Assessing the influence of global change on plant species distribution using statistical models

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Table of contents

Chapter 1

Introduction

Global change and its influence on biodiversity

Within the last two hundred years humans severely shaped the face of the Earth (Steffen et al. 2007). Structure and functioning of the Earth's systems are altered on a global scale by socioeconomic changes (demography, economy, energy and resource use, transport, and communication) which impacted biophysical systems (e.g. climate, carbon, nitrogen and water cycle, food chains, biological diversity). Among these factors the main drivers of changes in biodiversity of terrestrial ecosystems are land use change including habitat degradation and fragmentation, climate change, nutrient input/eutrophication, biological invasions and CO_2 increase (Vitousek 1994, Sala et al. 2000, Millennium Ecosystem Assessment 2005a). The resulting loss of biodiversity has been highlighted for several decades on a global and European scale (Wilson 1985, Heywood 1995, Thomas et al. 2004). Over the last 10 years the number of threatened plants and vertebrates almost doubled (IUCN 2008).

Global change constitutes not only a serious threat to biodiversity, ecosystems and ecosystem functioning, but also to human well-being (Millennium Ecosystem Assessment 2005b). Humanity benefits from the different types of ecosystem services comprising supporting services (e.g. nutrient cycle), provisioning services (e.g. food, water, fibre, wood), regulating services (e.g. climate regulation) and cultural values (e.g. aesthetic, spiritual). Strategies for policy and planning are needed to minimize anthropogenic pressures on biodiversity (Spangenberg 2007). Strong commitments have been expressed to reduce biodiversity loss significantly on a global scale (CBD 2002) and even to halt it in Europe by 2010 (European Council 2001). In order to meet those ambitious targets, to minimize and mitigate the impacts of global change and to adapt to future developments, one needs not only to describe and understand recent but also possible future responses of species and biodiversity to a changing environment. Within this study the influence of important components of global change that are among the main drivers of biodiversity, namely climate change, land use change and biological invasions are analysed. Furthermore, important limitations of methods that are commonly applied to estimate impacts of climate and land use change on biodiversity, namely species distribution models, are identified and discussed.

Climate change

The global surface temperature increased over the last 100 years on average about 0.74°C, with the strongest increases during the last decades and on continental areas of the Northern Hemisphere (IPCC 2007b). Recent climate change caused observable changes in phenology, such as earlier leafing, flowering and fruiting (Menzel et al. 2006), earlier reproduction times and advancements of passage dates of migratory birds (Parmesan 2006). Further, climate driven

changes in species abundance and composition (McCarty 2001), biotic interactions (Kozlov 2008) and a shifts of species ranges towards higher latitudes and elevations are reported (Walther et al. 2002, Parmesan and Yohe 2003). Especially species with restricted ranges show severe range contractions even leading to extinctions (Parmesan 2006). In addition, species-specific responses to climate change alter or even disrupt interactions between species of different trophic levels, e.g. unequal changes in a plant-herbivore-insectivore-avian predator system (Both et al. 2009).

Land use change

For 7000-9000 years humans settled in Europe, logged forests and changed them into pastures and arable fields (Jäger 1994, Poschlod et al. 2005). Humans changed the deciduous forests that more or less dominated central Europe into a richly structured landscape giving habitat to a higher number of species, containing both natives and introduced species from other parts of Europe and Asia. Thus, it is assumed that in the mid 19th century plant species richness peaked in Central Europe (Poschlod et al. 2005). Industrialisation and population pressure triggered an increasing land use intensity (land consolidation, mineral fertilizer, drainage, afforestation with non-indigenous trees) which caused a steady decrease in species numbers (Poschlod et al. 2005). Nowadays, most important land uses are agriculture, covering 50% of the land area, and forestry, covering 30% in western Europe (FAO 2007). Biodiversity in temperate regions of Europe is probably less affected by current and future land use change than in other parts of the world, because major land use changes already occurred in the past (Sala et al. 2000).

Biological invasions

Human-mediated transport of species in areas where they previously did not occur due to dispersal barriers (e.g. oceans, mountains, unsuitable climates) is the key step to biological invasions. Increasing overseas travel and trade led to an increasing translocation of species (Simberloff et al. 2005). The introduced species may undergo different steps within the invasion process (Richardson et al. 2000): casual occurance, sustaining reproducible populations (i.e., becoming naturalized), spreading and even become dominant and influence biodiversity (Richardson et al. 1996, Mack et al. 2000). Successful invasive species can cause high economic costs for control (Pimentel et al. 2000).

A main topic in invasion ecology is the identification of the drivers that allow a species being successful in the invasion process. Generally, invasions can be seen as a function of propagule pressure, abiotic characteristics of the invaded habitat and biotic characteristics of the recipient community and the invading species (Catford et al. 2009). The multitude of existing hypotheses

that try to explain invasion success illustrates that the process is very complex and our understanding rather incomplete. In order to derive general patterns, multi-species approaches and analyses over more than one stage of the invasion process are mandatory. Especially findings on biotic characteristics of species, a species' potential to invade and even cause harm or damage became recently relevant. Subsequently, transport and trade can be controlled or management strategies applied to prevent negative impacts.

Methods to estimate influence of global change on diversity and species distribution

Observations and Experiments

Observations and monitoring schemes are basic tools to record changes in diversity and distribution of species. Unfortunately, data are scarce and especially large-scale data are only in few cases available for more than one point or period in time. Causal relationships between changing environment and species can only be revealed by experimental approaches. Over the last decades these were increasingly used to study the impacts of climate change (Harte and Shaw 1995, Körner et al. 2005) or introduced species (Levine 2000). However, their application is mostly restricted to a few species and to a local scale, and thus, may suffer from a lack of generality. Large-scale manipulative experiments to investigate the effects of global change are difficult to manage both financially and logistically, but can also hardly be justified when outcomes are unpredictable and may have adverse effects on native ecosystems or even human populations (i.e., ethical issues of experimental species introductions).

Models

Models are an excellent tool to fill this gap and to estimate possible outcomes of global change on larger scales and for future scenarios. They are simplified representations of complex systems based on rules or mathematical representations of ecological assumptions. Generally, modelling approaches can be divided into three different groups: analytical, mechanistic and empirical models (Guisan and Zimmermann 2000).

Analytical models aim at a very precise mathematical description of relationships in a very simplified reality and are predominantly applied in theoretical ecology (Pickett et al. 1994). A common application is the Lotka-Volterra equation which is used to describe population dynamics for interacting species, e.g. predator and prey.

Mechanistic models aim to provide a more realistic description of processes and the resulting cause-effect relationships compared to analytical models. They are applied to describe element cycles, growth or population dynamics. Mechanistic models draw a functional but also very general picture of the world. The calibration of mechanistic models can be very time-

consuming and is limited by the knowledge available for causal relationships and ecological processes. Global vegetation models for example are only based on a restricted number of functional plant types and not on species (Sitch et al. 2003). Although mechanistic models are in principle able to include processes such as biotic interactions, dispersal rates or microevolution of species, their complex implementation is still under development.

Empirical models are pattern oriented and compare different types of observations and derive usually correlative rules of relatedness. This is the case for species distribution models, which are also termed as habitat models, environmental or ecological niche models, climate or bio-climatic envelope models. In ecological research they are established tools to analyse relationships between species and environment, but also to assess possible impacts of climate or land use changes (Guisan and Zimmermann 2000). Species distribution models correlate environmental conditions with the observed distributions of species (Kühn et al. 2009). This correlation is interpreted as causality and a multitude of different statistical techniques is available to derive such relationships. Species distribution models are based on the assumption that species occur in all areas with suitable conditions, i.e., the species is in a state of equilibrium with its environment (Hutchinson 1957). It is acknowledged that ranges are not only shaped by climatic variables but also by biotic interactions and limited dispersal (Pearson and Dawson 2003, Hampe 2004). Furthermore, in species distribution models species are treated as entities, which means that intraspecific variations of niche space caused by genetic variation or by plasticity are ignored. Species distribution models are fast and easy to calibrate, species ranges can be described very well with climate on a large scale and they are a good first method to provide a rough idea on the possible impacts of climate and land use changes. However, to enable a reliable interpretation of modelling results, it is necessary to understand prediction errors that result from the model assumptions but also from other sources of error such as data quality and species characteristics.

Scenarios

One way to assess possible developments and its impacts of complex and unpredictable systems are scenarios. They are descriptions of possible futures and incorporate qualitative narratives or storylines (e.g. socio-economical and political developments) and quantitative modelling results (e.g. physical effects of greenhouse gas concentration). Though scenarios are bound to be plausible, they are not designed to forecast or predict the future. Consequently, different scenarios are equally valid and no specific scenario is more probable to become true than another. Scenarios are thought experiments that may help to identify possible effects and risks connected to a certain development (Schweiger et al. 2010a). Climate change scenarios are

cornerstones of recent risk assessments (Millennium Ecosystem Assessment 2005b, IPCC 2007a).

Climate change scenarios provided by the Intergovernmental Panel on Climate Change (IPCC 2007) describe the "most likely" increase of mean annual temperature between 1.8 and 4.0°C up to 2100 over four different scenarios. In Europe mean temperature may rise even more strongly. Annual precipitation sums are expected to remain constant in Central Europe, but summer rainfall may be reduced and winter rainfall increased. Overall, the frequency of extreme events (e.g. storms, heavy rainfall, heat waves) increases.

Land use change scenarios up to 2080 describe a strong decrease in croplands and grasslands opposed by an increase in forestry areas, surplus areas and areas used for the production of biofuels (Rounsevell et al. 2006). However, changes in land use can vary strongly depending on basic scenario assumption such as global trade, agricultural productivity or biofuel production (Busch 2006).

Results from climate and land use change scenarios raised the question of how species distribution and biodiversity may respond to the described changes in environmental conditions. Species distribution models are commonly combined with quantitative scenarios and enable the estimation of potential impacts of environmental change on species' distributions and species numbers (Huntley et al. 1995, Thuiller et al. 2005b). Scenarios of species distribution and diversity, however, are only reliable when prediction errors and other sources of uncertainty are identified and reported. Otherwise uncertain or even unjustified modelling results may lead to inadequate policy or management strategies.

Objectives and structure

In this study, different aspects of the influence of global change on species distribution and selected methodological limitations are investigated. Throughout, vascular plants are used as study objects. These are of overall importance for ecosystems, since they are a fundamental structural component, provide habitat for many other species and have a basic position in most food chains. The following work is structured into four main chapters (Chapter 2-5).

Chapter 2 and chapter 3 deal with the identification and explanations of prediction errors that accompanies species distribution models. Chapter 2 concentrates on species specific error rates to answer the question of whether prediction errors are associated with species traits. The importance of species identity and ecological characteristics on prediction errors have been acknowledged in recent studies (McPherson and Jetz 2007). However, a comprehensive study about prediction errors of plant species distribution models using independent trait data is not yet available. Chapter 3 deals with patterns of prediction errors that occur when making

prediction in geographical space, analysing grid cell specific error rates. So far, such patterns have not been described but they are of general importance for predictive modelling. In this chapter patterns of prediction errors are identified and the magnitude of the errors explained by grid cell characteristics, influence of human land use and range characteristics.

In Chapter 4 it is shown how species distribution models can be applied to scenarios. The main question is which potential influence climate and land use change may have on plant species distribution in Germany. Species distribution models are calibrated on a European scale (50×50km² resolution) and applied to three climate and land use change scenarios for the average of the time period 2051-80 in Germany (6'×10' resolution). Species distributions are not only described by climate but also by soil conditions and land use, allowing a prediction on a smaller scale. The calibration of models with European data and the projection to Germany has two advantages. On one hand, it enables the a more comprehensive description of species' niches and on the other hand, species that do not yet occur in Germany but may expand their ranges under a changing environment can be considered as well.

Chapter 5 deals with the influence of biological invasions on distribution patterns of introduced plants and sources of its invasion success in Germany. Introduced plants considerable shape the flora in Germany and ornamental plants contribute very strongly: In Europe 40% of all established alien species are ornamentals (DAISIE 2009) and in Germany 30% (Kühn and Klotz 2003). Especially for ornamentals human influence such as breeding or pre-selection of specific characteristics may be important. This study investigates which part of the invasion success is explained by human influence and by species traits in different steps of the invasion process. Chapter 5 describes how the distributional patterns of introduced ornamental plant species in Germany can be explained by human influence and species characteristics.

Chapter 2

Predictive performance of plant species distribution models depends on species traits

with Ingolf Kühn, Sven Pompe and Stefan Klotz

Abstract

Predictive species distribution models are standard tools in ecological research and are used to address a variety of applied and conservation related issues. When making temporal or spatial predictions, uncertainty is inevitable and prediction errors may depend not only on data quality and modelling algorithm but on species characteristics. Here we applied a standard distribution modelling technique (generalized linear models) using European plant species distribution data and climatic parameters. Predictive performance was calculated using AUC, (Cohen's) Kappa and true skill statistic (TSS) which were subsequently correlated with biological and life-history traits. After accounting for phylogenetic dependence among species, model performance was poorest for species with a short life span and those occurring in human disturbed habitats. Our results clearly indicate that the performance of distribution models can be dependent on functional traits and provides further evidence that a species' ecology is likely to affect the ability of models to predict its distribution. Biased and less reliable predictions could misguide policy decisions and the management and conservation of our natural heritage.

Geographical patterns in prediction error of species distribution models

with Ingolf Kühn, Oliver Schweiger, Sven Pompe and Stefan Klotz
(submitted to *Global Ecology and Biogeography*)

Abstract

Aim To describe and explain geographical patterns of prediction errors, i.e. false absence and false presence rate, for commonly applied climate envelope models.

Location Europe.

Methods We calibrated climate envelope models using a set of climatic variables and gridded distribution data from the Atlas Florae Europaeae. We derived presence/absence maps for 1017 vascular plant species according to a threshold that maximizes Cohen's Kappa. Comparing observed and modelled species distribution we derived false absence rate, i.e. wrongly modelled as absent, and false presence rate, i.e. wrongly modelled as present, on a 50×50 km² grid. Subsequently, we related both error rates to range properties, land use and grid cell heterogeneity by means of simultaneous autoregressive models to correct for spatial autocorrelation.

Results Grid cell specific error rates were not evenly distributed across Europe. Mean false absence rate was 0.213 ± 0.136 (standard deviation) and mean false-presence rate 0.082 ± 0.052. False-absence rate was highest in south-western parts of Europe and the southern part of the South-East Europe while false presence rate was highest in the northern parts of South-East Europe, of the Iberian Peninsula and of Italy. False absence rate was larger when ranges of the occurring species where small (i.e. range size rarity was large), cover of artificial area high and altitudinal range large. False presence rate was negatively associated with range size rarity.

Main conclusions Multi-species predictions are not only accompanied by species specific but also by grid cell specific errors. The latter are associated with characteristics of the grid cells but also with range characteristics of occurring species. Uncertainties of predictive climate envelope models are not equally distributed in space and we would recommend to accompany maps of predicted distributions with a graphical representation of predictive performance.

Chapter 4

Climate and land use change impacts on plant distributions in Germany

Sven Pompe, Jan Hanspach, Franz Badeck, Stefan Klotz, Wilfried Thuiller and Ingolf Kühn

Abstract

We present niche-based modelling to project the distribution of 845 European plant species for Germany using three different models and three scenarios of climate and land use changes up to 2080. Projected changes suggested large effects over the coming decades, with consequences for the German flora. Even under a moderate scenario (approx. +2.2°C), 15–19% (across models) of the species we studied could be lost locally—averaged from 2995 grid cells in Germany. Models projected strong spatially varying impacts on the species composition. In particular, the eastern and southwestern parts of Germany were affected by species loss. Scenarios were characterized by an increased number of species occupying small ranges, as evidenced by changes in range-size rarity scores. It is anticipated that species with small ranges will be especially vulnerable to future climate change and other ecological stresses

Chapter 5

Correlates of naturalization and occupancy of introduced ornamentals in Germany

with Ingolf Kühn, Petr Pyšek, Evelin Boos, Stefan Klotz

Abstract

Invasions are multistage processes and the performance of a species at different stages depends on socio-economic, biogeographical, ecological and evolutionary factors. Most studies addressing the factors that determine invasion success focus on one particular stage, usually by examining data on introduced species that have successfully naturalized, whereas species that fail to naturalize are often not considered. In this study, we examined naturalization success (whether a species escaped from cultivation and became naturalized in the wild) and occupancy (the number of grid cells of 6´ longitude × 10´ latitude in which it is recorded) of up to 8018 ornamental plant species introduced into botanical gardens in Germany. Data on these introductions were extracted from the SYSTAX database (Information System of German Botanical Gardens), information on successful naturalization in Germany from the BiolFlor database and data on species traits from SYSTAX and the European Garden Flora. The effect of propagule pressure, biogeography, winter hardiness, life strategy, morphology and genetic variability on the probability of naturalization and the number of grid cells occupied was tested using regression models. The influence of phylogenetic dependence was considered within simple single variable models as a nested random effect. All traits that appeared significant in these simple models were combined in a multivariable model. The simplified multivariable model revealed an increasing probability of naturalization for species with a higher winter hardiness, a wider native range and a higher planting frequency in botanical gardens (Nagelkerke-R^2 of 0.196). Moreover, interactions between plant height and planting frequency and between growth form and winter hardiness also affected the probability of naturalization. The number of grid cells occupied was best explained by the winter hardiness (pseudo-R^2 of 0.61). The stratified pre-selection of ornamental plants by gardeners may hold the key to their successful escape from cultivation and subsequent naturalization.

Chapter 6

Synthesis

Prediction errors

Chapter 2 and chapter 3 showed patterns of prediction errors in plant species distribution models. Species specific error rates depended on species traits. A short lifespan, ruderal strategy and species' adaptation to human disturbance was associated with high error rates. These results complement findings from other groups such as trees (Guisan et al. 2007), butterflies (Pöyry et al. 2008) and birds (McPherson and Jetz 2007). Grid cell specific error rates were unevenly distributed and varied with grid cell characteristics such as grid cell heterogeneity and range size of the containing species. A suchlike error may be inherent to all modelled biodiversity patterns that were derived from gridded single species distribution models (Thuiller et al. 2005b, Araujo et al. 2006, Levinsky et al. 2007).

The results highlight the importance of three sources of prediction errors: data quality/resolution, niche filling and range size. Data quality is strongly influenced by mapping intensity (Mahecha and Schmidtlein 2008, Bierman et al. in press) and the inclusion of ecologically important variables (Fielding and Bell 1997). An inappropriate data resolution may lead to misspecification of the environmental niche of the species (Welk and Bruelheide 2006, Trivedi et al. 2008, Randin et al. 2009). Based on the results of this study it would be advisable to use fine resolution data for mountainous areas and to be aware of differences in mapping quality. The latter may lead to the exclusion of units with low mapping quality (see Kühn et al. 2006), improvement of data quality by novel approaches such as the inclusion of recording probability in species distribution models (Bierman et al. in press) or, if possible, attempts to collate additional information. This study shows a low predictive performance of species that are adapted to frequent disturbances. Consequently, it might be necessary to include measures of land use or human disturbances as an environmental variable when modelling suchlike species. Incomplete niche filling due to dispersal restrictions or biotic interactions is seen as a major drawback in species distribution modelling (Pearson and Dawson 2003, Hampe 2004, Pearson and Dawson 2004) and may contribute to the here presented prediction errors. Dispersal limitation has been shown for tracking of postglacial warming in Europe (Svenning et al. 2008) and especially reptiles and amphibians have a lower level of equilibrium with climate than birds or plants (Araújo and Pearson 2005). Estimating the influence of biotic interactions and dispersal abilities is a challenge to future research and might strongly enhance the quality of species distribution models (Araújo and Luoto 2007, Schweiger et al. 2008, Thuiller et al. 2008).

Though findings of this study do not directly allow reducing or handling prediction errors, the identification of errors and its possible sources raises awareness of uncertainties, allows for the interpretation of results and can direct future efforts to reduce prediction errors.

When species distribution models are used as a tool to estimate the impacts of environmental change, the thorough understanding of accompanying uncertainties is a basic requirement. Multi-species distribution models and biodiversity scenarios that are based on suchlike models should therefore be accompanied by a thorough assessment of prediction errors as shown in this study.

Climate and land use change

In chapter 4 the potential impacts of climate and land use change on plant species distribution were shown for the first time for the German national grid system. Species currently occurring in Germany may experience dramatic range losses. Due to regional differences in change within the scenarios, effects varied considerably among different regions of Germany. This study is one of the few studies in its field that uses calibration data that widely exceed the region of scenario prediction and covers a broad environmental gradient (Vaughan and Ormerod 2003). Commonly, the area used for model calibration equals the area of scenario prediction. In such an approach, the niches of marginal species, i.e. species only marginally ranging into the focal area, are described inadequately; truncated calibration data used for modelling at the edges of the study area may lead to the underestimation of the environmental niche and the overestimation of range losses (Thuiller et al. 2004, Thuiller et al. 2005a). The approach used in this study resulted in a more realistic estimation of species' ranges and includes species that might expand their ranges into Germany under scenario conditions. Depending on modelling strategy, roughly half of the "foreign" species could expand their potential ranges into Germany, which resulted to a net increase of biodiversity in some parts of Germany under the assumption of unrestricted dispersal. It is still a challenging question, how good species might be able to track climate change (Menéndez et al. 2006). Though frameworks that combine migrational models with predictions from species distribution models are available (Thuiller et al. 2008), data on dispersal rates are still rare. Within this study only the range of dispersal from a minimum of no dispersal to the maximum of unrestricted dispersal could be considered. Dispersal rates are highly species-specific and species with good dispersal and competitive ability may be better able to track changing climate (Menéndez et al. 2006). While habitat fragmentation and isolation for some species may slow down dispersal rates (Collingham and Huntley 2000), others may benefit from human mediated dispersal as shown in the field of biological invasions (Kowarik 2003, Von der Lippe and Kowarik 2007).

Model calibration in this study showed that climatic variables where most important to describe species distribution. Climatic variables explained on average 59% of the variation, while soil variables and land use explained 25% and 16%, respectively. Consequently, this might

underline that changing climate is a stronger driver of species distribution in the future compared to land use change (Sala et al. 2000) at least on this studies' scale. This study highlights the serious impacts of a changing climate that can potentially lead to the extinction of plant species on a local or even on a regional scale. Especially species at the southern or western range margin (the so called "trailing edge") and species adapted to cold and wet conditions might be confronted with this fate. The large potential rates of loss that were shown here and in related studies (Thuiller et al. 2005b) highlight the need to develop proactive nature conservation strategies to minimize the impact of climate and land use change (Hannah et al. 2002). For local application of management strategies specific conditions need to be considered thoroughly, since on the smaller scales microclimate, habitat availability and land use play a major role for species persistence (Randin et al. 2009).

Biological invasions

Factors that influenced the establishment and the degree of occupancy of introduced plants were identified with a dataset comprising a large number of introduced ornamentals and its invasion success at two different stages in chapter 5. On one hand, studies on naturalization success are rare (Milbau and Stout 2008) since it is normally unknown which species have been introduced but did not yet naturalize. On the other hand, considering more than one stage of the process allows for direct comparability while different studies rarely consider more than one stage (Pyšek and Richardson 2007, but see Pyšek et al. 2009). In this study, traits were identified that influenced either one of the two stages or both stages simultaneously. While planting frequency and native range size was also positively associated with the probability of naturalization, winter hardiness could facilitate success on both stages of the invasion process. Results from this study support the hypotheses that different stages are influenced by different factors and that early stages are strongly influenced by human activity (Williamson 2006). Propagule pressure that is caused by multiple introductions and planting activities is considered to be a strong driver of successful naturalization (Williamson and Fitter 1996, Lockwood et al. 2005). Although planting in botanical gardens is only a coarse proxy for propagule pressure, data on availability and prices of ornamentals in nursery catalogues corroborate this pattern (Dehnen-Schmutz et al. 2007). Especially for ornamental species this study shows that humans do not only act as an introducing agent but also facilitate the survival of introduced species and their spread, hence contributing considerably to the success of a species in the invasion process. A recent compilation of the 100 worst invasive species in Europe (DAISIE 2009) lists 18 terrestrial plants of which 14 have been introduced for ornamental purposes. Species once planted because they are large and showy such as *Fallopia japonica, Impatiens glandulifera* or

Heracleum mantegazzianum, grow now in dense stands in riparian habitats and disturbed places with good supply of water and nutrients, causing ecological and economical damage. They locally impede the growth of native plant populations and reduce biodiversity (*F. japonica, I. glandulifera, H. mantegazzianum*), cause flood hazards (*F. japonica*) or even be a danger to human health (*H. mantegazzianum*). The eradication of invasive species in Europe can cause large costs (Kettunen et al. 2008, Vilà et al. 2010) and the risks of future invasions need to be reduced. At this point, results from this study may contribute to effectively impede the establishment of introduced species, since reduced planting frequency significantly reduces the probability of naturalization. Banning the trade and planting of potentially invasive species might contribute to effective prevention and reduction of negative impacts of invasive species. Trait syndromes that have been identified to facilitate invasiveness such as a wide ecological niche, being invasive elsewhere or specific life-history characteristics (Goodwin et al. 1999, Pyšek and Richardson 2007, Pyšek et al. 2009) as well as results from this study can serve as a scientific basis for the development of such species lists or decision frameworks (Reichard and Hamilton 1997, Daehler et al. 2004, Křivánek and Pyšek 2006).

Conclusions

This study adds to the understanding of how global change influenced changes in biodiversity in the past through biological invasions and how it may influence changes in the future due to climate and land use change. In Central Europe climate change may strongly threat biodiversity in the future and human trade and planting of exotic species facilitate invasion success and the accompanying negative effects on biodiversity. In the face of these results the aim to stop biodiversity loss in Europe by 2010 (2013) (European Council 2001) seems naive.

Though the awareness of the future threats of climate change to biodiversity has been raised within the last decades, results from this study show that the reliability of modelling results needs to be thoroughly assessed. While Thuiller et al. (2005b) projected largest losses in plant species richness in the Mediterranean; this is also among the areas with highest rates of prediction error per grid cell. Further, species from North Africa might expand their ranges to Europe. Beside by this study, it is still barely addressed how species expanding their ranges from outside into a target area might influence biodiversity. It is likely, however, that this will lead to an increase of biodiversity compared to model output at least in the marginal areas. Nutrient enrichment (eutrophication) may favour competitive species such as many invasive species and habitat fragmentation and disturbance in combination with climate change may promote ruderal and synanthropic species. Again it should raise concern, that the prediction of suchlike species connected with highest prediction error, making it more difficult to assess the

effects of climate change. Recently, the importance of the interplay between different drivers of biodiversity has been highlighted for two-way interactions such as climate change and biotic invasions (Walther et al. 2009) and three-way interactions such as climate change, biological invasions and pollination (Schweiger et al. 2010b). While this study already integrated changes in climate and land use, interactive effects with biological invasions demand closer consideration, though due to complexity it is difficult to disentangle the driving forces.

Chapter 7

Summary

Global socio-economic changes in the last two hundred years led to the severe alteration of biophysical systems. Global change causes losses of biodiversity and degradation of ecosystem services and in consequence threats human well-being. In order to minimize the future impacts of global change, one has to understand how species responded to anthropogenic pressures in the past and how species may respond in the future. Within this study, main drivers of biodiversity, namely climate and land use change as well as biological invasions were selected and its influence on plant species distribution in Germany was analysed. Methodological limitations are analysed for species distribution models which are commonly applied to estimate impacts of climate and land use change.

Species distribution models correlate the occurance of species with environmental variables and derive a statistical description of the realized environmental niche. Subsequently, species distribution models can be combined with environmental change scenarios to estimate possible impacts of future changes. The validation of modelled species distribution with observations reveals the patterns of prediction errors. Predictive performance depends on data quality and the simplifying assumptions underlying species distribution models. Within this study, patterns of prediction errors per species and per mapping unit where analysed. Therefore, species distribution models were calibrated using distribution data from the Atlas Florae Europaeae and climatic variables. Species specific error rates were based on distribution models for 638 Central European plants and magnitude of error rate was correlated with species traits. Species with a short lifespan, ruderal strategy and species' adaptation to human disturbance were associated with high error rates. Error rates per mapping unit were calculated for each of 2219 grid cells (50×50km²) based on 1017 species distribution models. Mean size of false absence rate was 0.213±0.136 (±standard deviation) and mean false-presence rate 0.082±0.052. Error rates were unevenly distributed across Europe and varied depending on grid cell characteristics, such as grid cell heterogeneity, and in addition, on the species' range size. The identification of errors and its possible source allows for the interpretation of predictive species distribution models and can direct future efforts to reduce prediction errors.

In order to estimate possible future impacts of environmental change species distribution models for 845 plant species were combined with climate and land use change scenarios for Germany. Based on these models, several species currently occurring in Germany may experience dramatic range losses. Even under the moderate scenario (+2.2°C), 15–19% of the species could be lost locally. Due to regional differences in change within the scenarios, the effects varied considerably among different regions of Germany with highest losses in the eastern and south-western parts. Under the assumption of unrestricted dispersal, at least half of the 295 species not yet occurring in Germany might be able to expand their range into Germany.

The results show that climate and land use change may have severe impacts on species distribution and biodiversity. Though potential range expansion could account for regional losses of species, it is doubtful if species will be able to track the rapid change within the strongly fragmented landscape. Climate change is expected to be the strongest driver of changes in Central European biodiversity within the next decades and strategies need to be developed to minimize the impacts.

Biological invasions considerably influence species distribution and introduced species can negatively affect native biodiversity. Although the invasion processes are not new to science, drivers that influence the success within this process are not yet fully understood. Within the study, 8018 ornamental plants were selected to investigate the effect of species characteristics and human influence on the success on two different stages of the invasion success, namely naturalization and spread. Ornamentals represent an important part of introduced and naturalized plants in Central Europe and their introduction is at least partially documented. The results show that the probability of naturalization increased with planting frequency, and was higher for species with a wider native range and a higher winter hardiness. Degree of occupancy of naturalized species as a measure of spread was positively correlated with winter hardiness. These results demonstrate the stage specific influence of various drivers during the invasion process and show that humans do not only act as an introducing agent but also influence the invasion success by planting, i.e. by promoting propagule pressure. This indicates that trading restrictions to decrease propagule pressure could be an effective tool to reduce future invasion risks of potentially invasive ornamentals.

This study adds to the understanding of how global change has influenced changes in biodiversity in the past through biological invasions and how it may influence changes in the future due to climate and land use change. Some drawbacks of the different methodological approaches were investigated and may be the basis for more accurate estimation of possible impacts of environmental change on biodiversity.

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Appendix

Acknowledgements

Erklärung über den persönlichen Anteil an den Publikationen

Die folgende Auflistung gibt einen Überblick über meinen persönlichen Anteil an den hier zusammengestellten Publikationen mit Koautorenschaft:

Correlates of naturalization and occupancy of introduced ornamentals in Germany

Datenerhebung: 80% (Datenbankabfragen mit Evelin Boos)

Datenanalyse: 100%

Schriftliche Umsetzung: 90% (Korrekturen durch Ingolf Kühn, Petr Pyšek, Stefan Klotz)

Predictive performance of plant species distribution models depends on species traits

Datenerhebung: 80% (Klimadaten durch Sven Pompe zusammengestellt)

Datenanalyse: 100%

Schriftliche Umsetzung: 95% (Korrekturen durch Ingolf Kühn, Sven Pompe, Stefan Klotz)

Geographical patterns in prediction error of species distribution models

Datenerhebung: 80% (Klimadaten durch Sven Pompe zusammengestellt)

Datenanalyse: 100%

Schriftliche Umsetzung: 90% (Korrekturen durch Ingolf Kühn, Oliver Schweiger, Sven Pompe, Stefan Klotz)

Climate and land use change impacts on plant distributions in Germany

Datenerhebung: 30 % (Sven Pompe 60%, Franz Badeck & Ingolf Kühn 10%)

Datenanalyse: 10 % (Sven Pompe 75 %, Wilfried Thuiller & Ingolf Kühn 15%)

Schriftliche Umsetzung: 5 % (Sven Pompe 80 %, Korrekturen durch Franz Badeck, Stefan Klotz, Wilfried Thuiller, Ingolf Kühn)

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Publications

Hanspach, J., Kühn, I., Pyšek, P., Boos, E. & Klotz, S. (2008) Correlates of naturalization and occupancy of introduced ornamentals in Germany. *Perspectives in Plant Ecology, Evolution and Systematics*, 10, 241-250.

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Eigenständigkeitserklärung

Hiermit erkläre ich, dass diese Arbeit nicht bereits zu einem früheren Zeitpunkt der Naturwissenschaftlichen Falkultät I – Biowissenschaften der Martin-Luther-Universität Halle-Wittenberg oder einer anderen wissenschaftlichen Einrichtung zur Promotion vorgelegt wurde.

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