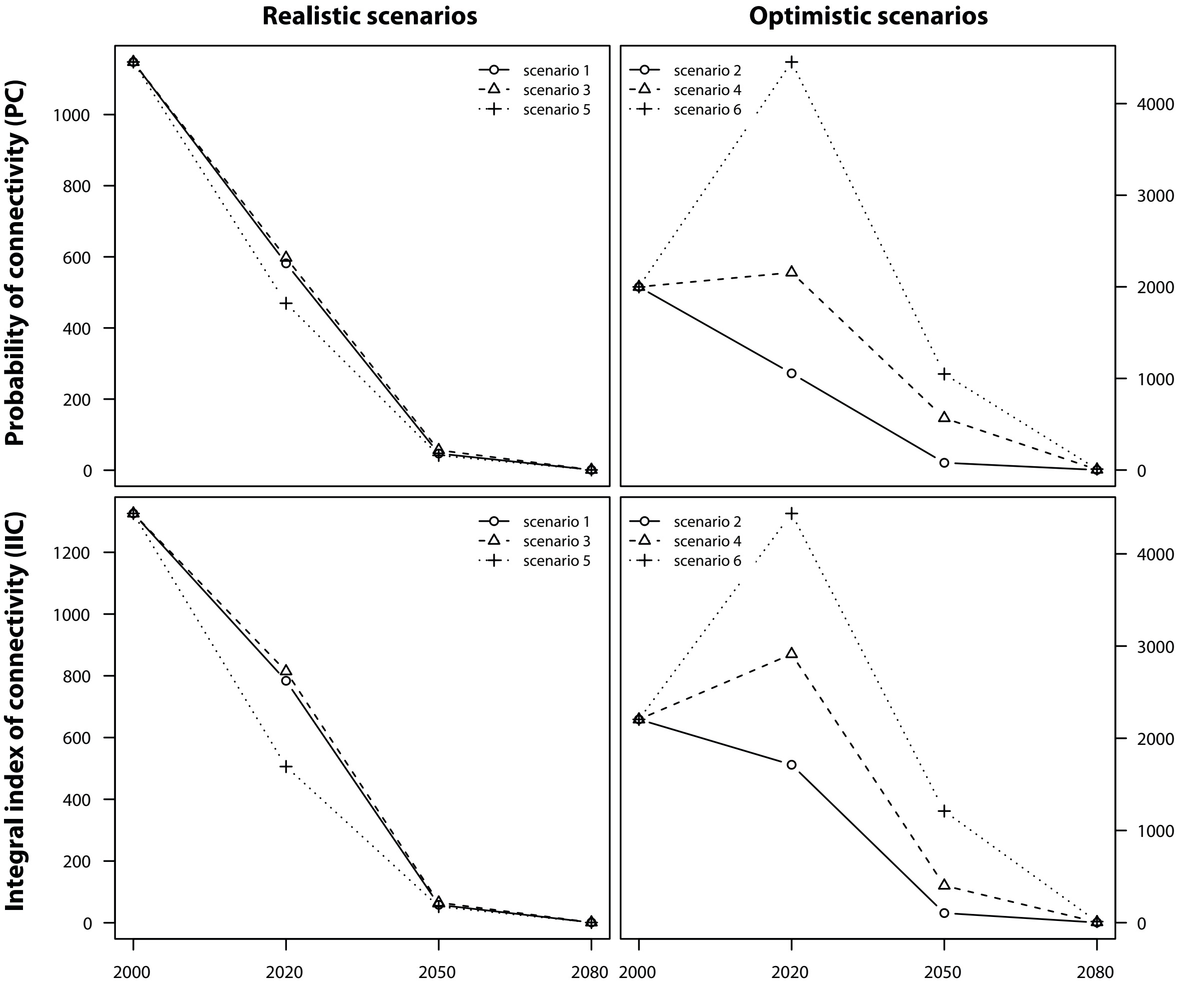


Fig. A13: Overall index values for "*Galio-Carpinetum* oak-hornbeam forests" (habitat type 9170) of the probability of connectivity index (PC) versus the integral index of connectivity (IIC) plotted separately for the realistic and the optimistic scenarios. Scenarios 1 & 2: null dispersal. Scenarios 3 & 4: realistic and optimistic dispersal / connectivity distance inside SCI Natura 2000 network under consideration of costs. Scenarios 5 & 6: realistic and optimistic dispersal / connectivity distance within Germany (except cities) under consideration of costs.

Article 5

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

revision submitted to Insect Conservation and Diversity on 2011-09-16
under review
submitted on 2011-04-14

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 in the modelling process.

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 *Leucorrhina caudalis* (up to -73%), whereas *Leucorrhinia pectoralis* is projected to gain distribution area (up to +37%) assuming either species-specific or unrestricted dispersal. Cross-validated AUC values range 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

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

Anja Jaeschke[1,2], Torsten Bittner[1,2], Björn Reineking[2], Carl Beierkuhnlein[1]

[1] Department of Biogeography, BayCEER, University of Bayreuth, Bayreuth, Germany
[2] Biogeographical Modelling, BayCEER, University of Bayreuth, Bayreuth, Germany

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 this 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/carto/; 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 HadCM3 climate model and covers the period 2021-50 (2035).

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).

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).

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'.

Tab. 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**
Coenagrion mercuriale	Up to 1 km/a	1 km/a	2 years	Thompson *et al.* (2003), Corbet et al. (2006)	14 km
Coenagrion ornatum	200m up to several km/a	1 km/a	2 years	Burbach *et al.* (1996)	14 km
Leucorrhinia albifrons	Up to 18 km/a	18 km/a	2 years	Mauersberger (2003a)	252 km
Leucorrhinia caudalis	Up to 7 km/a	7 km/a	2 years	Mauersberger (2003b), Corbet et al. (2006)	98 km
Leucorrhinia pectoralis	Up to 27 km/a	27 km/a	2 years	Wildermuth (1993), Corbet et al. (2006)	378 km
Ophiogomphus cecilia	Up to 10 km/a	10 km/a	3 years	Suhling et al. (2003), Corbet et al. (2006)	93 km

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), and 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 3). *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* 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.

Species show geographically differentiated responses to projected climate change (Fig. S1-S3). 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.

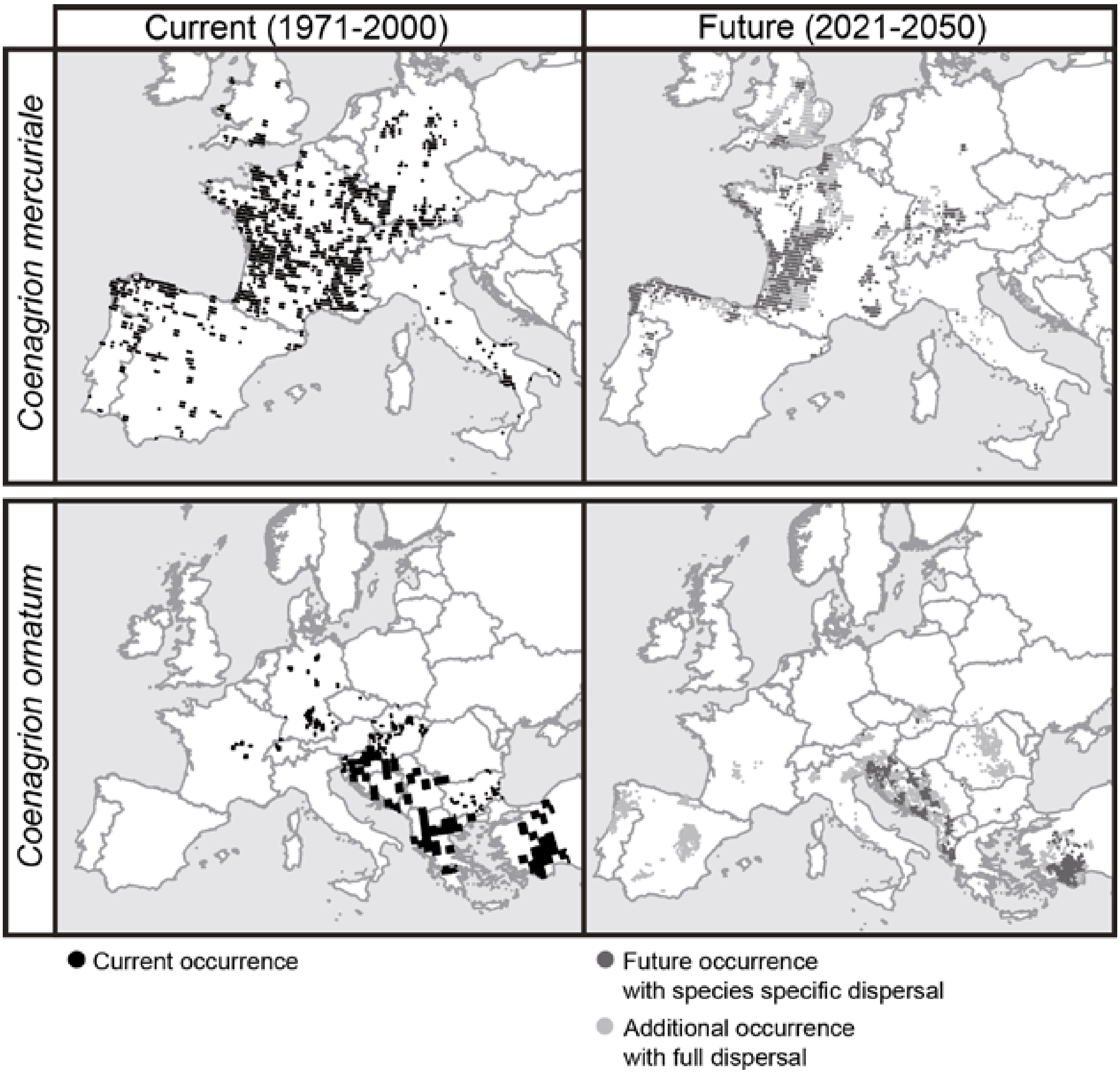


Fig. 1 Current and future projected distribution of Coenagrion mercuriale and Coenagrion ornatum in Europe. Both damselflies are projected to gain distribution area under the full dispersal scenario, but to lose distribution area under the species-specific dispersal scenario (1 km/a). Occurrence thresholds: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

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. 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 2). 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 hibernation, which is especially relevant for the survival of the larvae. Winter warming can interrupt the larval diapause via an increase in metabolism. This is highly energy consumptive, especially if this happens several times during hibernation. 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.

Tab. 2 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**					
Coenagrion mercuriale	0.66	0.64	0.89	0.88	TMN min 26.6%	PRE min 22.4%	PRE in May 22%	CLD in Jan 17%	DTR in Jan 12%
Coenagrion ornatum	0.59	0.55	0.79	0.77	DTR in Oct 64.2%	PRE in Apr 35.8%			
Leucorrhinia albifrons	0.60	0.81	0.92	0.92	CLD in Nov 36.5%	PRE in Apr 24.4%	PRE in Aug 19.7%	DTR in Nov 19.4%	
Leucorrhinia caudalis	0.48	0.82	0.84	0.88	CLD in Nov 43.5%	PRE in Apr 29.4%	PRE in Aug 27.1%		
Leucorrhinia pectoralis	0.54	0.73	0.83	0.80	CLD in Jan 26.2%	DTR in Jan 20.6%	GDD in Dec 20.1%	DTR in May 16.7%	PRE in Feb 16.3%
Ophiogomphus cecilia	0.50	0.53	0.81	0.77	CLD in Nov 32.8%	PRE in Feb 18%	DTR in Nov 17.3%	PRE max 16.5%	DTR in May 15.4%

Both modelling algorithms, GLM and BRT, performed well in predicting the current distribution of all six species (Table 2). All cross-validated AUC values are between 0.77 und 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).

Tab. 3 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**
Coenagrion mercuriale	- 71%	- 65%	- 52%	- 48%	+ 7%	+ 5%
Coenagrion ornatum	- 73%	- 77%	- 65%	- 68%	+ 23%	+ 17%
Leucorrhinia albifrons	- 64%	- 65%	- 39%	- 38%	- 35%	- 30%
Leucorrhinia caudalis	- 73%	- 71%	- 59%	- 57%	- 35%	- 34%
Leucorrhinia pectoralis	- 67%	- 67%	+ 34%	+ 7%	+ 37%	+ 7%
Ophiogomphus cecilia	- 58%	- 60%	- 16%	- 31%	+ 8%	+ 9%

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 the most likely one. The applied distance of one kilometre per generation is rather optimistic for a species with a mean dispersal distance of approximately 60 meters (Purse *et al.*, 2003). However, maximum dispersal distances of one kilometre can be also observed (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. 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. However, the problem with land cover is its coarse classification, especially on a continental scale, and its constraint predictability. On a European scale we cannot distinguish between e.g. types of forests. Therefore, this information cannot be interpreted in an ecological reasonable way.

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. In contrast, 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 influences the larval development time (Richter *et al.*, 2008).

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. 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.

Acknowledgements

We thank the Federal Agency for Nature Conservation Germany for funding this work (FKZ 3508 85 0600). We also thank two anonymous reviewers for their helpful comments on an earlier version of this manuscript.

References

Allouche, O., Steinitz, O., Rotem, D., Rosenfeld, A. & Kadmon, R. (2008) Incorporating distance constraints into species distribution models. *Journal of Applied Ecology*, **45**, 599–609.

Araújo, M.B. & Guisan, A. (2006) Five (or so) challenges for species distribution modelling. *Journal of Biogeography*, **33** (10), 1677–1688.

Bissonette, J.A. & Adair, W. (2008) Restoring habitat permeability to roaded landscapes with isometrically-scaled wildlife crossings. *Biological Conservation*, **141** (2), 482–488.

Bittner, T., Jaeschke, A., Reineking, B. & Beierkuhnlein, C. (2011) Comparing modelling approaches at two levels of biological organisation – Climate change impacts on selected Natura 2000 habitats. *Journal of Vegetation Science*, **22** (4), 699-710.

Boehning-Gaese, K., Caprano T, van Ewijk K & Veith M (2006) Range size: disentangling current traits and phylogenetic and biogeographic factors. *American Naturalist*, **167** (4), 555–567.

Bonte, D., Clercq, N. de, Zwertvaegher, I. & Lens, L. (2009) Repeatability of dispersal behaviour in a common dwarf spider: evidence for different mechanisms behind short- and long-distance dispersal. *Ecological Entomology*, **34** (2), 271–276.

Boudot, J.-P., Kalkman, V.J., Amorin, M.A., Bogdanovic, T., Rivera, A.C., Degabriele, G., Dommanget, J.-L., Ferreira, S., Garrigós, B., Jovic, M., Kotarac, M., Lopau, W., Marinov, M., Mihokovic, N., Riservato, E., Samraoui, B. & Schneider, W. (eds.) (2009) *Atlas of the Odonata of the Mediterranean and North Africa*. GdO, Börnsen.

Braune, E., Richter, O., Söndgerath, D. & Suhling, F. (2008) Voltinism flexibility of a riverine dragonfly along thermal gradients. *Global Change Biology*, **14**, 470–482.

Brooker, R.W., Travis, J.M.J., Clark, E.J. & Dytham, C. (2007) Modelling species' range shifts in a changing climate: The impacts of biotic interactions, dispersal distance and the rate of climate change. *Journal of Theoretical Biology*, **245** (1), 59–65.

Burbach, K., Faltin, I., Königsdorfer, M., Krach, E. & Winterholler, M. (1996) *Coenagrion ornatum* (SELYS) in Bayern (Zygoptera: Coenagrionidae). *Libellula*, **15** (3/4), 131–168.

Buse, J. & Griebeler, E.M. (2011) Incorporating classified dispersal assumptions in predictive distribution models – A case study with grasshoppers and bush-crickets. *Ecological Modelling*, **222** (13), 2130–2141.

Cabral, J.S. & Schurr, F.M. (2010) Estimating demographic models for the range dynamics of plant species. *Global Ecology and Biogeography*, **19**, 85–97.

Carvalho, S.B., Brito, J.C., Crespo, E.J. & Possingham, H.P. (2010) From climate change predictions to actions – conserving vulnerable animal groups in hotspots at a regional scale. *Global Change Biology*, **16**, 3257–3270.

Coetzee, B.W.T., Robertson, M.P., Erasmus, B.F.N., van Rensburg, B.J. & Thuiller, W. (2009) Ensemble models predict Important Bird Areas in southern Africa will become less effective for conserving endemic birds under climate change. *Global Ecology and Biogeography*, **18** (6), 701-710.

Corbet, P.S., Suhling, F. & Soendgerath, D. (2006) Voltinism of Odonata: a review. *International Journal of Odonatology*, **9** (1), 1–44.

Davidson, I. & Simkanin, C. (2008) Skeptical of assisted colonization. *Science*, **322** (5904), 1048–1049.

Dijkstra, K.-D.B. & Lewington, R. (2006) *Field Guide to the Dragonflies of Britain and Europe: Including western Turkey and north-western Africa*. British Wildlife Publishing, Dorset, UK.

Dormann, C.F., Purschke, O., Márquez, J.R.G., Lautenbach, S. & Schröder, B. (2008) Components of uncertainty in species distribution analysis: a case study of the Great Grey Shrike. *Ecology*, **89** (12), 3371–3386.

Dullinger, S., Dirnbock, T. & Grabherr, G. (2004) Modelling climate change-driven treeline shifts: relative effects of temperature increase, dispersal and invasibility. *Journal of Ecology*, **92** (2), 241–252.

EIONET (2009) *Central Data Repository(CDR)* <http://cdr.eionet.europa.eu/>.

Elith, J., Leathwick, J.R. & Hastie, T. (2008) A working guide to boosted regression trees. *Journal of Animal Ecology*, **77** (4), 802–813.

Elith, J. & Leathwick, J.R. (2009) Species distribution models: ecological explanation and prediction across space and time. *Annual Review of Ecology Evolution and Systematics*, **40**, 677–697.

European Topic Centre on Biological Diversity (ETC/BD) (2008) *Article 17 Technical Report (2001-2006)*. Annex J - Some specific analysis on conservation status.

Fitzpatrick, M.C., Sanders, N.J., Ferrier, S., Longino, J.T., Weiser, M.D. & Dunn, R. (2011) Forecasting the future of biodiversity: a test of single- and multi-species models for ants in North America. *Ecography*. doi: 10.1111/j.1600-0587.2011.06653.x.

Foltête, J.C., Berthier, K. & Cosson, J.F. (2008) Cost distance defined by a topological function of landscape. *Ecological Modelling*, **210**, 104–114.

Flenner, I. & Sahlén, G. (2008) Dragonfly community re-organisation in boreal forest lakes: rapid species turnover driven by climate change? *Insect Conservation and Diversity*, **1**, 169–179.

Franklin, J. (2010) Moving beyond static species distribution models in support of conservation biogeography. *Diversity and Distributions*, **16**, 321–330.

Freeman, E. (2007) PresenceAbsence: An R Package for Presence-Absence Model Evaluation, 507 25th street, Ogden, UT, USA.

Guisan, A. & Thuiller, W. (2005) Predicting species distribution: offering more than simple habitat models. *Ecology Letters*, **8** (9), 993–1009.

Harrell, F.E., Jr (2009) Design: Design Package <http://CRAN.R-project.org/package=Design>.

Hassall, C. & Thompson, D.J. (2008) The effects of environmental warming on Odonata: a review. *International Journal of Odonatology*, **11** (2), 131–153.

Hassall, C., Thompson, D. & Harvey, I. (2009) Variation in morphology between core and marginal populations of three British damselflies. *Aquatic Insects*, **31** (3), 187–197.

Hickling, R., Roy, D.B., Hill, J.K. & Thomas, C.D. (2005) A northward shift of range margins in British Odonata. *Global Change Biology*, **11** (3), 502–506.

Hickling, R., Roy, D.B., Hill, J.K., Fox, R. & Thomas, C.D. (2006) The distributions of a wide range of taxonomic groups are expanding polewards. *Global Change Biology*, **12**, 450–455.

Hill, J.K., Thomas, C.D. & Blakeley, D.S. (1999) Evolution of flight morphology in a butterfly that has recently expanded its geographic range. *Oecologia*, **121**, 165–170.

Hill, J.K., Griffiths, H.M. & Thomas, C.D. (2011) Climate change and evolutionary adaptations at species' range margins. *Annual Review of Entomology*, **56**, 143–159.

Hitch, A.T. & Leberg, P.L. (2007) Breeding distributions of North American bird species moving north as a result of climate change. *Conservation Biology*, **21** (2), 534–539.

Hoegh-Guldberg, O., Hughes, L., McIntyre, S., Lindenmayer, D.B., Parmesan, C., Possingham, H.P. & Thomas, C.D. (2008) Assisted colonization and rapid climate change. *Science*, **321** (5887), 345–346.

Kalkman, V.J., Boudot, J.-P., Bernard, R., Conze, K.-J., Knijf, G. de, Dyatlova, E., Ferreira, S., Jović, M., Ott, J., Riservato, E. & Sahlén, G. (2010) *European Red List of Dragonflies*, Luxembourg: Publications Office of the European Union.

Keller, D., Brodbeck, S., Flöss, I., Vonwil, G. & Holderegger, R. (2010) Ecological and genetic measurements of dispersal in a threatened dragonfly. *Biological Conservation*, **143** (11), 2658–2663.

Kreyling, J., Bittner, T., Jaeschke, A., Jentsch, A., Steinbauer, M.J., Thiel, D. & Beierkuhnlein, C. (2011) Assisted colonization: a question of focal units and recipient localities. *Restoration Ecology*, **19** (4), 433-440.

Lawler, J.J., Shafer, S.L., White, D., Kareiva, P., Maurer, E.P., Blaustein, A.R. & Bartlein, P.J. (2009) Projected climate-induced faunal change in the Western Hemisphere. *Ecology*, **90** (3), 588–597.

Massot, M., Clobert, J. & Ferrière, R. (2008) Climate warming, dispersal inhibition and extinction risk. *Global Change Biology*, **14**, 461–469.

Mauersberger, R. (2003a) Leucorrhinia albifrons (Burmeister, 1839). *Das europäische Schutzgebietssystem Natura 2000: Ökologie und Verbreitung von Arten der FFH-Richtlinie in Deutschland*. Band 1: Pflanzen und Wirbellose (ed. by B. Petersen, G. Ellwanger, G. Biewald, U. Hauke, G. Ludwig, P. Pretscher, E. Schröder and A. Ssymank), pp. 574–579: Landwirtschaftsverlag. Bonn - Bad Godesberg.

Mauersberger, R. (2003b) Leucorrhinia caudalis (Charpentier, 1840). *Das europäische Schutzgebietssystem Natura 2000: Ökologie und Verbreitung von Arten der FFH-Richtlinie in Deutschland*. Band 1: Pflanzen und Wirbellose (ed. by B. Petersen, G. Ellwanger, G. Biewald, U. Hauke, G. Ludwig, P. Pretscher, E. Schröder and A. Ssymank), pp. 580–585: Landwirtschaftsverlag. Bonn - Bad Godesberg.

Menéndez, R., González-Megías, A., Lewis, O., Shaw, M.R. & Thomas, C.D. (2008) Escape from natural enemies during climate-driven range expansion: a case study. *Ecological Entomology*, **33** (3), 413–421.

Mitchell, T.D., Carter, T.R., Jones, P.D., Hulme, M. & New, M. (2004) *A comprehensive set of high-resolution grids of monthly climate for Europe and the globe: the observed record (1901-2000) and 16 scenarios (2001-2100): Working Paper 55*.

Nathan, R. (2006) Long-Distance Dispersal of Plants. *Science*, **313**, 786–788.

Olsvik, H. & Dolmen, D. (1992) Distribution, habitat, and conservation status of threatened Odonata in Norway. *Fauna Norvegica, Series B*, **39**, 1–12.

Opdam, P., Steingröver, E. & van Rooij, S. (2006) Ecological networks: A spatial concept for multi-actor planning of sustainable landscapes. *Landscape and Urban Planning*, **75** (3-4), 322–332.

Ott, J. (2009) The Big Trek Northwards: Recent Changes in the European Dragonfly Fauna. *In Atlas of Biodiversity Risk* (ed. by J. Settele, L. Penev, T. Georgiev, R. Grabaum, V. Grobelnik, V. Hammen, S. Klotz, M. Kotarac and I. Kühn), pp. 78–79: Pensoft Publishers.

Ott, J. (2010) Dragonflies and climatic change - recent trends in Germany and Europe. *BioRisk*, **5**, 253–286.

Petersen, B., Ellwanger, G., Biewald, G., Hauke, U., Ludwig, G., Pretscher, P., Schröder, E. & Ssymank, A. (eds.) (2003) *Das europäische Schutzgebietssystem Natura 2000: Ökologie und Verbreitung von Arten der FFH-Richtlinie in Deutschland*. Band 1: Pflanzen und Wirbellose. Landwirtschaftsverlag, Bonn - Bad Godesberg.

Petersen, B. & Ellwanger, G. (eds.) (2006) *Das europäische Schutzgebietssystem Natura 2000: Ökologie und Verbreitung von Arten der FFH-Richtlinie in Deutschland*. Band 3: Arten der EU-Osterweiterung. Landwirtschaftsverlag, Bonn - Bad Godesberg.

Purse, B.V., Hopkins, G.W., Day, K.J. & Thompson, D.J. (2003) Dispersal characteristics and management of a rare damselfly. *Journal of Applied Ecology*, **40**, 716–728.

Reineking, B. & Schröder, B. (2006) Constrain to perform: Regularization of habitat models. *Ecological Modelling*, **193** (3-4), 675–690.

Ricciardi, A. & Simberloff, D. (2009) Assisted colonization is not a viable conservation strategy. *Trends in Ecology & Evolution*, **24** (5), 248–253.

Richter, O., Suhling, F., Müller, O. & Kern, D. (2008) A model for predicting the emergence of dragonflies in a changing climate. *Freshwater Biology*, **53**, 1868–1880.

R Development Core Team (2010) R: A Language and Environment for Statistical Computing, Vienna, Austria <http://www.R-project.org>.

Ridgeway, G. (2010) gbm: Generalized Boosted Regression Models <http://CRAN.R-project.org/package=gbm>.

Rouquette, J.R. & Thompson, D.J. (2007) Patterns of movement and dispersal in an endangered damselfly and the consequences for its management. *Journal of Applied Ecology*, **44**, 692–701.

Schlumprecht, H., Bittner, T., Jaeschke, A., Jentsch, A., Reinking, B. & Beierkuhnlein, C. (2010) Gefährdungsdisposition von FFH-Tierarten Deutschlands angesichts des Klimawandels: Eine vergleichende Sensitivitätsanalyse. *Naturschutz und Landschaftsplanung*, **42** (10), 293–303.

Schweiger, O., Settele, J., Kudrna, O., Klotz, S. & Kühn, I. (2008) Climate change can cause spatial mismatch of trophically interacting species. *Ecology*, **89** (12), 3472–3479.

Seo, C., Thorne, J.H., Hannah, L. & Thuiller, W. (2009) Scale effects in species distribution models: implications for conservation planning under climate change. *Biology Letters*, **5** (1), 39–43.

Settele, J., Hammen, V., Hulme, P., Karlson, U., Klotz, S., Kotarac, M., Kunin, W., Marion, G., O'Connor, M., Petanidou, T., Peterson, K., Potts, S., Pritchard, H., Pysek, P., Rounsevell, M., Spangenberg, J., Steffan-Dewenter, I., Sykes, M., Vighi, M., Zobel, M. & Kuhn, I. (2005) Alarm: Assessing Large-scale environmental Risks for biodiversity with tested Methods. *GAIA - Ecological Perspectives for Science and Society*, **14** (1), 69-72.

Smolik, M., Dullinger, S., Essl, F., Kleinbauer, I., Leitner, M., Peterseil, J., Stadler, L.-M. & Vogl, G. (2010) Integrating species distribution models and interacting particle systems to predict the spread of an invasive alien plant. *Journal of Biogeography*, **37** (3), 411–422.

Spangenberg, J.H. (2007) Integrated scenarios for assessing biodiversity risks. *Sustainable Development*, **15** (6), 343–356.

Sternberg, K. (1999) Coenagrion ornatum. *Die Libellen Baden-Württembergs. Bd. 1* (ed. by K. Sternberg and R. Buchwald), pp. 270-277: Ulmer. Stuttgart.

Sternberg, K., Buchwald, R. & Röske, W. (1999) Coenagrion mercuriale. *Die Libellen Baden-Württembergs. Bd. 1* (ed. by K. Sternberg and R. Buchwald), pp. 255-269: Ulmer. Stuttgart.

Sternberg, K. & Buchwald, R. (eds.) (1999) *Die Libellen Baden-Württembergs. Bd. 1*. Ulmer, Stuttgart.

Sternberg, K. & Buchwald, R. (eds.) (2000) *Die Libellen Baden-Württembergs. Bd. 2*. Ulmer, Stuttgart.

Sternberg, K., Höppner, B., Heitz, A. & Heitz, S. (2000) Ophiogomphus cecilia. *Die Libellen Baden-Württembergs. Bd. 2* (ed. by K. Sternberg and R. Buchwald), pp. 358-373: Ulmer. Stuttgart.

Suhling, F., Werzinger, J. & Müller, O. (2003) Ophiogomphus cecilia (Fourcroy, 1785). *Das europäische Schutzgebietssystem Natura 2000: Ökologie und Verbreitung von Arten der FFH-Richtlinie in Deutschland*. Band 1: Pflanzen und Wirbellose (ed. by B. Petersen, G. Ellwanger, G. Biewald, U. Hauke, G. Ludwig, P. Pretscher, E. Schröder and A. Ssymank), pp. 593–601: Landwirtschaftsverlag. Bonn - Bad Godesberg.

Swets, J.A. (1988) Measuring the accuracy of diagnostic systems. *Science* (240), 1285–1293.

Thompson, D.J., Rouquette, J.R. & Purse, B.V. (2003) *Ecology of the Southern Damselfly: Conserving Natura 2000 Rivers Ecology Series No. 8*, Peterborough.

Walther, G.-R., Beißner, S. & Burga, C.A. (2005) Trends in the upward shift of alpine plants. *Journal of Vegetation Science*, **16** (5), 541–548.

Wildermuth, H. (1993) Populationsbiologie von *Leucorrhinia pectoralis* (Charpentier) (Anisoptera: Libellulidae). *Libellula*, **12**, 269–275.

Supplemental figures

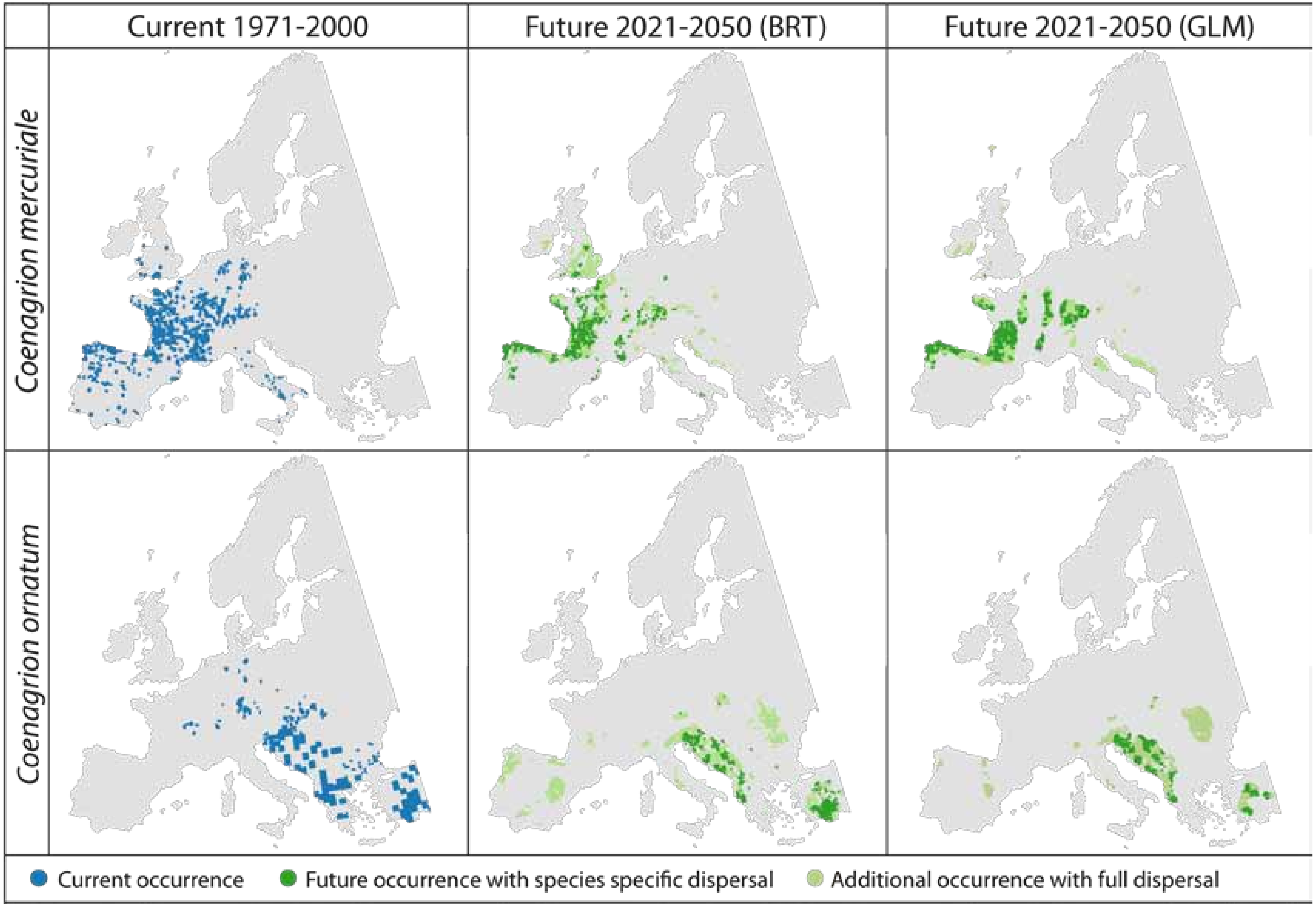


Fig. S1. Current and future projected distribution of *Coenagrion mercuriale* and *Coenagrion ornatum* in Europe. Both damselflies are projected to gain distribution area under the full dispersal scenario, but to lose distribution area under the species specific dispersal scenario (1 km/a). Occurrence 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*).

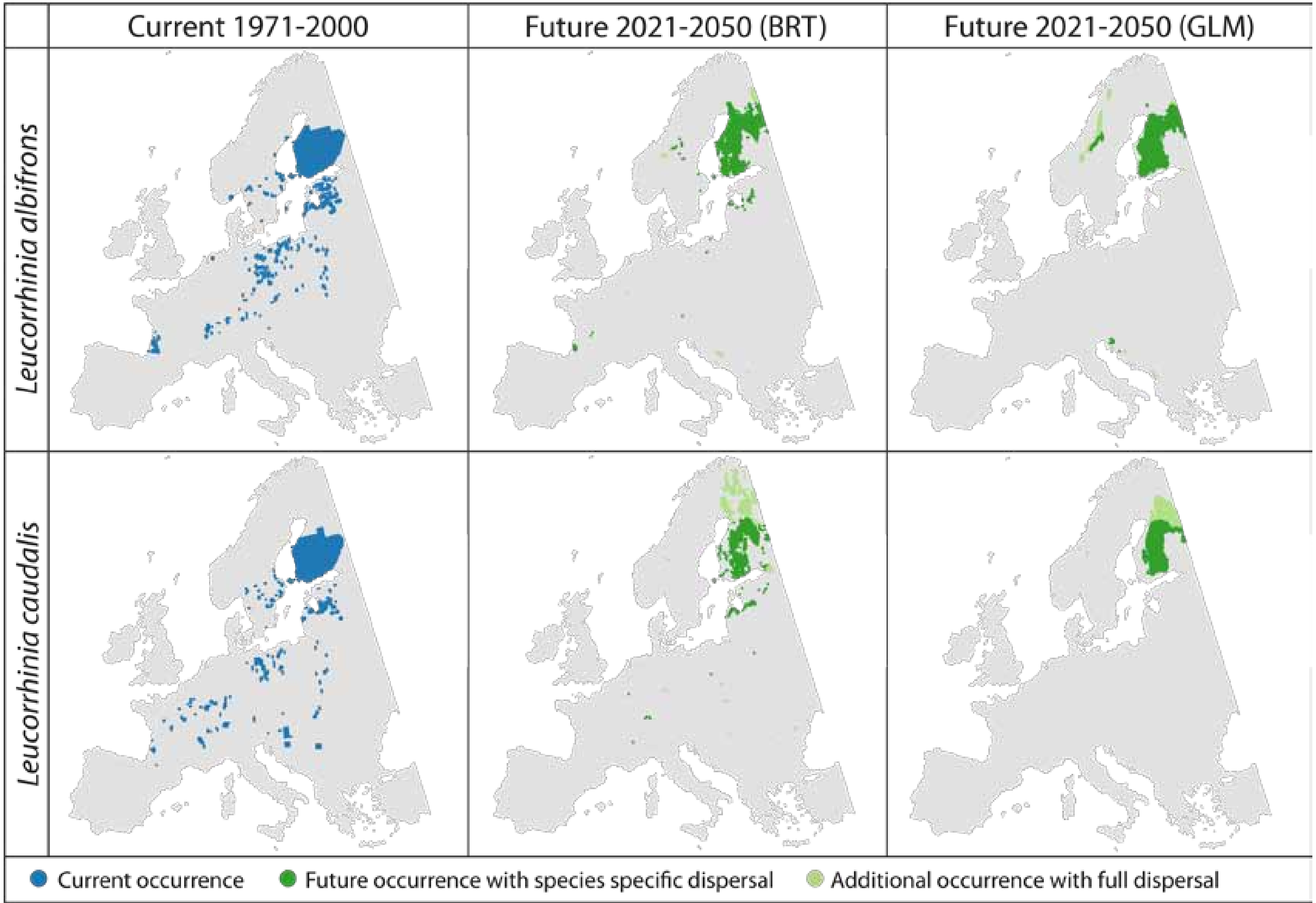


Fig. S2. Current and future projected distribution of *Leucorrhinia albifrons* and *Leucorrhinia caudalis* in Europe. Both dragonflies are projected to lose distribution area with all dispersal scenarios. Occurrence thresholds: BRT: 0.33 (*L. albifrons*), 0.27 (*L. caudalis*), GLM: 0.40 (*L. albifrons*), 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*).

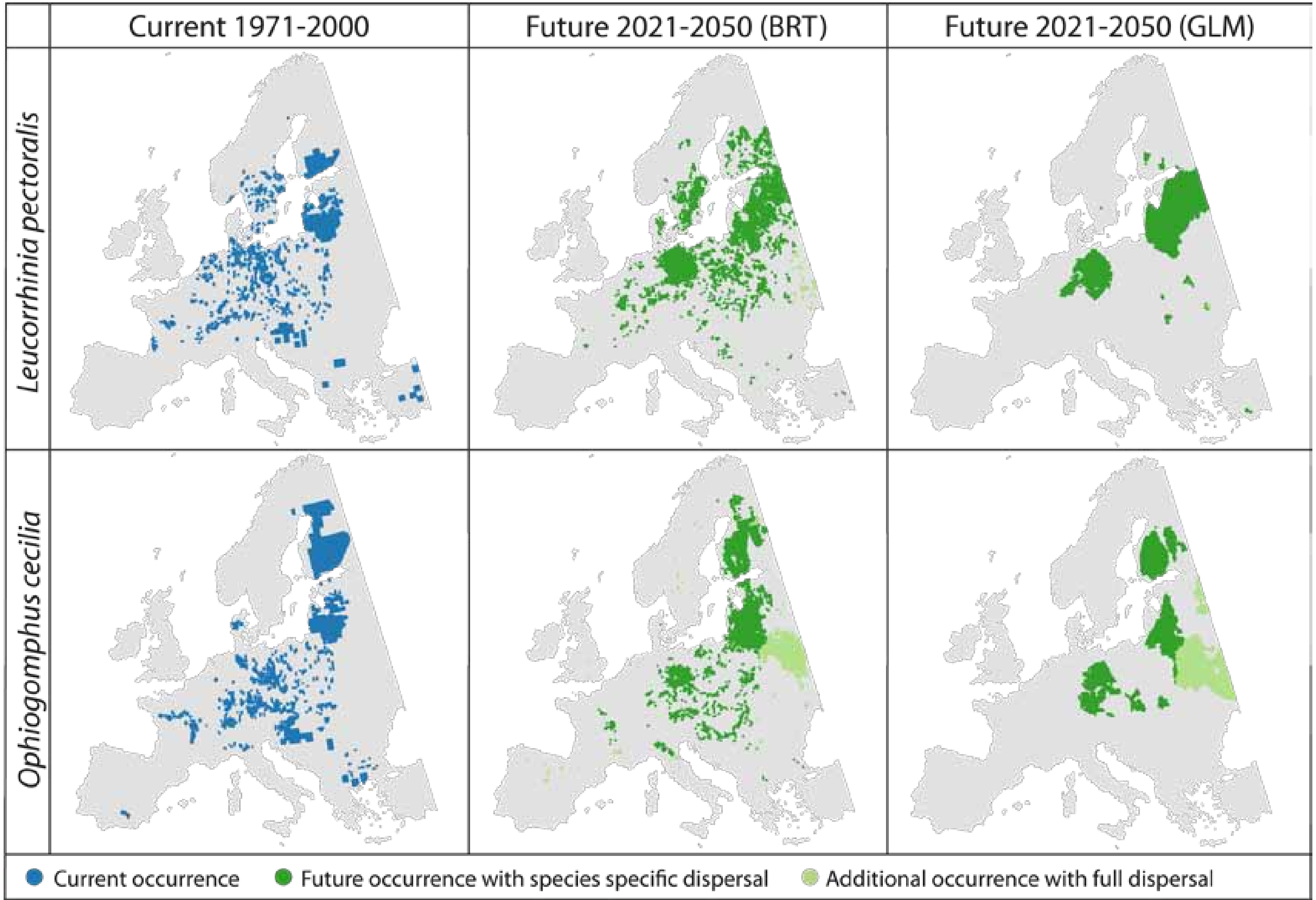


Fig. S3. Current and future projected distribution of *Leucorrhinia pectoralis* and *Ophiogomphus cecilia* in Europe. Both dragonflies are projected to gain distribution area under the full dispersal scenario, but *O. cecilia* is projected to lose distribution area with the species specific dispersal 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*).

Article 6

Assisted Colonization: A Question of Focal Units and Recipient Localities

Juergen Kreyling, Torsten Bittner, Anja Jaeschke, Anke Jentsch, Manuel Jonas Steinbauer, Daniel Thiel, Carl Beierkuhnlein

printed in Restoration Ecology 2011 19(4) 433–440
submitted 2010-01-18
accepted 2010-12-21

Abstract

Assisted colonization as an adaptation strategy to conserve or restore biodiversity in the face of climate change deservedly evokes controversy. Assisted colonization is perceived by some as a last option for conserving endangered species and by others as a risky and unwise management effort due to current gaps of knowledge. Based on the pros and cons of the recent debate, we show that the current discussion mainly focuses on the assisted colonization of rare and endangered species beyond their natural range of distribution. We suggest that a more useful approach for the conservation of endangered species could occur by focusing on the relevant foundation or keystone species, which ensure ecosystem integrity for a multitude of dependent species by governing the habitat structure and microclimate of the site. Examples of foundation species include dominant tree species in forests or dominant corals in coral reefs. For a given conservation or restoration need (e.g. conservation of rare species), we recommend the assisted colonization of pre-adapted ecotypes of the relevant foundation species from climates similar to future expectations for the target site. This approach could lead to climatesafe habitats for endangered species with minimal adverse effects on recipient ecosystems.

Keywords

adaptation strategy, assisted migration, core species, ecosystem engineers, managed relocation, managed translocation, species conservation.

Restoration Ecology
THE JOURNAL OF THE SOCIETY FOR ECOLOGICAL RESTORATION INTERNATIONAL

OPINION ARTICLE

Assisted Colonization: A Question of Focal Units and Recipient Localities

Juergen Kreyling,[1,2] Torsten Bittner,[1] Anja Jaeschke,[1] Anke Jentsch,[3] Manuel Jonas Steinbauer,[1] Daniel Thiel,[1] and Carl Beierkuhnlein[1]

[1] Biogeography, University of Bayreuth, D-95440 Bayreuth, Germany
[2] Address correspondence to J. Kreyling, email juergen.kreyling@uni-bayreuth.de
[3] Geoecology and Physical Geography, University of Koblenz-Landau, D-76829 Landau, Germany

Introduction

Assisted colonization as a conservation tool against the adverse effects of climate change on biodiversity is currently receiving a lot of attention (Hoegh-Guldberg et al. 2008 or Ricciardi & Simberloff 2009 and the various replies to these articles). This debate is based on the notion that global climate change leads to high regional extinction risks for species' populations (Thomas et al. 2004). Naturally rare species and species already exposed to habitat decline are assumed to be especially threatened by climate change (Ohlemüller et al. 2008). Yet, the degree to which such species are limited directly by climate or by biotic (Pelini et al. 2009) or other environmental factors (Harsch et al. 2009) remains largely unexplored. As a consequence of limited information, advocates and opponents of assisted colonization differ in their perception of the benefits and risks of this approach. Although it is usually regarded as a final option for conservation (e.g. Hoegh-Guldberg et al. 2008), assisted colonization has to be considered as one management option if preventing climate-driven extinction is a conservation priority (McLachlan et al. 2007; Richardson et al. 2009).

We define assisted colonization as "the intentional movement of focal units (ecotypes, species, taxa, functional types, life forms) to recipient localities, where these focal units are currently absent, and where they cannot be expected to colonize by natural means within a short time frame (i.e. years or decades)." We agree with Hunter (2007) that assisted colonization is a more appropriate term than assisted migration, because the final goal of this approach is not only to assist dispersal but rather the successful establishment of individuals and the subsequent development of self-sustaining populations, which is much more demanding. "Managed relocation" or "managed translocation" are further used as synonyms for this approach. However, these terms are not necessarily confined to the context of adaptation against climate change (Ricciardi & Simberloff 2009).

Evaluation of the applicability of assisted colonization needs to focus on the impacts of conducting (or not conducting) assisted colonization on a given focal unit and the impacts of assisted colonization on the recipient ecosystem (including aspects such as novel biotic interactions with other taxa, rapid genetic evolution at the recipient locality, changes in niche space within the recipient ecosystem, functional redundancy or complementarity to other species in the recipient community). Furthermore, the practical feasibility of conducting assisted colonization and the societal acceptability need to be considered (Richardson et al. 2009).

Assisted colonization is already taking place in various instances and therefore scientifically sound recommendations are urgently needed. Commercial nurseries in Europe, for example, have successfully assisted the colonization of at least 260 native European plant species by ornamental planting at an average of 1,000 km north of the species' natural northern range limits (van der Veken et al. 2008). During the early 20th century various cases of assisted colonization of plant species occurred in Central Europe. Their aim was to establish mainly thermophilous species in special microhabitats (e.g. steep south facing slopes) in order to enrich regional floras (e.g. Iris variegata, Linum austriacum, Verbascum phoeniceum). Several of these species are still present with stable populations (Walter 2003). Here, it should be noted that Pleistocene history provides evidence of the importance of localities differing in their micro-climate from the predominant macro-climate of a region for species survival (Bush 2002). In forestry, there is an extensive history of successful and unsuccessful assisted colonization trials (Zobel et al. 1987). Foresters move genetic resources from their point of origin to locations beyond their natural dispersal ranges, in particular during regeneration after timber harvesting. Here, managers are already making important decisions about the climatic tolerance and transferability of tree seeds (McKenney et al. 2009). In Canada, legislative recommendations concerning assisted colonization as a management tool to address climate change are already in place for British Columbia (O'Neill et al. 2008).

Here, we briefly present the arguments for and against assisted colonization. We then discuss the proposed schemes for the selection of focal units and recipient localities. We suggest focusing on local adaptations of foundation or keystone species (Ellison et al. 2005) and moving them within the species range in order to produce climate-safe habitats upon which endangered or rare species depend, rather than directly relocating endangered species. This approach provides a new dimension to the recent debate on assisted colonization and might help to reach a consensus between supporters and opponents of assisted colonization because it can be applied with minimal risks, especially in many restoration efforts.

Arguments in Favor of Assisted Colonization

The paramount argument for the intentional movement of focal units is to mitigate elevated extinction risk due to climate change (Thomas et al. 2004). The underlying assumption is that focal units lack adaptation and dispersal abilities to cope with rapid climate change. Other arguments that support assisted colonization (Table 1) are generally subordinate. Several points merely aim at defending the overall approach, such as the notion that low-risk situations can be identified and that a movement of species is generally not accompanied by any detrimental effects in the majority of studied cases. All of these considerations are based on the assumption that the risk of no action would be greater for biodiversity than the risks involved in assisted colonization. Most authors focus on the species level, but the maintenance of genetic diversity within certain species is also recognized as a goal of assisted colonization (del Castillo et al. 2009).

A different view prevails in forestry, where economic benefits (i.e. a high and stable productivity of ecosystems) are given top priority (Chapin et al. 2007; McKenney et al. 2009). This reasoning shifts the focus of attention from taxonomic units to the stability and productivity of a given geographic unit. The discussion about assisted colonization among conservationists might benefit from an acknowledgement of this view, as the creation of habitats adapted to climate change might meet several conservation goals.

Table 1. Arguments for assisted colonization.

The Pros	References (Not Comprehensive)
Reduced risk of extinction of focal units which lack adaptation and dispersal abilities to cope with climate change (intensified by fragmentation)	Hunter 2007; McLachlan et al. 2007; Davidson & Simkanin 2008; Hoegh-Guldberg et al. 2008; Mueller & Hellmann 2008; Pelini et al. 2009; Ricciardi & Simberloff 2009; Richardson et al. 2009; Willis et al. 2009
Conservation of genetic diversity	del Castillo et al. 2009
Identification of low-risk situations possible	Hoegh-Guldberg et al. 2008; Willis et al. 2009
Risks generally low, as the majority of studied historical species introductions were not detrimental	Mueller & Hellmann 2008
Risk of adverse effects on biodiversity from inaction higher	Schwartz et al. 2009
Conservation and restoration of diverse forests in the face of climate change	Chapin et al. 2007
Maintenance of the productive potential and stability (of forests)	Chapin et al. 2007; McKenney et al. 2009
Active conservation as opposed to documentation of losses for conservationists	Ricciardi & Simberloff 2009
Technical feasibility (at least for some taxa)	van der Veken et al. 2008; Willis et al. 2009
Pragmatic and cost-effective approach	Willis et al. 2009

Arguments Against Assisted Colonization, Including Open Research Questions

Intended and unintended species introductions can result in unpredictable consequences for the recipient ecosystems in terms of their nutrient cycling, productivity, disturbance regime, biotic interactions, and dispersal patterns (Ricciardi & Simberloff 2009). These notions serve as the main arguments against assisted colonization (Table 2). A primary focus of invasion biology over recent decades has been the search for predictors of the invasive potential of taxa. Thus far, these predictors have remained elusive (Levine et al. 2003) although some trait-based risk assessments have been made (e.g. Reichard & Hamilton 1997 for woody plants or Kolar & Lodge 2002 for fish). It has to be stressed, however, that the majority of unintended introductions do not lead to successful establishment of populations and only very few of those that establish do become invasive (Richardson & Pysek 2006).

An important research question with regard to assisted colonization is whether the target species are directly limited by specific climatic conditions. A direct dependence of species on current macro-climate is questionable for many species (Pearson & Dawson 2003; Guisan & Thuiller 2005). Even current patterns of ectotherm distributions are far from equilibrium with current macro-climate (Araujo & Pearson 2005). The biotic environment with its associated microclimates may be of higher relevance to many rare species than macro-climatic conditions (Ellison et al. 2005; Harsch et al. 2009; Pelini et al. 2009).

Another contribution to uncertainty is the limited knowledge on effective dispersal rates (Clark et al. 2003; Higgins et al. 2003). Rarity and stochasticity inherent in long-distance dispersal strongly limit our ability to forecast the spread of focal units (Nathan et al. 2008). Finally, recent findings indicate that environmental change, including climate change, can even cause rapid phenotypic change through both ecological and evolutionary processes especially in small populations (Ozgul et al. 2009). Common species, on the other hand, generally possess high genetic variability which allow for adaptation via selection (Bischoff et al. 2010). Species reproducing primarily through vegetative means, however, may be at a disadvantage. Such biotic adaptations are neglected in scenarios of biodiversity loss.

Table 2. Arguments against assisted colonization.

The Cons	References (Not Comprehensive)
Risk of adverse effects on native species composition and ecosystem functioning (as shown by examples of invasive species)	Chapin et al. 2007; Hunter 2007; McLachlan et al. 2007; Davidson & Simkanin 2008; Hoegh-Guldberg et al. 2008; Mueller & Hellmann 2008; van der Veken et al. 2008; Ricciardi & Simberloff 2009; Richardson et al. 2009; Willis et al. 2009
High risks for recipient ecosystems even for short-distance translocations	Davidson & Simkanin 2008; Mueller & Hellmann 2008; Ricciardi & Simberloff 2009
Single species approach untimely in conservation	Davidson & Simkanin 2008
Ex situ conservation more effective	Davidson & Simkanin 2008
Impediment of efforts to preserve or restore habitats	Hunter 2007; Ricciardi & Simberloff 2009; Richardson et al. 2009
Problematic identification of recipient localities with imperfect knowledge on ecology and climate change	Hunter 2007; McLachlan et al. 2007; del Castillo et al. 2009
Technical feasibility generally questionable	Pelini et al. 2009; Ricciardi & Simberloff 2009
Technical feasibility for rare and endangered species not provided	Hunter 2007; Mueller & Hellmann 2008
Lack of predictive methods for risk assessment	Ricciardi & Simberloff 2009
Some current climate conditions are without future definition, and assisted colonization for species from these climates is not feasible	Williams et al. 2007
Unknown costs and acceptability	Richardson et al. 2009
Creation of a biased flora or fauna	Schwartz et al. 2009
Biological homogenization	van der Veken et al. 2008

Focal Units—What Should be Moved?

Rare and endangered species are challenged most by climate change and are therefore usually discussed as focal units for assisted colonization. However, we see three reasons why rare and endangered species are not well suited for assisted colonization efforts:

1. For many rare and endangered species no adequate recipient locality can be found. Current centers of rare species distributions are located in areas with highly specific climate conditions, which are predicted to shrink disproportionately under future climate change (Ohlemüller et al. 2008) or even be lost globally (Williams et al. 2007). Novel conditions may further be produced by interactions among climate, local static environmental conditions (e.g. soils), and local species compositions.

2. The collection of sufficient numbers of individuals for establishment needs is hardly possible without harming local populations of endangered species. Willis et al. (2009) used two butterfly species and demonstrated the short-term (6 years) feasibility of assisted colonization in a field experiment. They worked with common species and

translocated 500 and 600 individuals of the two species, respectively. Based on a meta-analysis of published studies, Traill et al. (2007) suggest a minimum of 1,650–100,000 individuals for viable population sizes of insects in order to gain a persistence probability of 99% within a time frame of 40 generations. Collecting such numbers would cause extirpations of source populations without the insurance of successful colonization at the new locality.

3. Declining populations may have already passed through a genetic bottleneck and assisted colonization is doomed to fail in such cases. Remnant populations (Eriksson 1996) represent only a limited part of the previous gene pool. An excess extinction risk of naturally small populations of butterflies, for instance, can be related to inbreeding depression (Saccheri et al. 1998). The history of reintroduction projects (Mueller & Hellmann 2008) implies that the risk of failed translocations is considerably higher for rare species (54% failing) than for common species (only 14% failing) (Griffith et al. 1989; Wolf et al. 1996). Such failures are not only detrimental to the translocated individuals, but also to the source populations due to its depletion of individuals.

Based on these concerns, and taking also the decision tree provided by Hoegh-Guldberg et al. (2008) into account, assisted colonization might only be an option for a very limited number of endangered species with sufficiently large gene pools and well-known climatic and ecological constraints that can be met in new target localities. Those species most threatened by climate change would not appear to be suitable in most cases. The problem of a global loss of rare species cannot be addressed by this means. We conclude that assisted colonization of rare and endangered species themselves is risky, ineffective, and probably hazardous for both the focal units as well as for the recipient ecosystems in many cases.

The creation and conservation of climate-safe habitats, that is habitats that can be expected to withstand climate change without changes to their overall structure and functionality, may be more profitable in many cases. We have discussed that a direct dependence of species on current macro-climate appears questionable for many species. Fine-scale distributions can further be expected to depend strongly on micro-climatic variation within a landscape. Temperature variation due to exposition and vegetation cover within the same region and elevation is stronger than the projected increases in mean temperature until the end of this century (Scherrer & Koerner 2010). Based on these considerations, rare species might be conserved without the need to move them but by adapting their habitats. Such climate-safe habitats depend mainly on the climatic tolerance of the dominant plants, which determine structure and micro-climate. According to Ellison et al. (2005), such species could be called core species, keystone species, structural species, ecosystem engineers or, as further used here, foundation species, that is "single species that define much of the structure of a community by creating locally stable conditions for other species, and by modulating and stabilizing fundamental ecosystem processes".

Forestry has a long tradition in assisted colonization of foundation species (Zobel et al. 1987; Chapin et al. 2007; McKenney et al. 2009). Although the main concern in forestry is not the preservation of biodiversity, forest trees provide specific environments that serve as habitats for entire communities of plants, animals, and microorganisms. Ensuring the presence of these species supplies climate-safe habitats for a multitude of dependent species. For instance, several thousand species, such as plants, insects or fungi, depend on the European beech (Fagus sylvatica) as a foundation species (Kölling et al. 2005). The loss of such foundation species is expected to have cascading, adverse effects on biodiversity and ecosystem functioning. Replacing native species by exotic ones may safeguard biomass production in forestry, but would negatively affect conservation value. Furthermore, pollinator systems provide ample examples of rare species performance, sometimes even survival, depending on the presence of common species (e.g. Gibson et al. 2006). Coral species (Acroporidae) with wide ranges may serve as another example, as low-latitude coral populations exist which show higher temperature tolerances than those at higher latitudes (Berkelmans & van Oppen 2006). The latter have already declined or died off due to increased thermal stress. Introducing lower-latitude, heat-adapted ecotypes to these degraded sites may therefore serve as a useful management strategy (Berkelmans & van Oppen 2006). These examples and several related reviews (e.g. Simberloff 1998; Boogert et al. 2006) suggest that foundation species and their relationships with biodiversity are common phenomena. The main question is therefore how to retain or restore the foundation species in times of change.

Moving foundation species out of their natural range (i.e. the potential current range in the absence of human interference) can be expected to create even larger ecological problems (e.g. invasiveness) than moving rare species due to the generally higher competitive power of foundation species (Hunter 2007). Foundation species are commonly wide-ranging species (Ellison et al. 2005) that exhibit large genetic variation (Hamrick 2004). This is commonly displayed in strong local adaptation, especially to the climate (Joshi et al. 2001; McKay et al. 2005). Ecotypes can be found within the current distribution of the foundation species that are adapted to future climate conditions at locations further north or at higher altitudes (Fig. 1). Moving such pre-adapted genetic resources to sites where the species is already present or where it was present before human interference in case of sites subjected to restoration efforts would ensure ecosystem integrity by conserving the presence of foundation species and by providing climatesafe habitats for a host of dependant species. Within-species range translocation might also minimize potential problems with invasiveness (but see below).

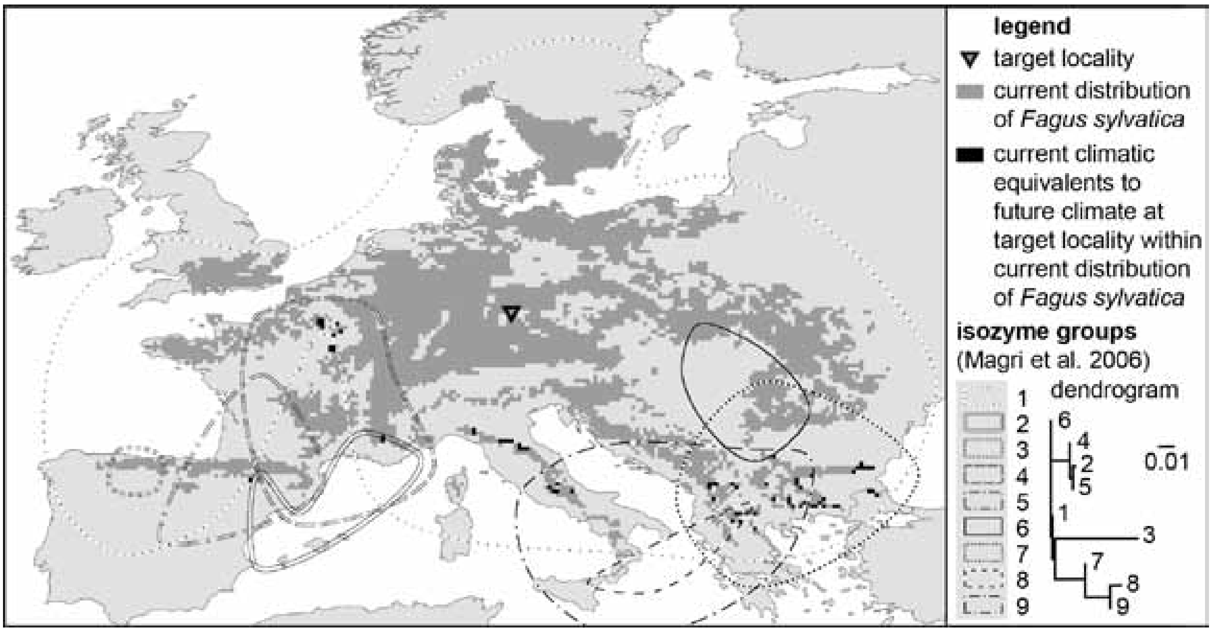


Figure 1. The proposed assisted ecotype colonization of foundation species exemplified for a given site at Bayreuth, Germany (triangle), where European beech (Fagus sylvatica) is the foundation species for the maintenance of (semi-) natural forests which contain a high number of specialized species (Kölling et al. 2005). Its current distribution according to EUFORGEN (2009) is shown in dark gray. Current climate equivalents for the target site at the end of this century (regional climate model: REMO-BfG [MPI-M Hamburg]; SRES: A1B) based on mean annual temperature ± 0.5°C, colder mean winter temperature, and lower summer precipitation are shown in black (current climate based on worldclim; Hijmans et al. 2005). Outlined are different genotypes of the target species (based on isozyme similarity; Magri et al. 2006), which imply that pre-adapted ecotypes of different genetic heritage would be available.

Genetic diversity of target species increases restoration success (Bischoff et al. 2010). It has also been proposed that a wider selection of "mixtures of genotypes from climatically local populations" might benefit short-term establishment and long-term adaptation potential (McKay et al. 2005). We suggest moving one step further by adding genetic resources from ecotypes of current climatic conditions comparable to the expected future climate of the target area (Fig. 1). Including this approach into general restoration concepts seems to be a promising scheme for the ecological adaptation of landscapes to climate change, which is an inevitable challenge for any current restoration effort. Based on the arguments made above, and on the associated uncertainties, the assisted colonization of pre-adapted ecotypes may more often be a successful management strategy than the assisted colonization of rare and endangered species (Fig. 2).

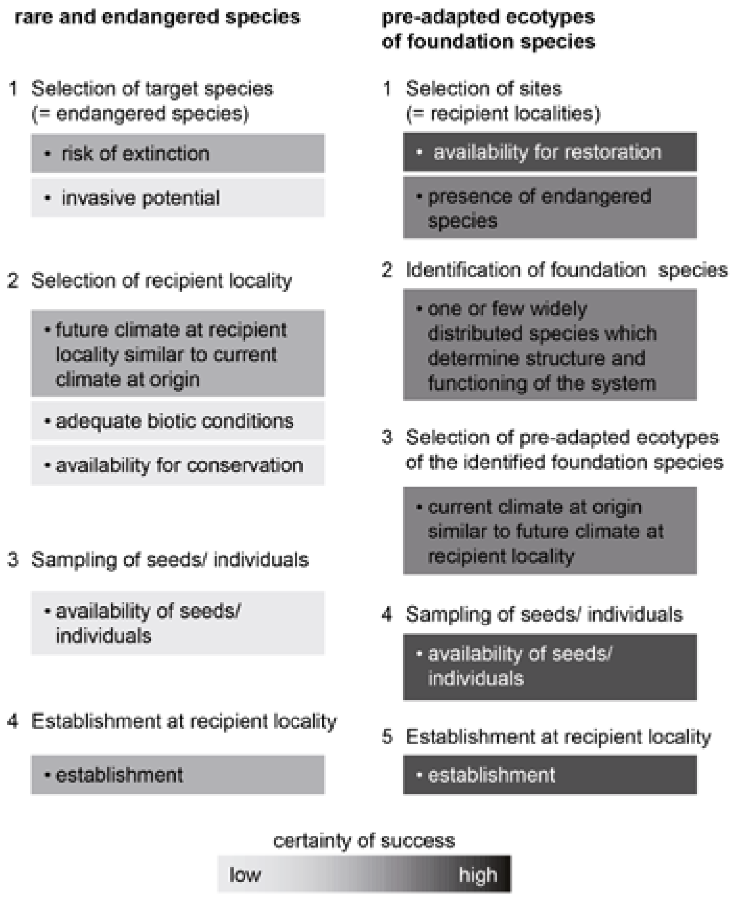


Figure 2. Conceptual comparison of the basic steps in assisted colonization for different focal units. The "pre-adapted ecotypes" approach starts from a given location where either is available for restoration or contains an endangered species and aims at the climate-safe adaptation of this given location. The expected certainty of success for each step is based on subjective expert knowledge by the authors.

This assisted ecotype colonization of foundation species does not come without risks. Two major aspects of genetic pollution, that is the introduction of non-native genetic information, have to be considered according to McKay et al. (2005). The first concern is that the introduction of nonlocal genotypes will create a large genetic load that causes the restoration to fail. To counter this, we strongly advise testing, experimentally, the potential suitability of target ecotypes and to use origins from matching climatic and environmental conditions (Fig. 1). The usage of more than one origin appears to be a further insurance for success. The second concern is that the nonlocal genotypes will eliminate locally adapted genotypes. Here, we argue that a high percentage of restoration efforts is carried out after the target species was already lost from the site and local adaptation, consequently, was lost as well. If the target species is still present, any superiority of local adaptation should also result in better fitness and (re-) selection of the best-adapted genotypes.

The consequences of an assisted colonization of pre-adapted ecotypes within the range of the target foundation species should be predictable. No adverse effects on the recipient system compared to the expected major risks of moving species outside of their natural range, and even outside of their biogeographical context, are expected simply because the species is or was already present, even dominant, in the system before the action (Fig. 2). Figure 1 displays an example of the proposed approach. In accordance with Hunter (2007), we strongly warn against the assisted colonization of foundation species outside their biogeographical contexts.

There are further caveats to the idea of assisted colonization in general, as it might not suffice to select recipient localities based on the similarity of their expected future average climate conditions (i.e. mean temperature and total precipitation) with the climate of the focal units‘ origin. Extreme weather events might put much higher selective pressure on survival than average climate conditions while hardly being quantifiable at a sufficient spatial resolution both in the past and in future expectations (Jentsch & Beierkuhnlein 2008). Experimental testing of the tolerance of target genotypes in the face of expected extreme events is, therefore, recommended.

Furthermore, the problem of targeting recipient localities with suitable climate conditions is a question of the appropriate time scale, as the recipient localities themselves are also subject to a changing climate. McKenney et al. (2009) suggest that the selection of recipient localities in forestry should depend on the silvicultural rotation lengths of the focal units, with climate conditions similar enough to the climate preferences of the focal units to enable a good survival rate while also ensuring good adaptation toward the end of the rotation. Comparable suggestions for the conservation of endangered species are missing. It is therefore important to explore how far species‘ distributions lag behind the shifting climatic conditions, especially in the anthropogenically modified landscape. Placing pre-adapted ecotypes of species at the leading edge of their current distribution may be the most effective (and conservative) intervention.

Conclusions

The debate about assisted colonization as a management tool to conserve biodiversity in the face of climate change is based largely on two opposing arguments. On the one hand, high extinction risks are projected due to the fact that focal units might not adapt fast enough to climate change through migration or genetic adaptation. Invasion biology, on the other hand, provides evidence that the intentional introduction of species may adversely affect recipient ecosystems. A more important consideration may be that assisted colonization will not be feasible for many endangered taxa due to their limited availability and due to a lack of recipient localities. We conclude that the assisted colonization of single endangered species is risky and not useful in many cases.

Therefore, we propose that the structure and micro-climate of habitats containing rare and endangered species could be the focus for climate change adaptation (i.e. climate-safe habitats) via the establishment of pre-adapted ecotypes of the relevant foundation species. We suggest moving ecotypes of foundation species within the species' natural range in order to minimize possible adverse effects. The assisted colonization of foundation species ecotypes might provide a means for sustainable climate change adaptation in restoration efforts. The history of conservation biology informs us that the restoration or conservation of suitable habitat including its dynamic processes (e.g. disturbance regimes) is the only sustainable option to manage endangered species. Building climate-safe habitats by the use of pre-adapted ecotypes of foundation species may therefore be a better investment toward the conservation of biodiversity than aiming at single endangered species.

Examples from forestry show that this approach is applicable with regard to societal or legislative dimensions. We see a strong need for future research on the role of foundation species, and on biotic interactions for ecosystem functioning in changing climates. Ultimately, the human dimension of assisted colonization, e.g. species selection, societal acceptance, legislative frameworks and costs, requires detailed consideration even if a consensus on ecological questions can be achieved.

Implications for Practice

- Assisted colonization of rare and endangered species is risky for the target species and the recipient localities and cannot be recommended in general.
- Some endangered species could be conserved on site by developing climate-safe habitats through the assisted colonization of pre-adapted ecotypes of the relevant foundation species (e.g. major forest trees or corals). This approach would conserve structure and micro-climate of the habitat and avoid moving species out of their natural range.
- Regardless of the conservation approach, restoration efforts need to design climate-safe communities. The integration of ecotypes adapted to the expected future climate should become one part of restoration concept plans.

Acknowledgments

This work was partly funded by the "Bavarian Climate Programme 2020" in the joint research center "FORKAST" and by the Federal Agency for Nature Conservation (BfN) in the project "Impacts of climate change on fauna, flora and habitats, as well as adaptation strategies". The authors thank two anonymous reviewers and the associated editor for valuable comments on an earlier version of this manuscript.

Literature cited

Araujo, M. B., and R. G. Pearson. 2005. Equilibrium of species' distributions with climate. Ecography 28:693–695.

Berkelmans, R., and M. J. H. van Oppen. 2006. The role of zooxanthellae in the thermal tolerance of corals: a 'nugget of hope' for coral reefs in an era of climate change. Proceedings of the Royal Society of London Series B Biological Sciences 273:2305–2312.

Bischoff, A., T. Steinger, and H. Mueller-Schaerer. 2010. The importance of plant provenance and genotypic diversity of seed material used for ecological restoration. Restoration Ecology 18:338–348.

Boogert, N. J., D. M. Paterson, and K. N. Laland. 2006. The implications of niche construction and ecosystem engineering for conservation biology. Bioscience 56:570–578.

Bush, M. B. 2002. Distributional change and conservation on the Andean flank: A palaeoecological perspective. Global Ecology and Biogeography 11:463–473.

Chapin, I. F. S., K. Danell, T. Elmqvist, C. Folke, and N. Fresco. 2007. Managing climate change impacts to enhance the resilience and sustainability of Fennoscandian forests. Ambio 36:528–533.

Clark, J. S., M. Lewis, J. S. McLachlan, and J. HilleRisLambers. 2003. Estimating population spread: what can we forecast and how well? Ecology 84:1979–1988.

Davidson, I., and C. Simkanin. 2008. Skeptical of assisted colonization. Science 322:1048–1049.

del Castillo, R. F., S. T. Argueta, and C. Saenz-Romero. 2009. Pinus chiapensis, a keystone species: genetics, ecology, and conservation. Forest Ecology and Management 257:2201–2208.

Ellison, A. M., M. S. Bank, B. D. Clinton, E. A. Colburn, K. Elliott, C. R. Ford, et al. 2005. Loss of foundation species: Consequences for the structure and dynamics of forested ecosystems. Frontiers in Ecology and the Environment 3:479–486.

Eriksson, O. 1996. Regional dynamics of plants: A review of evidence for remnant, source-sink and metapopulations. Oikos 77:248–258. EUFORGEN. 2009. Distribution map of Beech (Fagus sylvatica) (available from www.euforgen.org).

Gibson, R. H., I. L. Nelson, G. W. Hopkins, B. J. Hamlett, and J. Memmott. 2006. Pollinator webs, plant communities and the conservation of rare plants: arable weeds as a case study. Journal of Applied Ecology 43:246–257.

Griffith, B., J. M. Scott, J. W. Carpenter, and C. Reed. 1989. Translocation as a species conservation tool - status and strategy. Science 245: 477–480.

Guisan, A., and W. Thuiller. 2005. Predicting species distribution: offering more than simple habitat models. Ecology Letters 8:993–1009.

Hamrick, J. L. 2004. Response of forest trees to global environmental changes. Forest Ecology and Management 197:323–335.

Harsch, M. A., P. E. Hulme, M. S. McGlone, and R. P. Duncan. 2009. Are treelines advancing? A global meta-analysis of treeline response to climate warming. Ecology Letters 12:1040–1049.

Higgins, S. I., J. S. Clark, R. Nathan, T. Hovestadt, F. Schurr, J. M. V. Fragoso, M. R. Aguiar, E. Ribbens, and S. Lavorel. 2003. Forecasting plant migration rates: managing uncertainty for risk assessment. Journal of Ecology 91:341–347.

Hijmans, R. J., S. E. Cameron, J. L. Parra, P. G. Jones, and A. Jarvis. 2005. Very high resolution interpolated climate surfaces for global land areas. International Journal of Climatology 25:1965–1978.

Hoegh-Guldberg, O., L. Hughes, S. McIntyre, D. B. Lindenmayer, C. Parmesan, H. P. Possingham, and C. D. Thomas. 2008. Assisted colonization and rapid climate change. Science 321:345–346.

Hunter, M. L. 2007. Climate change and moving species: furthering the debate on assisted colonization. Conservation Biology 21:1356–1358.

Jentsch, A., and C. Beierkuhnlein. 2008. Research frontiers in climate change: effects of extreme meteorological events on ecosystems. Comptes Rendus Geoscience 340:621–628.

Joshi, J., B. Schmid, M. C. Caldeira, P. G. Dimitrakopoulos, J. Good, R. Harris, et al. 2001. Local adaptation enhances performance of common plant species. Ecology Letters 4:536–544.

Kolar, C. S., and D. M. Lodge. 2002. Ecological predictions and risk assessment for alien fishes in North America. Science 298:1233–1236.

Kölling, C., H. Walentowski, and H. Borchert. 2005. Die Buche in Mitteleuropa. AFZ - Der Wald 13:696–701.

Levine, J. M., M. Vila, C. M. D'Antonio, J. S. Dukes, K. Grigulis, and S. Lavorel. 2003. Mechanisms underlying the impacts of exotic plant invasions. Proceedings of the Royal Society London Series B Biological Sciences 270:775–781.

Magri, D., G. G. Vendramin, B. Comps, I. Dupanloup, T. Geburek, D. Gomory, et al. 2006. A new scenario for the Quaternary history of European beech populations: palaeobotanical evidence and genetic consequences. New Phytologist 171:199–221.

McKay, J. K., C. E. Christian, S. Harrison, and K. J. Rice. 2005. "How local is local?" - a review of practical and conceptual issues in the genetics of restoration. Restoration Ecology 13:432–440.

McKenney, D., J. Pedlar, and G. O'Neill. 2009. Climate change and forest seed zones: past trends, future prospects and challenges to ponder. Forestry Chronicle 85:258–266.

McLachlan, J. S., J. J. Hellmann, and M. W. Schwartz. 2007. A framework for debate of assisted migration in an era of climate change. Conservation Biology 21:297–302.

Mueller, J. M., and J. J. Hellmann. 2008. An assessment of invasion risk from assisted migration. Conservation Biology 22:562–567.

Nathan, R., F. M. Schurr, O. Spiegel, O. Steinitz, A. Trakhtenbrot, and A. Tsoar. 2008. Mechanisms of long-distance seed dispersal. Trends in Ecology and Evolution 23:638–647.

Ohlemüller, R., B. J. Anderson, M. B. Araujo, S. H. M. Butchart, O. Kudrna, R. S. Ridgely, and C. D. Thomas. 2008. The coincidence of climatic and species rarity: high risk to small-range species from climate change. Biology Letters 4:568–572.

O'Neill, G. A., N. K. Ukrainetz, M. Carlson, C. V. Cartwright, B. C. Jaquish, J. N. King, J. Krakowski, J. H. Russell, M. U. Stoehr, C.-Y. Xie, et al. 2008. Assisted migration to address climate change in British Columbia - recommendations for interim seed transfer standards. Ministry of Forests and Range, Forest Science Program, Tech Rep 048, Victoria, B.C.

Ozgul, A., S. Tuljapurkar, T. G. Benton, J. M. Pemberton, T. H. Clutton-Brock, and T. Coulson. 2009. The dynamics of phenotypic change and the shrinking sheep of St. Kilda. Science 325:464–467.

Pearson, R. G., and T. P. Dawson. 2003. Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? Global Ecology and Biogeography 12:361–371.

Pelini, S. L., J. D. K. Dzurisin, K. M. Prior, C. M. Williams, T. D. Marsico, B. J. Sinclair, and J. J. Hellmann. 2009. Translocation experiments with butterflies reveal limits to enhancement of poleward populations under climate change. Proceedings of the National Academy of Sciences USA 106:11160–11165.

Reichard, S. H., and C. W. Hamilton. 1997. Predicting invasions of woody plants introduced into North America. Conservation Biology 11: 193–203.

Ricciardi, A., and D. Simberloff. 2009. Assisted colonization is not a viable conservation strategy. Trends in Ecology and Evolution 24: 248–253.

Richardson, D. M., J. J. Hellmann, J. S. McLachlan, D. F. Sax, M. W. Schwartz, P. Gonzalez, et al. 2009. Multidimensional evaluation of managed relocation. Proceedings of the National Academy of Sciences of the United States of America 106:9721–9724.

Richardson, D. M., and P. Pysek. 2006. Plant invasions: merging the concepts of species invasiveness and community invasibility. Progress in Physical Geography 30:409–431.

Saccheri, I., M. Kuussaari, M. Kankare, P. Vikman, W. Fortelius, and I. Hanski. 1998. Inbreeding and extinction in a butterfly metapopulation. Nature 392:491–494.

Scherrer, D., and C. Koerner. 2010. Infra-red thermometry of alpine landscapes challenges climatic warming projections. Global Change Biology 16:2602–2613.

Schwartz, M. W., J. J. Hellmann, J. S. McLachlan. 2009. The precautionary principle in managed relocation is misguided advice. Trends in Ecology and Evolution 24:474.

Simberloff, D. 1998. Flagships, umbrellas, and keystones: is single-species management pass´e in the landscape era? Biological Conservation 83:247–257.

Thomas, C. D., A. Cameron, R. E. Green, M. Bakkenes, L. J. Beaumont, Y. C. Collingham, et al. 2004. Extinction risk from climate change. Nature 427:145–148.

Traill, L. W., C. J. A. Bradshaw, and B. W. Brook. 2007. Minimum viable population size: a meta-analysis of 30 years of published estimates. Biological Conservation 139:159–166.

van der Veken, S., M. Hermy, M. Vellend, A. Knapen, and K. Verheyen. 2008. Garden plants get a head start on climate change. Frontiers in Ecology and the Environment 6:212–216.

Walter, E. 2003. Florenverfälschung durch Ansalbung am Beispiel des NSG "Hohe und Zeyerner Wand" in Oberfranken. Bericht der Naturforschenden Gesellschaft Bamberg LXXVI:123–134.

Williams, J. W., S. T. Jackson, and J. E. Kutzbacht. 2007. Projected distributions of novel and disappearing climates by 2100 AD. Proceedings of the National Academy of Sciences of the United States of America 104:5738–5742.

Willis, S. G., J. K. Hill, C. D. Thomas, D. B. Roy, R. Fox, D. S. Blakeley, and B. Huntley. 2009. Assisted colonization in a changing climate: a test-study using two U.K. butterflies. Conservation Letters 2: 46–52.

Wolf, C. M., B. Griffith, C. Reed, and S. A. Temple. 1996. Avian and mammalian translocations: update and reanalysis of 1987 survey data. Conservation Biology 10:1142–1154.

Zobel, B. J., G. van Wyk, and P. Stahl. 1987. Growing exotic forests. Wiley, New York, New York.

Acknowledgements

First of all, I want thank Prof. Dr. Carl Beierkuhnlein for giving me the possibility to do my doctoral thesis at the Department of Biogeography and for his motivations, consultations, supervision and assessment of my work.

This thesis was realized at the University of Bayreuth at the Department of Biogeography within the research and development project 'Auswirkungen des Klimawandels auf Fauna, Flora und Lebensräume sowie Anpassungsstrategien des Naturschutzes' (FKZ 3508 85 0600) funded by the German Federal Agency for Nature Conservation. Thanks to Götz Ellwanger for excellent support in the project.

I would like to express my exceeding thanks to my colleague Anja Jaeschke for her elementary support, excellent cooperation and stimulating discussions. It was a great pleasure for me to work with you. It was inspiring to guide Samuel Rauhut (B.Sc.) and Holger Dempe (M.Sc.) during their final thesis within the project.

I want to enunciate special thanks to Prof. Dr. Björn Reineking for his technical and methodological supervising and Prof. Dr. Anke Jentsch for her motivating and encouraging support. Furthermore, I would like to thank Reinhold Stahlmann not only for always having a sympathetic ear in times of technical problems but also for intensive discussions about geek stuff and the life itself.

Moreover, I would like to thank Klara Dolos and Dominik Fischer for many fruitful discussions, scientific exchange but also for the many non-scientific events and their friendship. Thanks to all my colleagues in Bayreuth for having a great time, multifaceted conversations and scientific insights.

I thank my family and friends for their support while the whole thesis. First of all my partner Silva Donke, which accompanied me for years, supported me on my way and always brought me forward as well as our daughter Thea. You show me the real worth of life and give me daily strength.

Curriculum vitae

Persönliche Daten

- geboren am 18.08.1980 in Görlitz, Sachsen
- Familienstand: ledig / eine Tochter (*01.03.2010)

Schulbildung

- 6/2000 Abitur im naturwissenschaftlichen Juliot-Curie-Gymnasium, Görlitz

Zivildienst

- 7/2000-6/2001, Fahrdienst im DRK Görlitz

Akademische Laufbahn

- 10/2001- 3/2007 Studium der Biologie (Diplom) an der Friedrich-Alexander Universität Erlangen-Nürnberg - Abschluss gesamt: sehr gut
    - 10/2002-2/2007 Studentische Hilfskraft für die ‚Übungen zur Biologie und Systematik einheimischer Tiere I & II‘ (Prof. Dr. Hans-Werner Scheloske und Dr. Jürgen Schmidl)
    - 2002-2007 Mitglied der Arbeitsgruppe ‚Ökologie, Landschaft und Naturschutz‘ unter der Leitung von Dr. Jürgen Schmidl
    - Diplomprüfungen in Zoologie (Hauptfach): 1,7; Entwicklungsbiologie: 1,3; Geobotanik: 1,3; Paläontologie/Geologie: 1,3
    - 6/2006-3/2007 Diplomarbeit: ‚Entwicklung von Xylobionten-Zönosen an Stammtotholz und Mulmhöhlen‘ bei Dr. Jürgen Schmidl und Prof. Dr. Martin Klingler, LS für Entwicklungsbiologie Uni Erlangen.
- seit 2/2009 Promotionsstudium an der Universität Bayreuth am Lehrstuhl für Biogeografie. Bearbeitung des F&E Vorhabens: ‚Auswirkungen des Klimawandels auf Fauna, Flora und Lebensräume sowie Anpassungsstrategien des Naturschutzes‘ im Auftrag des Bundesamtes für Naturschutz (BfN)
- Anfertigung einer Disseration mit dem Titel ‘Diversity, habitats and climate change: From environmental envelope modelling to nature conservation strategies‘
- Betreuung verschiedener Abschlussarbeiten: Bachelorarbeiten in den Studiengängen Geografie und Geoökologie sowie Masterarbeiten im Studiengang Global Change Ecology
- Reviewer für internationale peer reviewed Journals (European Journal of Forest Research)

Weiterer fachlicher Werdegang und ausgewählte Projekte

- seit 3/2007 freiberufliche Tätigkeit als Biologe, Ökologe und Fachgutachter mit Schwerpunkt im Bereich Artenschutz, Landschaftsplanung und Faunistik (u.a. Libellen und xylobionter Käfer)
    - 5-8/2007 Freiberufliche Mitarbeit im Büro bufos - Büro für ökologisch-faunistische Studien in Nürnberg
    - 5-8/2007 Kartierung von potentiellen Brutbäumen der FFH-Art Osmoderma eremita (Eremit) in den Waldgebieten des FFH-Gebietes 6939-371 “Trockenhänge am Donaurandbruch“ (Auftraggeber: Regierung der Oberpfalz)
    - 8-11/2007 Freiberufliche Mitarbeit im Landschaftsplanungsbüro ANUVA Stadt- und Umweltplanung, Nürnberg

  - 5-7/2009 Hirschkäfer- und Hirschkäferlebensraumkartierung in den Trockengebieten an den Werntalhängen zwischen Karsbach und Stetten (im Auftrag von bufos - büro für faunistisch-ökologische studien Nürnberg)
  - 7/2009 Artenschutzrechtliche Prüfung der planungsrelevanten Käferarten zur Ortsumfahrung Schaippach (im Auftrag von bufos - büro für faunistisch-ökologische studien Nürnberg)
  - 8/2010 Artenschutzrechtliche Einschätzung unter besonderer Berücksichtigung von Osmoderma eremita - Zu der Ausbaumaßnahme GZ2 Ziementshausen -Maria Vesperbild (im Auftrag von bufos - büro für faunistisch-ökologische studien Nürnberg)
  - 6-9/2010 Kartierung der xylobionten Käferfauna im Altmühltal nahe Schönfeld. Unveröff. Bericht (im Auftrag von bufos - büro für faunistisch-ökologische studien Nürnberg)
- 11/2007-02/2009 Festanstellung bei ANUVA Stadt und Umweltplanung, Nürnberg; Aufgabenfeld: nationaler und europäischer Artenschutz, Umweltverträglichkeit, Projektkoordination faunistischer und artenschutzrechtlicher Projekte, Erarbeitung artenschutzrechtlicher Prüfungen, etc.
- Teilnahme an dem internationalen Biodiversitätsprojekt IBISCA:
  - 3-4/2007 in Australien, QLD. im Lamington Nationalpark. Projektteil: Käferlebensgemeinschaften an Rinde
  - 5/2008 in Frankreich, Auvergne. Projektteil: Käferlebensgemeinschaften an Rinde
- seit 10/2011 Anstellung als wissenschaftlicher Mitarbeiter bei der LUBW - Landesanstalt für Umwelt, Messungen und Naturschutz im Referat Arten- und Flächenschutz, Landschaftspflege

List of Publications

Peer-reviewed journals

Bittner, T., Rauhut, S., Fischer, D., Beierkuhnlein, C. (in prep.). The Natura 2000 Network in Germany – Characteristics, Disparities, Risk Assessment and Opportunities in a changing environment. Journal of Nature Conservation

Schmidl, J., Bittner, T. (in prep.). Gradients in beetle composition and diversity on tree barks in Lamington NP, Queensland, AU. Austral Ecology

Jaeschke, A., Bittner, T., Jentsch, A., Reineking, B., Schlumprecht, H., Beierkuhnlein, C. (in prep). Modelling biotic interactions facing climate change: A comparative study of three different approaches. Ecography

Dempe, H., Bittner, T., Jaeschke, A., Beierkuhnlein, C. (submitted). Habitat coherence and climate change: an analysis application for the Natura 2000 network in Germany. Ecological Applications

Bittner, T., Jaeschke, A., Reineking, B., Beierkuhnlein, C. (submitted). Climate change impacts on terrestrial Natura 2000 habitats: Distribution, projected environmental space, threats and potential management. Biodiversity and Conservation

Jaeschke, A., Bittner, T., Jentsch, A., Beierkuhnlein, C. (in review). Challenges for applied ecology and nature conservation in the face of climate change. Climatic Change

Jaeschke, A., Bittner, T., Reineking, B., Beierkuhnlein, C. (in press). Can they keep up with climate change? Integrating specific dispersal abilities of protected Odonata in species distribution modelling. Insect Conservation and Diversity

Thomas, S. M., Fischer, D., Fleischmann, S., Bittner, T., Beierkuhnlein, C. (2011). Risk assessment of dengue virus amplification in europe based on spatio-temporal high resolution climate change projections. Erdkunde 65 (2): 137-150

Bittner, T., Jaeschke, A., Reineking, B., Beierkuhnlein, C. (2011). Comparing modelling approaches at two levels of biological organisation – Climate change impacts on selected Natura 2000 habitats. Journal of Vegetation Science 22(4): 699-710.

Kreyling, J., Bittner, T., Jaeschke, A., Jentsch, A., Steinbauer, M. J., Thiel, D., Beierkuhnlein, C. (2011). Assisted colonization: a question of focal units and recipient localities. Restoration Ecology 19(4): 433-440.

Schlumprecht, H., Bittner, T., Jaeschke, A., Jentsch, A., Reineking, B., Beierkuhnlein, C. (2010). Gefährdungsdisposition von FFH-Tierarten Deutschlands angesichts des Klimawandels - Eine vergleichende Sensitivitätsanalyse. Naturschutz und Landschaftsplanung 42(10): 293-303.

Book chapters and non-refereed periodicals

Jaeschke, A., Bittner, T., Jentsch, A., Beierkuhnlein, C. (submitted). Einfluss des Klimawandels auf FFH-Schutzgebiete. Exkurs in Lingenhöhl, D. (Hrsg.): „Naturschutz in Europa - Konzepte, Erfolge und Rückschläge". Spektrum Akademischer Verlag

Auswirkungen des Klimawandels auf Fauna, Flora und Lebensräume sowie Anpassungsstrategien des Naturschutzes (2011, final coordination). Naturschutz und Biologische Vielfalt, ca. 400 Seiten

Natura 2000 und Klimawandel (in press). Broschüre für das Bundesamt für Naturschutz. 80 Seiten

Bittner, T., Wiegel, R. (2005) Chlaenius spoliatus (Rossi, 1790) in Bavaria (Coleoptera: Carabidae), Entomologische Zeitschrift 115 (3)

Schmidl, J., Bail, J., Bittner, T., Fröhlich, V. & Wiegel, R. (2004). Arthropoden-Gemeinschaften der Kiefern-Baumkronen als Indikatoren für Naturnähe und Standtortbedingungen verschiedener Flächen im Nürnberger Reichswald. LWF Wissen - 25 Jahre Naturwaldreservate in Bayern 46, 50-58.

Remark:

Typeset-versions of the articles Schlumprecht et al. 2011 and Thomas et al. 2011 listed in the Appendix of the submitted thesis were provided as supplemental information for the examinations board.

Erklärung

Hiermit erkläre ich an Eides statt,

dass ich vorliegende Arbeit selbständig verfasst habe, andere als die von mir angegebenen Quellen und Hilfsmitten nicht benutzt habe und die den benutzten Werken wörtlich oder inhaltlich entommenen Stellen als solche kenntlich gemacht habe.

Hiermit erkläre ich an Eides statt,

dass ich weder die vorliegende noch eine gleichartige Doktorprüfung an einer anderen Hochschule endgültig nicht bestanden habe.

Torsten Bittner

Bayreuth, im September 2011