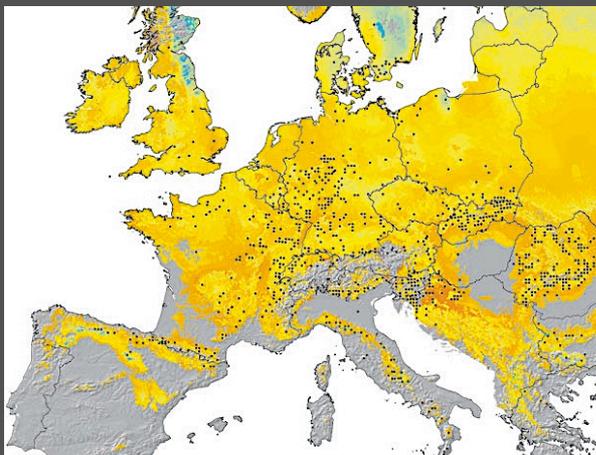
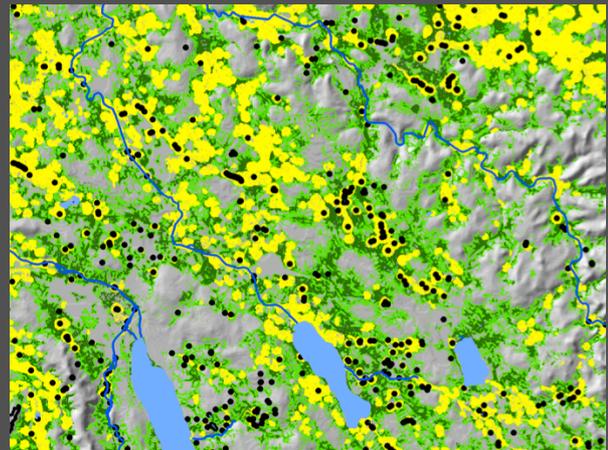


# MODELLING SPATIAL DYNAMICS OF PLANT DISTRIBUTIONS

Implementation of biotic interactions and migration improves large-scale projections of species distributions during climate and land-use change

Eliane S. Meier



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# MODELLING SPATIAL DYNAMICS OF PLANT DISTRIBUTIONS

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## IMPLEMENTATION OF BIOTIC INTERACTIONS AND MIGRATION IMPROVES LARGE-SCALE PROJECTIONS OF SPECIES DISTRIBUTIONS DURING CLIMATE AND LAND-USE CHANGE

A dissertation submitted to  
ETH ZURICH  
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"If a tree falls in a forest and no one is around to hear it, does it make a sound?"

Adapted from George Berkeley, 1734, *A Treatise Concerning the Principles of Human Knowledge*, section 45.



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## Abstracts

Global changes in climate, land-use and the economy rapidly alter large-scale distributions of animal and plant species. Under these varying climatic and land-use conditions, species may shift their distributions or, if they are too migration limited to do so, they can adapt to the new conditions or they may go extinct. Additionally, because of the increase in international trade, species are being introduced to new areas more frequently and, due to their ability to spread rapidly, are becoming one of the main reasons for species decline. The aim of this thesis was to investigate the factors that drive such long-term dynamics at different spatial scales by using species distribution models. The results showed that competition between species was a key factor influencing species distributions, especially under favourable climate conditions. It was further shown that migration limitation was an additional key factor shaping species distributions and was mainly caused by competition, adverse climatic conditions and habitat fragmentation. As a result, tree species that occur mainly in competitive environments may not be able to keep pace with climate and land-use change, while ruderal species may have only minor delays in the readjustment of their distributions. Another important finding was that knowledge on the variation in migration rates due to habitat heterogeneity can be used successfully for developing strategies to control invasive plants more economically. Overall, the findings of this thesis will be helpful for investigating and better predicting large-scale species distributions under global change scenarios and for developing mitigation strategies to reduce the effects of global change on species distributions.

Globale Veränderungen in Klima, Landnutzung und Wirtschaft wirken sich rasch auf die grossräumige Verbreitung von Tier- und Pflanzenarten aus. Durch die Klima- und Landnutzungsänderungen verschieben Arten ihre Verbreitungsgebiete, oder wenn sie in der Wanderung begrenzt sind, passen sie sich an die neuen Bedingungen an oder sterben aus. Mit dem zunehmenden internationalen Handel werden Arten eingeschleppt, welche durch ihre intensive Ausbreitung zu den Hauptgründen für den Artenrückgang zählen. Das Ziel dieser Arbeit war es, mit Hilfe von Artverbreitungsmodellen die Faktoren zu eruieren, welche solche langfristigen Dynamiken auf unterschiedlichen räumlichen Skalen antreiben. Die Ergebnisse zeigten auf, dass die Konkurrenz zwischen den Arten ein Schlüsselfaktor für Artverbreitungen ist, insbesondere unter günstigen klimatischen Bedingungen. Weiter zeigte sich, dass die Beschränkung der Wanderungsgeschwindigkeit ein zusätzlicher Schlüsselfaktor für Artverbreitungen ist. Solche Beschränkungen werden vor allem durch Konkurrenz, ungünstige klimatische Bedingungen und Habitatfragmentierung verursacht. Dadurch werden insbesondere Bäume, die hauptsächlich in konkurrenzstarken Gesellschaften vorkommen, kaum mit dem Klima- und Landnutzungswandel Schritt halten können, während ruderale Arten nur geringfügige Verzögerungen bei der Anpassung ihrer Verbreitungen aufweisen werden. Ein weiteres Ergebnis dieser Arbeit war, dass das Wissen über Unterschiede in der Wanderungsgeschwindigkeit aufgrund von Habitatheterogenität erfolgreich zur Entwicklung von Strategien zur wirtschaftlichen Bekämpfung invasiver Pflanzen genutzt werden kann. Die Ergebnisse dieser Arbeit können für die Untersuchung und Verbesserung von Projektionen von grossräumigen Artverbreitungen unter Szenarien des globalen Wandels genutzt werden, sowie zur Entwicklung von Strategien zur Milderung der Auswirkungen des globalen Wandels auf Artverbreitungen.



## Summary

Global change rapidly affects large-scale plant species distributions. On the one hand, in response to varying climate, plant species have to adjust their ranges in order to track suitable climatic conditions; if a species is too dispersal limited to track suitable conditions, it either has to adapt rapidly to the new conditions, or it goes extinct. On the other hand, and as a side effect of increased international trade during globalization, species are increasingly introduced into areas they would otherwise have been unlikely to have reached with natural dispersal alone, where they then start to spread expansively over large areas. To predict such changes in large-scale species distributions, species distribution models (SDMs) are valuable tools. However, the direction and magnitude of the effects predicted for large-scale species distributions during global change strongly depend on model quality, i.e. the data used, the modelling methods applied, and the theories and assumptions underlying the models. Whether or not different types of data and modelling methods meet required standards was evaluated in a vast number of studies. However, despite that the assumptions complementing the SDM implementation of the niche concept are widely acknowledged, the conditions under which they are applicable are, as of yet, hardly tested. In addition, several key assumptions contradict ecological concepts and the validity of the models under several conditions may thus be crucially compromised. Such key assumptions are that (1) large-scale species distributions are predominantly determined by climate constraints, (2) species are in pseudo-equilibrium with the current environment, and (3) species' niches do not vary. The first key assumption results from the expected spatial hierarchical importance of drivers, i.e. that on large scales only large-scale drivers are important. From the niche concept, however, we expect that local processes like competition also determine where species are found in nature, in addition to climate and independent of scale. Moreover, according to the stress-gradient hypothesis we further expect that species ranges are only shaped by climate under adverse conditions, while competition limits species ranges under favourable conditions. The second key assumption is based on the expectation that species had sufficient time to adapt to a relatively stable climate since the late Holocene. This assumption may be flawed by several ecological concepts, and also by the observation that several species spread rapidly once they are anthropogenically introduced into an area. The third key assumption is used as a justification to project SDMs to other areas or future climates. However, conceptually, species may rapidly adapt to the local conditions or may have different niches during their lifecycle. In conclusion, projections from SDMs may be flawed when considering the expectations of several ecological concepts. The exclusive use of mean climate to project species distributions across time and space may not be justified on the one hand, by the fact that observations of organisms in nature are by definition already shaped by species' interactions, land-use effects, climatic extremes, migration limitations and the interactions between these

processes, and on the other hand, by the assumption that these processes are only of minor importance and remain stable over time and space.

Despite increasing knowledge on individual drivers of species distributions, we still lack a broader understanding of the most important range shaping processes during global change and the way in which they interact on large spatial scales. Thus, it is important to evaluate the key assumptions of SDMs and the contrasting ecological concepts with empirical data and to potentially refine them. In my PhD, I evaluated the first two key assumptions of SDMs and the related ecological concepts by attempting to answer the following four questions: *Question 1*: How do abiotic and biotic variables contribute to shaping spatial patterns? *Question 2*: How do biotic interactions vary along macroclimatic gradients and how does this affect species ranges? *Question 3*: How strongly do migration limitations prevent species from tracking suitable habitats during climate and land-use change? *Question 4*: How can population management prevent invasive species from spreading across the landscape?

The study to answer *Question 1* showed that biotic and abiotic variables make mostly independent and equally large contributions when explaining tree species distributions within Switzerland. Further, mid- to late-successional tree species were more strongly affected by biotic predictors than early-successional tree species, possibly because they are exposed to stronger biotic interactions. Thus, the explicit inclusion of small-scale processes, such as biotic interactions, when projecting large-scale species distributions is essential to more completely depict the realized niche, not only for projections under current climate, but also for projections of future species range limits where species communities may change.

In attempting to answer *Question 2*, I found that the strength of biotic interactions varies considerably along environmental gradients and, hence, in geographic space. In line with the stress-gradient hypothesis, beech abundance was strongly linked to the abundance of its competitor species under abiotically favourable growing conditions (i.e. medium warm and wet climate), while this link weakened in conditions of high physiological stress (i.e. cold and dry climate). Translated to geographic space, this leads to the strongest interactions and reduced predicted abundance of the focal species occurring at low elevations and in southern Europe. When projecting such calibrated models to future climates, the limiting effect of competitive interactions was decreased because of the predicted spatial segregation of the major tree species.

Analyses to answer *Question 3* revealed that species characterized by especially low reproductive rates may be largely in disequilibrium with future climate. Thus, projected distributions of early-successional tree species during the 21st century from models that incorporate realistic migration matched with the unlimited migration assumption quite well (i.e. hardly no constraints to migration are present and thus no lags in the re-adjustment of ranges under climate change), while the

predicted distributions of mid- to late-successional tree species matched better with the no migration assumption (i.e. such species do not track changing climates and disappear in regions that become unsuitable). I further showed that inter-specific competition reduced range shift velocity of trees in Europe more than adverse macroclimatic conditions (i.e. very cold or dry climate), while habitat fragmentation increased this effect.

In answering *Question 4*, I demonstrated how the knowledge of effects from habitat heterogeneity on spread could be used to efficiently keep invasive species from reaching equilibrium conditions. Compared to random treatments within the landscape, which is currently most frequently done by practitioners, treating individuals of three hydrochorous plants according to specific spatial allocation patterns (i.e. removing individuals of large populations, small populations, outlying populations, cells in large connected habitats, cells along rivers, cells in upper reaches of rivers or in lower reaches) largely increased the effect of management actions on population growth and spread into uncolonized habitats, without increasing the costs considerably. The most efficient spatial allocation patterns varied mainly between vegetatively reproducing species (i.e. highest efficiency by removing large populations) and sexually reproducing species (i.e. highest efficiency by removing small populations), but not much between management goals (i.e. reducing spread, area, individuals or regeneration potential) or different levels of costs. Over the 15 years of simulation, effects of the most efficient management strategies increased, while costs remained the same or decreased. Furthermore, after a few years, very high costs approached the level of medium costs, but still had much higher effects, while very low costs were not very useful due to density regulation of stands whereby removed individuals were overcompensated by higher seed yields.

Overall, I could demonstrate that local processes, including biotic interactions, land-use and species' migration abilities, may have a strong influence on responses of large-scale species distributions to global change. When ignoring the effects of such processes, the validity of SDM projections for other areas or different climates may be crucially compromised. My results not only reveal conditions where projections from SDMs based on standard assumptions may be compromised, thus improving the interpretability of range shift maps from SDMs (i.e. under what conditions projections may be more uncertain due to out-competition and migration limitations), but they also improve species management strategies, e.g. when planning the assisted migration of economically and ecologically important species or reducing the spread of alien invasive species. However, the approaches used in this thesis also have limitations, e.g. that from data based on observations, it is hard to distinguish cause and effect, or that more complex models inherently contain more uncertainty. To underpin my findings, it would be necessary to investigate the direction of competitive interactions along climatic gradients in experimental setups designed to evaluate the models, or use Bayesian approaches to estimate the uncertainty in the models.



## Zusammenfassung

Der globale Wandel beeinflusst die grossräumige Verbreitung von vielen Tier- und Pflanzenarten rapide. Einerseits müssen die Arten ihre Verbreitungsgebiete dem sich wandelnden Klima anpassen. Falls sie nicht genug schnell wandern können, müssen sie sich entweder rasch genetisch an die neuen Bedingungen anpassen oder sterben aus. Andererseits, und als Nebeneffekt des verstärkten internationalen Handels während der Globalisierung, werden Arten zunehmend in Gebiete eingeschleppt in welche sie ohne fremde Hilfe kaum gelangt wären, sich nun aber dort intensiv über grosse Flächen ausbreiten. Um vorherzusagen auf welche Weise sich die grossräumigen Artverbreitungen verändern, werden häufig Artverbreitungsmodelle (SDMs) herbeigezogen. Die Richtung und das Ausmass der vorhergesagten Änderungen hängen jedoch stark von der Qualität der Modelle ab, d.h. von den verwendeten Daten, den verwendeten Methoden, und den Theorien und Annahmen der Modelle. Ob bestimmte Daten und Methoden entsprechende Normen erfüllen, wurde in einer Vielzahl von Studien untersucht. Hingegen sind die Annahmen auf welchen die Modelle beruhen zwar anerkannt, jedoch sind die Bedingungen unter welchen sie anwendbar sind noch kaum erprobt. Da mehrere dieser Annahmen wichtigen ökologischen Konzepten widersprechen, ist es gut möglich, dass die Gültigkeit der Modelle unter verschiedenen Bedingungen entscheidend beeinträchtigt ist. Solche Annahmen sind, dass (1) grossräumige Artverbreitungen hauptsächlich durch das Klima bestimmt werden, (2) sich die Arten in einem Gleichgewicht mit der heutigen Umwelt befinden, und (3) die Nischen von Arten kaum variieren. Die erste Annahme basiert auf der erwarteten hierarchischen Gliederung von Einflussfaktoren, so sind auf grossen räumlichen Skalen nur grossräumige Einflussfaktoren wichtig. Aufgrund des Nischenkonzepts wäre jedoch zu erwarten, dass auch lokale Prozesse wie Konkurrenz zwischen Arten darüber entscheiden, wo Arten in der Natur zu finden sind - zusätzlich zum Klima und unabhängig vom Massstab. Darüber hinaus ist aufgrund der Stress-Gradienten Hypothese zu erwarten, dass Artverbreitungen nur unter widrigen Klimabedingungen direkt vom Klima bestimmt werden, hingegen unter günstigen Bedingungen die Konkurrenz zwischen Arten ausschlaggebender ist. Die zweite Annahme basiert auf der Erwartung, dass Arten genügend Zeit hatten um sich an das heutige Klima anzupassen, welches seit dem späten Holozän relativ stabil ist. Diese Annahme steht im Gegensatz zu verschiedenen ökologischen Konzepten und zur Beobachtung von Arten die sich rasant ausbreiten, sobald sie in bestimmte Gebiete eingeführt werden. Die dritte zentrale Annahme gilt als Rechtfertigung, um SDMs auf unterschiedliche Orte oder zukünftige Klimabedingungen zu projizieren. Allerdings können sich gemäss ökologischen Konzepten Arten rasch evolutiv an örtliche Gegebenheiten anpassen und unterschiedliche Nischen im Verlaufe ihres Lebens aufweisen. Folglich können Projektionen fehlerhaft sein, welche auf der Erwartung beruhen, dass nur das Klima für die grossräumigen

Artverbreitung ausschlaggebend ist, weil die Beobachtungen von Organismen in der Natur bereits durch Konkurrenz, klimatische Extreme, Migration und Wechselwirkungen zwischen all diesen Prozessen geprägt sind, diese über Raum und Zeit stabil bleiben, und kleinräumige Prozesse sowieso nur von untergeordneter Bedeutung sind.

Trotz zunehmender Erkenntnisse über einzelne Einflussfaktoren von Artverbreitungen fehlt nach wie vor ein breiteres Verständnis dafür, welche dieser Faktoren während des globalen Wandels einen grossen Einfluss haben und wie diese Faktoren auf grossen räumlichen Skalen interagieren. Daher wäre es wichtig, die Grundannahmen von SDMs und die kontrastierenden ökologischen Konzepte mittels Daten zu untersuchen, um dabei potenzielle Einschränkungen der SDM-Annahmen und ökologischen Konzepte zu definieren. Deshalb habe ich in meiner Doktorarbeit die ersten beiden SDM-Grundannahmen und die damit verbundenen ökologischen Konzepte mittels der folgenden vier Fragen untersucht: *Frage 1:* Wie viel tragen abiotische und biotische Variablen zu grossräumigen Mustern von Artverbreitungen bei? *Frage 2:* Variieren biotische Interaktionen entlang von makroklimatischen Gradienten und wie wirkt sich diese Variation auf die Verbreitung von Arten aus? *Frage 3:* Wie stark werden Arten durch limitierte Migrationsgeschwindigkeiten daran gehindert, bei der Verschiebung von geeigneten Lebensräumen während dem Klima- und Landnutzungswandel mitzuhalten? *Frage 4:* Kann das Management gezielter Populationen von invasiven Arten diese dabei hindern sich in der Landschaft auszubreiten?

Die Studie zur *Frage 1* hat gezeigt, dass biotische und abiotische Variablen weitgehend unabhängig voneinander und zu gleichen Teilen zur Erklärung von Baumartenverbreitungen innerhalb der Schweiz beitragen. Ferner wurden spätsukzessionale Baumarten stärker durch biotische Variablen beeinflusst als frühsukzessionale, möglicherweise weil sie stärkeren biotischen Interaktionen ausgesetzt sind. Somit ist der explizite Einbezug von kleinräumigen Prozessen wie biotische Interaktionen wesentlich zur vollständigeren Erklärung der realisierten Nische und folglich bei der Projektion von grossräumigen Artverbreitungen.

In der Studie zur *Frage 2* konnte ich zeigen, dass biotische Interaktionen entlang von Klimagradienten und somit auch im geographischen Raum variieren. In Übereinstimmung mit der Stress-Gradienten Hypothese war das Buchenvorkommen unter abiotisch günstigen Wachstumsbedingungen (d.h. warmes und feuchtes Klima) stark vom Vorkommen von Konkurrenzarten abhängig, wobei sich diese Beziehung hin zu hohem physiologischen Stress (d.h. kaltes und trockenes Klima) immer mehr abgeschwächt hat. Im geographischen Raum führte dies zu den stärksten Interaktionen und folglich reduzierter Abundanz in tiefen Lagen und in Richtung Südeuropa. Diese Reduktion nahm bei Zukunftsszenarien wegen der vorhergesagten räumlichen Segregation der wichtigsten Baumarten ab.

Analysen zu *Frage 3* zeigten, dass sich besonders langsam reproduzierende Baumarten in einem starken Ungleichgewicht mit dem zukünftigen Klima befinden werden. Werden Migrationsraten von Bäumen in die grossräumigen Modelle miteinbezogen, entstehen in Europa für frühsukzessionale Baumarten keine Verzögerungen bei der Neujustierung ihrer Verbreitungen während dem Klima- und Landnutzungswandel im 21. Jahrhundert. Spätsukzessionale Baumarten hingegen werden hauptsächlich noch in einigen Gebieten ihrer heutigen Verbreitung vorkommen welche nach wie vor gute Bedingungen aufweisen. Weiter konnte ich zeigen, dass interspezifische Interaktionen die Migrationsgeschwindigkeiten stärker herabsetzen können als ungünstige Klimabedingungen. Habitatfragmentierung erhöhte diesen negativen Effekt auf die Migrationsgeschwindigkeiten.

Die Studie zur *Frage 4* zeigte, dass es für die kostengünstige Eindämmung invasiver Pflanzenarten eine grosse Rolle spielt, wo Individuen in einer Landschaft behandelt werden. Im Gegensatz zu zufällig in der Landschaft durchgeführten Behandlungen, was derzeit Standard ist, führten Behandlungen aufgrund von bestimmten räumlichen Mustern (d.h. Entfernen von grossen Populationen, kleinen Populationen, weitentfernten Populationen, grossen vernetzten Habitaten, Flussoberläufen oder -unterläufen) zu einer drastischen Reduktion der Populationszunahme und der Ausbreitung in derzeit unbesiedelte Lebensräume. Die effizientesten räumlichen Muster unterscheiden sich hauptsächlich zwischen vegetativ reproduzierenden Arten (d.h. Behandlung grosser Populationen) und sexuell reproduzierenden Arten (d.h. Behandlung kleiner Populationen), aber nur geringfügig zwischen Management-Zielen (d.h. Verringerung der Ausbreitung, Fläche, Adulten Individuen oder dem Regenerationspotenzial) oder unterschiedlichen Grössenordnungen von Kosten. Im Laufe der 15 jährigen Simulation erhöhten sich die Effekte der effizientesten Strategien, während dem die Kosten gleich blieben oder gesunken sind. Im Weiteren entsprachen die jährlichen Kosten nach wenigen Jahren dem Niveau der mittleren Kosten, hatten aber noch viel grössere Effekte. Sehr niedrige Kosten waren selten sinnvoll, da durch die Dichteregulation der Bestände die entfernten Individuen kompensiert oder gar überkompensiert wurden.

Insgesamt konnte ich zeigen, dass lokale Prozesse wie biotische Interaktionen, Landnutzung oder die Migrationsfähigkeit von Arten einen starken Einfluss auf die Reaktion von grossräumigen Artverbreitungen während des Globalen Wandels haben können. Werden solche lokalen Prozesse ignoriert, kann die Gültigkeit der Projektionen unter bestimmten Bedingungen entscheidend beeinträchtigt sein. Die Erkenntnisse helfen dabei die Interpretierbarkeit von Artverschiebungskarten zu verbessern, welche mit Standard-SDMs generiert wurden, und können für Artenmanagement-Strategien hilfreich sein, z.B. für die unterstützte Umsiedlung von wirtschaftlich oder ökologisch wichtigen Arten oder für die Eindämmung von invasiven Arten. Allerdings müssen dabei die Limitierungen der vorliegenden Ansätze berücksichtigt werden, z.B. dass aufgrund von Beobachtungsdaten nur schwer zwischen Ursache und Wirkung zu unterscheiden ist, und dass

komplexere Modelle mehr Modellunsicherheit enthalten als einfachere Modelle. Zur Untermauerung meiner Ergebnisse könnte z.B. untersucht werden, wie sich in einem experimentellen Versuchsaufbau die Richtung von kompetitiven Interaktionen entlang von klimatischen Gradienten verändert, oder es könnte mittels eines Bayes-Ansatzes die Unsicherheit in den Modellen geschätzt werden.

# 1 General introduction

Why species are found in certain geographical areas and how they got there has fascinated biogeographers and ecologists for more than two centuries (Humboldt, 1808; Darwin, 1859; Grinnell, 1917; Connell, 1961). As a basic unit of investigation for such questions, researchers often address the geographical range of a species, which is characterized by the complex interplay of a species' characteristics and its environment (Brown *et al.*, 1996). The geographical range of a species may be dynamic and can change within relatively short timescales, e.g. summer and winter ranges or breeding and non-breeding ranges of mobile species like most animals. For non-mobile species like plants, geographical ranges may only respond dynamically over longer time spans, since individuals often stay in the same place during their whole life cycle and dispersion is bound to reproduction, although wind, water, animals or humans may enhance their dispersal (Nathan & Muller-Landau, 2000). Consequently, current ranges of plants, especially of species with long life cycles, have emerged over long time periods. For instance, the ranges of most European trees started to take shape after the late glacial maximum when the climate in the northern hemisphere began to warm up and deglaciation was initiated (Cain *et al.*, 1998; Tinner & Lotter, 2006). Because the climate during the Holocene was relatively stable, it is expected that current ranges are a result of the adaptation of a species to the present environment, despite potentially low migration rates (Kullman & Kjallgren, 2000). Today, global change is assumed to rapidly alter large-scale plant species distributions (Parmesan & Yohe, 2003; Thomas, 2010). On the one hand, many species have to adjust their ranges at a rate equal to the shifting climate in order to track suitable environmental conditions (Parmesan *et al.*, 1999). However, if a species is highly limited in its ability to migrate, then it must either rapidly adapt to the new environmental conditions in their current habitat<sup>1</sup> (Pearman *et al.*, 2008), or it will go locally extinct (Channell & Lomolino, 2000). On the other hand, and as a side effect of increased international trade during globalization, humans introduce species into areas they would otherwise have been unlikely to have reached by natural dispersal alone. Following such introductions, species often start to spread intensively over large areas (Mack *et al.*, 2000). Thus, research on the key drivers of species distributions at large spatial scales is not only useful in furthering our understanding of ecological concepts, but is also important for improving species management strategies, especially in light of rapid global change. Despite that knowledge is accumulating due to a vast increase in the number of publications on individual aspects of drivers of species distributions, we still lack a broader

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<sup>1</sup>In my study I refer to "habitat" to express all climatically and biologically suitable geographic areas of a species. The term does not reflect the more plant community-oriented term "habitat" as used in conservation biology, e.g. xeric grasslands or riparian zone.

understanding of the most important range shaping processes and the way in which they interact over large spatial scales (Gaston, 2009).

To better understand how fast species can migrate to certain areas during global change, we have to broaden our understanding of the most important drivers of species distributions. Based on our current understanding, the known drivers operate at different spatial scales and with different magnitudes, although they may in some cases act in an interrelated fashion. At the continental scale, gradual trends in macroclimate are hypothesized to be the key factors shaping species ranges, while at regional scales topography and climatic extremes may play a key role for species distributions. At local scales, on the other hand, biotic interactions, soil or land-use may be among the most important drivers to explain species distributions (Pearson & Dawson, 2003). During the Holocene, species range shifts of up to 100 km per century were observed (Birks, 1989); range shifts of similar magnitude are expected under current climate change scenarios (Prentice *et al.*, 1992). However, such range shift projections are expected to be flawed in that new drivers may emerge and the known drivers that act on different hierarchical levels may be interrelated to some degree. Biotic interactions, for instance, may also limit species ranges if macro-climatic conditions are less severe (Maestre *et al.*, 2009). Further, the importance of these different drivers is not only expected to change between spatial scales, but may also be specific to the ecology of individual species, i.e. the relative importance of drivers may depend on the physiological tolerances, competitive ability or dispersal ability of a species. As a consequence, key drivers may be similar for species that are characterized by similar traits (Lavorel & Garnier, 2002).

Models are designed to reduce the complexity of nature to simple systems and are thus often used to test hypotheses on the drivers of large-scale plant species distributions and to simulate the potential magnitude and direction of the effects on species distributions when these drivers change. A vast number of models exist that deal with different spatial and temporal aspects of drivers of species distributions. The conceptual basis of modelling approaches to quantify and predict species-environment relationships in space and time is the ecological niche concept. The ecological niche concept *sensu* Hutchinson (1957) differentiates between the fundamental niche, which describes abiotic physiological limitations of a species, and the realized niche, which describes the fraction of the fundamental niche that a species can successfully colonize when considering additional constraints from biotic interactions. According to the implementation of this niche concept, the vast majority of models may be divided into two principal groups. Mechanistic species dynamics models (e.g. dynamic vegetation models or multispecies population dynamic models) parameterize the fundamental niche by calibrating physiological tolerances and by implementing rules of competitive behaviour that result in the predictions of the realized response (e.g. Shugart, 1984; Prentice *et al.*, 1992; Neilson, 1995; Humphries *et al.*, 1996; Bugmann, 2001; Sitch *et al.*, 2003). Therefore, many

mechanistic species dynamics models provide a suitable tool for studying demographic responses to spatiotemporal environmental variation and small-scale processes. However, such models cannot be easily applied to large spatial extents at a fine grain due to their high computational cost (Neilson *et al.*, 2005). Empirical species distribution models (SDMs), on the other hand, parameterize the realised niche implicitly by linking species occurrence data, which are driven by both local processes, such as biotic interactions, and physiological constraints, to environmental predictors in order to project suitable habitats of species in space and time (Guisan & Zimmermann, 2000). SDMs were not, however, meant to include dynamic processes and are based on several assumptions that may not hold in all circumstances (Guisan & Zimmermann, 2000; Guisan & Thuiller, 2005). Consequently, both of these two major groups of species distribution models have different limitations (more details on each model type are given in Box 1 and 2). Nevertheless, in order to test hypotheses on the key drivers of large-scale plant species distributions, and to simulate the potential magnitude and direction of effects on species distributions under transient conditions following global change, SDMs may still provide a useful starting point. To improve their usefulness and reliability, however, they may have to be extended by elements of mechanistic species dynamics models.

The precision of model predictions depends on the suitability of a model for the intended use and the developer's conceptual model description (Rykiel, 1996). SDMs are designed to project the most likely impact of global change on future species distributions (Guisan & Thuiller, 2005), with the ecological niche concept providing the basis for SDM projections. In order to further reduce the complexity of natural systems, several assumptions on ecological processes exist. However, these assumptions may not be applicable to all ecological circumstances that SDMs are applied to. Thus, in order to reduce the uncertainty in SDM projections, one may want to quantify the fraction of prediction uncertainty that arises due to the assumptions behind SDMs. The assumptions may then be refined accordingly. In addition, methodological assumptions also exist, e.g. on the spatial resolution, scale, modelling technique, evaluation method or data quality (e.g. Heikkinen *et al.*, 2006). However, the uncertainty originating from methodological assumptions are much better studied - for an overview please consult the numerous publications written in the last few years (e.g. Allouche *et al.*, 2006; M. P. Austin *et al.*, 2006; Elith *et al.*, 2006; Guisan *et al.*, 2007a; Elith & Leathwick, 2009; Zimmermann *et al.*, 2010). I thus focus here on elaborating the spatiotemporal variation in the applicability of SDM assumptions, with recognition that several ecological and methodological assumptions are deeply interrelated.

There are three main ecological assumptions of standard SDMs that complement the SDM implementation of the niche concept: (1) large-scale species distributions are mainly determined by climate constraints, (2) species distributions are in pseudo-equilibrium with the current environment, and (3) niches are stable over short time spans (Guisan & Theurillat, 2000). These three assumptions

help to simplify model calibration, but may not hold in all natural circumstances. The first SDM assumption is based on the hypothesis that drivers of species distributions operate at different spatial scales and at different magnitudes. As a consequence, and according to the first assumption for large-scale species distributions, only macroclimate plays a key role in shaping species distributions, while small-scale processes like biotic interactions may only exert a minor influence on the range of a species (Pearson & Dawson, 2003). This first assumption is contradicted by the ecological niche concept which hypothesizes that, even though the fundamental niche of a species is determined by abiotic factors, the realized niche is determined by the area where species can be observed in nature as a result of biotic interactions, independent of the scale (Hutchinson, 1957). Moreover, according to the stress-gradient hypothesis, we would expect stronger competitive replacement under abiotically favourable conditions than under physiologically stressful conditions (Connell, 1961; MacArthur, 1972; Bertness & Callaway, 1994). The second assumption that species are in pseudo-equilibrium with their environment is based on the expectation that current species ranges are more or less in equilibrium with current climate after having been instable in the late glacial and early Holocene period. However, this assumption may be flawed by the finding that species are absent from many suitable areas as modelled by SDMs (Svenning & Skov, 2007). Even more extreme examples include observations that several species begin to spread rapidly in areas where they have been anthropogenically introduced (Welk, 2004). Thus, the critical question is not whether or not current large-scale species distributions are in disequilibrium with current climate conditions, but rather how much they are in disequilibrium. The extent of disequilibrium may be dependent on the magnitude of historical incidents, recent climatic variability, species traits, the spatial configuration of suitable habitats and populations, source-sink populations or species management (Pulliam, 1988; Turner, 1989; Svenning *et al.*, 2004). The third assumption is built on several sub-hypotheses, i.e. that neither the fundamental niche nor the realised niche of a species varies in time or space, and does not change during ontogeny (Davis *et al.*, 1998). These hypotheses of niche-stasis are used as a justification for projecting SDMs to different locations or future climates (Pearman *et al.*, 2008). However, from an evolutionary biology perspective, we hypothesize that natural selection may change the genetically determined environmental tolerances of a species during range expansion (Ackerly, 2003). In addition, current results from the field of invasion biology suggest that, similar to exotic species that become highly invasive after experiencing a release from natural enemies in new environments (Broennimann *et al.*, 2007), the realized niche of native species might also change in time and space. Further, from a population biology point of view, we assume that juveniles are more vulnerable to adverse abiotic and biotic conditions than adults (Bazzaz, 1996): thus, one should address the niche of all ontogenetic stages instead of the adult niche alone in order to predict potential areas during climate change where only adults may survive and areas where regeneration may also be possible.

In the following sections, I will explain in more detail the ecological concepts and the first two SDM assumptions, followed by a discussion on the current research gaps. The main research questions that I derived from this discussion will then be described in the following chapters and discussed further in the synthesis. Due to reasons of focus, I decided not to tackle the third assumption of niche stability, resulting in the omission of a more detailed discussion of this hypothesis. Questions concerning the first two assumptions, however, have directly guided my thesis structure.

## *1.1 Issue 1: Which drivers are important for large-scale species distributions?*

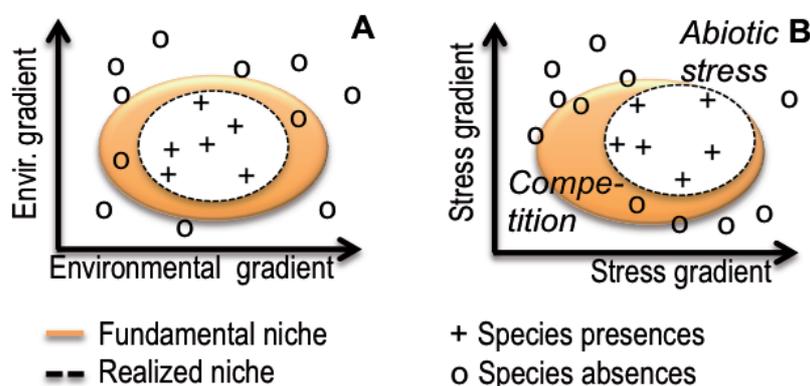
### 1.1.1 Ecological concepts

The geographic distribution of species is dependent on a number of external abiotic and biotic drivers, such as climate, topography, soil, disturbance, resource availability, competition, facilitation, and species management. The effect of these drivers strongly depends on the population dynamics of a species (i.e. regeneration, growth and mortality rates), their physiological tolerances, and their competitive and dispersal abilities (Begon *et al.*, 2006).

The ecological niche concept attempts to group together all of the factors that determine species distributions. Due to the variety of definitions attached to this concept, its usefulness was repeatedly challenged. Grinnell (1917) first coined the term niche, defining it primarily as a geographical and structural location. Elton (1924) tried to link niches with the functional role of a species in their environment, while Gause (1934) focused on describing the niche based on the competitive exclusion of species. Ellenberg (1953) carried out experiments with three competing species to determine the ‘ecological optimum’ (i.e. the space that a species actually fills in the presence of competition) and the ‘potential physiological domain’ of a species (i.e. the space that a species could fill without competitors). Hutchinson (1957) was the first in the English literature to define the concept of fundamental and realized niches (Fig. 1a) in a similar way to Ellenberg (1953). According to Hutchinson’s conceptual framework, the fundamental niche is determined by the abiotic physiological limitations of a species (i.e. the potential physiological domain *sensu* Ellenberg), and is approximated by the multidimensional environmental space of a species. The realized niche is the fraction within the fundamental niche that is actually occupied (i.e. the ecological optimum *sensu* Ellenberg). The discrepancy between the fundamental and the realized niche is primarily caused by biotic factors (i.e. most often competition). Leibold (1995) focused on the distinction between environmental requirements and environmental impacts of species. Pulliam (2000) and Chase and Leibold (2003) further discussed the relation of source-sink dynamics and the niche concept. In order

to avoid confusion between these various definitions, I refer to the ecological niche of a species according to Hutchinson's concept of the fundamental and realized niche, which states that even though the fundamental niche of a species is determined by abiotic factors, the realized niche, which is further determined by biotic factors and other small-scale processes, determines the area where species can be observed in nature.

Other ecological concepts have established relationships between the rather distinct niche aspects defined by Hutchinson (1957). According to the stress gradient hypothesis, it is expected that the strength and direction of species interactions vary along gradients of physiological stress (Connell, 1961; MacArthur, 1972; Bertness & Callaway, 1994). Facilitative interactions between species are assumed to be stronger under conditions of high physical stress or in communities with high consumer pressure, while competitive interactions are assumed to be stronger under abiotically more favourable conditions (Bertness & Callaway, 1994) (Fig. 1b). Plants are physiologically stressed under extreme conditions at the ends of temperature and moisture gradients (i.e. the two climatic gradients that strongly influence plant physiology) (M.P. Austin, 1990). In Europe, however, most plants are found to have primarily evolved within very warm and wet climates and are therefore rarely stressed under conditions towards the upper ends of the two gradients (i.e. in hot and wet conditions) (Wiens & Donoghue, 2004). Thus, we expect that cold and dry temperatures directly constrain the distribution of plant species in Europe (i.e. physiological limitations from frost effects and drought stress resulting in reproductive failure, growth reduction and killing of individuals), while under warm and wet conditions, competitive interactions between species are stronger and, hence, may constrain the distribution range of a species.



**Figure 1.** Conceptualization of (A) Hutchinson's niche model (1957) which is often used to demonstrate the relationship between a species' environmental constraints and its distribution. The concept differentiates between the fundamental niche (i.e. physiological tolerances of a species) and the realized niche (i.e. the fraction within the fundamental niche that is actually occupied due to competition); (B) The stress-gradient hypothesis which expects that the differences between the realized niche and the fundamental niche are greater under abiotically favourable conditions when competition is increased, than under conditions of physiological stress which directly limits species distributions.

### 1.1.2 SDM assumptions

SDMs assume that the drivers of species distributions operate at different spatial scales and at different magnitudes. At the continental scale, gradual trends in macroclimate are hypothesized to be among the key factors shaping species' distributions, while at regional scales topography and climatic extremes likely play a more important role. At local scales, biotic interactions, soil, or land-use may be among the most important drivers of species distributions (e.g. Woodward, 1987; Prentice *et al.*, 1992; Pearson & Dawson, 2003). Accordingly, for large-scale species distributions, only macroclimate has been assumed to play a key role, while small-scale processes, such as biotic interactions, have been assumed to exert only minor influences (Midgley *et al.*, 2002; Pearson & Dawson, 2003), which are unpredictable and idiosyncratic (Lewis, 2006). Furthermore, because observational data from nature will, by definition, describe the realized niche *sensu* Hutchinson (1957), it is often claimed that if a model is developed from observational data, interspecific interactions and other small scale processes, such as climatic extremes or land-use effects and the interaction between them, are sufficiently included in the model, especially given their relatively minor importance (Davis *et al.*, 1998). Thus, ignoring small-scale processes when projecting SDMs to different locations or to other points in time is assumed to have an insignificant effect on the predictions. In fact, few studies in which species distributions are predicted over large areas or future

climates explicitly include interspecific interactions and other small-scale processes (Thuiller *et al.*, 2004; Guisan & Thuiller, 2005; Heikkinen *et al.*, 2007). As a result, when assuming that species may track climate change without time lags, range shifts of up to 100 km per century are expected from SDM projections during climate change (Prentice *et al.*, 1992).

### 1.1.3 Research gaps

Analogous to the high level of invasiveness experienced by exotic species after being released from natural enemies in their introduced environments (Stohlgren & Schnase, 2006), the abundance of native species may also strongly depend on the importance of biotic interactions. The scale at which biotic interactions become important determinants of species distributions, and the variability in the importance of these biotic interactions for large-scale species distributions, is, however, unclear. On the one hand, ecological concepts attempt to structure the vast number of drivers of species distributions by grouping them into abiotic and biotic factors and by referring to the potential relationships between these two groups. They address the ecological rather than the geographical space and are thus formulated independent of spatial scale. Consequently, it is unclear if these concepts are also applicable to large-scale species distributions. SDMs, on the other hand, assume that biotic interactions are only relevant for small-scale distributions. However, the assumptions of ecological concepts and SDMs lack a thorough evaluation with empirical data.

If biotic interactions are identified to be important for large-scale distributions, and if they are shown to vary along stress-gradients, it may be insufficient to only include them implicitly into SDMs by using observational data that is already shaped by biotic interactions. One should instead include them explicitly by incorporating certain biotic predictors. Not only could this have an effect on the projections of current distributions, but the projections of distributions for future climates may be particularly influenced, especially if plant communities change due to the different velocities experienced by different species in tracking suitable climates, or when species are anthropogenically introduced into a new area (Davis *et al.*, 1998). Moreover, the degree to which climate acts as a key range-limiting factor compared to biotic processes may determine the extent to which species retract from their southern range margins and expand northwards as the climate warms.

Thus, it is important to evaluate (1) how important biotic and abiotic predictors are for large-scale range patterns, (2) how strongly the importance of biotic interactions varies along environmental gradients, and (3) how this variation affects current and future projections of large-scale species distributions. Additionally, it may be important to not only regard the mean adverse climate as a range determinant, but particularly the climatic extremes that may directly limit species distributions. Further, to better understand the effect of species interactions on species ranges, one may investigate if the importance of biotic interactions varies among species groups: biotic interactions may be less

important for species with a high competitive ability, compared to competitively subordinate species that are more often excluded (Guisan *et al.*, 2007b).

## *1.2 Issue 2: How strongly are species impeded in attaining equilibrium with their environment?*

### 1.2.1 Ecological concepts

A second key question affecting SDMs is to what degree species are or are not in equilibrium with their environment. If species are not in equilibrium, they may be in a time-lagged or in a space-lagged disequilibrium with their environment (M. P. Austin, 2002; Svenning & Skov, 2004; Araújo & Pearson, 2005). In the following paragraphs, I will discuss these two issues and provide relevant examples.

Time-lagged disequilibria may represent legacies from historical incidents or shifts in suitable habitats, often due to dispersal limitations. The importance of dispersal limitation for a species' distribution becomes apparent when looking at species that are introduced by humans into areas that they never would have reached by natural dispersal alone, but from where they then start to spread rapidly (Welk, 2004). Dispersal limitations that impede such (re-)filling of (temporally) non-colonized and suitable habitats may depend on the magnitude of the historical incident, species traits, abiotic and biotic habitat constraints, or the spatial configuration of suitable habitats and populations. The magnitude of a historical incident causing disequilibria is defined by the degree and frequency of the disturbance (Delcourt & Delcourt, 1988), since spatially and temporally small-scale disturbances (e.g. fire) and spatially and temporally large-scale disturbances (e.g. climate change) may generate different legacies. Severe historical incidents, coupled with migration limitations, might be responsible for the currently debated range filling limitations of European plants (Svenning & Skov, 2004; Svenning *et al.*, 2008). Species traits, such as dispersal agents (e.g. wind, water, animals, humans, or none at all) or traits that help to differentiate between early- and mid- to late-successional species, may also determine the degree of migration limitation and, hence, the degree to which species distributions are in disequilibrium with their environment (Buckley, 2008). For instance, early-successional species show longer seed dispersal distances than mid- to late- successional species. Yet, the competitive ability of early successional species is lower. According to the stress-gradient hypothesis, biotic constraints vary as a function of environmental gradients (Bertness & Callaway, 1994) and thus, depending on the degree of species' interactions and on the abiotic severity of the habitats through which species migrate, species may be more or less constrained in tracking the fluctuations in environmental conditions according to the traits that they have. The spatial

configuration of suitable habitats and populations may also impede species from tracking a changing climate. According to the percolation theory (Turner, 1989; Stauffer & Aharony, 1994), patches of different sizes, shape and connectivity may impede plant migration through the landscape with different intensities until a percolation value (i.e. percolation threshold) is undershot and species are no longer able to migrate. Further, the spatial arrangement of populations may also influence the spread of a species: core populations may be the principal sources of propagules (Hulme, 2003) and, hence, contribute much to long distance dispersal, while small outlying populations have a large edge to area ratio and, thus, may contribute more to the expansion within habitats (Moody & Mack, 1988; Taylor & Hastings, 2004).

Space-lagged disequilibria may arise from population dynamics. Sink populations of plants, defined as populations occupying habitats where the reproductive rate is less than the mortality rate, can only persist if enough seeds from more productive nearby source populations (where the reproductive success is greater than mortality) reach the site. If there is no source population within dispersal distance, sink populations will go extinct (Pulliam, 1988). Thus, for a species that occupies a sink habitat outside of its fundamental niche, the realised niche will seem larger than the fundamental niche. Likewise, anthropogenic species management may generate source and sink populations. Artificial plantations, for example, can act as source populations, while species removal at certain sites (e.g. because of the targeted eradication of alien invasive species) may act as sink populations.

### 1.2.2 SDM assumptions

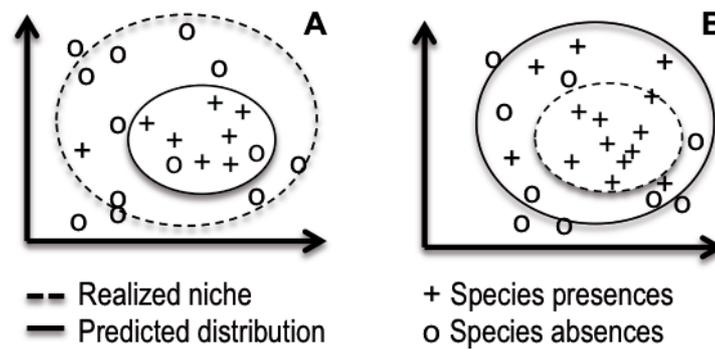
When applying SDMs, one implicitly assumes that species are in pseudo-equilibrium with the current environment (Guisan & Theurillat, 2000), and, in doing so, assumes time-lagged and space-lagged disequilibria effects to be unimportant for understanding and calibrating the ecological niche of a species. On the one hand, it is often argued that species generally had enough time to adjust their ranges to a relatively stable climate in the second half of the Holocene. Even if species are highly dispersal limited, they are assumed to be in equilibrium with the current environment because they had enough time to adapt to the environment (Peterson *et al.*, 1999; Ackerly, 2003; Losos *et al.*, 2003).

### 1.2.3 Research gaps

While the perception is that species are, in general, in (a possibly dynamic) equilibrium with their environment, it is still unclear to what degree species are in time-lagged and/or space-lagged disequilibria, at least for certain parts of their range. Ignoring potential disequilibria when applying SDMs may result in omission errors when species that have not yet colonized all suitable locations are included (Fig. 2a), and commission errors by including species with sink populations into the models, where a species may not be able to maintain sustainable populations over the longer term (Fig. 2b).

On the one hand, migration limitations may cause current species range limits to be in time-lagged disequilibria with the current environment and, thus, potentially suitable habitats may be underestimated if not all possible combinations of suitable environments for a species are included. Moreover, in addition to causing time-lagged disequilibria with the current environment, migration limitation may also cause time-lagged responses when colonising suitable habitats during on-going and future climate change. This may flaw scientific evaluations, lead to the overestimation of species' potential to track climate change, and could thus hamper species management decisions. On the other hand, because statistical models always describe an amalgam of the realised niche and sink areas (M. P. Austin, 2002), misinterpretation of the environmental envelope may occur if observations gathered from sink populations are used to model distribution without accounting for the ecological neighbourhood, i.e. the region within which an organism is active or has some influence during a certain time period (Addicott *et al.*, 1987).

Migration limitation is, to date, one of the most prominent uncertainties in predicting future species distributions. In order to make more reliable scientific and management decisions, a better understanding of the effect of migration limitations on species ranges is needed. This is primarily true for non-commercial species, which may not profit easily from assisted migration due to commercial reasoning. To explore such migration limitations for current and future species distributions at large scales, SDMs would profit from being coupled with mechanistic species dynamics models. Gained knowledge on the dynamic range shifts of a species may not only improve range shift projections during climate change, but may also invoke improvements in species management. For one thing, areas for ecologically and economically important species can be defined, where migration is very limited and species need to be artificially transplanted. In addition, the achieved knowledge may also help to improve the containment of the spread of invasive species by artificially introducing migration limitations.



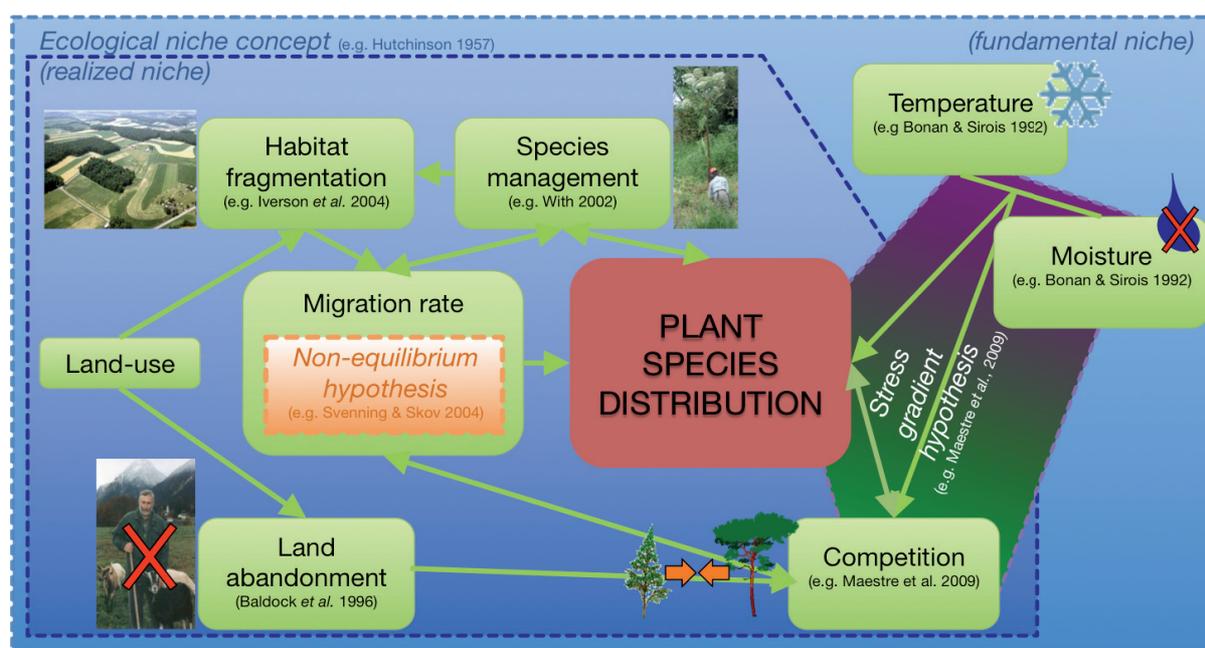
**Figure 2.** Processes that keep species from being in equilibrium with their environment and that may lead to a mismatch between the actual and the predicted distribution: (A) time-lagged disequilibria due to dispersal limitations like historical disturbance effects may lead to under-predictions of the realized niche and also to over-predictions of potentially reachable sites, (B) space-lagged disequilibria as a result of population dynamics (i.e. source-sink populations) may lead to over-predictions. This figure is partly adapted from Pulliam (2000).

### 1.3 Summary of research gaps

Despite the fact that knowledge is accumulating due to a large increase in the number of publications on individual aspects of drivers of species distributions, we still lack a broader understanding of the most important range shaping processes and the way in which they interact on large spatial scales (Gaston, 2009) and as an effect of constantly varying environments. Currently, it is still unclear how much abiotic and biotic variables contribute to large-scale species distributions, whether the importance of biotic interactions is linked to macroclimatic gradients and could thus vary in space, and how strongly migration limitations prevent species from attaining equilibrium with their environment (Table 1).

Emphasizing single constraints of species distributions does not assign a strong role for ecosystem processes in understanding nature (Naeem, 2002). Therefore, it is not only important to estimate the effects resulting from individual processes, but to also focus on the interlinked effects of several processes. For example, the degree to which species are migration limited, and thus in disequilibrium with the environment, may not only depend on individual processes impeding range adaptation, but also on the interlinked effects of climate, species interactions, landscape fragmentation, land abandonment and species management (Scheller & Mladenoff, 2008). Land-use change may lead to land abandonment, where tree species are expected to experience low interspecific-interactions in the initial phase on abandoned patches. Thus, conditions for tree migration would initially be favourable. However, if the abandoned patch is located in a highly fragmented landscape, then species migration may not be feasible across the landscape. Knowledge

on such interrelated processes would be necessary to better plan the assisted migration of economically and ecologically important species that are not able to reach suitable habitats unassisted and also to improve strategies aimed at controlling the spread of invasive species. So far, it is common to prioritize the clearing of areas that are or are becoming environmentally suitable under climate change (Richardson *et al.*, 2010). However, because not all suitable habitats may be colonisable, and not all areas may contribute equally to spatial spread and population growth within the colonisable habitat, a better knowledge of the interlinked processes involved will allow for more efficient management strategies. In Figure 3, I depict the expected dependencies among processes potentially shaping species distributions and the ecological concepts underlying these expected relationships.



**Figure 3.** Overview of expected dependencies among processes potentially shaping species distributions and ecological concepts underlying these expected relationships.

**Table 1.** Summary of SDM assumptions and contradicting ecological concepts.

| SDM assumptions   | Ecological concepts   | Research gaps  |
|---|---|--|
| <p>-For large-scale species distributions, gradual constraints have a high importance, while biotic interactions, climatic extremes, and land-use are only of high importance for small-scale species distributions (Pearson &amp; Dawson, 2003).</p> | <p>-The ecological niche concept differentiates between the fundamental and the realized niche, whereby the latter determines the area where species can be observed in nature - independent of the scale being addressed (Hutchinson, 1957).<br/>                     -The stress gradient hypothesis states that the strength and direction of species interactions vary along abiotic gradients of physiological stress (Berthess &amp; Callaway, 1994), and, thus, biotic interactions may also shape ranges and may act on multiple scales.</p>  | <p>-It is unclear how much abiotic and biotic variables contribute to large-scale species distributions.<br/>                     -It is unclear if the importance of biotic interactions is linked to macroclimatic gradients and thus may vary in space.</p> |
| <p><b>Issue 1: Which drivers are important for large-scale species distributions?</b></p>   |   |  |
| <p>-Species are in pseudo-equilibrium with their current environment (Guisan &amp; Theurillat, 2000).</p>   | <p>-The magnitude of historical incidents causing disequilibria is influenced by the degree and frequency of disturbances (Delcourt &amp; Delcourt, 1988).<br/>                     -Species traits may determine the degree of migration limitation and, hence, the degree to which species distributions are in disequilibrium with their environment (Buckley, 2008).<br/>                     -Spatial configuration of suitable habitats and populations may impede species from tracking changing climates (Moody &amp; Mack, 1988; Turner, 1989; Stauffer &amp; Aharony, 1994; Hulme, 2003; Taylor &amp; Hastings, 2004).<br/>                     -According to the stress-gradient hypothesis (Berthess &amp; Callaway, 1994), species migration may be limited to various extents either by biotic or by abiotic processes.<br/>                     -Populations may be either source populations, where the reproductive success is larger than mortality, or sink populations, where the reproductive success is smaller than mortality and the populations can be sustained only if individuals from source populations immigrate (i.e. space-lagged disequilibrium) (Pulliam, 2000).</p> | <p>-It is unclear how strong migration limitations prevent species from attaining equilibrium with their environment.</p>  |
| <p><b>Issue 2: How strongly are species in equilibrium with their environment?</b></p>  |   |  |
| <p>-Species management may remove species from suitable habitats.</p>   |   |  |

## *1.4 Overview of research questions*

Predictions of species distributions are based on several concepts and assumptions and must deal with a wide range of limitations. While these limitations are widely acknowledged, they may compromise the use of such models for developing reliable adaptation and mitigation strategies for species with ecological, conservation or economic importance. Among the most widely used models, few explicitly deal with species' interactions, land-use effects, climatic extremes, migration rates and the interaction between these processes, even though species ranges are expected to be strongly impacted by these factors according to several ecological concepts. Consequently, it is important to investigate how the most commonly used main climate factors shape current large-scale species distributions when combined with other factors (e.g. climatic extremes, biotic interactions, migration limitations, etc.). It is further important to assess if the relative importance of these major factors changes during global change, how alterations of these factors effect responses of large-scale species distributions to global change, and which traits explain whether species can track shifting suitable habitats, whether they can adapt rapidly, or whether they go extinct. Such investigations will allow us to better understand which of these major factors should be managed. For instance, the growth and survival of endangered species may be enhanced if one removes the strongest competitors that would outcompete them in climatically suitable habitats. Also, impacts from migration limitations may be mitigated if migration limited species are planted ahead of the slow moving, leading edge in habitats that become newly suitable under a changing climate. As a final example, the spatial spread of invasive alien species may be more efficiently contained if those populations that contribute the most to migration and population growth are treated.

In my PhD thesis, I evaluated the consequences of spatiotemporal variation for two key SDM assumptions when predicting large-scale distributions of plant species. The aim of my thesis was to attempt to refine SDMs in order to better incorporate important processes that are traditionally neglected. Ultimately, my goal was to apply improved models to develop optimal strategies for species management. Specifically, I attempted to answer the following four research questions:

- |             |   |
|-------------|---|
| Question 1) | How do abiotic and biotic variables contribute to shaping spatial patterns?<br><i>[Paper 1]</i>   |
| Question 2) | How do biotic interactions vary along macroclimatic gradients and how does this affect species ranges?<br><i>[Paper 2 &amp; Appendix Paper]</i> |
| Question 3) | How strongly do migration limitations prevent species from tracking suitable habitats during climate and land-use change?<br><i>[Paper 3]</i>   |
| Question 4) | How can population management prevent invasive species from spreading across the landscape?<br><i>[Paper 4]</i>                                 |

To answer these questions, I employed and adapted SDMs, dynamic vegetation models and hybrids between the two, and investigated the questions on different spatial scales (i.e. Europe, Switzerland and Swiss lowlands) and different species groups (i.e. European trees and alien invasive herbs). The choice of combining model approaches depended on the objectives. A better understanding of the distribution of the two selected species groups is of high importance. Trees in European forests deserve particularly intense study because of their unique management strategies and the susceptibility of tree species to climate change. Outside of Europe, forests are divided into sections for intensive wood production and sections for nature conservation and recreation. In Central Europe, however, forests often fulfil these multiple functions at one and the same site (Pretzsch *et al.*, 2008). In light of global change, there is an urgent need for systems knowledge and innovative planning methods, especially since the life-cycle of trees is very slow indicating that tree species may not be able to track climate change without assistance. Alien invasive herbs, on the other hand, which are, by definition, reproducing and spreading at very high rates, are amongst the largest threats for loss of biodiversity, next to habitat loss and degradation. To limit the invasion of alien species most effectively, i.e. at an early stage before the costs and efforts are too high, management strategies have to be optimized to fit the particular problem. Assessing the effect of various management strategies through experimentation is, however, prohibitively complex, both in terms of time and logistics. Therefore, models may provide suitable tools to gain rapid insight into optimizing management strategies. More details on data, study area and methods to answer the four research questions are given below.

## Question 1: How do abiotic and biotic variables contribute to shaping spatial patterns?

The relative importance of abiotic and biotic range determinants remains unclear and whether or not SDMs can help distinguish between environmental/physiological constraints that make up the fundamental niche and the biotic interactions that constrain species to occur within their realized niches is unresolved. In *Paper 1*, I approached these problems by examining the extent to which abiotic and biotic variables jointly and independently explain large-scale distributions of species belonging to different characteristic groups. More specifically, for 11 common tree species in Switzerland, I included, in addition to standard abiotic predictors, different types of biotic predictors into SDMs (i.e. generalized linear models, GLMs). Using a variation partitioning technique, I then estimated the proportion of variance explained by the abiotic and biotic predictors, jointly and independently, for each species individually and for species aggregated according to their traits. This allowed me to assess to what degree these two major predictor sets combine to shape species ranges. As species data, I used the National Forest Inventory of Switzerland (NFI1, 1983-1983, c. 10'500 plots; and NFI2, 1993-1995, c. 6500 plots), from which I also derived different types of response variables and biotic predictor variables. As response variables, I used presence-absence data (i.e. most frequently used response variable type in studies that model species distributions), and the proportional basal area of a target species compared to the total basal area recorded on the sample plot (i.e. a measure of competition in the stand). As biotic predictor variables, I used the NFI database to estimate the relative abundance of common species, the relative abundance of common species that are taller than the median height of the target species in a stand, and the total shading by all tall individuals. For trait analyses, I grouped the target species according to their response to disturbance and stress, seed dispersal distance, shade tolerance, or frequency and dominance in the landscape. As environmental data, I used degree-days, summer frost frequency, moisture index from March to August, precipitation days, potential yearly global radiation, topographic position and slope.

## Question 2: How do biotic interactions vary along macroclimatic gradients and how does this affect species ranges?

From the stress-gradient hypothesis, we expect that cold and dry temperatures directly constrain the distribution of plant species in Europe, while competitive interactions between species may become stronger under warm and wet conditions, and may hence constrain their range. However, an empirical quantification of the strength of interspecific competition along large-scale climatic gradients is still largely missing.

In *Paper 2*, I tested the climatic conditions under which biotic interactions are strongest and how the variation in the strength of biotic interactions along climatic gradients influences the projections of current and future large-scale species distributions. Specifically, I analysed the correlations between the relative abundance of European beech (*Fagus sylvatica*) and three major competitor species (*Picea abies*, *Pinus sylvestris* and *Quercus robur*) in environmental space, and then projected them to geographic space. I then evaluated where and how much the predicted beech distribution varies under current and future climates (A1fi and B2 climate scenarios for the years 2040, 2070 and 2100) if potential competitor species are included or excluded in the SDMs (i.e. generalized additive models, GAMs). I further evaluated if these areas coincide with current species co-occurrence patterns. Using the species data from the large-scale transnational survey of forest condition in Europe under the International Co-operative Programme on Assessment and Monitoring of Air Pollution Effects on Forests (ICP Forests Level 1, c. 6000 plots), I derived the relative abundance of each species per plot. As environmental data, I used degree-days, summer precipitation, soil texture, cation-exchange capacity of the topsoil, slope and topographic position.

Additionally, in the *Appendix Paper*, we tested the importance of climatic extremes as determinants of large-scale species distributions. From the stress-gradient hypothesis, it is expected that species ranges are directly constrained by physiological tolerances under unfavourable climatic conditions, while they are constrained by competition under favourable conditions. Therefore, we expected that when climatic extremes are included into SDMs for large-scale species distributions in addition to mean climate, which is standard, the description of the physiological tolerances of a species under adverse climate would be improved. This would be especially important to better predict changes at range edges of species that are physiologically constrained, i.e. diebacks (trailing edges) by increased drought and range expansions (trailing edge) by disappearing frost. To do so, we used SDMs (i.e. GAMs) to test whether climatic variability, in addition to climatic means, helps to explain patterns of tree species in Switzerland. As species data, we used the available data for 11 common species from the NFI database, as in *Paper 1*. As mean climate variables, we used mean winter temperature, mean summer moisture index, slope and topographic position. We expressed climatic variability as the year-to-year variability of winter temperature and summer moisture index.

### **Question 3: How strongly do migration limitations prevent species from tracking suitable habitats during climate and land-use change?**

Dispersal limitation is one of the main sources of uncertainty when predicting species distributions under changing climates. For this reason, in *Paper 3* I investigated how abiotic, biotic and contextual landscape conditions affect the migration rates of tree species in Europe. Finally, I compared early-

vs. mid- to late-successional tree species in order to reveal how these two groups differ in projected range shifts. Therefore, I distinguished three modes of migration, namely: (1) migration is assumed to be unlimited (species are assumed to track climate change immediately), (2) there is no migration (species only lose habitats that become unsuitable), and (3) species respond with realistic migration rates, for which I implemented a new migration module. The first two modes of migration were represented by standard implementations in SDMs; however, transient migration information is usually not used. In order to use realistic migration rates, I developed an approach that first derives migration rates for all possible current and future environmental conditions (i.e. competition, climate, soil, and habitat configuration) in a multi-factorial experiment using a dynamic population model (TreeMig). I then fit a statistical model from these experiments in order to explain the dependencies of migration rates on abiotic, biotic and contextual conditions. This resulted in a migration cost surface over the whole European continent that was implemented in SDM projections (here, GLMs). This allowed me to constrain species distributions predicted by SDMs and update for the changed conditions in ten-year time steps using realistic migration rates. I applied this approach to 14 common tree species in Europe. Species abundance data was acquired from the ICP Forest, Level I database. As environmental data, I used current and future land-use data (GRAS and SEDGE scenario until 2100 originating from the ALARM and downscaled in the ECOCHANGE EU-projects), current and future inter-decadal means and standard deviations of minimum winter temperature, degree-days, summer precipitation and drought stress index (A1fi and B1 scenarios until 2100), current water-holding capacity of the soil and soil texture, and slope and topographic position.

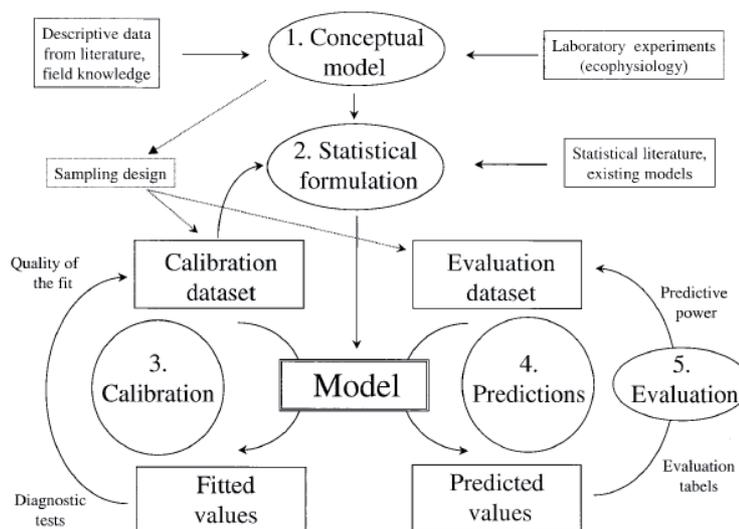
#### **Question 4: How can population management prevent invasive species from spreading across the landscape?**

Biological invasion affects ecosystem goods and services and causes considerable economic costs when the invaded areas have to be cleared. Therefore, efficient management strategies have to be developed in order to keep aggressively invasive species from spreading to economically and ecologically valuable habitats. Most current approaches address the problem at the local scale rather than at the landscape scale, despite the fact that changing population- or habitat-configurations at the level of the landscape may help to increase migration limitations thereby increasing the efficiency of management methods. In *Paper 4*, I assessed the degree to which space matters for constraining the spread and population growth of three hydrochorous invasive plant species, each with differing traits, by applying a set of management methods according to different spatial patterns. These methods differ in their local intensity, the area treated and in the frequency that they are applied. More specifically, I parameterized and adapted a spatial explicit hybrid model (CATS; simulates population demographics and dispersion among suitable habitats derived from SDMs that have been fitted to the three target species individually) in order to simulate the potential dispersal and population dynamics

of the three species (i.e. *Heracleum mantegazzianum*, *Impatiens glandulifera* and *Reynoutria japonica*) in the Canton of Zurich (i.e. north-eastern lowlands of Switzerland). I run the simulation experiments over a period of 15 years, incorporating the effect of population dynamics and initial spatial setting on spatial spread and population growth when the different control methods are applied in various spatial management schemes. Species characteristics used to parameterize the dynamic model were taken from literature. In order to set the initial conditions for the simulations and to model the potential equilibrium distribution of the three invasive species with SDMs (i.e. GLMs with spatial autocorrelation correction), I used the species data obtained from the Neophytenkataster of the Canton Zurich, which contains c. 2000 occurrences per investigated species. Environmental data used for the SDMs included degree-days, topographic position, potential yearly global radiation, aspect value, soil coarse fragment content, and land use, as well as the distances to a range of land use/cover classes, including buildings, forest edges, small and large roads, bridges, railroads, lakes, creeks and rivers, construction sites and gravel pits.

### Box 1: Empirical species distribution models

**How they work:** Empirical species distribution models (SDMs), also called niche-based species distribution models, predictive habitat distribution models (PHDM), ecological niche models (ENM) or habitat models, are spatially explicit statistical models that relate presence or abundance of species to environmental predictors in order to predict the dependency of presence or abundance on these predictors and to map suitable habitats of



*Overview of the successive steps of a general SDM-building process. [Figure from Guisan and Zimmermann 2000]*

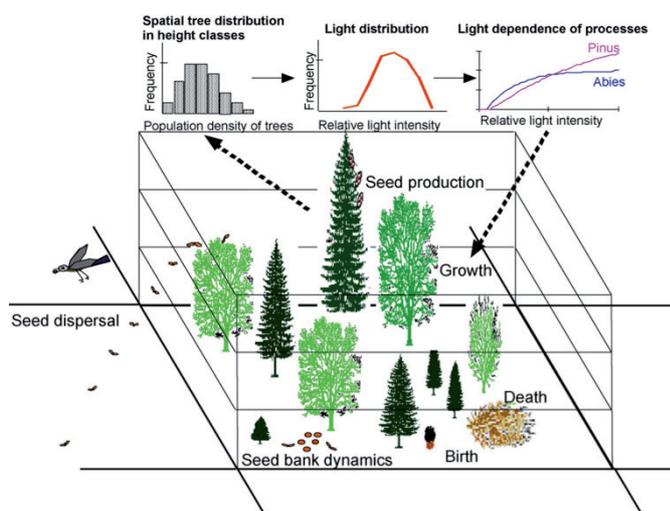
species through time. They are – as a general rule – regression type models employing explanatory variables that explain the outcome of more complex physiological and population dynamic processes. Statistical approaches include multiple regressions (e.g. generalized linear model, GLM; generalized additive model, GAM; multivariate adaptive regression splines, MARS; maximum entropy models, MAXENT), classification techniques (e.g. classification and regression trees, CART; random forests, randomForest; boosted regression trees, BRT), ordination techniques (e.g. canonical correspondence analysis, CCA), neural networks (e.g. artificial neural networks, ANN) and Bayesian approaches (Guisan & Zimmermann, 2000; Segurado & Araújo, 2004; Guisan & Thuiller, 2005; Elith *et al.*, 2006; Heikkinen *et al.*, 2006; M. P. Austin, 2007). An overview of the successive steps of conceptual model formulation to model evaluation when applying standard SDMs is given in the accompanying figure.

**Potential, limitations and assumptions:** For conservation management and planning it is critical to understand which habitats are most suitable for a particular species. To advise conservation managers for the design and evaluation of reserve networks, suitable habitats are often portrayed as map products. SDMs are an ideal approach to generate such suitability maps rapidly, and also have utility when forecasting the likely impact of global change on future species distributions (Guisan & Thuiller, 2005). Furthermore, SDMs are useful tools for exploring various questions in ecology, evolution and conservation. For instance, SDMs have been used to assess the impact of climate change on species distributions (Midgley *et al.*, 2003; Pearson & Dawson, 2003; Thuiller, 2004), to assess global species extinction risks (Thomas *et al.*, 2004), to predict invasion patterns (Peterson, 2003; Thuiller *et al.*, 2005), to study relationships between environmental parameters and species richness (MacNally & Fleishman, 2004), to reconstruct current and future patterns of communities from individual species

projections and assembly rules (Guisan & Thuiller, 2005), to predict the distribution of rare and endangered species (Engler *et al.*, 2004; Bomhard *et al.*, 2005), or to improve the sampling of rare species (Edwards *et al.*, 2005; Guisan *et al.*, 2006). Furthermore, SDMs have been applied at different spatial (Thuiller *et al.*, 2003) and temporal scales (Thuiller, 2004). Large efforts were made to test and improve most steps in the SDM-building process; i.e. a vast number of studies were dedicated to the statistical model formulation and model calibration (e.g. effect of grain size, extent and number of observations, generation of pseudo-absences for presence only data, comparisons of statistical models, spatial autocorrelation) and model evaluation (internal cross-validation vs. external validation; evaluation measures such as Kappa, AUC or TSS). However, projections from current SDMs still have partly unexplored limitations, as SDMs are based on several assumptions that may not hold in all found instances and often lack estimates for associated model uncertainties (M. P. Austin, 2002; Hirzel & Guisan, 2002; Thuiller, 2004; Guisan & Thuiller, 2005; Heikkinen *et al.*, 2006).

## Box 2: Mechanistic species dynamics models

**How they work:** Mechanistic models of species and ecosystem dynamics, including dynamic vegetation models or dynamic population models, typically use a bottom-up approach. By this, they describe processes that are based on causes and effects responsible for vegetation and population dynamics. Dynamic vegetation models, such as dynamic global vegetation models (DGVMs), are process-based models that simulate fluxes and pools of water, carbon or nutrients from biogeochemical and physiological processes for several functional types or biomes that either compete against each other or are prescribed (Prentice *et al.*,



*Concept of the multispecies population dynamic model 'TreeMig'. On each patch or cell, the stand dynamics are simulated (i.e. functional relationships formulating the processes of tree establishment, growth, and mortality) and seeds are redistributed among cells. [Figure from Lischke *et al.* 2006]*

1992; Thornton *et al.*, 2002; Sitch *et al.*, 2003). Dynamic population models, such as forest gap models, simulate the establishment, growth and mortality of individual trees as a function of abiotic and biotic factors. Mortality of large, dominating trees produces gaps in forests, which lead to a release of suppressed trees and increased mineralization and tree recruitment rates (Shugart, 1984; Humphries *et al.*, 1996; Budy *et al.*, 2008). Some of these forest gap models include, in addition to the density-dependent population processes such as growth, mortality or competition for light, seed dispersal kernels describing the spatial distribution of seeds from a parent plant (e.g. Lischke *et al.*, 2006).

**Potential, limitations and assumptions:** Field experiments are limited to rather short time periods and small extents. If temporal dimensions are long or spatial extents are large, mechanistic species dynamics models become useful tools as an alternative to conducting costly long-term landscape scale experiments (Mladenoff, 2004) used for ecosystem management. In forestry, for instance, dynamic vegetation models are used to predict forest productivity and carbon sequestration (Law *et al.*, 2001), which are tightly linked to timber supply (Martin *et al.*, 2005). For the management of sustainable rangeland ecosystems, grazing strategies are developed using dynamic population models (Simioni *et al.*, 2000), since non-adapted grazing strategies would lead to irreversible environmental problems (van Langevelde *et al.*, 2003). Additionally, dynamic population models including

dispersal are used to estimate the effects of global change, i.e. rates at which plants may track changing environmental conditions, or rates at which alien species invade habitats (Gustafson & Gardner, 1996; Schumaker, 1996; Clark *et al.*, 1999). However, there are computational and conceptual trade-offs. Computational trade-offs are related to the spatial resolution at which models are run, and to the maximum landscape extent included in simulations. Conceptual trade-offs are made between knowledge on functional relationships (reality), the applicability of a model to a range of instances (generality), and the degree to which a model incorporates mechanistic detail (precision) (Guisan & Zimmermann, 2000). Assumptions behind mechanistic species dynamics models are rather model-specific, because the models were developed with different objectives and conceptions.

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## 2 Biotic and abiotic variables show little redundancy in explaining tree species distributions [Paper 1]

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### 2.1 Abstract

Abiotic factors such as climate and soil determine the species fundamental niche, which is further constrained by biotic interactions such as interspecific competition. To parameterize this realized niche, species distribution models (SDMs) most often relate species occurrence data to abiotic variables, but few SDM studies include biotic predictors to help explain species distributions. Therefore, most predictions of species distributions under future climates assume implicitly that biotic interactions remain constant or exert only minor influence on large-scale spatial distributions, which is also largely expected for species with high competitive ability. We examined the extent to which variance explained by SDMs can be attributed to abiotic or biotic predictors and how this depends on species traits. We fit generalized linear models for 11 common tree species in Switzerland using three different sets of predictor variables: biotic, abiotic, and the combination of both sets. We used variance partitioning to estimate the proportion of the variance explained by biotic and abiotic predictors, jointly and independently. Inclusion of biotic predictors improved the SDMs substantially. The joint contribution of biotic and abiotic predictors to explained deviance was relatively small (~9%) compared to the contribution of each predictor set individually (~20% each), indicating that the

additional information on the realized niche brought by adding other species as predictors was largely independent of the abiotic (topo-climatic) predictors. The influence of biotic predictors was relatively high for species preferably growing under low disturbance and low abiotic stress, species with long seed dispersal distances, species with high shade tolerance as juveniles and adults, and species that occur frequently and are dominant across the landscape. The influence of biotic variables on SDM performance indicates that community composition and other local biotic factors or abiotic processes not included in the abiotic predictors strongly influence prediction of species distributions. Improved prediction of species' potential distributions in future climates and communities may assist strategies for sustainable forest management.

## *2.2 Introduction*

Effective nature management in the face of anthropogenic climate change challenges ecologists to improve predictions of how species distributions might respond to altered climate. Predictions of these responses are often generated with species distribution models (SDMs, Guisan and Zimmermann 2000, Guisan and Thuiller 2005, Elith et al. 2006). SDMs most often relate presence/absence or abundance of species to abiotic variables such as climatic, topographic or edaphic factors, and are used to assess factors that potentially control species distributions and to predict the distribution of suitable habitat of species. Nonetheless, biotic interactions such as competition, mutualism, amensalism or commensalism also affect species distributions, in addition to the effects of abiotic factors (Connell 1961, Loehle 1998, Soberón 2007). The relative importance of abiotic and biotic range determinants remains unclear. The tendency to omit biotic variables from models when predicting the effects of climate change does not eliminate the potential effects of biotic processes and adds an unknown amount of uncertainty to models used to predict climate change effect. Thus, we need to determine whether inclusion of biotic predictors can reduce uncertainty in models that are used to predict climate change impacts. It remains unresolved whether SDMs can help to distinguish between environmental/physiological constraints that make up the fundamental niche and the biotic interactions that constrain species to occur within their realized niches (Hutchinson 1957). The relative importance of biotic and abiotic influences on species distributions has generated a variety of opinions. Some authors argue that general species distribution patterns are not considerably influenced by biotic interactions (Huntley et al. 1995, Bakkenes et al. 2002) or only at small-scales (Pearson and Dawson 2003, Heikkinen et al. 2007), whereas others have argued for a strong role for biotic interactions, causing standard SDM predictions to be incomplete at best (Davis et al. 1998, Anderson et al. 2002, Araújo and Luoto 2007). Negative biotic interactions are often thought to mainly constrain species distributions at equatorial/lower limits, while positive biotic interactions and abiotic factors are expected being the dominant determinants of poleward/upper range limits

(MacArthur 1972, Brown et al. 1996, Loehle 1998, Vetaas 2002, Normand et al. 2009). Furthermore, biotic interactions might lead to a high degree of indeterminacy in species range responses to changes in the abiotic environment (Davis et al. 1998, Case et al. 2005). Indirect evidence of biotic interactions affecting models for trees at the regional scale are also suggested by early-successional species being more difficult to model than dominant late-successional species, most likely due to the realized niche of the former depending on the degree of range filling of the latter (Guisan et al. 2007, Pearman et al. 2008).

Predictions for any given location or for future and past climates are often based on the implicit assumption that biotic interactions remain constant, or are not important for the focal species (Guisan and Thuiller 2005). However, over large geographic ranges biotic interactions may not be constant, partly because of environment-dependant competitive abilities and partly because of spatial variation in the distribution of interacting species due to different environmentally constraining factors or due to anthropogenic influences. During climate change, biotic interactions may vary further, since species may shift their ranges individually as they migrate at different speeds and/or in differing directions (Davis and Shaw 2001, Suttle et al. 2007).

In this paper we approach the problem of identifying potential effects of biotic interactions on current large-scale distributions by including biotic predictors in SDMs. We address the following questions: 1) are SDM estimates of tree species distributions improved when data on other tree species are explicitly included as biotic predictors alongside abiotic (topographic and climatic) predictors? 2) What is the magnitude of the independent and joint contributions of abiotic and biotic predictors to reducing model variance? 3) Does the importance of biotic predictors for explaining species distributions depend on traits of the focal species, such as their response to disturbance and stress, seed dispersal distance, shade tolerance, or frequency and dominance in the landscape? In our study we examine correlations in species occurrences, which means that we cannot evaluate the direction of influence in interspecific interactions. Additional experiments would be required to disentangle the direction of influence in interspecific interactions. Further, we interpret the importance of biotic predictors on the performance of SDMs as an indication of the relevance of local biotic interactions (i.e. competition, mutualism, amensalism and commensalism) or local abiotic processes not included in the large-scale predictors for determining species distributions.

## 2.3 Material and methods

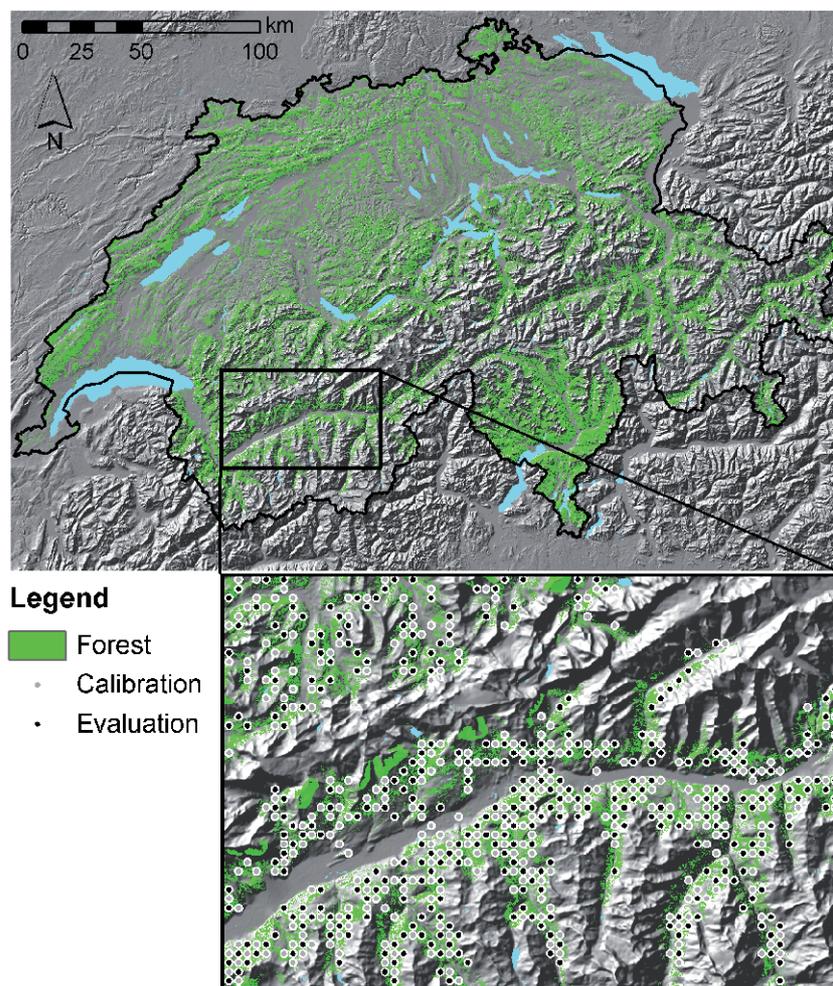
### 2.3.1 Study area

The study area (45°49'N-47°48'N, 5°57'E-10°29'E) in the central Alps encompassed 12340 km<sup>2</sup> of forested area, half of which was located above 1000 m. The climate is moist and mildly maritime north of the Alps, but dry and more continental in the interior valleys. The Alps act as a barrier separating the climates of southern (Mediterranean) and central Europe (Zimmermann and Kienast 1999). Public forest accounted for 68%, the rest being privately owned. Two thirds of the forest are frequently managed, 18% infrequently managed and 14% remain unmanaged (Brassel et al. 1999). Forest management is primarily practiced at low elevations, and selection forestry is the predominant management scheme. Thus, no larger-scale clear-cutting is applied, and natural regeneration is often furthered by management activities. The major change in species composition due to forest management is expected for *Picea abies* at the cost of the otherwise dominant *Fagus sylvatica*. *Picea abies* has its major distribution at high elevation in the subalpine belt, but is partly planted at low elevations on the Plateau. However, palynological studies demonstrate, that *P. abies* occurs naturally at low elevations. It has been present long before intense human activities have occurred and under similar climatic conditions as today (Burga 1988, Burga and Hussendorfer 2001). A simulation of natural forest succession using a dynamic forest succession model also reveals that *P. abies* is expected to naturally occur at the Swiss Plateau (Bolliger et al. 2000).

### 2.3.2 Data sources and study species

Species data was extracted from the National Forest Inventory of Switzerland (NFI). The database contains data on individual trees in 200 m<sup>2</sup> circular sample plots. The first inventory (NFI\_1, 1983—1985) was recorded on a 1-km regular grid, while NFI\_2 (1993—1995) was on a 1.4-km grid. All grid points located in forest were sampled (Fig. 1). A total of 5236 plots were repeated during NFI\_1 (n = 10419) and NFI\_2 (n = 6412). All trees with diameters at breast height (1.37 m above the ground; DBH) larger than 12 cm were measured for basal area. We selected eleven target tree species out of approximately 50 common species. The selected species are sufficiently abundant to be modeled (>100 observations), belong to two different functional groups (broadleaved deciduous and needleleaved evergreen), and combine to cover the full elevation gradient available in Switzerland, reaching from 180 m a.s.l. to the treeline situated at roughly 2450 m a.s.l. in the dry interior valleys. The seven broadleaved species included European beech *Fagus sylvatica*, sycamore *Acer pseudoplatanus*, European ash *Fraxinus excelsior*, silver birch *Betula pendula*, pedunculate oak *Quercus robur*, sessile oak *Quercus petraea*, and common whitebeam *Sorbus aria*; while the four conifers included Norway spruce *Picea abies*, silver fir *Abies alba*, Scots pine *Pinus sylvestris*, and

Swiss stone pine *Pinus cembra*. Eight of these species were also incorporated as biotic predictors (Table 1).



**Figure 1.** Distribution of study plots (circles of 200 m<sup>2</sup> represented by black and grey dots) within the forest of the central Alps (45°49'N-47°48'N, 5°57'E-10°29'E). Black dots represent the plots used for model calibration (n = 5236), grey dots represent plots used for external model evaluation (n = 5183).

**Table 1.** Species traits of the selected species for modeling and analyses.

| Species                    | Number of occurrences |        | Predictor species | CSR strategy | Seed dispersal | Shade tolerance |     | Freq.-domin. group |
|----------------------------|-----------------------|--------|-------------------|--------------|----------------|-----------------|-----|--------------------|
|                            | NFI_1c                | NFI_1e |                   |              |                | Juv.            | Ad. |                    |
| <i>Abies alba</i>          | 1520                  | 1610   | x                 | CS           | 100            | 3               | 1   | FD                 |
| <i>Acer pseudoplatanus</i> | 752                   | 737    | x                 | C            | 100            | 2               | 4   | IS                 |
| <i>Betula pendula</i>      | 218                   | 178    | x                 | R            | 200            | 7               | 9   | ID                 |
| <i>Fagus sylvatica</i>     | 2114                  | 2096   | x                 | CS           | 25             | 3               | 1   | FD                 |
| <i>Fraxinus excelsior</i>  | 684                   | 645    | x                 | C            | 100            | 4               | 6   | ID                 |
| <i>Picea abies</i>         | 3387                  | 3322   | x                 | CS           | 100            | 5               | 5   | FD                 |
| <i>Pinus cembra</i>        | 123                   | 114    |                   | S            | 25             | 6               | 5   | ID                 |
| <i>Pinus sylvestris</i>    | 436                   | 431    | x                 | CSR          | 100            | 7               | 9   | ID                 |
| <i>Quercus petraea</i>     | 226                   | 233    |                   | CS           | 25             | 6               | 7   | ID                 |
| <i>Quercus robur</i>       | 171                   | 159    | x                 | CS           | 25             | 7               | 9   | IS                 |
| <i>Sorbus aria</i>         | 167                   | 150    |                   | SR           | 25             | 6               | 7   | IS                 |

Notes: NFI\_1c are forest plots for calibration and NFI\_1e for external evaluation; seed dispersal shows the avg. seed dispersal distances [m]; predictor species (x) are species used as predictors in the models; shade tolerance of juveniles and adults indicate low values for high shade tolerance; freq.-domin. group indicates “F” for species with a frequent occurring in the landscape and “I” for infrequent occurring species, while “D” indicates high local abundance (i.e. dominant) and “S” low local abundance (i.e. subordinate).

### 2.3.2.1 Response variables

We analyzed two response variables: 1) presence-absence data (PA), where presence was recorded when a tree of a target species was present on the sample plot. This is frequently used in studies that model species distributions. 2) Basal area (BA), the basal area of a target species as a proportion of the total basal area recorded on the sample plot. Since basal area is a surrogate of biomass, it can also be used as a measure of competition in the stand (Waring and Running 2007).

### 2.3.2.2 Biotic predictor variables

We evaluated three species-specific variables to describe the influence of predictor species on the occurrence of a target species: 1) relative abundance (AB), defined as the number of stems of a predictor species as a proportion of total number of stems recorded in a sample. 2) Relative abundance of large individuals (AB\_L), defined as the number of stems of large individuals of a target species as a proportion of the total number of stems on the sample plot. An individual was considered large (L) if it was taller than the median height of the target species in a stand. Height is indicative of competitive ability for light because taller plants shade shorter plants. Competitive advantage can depend on relative rather than the absolute height (Falster and Westoby 2003). 3) Total

shading by large individuals (LAI\_L), defined by the cumulative leaf area index (*CumLAI*) of all large trees. Biotic predictors were all correlated  $< |0.5|$ .

In order to identify species heights for deriving AB\_L and LAI\_L, we first estimated actual tree height ( $H_a$ ; [cm]) according to Bugmann (1994):

$$H_a = 137 + b_1 \times D_a + b_2 \times D_a^2 \quad (1)$$

where  $D_a$  [cm] is the actual diameter of the individual trees as taken from NFI, and  $b_1$  and  $b_2$  are species-specific parameters derived as follows (eq. 2 and 3):

$$b_1 = \frac{2(H_{\max} - 137)}{D_{\max}} \quad (2)$$

$$b_2 = -\frac{b_1}{2 \times D_{\max}} \quad (3)$$

where  $H_{\max}$  is the maximum possible height of a tree species in cm, and  $D_{\max}$  the maximum possible DBH (i.e. at 137 cm above ground), also in cm (Supplementary material Appendix 1). For a target species, we first calculated median tree height in each plot and then calculated the fraction of individuals of the relevant predictor species larger than the median (AB\_L). Formulas for estimating LAI\_L are found in Supplementary material Appendix 2.

### 2.3.2.3 Species traits

We selected several species traits to group the species accordingly and test whether the contributions of the biotic and abiotic sets of predictors differ as a function of species traits. We formulate hypotheses regarding effects of biotic variables on species that differ in their traits (Table 1, 2). We base our hypotheses on the general expectation that more competitive species are associated with higher effects from biotic variables, since we cannot evaluate the direction of the influence when using correlative methods.

CSR strategies: species were grouped according to their strategies in response to disturbance (factors reducing biomass) and stress (factors restricting productivity, Grime 1979). According to the stress gradient hypothesis (Bertness and Callaway 1994) species occurring in undisturbed, low-stress environments (C strategy) should be involved in intense exclusionary biotic interactions (i.e. interspecific competition) compared to species adapted to frequent disturbances (R strategy) or high stress (S strategy) that may be involved in mutualistic biotic interactions. We expected exclusionary biotic interactions to be strongest compared to other types of biotic interactions, and thus, two groups

were considered, one with species with R, S or SR strategies and one with C strategy species. Due to unequal number of species assigned to the two groups, the results must be considered with care. CSR strategies were assigned according to Brzeziecki and Kienast (1994).

Seed dispersal distances: consideration of seed dispersal distance leads to contrasting predictions regarding the importance of biotic predictors. On the one hand, we expect that models for species with longer seed dispersal distances are more influenced by biotic predictors than models for species with shorter seed dispersal distances. Intra-specific biotic interactions with parent trees are replaced with increased separation by interspecific interactions (Howe and Smallwood 1982), resulting in increasing contribution of biotic predictors with increasing seed dispersal distance. On the other hand, seed dispersal is an essential mechanism for plants to tackle temporal and spatial habitat changes (Gleason 1926, Cain et al. 2000). Seed dispersal distance is closely linked to successional stage on which a species is dominant. Early-successional plant species typically have fat tailed dispersal kernels (i.e. a larger proportion of long-distance movements) and rapid growth rates that enable them to respond quickly to disturbance. Late-successional species usually demonstrate contrasting tendencies (Tilman 1994). In the absence of disturbance in high-resource environments, late-successional species generally competitively exclude early-successional species due to better resource use efficiency (Rees et al. 2001). Accordingly, species with shorter seed dispersal distances tend to occur in late-successional environments with strong biotic interactions, and thus, may have models with higher contributions of biotic predictors. However, we expect that this effect is weak compared to the effect from the transition from intra to interspecific interactions with distance to parent. To examine these alternatives, we grouped species according to Lischke et al. (2004) into species with short seed dispersal distances (25 m) and species with long seed dispersal distances (100-200 m).

Shade tolerance: forest succession is driven largely by interspecific differences in shade tolerance (Kobe et al. 1995). Shade-tolerant species are evolutionarily better adapted for photosynthesis in low light than are shade-intolerant species (Boardman 1977, Kobe et al. 1995). Therefore, shade-tolerant species have an advantage over similar-sized species during competition for moisture and nutrients (Kimmins 2004). Since the degree of shade tolerance also varies by age (Ellenberg 1992), we tested whether models for species with differing juvenile and adult shade tolerance are differentially affected by biotic predictor variables. We derived species-specific shade-tolerance values from Bugmann (1994). We expect stronger effects for shade-intolerant species (values >5) than for shade-tolerant (values <5) because species with higher shade tolerance are unlikely outcompeted for light, and thus, may occur in many abiotically suitable habitats. We also expect stronger biotic effects for juveniles than for adults, because tall adults of shade intolerant species may still reach the canopy and thus sufficient light, which may not be the case for juveniles.

Frequency-dominance groups: species can be classified according their frequency in the landscape and their local dominance (Collins et al. 1993, Zimmermann et al. 2007). Here, we classified species as “frequent” when occurring in >25% of all forest plots. Species were classified as “dominant” if the average relative abundance (AB) per plot among all NFI plots was >25% in plots where the species was present. Because frequency of occurrence of species may depend on local abundance (Hanski 1982, Collins et al. 1993), we predict that locally dominant species due to their competitiveness occur more frequently in suitable habitats than do subordinate species. Thus, we expect greater model improvement from adding biotic predictors to models of less dominant and less frequent species than when modeling dominant, frequent species. Several previous studies have indeed shown that tree species frequency in forested landscapes increases with the key competitive trait, shade-tolerance (Pacala et al. 1996, Svenning et al. 2004).

**Table 2.** Species traits in relation to the expected effect of biotic predictors on species distributions. For definitions of the traits see text.

| Trait                     | Weak effect expected      | Strong effect expected         |
|---------------------------|---------------------------|--------------------------------|
| CSR strategy              | R and S strategy          | C strategy                     |
| Seed dispersal distance   | Short distance            | Long distance                  |
| Shade tolerance           | Shade tolerant            | Shade intolerant               |
| Frequency-dominance group | Frequent-dominant species | Infrequent-subordinate species |

#### 2.3.2.4 Abiotic predictor variables

We chose a comprehensive set of topo-climatic variables as abiotic predictors on the basis of their relevance to plant physiology and for explaining spatial patterns. The topo-climatic data were generated at a 25-m spatial resolution following Zimmermann and Kienast (1999) and Guisan et al. (2007). We selected only predictors with correlations  $< |0.5|$  to avoid problems with multicollinearity. This left seven topo-climatic predictors: 1) degree-days with a 5.56°C threshold (DDEG556, [°C x d]), 2) summer frost frequency (SFROY, [d]) expressing the sum of frost events during the frost-sensitive time of the year, 3) moisture index from March to August (MIND38, [mm d<sup>-1</sup>]) as a measure of the water balance of an area in terms of gains from precipitation and losses from potential evapotranspiration, 4) precipitation days (PDAY, [ndays]) as the number of days per year with precipitation higher than 1 mm, 5) potential yearly global radiation (SRADYY, [kJ m<sup>-2</sup> d<sup>-1</sup>]) expressing the potential amount of direct and indirect solar energy irradiated to the surface, 6) topographic position (TOPOS, [range]) as the difference between the average elevation in a circular moving window applied to a 25-m digital elevation model (DEM) and the centre cell of the window (representing soil properties such as soil depth and nutrient availability), and 7) slope (SLP, [°])

expressing the slope angle in degrees derived from the DEM (subsuming gravitational disturbance processes such as rock fall, solifluction, and avalanches).

### 2.3.3 Data analysis

We used a variance partitioning approach (Mood 1971, Borcard et al. 1992, Fig. 2) by fitting generalized linear models (GLM, McCullagh and Nelder 1989) using three different combinations of predictors for each tree species: just the abiotic (ABIOT) or just the biotic (BIOT) predictor variables, or the abiotic and biotic predictor sets combined (FULL). Each model was calibrated using different types of species responses (PA and BA) and BIOT and FULL models using different biotic predictors (AB, AB\_L and LAI\_L).

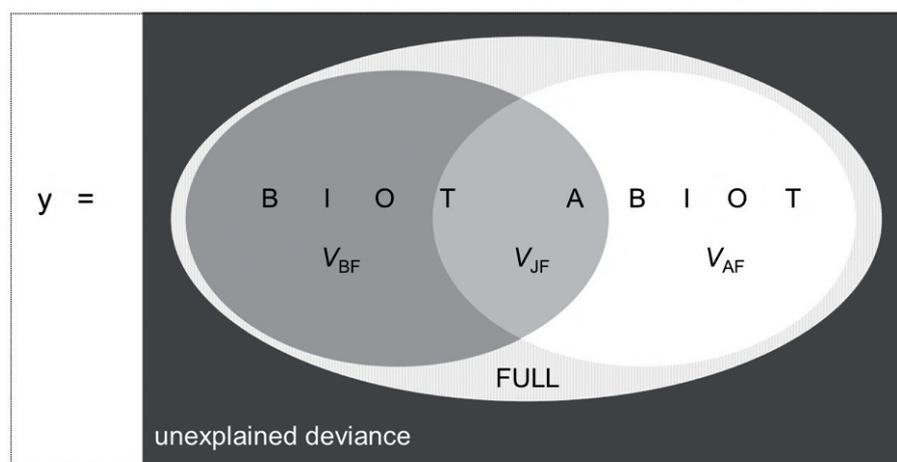
We built GLMs with logit links (assuming a binomial distribution) followed by both backward and forward stepwise variable selection based on AIC (Akaike's information criterion, Akaike 1974) and BIC (Bayesian information criterion, Schwarz 1978). Here, we only report AIC-based results because both criteria led to the same models, likely because of the large sample sizes. For proportional response variables (BA- and AB-models) we used weighted GLMs to account for the total number of tree individuals and stand basal area of all trees per plot, respectively (Dalgaard 2002). For binary response variables (PA-models) no weights were used. Predictors were entered both as linear and quadratic terms to allow for nonlinear responses. For model calibration we used tree species data from NFI\_1 from plots intersecting with NFI\_2 (i.e. NFI\_1c).

Model fit was evaluated by the adjusted  $D^2$  ( $adj.D^2$ ) following Weisberg (1980) for each of the selected species, a measure that adjusts the deviance explained ("deviance" is the variance in likelihood methods;  $D^2$ ) by the number of fitted regression parameters and the number of observations. To partial out the deviance explained by the abiotic and biotic predictor sets, we followed earlier work using GLMs (Lobo et al. 2001, Zimmermann et al. 2007). The contribution of each set of predictors was estimated by subtracting the  $adj. D^2$  of the opposite set of predictors from the FULL model, so that  $V_{BF} = V_{FULL} - V_{ABIOT}$ , and  $V_{AF} = V_{FULL} - V_{BIOT}$ .  $V_{BF}$  and  $V_{AF}$  are the pure contributions of the biotic and abiotic predictor sets to the total deviance explained, while the joint contribution ( $V_{JF}$ ) of the two predictor sets was calculated as  $V_{JF} = V_{FULL} - (V_{ABIOT} + V_{BIOT})$ . In rare cases,  $V_{JF}$  may become negative as a result of opposing effects of the two sets of predictors in the FULL model (Legendre 1998).

Partial  $adj.D^2$  values were then further evaluated to test whether the pure and joint contributions to the  $adj.D^2$  followed patterns that matched species groups according to their traits. We used the Mann—Whitney U test and the Kruskal—Wallis test to compare the effect of traits classified into two and three groups, respectively.

In addition to the variance partitioning, we evaluated model accuracy internally by 10-fold cross-validation (Venables et al. 2002) and externally by testing the models against the NFI\_1 plots

that were not part of NFI\_2 (i.e. NFI\_1e). We used Cohen's kappa (Cohen 1960) and area under the receiver characteristic curve (ROC) (AUC; Fielding and Bell 1997) for models calibrated with binary response variables (PA-models). For models calibrating proportional responses (BA-models) we used mean absolute error (MAE, Voltz and Webster 1990), root mean square error (RMSE, Voltz and Webster 1990) and the coefficient of determination,  $R^2$  (Menard 2002). All data was prepared and analyzed using R (R Development Core Team 2008) and ArcGIS 9.2 (ESRI 2006).



**Figure 2.** Variance partitioning concept. BIOT: deviance explained by biotic predictor set; ABIOT: deviance explained by abiotic predictor set; FULL: deviance explained by both biotic and abiotic predictor sets;  $V_{BF}$ : alone contribution to deviance explained by biotic predictor set;  $V_{JF}$ : joint contribution of both predictor sets; and  $V_{AF}$ : alone contribution of the abiotic predictor set. Adapted from Legendre (1993).

## 2.4 Results

### 2.4.1 Model qualities using different types of biotic variables

The explicit inclusion of biotic predictors improved model fit (Table 3). However, model quality varied among tree species, chosen response variable and selected biotic predictors. Since the amount of shade (LAI\_L) was never significant, we did not consider it further. The explained deviance was significantly lower for presence-absence models (PA) than for proportional basal-area models (BA, paired t-test,  $p < 0.001$ ; Table 3).

For presence-absence models the accuracies of the two partial models (ABIOT and BIOT) were similar, but significantly exceeded by the FULL model (paired t-test,  $p < 0.001$  and see Table 4). Further, model accuracies as estimated with 10-fold cross validation and external validation on NFI\_1 data not used for model calibration (NFI\_1e) did not differ significantly, which indicates that we obtained stable models with low bias (Supplementary material Appendix 3). For the proportional

basal-area models MAE was similar for the two partial models, but significantly smaller for the FULL model (paired t-test,  $p < 0.001$  and see Table 6). However, for most modeled tree species MAE and RMSE differed substantially, indicating large variance in individual errors in the sample (Supplementary material Appendix 4). Likewise, model quality ( $R^2$ ) was similar for the two partial models, but higher for the FULL model. For these proportional models, accuracies estimated by 10-fold cross validation and by external validation using NFI\_1e data did not differ significantly.

When comparing the three types of biotic predictor variables, we found that species-specific relative abundances (AB) explained the most deviance in fitted models (Table 5). Relative abundances of large individuals (AB\_L) explained considerably less deviance (paired t-test,  $p = 0.001$ ; Table 5) and the amount of shade as measured by LAI (LAI\_L) failed to explain patterns. Model accuracies for models with relative abundances were similar to models with relative abundances of large individuals in terms of errors (MAE, RMSE), but were higher in terms of model quality ( $R^2$ , Table 6). In general, models with relative abundances of large individuals had similar MAE for the two partial models and the FULL model. However, their RMSE was highest for the BIOT model, lower for the FULL model, and lowest for the ABIOT model, indicating large variance in individual model errors (Table 6). Model quality ( $R^2$ ) was highest for the FULL model, lower for the ABIOT model and lowest for the BIOT model. Model accuracies taken from 10-fold cross validation were not significantly different from external validation using NFI\_1e data.

When proportional basal area was the response, the deviance explained by individual predictors within the ABIOT and BIOT groups varied considerably among species. Degree-days was generally the strongest ABIOT predictor, while *Picea abies* had similar strength and was the strongest BIOT predictor (Table 7). The other tree species generally declined with increasing abundance of *Picea abies*, although the relationship was unimodal for *Abies alba* and *Pinus sylvestris* (Table 7).

**Table 3.** Deviance explained (*adj. D*<sup>2</sup>) for ABIOT, BIOT and FULL models for PA and BA responses and species-specific relative abundances as biotic predictors. Bold face indicates the model with the highest fit.

| Species                    | ABIOT |      | BIOT |      | FULL |             |
|----------------------------|-------|------|------|------|------|-------------|
|                            | PA    | BA   | PA   | BA   | PA   | BA          |
| <i>Abies alba</i>          | 0.18  | 0.19 | 0.23 | 0.40 | 0.40 | <b>0.61</b> |
| <i>Acer pseudoplatanus</i> | 0.11  | 0.10 | 0.15 | 0.25 | 0.26 | <b>0.41</b> |
| <i>Betula pendula</i>      | 0.25  | 0.36 | 0.20 | 0.34 | 0.35 | <b>0.51</b> |
| <i>Fagus sylvatica</i>     | 0.26  | 0.26 | 0.27 | 0.48 | 0.47 | <b>0.65</b> |
| <i>Fraxinus excelsior</i>  | 0.18  | 0.20 | 0.19 | 0.32 | 0.34 | <b>0.49</b> |
| <i>Picea abies</i>         | 0.19  | 0.25 | 0.20 | 0.44 | 0.36 | <b>0.59</b> |
| <i>Pinus cembra</i>        | 0.62  | 0.71 | 0.38 | 0.51 | 0.65 | <b>0.75</b> |
| <i>Pinus sylvestris</i>    | 0.19  | 0.25 | 0.14 | 0.29 | 0.31 | <b>0.48</b> |
| <i>Quercus petraea</i>     | 0.23  | 0.29 | 0.20 | 0.33 | 0.37 | <b>0.54</b> |
| <i>Quercus robur</i>       | 0.24  | 0.28 | 0.12 | 0.21 | 0.31 | <b>0.41</b> |
| <i>Sorbus aria</i>         | 0.12  | 0.15 | 0.09 | 0.16 | 0.17 | <b>0.29</b> |
| Mean                       | 0.23  | 0.28 | 0.20 | 0.34 | 0.36 | 0.52        |
| Stdv                       | 0.14  | 0.16 | 0.08 | 0.11 | 0.12 | 0.13        |

**Table 4.** Mean model accuracy among species (Kappa, AUC) of ABIOT, BIOT and FULL models calibrated with PA data as species response and species-specific relative abundances as biotic predictors. Model accuracy was derived by 10-fold cross validation (CV) and external validation on NFI\_1e.

|       | 10-fold CV  |             | External validation |             |
|-------|-------------|-------------|---------------------|-------------|
|       | Kappa       | AUC         | Kappa               | AUC         |
| ABIOT | 0.24 ± 0.12 | 0.82 ± 0.07 | 0.23 ± 0.12         | 0.81 ± 0.07 |
| BIOT  | 0.22 ± 0.14 | 0.80 ± 0.05 | 0.22 ± 0.13         | 0.81 ± 0.05 |
| FULL  | 0.36 ± 0.18 | 0.89 ± 0.05 | 0.35 ± 0.18         | 0.89 ± 0.04 |

**Table 5.** Deviance explained (*adj. D*<sup>2</sup>) for ABIOT, BIOT and FULL models for BA responses and species-specific relative abundances (AB) and species-specific relative abundances of large trees (AB\_L) as biotic predictors. Bold face indicates the model with the highest fit.

| Species                    | ABIOT | BIOT |      | FULL        |             |
|----------------------------|-------|------|------|-------------|-------------|
|                            |       | AB   | AB_L | AB          | AB_L        |
| <i>Abies alba</i>          | 0.19  | 0.40 | 0.11 | <b>0.61</b> | 0.33        |
| <i>Acer pseudoplatanus</i> | 0.10  | 0.25 | 0.06 | <b>0.41</b> | 0.15        |
| <i>Betula pendula</i>      | 0.36  | 0.34 | 0.24 | <b>0.51</b> | 0.44        |
| <i>Fagus sylvatica</i>     | 0.26  | 0.48 | 0.11 | <b>0.65</b> | 0.36        |
| <i>Fraxinus excelsior</i>  | 0.20  | 0.32 | 0.10 | <b>0.49</b> | 0.31        |
| <i>Picea abies</i>         | 0.25  | 0.44 | 0.31 | <b>0.59</b> | 0.44        |
| <i>Pinus cembra</i>        | 0.71  | 0.51 | 0.38 | <b>0.75</b> | 0.72        |
| <i>Pinus sylvestris</i>    | 0.25  | 0.29 | 0.30 | 0.48        | <b>0.53</b> |
| <i>Quercus petraea</i>     | 0.29  | 0.33 | 0.12 | <b>0.54</b> | 0.36        |
| <i>Quercus robur</i>       | 0.28  | 0.21 | 0.09 | <b>0.41</b> | 0.33        |
| <i>Sorbus aria</i>         | 0.15  | 0.16 | 0.14 | <b>0.29</b> | 0.26        |
| Mean                       | 0.28  | 0.34 | 0.18 | 0.52        | 0.39        |
| Stdv                       | 0.16  | 0.11 | 0.11 | 0.13        | 0.15        |

**Table 6.** Mean model accuracy (MAE, RMSE, R<sup>2</sup>) of ABIOT, BIOT and FULL models calibrated with BA data as species response and species-specific relative abundances (AB) and species-specific relative abundances of large trees (AB\_L) as biotic predictors. Model accuracy was derived by 10-fold cross validation (CV) and external validation on NFI\_1e.

|                      | 10-fold CV  |             |                | External validation |             |                |
|----------------------|-------------|-------------|----------------|---------------------|-------------|----------------|
|                      | MAE         | RMSE        | R <sup>2</sup> | MAE                 | RMSE        | R <sup>2</sup> |
| ABIOT                | 0.08 ± 0.09 | 0.57 ± 0.87 | 12.52 ± 11.06  | 0.08 ± 0.09         | 0.47 ± 0.91 | 11.21 ± 9.44   |
| BIOT <sub>AB</sub>   | 0.07 ± 0.07 | 0.86 ± 1.35 | 14.09 ± 13.72  | 0.07 ± 0.07         | 0.89 ± 1.47 | 13.22 ± 13.51  |
| BIOT <sub>AB_L</sub> | 0.08 ± 0.09 | 0.96 ± 1.56 | 6.25 ± 7.46    | 0.08 ± 0.10         | 0.97 ± 1.76 | 5.16 ± 6.69    |
| FULL <sub>AB</sub>   | 0.05 ± 0.05 | 0.75 ± 1.11 | 30.13 ± 20.77  | 0.05 ± 0.05         | 0.71 ± 1.13 | 28.98 ± 20.99  |
| FULL <sub>AB_L</sub> | 0.07 ± 0.08 | 0.86 ± 1.33 | 19.22 ± 14.01  | 0.07 ± 0.08         | 0.85 ± 1.42 | 17.54 ± 12.16  |

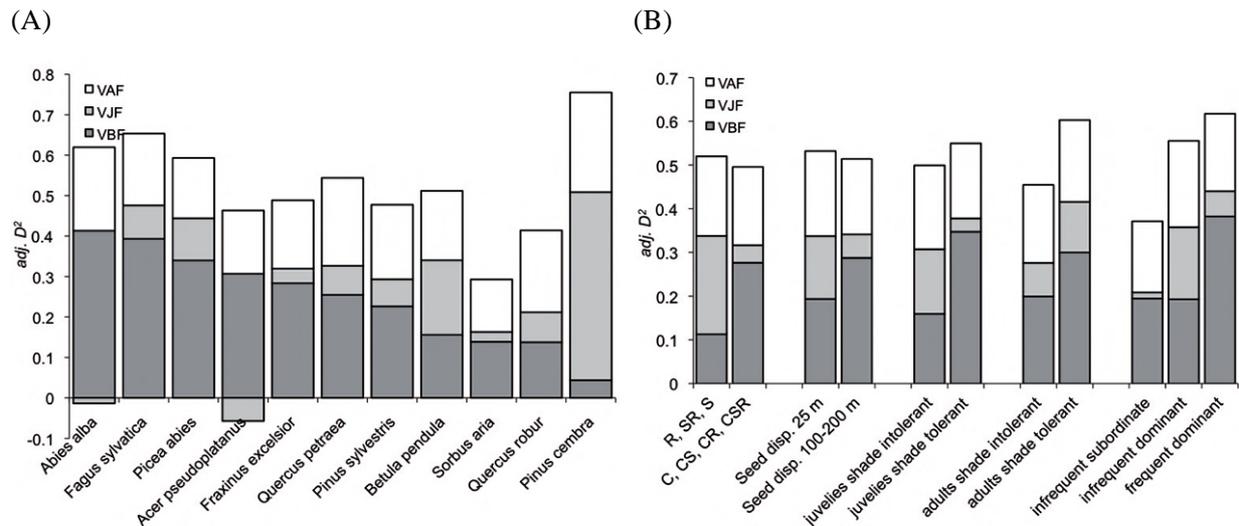
Table 7. Deviance explained (*adj. D*<sup>2</sup>) by individual predictors, derived from single variable GLMs with proportions of basal areas (BA) as response variable and abiotic and biotic predictors (only AB predictors are shown). Acronyms for the modeled species: first letter of genus plus two first letters of species epithet. Numbers indicate the *adj. D*<sup>2</sup> explained by the predictor. The direction of the trend between the predictor and the response species is indicated in parenthesis as positive linear “+”, negative linear “-”, positive unimodal “∩”, negative unimodal “∪”, or with no clear trend “N”. Bold-face indicate *adj. D*<sup>2</sup> ≥ 0.10.

| Predictor                | <i>Aal</i>   | <i>Aps</i>   | <i>Bpe</i>   | <i>Fsy</i>   | <i>Fex</i>   | <i>Pab</i>   | <i>Fce</i>   | <i>Psy</i> | <i>Qpe</i>   | <i>Qro</i>   | <i>Sar</i> | Mean        | Stdv |
|--------------------------|--------------|--------------|--------------|--------------|--------------|--------------|--------------|------------|--------------|--------------|------------|-------------|------|
| SLP25                    | 0.01—        | 0.01∩        | 0.04+        | 0.00—        | 0.02—        | 0.00—        | 0.06∩        | 0.01U      | 0.05U        | 0.09—        | 0.04+      | 0.03        | 0.03 |
| MIND38                   | 0.01∩        | 0.00∩        | 0.01+        | 0.02—        | 0.07—        | 0.06+        | 0.09∩        | 0.16—      | 0.20—        | 0.19—        | 0.01∩      | 0.08        | 0.07 |
| SFROY                    | 0.02—        | 0.02—        | 0.05—        | 0.03—        | 0.03U        | 0.03∩        | <b>0.43+</b> | 0.01—      | 0.02—        | 0.02—        | 0.01—      | 0.06        | 0.12 |
| DDEG556                  | <b>0.15∩</b> | 0.05∩        | 0.08∩        | <b>0.20∩</b> | <b>0.17∩</b> | <b>0.16—</b> | <b>0.58—</b> | 0.05∩      | <b>0.20∩</b> | <b>0.23∩</b> | 0.04∩      | <b>0.17</b> | 0.15 |
| PDAY                     | 0.03∩        | 0.03∩        | <b>0.17∩</b> | 0.01∩        | 0.01∩        | 0.08+        | 0.07∩        | 0.06—      | <b>0.12∩</b> | 0.07∩        | 0.00∩      | 0.06        | 0.05 |
| SRADYY                   | 0.00∩        | 0.00—        | 0.01U        | 0.00U        | 0.02∩        | 0.00+        | 0.04—        | 0.03+      | 0.04+        | 0.06∩        | 0.02U      | 0.02        | 0.02 |
| TOPOS                    | 0.01∩        | 0.01—        | 0.01U        | 0.00∩        | 0.02∩        | 0.00U        | 0.00U        | 0.00∩      | 0.02∩        | 0.06∩        | 0.01+      | 0.01        | 0.02 |
| <i>A. alba</i>           | -            | 0.02∩        | 0.06—        | 0.02∩        | 0.02—        | 0.07—        | 0.09N        | 0.04—      | 0.03—        | 0.01—        | 0.01—      | 0.04        | 0.03 |
| <i>A. pseudoplatanus</i> | 0.01∩        | -            | 0.01—        | 0.01∩        | 0.05∩        | 0.02—        | 0.03N        | 0.02—      | 0.01N        | 0.00+        | 0.02∩      | 0.02        | 0.01 |
| <i>B. pendula</i>        | 0.01—        | 0.00—        | -            | 0.00∩        | 0.00N        | 0.01—        | 0.00—        | 0.00∩      | 0.00∩        | 0.00N        | 0.00+      | 0.00        | 0.00 |
| <i>F. sylvatica</i>      | 0.07∩        | 0.03∩        | 0.01—        | -            | 0.01∩        | <b>0.20—</b> | <b>0.12N</b> | 0.01∩      | 0.02∩        | 0.02∩        | 0.03∩      | 0.05        | 0.06 |
| <i>F. excelsior</i>      | 0.01—        | 0.05∩        | 0.00—        | 0.01∩        | -            | 0.04—        | 0.03N        | 0.00—      | 0.00—        | 0.04∩        | 0.00—      | 0.02        | 0.02 |
| <i>P. abies</i>          | <b>0.19∩</b> | <b>0.11—</b> | <b>0.15—</b> | <b>0.33—</b> | <b>0.15—</b> | -            | 0.08—        | 0.09∩      | <b>0.15—</b> | 0.09—        | 0.10—      | <b>0.14</b> | 0.07 |
| <i>P. sylvestris</i>     | 0.02—        | 0.01—        | 0.00N        | 0.01∩        | 0.01—        | 0.03—        | 0.02—        | -          | 0.01∩        | 0.01∩        | 0.02∩      | 0.01        | 0.01 |
| <i>Q. robur</i>          | 0.00—        | 0.00—        | 0.00N        | 0.00∩        | 0.01∩        | 0.01—        | 0.01N        | 0.00N      | 0.00—        | -            | 0.00N      | 0.00        | 0.00 |

## 2.4.2 Variance partitioning of biotic and abiotic predictors

We report variance partitioning as applied to models with proportional basal areas as response and topo-climatic and/or relative abundance as abiotic and biotic predictor sets, respectively, because these were the predictors that best describe tree distributions. The pure contribution of abiotic ( $V_{AF}$ ) and of biotic ( $V_{BF}$ ) predictors to explanation of model deviance differed among species (Fig. 3A). Across species, the biotic contribution ( $0.25 \pm 0.12$ ) was larger than the abiotic contribution ( $0.18 \pm 0.03$ ), and the joint contribution ( $V_{JF}$ ) was comparably small ( $0.09 \pm 0.14$ ).

When accounting for species traits, species adapted to undisturbed low-stress environments (C, CS, CR, CSR) showed significantly higher contributions to explained deviance from biotic predictors than do species adapted to disturbed or stressful environments (R, S, SR; Mann—Whitney U test,  $p = 0.04$ ; Fig. 3B). Further, species with medium to long seed dispersal distances (avg. = 100—200 m) tended to have larger contributions to explained deviance from biotic predictors than species with short seed dispersal distances (avg. = 25 m; Mann—Whitney U test,  $p = 0.17$ ; Fig. 3B). Models of species with shade-tolerant juveniles had significantly larger contributions from biotic predictors than did models of species with shade intolerant juveniles (Mann—Whitney U test,  $p = 0.004$ ; Fig. 3B). A similar, but non-significant tendency was found from analyzing the effect of adult shade tolerance (Mann—Whitney U test,  $p = 0.12$ ). Further, models of dominant species that occur frequently in a landscape showed significantly higher contributions to the deviance explained from biotic predictors than did models of dominant and subordinate species that demonstrate infrequent occurrence (Kruskal—Wallis test,  $p = 0.04$ ; Fig. 3B). Abiotic and joint contributions did not differ significantly within characteristic species groups (Mann—Whitney U test and Kruskal—Wallis test, all  $p > 0.27$ ).



**Figure 3.** Graphical representation of variance partitioning results. (A) Partial deviance explained ( $adj. D^2$ ) by the two sets of predictors for individual tree species.  $V_{BF}$  is the pure contribution of the biotic set of predictors,  $V_{AF}$  is the pure contribution of the abiotic set and  $V_{JF}$  is the joint fraction of both predictor sets. (B) Mean contributions of species adapted to undisturbed low-stress environments (C, CS, CRS) and stressful environments (R, S, RS); species with medium to long seed dispersal distances (average dispersal distance of 100–200 m) and short seed dispersal (average dispersal distance of 25 m); species with shade-tolerant juveniles and adults (values  $\leq 5$ ) and shade-intolerant juveniles and adults (values  $> 5$ ); and dominant species that occur frequently at the landscape and subordinate and dominant species that occur infrequently.

## 2.5 Discussion

### 2.5.1 Biotic predictors and model quality

We find that biotic variables considerably improved predictions of tree species distributions in Switzerland, with their effect being largely independent of abiotic topo-climatic factors. Several previous studies have extended SDMs by including biotic predictors (Rouget et al. 2001, Leathwick 2002, Araújo and Luoto 2007, Heikkinen et al. 2007, Sutherst et al. 2007). Similar to our findings, these studies generally demonstrate improved predictions when adding biotic predictors. For instance, the abundance of *Nothofagus* species in New Zealand is dependent on the presence or absence of their congeners (Leathwick 2002), while presence of host plant species is an important occurrence predictor for butterfly species in Europe (Araújo and Luoto 2007). Some owl species appear to facilitate the presence of other owl species in Finland (Heikkinen et al. 2007). In our study, we specifically demonstrate that the statistical contribution of the biotic predictors, which we assume reflect biotic interactions, small-scale information on species co-occurrence and local abiotic conditions (e.g. soil, nitrogen content), is largely independent of the contribution of macro-climatic factors. Our results also show that different ways of expressing biotic variables can have a large

influence on model quality. Overall, biotic predictors have the potential to elucidate important aspects of species distribution patterns that are not easily represented by large-scale abiotic predictors.

### 2.5.2 Partitioning the biotic and abiotic predictor contribution

In our analysis of the respective contributions of biotic and abiotic factors in SDMs, we find that the joint contribution of both predictor sets is consistently small (except for *Pinus cembra*). This indicates that biotic predictors are largely independent of the abiotic predictors in their explanatory capacity. Abiotic predictors (topography and climate) may reflect constraints of the fundamental niche of the tree species, and hence, are expected to determine large-scale species ranges (Pearson and Dawson 2003). In contrast, small-scale distribution patterns are expected to be more strongly influenced by biotic processes such as competition or facilitation, as well as land-use, stochastic processes and local abiotic conditions (micro-climate, soil, nitrogen content). The largely unique influence of abiotic and biotic predictors in our study probably reflects that the small-scale processes are relatively independent of the effects of large-scale topo-climatic gradients. The main exception occurs with *Pinus cembra*, a species adapted to relatively extreme (cold) habitats. Abiotic predictors, with no independent contribution of the biotic predictors, constitute the main range determinants for this species. Furthermore, the large joint contribution of the two predictor sets for *P. cembra* indicates that influence of biotic processes likely mediates the influence of the abiotic environment. Notably, *P. cembra* mainly occurs where it is too cold for strong competitors such as *Picea abies* (cf. Table 7). As a consequence of our findings, we expect the addition of biotic predictors to improve the ability of species distribution models to predict small-scale distribution and abundance patterns, but not necessarily to produce a clear improvement in the prediction of species large-scale ranges.

### 2.5.3 Biotic predictor component and species traits

We find clear differences in the relative contribution of abiotic and biotic predictors when species are grouped according to traits. With the exception of the hypothesized effects of biotic predictors on models of species belonging to different shade tolerance groups and CSR-strategies, the data support our hypothesis regarding effects of biotic predictors on species that differ in their traits. The tree species whose modeled distribution are most strongly influenced by biotic predictors are adapted to undisturbed low-stress environments (competitive strategy), shade-tolerant as juveniles and adults, frequent dominants, and tend to have long distance seed dispersal. All these traits point to late-successional species with high competitive ability. A principle exception is the dispersal distance relationship where the effect from the transition from intra to interspecific interactions with distance from parent may be overriding. Thus, our results support the idea that models of species typified by occurrence in stressful or disturbed environments seem to profit less from biotic predictors, despite

these species may be outcompeted during succession by species with a higher competitive ability, and thus, occur less often in abiotically suitable habitats due to negative biotic interactions.

Our results are in line with the assumption of Grime (1979), where species experience stronger biotic interactions in less disturbed, productive environments compared to more disturbed, stressed environments. For trees, biotic interactions are thus more likely important for competitive, shade-tolerant species, which primarily occur in late-successional, productive environments, where competition plays a strong structuring role, while they are less likely important for ruderal and stress-adapted, shade-intolerant species, which mainly occur in low-competition environments. In terms of species, we find that the strongest effects of biotic variables on tree species distributions were for the late-successional species *Picea abies* and *Fagus sylvatica* (Table 7). We caution that our correlative analyses detect only the shape of the mutual response, but not the direction of the effect. If one species imposes e.g. shade and thus reduces the abundance of another species, then the two species show a correlation. If two SDMs are fitted, where each species is once the dependent and once the predictor variable, we would find negative response directions for both. Accordingly, we interpret the large contribution of the biotic predictor set if strong competitors are used as dependent variables such that these competitive species impose stronger competitive control over others that we have added as predictors. This inversion of the influence was much lower if early-successional, and shade-intolerant species are considered. Experiments would be needed to detect causal relationships.

#### 2.5.4 Predictive power of different biotic predictor sets and single predictors

In our analysis, use of presence-absence (PA) as a response variable in the models results in less explained deviance than do models using proportional data on basal areas (BA). This may indicate that our estimated realized niche of a species is better characterized with species performance data than with simple occurrence data, which is in line with the original definition of the realized niche based on net growth rate of populations (Pulliam 2000). Further, despite our original expectation that larger trees directly influence the occurrence of smaller trees since small trees are likely to suffer or die from competition by larger trees, species-specific relative abundances of large individuals (AB\_L) explained significantly less deviance than did AB. If the species-specific component is removed and only overall shading of large individuals (LAI\_L) was addressed, hardly any deviation is explained. This is surprising since leaf area and not biomass is assumed to be the underlying mechanism behind the self-thinning rule (Westoby 1984). Possibly, the method needs to be improved to accurately portray the influence by shading on target trees, i.e. leaves of trees from the same species are likely at least as important for shading effects as are the effects of shading from leaves of other species.

Degree days (5.56°C threshold) and moisture index from March to August were the best single predictors of the abiotic predictors set. These factors are important for species that grow

primarily under cold (*Pinus cembra*) or dry (*Quercus petraea* and *Q. robur*) conditions. In contrast, models of *Abies alba*, *Picea abies* and *Fagus sylvatica* show the highest impact by biotic variables (i.e. biomass of other species). As mentioned above, we interpret this as competitive strength of these three species compared to other species. The inclusion of the presence/absence or abundance of additional species as predictor variables need not reflect biotic interactions. It may also represent consequences of forest management, or simply the occurrence of co-varying distributions between pairs of species that do not necessarily interact. For example, *P. abies* is dominant at high elevations and naturally occurs less frequent at low elevations. However, since it is commercially the most important tree species in the central Alps, it is sometimes planted at low elevations. Hence, biotic influences subsumed in this predictor may not only contain the natural interactions between tree species, but in some cases the effects of management. Finally, deviance in co-occurrence may also represent unmeasured or incompletely measured environmental deviance, notably micro-environmental heterogeneity that might not be captured by larger scale abiotic GIS layers. The direction of the trend between the biotic predictor and the response may indicate that species tend to occur in mixed stands or in stands with only one dominant tree species. Unimodal distributions, as seen in the responses of *F. sylvatica* and *Abies alba*, reflect a tendency of a species to occur often in mixed stands at intermediate densities.

## 2.6 Conclusion

Models are generally improved by representing other species as predictor variables in the models. Species that reflect interspecific facilitation, such as root symbionts, may be beneficial for better understanding the small-scale drivers of plant distribution. However, spatially explicit information of fungal or bacterial symbionts is difficult to obtain. Furthermore, to prevent overfitting, only few such predictor species can be included in a model. Hence, even where data are available, inclusion of these variables should be contingent on prior ecological knowledge to avoid fitting models with spurious interactions. Given the effects of biotic variables on the modeled distribution of trees, it seems unlikely that predictions for global warming at small spatial scales (resolution or grain) are credible if they are based solely on topo-climatic gradients. These predictions for global change could be improved by including community information and seed dispersal or migration effects (Engler and Guisan 2009). Further and more generally, biotic interactions may not only be dependent on species traits, but also on the position of sample locations along key climatic gradients (temperature, moisture). Competition, for instance, may be stronger towards the more favorable growing conditions (Bertness and Callaway 1994, Brown et al. 1996). These interactions may variably change in a changing climate.

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## 2.9 Supplementary material

### Appendix 1 – Parameters

**Table S1.** Species-specific parameters for tree-height and LAI calculation.

| Species                    | $H_{max}$ | $D_{max}$ | $A_1$ | $A_2$ | $C_2$ |
|----------------------------|-----------|-----------|-------|-------|-------|
| <i>Abies alba</i>          | 60        | 2.15      | 0.22  | 1.6   | 6     |
| <i>Acer pseudoplatanus</i> | 37        | 2.15      | 0.06  | 1.7   | 12    |
| <i>Betula pendula</i>      | 29        | 1.15      | 0.08  | 1.4   | 12    |
| <i>Fagus sylvatica</i>     | 45        | 2.25      | 0.06  | 1.7   | 12    |
| <i>Fraxinus excelsior</i>  | 42        | 1.90      | 0.10  | 1.4   | 12    |
| <i>Picea abies</i>         | 58        | 2.10      | 0.22  | 1.6   | 6     |
| <i>Pinus cembra</i>        | 26        | 1.80      | 0.22  | 1.6   | 6     |
| <i>Pinus sylvestris</i>    | 45        | 1.55      | 0.17  | 1.4   | 6     |
| <i>Quercus petraea</i>     | 45        | 2.85      | 0.06  | 1.7   | 12    |
| <i>Quercus robur</i>       | 52        | 3.20      | 0.06  | 1.7   | 12    |
| <i>Sorbus aria</i>         | 22        | 0.55      | 0.10  | 1.4   | 12    |

Notes:  $H_{max}$ : maximum height used for calculation of actual tree height [m];  $D_{max}$ : maximum diameter at breast height [m] used for calculation of actual tree height and LAI;  $A_1$ ,  $A_2$  and  $C_2$ : parameter values used for LAI estimation.

## Appendix 2 – Leaf area index (LAI)

LAI is defined as the projected leaf area [ $\text{m}^2 \text{m}^{-2}$ ], and indicates the amount of shade produced by canopies. The cumulative leaf area index (*CumLAI*; eq. S1) of large predictor trees relative to a response species is a function of the size of the forest plot (*PS*; [ $\text{m}^2$ ]) and the species-specific double-sided foliage area (*FolA<sub>i</sub>*; [ $\text{m}^2$ ]; eq. S2) of an individual tree *i* if it is taller than the actual median height of all species in a stand (*H<sub>am</sub>*). This quantity is calculated from the foliage dry weight (*FolW<sub>i</sub>*; [kg]; eq. S3; Burger 1945–1953):

$$CumLAI = \frac{1}{PS} \times \sum_{i | H_i \geq H_{am}}^n FolA_i \quad (S1)$$

with

$$FolA_i = \frac{C_{2i}}{C_{1i}} \times FolW_i \quad (S2)$$

where  $C_{1i}$  [%/100] is the dry-to-wet ratio of foliage and  $C_{2i}$  [ $\text{m}^2 \text{kg}^{-1}$ ] is the foliage area per unit foliage weight, and

$$FolW_i = C_{1i} \times A_{1i} \times D_{ai}^{A_{2i}} \quad (S3)$$

where  $A_{1i}$  [ $\text{kg cm}^{-1}$ ] and  $A_{2i}$  [–] are allometric parameters for foliage weight. The species-specific parameter values ( $C_{1i}$ ,  $A_{1i}$  and  $A_{2i}$ ) were taken from Bugmann (1994). For each target response species we estimated the LAI\_L of predictor species of individuals that were larger than the median of the response species in each plot.

## Appendix 3 – Model accuracies

Summary table of model accuracies of ABIOT, BIOT and FULL-models calibrated with presence-absence data (PA; K, AUC) as response variable and topographic (topo-clim), species-specific proportions of abundance (AB) and species specific proportion of large individuals (AB<sub>L</sub>) as predictors. Accuracies were derived by 10-fold cross validation (CV) and external validation on NFI\_1e (NFI\_1 data from plots not used for model calibration).

|                            | ABIOT |      |      |      |      |      | BIOT <sub>AB</sub> |      |      |      |      |      | BIOT <sub>AB,L</sub> |      |      |      |      |      | FULL <sub>AB</sub> |      |      |      |      |      | FULL <sub>AB,L</sub> |      |      |      |      |      |
|----------------------------|-------|------|------|------|------|------|--------------------|------|------|------|------|------|----------------------|------|------|------|------|------|--------------------|------|------|------|------|------|----------------------|------|------|------|------|------|
|                            | CV    |      | EXT  |      | EXT  |      | CV                 |      | EXT  |      | EXT  |      | CV                   |      | EXT  |      | EXT  |      | CV                 |      | EXT  |      | EXT  |      | CV                   |      | EXT  |      | EXT  |      |
|                            | K     | AUC  | K    | AUC  | K    | AUC  | K                  | AUC  | K    | AUC  | K    | AUC  | K                    | AUC  | K    | AUC  | K    | AUC  | K                  | AUC  | K    | AUC  | K    | AUC  | K                    | AUC  | K    | AUC  | K    | AUC  |
| <i>Abies alba</i>          | 0.34  | 0.78 | 0.35 | 0.78 | 0.37 | 0.81 | 0.37               | 0.81 | 0.37 | 0.81 | 0.32 | 0.7  | 0.31                 | 0.69 | 0.57 | 0.89 | 0.58 | 0.9  | 0.49               | 0.86 | 0.48 | 0.86 | 0.48 | 0.86 | 0.49                 | 0.86 | 0.48 | 0.86 | 0.48 | 0.86 |
| <i>Acer pseudoplatanus</i> | 0.19  | 0.73 | 0.16 | 0.7  | 0.18 | 0.77 | 0.19               | 0.77 | 0.12 | 0.68 | 0.12 | 0.68 | 0.11                 | 0.67 | 0.35 | 0.85 | 0.33 | 0.84 | 0.24               | 0.77 | 0.2  | 0.74 | 0.2  | 0.74 | 0.24                 | 0.77 | 0.2  | 0.74 | 0.24 | 0.74 |
| <i>Betula pendula</i>      | 0.22  | 0.83 | 0.17 | 0.8  | 0.15 | 0.83 | 0.12               | 0.81 | 0.12 | 0.78 | 0.12 | 0.78 | 0.09                 | 0.78 | 0.25 | 0.89 | 0.19 | 0.88 | 0.21               | 0.87 | 0.17 | 0.86 | 0.17 | 0.86 | 0.21                 | 0.87 | 0.17 | 0.86 | 0.21 | 0.86 |
| <i>Fagus sylvatica</i>     | 0.45  | 0.81 | 0.44 | 0.81 | 0.45 | 0.83 | 0.42               | 0.82 | 0.2  | 0.66 | 0.23 | 0.68 | 0.23                 | 0.68 | 0.64 | 0.91 | 0.64 | 0.91 | 0.5                | 0.83 | 0.49 | 0.83 | 0.49 | 0.83 | 0.5                  | 0.83 | 0.49 | 0.83 | 0.5  | 0.83 |
| <i>Fraxinus excelsior</i>  | 0.2   | 0.78 | 0.2  | 0.78 | 0.27 | 0.8  | 0.25               | 0.8  | 0.15 | 0.67 | 0.13 | 0.63 | 0.13                 | 0.63 | 0.39 | 0.89 | 0.39 | 0.89 | 0.28               | 0.83 | 0.24 | 0.81 | 0.24 | 0.81 | 0.28                 | 0.83 | 0.24 | 0.81 | 0.28 | 0.81 |
| <i>Picea abies</i>         | 0.37  | 0.78 | 0.35 | 0.76 | 0.43 | 0.76 | 0.41               | 0.77 | 0.54 | 0.8  | 0.53 | 0.8  | 0.53                 | 0.8  | 0.58 | 0.87 | 0.57 | 0.87 | 0.61               | 0.88 | 0.59 | 0.87 | 0.59 | 0.87 | 0.61                 | 0.88 | 0.59 | 0.87 | 0.61 | 0.87 |
| <i>Pinus cembra</i>        | 0.36  | 0.98 | 0.33 | 0.98 | 0.21 | 0.93 | 0.21               | 0.94 | 0.21 | 0.94 | 0.21 | 0.9  | 0.19                 | 0.89 | 0.42 | 0.99 | 0.4  | 0.98 | 0.39               | 0.98 | 0.37 | 0.98 | 0.37 | 0.98 | 0.39                 | 0.98 | 0.37 | 0.98 | 0.39 | 0.98 |
| <i>Pinus sylvestris</i>    | 0.19  | 0.81 | 0.19 | 0.81 | 0.17 | 0.78 | 0.16               | 0.78 | 0.3  | 0.84 | 0.3  | 0.84 | 0.3                  | 0.84 | 0.31 | 0.88 | 0.3  | 0.88 | 0.38               | 0.92 | 0.37 | 0.92 | 0.37 | 0.92 | 0.38                 | 0.92 | 0.37 | 0.92 | 0.38 | 0.92 |
| <i>Quercus petraea</i>     | 0.14  | 0.86 | 0.16 | 0.87 | 0.14 | 0.84 | 0.15               | 0.85 | 0.08 | 0.72 | 0.09 | 0.76 | 0.09                 | 0.76 | 0.24 | 0.92 | 0.25 | 0.93 | 0.16               | 0.88 | 0.18 | 0.89 | 0.18 | 0.89 | 0.16                 | 0.88 | 0.18 | 0.89 | 0.16 | 0.88 |
| <i>Quercus robur</i>       | 0.12  | 0.87 | 0.11 | 0.86 | 0.06 | 0.76 | 0.07               | 0.79 | 0.04 | 0.66 | 0.04 | 0.66 | 0.04                 | 0.66 | 0.16 | 0.9  | 0.16 | 0.91 | 0.13               | 0.88 | 0.12 | 0.87 | 0.12 | 0.87 | 0.13                 | 0.88 | 0.12 | 0.87 | 0.13 | 0.87 |
| <i>Sorbus aria</i>         | 0.07  | 0.75 | 0.06 | 0.74 | 0.04 | 0.74 | 0.04               | 0.74 | 0.09 | 0.72 | 0.09 | 0.72 | 0.06                 | 0.7  | 0.08 | 0.8  | 0.08 | 0.81 | 0.11               | 0.82 | 0.08 | 0.78 | 0.08 | 0.78 | 0.11                 | 0.82 | 0.08 | 0.78 | 0.11 | 0.82 |
| Mean                       | 0.24  | 0.82 | 0.23 | 0.81 | 0.22 | 0.8  | 0.22               | 0.81 | 0.2  | 0.74 | 0.19 | 0.74 | 0.19                 | 0.74 | 0.36 | 0.89 | 0.35 | 0.89 | 0.32               | 0.87 | 0.3  | 0.86 | 0.3  | 0.86 | 0.32                 | 0.87 | 0.3  | 0.86 | 0.32 | 0.86 |
| Stdv                       | 0.12  | 0.07 | 0.12 | 0.07 | 0.14 | 0.05 | 0.13               | 0.05 | 0.15 | 0.08 | 0.14 | 0.08 | 0.14                 | 0.08 | 0.18 | 0.05 | 0.18 | 0.04 | 0.17               | 0.06 | 0.17 | 0.07 | 0.07 | 0.07 | 0.17                 | 0.06 | 0.17 | 0.07 | 0.07 | 0.07 |

## Appendix 4 – Model accuracies

Summary table of model accuracies of ABIOT, BIOT and FULL-models calibrated with proportions of basal areas (BA; MAE, RMSE and R<sup>2</sup>) as response variable and topo-climatic (topo-clim), species-specific proportions of abundance (AB) and species-specific proportion of large individuals (AB<sub>L</sub>) as predictors. Accuracies are derived by 10-fold cross validation (CV) and external validation on NFL\_1e (NFL\_1 data from plots not used for model calibration).

|                            | ABIOT |      |                | BIOT <sub>AB</sub> |      |                | BIOT <sub>AB,L</sub> |      |                | FULL <sub>AB</sub> |      |                | FULL <sub>AB,L</sub> |      |                |      |      |       |      |      |       |      |      |       |      |      |       |      |      |       |
|----------------------------|-------|------|----------------|--------------------|------|----------------|----------------------|------|----------------|--------------------|------|----------------|----------------------|------|----------------|------|------|-------|------|------|-------|------|------|-------|------|------|-------|------|------|-------|
|                            | CV    | EXT  | R <sup>2</sup> | CV                 | EXT  | R <sup>2</sup> | CV                   | EXT  | R <sup>2</sup> | CV                 | EXT  | R <sup>2</sup> | CV                   | EXT  | R <sup>2</sup> |      |      |       |      |      |       |      |      |       |      |      |       |      |      |       |
| <i>Abies alba</i>          | 0.15  | 0.79 | 12.86          | 0.15               | 0.21 | 14.01          | 0.13                 | 1.51 | 25.19          | 0.13               | 1.20 | 24.80          | 0.16                 | 1.24 | 6.07           | 0.17 | 0.94 | 5.55  | 0.08 | 1.16 | 53.79 | 0.09 | 0.85 | 55.18 | 0.13 | 0.94 | 25.91 | 0.13 | 0.77 | 26.31 |
| <i>Acer pseudoplatanus</i> | 0.04  | 0.53 | 1.96           | 0.04               | 0.52 | 1.31           | 0.05                 | 0.57 | 8.77           | 0.05               | 0.68 | 8.03           | 0.05                 | 0.77 | 0.91           | 0.05 | 0.90 | 0.18  | 0.04 | 0.39 | 16.66 | 0.04 | 0.53 | 20.10 | 0.05 | 0.75 | 3.24  | 0.05 | 0.89 | 2.28  |
| <i>Betula pendula</i>      | 0.02  | 0.40 | 12.99          | 0.02               | 0.28 | 8.68           | 0.02                 | 0.39 | 6.74           | 0.02               | 0.22 | 5.95           | 0.02                 | 0.43 | 4.50           | 0.02 | 0.27 | 4.46  | 0.02 | 0.39 | 23.08 | 0.02 | 0.26 | 21.05 | 0.02 | 0.43 | 18.98 | 0.02 | 0.28 | 16.55 |
| <i>Fagus sylvatica</i>     | 0.18  | 0.33 | 18.79          | 0.18               | 0.04 | 17.44          | 0.16                 | 0.15 | 32.02          | 0.16               | 0.43 | 31.51          | 0.22                 | 0.50 | 7.80           | 0.22 | 0.31 | 7.42  | 0.11 | 0.42 | 59.17 | 0.11 | 0.29 | 58.15 | 0.17 | 0.71 | 29.82 | 0.17 | 0.47 | 27.23 |
| <i>Fraxinus excelsior</i>  | 0.05  | 0.65 | 4.80           | 0.05               | 0.36 | 4.85           | 0.05                 | 0.32 | 14.71          | 0.05               | 0.11 | 13.74          | 0.06                 | 0.57 | 4.02           | 0.05 | 0.34 | 3.50  | 0.04 | 0.33 | 26.77 | 0.04 | 0.16 | 27.73 | 0.05 | 0.54 | 12.48 | 0.05 | 0.37 | 13.44 |
| <i>Picea abies</i>         | 0.29  | 3.08 | 26.52          | 0.30               | 3.17 | 23.93          | 0.20                 | 4.69 | 43.38          | 0.21               | 5.14 | 41.10          | 0.28                 | 5.50 | 26.26          | 0.29 | 6.13 | 23.64 | 0.16 | 3.92 | 61.77 | 0.16 | 3.97 | 61.75 | 0.23 | 4.72 | 41.59 | 0.24 | 4.99 | 39.11 |
| <i>Pinus cembra</i>        | 0.01  | 0.02 | 35.25          | 0.01               | 0.01 | 30.56          | 0.02                 | 0.17 | 10.91          | 0.02               | 0.29 | 7.72           | 0.02                 | 0.01 | 8.03           | 0.02 | 0.12 | 4.96  | 0.01 | 0.05 | 38.12 | 0.01 | 0.07 | 33.46 | 0.01 | 0.00 | 32.62 | 0.01 | 0.01 | 29.52 |
| <i>Pinus sylvestris</i>    | 0.06  | 0.24 | 15.94          | 0.06               | 0.36 | 8.63           | 0.06                 | 1.14 | 4.91           | 0.06               | 1.26 | 2.49           | 0.05                 | 1.10 | 9.57           | 0.06 | 1.28 | 4.54  | 0.04 | 1.04 | 25.16 | 0.04 | 1.18 | 18.08 | 0.04 | 0.95 | 32.09 | 0.04 | 1.14 | 17.91 |
| <i>Quercus petraea</i>     | 0.02  | 0.10 | 5.13           | 0.02               | 0.15 | 7.47           | 0.02                 | 0.13 | 6.46           | 0.02               | 0.14 | 9.78           | 0.02                 | 0.03 | 2.07           | 0.02 | 0.00 | 4.16  | 0.02 | 0.13 | 21.50 | 0.02 | 0.21 | 18.16 | 0.02 | 0.06 | 10.16 | 0.02 | 0.08 | 15.03 |
| <i>Quercus robur</i>       | 0.02  | 0.02 | 2.71           | 0.02               | 0.05 | 6.01           | 0.02                 | 0.20 | 1.19           | 0.02               | 0.22 | -0.36          | 0.02                 | 0.14 | -0.67          | 0.02 | 0.15 | -1.41 | 0.01 | 0.16 | 1.60  | 0.01 | 0.21 | 3.37  | 0.01 | 0.12 | 2.37  | 0.01 | 0.16 | 4.74  |
| <i>Sorbus aria</i>         | 0.00  | 0.07 | 0.81           | 0.00               | 0.02 | 0.42           | 0.01                 | 0.22 | 0.70           | 0.01               | 0.15 | 0.68           | 0.01                 | 0.23 | 0.18           | 0.01 | 0.16 | -0.19 | 0.01 | 0.21 | 3.87  | 0.01 | 0.13 | 1.75  | 0.01 | 0.23 | 2.13  | 0.01 | 0.16 | 0.86  |
| Mean                       | 0.08  | 0.57 | 12.52          | 0.08               | 0.47 | 11.21          | 0.07                 | 0.86 | 14.09          | 0.07               | 0.89 | 13.22          | 0.08                 | 0.96 | 6.25           | 0.08 | 0.97 | 5.16  | 0.05 | 0.75 | 30.13 | 0.05 | 0.71 | 28.98 | 0.07 | 0.86 | 19.22 | 0.07 | 0.85 | 17.54 |
| Stdv                       | 0.09  | 0.87 | 11.06          | 0.09               | 0.91 | 9.44           | 0.07                 | 1.35 | 13.72          | 0.07               | 1.47 | 13.51          | 0.09                 | 1.56 | 7.46           | 0.10 | 1.76 | 6.69  | 0.05 | 1.11 | 20.77 | 0.05 | 1.13 | 20.99 | 0.08 | 1.33 | 14.01 | 0.08 | 1.42 | 12.16 |

### 3 Co-occurrence patterns of trees along macro-climatic gradients and their potential influence on the present and future distribution of *Fagus sylvatica* L. [Paper 2]

Meier E.S.<sup>1</sup>, T.C. Edwards<sup>2</sup>, F. Kienast<sup>1</sup>, M. Dobbertin<sup>3</sup> and N.E. Zimmermann<sup>1</sup>. 2011. Co-occurrence patterns of trees along macro-climatic gradients and their potential influence on the present and future distribution of *Fagus sylvatica* L.. *Journal of Biogeography* **38**:371-382.

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#### 3.1 Abstract

**Aim** During recent and future climate change, shifts in large-scale species ranges are expected due to the hypothesized major role of climatic factors in regulating species distributions. The stress-gradient hypothesis suggests that biotic interactions may act as major constraints on species distributions under more favourable growing conditions, while climatic constraints may dominate under unfavourable conditions. We tested this hypothesis for one focal tree species having three major competitors using broad-scale environmental data. We evaluated the variation of species co-occurrence patterns in climate space and estimated the influence of these patterns on the distribution of the focal species for current and projected future climates.

**Location** Europe.

**Methods** We used ICP Forest Level 1 data as well as climatic, topographic and edaphic variables. First, correlations between the relative abundance of European beech (*Fagus sylvatica*) and three major competitor species (*Picea abies*, *Pinus sylvestris* and *Quercus robur*) were analysed in environmental space, and then projected to geographic space. Second, a sensitivity analysis was performed using generalized additive models (GAM) to evaluate where and how much the predicted *F. sylvatica* distribution varied under current and future climates if potential competitor species were

included or excluded. We evaluated if these areas coincide with current species co-occurrence patterns.

**Results** Correlation analyses supported the stress-gradient hypothesis: towards favourable growing conditions of *F. sylvatica*, its abundance was strongly linked to the abundance of its competitors, while this link weakened towards unfavourable growing conditions, with stronger correlations in the south and at low elevations than in the north and at high elevations. The sensitivity analysis showed a potential spatial segregation of species with changing climate and a pronounced shift of zones where co-occurrence patterns may play a major role.

**Main conclusions** Our results demonstrate the importance of species co-occurrence patterns for calibrating improved species distribution models for use in projections of climate effects. The correlation approach is able to localize European areas where inclusion of biotic predictors is effective. The climate-induced spatial segregation of the major tree species could have ecological and economic consequences.

**Keywords** Climate change, environmental gradients, Europe, forest, generalized additive models, relative abundance, species distribution model, species interactions, stress-gradient hypothesis.

### 3.2 Introduction

Species responses along macro-climatic gradients have often been interpreted to represent the realized ecological niche sensu Hutchinson (Austin et al., 1990; Araújo & Guisan, 2006). This means that large-scale species patterns are not only influenced by macro-climatic and other abiotic environmental predictors, but also by species (i.e. biotic) interactions. The importance of biotic interactions may vary according to scale and position along environmental gradients. For instance, biotic interactions are recognized as important local filters of species distributions (Lortie et al., 2004; Meier et al., 2010). This local filtering is inherent in the stress-gradient hypothesis (e.g. Bertness & Callaway, 1994; Callaway & Walker, 1997), which predicts negative interspecific biotic interactions (i.e. competition) mainly towards favourable growing conditions, and positive interspecific biotic interactions (i.e. facilitation) and physiological stress towards unfavourable growing conditions. The stress-gradient hypothesis has been widely supported in the theoretical literature (Bertness & Callaway, 1994) and by a broad range of small-scale studies based on experiments and surveys of population dynamics (e.g. Callaway et al., 2002; Saccone et al., 2009). Still largely missing, however, is empirical quantification of the strength of interspecific competition along large-scale climate gradients (but see Normand et al., 2009).

Species distribution models (SDMs) are powerful tools for relating species occurrences to environmental variables (Guisan & Zimmermann, 2000; Guisan & Thuiller, 2005). Abiotic factors play a prominent role in SDMs, whereas biotic interactions are frequently subsumed in the abiotic predictors. This may lead to an under- or overestimation of biotic interactions and to bias in the predicted distribution of species. Altered temperature and moisture regimes under projected climate change may even aggravate these biases. Thus, efforts are needed to improve SDMs by incorporating, for example, biotic interactions (Leathwick & Austin, 2001; Araújo & Luoto, 2007; Heikkinen et al., 2007). Knowledge of climatic conditions where biotic interactions may act as relevant constraints on large-scale species distributions would help ecologists and conservationists understand how species might shift their ranges in the future (Davis et al., 1998; Williams & Jackson, 2007). In forest management, for example, altered climate regimes may affect silvicultural planting decisions, requiring consideration of tree species adapted to both current and projected future climate. According to some current predictions, treelines may shift upwards if future temperatures rise (Dullinger et al., 2004), while in forests tree species may experience drought stress and die back, or may experience changes in composition as a result of species-specific migration rates.

However, if the relative importance of species interactions along macro-climatic gradients is included in climate effects models, these predictions may be different. In silviculture, for instance, partial failure of commercial tree plantings can occur not only because trees have been planted outside the range of their physiological tolerance (e.g. too cold or dry), but also because trees were planted in areas where interspecific competition was high (Kimmins, 2004). Thus, the distribution of a species may change not only because of altered climatic conditions, but also because of altered competitive interactions that themselves change as potential competitors move in response to climate change.

Competition between species for light, soil nutrients, soil moisture or space may result in a reduction of the above- and below-ground growth or abundance of species in co-existence, or it may even act as a filter for determining whether a species may or may not become established in a given community (Grime, 1979; Begon et al., 2006). Therefore, competitive effects may be measured by reduced biomass or abundance of a focal species if competitors are present, and by a strong link between the biomass or abundance of the focal species and the competitors. Competitive abilities of species may vary in space either because of variation in the biotic and abiotic environment (e.g. Smith et al., 1971) or because of intraspecific genetic variation (e.g. Bradshaw & Snaydon, 1959).

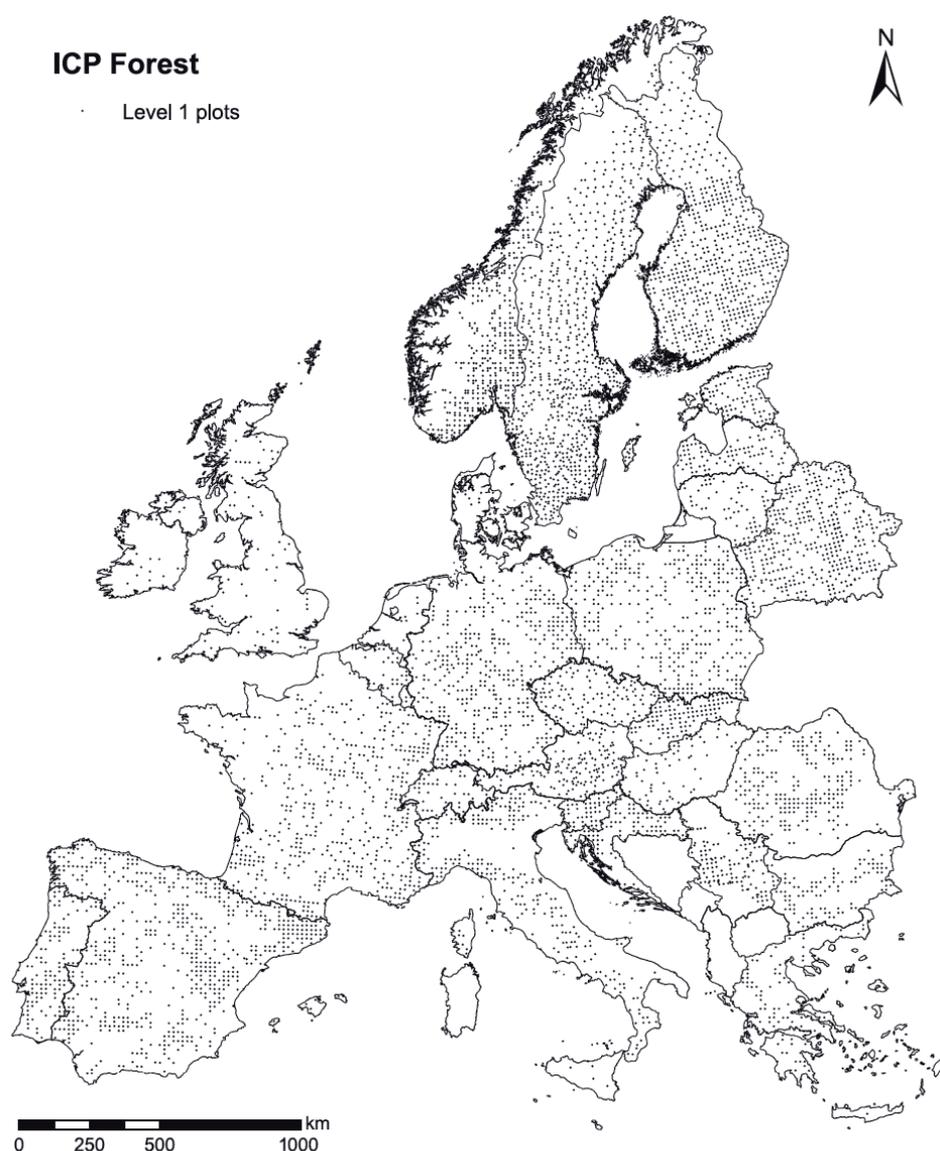
In this paper: (1) we evaluate how correlation patterns of the relative abundance of European beech (*Fagus sylvatica* L.) with three species, each of which act as major competitors under specific environmental conditions [Norway spruce, *Picea abies* (L.) H. Karsten; Scots pine, *Pinus sylvestris* L.; and pedunculate oak, *Quercus robur* L.], change along two main macro-climatic

gradients (temperature and moisture); (2) we project these patterns into geographic space; (3) we evaluate where and how much predictions of *F. sylvatica* distributions for current and future climate differ when comparing models that are based solely on climate, soil and topography against models that additionally include the predicted relative abundance of the three competitor species; and (4) we assess if these areas coincide with the correlation patterns in geographic space. The selected tree species are common and commercially important in Europe, and are expected to compete at different strengths under different macro-climatic conditions (Woodward, 1987; Ellenberg, 1996; Bolte et al., 2007). We expect from the stress-gradient hypothesis that the link between species co-occurrences may be strong towards favourable growing conditions of *F. sylvatica* and weak towards unfavourable growing conditions. In geographic space, this would lead to a large variance in co-occurrence patterns along a north–south gradient, and along an elevational gradient. Because of altered climatic conditions in the future, followed by range changes and a potential spatial segregation of the competitor species, we expect that the effects from the co-occurrence patterns in geographic space on *F. sylvatica* distribution may change in the future.

### 3.3 *Material and methods*

#### 3.3.1 Study area

The study area encompassed all of Europe (34–72°N, 11°W–32°E; c. 5.7 x 10<sup>6</sup> km<sup>2</sup>; Fig. 1). Around 80–90% of Europe was once covered by forest, but due to deforestation more than two-thirds of the natural forest areas have disappeared, although many trees have been planted. In recent years, many monoculture plantations of conifers have been replaced by more natural mixed forest, resulting in semi-natural forests of broadleaf and coniferous species. The most important species in Central and Western Europe are *F. sylvatica* and *Quercus* spp., whereas *Picea* spp., *Pinus* spp. and *Betula* spp. dominate the taiga in the north.

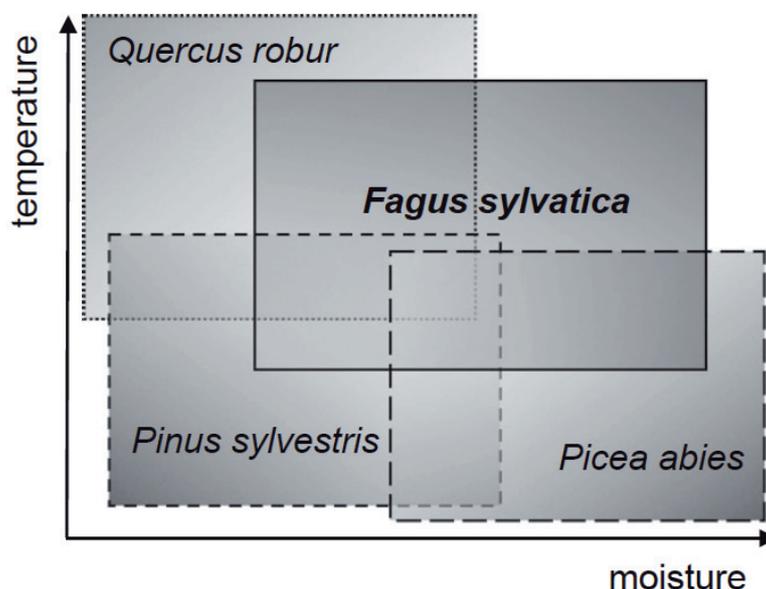


**Figure 1** Distribution of the ICP Forest Level 1 plots. The plots are distributed nationally on a systematic grid of c. 16 x 16 km using national projections, covering c. 6000 forest plots.

### 3.3.2 Species data

Our focal tree species was European beech (*Fagus sylvatica*, nplots = 831; see Appendix S1 in the Supporting Information). We selected as potential competitor species Norway spruce (*Picea abies*, nplots = 2118), Scots pine (*Pinus sylvestris*, nplots = 2570) and pedunculate oak (*Quercus robur*, nplots = 548; see Appendix S1). The selected tree species are abundant and commercially important in Europe, and are expected to compete under different climatic conditions at varying strengths (Fig. 2) (Woodward, 1987; Ellenberg, 1996). *Fagus sylvatica* is expected to dominate under moderately

warm and wet conditions. Relative to *F. sylvatica*, *P. abies* dominates under colder conditions, *P. sylvestris* under colder and drier conditions, and *Q. robur* under warmer and drier conditions.



**Figure 2** Expected competitive abilities of *Fagus sylvatica* and its potential competitors in relation to the climatic condition (dark: high competitive ability, bright: low competitive ability).

Species data were extracted from the large-scale transnational survey of forest condition in Europe under the International Co-operative Programme on Assessment and Monitoring of Air Pollution Effects on Forests (ICP Forests Level 1; Lorenz, 1995). The database contains information on individual trees of every species occurring in predefined plots. The plots are distributed on systematic national grids of c.16 x 16 km throughout Europe, covering c. 6000 plots (Fig. 1). Relevant data for this study, the number of individuals per species, were recorded in four sub-plots at a distance of 25 m from the centre grid point (Eichhorn et al., 2006). On each subplot a minimum of six trees (with a minimum height of 60 cm) nearest to the subplot centre were recorded, resulting in > 24 trees per plot. Data used for the analyses were collected in 2005 and 2006.

Competition between species may be expressed as a reduction of the relative above-and below-ground biomass or abundance of species in co-existence. Because relative basal area (a surrogate of biomass) has been shown to be highly correlated with relative abundance (Meier et al., 2010), we estimated effects from species co-occurrence patterns along climatic gradients by variation in the relative abundance of species. Relative abundance is defined as the proportion of the stem number of a focal species relative to the total number of stems of every species recorded in a plot.

Correlations among the relative abundance values of the three selected potential competitor species of *F. sylvatica* in the European forest inventory were all  $< |0.5|$  (see Appendix S2), avoiding multicollinearity problems when adding the species as biotic predictors in regression models.

### 3.3.3 Environmental data

We selected environmental data from a comprehensive set of climatic, edaphic and topographic variables on the basis of their relevance to plant physiology and for explaining large-scale spatial patterns. The selected variables all had correlations  $< |0.5|$  (see Appendix S2), which reduced potential problems regarding multicollinearity. Environmental data were generated at a 750-m spatial resolution for all of Europe.

Climate data were based on monthly averages of temperature and precipitation maps of WorldClim (30 arc s resolution c. 750 m resolution over Europe) for current climate (1950–2000, <http://www.worldclim.org>; Hijmans et al., 2005) and the years 2040, 2070 and 2100 for two climate scenarios originating from the Hadley Centre Coupled Model, version 3 (HadCM3). Future climates are calculated using SRES scenarios as specified by the Intergovernmental Panel on Climate Change. We used the A1fi scenario, which represents a global economic and fossil fuel-intensive world with a global average surface warming of c. 4 °C until 2100 relative to 1980–99; and the B2 scenario, which represents a regional environmental world with a global average surface warming of c. 2.4 °C. Following Zimmermann & Kienast (1999), we derived degree-days with a 5.56 °C threshold (DDEG556, °C\*days) and summer precipitation (PRSU, average of April–September, mm).

Soil data used included texture (TEXT, percentage of clay and sand) and cation-exchange capacity of the topsoil (CEC\_TOP, cmol kg<sup>-1</sup>). Variables were derived from polygon maps of the European Soil Bureau Network and the European Commission (2004).

Topography data included slope (SLOPE, degrees) derived from a global digital elevation model (GTopo30, 30 arc s resolution); and topographic position (TOPOS, range) expressed as the difference between the average elevation in a circular moving window applied to the global digital elevation model and the centre cell of the window (Zimmermann et al., 2007).

### 3.3.4 Statistical analyses

#### 3.3.4.1 Correlation analysis of species pairs

To examine the co-occurrence patterns of species pairs in climatic space (DDEG, PRSU), we analysed the correlation between the relative abundance of each species pair in moving windows. The values of the grid cells of the two climate variables were split according to the range of the values into 40 equally sized bins (climate cells, hereafter). The size of the analysis window was 5 x 5 climate

cells. The window was moved from cell to cell through climate space. If at least 15 abundance values  $> 0$  of both species were present in an analysis window, a correlation value was written to the centre climate cell of the moving window. Finally, we projected correlations between species pairs from climate space into geographic space using look-up tables. We used Spearman's rank correlation coefficient ( $r_s$ ) because of the proportional data (i.e. relative abundance per species and plot) and because of the partly small sample sizes.

We tested if the variation in correlations was an artefact of 'spurious correlations' (Köhler et al., 2007) rather than an effect from variation in species co-occurrence patterns. Spurious correlations may occur if the two species are highly abundant, and their relative abundance in a forest plot sums to almost 100%. We therefore assessed whether correlations increased with increasing sums of relative abundance of the two species. However, we found no such patterns, therefore we concluded that spurious correlations were marginal and unimportant in successive analyses.

#### 3.3.4.2 Predictions of species distributions

To map the degree of the effect of co-occurrence patterns relative to the climatic condition on current and future relative *F. sylvatica* abundance, we constructed generalized additive models (GAM) with and without the relative abundance of the three potential competitor species as biotic predictors. We used climatic, topographic and edaphic variables as abiotic predictors. Our response variable was the proportion of individual beech trees in a forest plot. In order to exclude possible effects originating from differing numbers of individuals, we used weighted GAMs where the total number of individuals of all tree species in a plot was used as weight. All GAMs were built using the R package *mgcv*, where the degree of smoothing is selected by internal cross-validation maximizing model predictive accuracy (Wood, 2008).

Models were predicted to all of Europe for current and future climates. For models with biotic predictors, we first mapped the potential distribution of the relative abundance of the competitor species using GAMs with climatic, topographic and edaphic predictors for current and future climates. We next used these competitor maps for the predictions of *F. sylvatica*. In order to keep the models parsimonious, we used only abiotic envelopes for the potential competitor species. Adding biotic drivers for the competitor species would require us to consider additional competitors of oak, spruce and pine. Furthermore, we have good ecological reasons (see Discussion) to assume that *F. sylvatica* is the strongest of the four competitors and consequently experiencing the least negative influence from the presence of the other species.

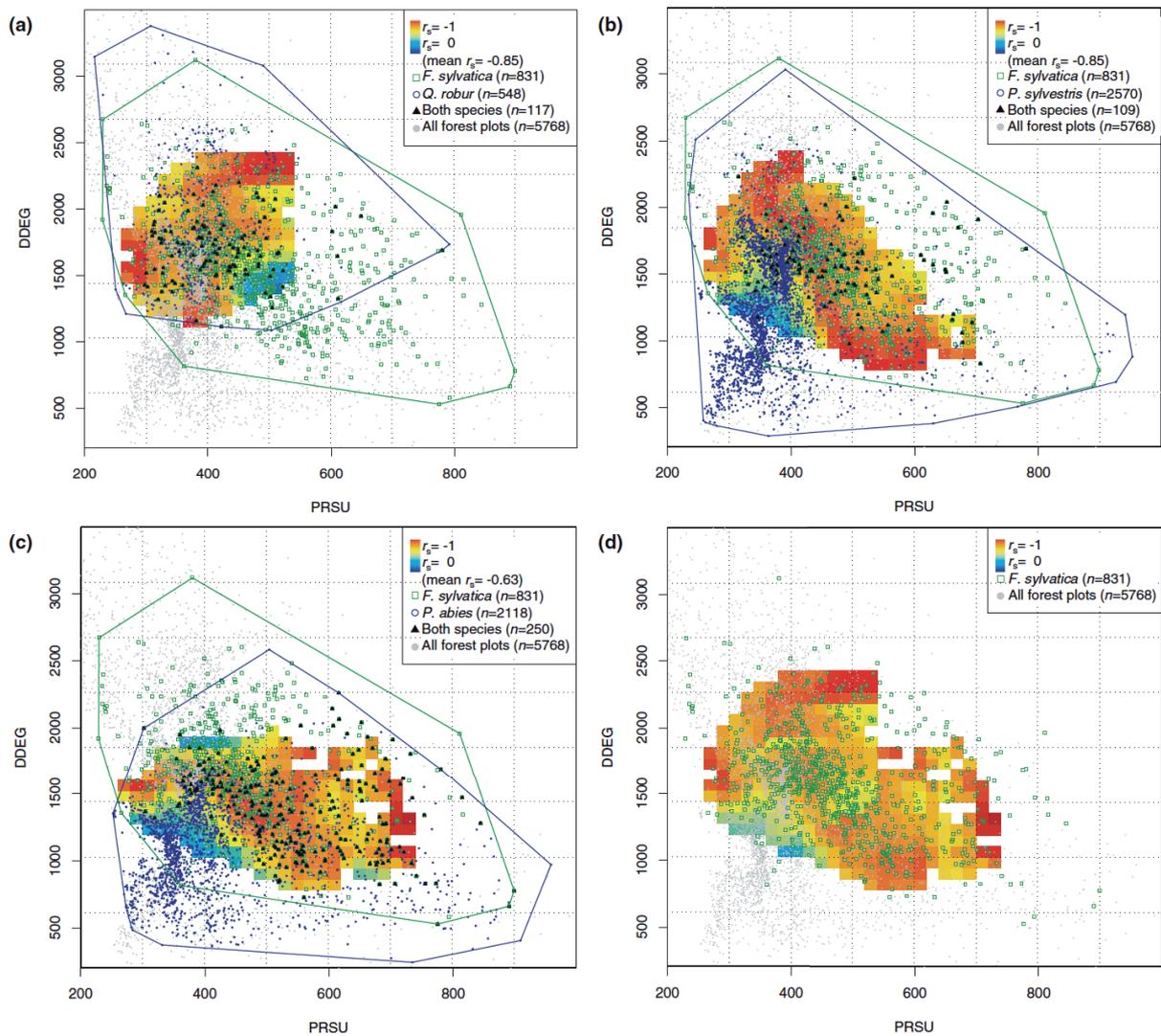
Model fit was evaluated by the adj.  $D^2$ ; model errors and quality were assessed by a 10-fold cross-validation, where we calculated the mean absolute error (MAE), root mean square error

(RMSE) and the coefficient of determination ( $R^2$ ). All data were analysed and prepared using R (R Development Core Team, 2008) and ArcGIS 9.2 (ESRI, 2006).

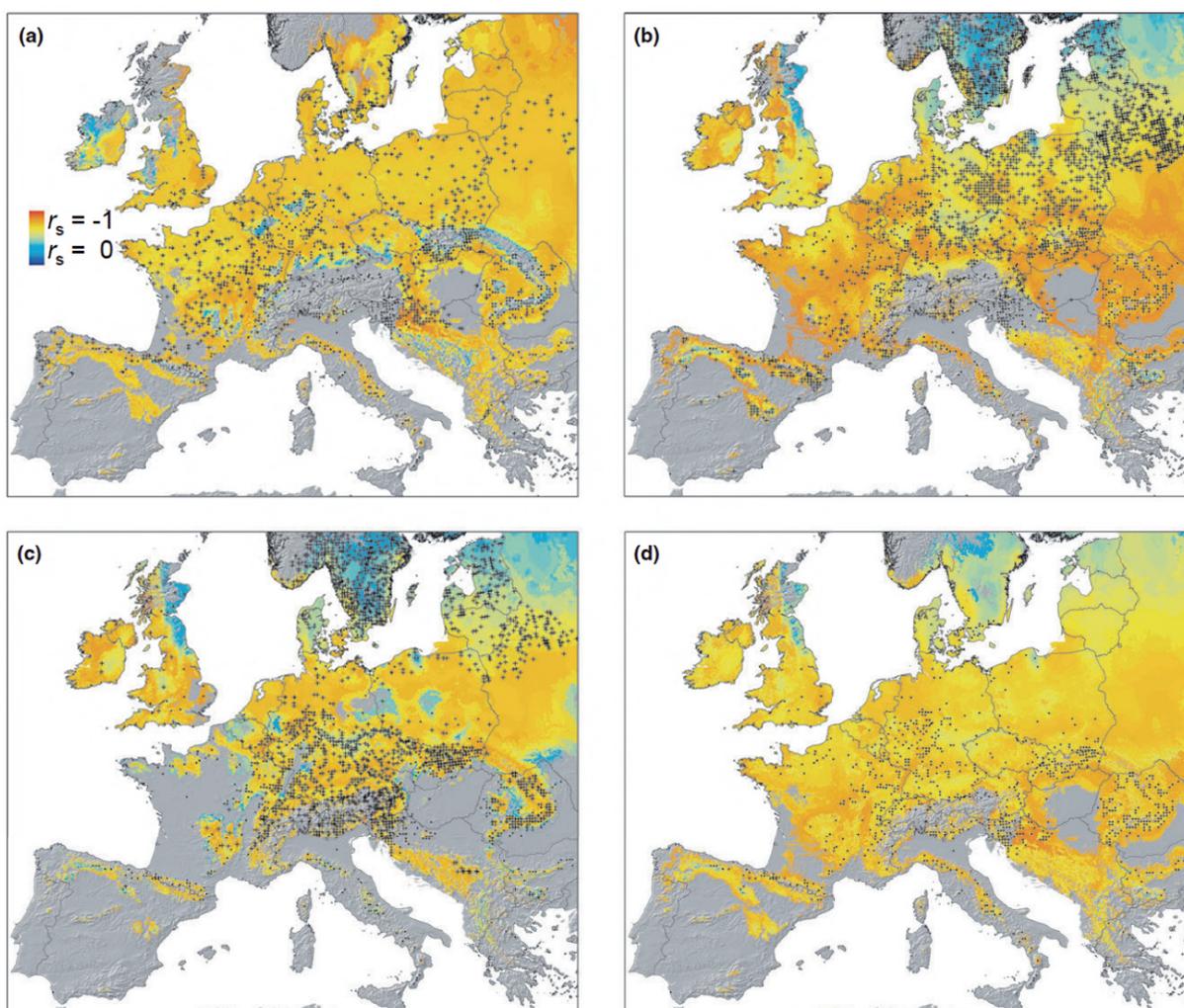
## 3.4 Results

### 3.4.1 Correlation analysis of species pairs

Correlation patterns in climate space differ between each of the potential competitor species and *F. sylvatica* (Kruskal–Wallis chi-square test,  $P < 0.001$ ; see Appendix S3). However, they all reveal stronger correlations towards warm and/or wet conditions, and weaker correlations towards colder and drier conditions, except for *Q. robur*, which is only weakly correlated with *F. sylvatica* under cold and wet conditions (Fig. 3). This pattern becomes stronger once all three correlation maps are averaged (Fig. 3d). This mean correlation among species reveals strong geographic patterns. We found significant correlations with latitude ( $r_s = -0.60$ ,  $P < 0.001$ ) and elevation ( $r_s = 0.25$ ,  $P < 0.001$ ) over the scale of Europe, with stronger correlations at more southern latitudes and lower elevations and with lower correlations at more northern latitudes and higher elevations (Fig. 4).



**Figure 3** Spearman's rank correlation patterns of *Fagus sylvatica* and three competitor species along temperature (DDEG: degree-days using a 5.56 °C threshold) and moisture (PRSU: summer precipitation sum) gradients. Panels show correlation pattern of *Fagus sylvatica* with (a) *Quercus robur*, (b) *Pinus sylvestris* and (c) *Picea abies* in the climate space where each of the species occurs (polygons), while the mean among the tree correlations is mapped in (d). Numbers in brackets represent numbers of forest plots. Mean Spearman's rank correlation coefficient (mean  $r_s$ ) indicates the overall correlation between each species pair across the whole climate space.



**Figure 4** Spearman's rank correlations along temperature and moisture gradients (see Fig. 3 for details) between *Fagus sylvatica* (•) and the selected competitor species (+) projected to the geographic space: (a) *Quercus robur*, (b) *Pinus sylvestris*, (c) *Picea abies*. The mean among the three maps (d) was derived by averaging the three species-specific correlations.

### 3.4.2 Predictions of species distributions

The distribution model for *F. sylvatica* calibrated without biotic predictors has lower adj.  $D^2$  and  $R^2$  fits, and higher MAE and RMSE errors than the model that included biotic predictors (Table 1). Adj.  $D^2$  of individual predictors is given in Appendix S4.

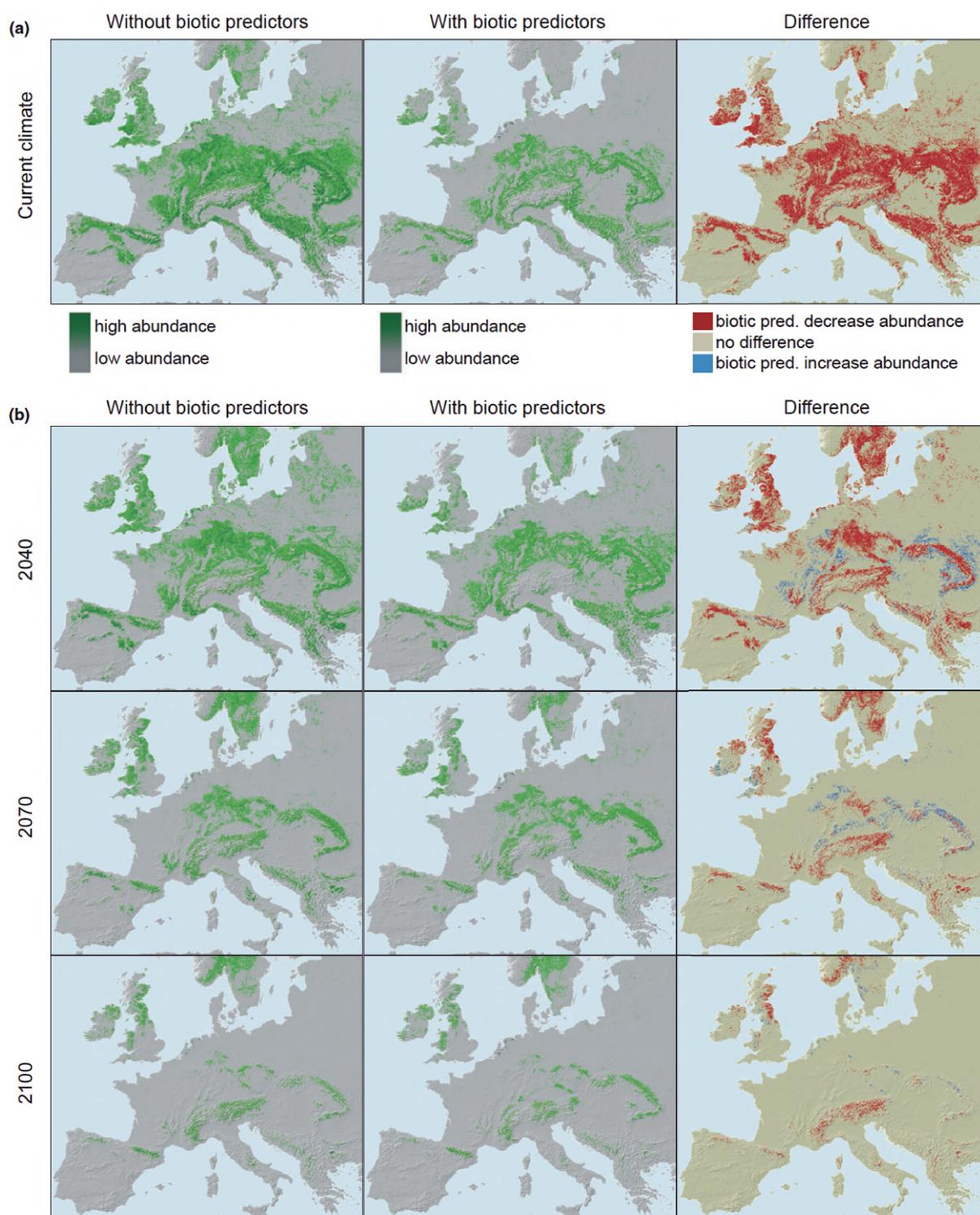
Under current climatic conditions, the inclusion of the biotic predictors reduces the predicted *F. sylvatica* range more in lower elevations and southward than in higher elevations and northward (Fig. 5a). This is demonstrated by significant correlations between changes in the predicted *F. sylvatica* abundance when adding biotic predictors on the one hand, and latitude ( $r_s = 0.39$ ,  $P <$

0.001) or elevation ( $r_s = 0.29$ ,  $P < 0.001$ ) on the other hand. These areas coincide with the geographic regions where strong correlations between *F. sylvatica* and its three potential competitors were found. Under future climate scenario conditions (years 2040, 2070 and 2100 for A1fi and B2 SRES scenarios), the use of biotic predictors generates less prominent effects, that is, the differences in predicted distribution patterns with or without including biotic predictors are smaller and the geographic patterns generally change (Fig. 5b,c).

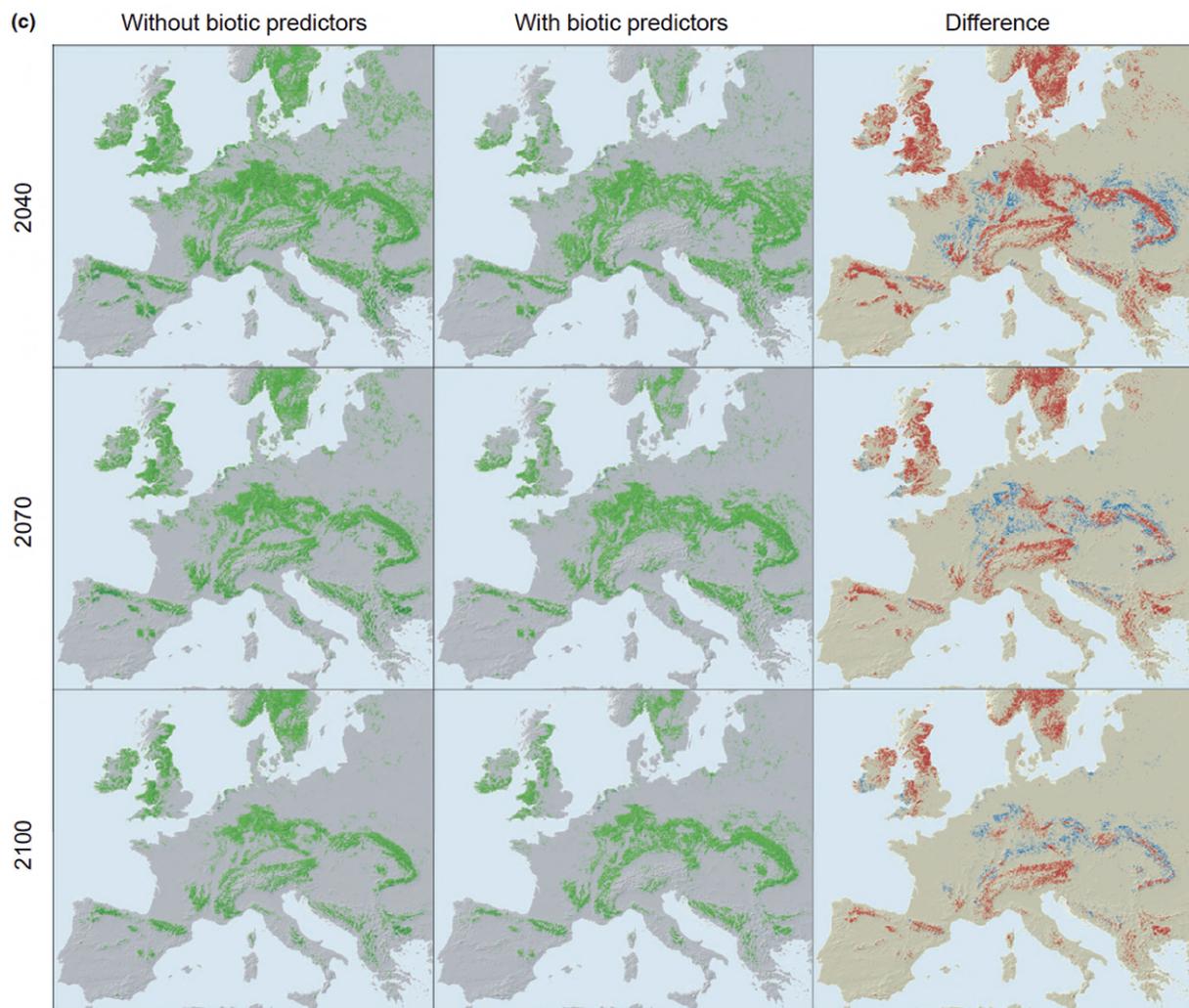
The most prominent changes are as follows: in the A1fi scenario (Fig. 5b) for the year 2040, areas at low elevations emerge where biotic predictors enhance the predicted abundance. For the year 2070, areas where biotic predictors reduce predicted high abundance in *F. sylvatica* are restricted to mid and high elevations, and areas where biotic predictors enhance the predicted abundance are occurring at mid elevation. For the year 2100, areas where biotic predictors reduce the predicted patterns are restricted to high elevations, and areas where biotic predictors enhance the predicted abundance have almost disappeared. The same effects, although less strong, can also be seen for the B2 scenario (Fig. 5c). Averaged over the entire continent, the inclusion of biotic predictors leads to a consistent decrease of the predicted relative abundance of *F. sylvatica* over Europe (Fig. 6). The effect decreases over time, with the 2100 predictions showing the lowest effect.

**Table 1** Model fit (adj.  $D^2$ ), model errors (MAE, mean absolute error; RMSE, root mean square error) and model quality ( $R^2$ ) of the generalized additive models for current *Fagus sylvatica* distribution calibrated with and without biotic predictors, assessed by a 10-fold cross-validation.

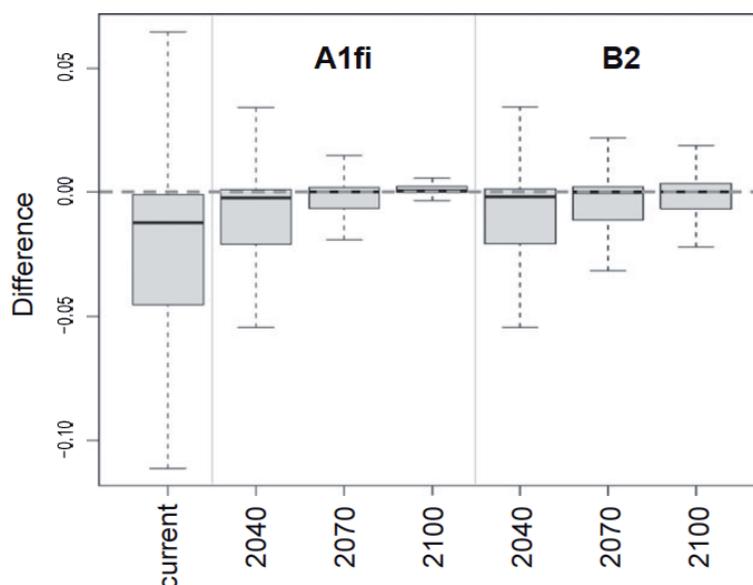
|                           | adj. $D^2$ | MAE  | RMSE | $R^2$ |
|---------------------------|------------|------|------|-------|
| Without biotic predictors | 0.38       | 0.11 | 0.71 | 17.36 |
| With biotic predictors    | 0.60       | 0.08 | 0.60 | 35.33 |



**Figure 5** Predictions of the relative abundance of *Fagus sylvatica* in Europe (a) for current climate; (b,c) for 2040, 2070 and 2100 according to (b) the A1fi scenario and (c) the B2 SRES scenario from models calibrated with climatic, edaphic and topographic predictors and from models calibrated additionally with biotic predictors.



**Figure 5** Continued



**Figure 6** Difference in predicted relative tree abundance of *Fagus sylvatica* across Europe with and without biotic predictors for current and future climate according to the A1fi and B2 SRES scenarios. If the difference of the relative abundance is positive, the model that includes biotic predictors yields higher abundances than the model without biotic predictors.

### 3.5 Discussion

Predictions from SDMs based only on abiotic factors have been criticised as incomplete representations of natural patterns because they ignore important aspects such as competition, human activities and other local processes (Rouget et al., 2001; Araújo & Luoto, 2007). Despite this shortcoming, SDMs still remain the best available tool for rapid species-specific assessments of potential ranges under current or potentially changed conditions (Pearson & Dawson, 2003). Our results highlight the climatic conditions under which omitting biotic predictors subsuming local biotic and abiotic processes may be especially critical for generating reliable prediction maps, and may thus help to interpret maps generated by SDMs. To ensure a correct interpretation of our results, we mention several critical discussion points below.

First, our analysis was restricted to four species. We examined correlation patterns among European beech (*F. sylvatica*) and three of its key competitor species, and estimated the potential influence of the abundance of these competitors on the distribution of *F. sylvatica* under current and projected future climate. Further species may be tested for similar effects.

Second, we used an observational approach. Competition for limited resources such as light, soil moisture, nutrients and space between and among species may result in a reduction of fitness (e.g.

Tilman, 1994; Rouget et al., 2001), while the individual strength of competition depends on the carrying capacity of the environment (Grime, 1979). Based on this definition, observational studies often assume that the relative abundance of species is reduced if competitor species are present (e.g. Rouget et al., 2001; Latimer et al., 2009). However, variation in correlations may also be associated with interspecific facilitation, local habitat heterogeneity, evolutionary history or stochastic processes (Bell, 2003; Veech, 2006). Thus, we cannot directly demonstrate competition with our analysis even though we used small-scale species data.

Third, cause and effect of co-occurrence patterns are hard to separate (Huston, 1997), particularly with observational approaches. Experimental studies where species are grown in manipulated mixtures (e.g. Perkins et al., 2007; Rewald & Leuschner, 2009) clearly provide greater inference. However, we would have had the disadvantage of studying only a few climatic conditions with relatively few replicates, and therefore it would still have been difficult to demonstrate the variability of competition or other forms of biotic interaction along multiple environmental gradients and over large spatial scales with several interacting species.

Fourth, it is unclear from co-occurrence patterns alone which species is influencing the distribution of the others. We selected species that are expected to compete under different climatic conditions at varying strengths. Our focal species, *F. sylvatica*, is the strongest competitor under moderately warm and wet conditions because of a medium frost and heat tolerance, and a high potential to access topsoil moisture and nutrients due to its fine-root structure (Bolte & Villanueva, 2006). It has the highest shade tolerance compared with the other species selected for this study (Ellenberg, 1996), and may also have an advantage in the competition for soil moisture and nutrients (Kobe et al., 1995; Welander & Ottosson, 1998). *Picea abies* is more competitive under colder conditions because of its higher frost tolerance but lower heat tolerance. Under optimal conditions, *P. abies* is co-dominant with *F. sylvatica*; despite having a slightly lower shade tolerance, it grows quickly and can reach the highest size among the forest trees in Europe (Bugmann, 1994), thus gaining direct access to light. *Pinus sylvestris* is more dominant under colder and drier conditions because of its higher frost tolerance but lower heat tolerance, and its higher drought tolerance due to tap-roots whereby it can access deep water-bearing strata (Burns & Honkala, 1990). *Quercus robur* dominates under warmer and drier conditions because of its lower frost tolerance but higher heat tolerance, and its higher drought tolerance due to a fibrous root system allowing it access to both deep waterbearing strata and upper strata, containing more nutrients (van Hees, 1997). However, *Q. robur* may be the weakest competitor among the four species included in this study (Björkman & Bradshaw, 1996).

Fifth, the modelled partial segregation of the ranges of *F. sylvatica* and its three competitor species under future climatic conditions may be biased, given that not all competitor species may be able to colonize potentially suitable habitats due to limited migration. Although we did not address this issue in our analyses, we acknowledge that predicted distributions of competitor species may be different under future climates. Nevertheless, the general patterns we found in the climatic space should not be affected by this shortcoming.

Sixth, biotic predictors in models can include not only biotic interactions, but also a broad range of local processes such as dispersal, disturbance or human influences (Meier et al., 2010). For example, forest composition across Europe is influenced by country-specific forestry practices that have resulted in large differences in forests between Western and Eastern European countries, despite similarities in regional climates. Forest composition and cover in Eastern European countries is still largely influenced by the socialist period (Kissling-Näf & Bisang, 2001; Kuemmerle et al., 2006), where there were large differences in broad-scale socioeconomic and political factors relative to Western Europe, and *F. sylvatica* was often replaced through clear-cuts by coniferous forest (mainly *P. abies*). These large contrasts are readily observed when comparing adjacent forest areas in countries that were or were not former Soviet Union countries, for example in the comparison between Sweden and Finland and the former Soviet Union countries (Lazdinis & Angelstam, 2005) or Poland, Slovakia and Ukraine (Kuemmerle et al., 2006). Given these differences in current and historical forest management, our results may be biased. However, because of the large number of forest plots used in the study and the small number of plots located in former Soviet countries, the effects on the modelled distribution are likely to be marginal.

Despite these critical points, our results provide two major insights. First, correlation patterns between the three potential competitor species and *F. sylvatica* in environmental space showed a general trend towards low correlations under cold and dry conditions, and high correlations under warm and wet conditions, except for *Q. robur*, where the correlations were lowest under cold and wet conditions. When averaging all three partial correlations, this leads to a general latitudinal and an elevational gradient correlation trend over Europe: correlations generally increase towards the south and towards low elevations. This is in agreement with the stress-gradient hypothesis, which expects a context-sensitive rather than a global competition. Therefore, under less favourable environmental conditions (i.e. increased frost or drought events), competition appears to decrease (Bertness & Callaway, 1994; Normand et al., 2009). With decreasing competition, positive interactions between other species (e.g. mutualism) may become more important (Bertness & Callaway, 1994). In our study, we did not detect strong positive correlations that we could interpret as facilitation. Facilitation may still occur among the four species, but we were unlikely to be able to detect it at the given analysis scale.

Second, under current climate, the inclusion of biotic predictors reduces the predicted relative abundance of *F. sylvatica* in some parts of Europe, specifically at more southerly and lower-elevation sites, which coincides with the observed co-occurrence patterns. Under future climate scenarios, differences in predicted distribution patterns become smaller and patterns change generally. Areas emerge, for example, where biotic predictors do not reduce but rather enhance the abundance of *F. sylvatica*. By 2100, areas where biotic predictors reduce the predicted abundance of *F. sylvatica* are restricted to high elevations, and areas where biotic predictors enhance the predicted abundance almost disappear under the A1fi scenario. However, these areas are still available under the B2 scenario. This is probably the result of the predicted climate change inducing general but individually differing range shifts of *F. sylvatica* and the three potential competitor species to higher elevations and more northern latitudes. Due to this predicted spatial segregation between the ranges of *F. sylvatica* and its current competitor species, the difference between the predicted relative abundance of *F. sylvatica* from models with and without biotic predictors becomes smaller for future climate. It remains unclear, however, if new competitor species will replace the former species in the future. It has been shown, for instance, that growth rates of immigrant species from currently warmer and more arid regions were comparable with those of the local species because the soil moisture requirements of the potential immigrants were similar to those of the local species (Ibáñez et al., 2009).

Our study has a number of consequences for using SDMs to assess the effects of climate change on species distributions. We have demonstrated that including biotic predictors together with environmental variables in models has an effect on the predicted range patterns of species. However, the magnitude of this effect changed under projections of future climate, probably due to a predicted spatial segregation of species' future ranges. Because it remains partly unclear how quickly individual species will migrate, and thus equally unclear whether and which competitors will invade the habitats of existing trees, we have to evaluate carefully large-scale projections for future climates (Baselga & Araújo, 2009). Consequently, future research should focus on a mechanistic implementation of expected competitive relations and implementation of migration rates. This can be achieved, for instance, through a set of experimental evaluations of species pairs along large-scale environmental gradients, or by process models, which in turn may be linked to statistical models.

### 3.6 Acknowledgements

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Belarus. This research was conducted as part of the 6th & 7th European Framework Programme Grants GOCE-CT-2007-036866 (ECOCHANGE) and ENV-CT-2009-226544 (MOTIVE). Use of any particular product in this research does not constitute endorsement by the US Geological Survey.

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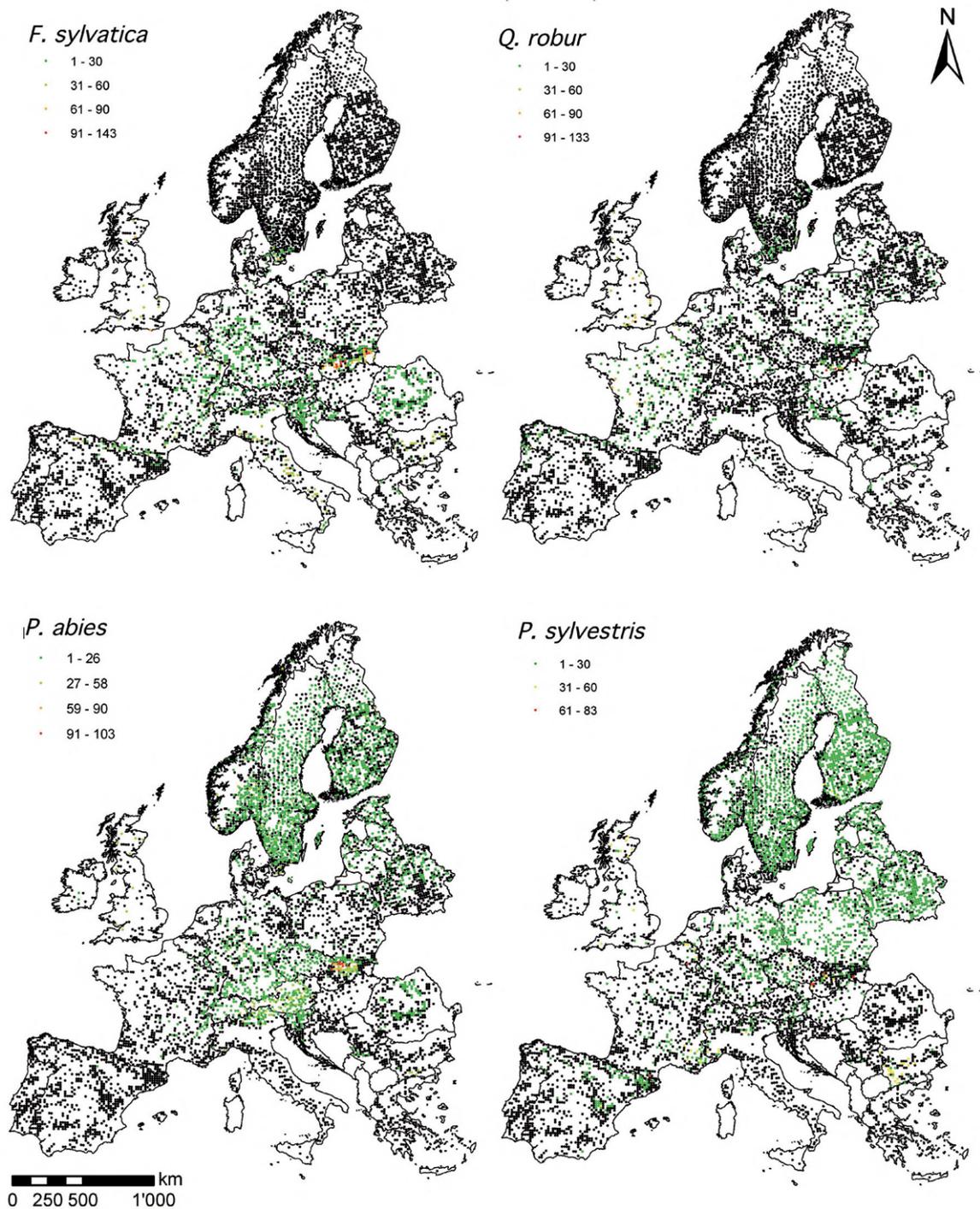
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### 3.8 Supporting information

#### Appendix S1 – Current species distributions



**Appendix S1** Numbers of individuals of *Fagus sylvatica*, *Quercus robur*, *Pinus sylvestris* and *Picea abies* per forest plot (ICP Forest Level 1).

## Appendix S2 – Correlation coefficients of predictors

**Appendix S2** Correlation coefficients of predictor variables for modelling *Fagus sylvatica* distribution.

|                      | <i>Picea abies</i> | <i>Pinus sylvestris</i> | <i>Quercus robur</i> | DDEG556 | PRSU  | TEXT | CEC_TOP | SLOPE |
|----------------------|--------------------|-------------------------|----------------------|---------|-------|------|---------|-------|
| <i>P. sylvestris</i> | -0.27              | -                       | -                    | -       | -     | -    | -       | -     |
| <i>Q. robur</i>      | -0.12              | -0.13                   | -                    | -       | -     | -    | -       | -     |
| DDEG556              | -0.39              | -0.28                   | 0.10                 | -       | -     | -    | -       | -     |
| PRSU                 | 0.29               | -0.11                   | -0.01                | -0.45   | -     | -    | -       | -     |
| TEXT                 | -0.06              | -0.23                   | 0.06                 | 0.25    | -0.08 | -    | -       | -     |
| CEC_TOP              | 0.05               | -0.08                   | 0.03                 | -0.04   | 0.01  | 0.44 | -       | -     |
| SLOPE                | 0.07               | -0.26                   | -0.09                | -0.08   | 0.41  | 0.02 | 0.03    | -     |
| TOPOS                | 0.02               | -0.03                   | 0.00                 | -0.04   | 0.01  | 0.06 | 0.00    | -0.04 |

DDEG556, degree-days with a 5.56°C threshold; PRSU, summer precipitation; TEXT, soil texture; CEC\_TOP, cation exchange capacity of the topsoil; SLOPE, slope; TOPOS, topographic position.

## Appendix S3 – Correlation coefficients of species

**Appendix S3** Statistics of Spearman's rank correlation coefficients ( $r_s$ ) between *Fagus sylvatica* and each competitor species in moving analysis windows (5 x 5 climate cells) along the two climatic gradients.

|                         | mean±SD    | min.  | max.  |
|-------------------------|------------|-------|-------|
| <i>Quercus robur</i>    | -0.73±0.08 | -0.25 | -0.87 |
| <i>Picea abies</i>      | -0.62±0.16 | -0.25 | -0.91 |
| <i>Pinus sylvestris</i> | -0.67±0.15 | -0.28 | -0.87 |

## Appendix S4 – Adj. $D^2$ of individual predictors

**Appendix S4** Adj.  $D^2$  of individual predictors of *Fagus sylvatica* distribution.

| Predictor               | Adj. $D^2$ |
|-------------------------|------------|
| DDEG556                 | 0.176      |
| PRSU                    | 0.223      |
| TEXT                    | 0.124      |
| CEC_TOP                 | 0.100      |
| SLOPE                   | 0.170      |
| TOPOS                   | 0.146      |
| <i>Quercus robur</i>    | 0.109      |
| <i>Pinus sylvestris</i> | 0.148      |
| <i>Picea abies</i>      | 0.122      |



## 4 Climate, competition and connectivity affect future migration and ranges of European trees [Paper 3]

Meier E.S.<sup>1</sup>, H. Lischke<sup>1</sup>, D.R. Schmatz<sup>1</sup> and N.E. Zimmermann<sup>1</sup>. 2011. Climate, competition and connectivity affect future migration and ranges of European trees. *Global Ecology and Biogeography*, DOI: 10.1111/j.1466-8238.2011.00669.x.

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### 4.1 Abstract

**Aim** Species ranges have adapted during the Holocene to altering climate conditions, but it remains unclear if species will be able to keep pace with recent and future climate change. The goal of our study is to assess the influence of changing macroclimate, competition and habitat connectivity on the migration rates of 14 tree species. We also compare the projections of range shifts from species distribution models (SDMs) that incorporate realistic migration rates with classical models that assume no or unlimited migration.

**Location** Europe.

**Methods** We calibrated SDMs with species abundance data from 5768 forest plots from ICP Forest Level 1 in relation to climate, topography, soil and land-use data to predict current and future tree distributions. To predict future species ranges from these models, we applied three migration scenarios: no migration, unlimited migration and realistic migration. The migration rates for the SDMs incorporating realistic migration were estimated according to macroclimate, interspecific competition and habitat connectivity from simulation experiments with a spatially explicit process model (TreeMig). From these relationships, we then developed a migration cost surface to constrain the predicted distributions of the SDMs.

**Results** The distributions of early-successional species during the 21st century predicted by SDMs that incorporate realistic migration matched quite well with the unlimited migration assumption (mean migration rate over Europe for A1fi/GRAS climate and land-use change scenario  $156.7 \pm 79.1$  m year<sup>-1</sup> and for B1/SEDG  $164.3 \pm 84.2$  m year<sup>-1</sup>). The predicted distributions of mid- to late-successional species matched better with the no migration assumption (A1fi/GRAS,  $15.2 \pm 24.5$  m year<sup>-1</sup> and B1/SEDG,  $16.0 \pm 25.6$  m year<sup>-1</sup>). Inter-specific competition, which is higher under favourable

growing conditions, reduced range shift velocity more than did adverse macroclimatic conditions (i.e. very cold or dry climate). Habitat fragmentation also led to considerable time lags in range shifts.

**Main conclusions** Migration rates depend on species traits, competition, spatial habitat configuration and climatic conditions. As a result, re-adjustments of species ranges to climate and land-use change are complex and very individualistic, yet still quite predictable. Early-successional species track climate change almost instantaneously while mid- to late- successional species were predicted to migrate very slowly.

### **Keywords**

Climate change projection, dynamic vegetation model, environmental gradient, generalized linear models, migration limitation, species distribution model, TreeMig.

## **4.2 Introduction**

Macroclimate plays a key role in shaping large-scale species distributions (Woodward, 1987). Changes in annual climate means and extremes are thus expected to lead to geographical shifts in the habitats suitable for many species (Parmesan & Yohe, 2003; Zimmermann et al., 2009). This expectation is consistent with data on Holocene climate change, where species ranges shifted in response to changing climate conditions (Davis & Shaw, 2001). It remains unclear, however, whether all species will be able to keep pace with ongoing climate change (Iverson et al., 2004). Several factors are likely to influence the ability to anticipate future range adjustments. First, global warming is predicted to occur at a faster pace than past climate changes, and thus implausibly higher migration rates would be necessary to match climate shifts in the future (Davis & Shaw, 2001). Second, new dispersal limitations have developed, such as anthropogenic landscape fragmentation, which may leave newly emerging habitats insufficiently connected. Third, the potential effect of biotic interactions (e.g. inter-specific competition, facilitation) has so far largely been ignored in analyses of species ranges. The migration rates of species are likely to be limited and to depend on inter-linked effects of climate, inter-specific competition and landscape fragmentation (Scheller & Mladenoff, 2008), which means that the patterns of potentially suitable and potentially colonizable habitats may vary greatly.

Migration limitation has to date been one of the most prominent uncertainties in predicting future species distributions (Neilson et al., 2005). Even if only climate is considered, the migration rates of non-vagile species may not be sufficient to reach the predicted potential distributions within reasonable time (Davis & Shaw, 2001). Moreover, according to the ‘stress-gradient hypothesis’,

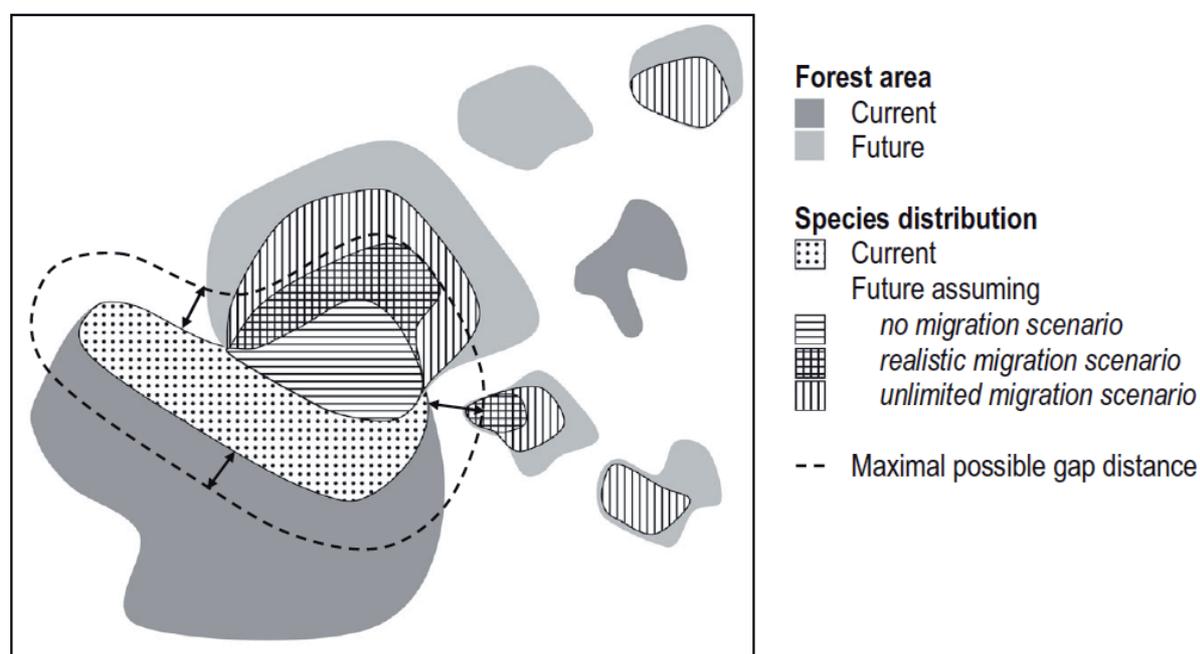
abiotic factors such as climate, topography and soil will directly constrain species distributions probably only where conditions for plant growth are adverse. Where abiotic conditions are more favourable, biotic interactions will be increased and competition may constrain species ranges (Bertness & Callaway, 1994). This constraining effect of interlinked abiotic and biotic processes may be important not only for predicting current species distributions (Meier et al., 2011) but also perhaps even more important for relating species range shifts to changing environmental conditions. Range shifts are mainly determined by the rate of plant establishment, growth and survival at new locations and by their dispersal abilities (Higgins et al., 2003), and thus are strongly linked to both abiotic and biotic conditions. Furthermore, landscapes today are strongly shaped by different land uses. Because of the high fragmentation of most modern landscapes, they contain fewer individuals that produce propagules, as well as fewer and more distant sites for propagules to colonize. This may further slow down migration rates (Iverson et al., 2004). On the other hand, due to land abandonment many forest patches have recently emerged where inter-specific interactions in the initial phase are low, and hence conditions for species migration are favourable. Thus, it is essential to include the inter-linked effects of macroclimate, inter-specific competition and habitat fragmentation on migration rates when predicting of the rate of readjustments of species to global change.

It is difficult to study demographic responses to large-scale spatiotemporal environmental variation (Ibáñez et al., 2007). Dynamic vegetation models (Cramer et al., 2001), on the one hand, often include small-scale processes, such as species interactions and dispersal, but they have not been applied on any large scales at a fine spatial resolution (e.g. 1 km<sup>2</sup>) due to their high computational cost (Neilson et al., 2005). Niche-based species distribution models (SDMs), on the other hand, have been widely used to forecast the potential effects of global change on large-scale species distributions as they are capable of mapping suitable habitats under current and altered climate conditions based on certain assumptions (Guisan & Zimmermann, 2000; Guisan & Thuiller, 2005), but they hardly include small-scale processes. In most SDMs, macroclimatic predictors play a key – if not a unique – role, and therefore models predict northwards expansion of biomes of up to 100 km per century under climate change (Prentice et al., 1992). What SDMs usually do not incorporate are species interactions (but see Meier et al., 2010, 2011), land-use effects (but see Thuiller et al., 2004) and species migration (but see, e.g., Dullinger et al., 2004; Iverson et al., 2004; Engler et al., 2009). Despite the knowledge gained from these various studies, we still lack a broader understanding of these important range-shaping processes and how they interact on large spatial scales.

This paper focuses on the migration rates of European tree species under projected future climates and land uses on a continental scale. We developed a method that implements migration rates into SDMs, taking into account competition, climate and habitat connectivity derived from a dynamic vegetation model. We address the following questions: (1) How do abiotic (i.e. climate, soil and

topography), biotic (i.e. inter-specific competition) and contextual (i.e. varying gap distances due to forest fragmentation) conditions affect migration rates? (2) What geographical patterns in migration rates emerge from these dependences? (3) How do range predictions differ if they assume no migration (i.e. the future distribution of a species is the overlap between current and future suitable distributions), unlimited migration (i.e. species fill the entire area projected to become suitable by SDMs), and realistic migration (i.e. implementation of migration rates into SDMs)?

We tackle these questions by deriving the dependence of migration rates on different biotic, abiotic and contextual conditions from simulation experiments based on the dynamic, spatially linked, forest-landscape model TreeMig (Lischke et al., 2006). The migration rates derived from these experiments are then translated into a migration cost surface to constrain species distributional responses to global change modelled with SDMs (Fig. 1 and see Appendix S1 in Supporting Information). These predictions could then be compared with SDMs assuming no and unlimited migration. The dependences of large-scale migration and distribution of 14 focal tree species in Europe during the 21st century were evaluated for each species individually as well as for species groups according to their successional status (early- versus mid- to late-successional species).



**Figure 1** Migration scenarios. Assuming no migration, species are in future restricted only to areas of current distribution still suitable under future conditions. Assuming unlimited migration, species are restricted to any areas suitable under future conditions. The realistic migration scenario incorporates species- and site-specific migration rates and maximal possible gap distances that a species can overcome (from the current distribution to not yet colonized forest patches).

## 4.3 Data and methods

### 4.3.1 Study area

The study area encompasses Europe. Mixed forests primarily constitute the natural vegetation cover (c. 44%). About 87% of the forest area is classified as semi-natural, 8% as plantations and 5% as undisturbed. The forest area has increased during recent decades, mainly due to agricultural land being abandoned (MCPFE, 2007).

### 4.3.2 Species occurrence data

We used tree abundance data from the trans-national survey of forest conditions in Europe under the international cooperative programme on assessment and monitoring of air pollution effects on forests (ICP Forest Level 1; Lorenz, 1995). The database consists of 5768 plots allocated on systematic national grids, c. 16 x 16 km each. In four subplots at a distance of 25 m from the centre point of each plot, a minimum of six trees (with a minimum height of 60 cm) nearest to the subplot centre were sampled, resulting in a minimum of 24 sample trees per plot. The data used in our analyses was collected in 2005 and 2006.

The species selected for our analyses are abundant in Europe (> 100 occurrences in the IPC Forest database) and parameterized in the dynamic model TreeMig. We selected 14 focal species: four coniferous trees (*Abies alba* Mill., *Larix decidua* Mill., *Picea abies* (L.) H. Karst., *Pinus sylvestris* L.) and 10 deciduous trees (*Acer pseudoplatanus* L., *Alnus glutinosa* (L.) Gaertn., *Betula pendula* Roth, *Carpinus betulus* L., *Fagus sylvatica* L., *Fraxinus excelsior* L., *Populus tremula* L., *Quercus petraea* (Mattuschka) Liebl., *Quercus pubescens* Willd., *Quercus robur* L.). For simulations with the dynamic model, we also used 16 common species parameterized in TreeMig to simulate the forest matrix (see Appendix S2). All focal species were classified as ‘early successional’ or ‘mid- to late successional’ by clustering their dispersal abilities in climatic space (moisture and temperature). The early-successional species, *B. pendula* and *P. tremula*, *L. decidua* and *P. sylvestris*, are generally fast dispersers. All other trees were considered mid- to late-successional species, i.e. generally slow dispersers. This largely conforms to other classifications of the successional status of trees (e.g. Brzeziecki & Kienast, 1994).

### 4.3.3 Environmental data

All environmental data described below were prepared at a spatial resolution of 1 km.

#### *Land-use maps*

We derived the forest areas from current land-use maps (CLC2000; EEA, 2000) and from downscaled

ALARM land-use scenarios for 2020, 2050 and 2080 (GRAS and SEDG scenario; <http://www.alarmproject.net.ufz.de>; Dendoncker *et al.*, 2006). We generated 10-year time steps by randomly removing and adding proportional fractions of disappearing and appearing forest areas. From these current and projected forest areas we calculated: (1) the Euclidean distance between colonized and potentially colonizable disconnected forest patches, and (2) the age of forest patches, distinguishing between newly emerged forest patches where competition between tree species may be low, and those established more than a decade ago where competition may be high.

#### *Soil and topo-climatic maps*

We used water-holding capacity [WHC ( $\text{cm m}^{-1}$ ); Batjes, 2006], soil texture [TEXT (%), percentage of clay and sand; ESNB, 2004] and cation-exchange capacity [CEC ( $\text{cmol kg}^{-1}$ ); ESNB, 2004]. Slope (SLP,  $^{\circ}$ ), aspect (ASP,  $^{\circ}$ ) and topographic position [TOPOS ( $\pm 100$ ); Zimmermann *et al.*, 2007] were derived from the GTOPO30 digital elevation model. Minimum winter temperature (MiWiT,  $^{\circ}\text{C}$ ), degree-days with a  $5.5^{\circ}\text{C}$  threshold (DDEG,  $^{\circ}\text{C days}$ ) and summer precipitation [PRSU (mm), April–September] were derived from monthly temperature and precipitation maps for the current climate (1950–2000; <http://www.worldclim.org>) and future climates [2000–2100 for A1fi and B1 climate change scenarios outlined by the Intergovernmental Panel on Climate Change (IPCC); maps from CRU based on HadCM3 (Mitchell *et al.*, 2004) downscaled to  $1 \text{ km}^2$  resolution]. Drought stress index (DrSt) was calculated according to ForClim-E (Bugmann & Cramer, 1998) by using monthly temperature, WHC, SLP and ASP. From the yearly maps of DDEG, MiWiT and DrStr, we estimated for each decade the mean and standard deviation (noted as ‘av.’ and ‘sd.’) and the proportion of years with no drought stress (PODrStr, %) for current and future climate.

#### 4.3.4 Modelling of species distributions assuming no or unlimited migration

The distribution of each species in geographical space was mapped in potential forest areas under current and future climates using generalized linear models (GLMs). As the dependent variable we used the proportion of individuals of each focal tree species per ICPF forest plot. A binomial error distribution was assumed in the GLMs. The total number of individuals of all tree species in each plot was taken to weight the observed species frequencies used in training the models to give more weight to observations with less associated error. The explanatory variables included climatic (av.PRSU, av.MiWiT, av.DDEG and sd.DrStr), edaphic (TEXT) and topographic variables (SLP and TOPOS). Except for av.MiWiT and av.DDEG, all correlations were  $< |0.5|$ , reducing multicollinearity problems. A variance inflation test gave a factor close to one for all predictors, indicating low effects of multicollinearity even for the latter two variables. We included the explanatory variables as linear and quadratic terms and applied stepwise variable selection from a full model. Model fit was

evaluated for current distributions by the adjusted  $D^2$  (Weisberg, 1980), a measure that adjusts the deviance explained ( $D^2$ ) by the number of fitted regression parameters and the number of observations. Model errors and quality were assessed in a 10-fold cross-validation, where we calculated the mean absolute error (MAE; Voltz & Webster, 1990), the root mean square error (RMSE; Voltz & Webster, 1990) and the coefficient of determination ( $R^2$ ; Menard, 2002).

To generate maps that most accurately represent the current range of our focal tree species, we further constricted the predictions of current species distributions to species occurrences within the 50 x 50 km<sup>2</sup> quadrats from the Atlas Flora Europaeae (Jalas & Suominen, 1972–1996). *Acer pseudoplatanus* and *F. excelsior* are not reported in the atlas, so data from EUFORGEN (2009) was used. The distributions of *Fagus sylvatica*, *Abies alba* and *L. decidua* are in strong disequilibrium with today's climate because their dispersal is very limited (Svenning & Skov, 2004; Bolte *et al.*, 2007), so that they cannot be modelled accurately with SDMs. To maximize the concordance between predicted current distributions and the observed atlas distribution data, we adjusted the predicted distributions of these three species to areas where their predicted abundance was > 2.5%. The respective threshold for all other species was set to > 0.1%.

When applying climate change scenarios, the potential future species ranges represent the full migration assumption, as no delay in range filling is expected. For the no-migration scenarios, ranges are constricted to the overlap between current and future suitable distributions.

#### 4.3.5 Dependences of migration rates on abiotic, biotic and contextual conditions

The dynamic forest landscape model TreeMig (Lischke *et al.*, 2006) was used to estimate migration rates under combinations of different environmental, forest compositional and habitat connectivity conditions. In TreeMig, stand structure is adjusted yearly by computing species-specific local population dynamics driven by competition for light, by the growth constraints of moisture availability and temperature, and by mortality and regeneration processes. Migration speed is determined by combining local population dynamics with seed dispersal and seed bank dynamics. For our migration rate simulations, we ran TreeMig for 6756 different climate conditions (climate bins), defined by the mean and standard deviation of DDEG, MiWiT, DrStr and P0DrStr, and high versus low inter-specific competition (COMP; see Appendix S3). According to Elton's diversity invasion hypothesis (Elton, 1958; Naeem *et al.*, 2000), we used as proxy for the degree of competition the number of competing species per simulation cell (DIV). The effect of habitat connectivity was measured by calculating migration time lags with different gap sizes. See Appendix S3 for a detailed description of the derivation of migration rates, and Lischke *et al.* (2006) for details about TreeMig.

The combinations of simulations described above resulted in 1 229 592 simulations of

migration rates per focal species. These migration rates were regressed using GLMs against DIV, COMP, av.DDEG, sd.DDEG, sd.MiWiT, sd.DrStr and P0DrSt (Poisson error structure, predictors as linear and quadratic terms; correlations between predictors  $< |0.5|$ ). We then fitted these experimentally derived migration rates to the two most important predictors (DIV and av.DDEG) using GLMs, and graphically represented this dependence in three-dimensional plots. We next calibrated GLMs with all predictors (except DIV, see below) to predict migration rates at each location in Europe. The climate and contextual layers could be directly linked to geographical space. Inter-specific competition (COMP) was accounted for through a binary variable with values of 1 (high competition) associated with forest patches colonized for more than 10 years and values of 0 associated with forested patches colonized for less than 10 years. As we had no spatial information for DIV, we omitted DIV when generating migration rate maps, although it is the variable that explains migration rates most. We further estimated the migrational lag effects of increasingly larger gaps introduced between colonizable cells for each set of conditions tested with TreeMig, which we then spatially mapped with the same GLM settings as for mapping migration rates.

#### 4.3.6 Species distributions assuming realistic migration

To map range shifts assuming realistic migration for each focal species, we conducted the following four steps. First, we predicted migration rates in suitable forest patches at time step  $t_{i+1}$  and inverted them to obtain the time used to cross a cell. Second, we calculated, with a cost-path analysis, the time used to reach each newly suitable cell at time step  $t_{i+1}$  from colonized cells at time step  $t_i$ . The cost-path analysis calculates the accumulated travel cost from each cell to the nearest cell in the set of source cells (ESRI, 2006). Third, we added the predicted time lags for overcoming gaps between the colonized forest patches at time step  $t_i$  and the edges of suitable forest patches at time step  $t_{i+1}$ . Fourth, we constrained the suitable habitats at time step  $t_{i+1}$  to cells reachable within 10 years. These four steps were repeated for each decade until 2100 for the A1fi/GRAS and B1/SEDG climate and land-use scenarios, while we updated the migration surface and species distribution matrix after each decade.

All statistical analyses were carried out in R (R Development Core Team, 2008).

## 4.4 Results

### 4.4.1 Current species distributions

Current species distributions were best explained by degree-days (av.DDEG), minimum winter temperature (av.MiWiT) and slope (SLP; Table 1). Among all species, models explained on average 27% of the variation of current species distributions and had a sound model quality estimated by 10-

fold cross validation (Table 1, mean MAE = 0.06, mean RMSE = 0.26).

**Table 1** Predictions of current species distributions. Model fit (adj.  $D^2$ ) of individual predictors and of the ‘full model’ (dependent variable: relative species abundance; the best explanatory predictors are in bold), and model errors [mean absolute error (MAE), root mean squared error (RMSE) and  $R^2$ ] of the ‘full model’ estimated with a 10-fold cross validation.

| Species                 | av.DDEG     | av.MiWiT    | av.PRSU     | sd.DrStr    | SLP         | TOPOS       | TEXT        | CEC         | full model  | MAE         | RMSE        | $R^2$        |
|-------------------------|-------------|-------------|-------------|-------------|-------------|-------------|-------------|-------------|-------------|-------------|-------------|--------------|
| <i>A.alba</i>           | <b>0.11</b> | 0.08        | 0.08        | 0.00        | 0.08        | 0.01        | 0.02        | 0.00        | 0.26        | 0.02        | 0.09        | 6.79         |
| <i>L.decidua</i>        | 0.08        | 0.13        | 0.12        | 0.01        | <b>0.21</b> | 0.07        | 0.02        | 0.02        | 0.34        | 0.02        | 0.03        | 7.95         |
| <i>P.abies</i>          | <b>0.29</b> | 0.17        | 0.17        | 0.04        | 0.00        | 0.00        | 0.01        | 0.00        | 0.36        | 0.20        | 0.25        | 25.99        |
| <i>P.sylvestris</i>     | 0.15        | <b>0.16</b> | 0.06        | 0.00        | 0.15        | 0.03        | 0.06        | 0.00        | 0.31        | 0.25        | 1.46        | 29.19        |
| <i>A.pseudoplatanus</i> | 0.07        | <b>0.07</b> | 0.05        | 0.00        | 0.03        | 0.02        | 0.04        | 0.00        | 0.18        | 0.01        | 0.01        | 2.17         |
| <i>A.glutinosa</i>      | 0.08        | 0.05        | 0.04        | 0.00        | <b>0.08</b> | 0.04        | 0.02        | 0.01        | 0.20        | 0.02        | 0.06        | 3.26         |
| <i>B.pendula</i>        | <b>0.13</b> | 0.11        | 0.08        | 0.01        | 0.11        | 0.02        | 0.01        | 0.00        | 0.23        | 0.05        | 0.10        | 8.89         |
| <i>C.betulus</i>        | <b>0.19</b> | 0.09        | 0.04        | 0.10        | 0.04        | 0.02        | 0.04        | 0.00        | 0.36        | 0.02        | 0.05        | 13.04        |
| <i>F.sylvatica</i>      | <b>0.11</b> | 0.10        | 0.02        | 0.00        | 0.09        | 0.01        | 0.06        | 0.00        | 0.25        | 0.11        | 0.92        | 15.22        |
| <i>F.excelisior</i>     | <b>0.11</b> | 0.07        | 0.03        | 0.01        | 0.00        | 0.01        | 0.03        | 0.01        | 0.18        | 0.01        | 0.02        | 2.50         |
| <i>P.tremula</i>        | 0.07        | 0.08        | 0.06        | 0.03        | <b>0.08</b> | 0.01        | 0.00        | 0.00        | 0.17        | 0.02        | 0.00        | 4.35         |
| <i>Q.petraea</i>        | <b>0.22</b> | 0.15        | 0.00        | 0.07        | 0.01        | 0.00        | 0.04        | 0.00        | 0.28        | 0.04        | 0.01        | 10.76        |
| <i>Q.pubescens</i>      | <b>0.28</b> | 0.24        | 0.06        | 0.03        | 0.06        | 0.00        | 0.04        | 0.01        | 0.42        | 0.02        | 0.19        | 9.02         |
| <i>Q.robur</i>          | <b>0.14</b> | 0.09        | 0.04        | 0.02        | 0.04        | 0.02        | 0.01        | 0.00        | 0.26        | 0.06        | 0.42        | 10.82        |
| Mean over all spp.      | <b>0.15</b> | <i>0.11</i> | <i>0.06</i> | <i>0.02</i> | <i>0.07</i> | <i>0.02</i> | <i>0.03</i> | <i>0.00</i> | <i>0.27</i> | <i>0.06</i> | <i>0.26</i> | <i>10.71</i> |

av.DDEG, averaged degree-days; av.MiWiT, averaged minimal winter temperatures; av.PRSU, averaged summer precipitation; sd.DrStr, standard deviation of drought stress; SLP, slope; TOPOS, topographic position; TEXT, soil texture; CEC, soil cation exchange capacity.

#### 4.4.2 Key factors influencing migration rates

The migration rates of focal tree species were largely explained by the biotic and abiotic predictors tested (Table 2). GLMs with individual predictors indicate that DIV, COMP, av.DDEG and P0DrStr are very important (Table 2). Generally, within established forests species migrated at about half the rate compared with low-competition conditions (COMP; Mann–Whitney U-test, all  $P < 0.001$ ), and migration rates were decreased with increasing numbers of competing species (DIV; Kruskal–Wallis test, all  $P < 0.001$ ). The directions of climatic responses to migration rates varied more between species. Focusing on the interlinked effects of the two best predictors among all focal species (DIV and av.DDEG), we found the lowest migration rates for most species at medium av.DDEG combined

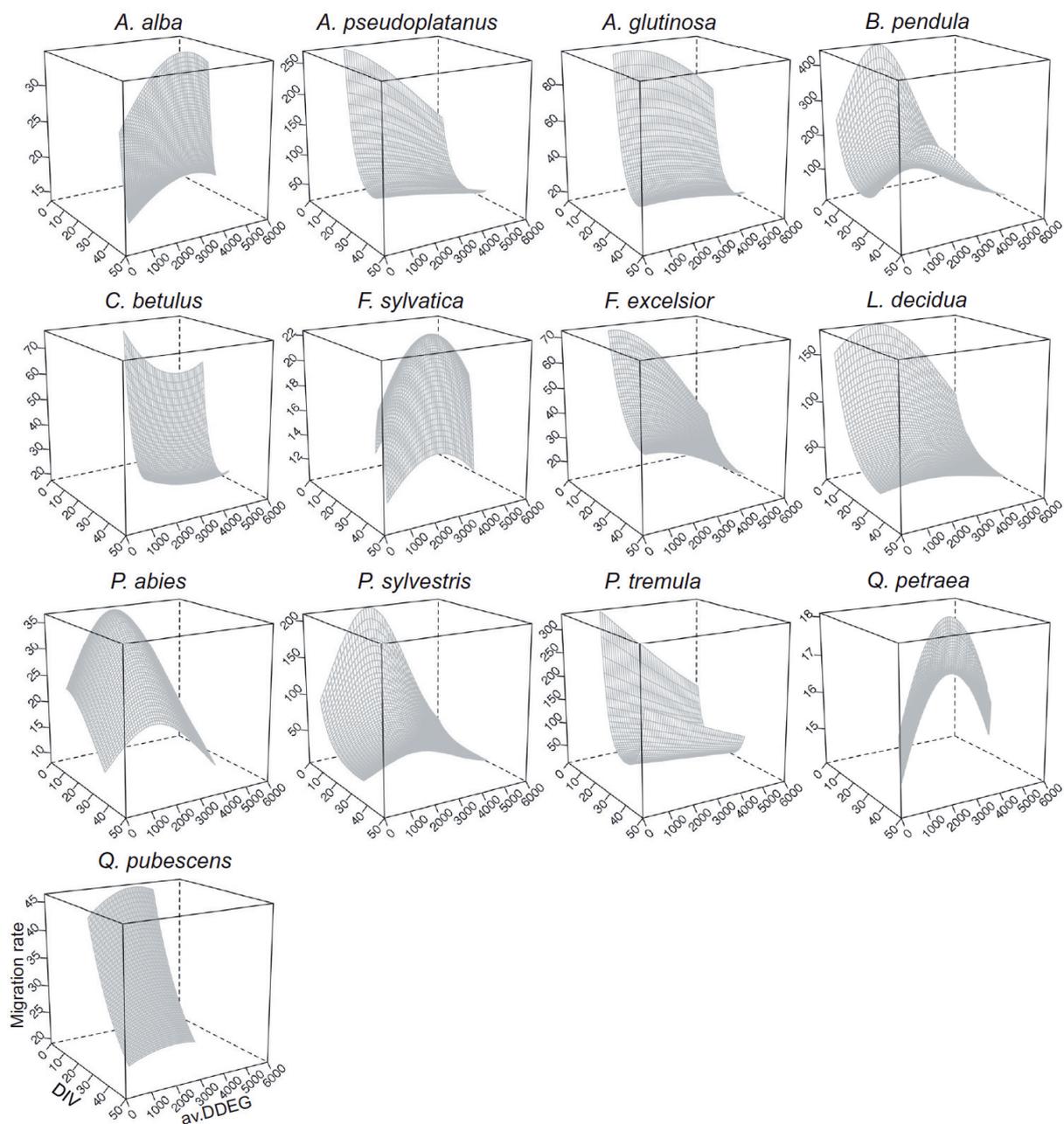
with high DIV (Fig. 2). The time lags needed to cross gaps are large under abiotic and biotic conditions where migration is already slow. With increasing gap size, the time lag increases (Kruskal–Wallis test, all  $P < 0.001$ ). The largest gap size overcome within the tested time frame was 4 km. This may be an artefact of the dynamic model as it underestimates long-distance dispersal, which tree migration rates are known to be sensitive to (e.g. Clark et al., 2003). *Quercus robur* is not listed in Table 2 or Fig. 2 because it did not migrate far enough within the tested time frame.

For all tested conditions of climate and competition, early-successional species had a significantly higher migration rate (mean =  $108.2 \pm 69.3$  m year<sup>-1</sup>) than mid- to late-successional species (mean =  $11.7 \pm 8.6$  m year<sup>-1</sup>, Kruskal–Wallis test:  $P = 0.007$ ). Their migration lags within the 1000 years measured to overcome gaps up to 4 km were significantly smaller (mean =  $669.5 \pm 61.1$  year) than for mid- to late-successional species (mean =  $906.3 \pm 36.3$  year; Kruskal–Wallis test,  $P = 0.001$ , Fig. 3).

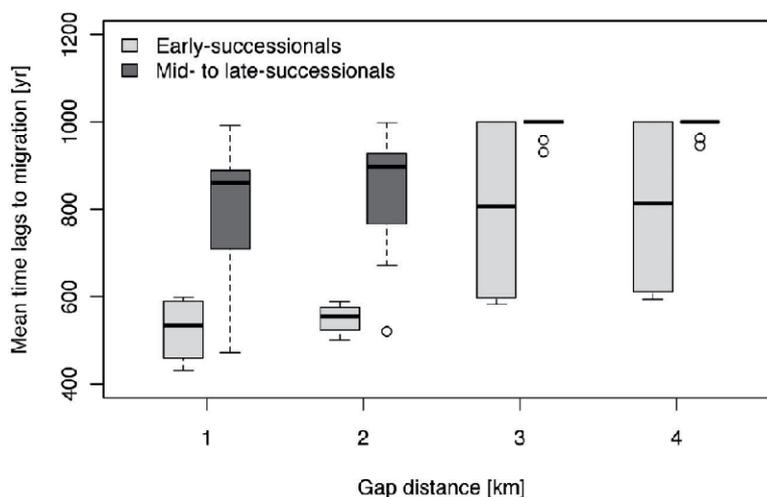
**Table 2** Predictions of migration rates. Model fit (adj.  $D^2$ ) of individual predictors and model fit and model errors [mean absolute error (MAE), root mean squared error (RMSE) and  $R^2$ ] of the ‘full model’\* estimated with a 10-fold cross validation. The best explanatory individual predictors are in bold.

| Species                 | DIV*        | COMP        | av.DDEG     | sd.DDEG | sd.MiWiT | sd.DrStr | P0DrSt      | full model | MAE                   | RMSE                  | $R^2$ |
|-------------------------|-------------|-------------|-------------|---------|----------|----------|-------------|------------|-----------------------|-----------------------|-------|
| <i>A.alba</i>           | <b>0.99</b> | 0.01        | 0.15        | 0.01    | 0.00     | 0.01     | <b>0.21</b> | 0.42       | $3.16 \times 10^{-3}$ | $2.03 \times 10^{-4}$ | 43.03 |
| <i>L.decidua</i>        | <b>0.13</b> | 0.09        | <b>0.09</b> | 0.02    | 0.00     | 0.05     | 0.01        | 0.25       | $3.57 \times 10^{-2}$ | $1.65 \times 10^{-4}$ | 23.86 |
| <i>P.abies</i>          | <b>0.8</b>  | 0.01        | 0.07        | 0.00    | 0.00     | 0.03     | <b>0.07</b> | 0.17       | $7.56 \times 10^{-3}$ | $5.41 \times 10^{-5}$ | 18.50 |
| <i>P.sylvestris</i>     | <b>0.09</b> | 0.07        | 0.04        | 0.01    | 0.01     | 0.06     | <b>0.08</b> | 0.27       | $2.62 \times 10^{-2}$ | $1.39 \times 10^{-4}$ | 26.18 |
| <i>A.pseudoplatanus</i> | <b>0.33</b> | 0.03        | <b>0.34</b> | 0.03    | 0.00     | 0.01     | 0.05        | 0.47       | $3.39 \times 10^{-2}$ | $8.14 \times 10^{-4}$ | 46.27 |
| <i>A.glutinosa</i>      | <b>0.76</b> | 0.02        | 0.16        | 0.03    | 0.00     | 0.01     | <b>0.23</b> | 0.53       | $9.65 \times 10^{-3}$ | $1.20 \times 10^{-4}$ | 59.62 |
| <i>B.pendula</i>        | 0.01        | <b>0.13</b> | <b>0.35</b> | 0.05    | 0.01     | 0.01     | 0.01        | 0.54       | $9.23 \times 10^{-2}$ | $3.20 \times 10^{-4}$ | 53.92 |
| <i>C.betulus</i>        | <b>0.88</b> | 0.01        | <b>0.42</b> | 0.04    | 0.01     | 0.03     | 0.07        | 0.60       | $5.59 \times 10^{-3}$ | $1.22 \times 10^{-4}$ | 54.00 |
| <i>F.sylvatica</i>      | <b>1.00</b> | 0.12        | <b>0.12</b> | 0.01    | 0.02     | 0.01     | 0.09        | 0.39       | $1.64 \times 10^{-3}$ | $1.09 \times 10^{-4}$ | 29.95 |
| <i>F.excelisior</i>     | <b>0.86</b> | 0.01        | <b>0.29</b> | 0.02    | 0.01     | 0.02     | 0.04        | 0.39       | $1.20 \times 10^{-2}$ | $3.14 \times 10^{-4}$ | 39.81 |
| <i>P.tremula</i>        | <b>0.16</b> | 0.09        | <b>0.36</b> | 0.03    | 0.00     | 0.01     | 0.03        | 0.52       | $7.34 \times 10^{-2}$ | $1.29 \times 10^{-3}$ | 50.75 |
| <i>Q.petraea</i>        | <b>1.00</b> | 0.25        | 0.10        | 0.01    | 0.01     | 0.00     | <b>0.14</b> | 0.54       | $1.12 \times 10^{-3}$ | $3.13 \times 10^{-5}$ | 40.44 |
| <i>Q.pubescens</i>      | <b>0.85</b> | 0.02        | <b>0.22</b> | 0.01    | 0.00     | 0.02     | 0.15        | 0.39       | $6.88 \times 10^{-3}$ | $1.02 \times 10^{-4}$ | 28.52 |
| All species             | <b>0.6</b>  | 0.07        | <b>0.21</b> | 0.02    | 0.01     | 0.02     | 0.09        | 0.42       | $2.38 \times 10^{-2}$ | $2.91 \times 10^{-4}$ | 39.60 |

\*We excluded DIV when calibrating the ‘full model’ because we do not have a map of tree species diversity (current or future) across Europe for model predictions. DIV, number of species present; COMP, distinguishing ‘low competition’ in newly emerged forest patches and ‘high competition’ in forest patches established more than a decade ago; av.DDEG, averaged degree-days; sd.DDEG, standard deviation of degree-days; sd.MiWiT, standard deviation of minimal winter temperature; P0DrStr, proportion of years with zero drought stress.



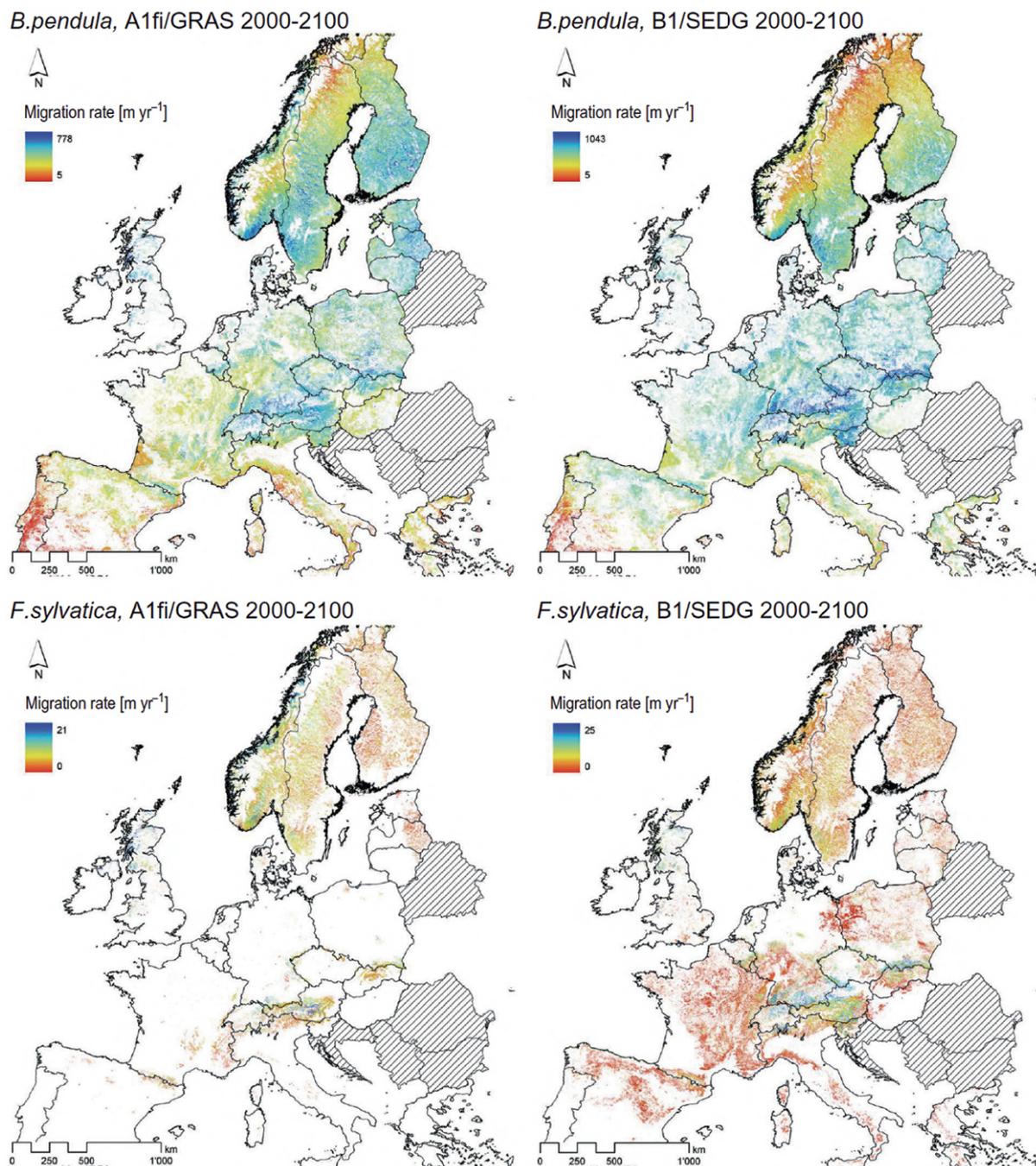
**Figure 2** Migration rates (m year<sup>-1</sup>) estimated by the dynamic model depending on the two best explanatory predictor variables among all focal species (see Table 2), i.e. the number of species present in the migratory matrix (DIV) and averaged degree-days (av.DDEG).



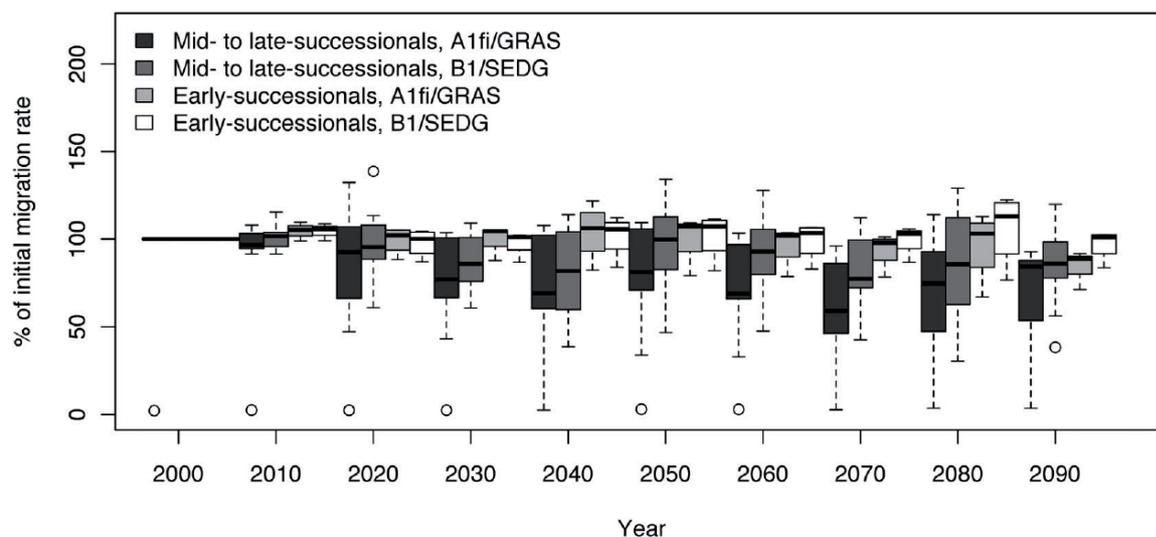
**Figure 3** Mean time lags in migration to overcome uninhabitable gaps of early- and mid- to late-successional species over all tested conditions estimated by the dynamic model. The central lines are the mean, the boxes are the inter-quartiles, the lower whiskers are the datapoints within 1.5 inter-quartile range (IRQ) of the lower quartile (analogous for the upper whiskers), and the points are the outliers (i.e. datapoints outside of 1.5 IQR).

#### 4.4.3 Patterns of migration rates within Europe

We found that migration rates differed substantially in geographical space. Migration rates were, for all species except *L. decidua* and *P. sylvestris*, especially high in the Alps and particularly low in northern and southern Europe (Fig. 4 and Appendix S4). Differences between the migration rates of early-successional species (mean for Europe in the 21st century for A1fi/GRAS  $153.1 \pm 90.0$  m year<sup>-1</sup> and B1/SEDG  $158.0 \pm 98.3$  m year<sup>-1</sup>) and mid- to late-successional species (A1fi/GRAS  $15.2 \pm 24.5$  m year<sup>-1</sup> and B1/SEDG  $15.9 \pm 25.6$  m yr<sup>-1</sup>) were also considerable. During the 21st century, mean migration rates have declined overall, but less for early-successional species than for mid- to late-successional species, and less for B1/SEDG climate and land-use scenarios than for A1fi/GRAS (Fig. 5).



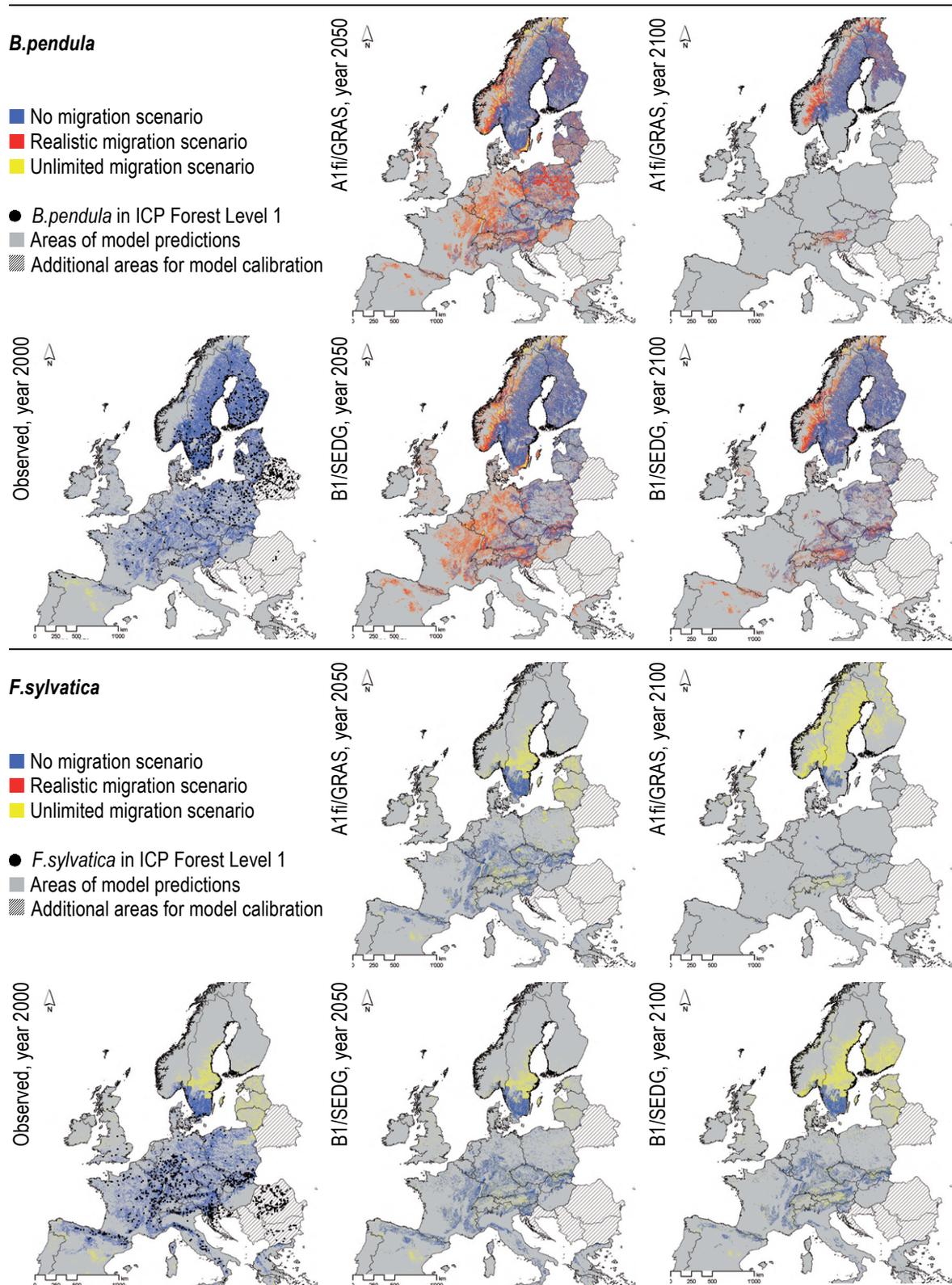
**Figure 4** Mean migration rate (including time lags due to forest fragmentation) since 2000 across potentially suitable habitats of an exemplary early-successional broadleaf species (*Betula pendula*) and an exemplary late-successional broadleaf species (*Fagus sylvatica*) for the A1fi/GRAS and B1/SEDG climate and land-use scenarios. ‘Striped’ countries indicate additional areas for model calibration.



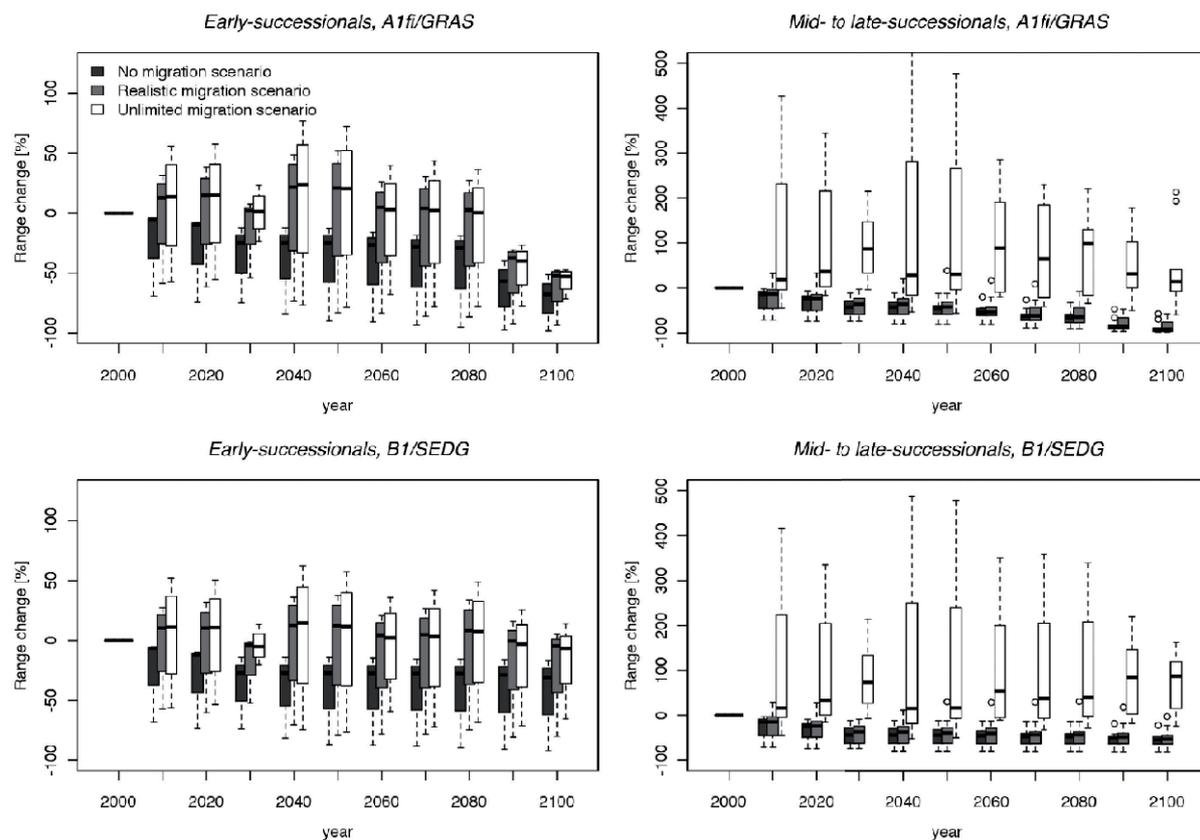
**Figure 5** Percentage of migration rates (including time lags due to forest fragmentation) in relation to the initial migration rate of early- and mid- to late-successional species over time for A1fi/GRAS and B1/SEDG climate and land-use scenarios. The central lines are the mean, the boxes are the inter-quartiles, the lower whiskers are the datapoints within 1.5 inter-quartile range (IRQ) of the lower quartile (analogous for the upper whiskers), and the points are the outliers (i.e. datapoints outside of 1.5 IQR).

#### 4.4.4 Differences between migration scenarios

Tree distributions estimated from the niche-based modelling approach incorporating migration matched for early-successional species better with SDM projections assuming unlimited migration than with projections assuming no migration (Fig. 6 and Appendix S5). With mid- to late-successional the relationship was reversed (Fig. 6 and Appendix S5). Therefore, differences in the projected range sizes between the models with the three different migration-limitation assumptions were especially large for mid- to late-successional species. These differences did not change in the 21st century for A1fi/GRAS and B1/SEDG climate and land-use change scenarios (Fig. 7).



**Figure 6** Predicted distributions of an exemplary early- (*Betula pendula*) and late-successional (*Fagus sylvatica*) species for 2000, 2050 and 2100 (A1fi/GRAS and B1/SEDG climate and land-use scenarios) for the no migration (top layer), realistic migration (middle layer) and unlimited migration scenario (bottom layer).



**Figure 7** Percentage of range gain and loss for each decade from 2000 until 2100 of early- and mid- to late-successional species predicted for the no, realistic and unlimited migration scenario for the A1fi/GRAS and B1/SEDG climate and land-use scenarios. The central lines are the medians, the boxes are the inter-quartiles, the lower whiskers are the datapoints within 1.5 inter-quartile range (IRQ) of the lower quartile (analogue for the upper whiskers), and the points are the outliers (i.e. datapoints outside of 1.5 IQR).

## 4.5 Discussion

Dispersal limitation is one of the main sources of uncertainty when predicting species distributions under changing climate (Araújo & Guisan, 2006). Implementing migration rates that depend on climate, competition and habitat connectivity into niche-based models has thus a great potential to substantially reduce uncertainty in future projections under changing climates. Our analyses showed clearly that early-successional species were considerably less limited in range re-adjustments than mid- to late-successional species. Further, inter-specific competition, which is especially high under favourable macroclimatic conditions, reduced range shift velocity more than adverse macroclimatic conditions. Landscape fragmentation led to considerable time lags in range shifts, especially for mid- to late-successional species. To ensure a correct interpretation of our results, we first discuss three main critical points below.

First, more complex models inherently contain more uncertainty (Midgley *et al.*, 2006; Thuiller *et al.*, 2008). In our distribution model with estimated realistic migration rates, uncertainty is inherent in: (1) SDM calibration of potential current and future habitats; (2) the processes of the dynamic model (TreeMig); and (3) the reduction in the variability of the migration rate estimates from the dynamic model to mean trends when predicting migration rates in geographical space. For example, omitting DIV reduced the proportion of explained variance (adj.  $D^2$ ) from 0.75 to 0.42. Findings from such complex models as ours may still be useful for conservation planners and forest managers (Midgley & Thuiller, 2005) because they are among the best approaches to assessing migration limitations on the large-scale distributions of species during climate change.

Second, our estimates of migration rates may be biased because: (1) the dynamic model may not be properly parameterized for individuals near their range limits or for rapid climate change; (2) we treated the different land-use types as equally strong barriers to dispersal; and (3) we used only single gaps to estimate time lags from landscape fragmentation. Individuals at their range edges tend to have higher dispersal abilities than individuals at their range centres (e.g. Darling *et al.*, 2008), possibly due to genetic selection or an interference of preemptive intra- or inter-specific competition. If expanding edges contain individuals with higher dispersal ability, then this may result in a spatial sorting of dispersal ability and it will affect the shape of the dispersal kernel (Phillips *et al.*, 2008). Dispersal kernels in TreeMig, however, were fixed for individuals of the same species. Regarding the impact of land use on migration rates, it is known that parks in cities and abandoned agricultural areas can act as stepping-stones for tree migration (Jim, 2004). Moreover, the behaviour of dispersal agents is strongly influenced by landscape structures (Nathan *et al.*, 2002). In our study, we only considered abandoned land as potentially colonisable sites outside forests, and only used a dispersal kernel calibrated under forest conditions because TreeMig is not parameterized to take into account land-use types having different dispersal agents. The third potential source of bias may arise from measuring the time lag for overcoming only single gaps of differing size in order to implement the resulting migration rates in SDMs. Addressing the time lags associated with just one gap at a time may differ from overcoming a second gap, even though the conditions and the gap size may remain the same. Multiple small barriers may slow down migration more than a single large barrier (e.g. Malanson & Cairns, 1997; Collingham & Huntley, 2000).

The third critical point is that the equilibrium assumption, which is a basic assumption of SDMs, may already be violated under current conditions. Current species distributions may be influenced by migration limitations during Holocene climate change and by past and current country-specific forest practices. In our study, for instance, *L. decidua*, *A. alba* and *F. sylvatica* were predicted to occur too far north under current conditions, possibly due to persisting migration limitations of these species (Svenning & Skov, 2004). On the other hand, *P. abies* distribution was predicted too far

south under current conditions, probably because plantations at low elevations are present in the database (Meier *et al.*, 2011).

Despite these three potential shortcomings, modelling transient dynamics across large spatial scales still provides valuable insights into the magnitude and the time-scale over which range shifts may occur, especially as little is known about the range restrictions of most species (Gaston, 2009), although some progress has been made (e.g. Normand *et al.*, 2009; Zimmermann *et al.*, 2009). One major reason may be that we do not know enough about the effects of local population dynamics and habitat fragmentation on large-scale migration rates (e.g. Schwartz, 1993). Our results showed strong effects of interspecific interactions on migration rates and large differences between the migration rates of early- and mid- to late-successional species. The discrepancy between the estimated migration rates from palaeoecological data, which assumes migration rates of the order of  $10^2$  and  $10^3$  m year<sup>-1</sup> (e.g. Huntley & Birks, 1983; Birks, 1989), and the migration rates in our study varied with species. Generally, migration rates from early-successional species were in the range of those obtained from palaeoecological data, while mid- to late-successional species migrated more slowly than expected. This may be because species in our model had to cope with the specific conditions found today, i.e. they had to spread through a landscape whose spatial structure and potential for plant establishment has been modified considerably (Pitelka *et al.*, 1997). However, it may also result from TreeMig not accounting for long-distance dispersal sufficiently well, which may play a crucial role for some species (e.g. Clark *et al.*, 2003).

Inter-specific competition, which is important for tree establishment, reduced migration rates in our simulations considerably. Because competition may not affect species linearly (Malanson & Cairns, 1997), we further investigated the effect of different degrees of competition. According to Elton's diversity invasion hypothesis (Elton, 1958; Naeem *et al.*, 2000), diversity may be used as a proxy for the degree of competition from resident species to immigrating species. Our analysis showed that, where only a few species had become established, migration rates remained high. Where species were advancing into areas already colonized by a high diversity of species, migration slowed down greatly, probably because newcomers are more likely to encounter a dominant competitor if more species are present (Wardle & Peltzer, 2003). Local disturbance events, such as fires or storms, may reduce this competitive inhibition (Björkman & Bradshaw, 1996), but we did not specifically test this in our study. From studies in Sweden we know that *P. abies* was able to invade the existing forest within one generation, while the establishment of *F. sylvatica* was delayed for almost 1000 years until ground fires created suitable seed bed conditions (Björkman & Bradshaw, 1996). Thus, predictions of trailing edge responses are also more uncertain. If, under future climate change, resident species die back prior to the immigration of newcomers (e.g. Solomon, 1986), competitive restrictions on migration rates may be less important than if resident species exhibit inertia (e.g. Hansen *et al.*, 2001).

The effect of inter-specific competition on migration rates was linked to climate. Migration rates were lowest at medium temperatures where species diversity was high. This relationship is in line with the stress gradient hypothesis (Maestre *et al.*, 2009) and the findings of Bonan & Sirois (1992), that growth would often increase with rising temperatures towards southern range limits. However, with rising temperatures competition, and to some extent drought, also increase, which limit species ranges and thus may also reduce migration.

Our results confirm that human-driven habitat fragmentation makes it difficult for many species to migrate (Pitelka *et al.*, 1997). Migration was delayed considerably by even small gaps between forest habitats. Other studies have similarly found that migration rates slowed down markedly when habitat availability fell below a certain threshold in landscapes composed of only few large habitat patches (Collingham & Huntley, 2000; King & With, 2002). Thus, standard SDMs may greatly underestimate the constraining effect of habitat fragmentation, whereas the dynamic model TreeMig may overestimate the time it takes to overcome gaps and underestimate the maximal distances that can be overcome between patches.

In geographical space, the effects of latitudinal climate gradients combined with patterns of land abandonment and habitat connectivity have resulted in an overall similar pattern for most species. Migration rates tend to be slow in the north and south of Europe where the climate is either very cold or very dry, which prolongs life cycles and reduces the growth of species and hence slows down migration. On the other hand, migration seems to be especially high in the Alps where extensive farming has traditionally dominated, so that the land is particularly vulnerable to abandonment (Baldock *et al.*, 1996). When land is abandoned, many forest patches emerge with low inter-specific interactions in the initial phase, which promotes species migration. The degree of competition in old forest patches may be overestimated in our model because dominant trees are not present at all locations due to migration limitations, in contrast to the migration experiment with TreeMig.

Early-successional species migrated about 10 times faster than mid- to late-successional species. This is because early-successional species generally have rapid growth rates, large amounts of seed and long seed-dispersal distances, while mid- to late-successional species usually have rather different characteristics (Meier *et al.*, 2010). This causes mid- to late-successional species to migrate predominantly into previously colonized forest habitats where inter-specific competition is higher. Their higher shade tolerance cannot outbalance this disadvantage, and thus their already lower migration rates are decreased even further. This strong migration limitation of mid- to late-successional species means they tend not to colonize new habitats that become potentially suitable under climate change. Only areas with short and steep environmental gradients, such as mountains, may facilitate the persistence of these poor dispersers (Cowling *et al.*, 1999). In contrast, early-successional species colonized new potentially suitable habitats much faster due to their lower

migration limitation (Ravazzi, 2002). Although estimated migration rates have not changed dramatically since 2000 for the global change scenarios tested, differences in migration rates between individual species and species groups have a large impact on the potential range shifts for global change scenarios. Naturally regenerating forests may become less diverse because they may be dominated by early-successional species with wide ecological amplitudes and contain less biomass than they would if mid- to late-successional species could keep pace (Sykes & Prentice, 1996).

Compared with standard SDM approaches that assume no or unlimited migration (e.g. Thomas *et al.*, 2004; Thuiller *et al.*, 2005; Araújo *et al.*, 2006), our approach using realistic migration rates enabled us to deduce rules for the degree of migration limitation on individual species or species groups related to their range-shifting behaviour under climate change. Depending on the limitation on migration identified, it may be possible to plan and assist their migration better. Species with large shifts in range under future climates and strong migration limitations should, in particular, be assisted. This applies not only for economically important species, but also for species that are important for biodiversity. Evaluating the degree of migration limitation is not only relevant for tree species, but also for many other potentially migration-limited plants and animals.

In conclusion, many slowly reproducing mid- to late-successional species may not be able to keep pace with recent and future climate change. At favourable locations, range shifts are limited by slow migration rates due to biotic interactions, while at unfavourable locations range shifts are limited directly by climate. Land-use change is a mixed blessing: while land abandonment creates patches with low inter-specific competition and thus promotes species migration, the fragmented character of many landscapes presents strong barriers to dispersal. Assessing the effects on migration rates and species ranges of inter-linked processes such as climate, inter-specific interactions and landscape fragmentation on a continental scale should help to identify the conditions that enhance or inhibit range shifts. This should help in the interpretation of range shift maps from SDMs and how these are affected by assuming no migration, or alternatively, unlimited migration. When including migration rates in projections of large-scale species distributions under climate change scenarios, the calculation of extinction risks can be improved, reserve networks can be better designed, and efforts to assist the migration of species with strong migration limitations can be better focused.

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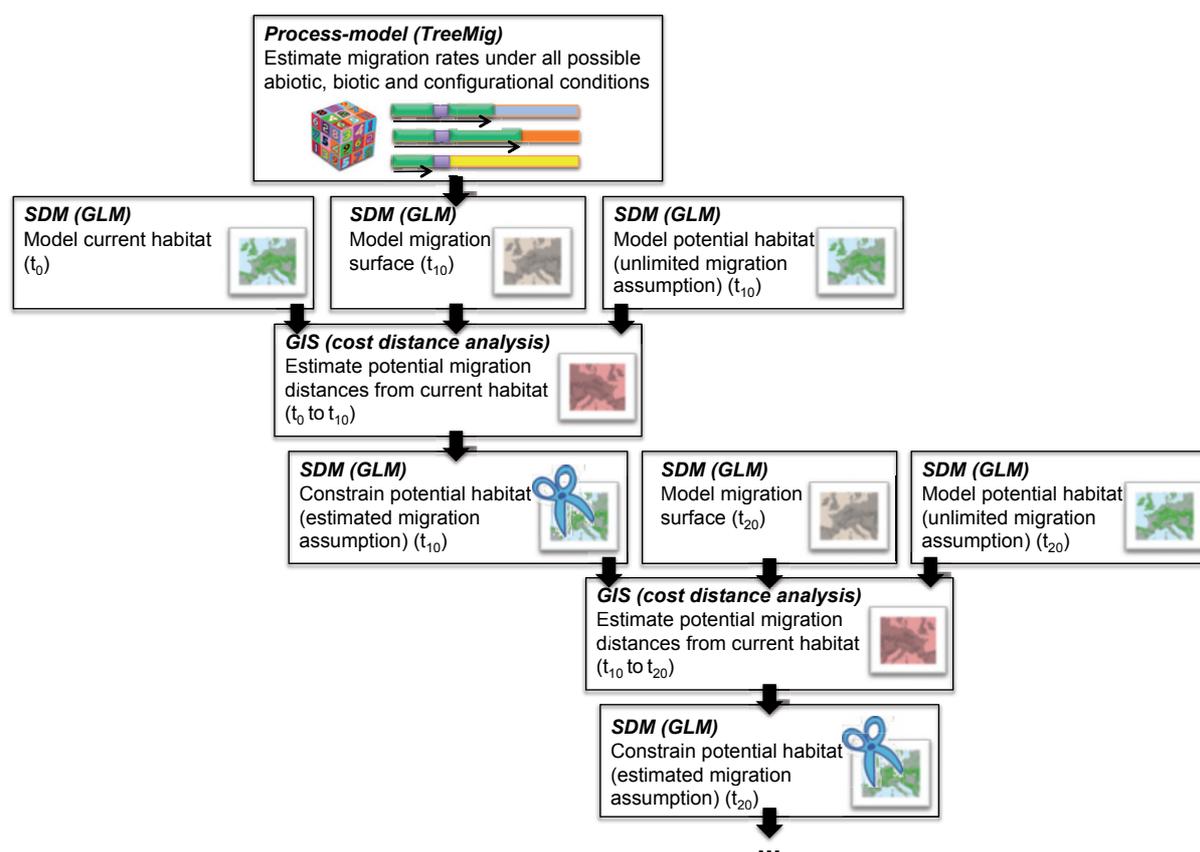
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## 4.8 Supporting information

### Appendix S1 – Model setup

We estimated with the process-model ‘TreeMig’ (Lischke et al., 2006) migration rates under all possible combinations of abiotic (i.e. climate, topography and soil), biotic (i.e. inter-specific competition) and contextual (i.e. gap distance between forest patches) conditions. These dependencies were used to model a migration-rate surface over Europe for time  $t_0$  to  $t_{10}$ . This migration-rate surface was then combined with colonisable habitats at  $t_0$  with a cost distance analysis (ESRI, 2006) to constrain potential species distributions at  $t_{10}$  (i.e. ‘unlimited migration’) to colonizable habitats at  $t_{10}$  (i.e. ‘realistic migration’). These steps were repeated for each decade until 2100 for A1fi/GRAS and B1/SEDG climate and land-use scenarios.



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## Appendix S2 – Selection of tree species

We selected 14 species from the ICP Forest Level 1 dataset as focal species for our analyses, which were both abundant enough for fitting statistical models (occurring in >100 forest plots) and were calibrated in the dynamic model TreeMig: four coniferous trees (*Abies alba* Mill., *Larix decidua* Mill., *Picea abies* (L.) H. Karst., *Pinus sylvestris* L.) and ten deciduous trees (*Acer pseudoplatanus* L., *Alnus glutinosa* (L.) Gaertn., *Betula pendula* Roth, *Carpinus betulus* L., *Fagus sylvatica* L., *Fraxinus excelsior* L., *Populus tremula* L., *Quercus petraea* (Mattuschka) Liebl., *Quercus pubescens* Willd., *Quercus robur* L.).

To create the forest matrix in the TreeMig simulations, we used in addition to the selected 14 focal species, 16 fairly common species parameterized in TreeMig: *Pinus cembra* L., *Pinus mugo* Turra, *Taxus baccata* L., *Acer campestre* L., *Acer platanoides* L., *Alnus incana* (L.) Moench, *Alnus viridis* (Chaix) DC., *Castanea sativa* Mill., *Corylus avellana* L., *Populus nigra* L., *Salix alba* L., *Sorbus aria* (L.) Crantz, *Sorbus aucuparia* L., *Tilia cordata* P. Mill., *Tilia platyphyllos* Scop. and *Ulmus glabra* Huds..

## Appendix S3 – Design of the migration experiments using TreeMig

Below, we describe the structure of the migration experiments, which we set up in order to estimate realistic and continent-wide migration rate surfaces depending on the climate, competition and habitat-connectivity for the 14 European tree species.

### *Classifying environmental conditions*

We first analyzed the environmental space between 1950 and 2100 (current climate and A1Fi climate scenario); i.e. we analyzed the absolute minimum and maximum of decadal means and standard deviations of DDEG, MiWiT, DrStr and P0DrStr, which represent the environmental drivers of the TreeMig model (Lischke et al., 2006). We then classified each of the mean variables (i.e. identified with ‘av.’) into 9 equally sized bins, the standard deviation variables (i.e. identified with ‘sd.’) into 5 equally sized bins, and P0DrStr into 3 equally sized bins. All combinations of bins that occurred under current or future climates were then used for the migration simulations ( $n = 6756$ ), allowing us to evaluate migration rates for all possible current and future climates. See the Data and Methods chapter in the text for a description of these climate variables.

### *Setting up and running TreeMig*

We used the dynamic, lattice-based, spatio-temporal, height-structured tree species model TreeMig (Lischke et al., 2006) to estimate the migration rates under these various climate conditions. TreeMig is one of very few models that have density-dependent population processes and seed dispersal implemented in a spatially explicit form (Thuiller et al., 2008). The model calculates local tree species population dynamics in each 1 km<sup>2</sup> grid cell, including seed bank dynamics, intra-specific density regulation of the seeds, germination, growth, competition for light, mortality and seed production. The process functions depend on climate variables (DDEG, MiWiT, and DrSt) and on light. The vertical structure leads to hierarchical competition. Within-cell heterogeneity is depicted by frequency distributions of tree density and consequently light intensity. Parameters describing the local dynamics stem from the gap-model ForClim (Bugmann, 1994). Medium scale heterogeneity, e.g. a migration front within a cell, is not taken into account explicitly. Interactions between the cells occur by seed dispersal, described by a dispersal kernel consisting of two negative exponentials, accounting for frequent short- and rare long-distance dispersal events (Lischke & Löffler, 2006). The species-specific mean dispersal distances for wind-dispersed seeds were estimated from sinking velocities and wind speed distributions, and dispersal distances for ballistic and animal dispersal were derived from literature (Lischke & Löffler, 2006). Species parameters reflect trade-offs, e.g. between shade-tolerance and seed production, dispersal distance and maximum growth. Small-scale disturbances are depicted by randomly increased mortality of 80% at return intervals of 1000 years.

For our experiments, we set up transects with the dimension 1x100 cells and a cell size of 1 km<sup>2</sup>. In order to avoid edge effects, we used cylindrical boundary conditions, assuming periodic boundaries on the narrow sides of the transect.

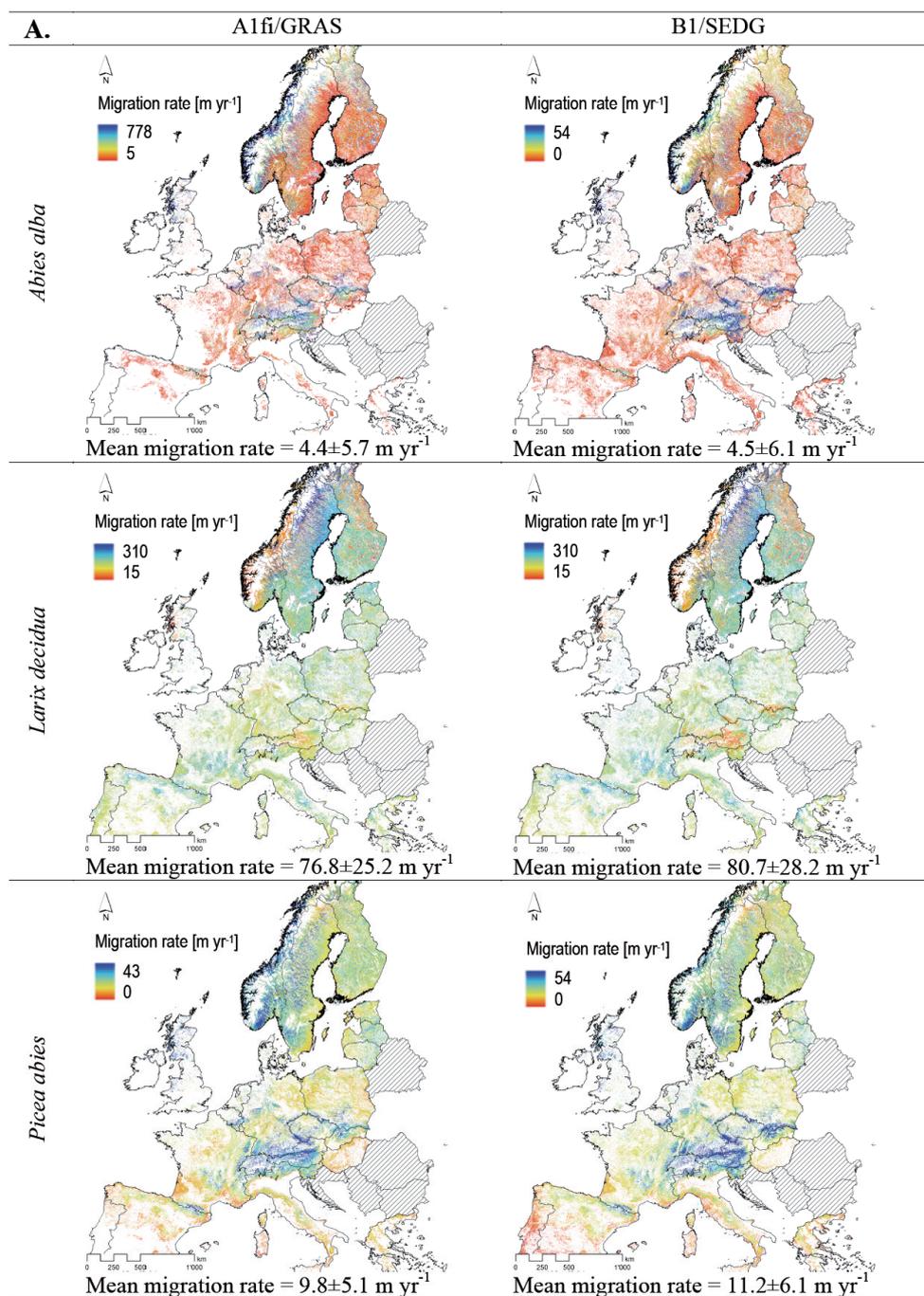
To test the effect of climate, we let each focal species migrate under each of the various climate conditions, which were held constant per run. A spin-up of 400 years was run to set up the initial forest conditions on the first cell under each climate condition. To test the effect of competition, we ran two tests where, in the first, we excluded the focal species during the spin-up run on all but the first cell, and in the second we kept all but the first cell empty. To test the effect of habitat connectivity, we introduced a gap of increasing size with each run along the transect, ranging from 1 km to 90 km in 1 km steps. This means that we repeated the two competition simulations for each gap distance. From these runs, we calculated the time-lags resulting from overcoming increasing gap distances compared to no gap conditions, and we measured the maximum gap distance the focal species was able to overcome. Under all combinations of conditions, we then let all species migrate for 1000 years after spin-up. We estimated the migration rate between the 10th (in order to reduce effects of the initialization period) and the 100th cell (or the last cell reached after 1000 years). When introducing gaps, we estimated the time lag at the first cell after the gap compared to no gap. Presence of a species was recorded if the species reached a biomass of 10 t km<sup>-2</sup> in a cell. In summary, we run simulations for 6756 climatic conditions, and for each set we ran one simulation without a gap, and an additional 90 simulations with increasing gap size each, both with and without forest as matrix to migrate through, and for a total of 14 species each. This resulted in 6756 x 91 x 2 x 14 = 17'214'288 simulations (or 1'229'592 simulations per focal species).

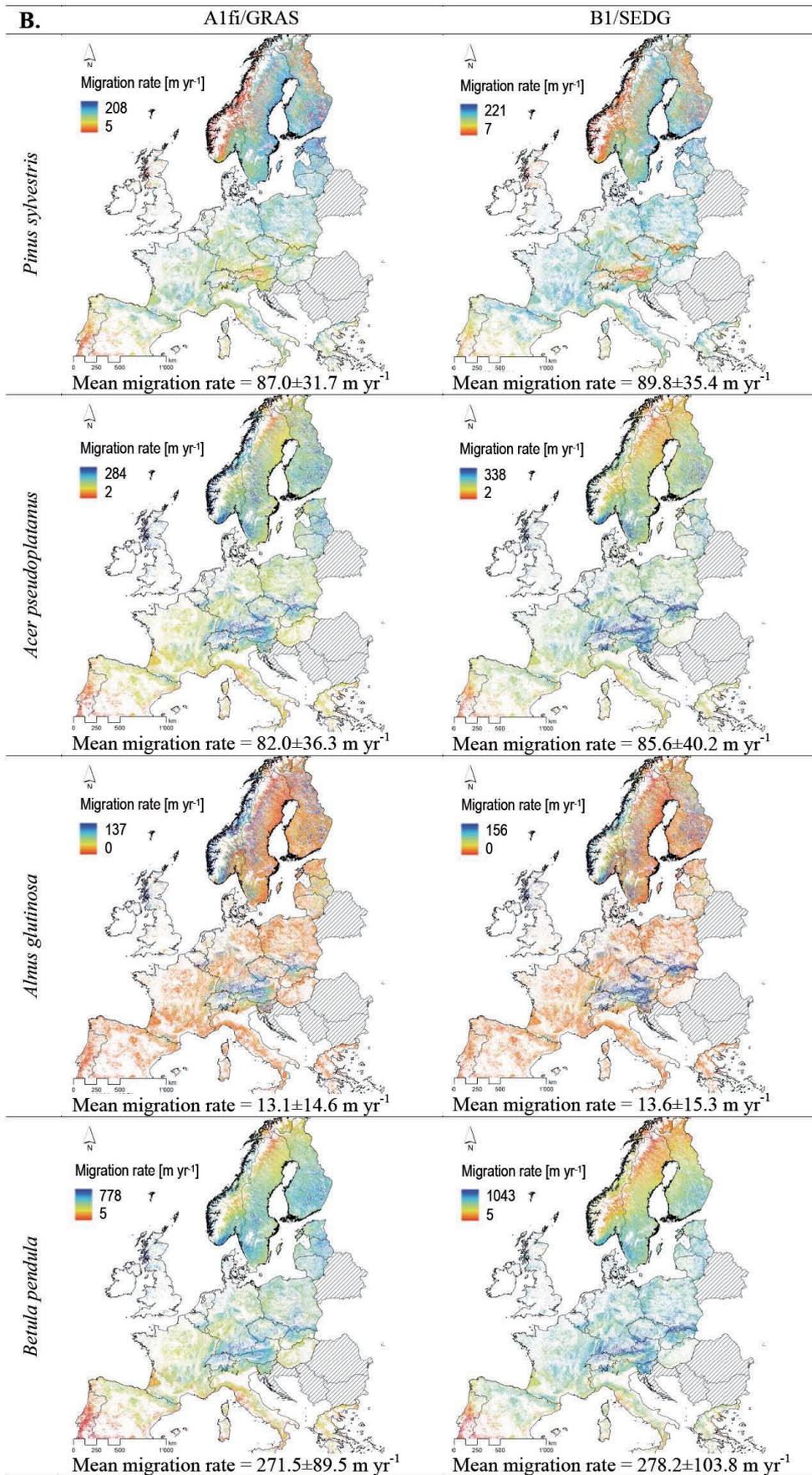
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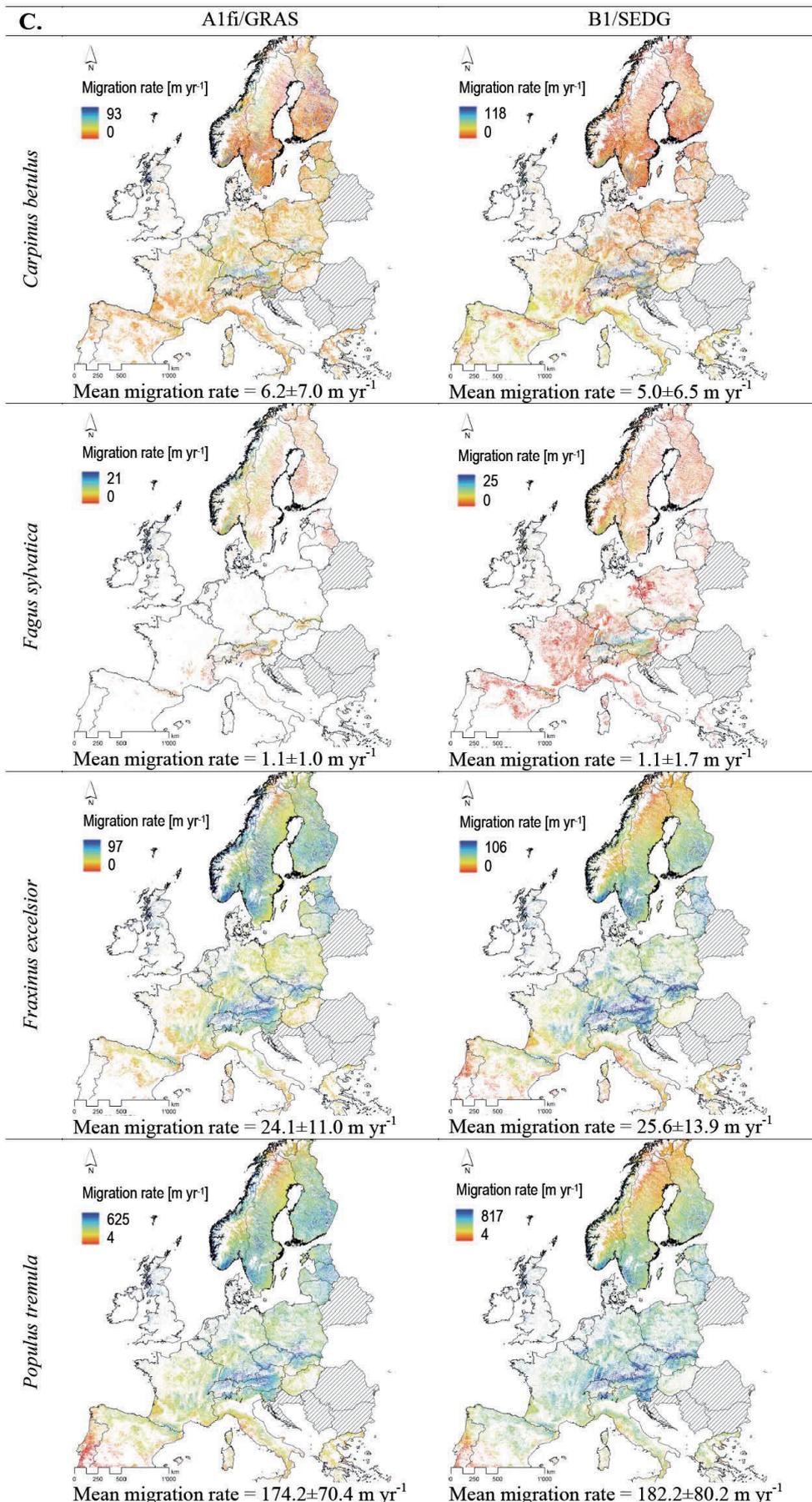
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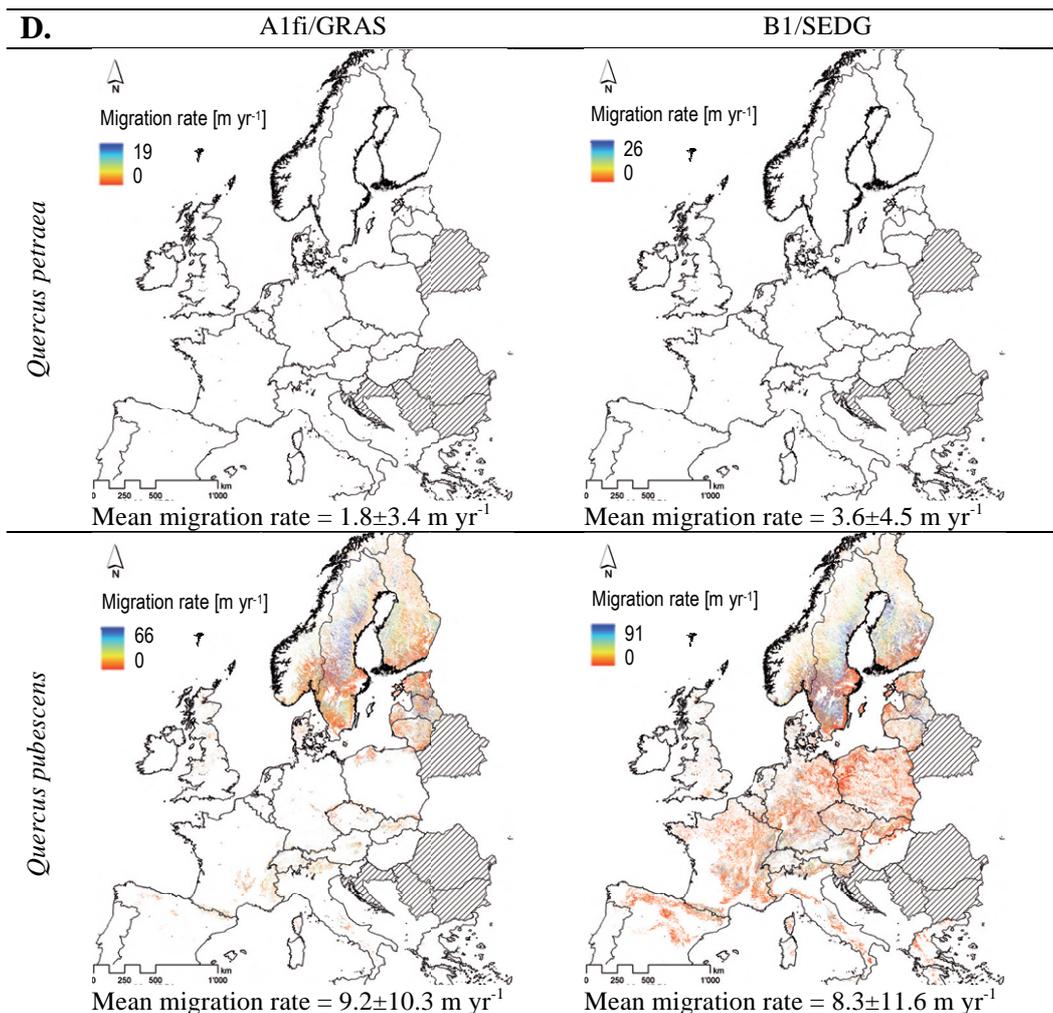
## Appendix S4 – Predicted migration rates

Predicted mean migration rates for the 14 focal tree species (plates A-D) across potentially suitable habitats in the 21st century for the A1fi/GRAS and B1/SEDG climate and land-use scenarios. Minima and maxima of mean migration rates since 2000 are given in the legend; averages and standard deviation of mean migration rates within Europe are indicated below each figure. Countries white highlighted represent areas of model predictions; countries with stripes represent additional areas for model calibration.



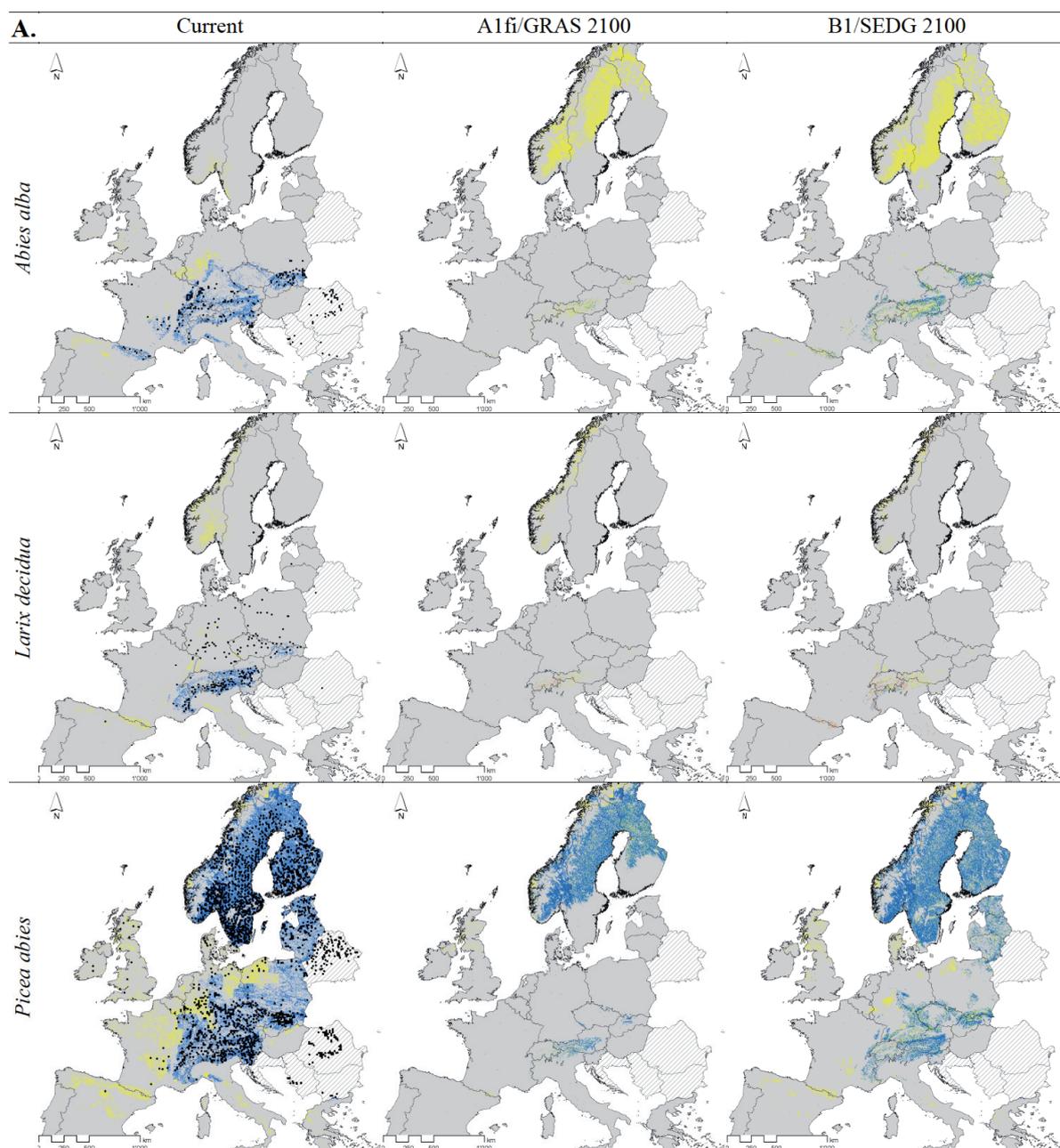


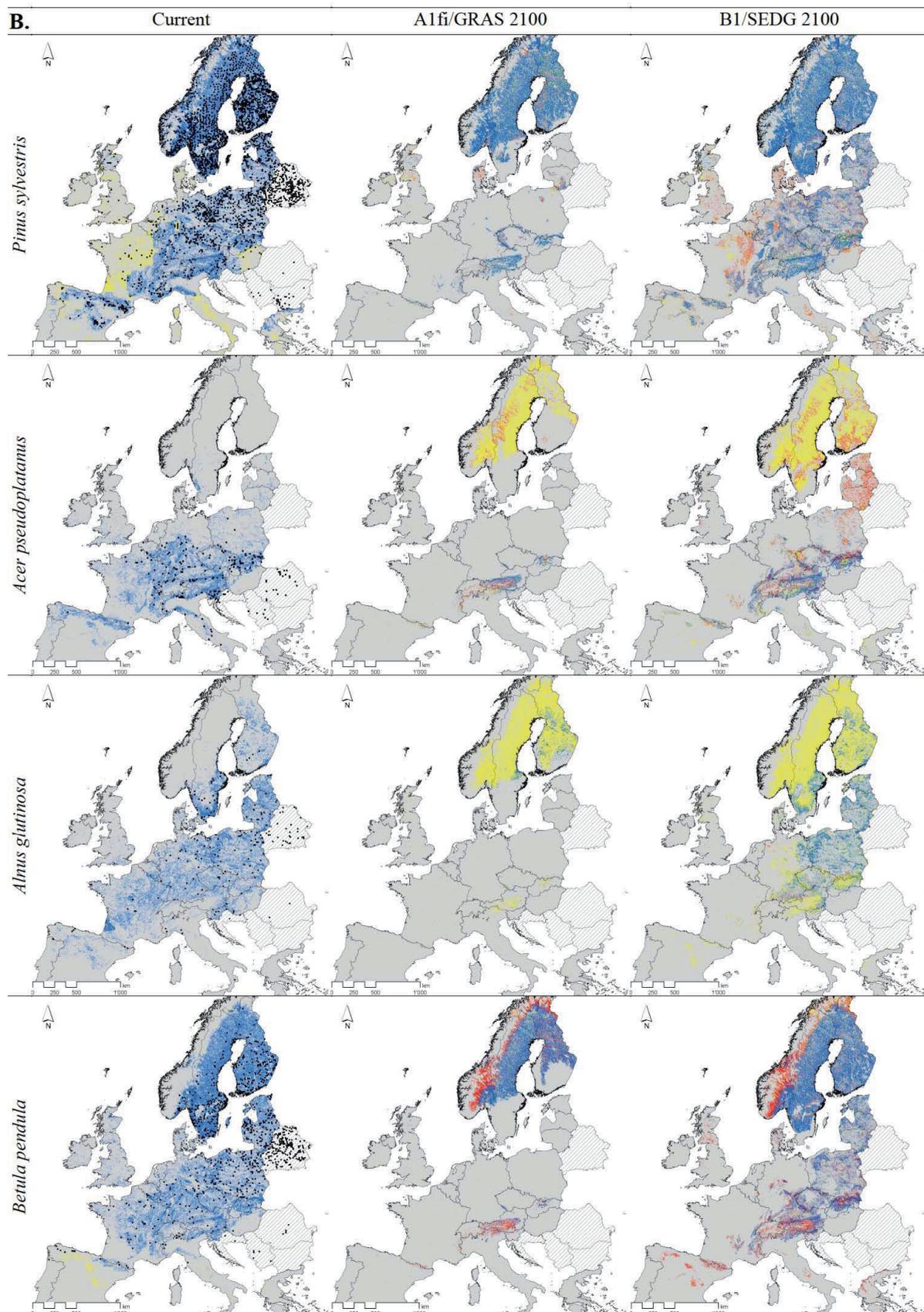


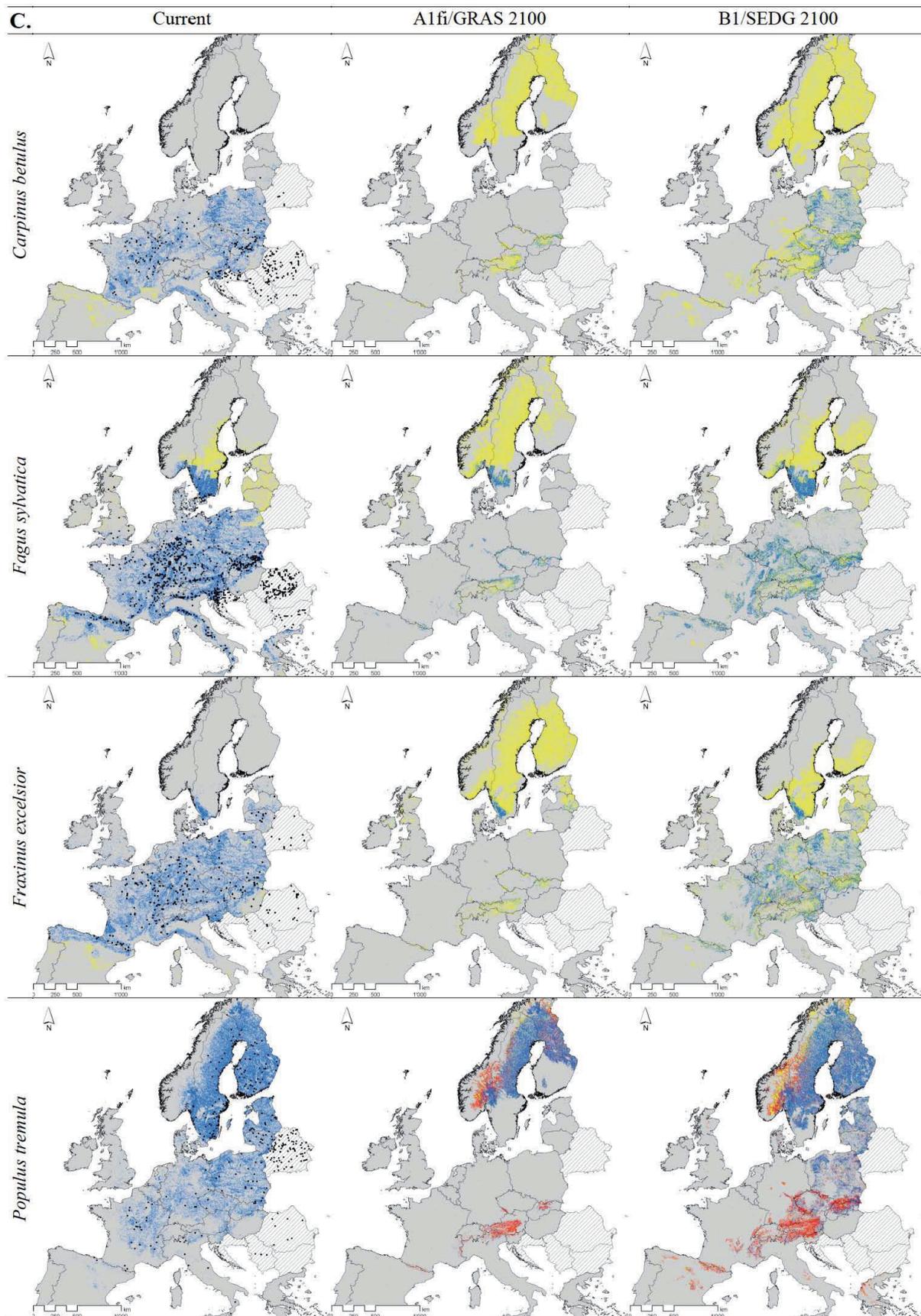


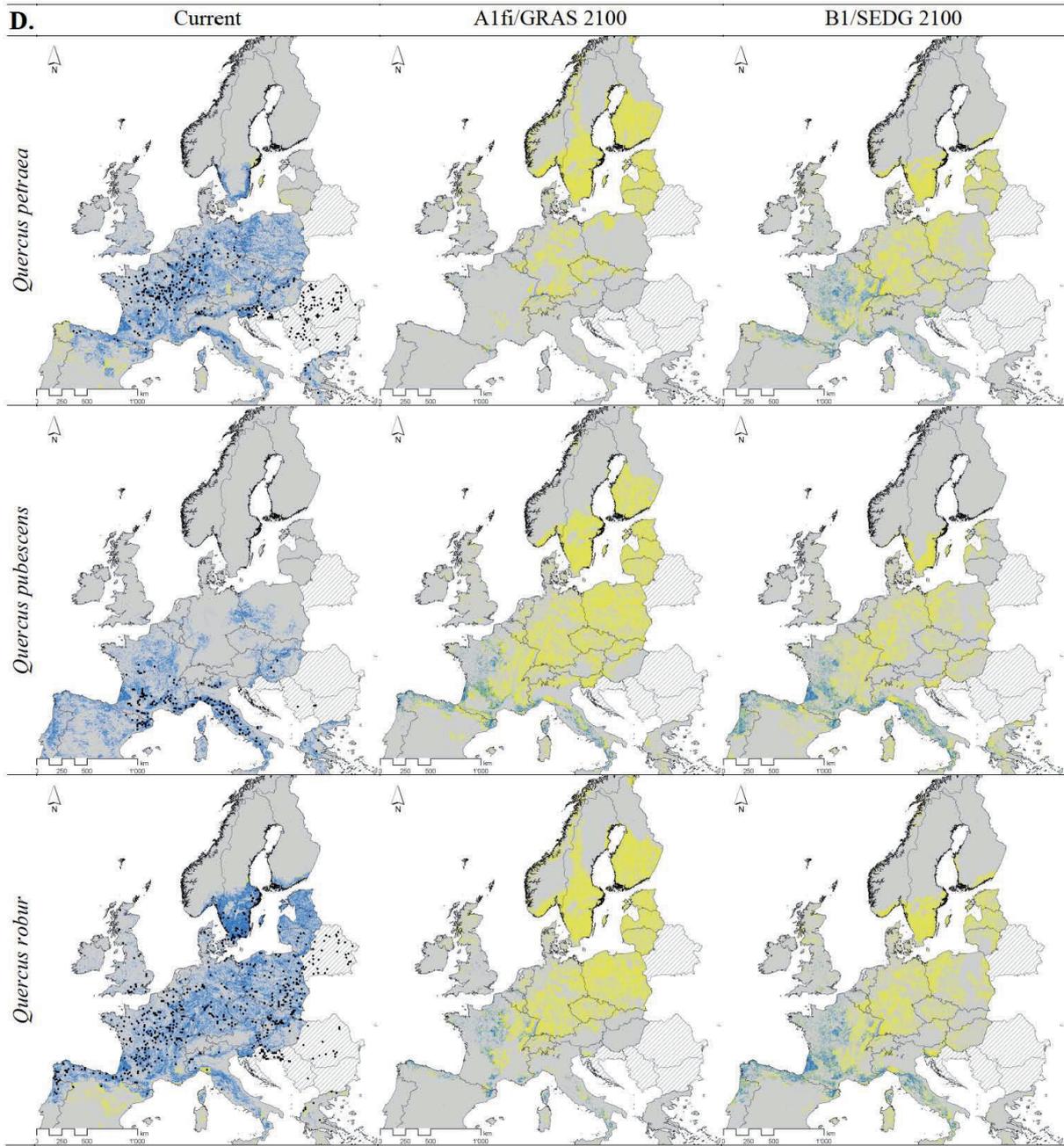
## Appendix S5 – Predicted species distributions

Predicted species distributions of the 14 focal tree species (plates A-D) until 2100 (A1fi/GRAS and B1/SEDG climate and land-use scenarios) for no, realistic and unlimited migration scenarios. Predicted species distributions assuming no migration are coloured blue (top layer), distributions assuming realistic migration red (medium layer) and distributions assuming unlimited migration scenarios yellow (bottom layer). Black points in the current distribution represent actual species occurrences in ICP Forest Level 1 data. Countries grey highlighted represent areas of model predictions; countries with stripes represent additional areas for model calibration.









## 5 Space matters when defining efficient management for invasive alien plants [Paper 4]

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Space matters when defining efficient management strategies for invasive alien plants.

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### 5.1 Summary

**1.** Invasive alien species cause harm to humans, animals and infrastructure and are among the largest threats to biodiversity across the globe. To reduce such losses of ecosystem services, management actions need to be developed that efficiently decrease population growth and spatial spread of invasive alien species. Currently, the efficiency of management is largely optimized locally by adjusting the intensity and frequency. However, to further increase the efficiency of management in complex landscapes, management may be targeted and spatially designed. Here, we evaluated in a simulation experiment the efficiency of such management strategies to control widespread invasive alien plants (IAPs) in complex landscapes.

**2.** To simulate costs and effects of 217 management strategies differing in local intensity, frequency, area and spatial allocation for controlling three widespread hydrochorous IAPs (i.e. *Heracleum mantegazzianum*, *Impatiens glandulifera* and *Reynoutria japonica*) across north-eastern Switzerland, we predicted habitat suitability with species distribution models and simulated demography and spread influenced by management strategies based on these suitability maps.

**3.** The spatial allocation of treatments strongly affected the efficiency of management strategies in complex landscapes. Most efficient management strategies treated small populations of sexually reproducing species and large populations of vegetatively reproducing species with highest local intensity, while primarily the frequency affected management costs. Without spatial strategy stands overcompensated management actions by higher vital rates, which lead to even stronger spread than without management. Further, we confirmed that effective early management largely increases the efficiency.

**4. Synthesis and applications.** Our results demonstrated that the efficiency of management is largely increased if treatments are targeted and spatially designed, and specifically, if early management is very effective. This highlights the need to carefully act early when IAPs start spreading, in order to achieve in the long-term higher protection at lower costs. Further, knowledge on maximally achievable effects from management strategies for different levels of costs is crucial for decision makers to compare policy options. Thus, our modelling approach may serve as a standard protocol to evaluate the efficiency of management strategies to reduce various IAPs in complex landscapes.

**Key words:** complex landscapes, *Heracleum mantegazzianum*, *Impatiens glandulifera*, invasive species, management strategy, population growth, *Reynoutria japonica*, riparian habitats, spatial spread, species distribution model.

## 5.2 Introduction

Biological invasions reduce ecosystem services by outcompeting native plants (Sala *et al.* 2000), harming the health of humans and domestic animals (Page *et al.* 2006), damaging infrastructure (Bohren 2010), providing feeding niches for other pests (Boppré *et al.* 1992), altering nutrient cycling (Asner & Vitousek 2005) or changing fire and water regimes (Schmitz *et al.* 1997). Further, they cause considerable economic costs when invaded areas have to be cleared (Pimentel *et al.* 2000). To reduce damage and costs from population growth and spread across landscapes, biological invasions should be controlled efficiently as early as possible (Mack *et al.* 2000; Hulme 2006). Therefore, various studies investigated the efficiency of early control approaches (e.g. Brabec & Pyšek 2000; Shea *et al.* 2010). However, these studies focused rather on local management than on landscape-wide management strategies. Local management concerns the efficiency of local treatments and includes for instance effects of chemicals, mechanical treatments or biological agents on local population growth and spatial spread. Such treatments are usually applied to vulnerable life-stages, i.e. for invasive alien plants (IAPs) this is typically the time of reproduction when dispersal occurs (Byers *et al.* 2002; Caswell, Lensink & Neubert 2003; Shea *et al.* 2010). In the practice, such local management approaches are often applied, but the rather uncoordinated manner hampers the deduction of general conclusions. Management strategies, on the other hand, focus on the temporal and spatial allocation of resources, namely when, where and how much control should be applied (Epanchin-Niell & Hastings 2010). To date, studies related to management strategies are rare and application in practice is scarce (De Waal 1994). Yet, many invasive species have become widespread and financial resources to control them are limited. Therefore, a refinement of prioritisation strategies remains an important challenge.

Management strategies often prioritize areas that are or will become suitable for IAPs under climate change (Thuiller *et al.* 2005; Ibáñez *et al.* 2009). However, limited resources require better-designed strategies, which may also include effects of dispersal limitations (Richardson *et al.* 2010) or may focus on identifying habitats or populations that most strongly contribute to spatial spread and population growth (Andrew & Ustin 2010). Few studies tested these two aspects, however they present conflicting results and conclusions. For example, one study has advised prioritization of large populations for control because these are principal sources of propagules in metapopulation theory (Hulme 2003). Other studies have advised to prioritize small outlying populations because from a population dynamics perspective they contribute most to range expansion due to their large edge-to-area ratio (Moody & Mack 1988; Higgins, Richardson & Cowling 2000; Taylor & Hastings 2004). Some have advised to prioritize large connected habitats because according to the percolation theory (Turner 1989) migration is reduced with increasing habitat fragmentation (With 2002), while others proposed to treat the main pathways of assisted dispersal (Wadsworth *et al.* 2000) because in comparison to animals the navigation capacity of plants is lacking and dispersal is linked to movement of external vectors such as flowing waters, animals or humans (Damschen *et al.* 2008). Accordingly, hydrochorous IAP populations near streams and especially at upper reaches may be prioritized in order to reduce the sources for downstream colonisation (Wadsworth *et al.* 2000). Next to being partly contradictory, the majority of these studies only estimated the efficiency of management strategies for species that were not yet widespread and none of them addressed strategies for species occurring in complex landscapes despite variation in habitat suitability and habitat fragmentation may greatly influence patterns of spread (Meier *et al.* 2011). This lack of synoptic, profound scientific insights may lead to high costs with unclear success.

Economic efficiency refers to the use of resources such as to maximize the production of goods and services (Standish 2000). Translated to management strategies for IAPs, efficiency refers to the use of costs such as to maximize the effects on species occurrences and spread. Effects may be measured by the duration until a population falls below an arbitrary size or is locally extinguished (Regan *et al.* 2006). However, this makes only sense for isolated populations (Solow *et al.* 2008). Otherwise, individuals may always continue to invade by long-distance dispersal from conjoint areas. In such cases, effects may be measured by the ability of reducing local population growth or spatial spread (Shea *et al.* 2010). Yet, even though a management strategy may be very effective, its costs may still be tremendous. Thus, one may examine management options for different levels of costs, either estimated by real financial costs (Regan *et al.* 2006) or by cost proxies, such as area treated (Naidoo *et al.* 2006), frequency of treatment in time or number of removed individuals (Higgins, Richardson & Cowling 2000). Cost proxies are generally more intuitive to develop and understand than real financial costs. Moreover, the use of cost proxies is advisable if sound data on specific costs are lacking and where real financial costs are highly volatile because they heavily depend on variable

costs for labour, material, local detection probability of IAPs (Hauser & McCarthy 2009), reachability and size of the area that has to be treated (i.e. economy of scales). The use of proxies may also be preferred where monetizing impact costs on ecosystem goods and services (Yokomizo *et al.* 2009) are difficult. Consequently, to adequately evaluate the efficiency of management strategies for rather widespread IAPs in complex and fragmented landscapes, one may target a maximal reduction of spatial spread and population growth for certain levels of costs proxies.

Optimizing management strategies experimentally is costly, and therefore using models to assess the effect of IAP management strategies is highly promising (Buckley, Briese & Rees 2003). Currently, most models on invasion control are based on reaction-diffusion processes (e.g. Flather & Bevers 2002), integro-difference equations (e.g. Kot, Lewis & vandenDriessche 1996), matrix models (e.g. Hooten *et al.* 2007), gravity models (e.g. Bossenbroek, Kraft & Nekola 2001) or cellular automata (e.g. Higgins, Richardson & Cowling 2000). Using such models in sensitivity analyses has proven useful to determine the intensity and frequency of treating most vulnerable life-stages (Byers *et al.* 2002; Caswell, Lensink & Neubert 2003; Shea *et al.* 2010) and to determine the efficiency of management strategies within simple landscapes (Moody & Mack 1988; Wadsworth *et al.* 2000). However, most of these models lack the capacity to evaluate management strategies in complex and fragmented landscapes. We therefore believe that a promising approach is to combine a population spread model with species distribution models (SDMs; Guisan & Zimmermann 2000).

In this study, we used such a hybrid model to evaluate the efficiency of different management strategies for various cost levels and management goals for widespread IAPs in complex landscapes. Specifically, we addressed the following three main questions: (1) Is the efficiency of management actions higher, if they are allocated according to specific spatial patterns across the landscape? (2) Do most efficient strategies vary between species with different traits, between management goals (i.e. reducing spread, area, individuals, regeneration or overall) or between different cost levels? (3) How do effects and costs change during 15 years of simulation and are the accumulated costs at the end of the simulation correlated with the magnitude of effects? To tackle these questions, we adapted the hybrid model 'CATS' (Dullinger, Hülber & Gattringer unpubl.) in order to simulate effects on population growth and spatial spread by 217 management strategies differing in local intensity, area treated, treatment frequency and spatial allocation applied over 15 simulation years. We selected three IAPs that have extensively spread in riparian habitats and differ in life form, i.e. giant hogweed (*Heracleum mantegazzianum*), Himalayan balsam (*Impatiens glandulifera*) and Japanese knotweed (*Reynoutria japonica*). As study area we selected the Swiss plateau, a hub of biological invasions due to a high proportion of urban areas at low altitude (Nobis, Jaeger & Zimmermann 2009).

## 5.3 Materials and methods

### 5.3.1 Study area

Our study area comprised the Canton Zurich (1729 km<sup>2</sup>; 47°09'N-47°41'N, 8°21'E-8°59'E) located in northeastern Switzerland. Compared to Europe the number of IAPs in Switzerland is above average (EEA/SEBI 2010), while the metropolitan area around Zurich is a hub of human mediated invasions due to its high population density and percentage of agricultural area. The climate is moist and mildly maritime, elevation ranges from 330-1289 m a.s.l., and numerous river valleys provide suitable habitats for hydrochorous IAPs.

### 5.3.2 Species data

As study species we used giant hogweed (*Heracleum mantegazzianum* Sommier et Levier), Himalayan balsam (*Impatiens glandulifera* Royle) and Japanese knotweed (*Reynoutria japonica* Houtt.). They are widespread in the study area and affect their environment by rapidly colonizing habitats of native species. Further, *H.mantegazzianum* harms the health of humans and domestic animals, while *I.glandulifera* and *R.japonica* erode riverbanks and damage infrastructure. The study species all spread predominantly in ruderal riparian habitats but differ in life form: *H.mantegazzianum* is monocarpic perennial, *I.glandulifera* is annual and *R.japonica* is polycarpic perennial but disperses in Europe exclusively vegetatively by plant fragments and rhizomes (see also Table S1 in Supporting Information).

Occurrence data was derived from the 'Neophytenkataster' of the Canton of Zurich ([www.gis.zh.ch/dokus/awel/abfallwirtschaft/neophyten.html](http://www.gis.zh.ch/dokus/awel/abfallwirtschaft/neophyten.html)), which contains point and polygon data on species abundance and area occupied. For *H.mantegazzianum* we used  $n=1216$  observations, for *I.glandulifera*  $n=2251$  and for *R.japonica*  $n=2346$ , which were all collected between 2006 and 2010 by community employees, nature conservation authorities and private persons. Because an overall sampling design was lacking, communities were sampled quite unevenly. Communities where most occurrences were documented we refer to as 'well-sampled communities', while communities with lower documented percentages we refer to as 'insufficiently-sampled communities'.

### 5.3.3 Environmental data

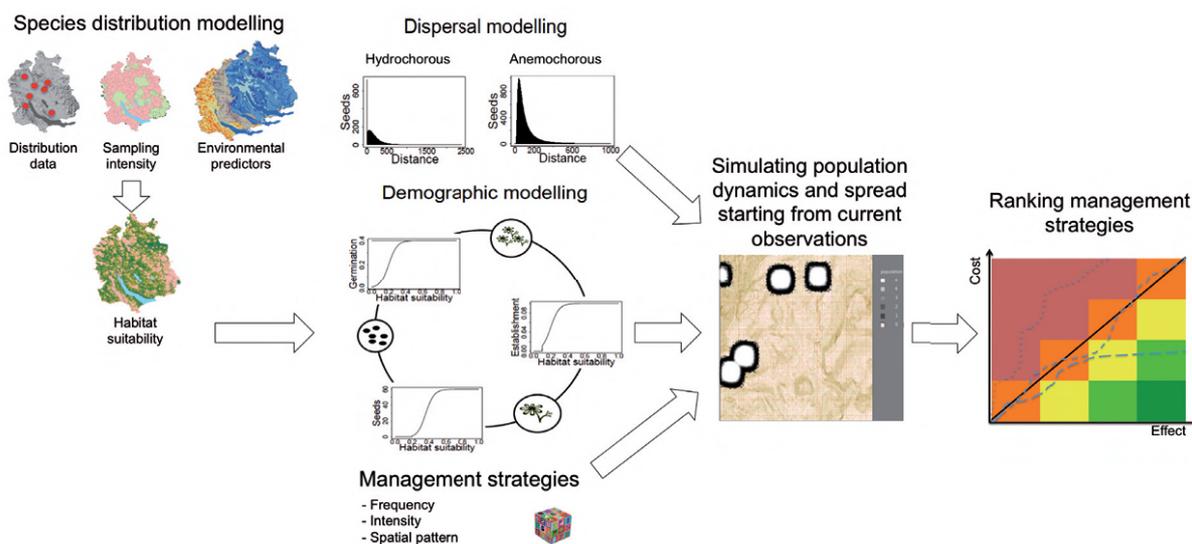
We selected 17 out of a more comprehensive set of environmental variables describing habitat quality and propagule pressure. All selected variables had correlations  $r_s < |0.6|$  to reduce multicollinearity problems. All environmental data was generated at 25 m spatial resolution.

As climate variable we used degree-days with a 5.56°C threshold [°C x d] estimated from downscaled monthly temperature maps for current climate (1950-2000; [www.worldclim.org](http://www.worldclim.org)). As

topographic variables we used aspect value [0-100 for south- to north-facing slopes], potential yearly global radiation [ $\text{kJ m}^{-2} \text{d}^{-1}$ ] and topographic position [range] estimated from a digital elevation model (DEM25; Swisstopo 2003). As soil variable we used coarse fragment content [five categories] from a soil suitability map (BEK200; BFS GEOSTAT 2000). As land-use variable we used land-use categories ‘settlement’, ‘agriculture’, ‘forest’, ‘nature reserve’ and ‘water bodies’ from the cantonal structure plan (Canton Zurich 2001). As distance variables we used distance to open gravel pits estimated from the gravel cadastre (Canton Zurich 2008); distance to house building activities estimated from the cantonal structure plan; distance to buildings, distance to forest edges, distance to small roads without tunnels, distance to large roads without tunnels, distance to railroads and distance to bridges estimated from VECTOR25 data (Swisstopo 2008); and distance to non-covered creeks, distance to non-covered rivers and distance to lakes estimated from the ecomorphological survey of flowing waters (Canton Zurich 2007).

### 5.3.4 Statistical analyses

To evaluate the efficiency of management strategies for widespread hydrochorous IAPs in complex landscapes we used the hybrid model CATS (Dullinger, Hülber & Gattringer unpubl.), which simulates, starting from known current occurrences, site-specific vital rates and spread based on habitat suitability maps. Therefore, we (1) mapped suitable habitats with SDMs, (2) mitigated unequal sampling of recorded occurrences, (3) parameterized and extended the hybrid model ‘CATS’ in order to account for hydrochory and management strategies, and (4) ranked the 217 tested management strategies per species according to cost proxies and effects in order to estimate the efficiency of the management strategies (Fig. 1).



**Fig. 1** Overview of model setup. Species distribution models were used to estimate habitat suitability. Habitat suitability determined within the hybrid model ‘CATS’ the rates of local demographic processes, which controlled the number of individuals at a site and the number of seeds produced by these individuals. The 217 management strategies removed juveniles and adults just before seeding. Local seed yields were re-distributed according to water and wind dispersal kernels. Efficiencies of management strategies were assigned by evaluating costs and effects.

#### 5.3.4.1 Mapping suitable habitats with SDMs

We mapped habitat suitability with SDMs using generalized linear models (GLMs), because they represent a good trade-off between complexity and performance. Further, GLMs allow for spatial autocorrelation correction and require presence-absence data. Spatial autocorrelation correction is required, because SDMs assume independently distributed errors (Anselin *et al.* 1996). Yet, most IAPs are still spreading from nascent foci, whereby their distribution patterns exhibit high degrees of spatial autocorrelation (Welk 2004). In order to prohibit incorrect statistical estimates of habitat parameters, spatial autocorrelation has to be addressed explicitly (Dormann *et al.* 2007). We applied a spatial eigenvector filtering method by using the R-library ‘spacemaker’ (SEVM-v3; Bini *et al.* 2009), which calculates spatial eigenvectors that can be included into SDMs. Further, because our dataset only included reported presences, we generated a set of pseudo-absences. In order to reduce the probability of generating pseudo-absences at locations where IAPs are present, we randomly generated 80% in well-sampled communities but excluded areas within a 25m buffer of recorded IAP locations. The total number of pseudo-absences was set equal to the number of presences of each species.

GLMs were calibrated with presences and pseudo-absences as binary response variable and the 17 environmental variables and the significant spatial eigenvectors as predictors. Environmental

variables were entered both as linear and quadratic terms to allow for non-linear responses. GLMs were built assuming binomial distributions with logit links followed by both backward and forward stepwise variable selection based on BIC. Model fit was evaluated by the adjusted  $D^2$  and model accuracy was evaluated by estimating Cohen's kappa and area under the receiver characteristic curve (AUC) by applying a 10-fold cross-validation. Non-colonizable areas such as buildings and lakes were set to unsuitable when mapping.

#### 5.3.4.2 Mitigating unequal sampling of current occurrences

As initial populations for the CATS runs we used the sum of occurrences of the last five years and we additionally generated nine sets of artificial populations to balance the unequal sampling efforts across the study area. These artificial population sets are important because patterns of spread depend on the initial spatial arrangement of species (Marchetto *et al.* 2010). To evaluate the degree of undersampling, we extrapolated the number of missing individuals per suitable habitat area of insufficiently-sampled communities from the ratio of individuals per suitable habitat area of well-sampled communities. Artificial population sizes were estimated by  $\text{mean} \pm \text{sd}$  of recorded population sizes in well-sampled communities and reached  $118.9 \pm 57.5$ ,  $152.2 \pm 105.5$ ,  $108.8 \pm 89.3$  for *H.mantegazzianum*, *I.glandulifera*, and *R.japonica*, respectively. This translated for the three species to additional 2675, 5767, and 902 populations respectively, which were randomly generated in under-sampled suitable habitat.

#### 5.3.4.3 Parameterizing and extending CATS

CATS is a population model that uses habitat suitability maps from SDMs to determine site-specific vital rates like germination, juvenile survival, juvenile to adult transition, seed yield, clonal reproduction and adult mortality, while density-dependent regulation decreases some of these vital rates. Seeds are re-distributed at the end of each growing season according to wind dispersal kernels that account for short and long distance dispersal (WALD model; Katul *et al.* 2005). For this study we integrated into CATS management strategies that remove juveniles and adults just before seeds were produced, and we added water dispersal that redistributes seeds and plant fragments along creeks and rivers after wind dispersal (i.e. negative exponential kernel for unidirectional dispersal in flow direction along the riverbed and riverside, Groves *et al.* 2009). Model parameters we derived from literature and few parameters we fitted by sensitivity analyses (Table S1).

Implemented management strategies included additional to the 'do nothing'-strategy 216 strategies representing combinations of frequency, local intensity, area and patterns of spatial allocation (Table 1). The frequency was selected according to common policies of practitioners, i.e. annual, bi-annual or five-annual treatments, while the first treatment was applied in the 1<sup>st</sup>, 2<sup>nd</sup> or 5<sup>th</sup> year. The intensity was affected by the local intensity of treatments (i.e. 25, 55 and 90% of juveniles

and adults were removed within a treated cell, while seed banks were only affected by reduced supply) and by the area treated (i.e. 5, 25 and 50% of cells with IAP occurrence were treated). The addressed local intensity of treatments reflected the range of most common treatments applied by practitioners, i.e. mechanical treatments (e.g. removal of stems or roots), chemical treatments (e.g. foliar- or soil-active chemicals), cultural treatments (e.g. grazing, re-vegetation, competition plantations, fertilization or fire) or biological treatments (e.g. augment or release native enemies or release enemies from the native IAP distribution) (Masters & Sheley 2001). These vary in local intensity between ca. 25% (e.g. sheep grazing for *H.mantagazzianum* (Andersen 1994)) and ca. 90% (e.g. Glyphosate spraying 3-4 times a year for *R.japonica* (De Micheli *et al.* 2006)). Patterns for spatial allocation of treatments were selected according to the biology of dispersal and focused on eight different spatial allocation strategies. First, we targeted large populations as they may reflect core populations that represent principal sources of propagules (Hulme 2003). Second, we targeted small populations as they have large edge-to-area ratios and hence may contribute most to range expansion (Moody & Mack 1988; Taylor & Hastings 2004). Third, we targeted outlier populations as these are surrounded mostly by non-colonized habitats into which they may spread. Fourth, we targeted cells within well-connected suitable habitats because according to the percolation theory high fragmentation may effectively reduce migration through corridors (Turner 1989; With 2002). Fifth, we targeted cells on riverbanks, because rivers are the main dispersal pathways of hydrochorous plants. Sixth, we targeted upper reaches of rivers, which may reduce the propagule sources for downstream colonisation (Wadsworth *et al.* 2000). Seventh, we targeted lower reaches of rivers, which reduces only the arriving propagules that could establish. Eighth, we targeted cells randomly to test the null hypothesis that the spatial allocation of treatments has no influence on efficiency. For further details on spatial patterns see Appendix S2. In summary, combinations of three treatment frequencies, three local intensities, three sizes of area treated and eight patterns of spatial allocation plus one 'do nothing'-strategy as a comparison for evaluating treatment efficiency resulted in 217 management strategies (Table 1). According to these management strategies, individuals were either cleared in entire cells that were randomly selected within predefined areas (i.e. well-connected habitats, riverbanks, upper reaches of rivers, lower reaches of rivers or random allocation over the whole study area) or in entire populations that were sequentially selected (i.e. large populations, small populations or outlying populations; populations were defined by colonized cells with common edges). As a result, management strategies differing only in their pattern of spatial allocation may treat unequal areas, because not all randomly selected cells in predefined areas may be colonized by IAPs and predefined areas may be too limited to contain the specified size of area to be treated.

Simulations with CATS were run over fifteen years for three species, nine initial conditions and 217 management strategies (Table 1). During each run we recorded yearly parameters related to management costs (i.e. the frequency, area, intensity, number of treated cells, number of treated adults

and number of treated juveniles) and management effects (i.e. number of colonized cells, number of adults, number of juveniles, number of seeds and spreading into uncolonized habitats). Because CATS is initialized only with adult populations, which produce propagules in the first simulation year and then die, the yearly values in the first years may be awkward especially for the monocarpic *H.mantegazzianum*, while we expect negligible biases for the annual *I.glandulifera* and for *R.japonica* that produces fragments that become adults within the same year.

**Table 1.** Overview of characteristics that were combined to set up management strategies. Additionally, we included a ‘do nothing’-strategy, which only addresses combinations of species and start populations. All these combinations resulted in 5859 model runs.

| Species                  | Start population | Frequency   | Intensity       |      | Spatial allocation      |
|--------------------------|------------------|-------------|-----------------|------|-------------------------|
|                          |                  |             | Local intensity | Area |                         |
| <i>H. mantegazzianum</i> | 1-9              | Annual      | 25%             | 5%   | Large populations       |
| <i>I. glandulifera</i>   |                  | Bi-annual   | 55%             | 25%  | Small populations       |
| <i>R. japonica</i>       |                  | Five-annual | 90%             | 50%  | Outlying populations    |
|                          |                  |             |                 |      | Well-connected habitats |
|                          |                  |             |                 |      | Riverbanks              |
|                          |                  |             |                 |      | Upper reaches of rivers |
|                          |                  |             |                 |      | Lower reaches of rivers |
|                          |                  |             |                 |      | Random                  |

#### 5.3.4.4 Efficiency of management strategies

To estimate the efficiency of management strategies for different cost levels, we first averaged the output values of the model runs among the nine initial conditions. Second, we corrected for the decrease in spread rate due to crowding by multiplying the spread rates with the percentage of colonized suitable habitat cells. We did so because spread rates into vacant suitable habitats drop with decreasing proportion of vacant sites (Loreau & Mouquet 1999). Third, we estimated for each of the 217 management strategies for each year and after 15 years of simulation the relative effects by using the ‘do nothing’-strategy as baseline, while costs we estimated by using the values of the ‘do nothing’-strategy as potential maximum. Effects were addressed using four goals, i.e. the ability to reduce (i) spread into uncolonized habitats, (ii) area of distribution by juveniles and adults, (iii) number of adult individuals and (iv) regeneration potential (i.e. giving equal weights to the number of juveniles and the number of seeds). Costs were not equal each year as they were calculated yearly from fractions of maximal area and number of individuals to be treated based on actual occurrence. Therefore, we evaluated a combined cost proxy by giving 30% weight to frequency of treatments,

30% weight to number of treated cells and 40% weight to number of treated juveniles and adults. Efficiency was defined by estimating for each management goal the most effective management strategy for each of four levels of costs (i.e. <10, 10-25, 25-40 and >40%).

## 5.4 Results

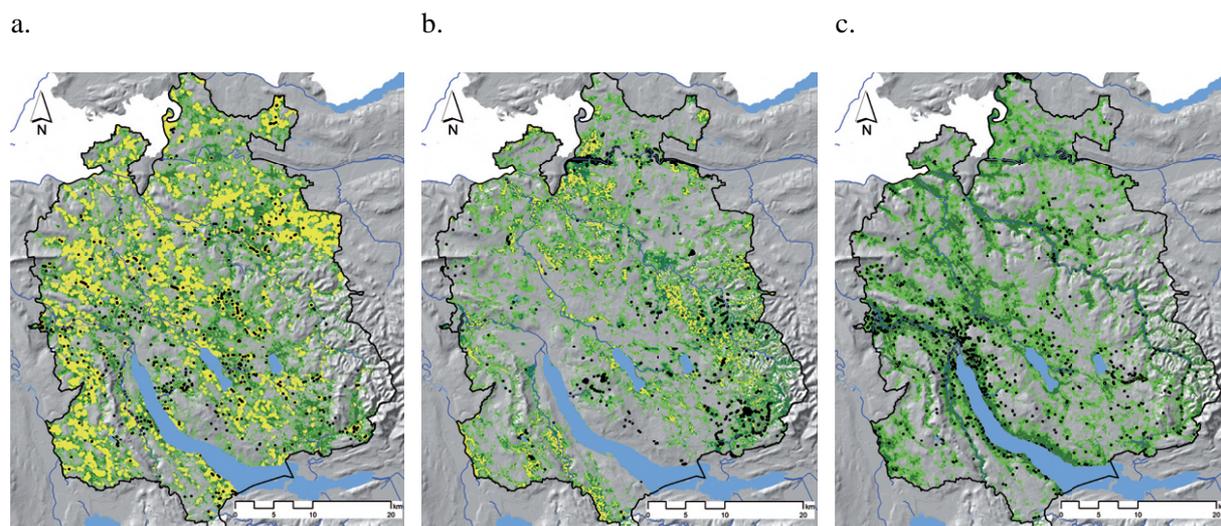
### 5.4.1 Colonization of suitable habitats

SDM quality was high for all three species (Table 2) and AUC and Kappa values for *H.mantegazzianum*, *I.glandulifera* and *R.japonica* models reached 0.89, 0.91, 0.90 and 0.62, 0.66, 0.64, respectively. The importance of single predictors for current distribution varied strongly among the species (Table 2). Current distribution of *H.mantegazzianum* was best explained by short distances to large roads and bridges and increasing degree-days, while *I.glandulifera* was mainly occurring in recreation areas, nature conservation areas and forests, near forest edges and near small roads. *R.japonica* was occurring more in pits than on ridges, near bridges, in forest and agriculture areas, at higher degree-days, near house building activities and on soils with high coarse fragment contents.

**Table 2.** Partial deviance explained (adjusted  $D^2$ ) for individual variables after spatial eigenvector filtering and overall explained deviance. Bold face indicate adjusted  $D^2$  from individual predictors > 0.05.

| Predictor                         | <i>H.mantegazzianum</i> | <i>I.glandulifera</i> | <i>R.japonica</i> |
|-----------------------------------|-------------------------|-----------------------|-------------------|
| Degree-days                       | <b>0.05</b>             | 0.01                  | <b>0.05</b>       |
| Aspect value                      | 0.00                    | 0.01                  | 0.00              |
| Potential yearly global radiation | 0.02                    | 0.02                  | 0.02              |
| Topographic position              | 0.04                    | 0.02                  | <b>0.08</b>       |
| Coarse fragment content           | 0.01                    | 0.01                  | <b>0.05</b>       |
| Land-use                          | 0.04                    | <b>0.09</b>           | <b>0.06</b>       |
| Gravel pits                       | 0.02                    | 0.04                  | 0.01              |
| House building activities         | 0.04                    | 0.03                  | <b>0.05</b>       |
| Buildings                         | 0.03                    | 0.03                  | 0.04              |
| Forest edges                      | 0.01                    | <b>0.06</b>           | 0.00              |
| Small roads                       | 0.03                    | <b>0.05</b>           | 0.01              |
| Large roads                       | <b>0.06</b>             | 0.01                  | 0.04              |
| Rail roads                        | 0.01                    | 0.04                  | 0.04              |
| Bridges                           | <b>0.05</b>             | 0.01                  | <b>0.07</b>       |
| Non-covered creeks                | 0.02                    | 0.03                  | 0.00              |
| Non-covered rivers                | 0.02                    | 0.03                  | 0.04              |
| Lakes                             | 0.02                    | 0.01                  | 0.02              |
| <i>Final model:</i>               | <i>0.24</i>             | <i>0.33</i>           | <i>0.24</i>       |

Colonisation rates of suitable habitats under no treatment differed strongly between the tree species. The simulated rate of area increase over 15 years on the Swiss plateau was highest for *H.mantegazzianum* (from 0.2% to 38.1% within 925 km<sup>2</sup> of suitable habitat area in the study area; Fig. 2a), lower for *I.glandulifera* (from 0.7% to 17.6% within 689 km<sup>2</sup> of suitable habitat area; Fig. 2b) and lowest for *R.japonica* (from 0.2% to 0.8% within 735 km<sup>2</sup> of suitable habitat area; Fig. 2c).



**Fig. 2.** Predicted potential habitats and colonised habitats after 15 years without control of *H.mantegazzianum* (a), *I.glandulifera* (b) and *R.japonica* (c). Black points represent current observation points, yellow areas represent areas colonized after 15 years without control, dark green areas represent potential habitats with a high probability of occurrence ( $> \max. \text{Kappa}$ ) and light green areas represent potential habitats with a low probability of occurrence (false negative rate  $< 0.05$ ).

#### 5.4.2 Efficiency of management strategies

Tested management strategies were not able to reduce the area, number of adults and regeneration potential below current levels, except for *R.japonica* where a few strategies were even able to eradicate the species (Fig. S3). Nevertheless, compared to the ‘do nothing’-strategy, the efficiency of treatments was partly very high if it followed a non-random spatial strategy at the landscape scale (Fig. 3, 4, 5 and Table S4). Among all management goals, most effective management strategies per cost level reduced *H.mantegazzianum*, *I.glandulifera*, *R.japonica* compared to the ‘do nothing’-strategy on average by -38.7%, -35.6%, -61.0%, while the most effective random strategies only reduced the three species by -5.2%, -2.1%, -1.1%. The average annual costs per cost level expressed as a fraction of costs when eradicating all populations under the ‘do nothing’-strategy was for the most effective strategies 27.9%, 29.0%, 26.9% compared to 19.2%, 17.7%, 16.9% for the most effective random strategies (Fig. 3 and Table S4). This means that efficient management strategies are

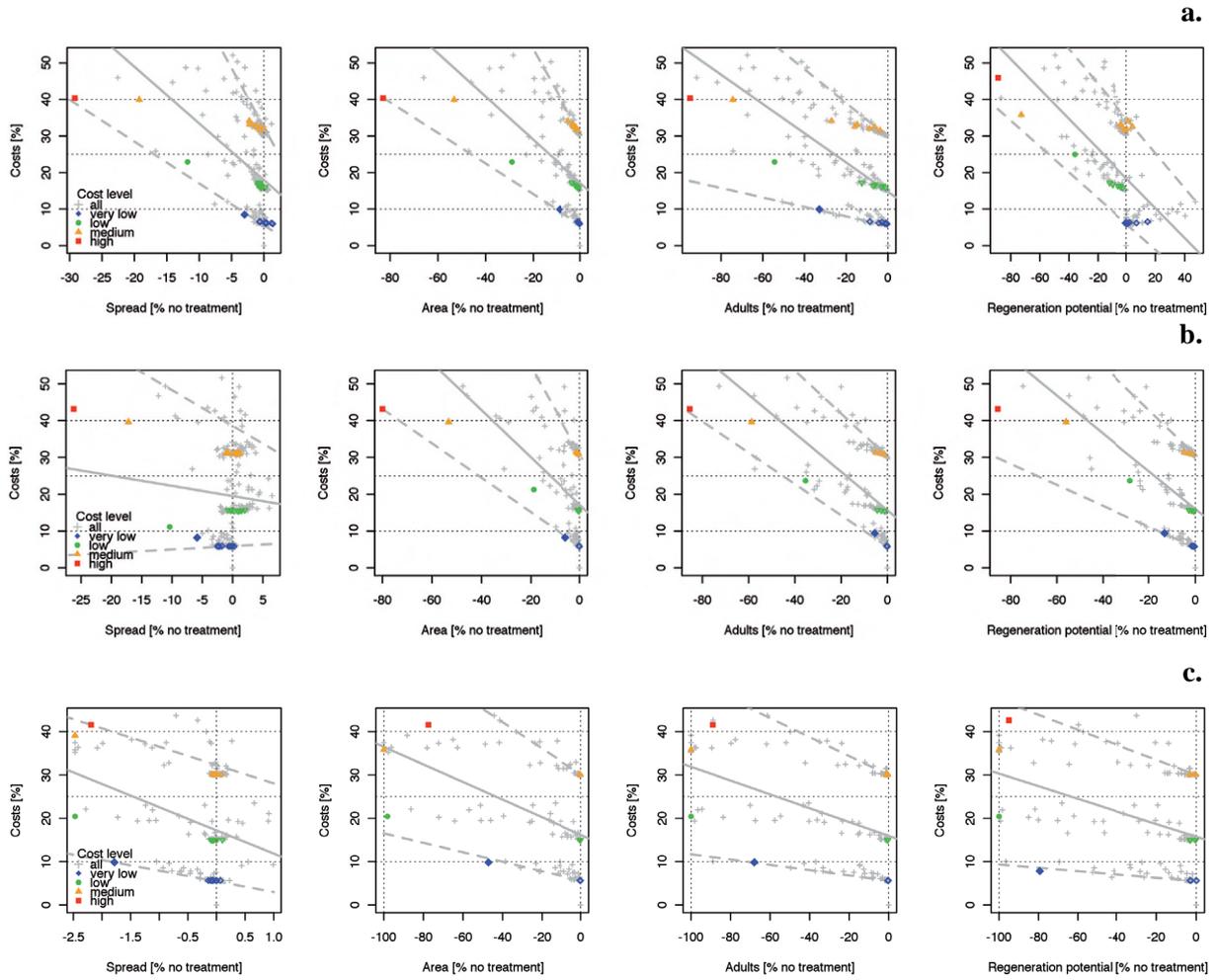
roughly 10% more expensive than random strategies, yet they are 30-60% more effective. Moreover, ineffective strategies (e.g. random) often even showed contrary effects despite comparably high costs to effective strategies. Without effective strategic removal of individuals, stands tended to overcompensate for the removed individuals by higher germination, juvenile survival and clonal propagation, which lead to stronger spread into non-colonized suitable habitats (Fig. 3, 4).

To reduce IAPs most efficiently in complex landscapes, primarily whole populations should be treated with highest possible local intensity, namely small populations for sexually reproducing species and large populations for vegetatively reproducing species (Table 3). Different cost levels result from changing the frequency rather than from changing the spatial allocation patterns and the intensity per area treated (Table 3). Management goals do not need to be addressed separately as most efficient treatments do not vary much between the different goals (Table 3).

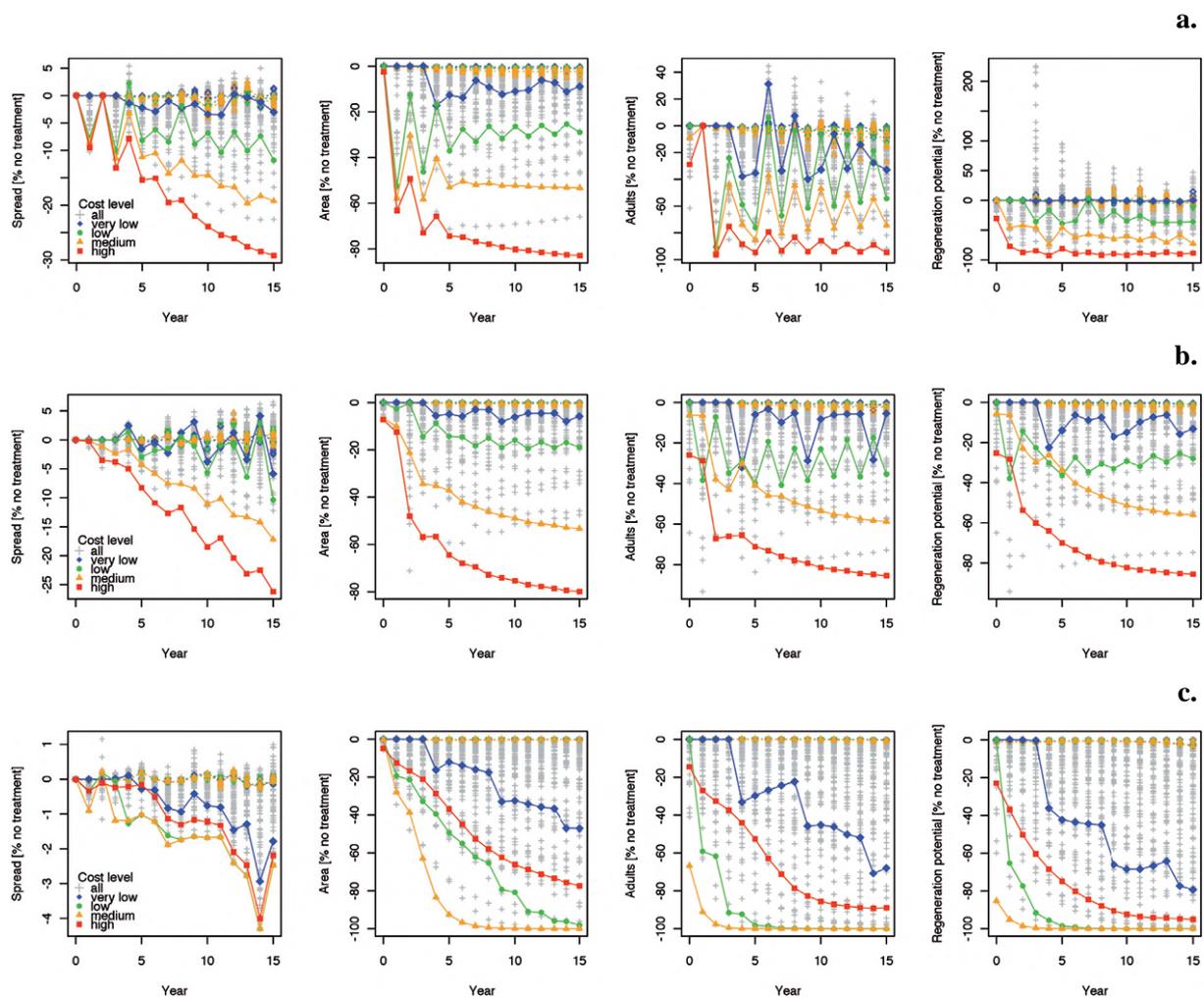
With increasing overall costs, larger effects were achieved (Fig. 3). However, over the 15 simulation years, yearly effects increased while yearly costs decreased (Fig. 4, 5). Moreover, the magnitude of effects achieved at early stages had a strong impact on the costs and effects in the following years, whereby strategies with high initial costs and effects achieved higher effects and lower overall costs than strategies with low initial costs and effects (Fig. 3, 4, 5). Thus, for *R.japonica* most effective strategies for low and medium cost levels reached even larger effects than the most effective strategy for the high cost level over the 15 years (Fig. 4, 5).

**Table 3.** Overview of most effective strategies for each species per management goal and cost level. ‘Very low’ cost levels refer to total overall costs of <10%, ‘low’ to 10-25%, ‘medium’ to 25-40% and ‘high’ to >40%; ‘Allocation’ refers to the applied pattern of treatments; intensity refers to habitat area treated (‘Area’, [%]) and locally applied intensity (‘Int.’, [%]); and frequency of treatments (‘Freq.’) is given in years.

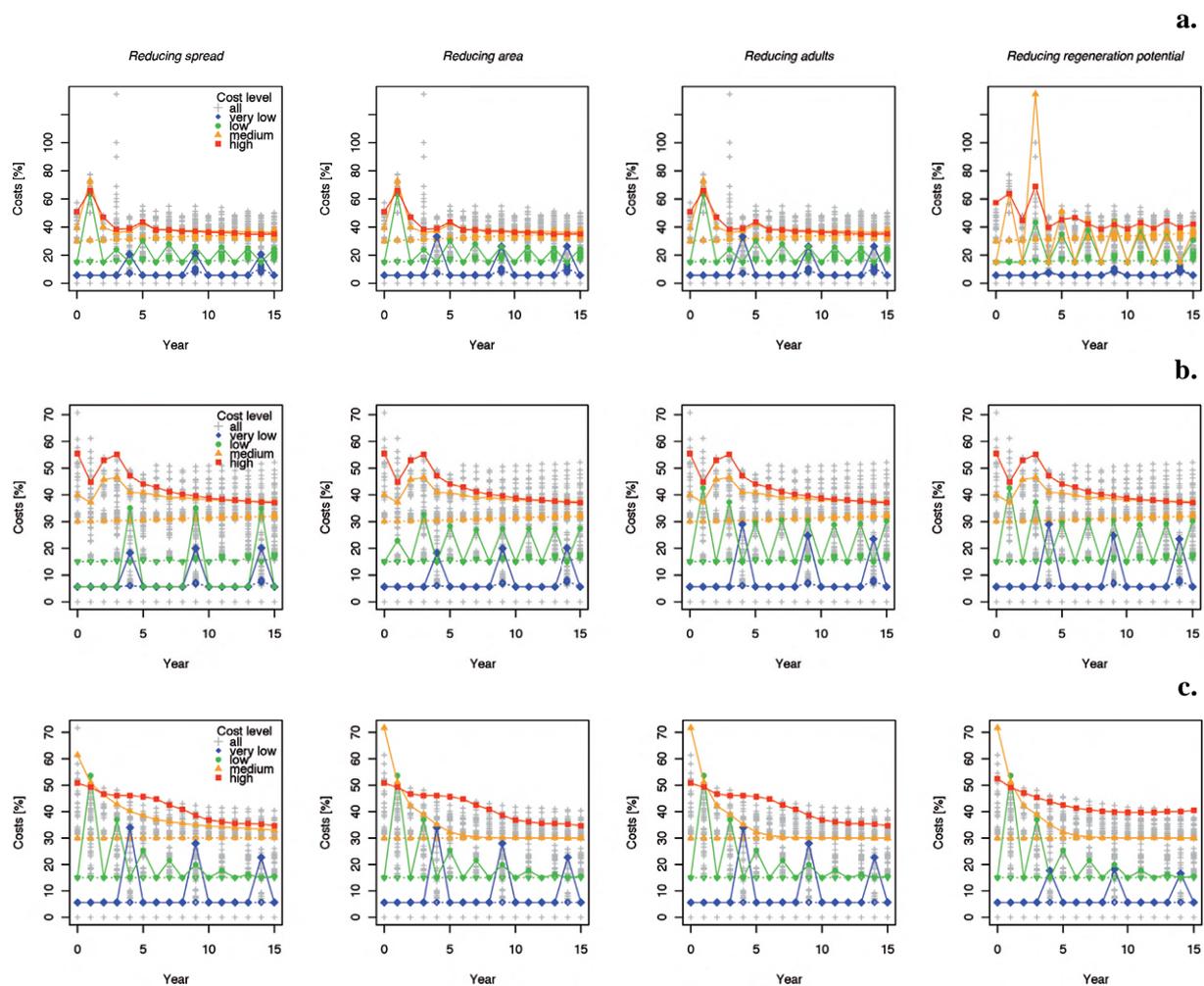
| Management goal        | Cost level | <i>H.mantegazzianum</i> |      |      |       | <i>I.glandulifera</i> |      |      |       | <i>R.japonica</i> |      |      |       |
|------------------------|------------|-------------------------|------|------|-------|-----------------------|------|------|-------|-------------------|------|------|-------|
|                        |            | Allocation              | Area | Int. | Freq. | Allocation            | Area | Int. | Freq. | Allocation        | Area | Int. | Freq. |
| Reducing spread        | very low   | Small pop.              | 25   | 90   | 5     | Small pop.            | 25   | 90   | 5     | Small pop.        | 50   | 90   | 5     |
|                        | low        | Small pop.              | 25   | 90   | 2     | Small pop.            | 50   | 90   | 5     | Large pop.        | 50   | 90   | 2     |
|                        | medium     | Small pop.              | 25   | 90   | 1     | Small pop.            | 25   | 90   | 1     | Large pop.        | 50   | 55   | 1     |
|                        | high       | Small pop.              | 50   | 90   | 1     | Small pop.            | 50   | 90   | 1     | Small pop.        | 50   | 55   | 1     |
| Reducing area          | very low   | Outlying pop.           | 50   | 90   | 5     | Small pop.            | 25   | 90   | 5     | Small pop.        | 50   | 90   | 5     |
|                        | low        | Small pop.              | 25   | 90   | 2     | Small pop.            | 25   | 90   | 2     | Large pop.        | 50   | 90   | 2     |
|                        | medium     | Small pop.              | 25   | 90   | 1     | Small pop.            | 25   | 90   | 1     | Large pop.        | 50   | 90   | 1     |
|                        | high       | Small pop.              | 50   | 90   | 1     | Small pop.            | 50   | 90   | 1     | Small pop.        | 50   | 55   | 1     |
| Reducing mature plants | very low   | Outlying pop.           | 50   | 90   | 5     | Outlying pop.         | 50   | 90   | 5     | Small pop.        | 50   | 90   | 5     |
|                        | low        | Small pop.              | 25   | 90   | 2     | Outlying pop.         | 50   | 90   | 2     | Large pop.        | 50   | 90   | 2     |
|                        | medium     | Small pop.              | 25   | 90   | 1     | Small pop.            | 25   | 90   | 1     | Large pop.        | 50   | 90   | 1     |
|                        | high       | Small pop.              | 50   | 90   | 1     | Small pop.            | 50   | 90   | 1     | Small pop.        | 50   | 55   | 1     |
| Reducing regeneration  | very low   | Outlying pop.           | 5    | 25   | 5     | Outlying pop.         | 50   | 90   | 5     | Large pop.        | 25   | 90   | 5     |
|                        | low        | Outlying pop.           | 50   | 90   | 2     | Outlying pop.         | 50   | 90   | 2     | Large pop.        | 50   | 90   | 2     |
|                        | medium     | Large pop.              | 50   | 90   | 2     | Small pop.            | 25   | 90   | 1     | Large pop.        | 50   | 90   | 1     |
|                        | high       | Large pop.              | 50   | 90   | 1     | Small pop.            | 50   | 90   | 1     | Large pop.        | 50   | 25   | 1     |



**Fig. 3.** Accumulated costs over 15 years and effects achieved after 15 years per management goal for *H.mantegazzianum* (a), *I.glandulifera* (b) and *R.japonica* (c). Filled symbols indicate most effective strategies, while empty symbols indicate random strategies. Grey lines indicate the mean and the 95% confidence intervals of all simulations, whereby dots below the mean line represent strategies that perform better than average.



**Fig. 4.** Achieved effects over 15 years of simulation per management goal for *H.mantegazzianum* (a), *I.glandulifera* (b) and *R.japonica* (c). Filled symbols and solid lines indicate most effective strategies, while empty symbols and dashed lines indicate random strategies.



**Fig. 5.** Used costs over 15 years of simulation per management goal for *H.mantegazzianum* (a), *I.glandulifera* (b) and *R.japonica* (c). Filled symbols and solid lines indicate most effective strategies, while empty symbols and dashed lines indicate random strategies.

## 5.5 Discussion

Only if management is efficiently applied, the relatively high financial costs to reduce ecological and societal impacts of IAPs are justified. In our study, we demonstrated how management strategies can be optimized as to where, when, how much control optimally could be applied to IPAs. Most efficient strategies treated entire populations (i.e. small or large populations depending on species traits) with highest possible local intensity, while the frequency of treatments rather affected costs. Further, we confirmed that effective treatment of species early during invasion increase the efficiency of control efforts. Below, we first discuss management implications followed by a discussion of the model performance and capacity.

### 5.5.1 Efficiency of management strategies

Most current management approaches to control biological invasions are costly because treatments are applied only locally without spatial strategy. This is likely because the responsibility for taking management decisions is too much at a local level (Epanchin-Niell & Hastings 2010) and because scientific insight is lacking. In order to evaluate efficient management strategies, various spatial allocation patterns were derived from the biology of invasions. We found large improvements by applying designed spatial strategies over simple random treatments. Yet, the tested strategies were only able to crucially reduce spread and growth of populations and were not able (except for *R.japonica*) to contain or eradicate the species because they re-invaded too rapidly from uncontrolled neighbouring patches. One key result of our study was that without efficient strategic removal of individuals, the simulated stands tended to overcompensate the removed individuals by higher germination rate, juvenile survival and clonal propagation, leading to even faster spread into non-colonized suitable habitats than without treatments.

Management strategies that affected whole populations were found to be the most efficient for widespread IAPs in fragmented landscapes. For vegetatively reproducing species, highest efficiency was achieved by primarily treating large populations, probably because fragment production is unlike seed production not density regulated. Contrarily, for sexually reproducing species, highest efficiency was achieved by primarily treating small populations, probably because of the fast radial spread into formerly vacant habitats by wind dispersal of seeds (Moody & Mack 1988; Taylor & Hastings 2004). The high efficiency of treating outlying populations under very low cost scenarios may result from the low costs required to control weak invasion pathways (Keller 2009). However, we did not find the expected benefits from treatments that decreased habitat connectivity (Minor *et al.* 2009; Meier *et al.* 2011) or treatments of secondary dispersal vectors (Wadsworth *et al.* 2000).

Efficient management strategies predominantly resulted from highest local intensity, which may be generally only be achieved from using chemicals such as Glyphosate (De Micheli *et al.* 2006). However, in several countries the use of chemicals is restricted at specific sites such as along roads, in gravel pits, in nature conservation areas, and on banks of rivers and lakes. This results in difficult management trade-offs between the efficient control of invasives and the reduction in use of chemicals. Different cost levels are achieved by changing the frequency rather than by changing the spatial allocation patterns and the intensity per area treated. This contradicts Taylor and Hastings (2004) who found that the optimal strategy was dependent on the annual budget available for control (i.e. removal of low-density areas for low and medium costs and removal of high-density areas for high costs). Furthermore, despite expectations from studies in more homogeneous landscapes saying that the most efficient strategies to reduce population growth differ from those that most effectively reduce spread (Shea *et al.* 2010), we found that the most efficient management strategies did not vary

considerably between the different management goals.

Over 15 simulation years the effects of most efficient management strategies generally increased, while the costs remained stable or even decreased. Further, applying treatments that share initially very high costs resulted in a clear cost reduction after a few years, and thus, in a high efficiency. In turn, treatments with low initial costs but higher yearly efforts did not provide sustainable alternatives. Thus, we confirm that effective early treatments of invasive species increase the efficiency of control efforts (Hulme 2006).

### 5.5.2 Invasion pattern

Habitat characteristics determined by our SDMs were largely in line with the habitat characteristics determined in other studies. According to these characteristics it became apparent that the IAPs rapidly spread away from their introduction sites into disturbed suitable areas. Our findings are in line with Pysek & Prach (1993) who pointed out, that *H.mantegazzianum*, which was originally introduced as a garden plant and primarily had dispersed from there along rivers, already has spread massively into other disturbed areas such road sides. *I.glandulifera*, which was introduced as honey plant by beekeepers along forest edges and first spread from there along streams (Beerling & Perrins 1993), now spreads massively along small roads and into recreation areas and nature conservation sites, probably assisted by humans who re-allocate infested deposits from rivers. *R.japonica* was primarily introduced as an ornamental plant into gardens and parks and was used as agricultural forage plant and for erosion control of riverbanks. From there it spread along flowing waters and is anthropogenically dispersed by soil re-allocations, from where it further spreads over large areas where frost events are rare and soils contain high coarse fragment contents (Beerling, Bailey & Conolly 1994). The difference among the three species in invasion rates may mainly be caused by the varying proportion of long-distance dispersal by wind (Pysek & Prach 1993).

### 5.5.3 Model evaluation

Quantifying uncertainty in models is crucial but generally complex. Comparisons against observations are hampered due to the large spatial and temporal scales and the lack of relevant historical data. Our SDMs were cross-validated and spread estimates were compared to literature. Cross-validations resulted in reasonable model accuracies. However, IAPs in our study area may not yet have spread to all suitable sites and therefore the potential environmental envelope may be too small. Calibrating SDMs from the native distribution and applying them to the invaded habitat is an alternative (e.g. Thuiller *et al.* 2005). However, since interactions between biotic and abiotic factors may be different between native and introduced ranges (Stohlgren & Schnase 2006) and species may have rapidly evolved in the invaded range (Cox 2004), we found it more advisable to analyse the habitat suitability only in the invaded range and to study only species that are already well spread. Spread estimates

within these potential habitats were consistent with literature on reconstructed invasion patterns during the exponential phase on the basis of floristic records (e.g. Pysek & Prach 1993; Pysek & Prach 1995; Mandak, Pysek & Bimova 2004; Pysek *et al.* 2008), i.e. the simulated increase in colonized cells if no management was applied was highest for *H.mantegazzianum*, lower for *I.glandulifera* and lowest for *R.japonica*.

Although some progress was made regarding management strategies for widespread IAPs in heterogeneous landscapes (e.g. Wadsworth *et al.* 2000; Jongejans *et al.* 2008; Blackwood, Hastings & Costello 2010), synoptic insights for large complex landscapes are lacking. Incorporating habitat complexity into simulations seems important because invasions are not uniform across the landscape. IAPs may follow linear landscape features such as rivers or roads (Buckley, Bolker & Rees 2007; Predick & Turner 2008; Christen & Matlack 2009) and several habitat patches may promote competitive advantages to IAPs, and thus, reduce the chance of being eliminated from such habitats simply due to demographic stochasticity (Vuilleumier *et al.* 2011). Once IAPs are established in such patches they may colonize the landscape rapidly from there. Riparian ecosystems provide numerous of such patches because flooding creates openings with suitable nutrient conditions and intensive human activities further disturb riparian habitat composition (Richardson *et al.* 2007). We believe that our hybrid model was able to capture such complex interactions well.

#### 5.5.4 Potential drawbacks

We assumed in our models that (1) invasibility of habitats is not affected by interspecific interactions, (2) human activities only affect potential habitats but do not act as secondary dispersal vectors, (3) the lack of a complete recording of initial populations may introduce a strong bias in spread estimates, and (4) cost proxies (instead of real financial costs) are appropriate for evaluating the efficiency of management strategies. If these assumptions are severely challenged, our simulation results may be biased.

First, we are aware that invasibility of habitats can be affected by interspecific interactions (Naeem *et al.* 2000; Meier *et al.* 2011). However, our study species are highly competitive in ruderal habitats, and therefore they may be affected only little by potential competitors (Meier *et al.* 2010). Second, we assumed that human activities only affect potential habitats but do not act as secondary dispersal vectors like wind or water. Secondary dispersal vectors are indeed of high importance to augment the autochorous dispersal of many IAPs. For instance, with autochorous dispersal alone, spread of *I.glandulifera* was estimated at 2-3 m yr<sup>-1</sup>, while when augmented by secondary dispersal vectors it was estimated from historical data at 38 km yr<sup>-1</sup> (Perrins, Fitter & Williamson 1993). For our study species, the most important secondary dispersal vectors of seeds were wind, water, animals and humans, while plant fragments were mainly distributed by water and humans (Pysek & Prach 1993;

Bullock, Shea & Skarpaas 2006). In our simulations, wind dispersal only occurred over relatively limited distances due to the heavy of seeds, while fragments were not dispersed by wind at all. By contrast, streams carried seeds and fragments over relatively long distances and therefore played an important role for large-scale patterns as was shown in other studies (Campbell, Blackwell & Woodward 2002). We did not calibrate animal and human dispersal as of its high complexity (Hodkinson & Thompson 1997). Thus, our spread estimates might especially for *R.japonica* be overly conservative. Third, invasion patterns are hypothesized to strongly depend on the initial spatial arrangement of a species (Marchetto *et al.* 2010), and therefore the lack of complete recording of initial populations may introduce a large bias in spread estimates. To mitigate this implication, we complemented the incompletely sampled distribution of invasives by allocating additional initial populations in suitable habitats of under-sampled areas. We did so by replicating this allocation nine times, but did not find clear differences between these nine replicates. Fourth, we assumed that cost proxies are appropriate for evaluating the efficiency of management strategies. Cost proxies are more intuitive to understand and develop than economic costs expressed in dollar terms (Naidoo *et al.* 2006). However, assessments with real costs may be important particularly for the discussion with stakeholders, because costs do not only depend on area, local intensity and frequency, but also on payment of workforces, material or location. However, we lacked sufficient data to populate a meaningful cost estimate.

### 5.5.5 Synthesis and applications

Knowledge on the efficiency of spatially explicit management strategies to contain IAPs derived from biological knowledge on invasion processes for different levels of costs is crucial for decision makers to design optimized treatments and to compare policy options. We demonstrate that treatments are much more effective when addressing species management from a landscape perspective with spatially optimized control actions instead of applying a local view only. However, because species traits, invasion size and landscape- and population-configurations may differ among invasions, there is no single management strategy that ensures most efficient control for all species and landscapes. Therefore, the presented approach may be used as a standard protocol to test possible management strategies to contain population growth and spatial spread of IAPs within different complex landscapes.

Not all of these spatially explicit strategies may be equally easy to implement. For instance, one may provide practitioners with maps for controlling species in highly connected habitats or along upper reaches of rivers. Advising them to contain large or small populations, or populations that are more or less far away from each other is much more complex tough, because population sizes and distances are highly volatile and hence may not be easily mapped. This calls, however, for both early treatment and sound monitoring. The first ascertains rapid success, while the second assists treatment

planning considerably.

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## 5.8 Appendices

### 5.8.1 Appendix S1 – Traits of species

**Table S1.** Traits of *Heracleum mantegazzianum*, *Impatiens glandulifera* and *Reynoutria japonica*. If several values per parameter were available from the literature, we excluded values from greenhouses; if still several parameters were available, we used the median or the mean for even values ('\*' represent used parameters). '+' represent parameters fitted by sensitivity analyses.

| Parameter                                   | <i>H. mantegazzianum</i>   | <i>I. glandulifera</i>   | <i>R. japonica</i>  |
|---|--|--|---|
| Family                                      | Umbelliferae   | Balsaminaceae  | Polygonaceae  |
| Life form                                   | Biennial or perennial monocarpic herb [1]  | Annual herb [2]  | Perennial polycarpic herb that disperses only vegetative in Europe [2]  |
| Height [m]                                  | 2-5 [1]  | 1-2 [3]  | 3 [4]   |
| Dispersal vectors                           | Wind [2], water [2], translocation of top soil contaminated with seeds [5], animals [2]  | Water [2], translocation of top soil contaminated with seeds [6], explosive seed capsule [2] | Water [2], man (e.g. translocation of top soil contaminated with plant fragments, garden waste) [2], vegetative [2] |
| Regeneration                                | Seeds, tuberous root [2]   | Seeds [2]  | Vegetative by stem and leaf fragments, rhizomes and rhizome fragments [2]   |
| Natural area                                | Caucasus [1]   | Himalayas [2]  | Eastern Asia (i.e. China, Korea, Japan, Taiwan, Vietnam) [7]  |
| Natural habitat                             | Forest edges and glades, mountain streams [1]  | Mountain streams [3]   | Dry infertile gravelly soils to wet nutrient-rich soils [7]   |
| Date of first Swiss record                  | 1912 [8]   | 1904 [6]   | 1950 [8]  |
| Source of most introductions                | Garden plant [5], bee fodder [9]   | Garden plant [6], bee fodder [6]   | Garden plant [7], bee and cattle fodder [7], bank reinforcement [7]   |
| <i>Water dispersal</i>                      |  |  |   |
| Mean distance [km]                          | 1 [10]   | 3 [10]   | 3 [11]  |
| Maximal distance [km]                       | 10 [5, 10]   | 20 [10]  | 20 [11]   |
| <i>Wind dispersal</i>                       |  |  |   |
| Seed release height [m]                     | 4 [5]  | 2 [3]  | -   |
| Seed terminal velocity [m s <sup>-1</sup> ] | 1.92-2.66 [12]   | 4.24-4.72 [12]   | -   |
| Height of the surrounding vegetation [m]    | c. 80% lower (meadows, parks, banks), c. 20% higher (forest edges and glades, shrub) [1] | c. 50% lower (banks), c. 50% higher (forest edges and glades, shrub) [2]                     | -   |

Table S1. Continued.

| <i>Demographic parameters</i>                             |  |  |  |
|---|--|--|--|
| Seedbank persistence [yr]                                 | 5 [13], 6* [5], 7 [www.neoflora.de]  | 2 [3]  | Fragments: <5 [notes Canton Zurich]  |
| Years until seeds germinate                               | 1 [5]  | 1 [3]  | Fragments: 0 [14]  |
| Maximal germination rate                                  | 0.1 germinate and 0.02 survive to the first year [13], which results in a overall germination rate of 0.002; 0.27-0.9 germinate and 0.012-0.137 survive the first season [5], which results in a overall germination rate of 0.00324-0.1233*; 0.8-0.85 germinate and 0.6-0.8 survive [15], which results in a overall germination rate of 0.48-0.68. | 0.105-0.739 germinate, while most of the seedlings survive for low germination and only few survive for high germination [15], which results in a overall germination rate of 0.105; 5000-6000 seeds m <sup>-2</sup> [16] and 50-70 adults m <sup>-2</sup> [17] results in a overall germination rate of 0.01; Mean: 0.0575* | Regenerating fragments: 0.39* [18]; 0.6 from 2 nodes [19].   |
| Maximal yearly juvenile survival rate                     | 0.23 of the seedlings survive to maturity [5], the yearly rate is hence 0.48*; 0.3-0.7 [15]  | 1.0 †  | 1.0 [20]   |
| Minimal juvenile to adult transition rate                 | 0.1 [1]  | 0.1 †  | 0.1 †  |
| Demographic slope   | 6 †  | 24 †   | 3 †  |
| First flowering [yr]                                      | 2 [5]  | 1 [2]  | 1 [14]   |
| Latest flowering [yr]                                     | 5 [5]  | 1 [2]  | 1 [14]   |
| Maximal percentage of flowering adults                    | 1.0 [1]; We used 0.25 because in reality adults die after flowering, which was not accounted for in the model.   | 1.0 [21]   | Fragments: 1.0 [14]  |
| Maximal number of seeds produced per individual in a year | Mean c. 20'000 [13]; Maximum c. 20'000-100'000 [5]; Mean: 50'000*  | 800 [17]; 1886 x [(2 x plant density) <sup>-0.367</sup> ] [3] results in 348 at carrying capacity and up to 1010 for very low density stands with only 2-3 individuals per m <sup>-2</sup> ; Mean: 905*  | 9.7 stem fragments + 2000 rhizome fragments m <sup>-2</sup> / 42 individuals m <sup>-2</sup> results in c. 60 fragments per individual [20] along the river, else 1. |
| Adult carrying capacity [adults m <sup>-2</sup> ]         | 2 [5] results in 1250 in a 625m <sup>2</sup> -cell; juvenile carrying capacity: 20 [5]   | 30-40* [3] results in 25'000 in a 625m <sup>2</sup> -cell; 50-70 [17]; 20-80 [15]  | 42 [20] results in 26'250 in a 625m <sup>2</sup> -cell   |
| Number of individuals after clonal growth                 | 1 [22]   | 1 [3]  | 6 [23]   |
| Maximal age [yr]  | 5 [5]  | 1 [3]  | 5 [24]   |

Table S1. Continued.

| <i>Other parameters</i>   |      |      |      |
|---|------|------|------|
| Occurrence-probability threshold to translate predictions into binary presence-absence forecasts (OT; best Cohen's kappa) | 0.45 | 0.50 | 0.50 |
| Occurrence-probability where below transition rates drop to 0 (ZT; false negative rate <0.05)                             | 0.20 | 0.20 | 0.20 |

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## 5.8.2 Appendix S2 – Details on patterns for spatial allocation of treatments

Patterns for spatial allocation of treatments were selected according to the biology of dispersal and focused on eight different spatial allocation strategies.

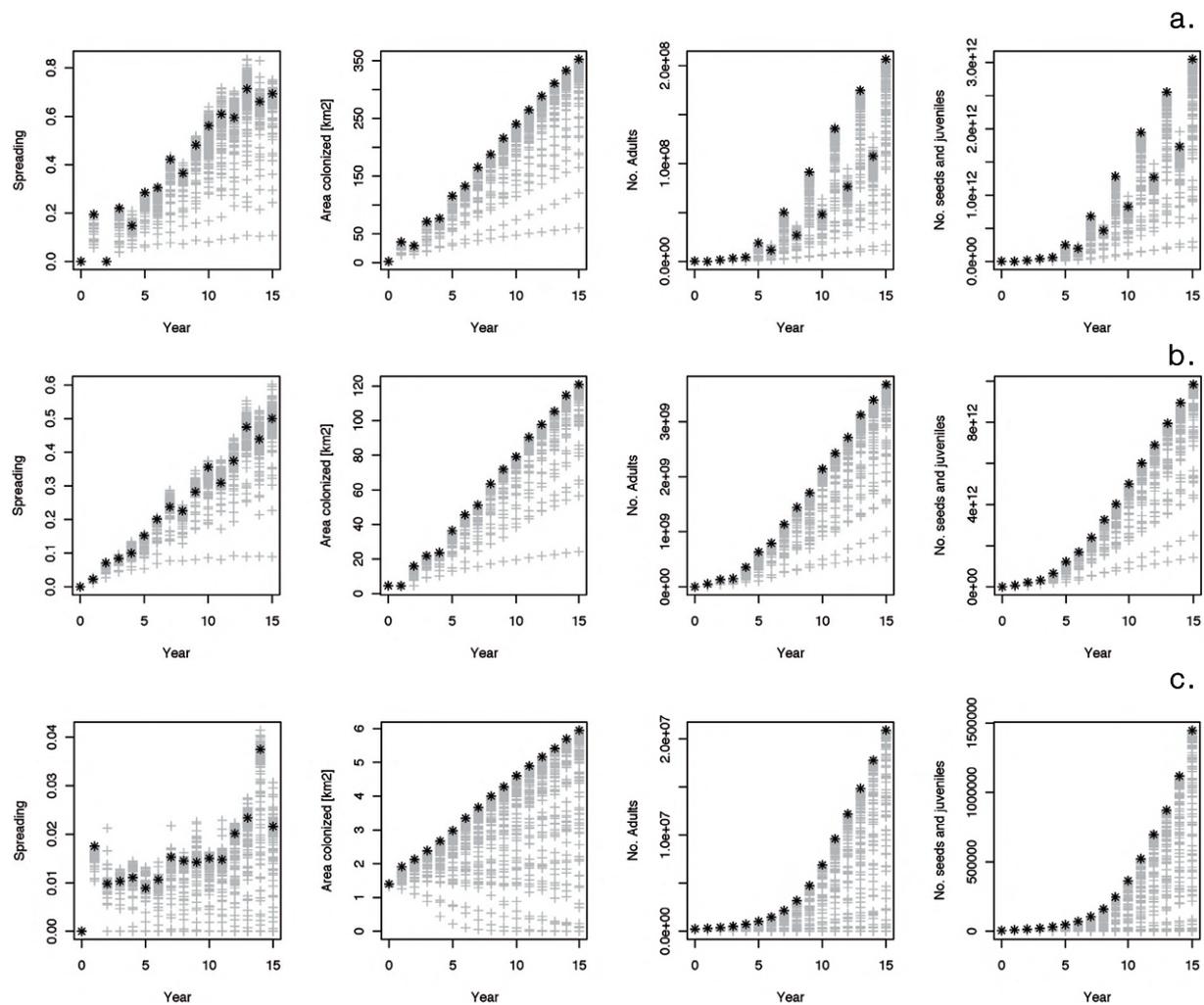
First, we targeted large populations as they may reflect core populations that represent principal sources of propagules (Hulme, 2003). Second, we targeted small populations as they have large edge-to-area ratios and hence may contribute most to range expansion (Moody & Mack, 1988; Taylor & Hastings, 2004). To disentangle large from small populations, we first defined population sizes by summing up individuals of cells with common edges. Then, we started to remove individuals in largest and smallest populations, respectively, and continued in populations with decreasing and increasing size, respectively, until the clearing area and local intensity were exhausted. Third, we targeted outlier populations as these are surrounded mostly by non-colonized habitats into which they may spread. The isolation of populations was estimated by calculating the minimal distance between centroids of populations, while populations were defined according to cells with common edges. Then, we started to remove populations with decreasing isolation until the clearing area and local intensity were exhausted. Fourth, we targeted cells within large well-connected suitable habitats because according to the percolation theory high fragmentation may effectively reduce migration through corridors (Turner, 1989; With, 2002). Therefore, we defined large connected habitats habitat areas with high connectivity with Fragstats 3.3, by first calculating with a 4 and 8 neighbours rule in a moving window of different sizes (100m, 250m, 500m radius) the total habitat area (TCA) and the largest patch index (LPI). TCA we then divided by the window size to get the percentages of habitat per window (PLAND). Next, we plotted LPI against PLAND and determined PLAND where LPI suddenly rises >80%. We estimated this for each combination of neighbourhood rule and window size. However, because habitat areas were all highly connected and not random within the landscape, the breakpoint was for each combination of neighbourhood rules and window sizes similar. Therefore, we selected large connected habitats according to the 500 m radius with the 8 neighbours-rule where PLAND was >40% and LPI<80%. Within these large connected habitats, we then removed random cells until the clearing area and local intensity were exhausted. Fifth, we targeted cells on riverbanks, because rivers are the main dispersal pathways of hydrochorous plants. Sixth, we targeted upper reaches of rivers, which may reduce the propagule sources for downstream colonisation (Wadsworth *et al.*, 2000). Seventh, we targeted lower reaches of rivers, which reduces only the arriving propagules that could establish. We defined upper and lower reaches by assigning the river sections according to the distance to their sources. Treatments were performed in random cells within a 50 m buffer along rivers or river sections until the clearing area and local intensity were exhausted. Eight, we targeted

cells randomly to test the null hypothesis that the spatial allocation of treatments has no influence on efficiency.

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### 5.8.3 Appendix S3 – Effect of management strategies



**Figure S3.** Spread, colonized area, number of adults and regeneration potential over 15 years for the ‘do nothing’-strategies and all management strategies for *H.mantegazzianum* (a), *I.glandulifera* (b) and *R.japonica* (c). Grey symbols indicate all management strategies, while black symbols indicate the ‘do nothing’-strategy.

## 5.8.4 Appendix S4 – Overview of most effective management strategies

Table S4. Overview of most effective management strategies per species, cost level and management goal, compared to most effective random strategies. 'Very low' cost levels refer to total overall costs of <10%, 'low' to 10–25%, 'medium' to 25–40% and 'high' to >40%; intensity refers to treated habitat area ('a', [%]) and to the locally applied intensity ('i', [%]); frequency is given in years; effects represent percentages of values compared to the 'do nothing' strategy after 15 years, and costs represent percentages accumulated over 15 years. The first sub-table is for *Heracleum mantegazzianum*.

| Management goal        | Cost level | Spatial allocation   | Intensity |    | Frequency | Effect on spread | Effect on area | Effect on adults | Effect on regeneration | Cost |
|------------------------|------------|----------------------|-----------|----|-----------|------------------|----------------|------------------|------------------------|------|
|                        |            |                      | a         | i  |           |                  |                |                  |                        |      |
| Reducing spread        | Very low   | Small populations    | 25        | 90 | 5         | -3.0             | -7.5           | -23.4            | 20.4                   | 8.5  |
|                        |            | Random cells         | 50        | 90 | 5         | -0.7             | -1.0           | -8.7             | 14.6                   | 6.5  |
|                        | Low        | Small populations    | 25        | 90 | 2         | -11.8            | -29.0          | -54.4            | -21.7                  | 22.9 |
|                        |            | Random cells         | 50        | 55 | 2         | -1.0             | -2.1           | -6.0             | -9.8                   | 16.7 |
|                        | Medium     | Small populations    | 25        | 90 | 1         | -19.2            | -53.2          | -74.3            | -47.9                  | 39.9 |
|                        |            | Random cells         | 50        | 90 | 1         | -2.3             | -5.0           | -27.1            | 1.5                    | 34.1 |
|                        | High       | Small populations    | 50        | 90 | 1         | -29.2            | -82.9          | -94.8            | -86.7                  | 40.4 |
|                        |            | Random cells         | -         | -  | -         | -                | -              | -                | -                      | -    |
| Reducing area          | Very low   | Outlying populations | 50        | 90 | 5         | -2.6             | -8.9           | -32.9            | 31.5                   | 9.9  |
|                        |            | Random cells         | 50        | 90 | 5         | -0.7             | -1.0           | -8.7             | 14.6                   | 6.5  |
|                        | Low        | Small populations    | 25        | 90 | 2         | -11.8            | -29.0          | -54.4            | -21.7                  | 22.9 |
|                        |            | Random cells         | 50        | 90 | 2         | -0.6             | -3.4           | -12.5            | -12.0                  | 17.2 |
|                        | Medium     | Small populations    | 25        | 90 | 1         | -19.2            | -53.2          | -74.3            | -47.9                  | 39.9 |
|                        |            | Random cells         | 50        | 90 | 1         | -2.3             | -5.0           | -27.1            | 1.5                    | 34.1 |
|                        | High       | Small populations    | 50        | 90 | 1         | -29.2            | -82.9          | -94.8            | -86.7                  | 40.4 |
|                        |            | Random cells         | -         | -  | -         | -                | -              | -                | -                      | -    |
| Reducing mature plants | Very low   | Outlying populations | 50        | 90 | 5         | -2.6             | -8.9           | -32.9            | 31.5                   | 9.9  |
|                        |            | Random cells         | 50        | 90 | 5         | -0.7             | -1.0           | -8.7             | 14.6                   | 6.5  |
|                        | Low        | Small populations    | 25        | 90 | 2         | -11.8            | -29.0          | -54.4            | -21.7                  | 22.9 |
|                        |            | Random cells         | 50        | 90 | 2         | -0.9             | -3.4           | -12.5            | -12.0                  | 17.2 |
|                        | Medium     | Small populations    | 25        | 90 | 1         | -19.2            | -53.2          | -74.3            | -47.9                  | 39.9 |
|                        |            | Random cells         | 50        | 90 | 1         | -2.3             | -5.0           | -27.1            | 1.5                    | 34.1 |
|                        | High       | Small populations    | 50        | 90 | 1         | -29.2            | -82.9          | -94.8            | -86.7                  | 40.4 |
|                        |            | Random cells         | -         | -  | -         | -                | -              | -                | -                      | -    |
| Reducing regeneration  | Very low   | Outlying populations | 5         | 25 | 5         | 0.5              | -0.3           | -0.7             | -0.1                   | 6.2  |
|                        |            | Random cells         | 5         | 25 | 5         | 1.4              | -0.2           | -0.4             | 0.1                    | 5.9  |
|                        | Low        | Outlying populations | 50        | 90 | 2         | -8.6             | -23.0          | -46.8            | -35.9                  | 25.0 |
|                        |            | Random cells         | 50        | 90 | 2         | -0.6             | -3.4           | -12.5            | -12.0                  | 17.2 |
|                        | Medium     | Large populations    | 50        | 90 | 2         | -9.5             | -37.6          | -67.4            | -72.8                  | 35.8 |
|                        |            | Random cells         | 25        | 55 | 1         | -1.8             | -3.1           | -14.8            | -3.8                   | 33.2 |
|                        | High       | Large populations    | 50        | 90 | 1         | -22.6            | -65.9          | -91.7            | -88.6                  | 46.0 |
|                        |            | Random cells         | -         | -  | -         | -                | -              | -                | -                      | -    |

Table S4. Continued for *Impatiens glandulifera*

| Management goal        | Cost level            | Spatial allocation   | Intensity            | Frequency | Effect on spread | Effect on area | Effect on adults | Effect on regeneration | Cost  |     |
|------------------------|-----------------------|----------------------|----------------------|-----------|------------------|----------------|------------------|------------------------|-------|-----|
| Reducing spread        | Very low              | Small populations    | 25                   | 90        | -5.9             | -5.8           | -5.4             | -9.5                   | 8.2   |     |
|                        |                       | Random cells         | 50                   | 55        | -2.5             | -0.1           | -0.1             | -0.8                   | 5.9   |     |
|                        | Low                   | Small populations    | 50                   | 90        | -10.4            | -9.9           | -10.3            | -20.9                  | 11.1  |     |
|                        |                       | Random cells         | 25                   | 90        | -0.8             | -0.8           | -4.4             | -2.8                   | 15.7  |     |
|                        | Medium                | Small populations    | 25                   | 90        | -17.2            | -53.2          | -58.7            | -56.0                  | 39.6  |     |
|                        |                       | Random cells         | 5                    | 55        | -1.1             | -0.7           | -3.1             | -2.8                   | 31.1  |     |
|                        | High                  | Small populations    | 50                   | 90        | -26.2            | -79.9          | -85.4            | -85.6                  | 43.1  |     |
|                        |                       | Random cells         | -                    | -         | -                | -              | -                | -                      | -     |     |
|                        | Reducing area         | Very low             | Small populations    | 25        | 90               | -5.9           | -5.8             | -5.4                   | -9.5  | 8.2 |
|                        |                       |                      | Random cells         | 5         | 90               | -1.8           | -0.2             | -0.4                   | -1.5  | 5.9 |
| Low                    |                       | Small populations    | 25                   | 90        | -0.9             | -18.9          | -31.7            | -22.5                  | 21.3  |     |
|                        |                       | Random cells         | 5                    | 90        | 2.0              | -0.8           | -4.4             | -2.8                   | 15.7  |     |
| Medium                 |                       | Small populations    | 25                   | 90        | -17.2            | -53.2          | -58.7            | -56.0                  | 39.6  |     |
|                        |                       | Random cells         | 50                   | 90        | 0.2              | -1.3           | -5.1             | -4.8                   | 31.3  |     |
| High                   |                       | Small populations    | 50                   | 90        | -26.2            | -79.9          | -85.4            | -85.6                  | 43.1  |     |
|                        |                       | Random cells         | -                    | -         | -                | -              | -                | -                      | -     |     |
| Reducing mature plants |                       | Very low             | Outlying populations | 50        | 90               | -5.0           | -4.8             | -5.4                   | -13.2 | 9.4 |
|                        |                       |                      | Random cells         | 5         | 90               | -1.8           | -0.2             | -0.4                   | -1.5  | 5.9 |
|                        | Low                   | Outlying populations | 50                   | 90        | -0.8             | -15.2          | -35.4            | -28.0                  | 23.7  |     |
|                        |                       | Random cells         | 5                    | 90        | 2.0              | -0.8           | -4.4             | -2.8                   | 15.7  |     |
|                        | Medium                | Small populations    | 25                   | 90        | -17.2            | -53.2          | -58.7            | -56.0                  | 39.6  |     |
|                        |                       | Random cells         | 25                   | 90        | 0.8              | -1.3           | -5.1             | -4.8                   | 31.3  |     |
|                        | High                  | Small populations    | 50                   | 90        | -26.2            | -79.9          | -85.4            | -85.6                  | 43.1  |     |
|                        |                       | Random cells         | -                    | -         | -                | -              | -                | -                      | -     |     |
|                        | Reducing regeneration | Very low             | Outlying populations | 50        | 90               | -5.0           | -4.8             | -5.4                   | -13.2 | 9.4 |
|                        |                       |                      | Random cells         | 5         | 90               | -1.8           | -0.2             | -0.4                   | -1.5  | 5.9 |
| Low                    |                       | Outlying populations | 50                   | 90        | -0.8             | -15.2          | -35.4            | -28.0                  | 23.7  |     |
|                        |                       | Random cells         | 25                   | 90        | -0.8             | -0.8           | -4.4             | -2.8                   | 15.7  |     |
| Medium                 |                       | Small populations    | 25                   | 90        | -17.2            | -53.2          | -58.7            | -56.0                  | 39.6  |     |
|                        |                       | Random cells         | 25                   | 90        | 0.8              | -1.3           | -5.1             | -4.8                   | 31.3  |     |
| High                   |                       | Small populations    | 50                   | 90        | -26.2            | -79.9          | -85.4            | -85.6                  | 43.1  |     |
|                        |                       | Random cells         | -                    | -         | -                | -              | -                | -                      | -     |     |

Table S4. Continued for *Reynoutria japonica*

| Management goal        | Cost level            | Spatial allocation | Intensity         |      | Frequency | Effect on |        |        | Cost   |              |
|------------------------|-----------------------|--------------------|-------------------|------|-----------|-----------|--------|--------|--------|--------------|
|                        |                       |                    | a                 | i.i. |           | spread    | area   | adults |        | regeneration |
| Reducing spread        | Very low              | Small populations  | 50                | 90   | 5         | -1.8      | -47.1  | -67.9  | -27.2  | 9.9          |
|                        |                       | Random cells       | 50                | 25   | 5         | -0.1      | -0.2   | -0.4   | -2.8   | 5.6          |
|                        | Low                   | Large populations  | 50                | 90   | 2         | -2.5      | -98.1  | -100.0 | -100.0 | 20.4         |
|                        |                       | Random cells       | 25                | 90   | 2         | -0.1      | 0.0    | -0.5   | -0.3   | 15.0         |
|                        | Medium                | Large populations  | 50                | 55   | 1         | -2.5      | -88.2  | -100.0 | -100.0 | 39.1         |
|                        |                       | Random cells       | 25                | 55   | 1         | -0.1      | -0.2   | -0.4   | -0.1   | 30.1         |
|                        | High                  | Small populations  | 50                | 55   | 1         | -2.2      | -77.5  | -88.9  | -59.7  | 41.6         |
|                        | Reducing area         | Very low           | Small populations | 50   | 90        | 5         | -1.8   | -47.1  | -67.9  | -27.2        |
| Random cells           |                       |                    | 50                | 55   | 5         | -0.1      | -0.3   | -0.4   | -2.9   | 5.6          |
| Low                    |                       | Large populations  | 50                | 90   | 2         | -2.5      | -98.1  | -100.0 | -100.0 | 20.4         |
|                        |                       | Random cells       | 5                 | 90   | 2         | -0.1      | -0.4   | -0.8   | -3.1   | 15.0         |
| Medium                 |                       | Large populations  | 50                | 90   | 1         | -2.5      | -100.0 | -100.0 | -100.0 | 35.8         |
|                        |                       | Random cells       | 5                 | 90   | 1         | 0.0       | -0.5   | -1.3   | -3.1   | 30.1         |
| High                   |                       | Small populations  | 50                | 55   | 1         | -2.2      | -77.5  | -88.9  | -59.7  | 41.6         |
| Reducing mature plants |                       | Very low           | Small populations | 50   | 90        | 5         | -1.8   | -47.1  | -67.9  | -27.2        |
|                        | Random cells          |                    | 25                | 90   | 5         | -0.1      | -0.1   | -0.5   | -2.9   | 5.6          |
|                        | Low                   | Large populations  | 50                | 90   | 2         | -2.5      | -98.1  | -100.0 | -100.0 | 20.4         |
|                        |                       | Random cells       | 5                 | 90   | 2         | -0.1      | -0.4   | -0.8   | -3.1   | 15.0         |
|                        | Medium                | Large populations  | 50                | 90   | 1         | -2.5      | -100.0 | -100.0 | -100.0 | 35.8         |
|                        |                       | Random cells       | 25                | 90   | 1         | 0.0       | -0.5   | -1.3   | -3.2   | 30.1         |
|                        | High                  | Small populations  | 50                | 55   | 1         | -2.2      | -77.5  | -88.9  | -59.7  | 41.6         |
|                        | Reducing regeneration | Very low           | Large populations | 25   | 90        | 5         | -0.5   | -10.4  | -33.3  | -79.3        |
| Random cells           |                       |                    | 5                 | 90   | 5         | 0.1       | -0.2   | -0.5   | -3.0   | 5.6          |
| Low                    |                       | Large populations  | 50                | 90   | 2         | -2.5      | -98.1  | -100.0 | -100.0 | 20.4         |
|                        |                       | Random cells       | 5                 | 90   | 2         | -0.1      | -0.4   | -0.8   | -3.1   | 15.0         |
| Medium                 |                       | Large populations  | 50                | 90   | 1         | -2.5      | -100.0 | -100.0 | -100.0 | 35.8         |
|                        |                       | Random cells       | 25                | 90   | 1         | 0.0       | -0.5   | -1.3   | -3.2   | 30.1         |
| High                   |                       | Large populations  | 50                | 25   | 1         | -0.3      | -41.4  | -88.9  | -95.0  | 42.6         |
|                        |                       |                    | Random cells      | -    | -         | -         | -      | -      | -      | -            |



## 6 Synthesis

Ongoing climate change, land-use change, and biological invasion may alter large-scale species distributions dramatically in the near future (Sala *et al.*, 2000). Therefore, the understanding of the interplay of these key impacts is of major importance when predicting the potential distribution of species under global change (Gaston, 2009). Species distribution models (SDMs), which link species occurrences to ecological and environmental data over large spatial scales, are widely used to estimate species' ecological requirements, and accordingly, to predict future species ranges or extinction risks (Guisan & Zimmermann, 2000). However, the degree to which the interplay of predictors for species distributions can be unveiled strongly depends on the adequacy of the predictors included in the model (Syphard & Franklin, 2009). Most often, predictor selection is based only on weakly tested expectations (Guisan & Zimmermann, 2000). Thus, in this thesis, I assessed several potential key drivers of long-term dynamics of large-scale species distributions, which themselves are expected to alter and adjust to global change.

To spot key drivers that shape current large-scale species distributions and that alter the dynamics of large-scale species distributions during global change, one would have to evaluate a vast number of small- and large-scale processes. In order to focus on potentially important range shaping processes, I used the currently debated key assumptions of SDMs as a starting point, and contrasted them with assumptions on species-environment relations from ecological concepts. With this, I was able to contribute to a refinement of SDM applicability and demonstrated how certain limitations of SDMs could be overcome. This allows for the formation of more reliable scientific and management decisions based on improved predictions over time and space.

### 6.1 Thesis findings and limitations

The two main objectives of this thesis were (1) to estimate the importance of small-scale biotic interaction processes for large-scale species distributions, and (2) to estimate the magnitude to which species lag behind in attaining equilibrium with their environment due to migration limitations. To evaluate these two rather broad issues, I examined to what extent abiotic and biotic variables contribute to the accuracy of models for large-scale species distributions, and whether the magnitude of these effects is related to species traits (*Question 1*). I also evaluated under which climatic conditions biotic interactions are strongest, and how this variation in the strength of biotic interactions along climatic gradients influences the projections of current and future large-scale species distributions (*Question 2*). Furthermore, I investigated how strongly migration limitations

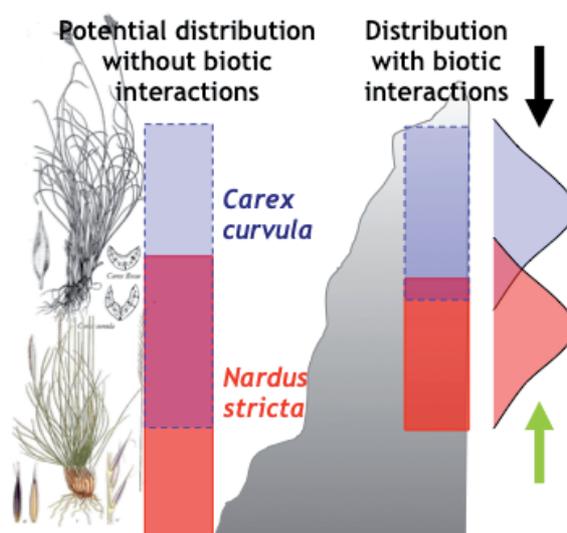
prevent species from tracking suitable habitats during climate change, and whether these migration limitations are related to abiotic and biotic conditions, the degree of landscape fragmentation, and species traits (*Question 3*). Finally, I studied how much invasive species can be kept from spreading and eventually reaching equilibrium conditions by applying spatial explicit control strategies (*Question 4*). These four questions are discussed in the following chapters in the context of the two overarching issues.

## **Question 1: How do abiotic and biotic variables contribute to shaping spatial patterns?**

To date, the relative importance of abiotic and biotic range determinants is unclear (Araújo & Guisan, 2006). The results I obtained from *Paper 1* revealed that biotic variables, which are often said to only affect local species distributions, also affect large-scale species ranges by adding important local information on biotic interactions and other small-scale processes. Among all investigated tree species, biotic and abiotic variables contributed mostly independently from each other and equally as much to explain spatial range patterns. I further showed that biotic predictors helped to explain the distribution of mid- to late-successional tree species more accurately. This successional group is, by definition, more competitive than early successional species, which avoid competition as a strategy. These results led me to conclude that the implicit inclusion of biotic interactions is insufficient when using species occurrence data to predict large-scale species patterns, although such data inherently depict the realized niche. Consequently, standard SDMs are incapable of exclusively fitting environmental constraints (i.e. that make up the fundamental niche), nor do they implicitly fit biotic interactions (i.e. that constrain the realized niche). To depict the realized niche more completely, it is essential to include biotic predictors explicitly into SDMs, especially for predictions of highly competitive environments and future climates. However, it should be noted that the general shape of pan-European ranges did not dramatically change when including biotic predictors (see *Paper 2*). Most variation explained by biotic predictors occurred at smaller spatial scales by modifying predictions within species ranges. In any case, models developed to include both biotic and abiotic predictors were more accurate and showed somewhat constrained spatial domains, implying that the inclusion of biotic predictors also affected range shapes.

Plant communities (and, hence, interspecific interactions) may be altered during global change, since species will likely track suitable climates with different velocities (Ackerly, 2003) and human introductions of non-native species are likely to continue (Thomas, 2010). To predict changes in distributions during global change, I conclude that explicitly addressing biotic interactions reduces the projection uncertainty. However, the inclusion of biotic interactions into SDMs can still be improved, possibly by better calibrating bi-directional effects through the use of Bayesian models.

From observation data alone, it is hard to disentangle the various local processes included in the biotic predictors – local communities may not only be influenced by competition, but also by species management and micro-topography. To further disentangle these local processes and the direction of biotic interactions, one should conduct experiments on the physiological tolerances and competitive abilities of the species. Originally, I had planned such an experiment to better separate the effects of abiotic and biotic predictors and also to estimate the direction of influence in interspecific interactions (cf. *Question 2*). In particular, I intended to compare the physiological frost tolerance of juveniles and adults of two non-economically used species replacing each other along an altitudinal gradient at high altitudes in the Alps, in order to compare their potential distributions based on climatic tolerance and their actual distribution constrained by biotic interactions. However, the seeds of one of the two species used in the experimental setup (i.e. *Carex curvula* and *Nardus stricta*) failed to germinate during two seasons despite diverse attempts to break their dormancy.



**Figure 1.** Expected effect of biotic interactions for two species replacing each other along an altitudinal gradient. It is expected that a species which grows under more favourable conditions (i.e. the species growing at a lower elevation and thus under warmer conditions), constrains the occurrence of the species growing under less favourable (colder) conditions.

## Question 2: How do biotic interactions vary along macroclimatic gradients and how does this affect species ranges?

Until now, empirical quantifications of the variation in the strength of interspecific competition along large-scale climate gradients, and of the potential effect of this variation on current and future species

ranges, were largely missing (Gaston, 2009). Results from *Paper 2* demonstrated that the strength of biotic interactions not only varies between species of differing traits (cf. *Paper 1*), but also along environmental gradients. In line with the stress-gradient hypothesis, beech abundance was strongly linked to the abundance of its competitor species under abiotically favourable growing conditions (i.e. moderately warm and moist climate). This link became weaker towards conditions of high physiological stress (i.e. cold and/or dry climate). Translated to geographic space, this led to the strongest biotic interactions occurring at low elevations and in southern Central Europe, and thus to strong reductions in the predicted spatial beech distribution when biotic predictors were explicitly included in SDMs. When projecting such calibrated models to future climates, the effect from competitive interactions was reduced because of a predicted spatial segregation of the major competitors of beech. I conclude that the explicit inclusion of biotic predictors assists to reduce the uncertainty when projecting large-scale SDMs to current or future climate, especially under favourable growing conditions. Moreover, knowledge on climatic conditions under which competition is strong may improve species management strategies; e.g. one can reduce competitors in order to enhance the occurrence of endangered species. However, these findings also have limitations. First, it is hard to distinguish between cause and effect when using observational data alone and thus to determine which species outcompetes or facilitates which other species. This means that the direction of biotic effects cannot easily be retrieved from observational presence/absence data alone. Second, we assumed shifts of species distributions to be unlimited under future climate when projecting future species patterns under the inclusion of biotic interactions. *Paper 3* demonstrates that this is not a realistic scenario for mid- to late-successional species. To improve the resolution of these issues, one could use experiments to test the competitive abilities of species under different climate conditions (cf. *Question 1*) and implement more realistic migration rates for range shift projections.

In the *Appendix Paper* we additionally tested the importance of climatic extremes as range determinants. We found that climatic extremes improve predictions of large-scale species distributions to a small, but significant, degree, and that the improvement is primarily due to spatially correcting over- and under-predictions compared to using mean climate variables alone. However, the effects of extremes and means were not easy to separate due to the high correlation between mean values and percentiles as measures of extremes. Accordingly, some corrections occur at range margins, while others help to improve the spatial performance inside the species' range. Thereby, the added extremes variables help to detect local extinctions (reduce over-predictions) and sink populations (reduce under-prediction). Specifically, our findings are important for projecting the front and the trailing edge of species ranges during global change where climatic variability may increase (Giesecke *et al.*, 2010).

### Question 3: How strongly do migration limitations prevent species from tracking suitable habitats during climate and land-use change?

Projecting the adjustment of species ranges to changing environmental conditions requires the implementation of migration processes at large scales, for which no standard approach currently exists. Therefore, dispersal limitation was one of the main sources of uncertainty when projecting species distributions under a changing climate (Araújo & Guisan, 2006). A few dynamic vegetation models include dispersal (e.g. Lischke *et al.*, 2006), but these have not been applied to large spatial scales at a fine spatial resolution due to high computational demands (Neilson *et al.*, 2005). SDMs, on the other hand, are capable of projecting species distributions over large spatial scales; however, they do not account for dispersal (Guisan & Zimmermann, 2000; Engler *et al.*, 2009). Integrating migration processes into SDMs has therefore been considered as one of the most important needs for improving projections under changing conditions (Araújo *et al.*, 2005; Guisan & Thuiller, 2005; Heikkinen *et al.*, 2006; Zurell *et al.*, 2009). For this reason, in *Paper 3* I aimed at applying realistic migration rates in an SDM-based projection framework, in which migration depends on abiotic constraints, biotic interactions and landscape fragmentation. MigClim (Engler & Guisan, 2009) also addresses migration in combination with SDMs. However, MigClim uses only generation time to depict demography and assigns each plant species randomly to one of seven identified major dispersal types without evaluating the population biology of a species in particular. Also, landscape fragmentation was only considered at the level of dispersal barriers. TreeMig on the contrary, simulates demographic processes (regeneration, growth, mortality, seed numbers, seedbank behaviour, regeneration rate, seed dispersal distance, etc.) explicitly and calibrated to the species. Therefore, I believe that the found migration rates are more realistic and represent the ecology of a species better than does MigClim.

With my approach, I was able to investigate how abiotic, biotic and contextual conditions affect the migration rates of species throughout the continent. I was further able to investigate the geographical patterns of migration rates that emerged from these dependencies and was able to compare estimated shifts in distributions when migration was assumed to be unlimited or totally limited (i.e. the standard migration assumptions of SDMs for defining the upper and the lower bound of the projections) or when realistic migration rates were applied. The results showed that within Europe, inter-specific competition, which is higher under favourable growing conditions than under more adverse conditions for a given species (cf. *Paper 2*), reduced range shift velocity more than the adverse macroclimatic conditions (i.e. very cold or dry climate) did. Additionally, the results from *Paper 3* clearly indicate that habitat fragmentation acts to slow down migration rates. When applying these relationships to geographic space, early-successional tree species migrated about ten times faster

than mid- to late-successional species. This is because early-successional species are generally characterized by rapid growth rates, produce large amounts of seed and often reveal longer seed-dispersal distances compared to mid- to late-successional species. This causes mid- to late-successional species to migrate predominantly into previously colonized forest habitats where inter-specific competition is higher. Their higher shade tolerance cannot outbalance this disadvantage, resulting in their already lower migration rates to decrease further. Therefore, the projected distribution of early-successional species during the 21st century from models that incorporate realistic migration matched well with the unlimited migration assumption (i.e. hardly no constraints to migration and thus no lags in the re-adjustment of ranges under climate change), while the projected distribution of mid- to late-successional species using transient shifts from realistic migration rates showed high similarities with the no migration assumption (i.e. species do not track changing climates and disappear in regions that become unsuitable). Thus, under a future scenario of a changing environment, the mid- to late-successional species may largely fail to track suitable climates and will be in non-equilibrium with their environment. Moreover, since the degree to which species are in equilibrium with current climate may be inversely related to the species' ability to track future climate changes (Araújo & Pearson, 2005), one can deduce from these results that mid- to late-successional species may have already failed under the current climate to reach equilibrium, despite the relatively stable climate in the Holocene. The results from *Paper 3* may help to improve the interpretation of range shift maps from SDMs (i.e. to assign a more realistic migration assumption for a given species), to better estimate extinction risks, to design reserve networks, and to assist in the migration of ecologically or economically important species with strong migration limitations. However, when deducing the applicability of results obtained from such hybrid models, one has to keep in mind that more complex models implicitly contain more uncertainty. To estimate the uncertainty of such models and to include it into the analyses, Bayesian approaches may prove very useful.

#### **Question 4: How can population management prevent invasive species from spreading across the landscape?**

Most current approaches to controlling biological invasions require significant financial resources, not the least because most of the methods are applied locally without any strategy at the landscape level (Epanchin-Niell & Hastings, 2010). Thus, in *Paper 4* I tested if space matters when applying different control methods (i.e. methods that differ in local intensity, area treated and in the frequency that they are applied) to keep invasive alien plant species from spreading and reaching equilibrium with the environment. I used simulation experiments with a dynamic demography model calibrated to individual species and set up experiments to show improvements of specific management scenarios over simple random treatments with no designed strategy (a method often applied, since larger scale landscape-level management is frequently missing). The results show that treating individuals of three

hydrochorous plants according to landscape-wide strategies (i.e. removing individuals from large populations, small populations, outlying populations, cells in large connected habitats, cells along rivers, cells in upper reaches of rivers and in lower reaches) increased the effect of reducing different population characteristics (i.e. population growth and spreading into uncolonized habitats) more clearly compared to random treatments within the landscape. I further demonstrated that this can be achieved without considerably increasing the costs.

I found clear differences in the most efficient management strategies for vegetatively reproducing (i.e. highest efficiency by removing large populations) and sexually reproducing (i.e. highest efficiency by removing small populations) species. On the other hand, I did not find a clear effect when considering different management goals (i.e. reducing spread, area, individuals or regeneration potential) or different levels of costs. Over the 15 simulation years, the effects of the most efficient management strategies generally increased, while the costs remained stable or decreased during simulations. Further, applying treatments that initially share very high costs resulted in a clear cost reduction to the level of medium costs after only a few years. This approach thus proved to be very efficient. In turn, extremely low cost treatments were not very useful and did not provide sustainable alternatives. This is likely due to the density regulation within stands whereby removed individuals were overcompensated by higher seed yields from the remaining individuals. These findings can be used to help increase the efficiency of control methods and to provide a tool to improve success of the control at the landscape scale. However, these findings may come with several limitations which have to be addressed in order to make conclusive management decisions. For instance, I did not include biotic interactions in this study, even though my previous studies highlighted its importance. In any case, competition may be less important for my study species because they are highly competitive in ruderal habitats and thus less affected by potential competitors (cf. *Paper 1*). Unlike for forest dynamic simulations, there are currently no useful models developed that easily include biotic interactions in non-tree habitats. To test if interspecific competition has an influence on my findings, one could either explicitly include biotic interactions in the SDM-part of the hybrid model, or include competitive processes from gap models into the dynamic part. Because of the vast number of non-woody species, one would likely have to operate with functional groups rather than with individual species, an approach used in the BIOMOVE model (Midgley *et al.*, 2010). In addition, it may be important to estimate the real monetary costs and not only cost proxies (i.e. area or number of individuals treated). This may be achieved by creating a survey together with practitioners designed to estimate the costs for different species under different preconditions. This could then be linked back to space, which may be especially important if stakeholders have to optimize the allocation of financial resources for treatment effects.

## Issue 1 & 2: Overall findings

Despite the potential shortcomings when answering the four main research questions, estimating the range shaping effect of biotic interactions and modelling transient dynamics across large spatial scales provided valuable insights on the magnitude and the timescale over which range shifts may occur, especially as little is known about the range restrictions of most species (Gaston, 2009). To recapitulate the loosely formulated questions presented above, I demonstrated that (1) for large-scale species distributions, small-scale drivers like biotic interactions are just as important as large-scale drivers like macroclimate, although the importance of biotic interactions itself varies along macroclimate gradients; and (2) species ranges are affected by migration limitations, where the degree of limitation depends on species traits and the landscape characteristics through which a species must migrate. These findings contribute to a broader understanding of the most important range shaping processes for a species and the way in which they interact on large spatial scales. This ultimately improves the ability to project the responses of large-scale species distributions to climate change, thereby helping to improve scientific and management decisions.

### *6.2 Scientific significance and implications*

Identifying appropriate scales of analysis for different environmental drivers is recognised as an important area of research (Allen & Starr, 1982; Pearson & Dawson, 2003). Based on the findings of my PhD, I will improve the concepts related to the hierarchical spatial structure of processes in ecological systems. However, because several terms are used in the literature in an ambiguous manner, I will first clarify the terminology used. First, the spatial scale of the processes that I refer to does not represent the spatial scale at which these processes act, but rather the spatial scale at which these processes affect species distributions. Biotic interactions, for instance, act only on local scales, e.g. by interference or resource-exploitation (Begon *et al.*, 2006). If competition is however linked to large-scale drivers like macroclimate, it may affect species responses and distributions not only on local scales but also on large spatial scales. Second, the term spatial scale (i.e. continental, regional and local scale) does not address the extent of the study area, but rather the scale of the species distribution pattern. The continental scale refers to processes determining the total range margins of a species, the regional scale to processes affecting regional distributions within these range margins, and the local scale to processes affecting only the very local spatial arrangement of species, e.g. within a few square meters. Third, it is important to differentiate between processes that affect the response of species distributions to changing environments (because such changes matter for the physiology, the demography, etc.) and processes that constrain the distribution limits of species (i.e. if they would have indefinite time to migrate). Land use and spatial habitat configuration, for instance,

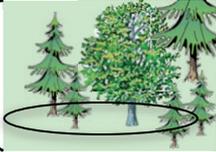
may influence species' responses to changing conditions, but will not prevent species from growing in an area that they have successfully reached – in contrast to an adverse macroclimate which would also prevent them from growing there.

The hierarchy of spatial scales at which factors operate is considered as a useful framework for addressing environment-biota relationships (Pearson & Dawson, 2003). It implicates that analyses on specific spatial scales may only address the phenomena that are dominant at this specific spatial scale (Turner *et al.*, 2001). For large-scale species distributions (i.e. regional to continental scales) this implies that, according to current expectations, only climate needs to be considered as the dominant driver (Midgley *et al.*, 2003; Pearson & Dawson, 2003). My findings, however, suggest that the general expectation of climate as being the only main driver of species distributions at large scales should be rejected, since small-scale processes also have major impacts on large-scale species distributions (Table 1). Biotic interactions, which were assumed to have an effect only at local-scale distributions (Midgley *et al.*, 2003; Pearson & Dawson, 2003), was also shown to have a strong influence - almost equally as strong as climatic factors - on regional distributions. Moreover, because their importance is linked to gradual macroclimate, they also affect continental scale distributions (i.e. competition was shown to be especially high under favourable climate conditions, which primarily affects the southern range margins of Europe, unless drought is the main range limiting factor). Land-use and spatial habitat configuration, which were expected to be important only at local scales (Thuiller *et al.*, 2004), are also shown to be important at the regional scale by altering biotic interactions (e.g. land-abandonment of agricultural areas creates low competition habitats for tree species). Moreover, the principal effect of land use is to reduce the effectiveness of species responses to global change, especially when very scattered habitats or populations are created. Climatic extremes, topography, and soil were also found to be important for regional species distributions; however, as drivers on continental scales, they are less important. Accordingly, I suggest that the hierarchical concept of drivers influencing species distribution patterns should be redefined (Table 1) in order to reduce the uncertainty when modelling large-scale species distributions.

Using current standard approaches, it was not easily possible to address transient responses of large-scale species distributions to global change (Neilson *et al.*, 2005). For a better understanding of species range restrictions and for improved projections of the transient dynamics of species ranges induced by global change, the most accepted means of progress was a convergence of empirical and mechanistic model approaches (Guisan & Thuiller, 2005; Heikkinen *et al.*, 2006; Zurell *et al.*, 2009). Indeed, with such hybrid models I was able to demonstrate, that the ability of a plant species to migrate is a function of the species' characteristics and of the landscape through which a species migrates. Whether or not a species is able to track suitable environmental conditions during global change depends particularly on (1) the community structure of the habitats a species has to

move across, (2) the spatial configurations of the habitats through which a species migrates, and (3) the climatic conditions that the habitats exhibit. Due to dispersal limitations, several species are or will be in a strong disequilibrium with their environment and will thus lag behind in tracking potentially suitable habitats. Late-successional species may find it especially difficult to achieve equilibrium with a constantly changing climate. Invasive species, on the other hand, which represent fast-spreading, ruderal species, would rapidly achieve equilibrium with their environment without control. To minimize their spread, one could manipulate spread behaviour in the most sensitive populations, since these are the principal sources of population growth and spread within the landscape. In conclusion, whether or not species are able to colonize future suitable habitats strongly depends on a species' ability to migrate through dynamically changing heterogeneous landscapes within the constraints of the bioclimatic envelopes. Although the interplay of all of the processes affecting large-scale species distributions is quite complex and individualistic, the responses of large-scale species distributions to changing environments are rather predictable.

**Table 1.** Scale at which processes affect species ranges and responses to climate change. The table compares current expectations (blue arrows) and redefined hypotheses from my PhD (red arrows). Dashed lines express processes that only affect the responses of species distributions to changing environment but not the equilibrium distributions.

|                               | Continental scale<br> | Regional scale<br> | Local scale<br> |
|-------------------------------|--|--|--|
| Climate                       | <i>Paper 2, 3</i>  | <i>Paper 1, 2, 3, 4,</i><br><i>Appendix Paper</i>  |  |
| Biotic interactions           | <i>Paper 2, 3</i>  | <i>Paper 1, 2, 3</i>   | <i>Paper 1, 2, 3</i>   |
| Land-use                      |  | <i>Paper 4</i>   | <i>Paper 4</i>   |
| Spatial habitat configuration | <i>Paper 3</i>   | <i>Paper 4</i>   | <i>Paper 4</i>   |
| Climatic extremes             |  | <i>Appendix Paper</i>  | <i>Appendix Paper</i>  |
| Topography                    |  | <i>Paper 1, 2, 3, 4,</i><br><i>Appendix Paper</i>  | <i>Paper 1, 2, 3, 4,</i><br><i>Appendix Paper</i>  |
| Soil                          |  | <i>Paper 2, 3, 4</i>   | <i>Paper 2, 3, 4</i>   |

### ***6.3 Societal and economic significance and implications***

Mitigation strategies are urgently required to slow down the erosion of biodiversity. The knowledge gained from my research may improve the projection and mitigation of extinction risks due to global change, and could help to develop and test strategies for species management. However, the development of a target state is always a process of negotiation with the people involved, e.g. forest owners and other stakeholders. Thus, my results are not yet a fixed solution for mitigation strategies of global change effects on species distributions. Nevertheless, my results may eventually be used to help improve the interpretation of maps that portray species ranges when designing reserve networks (i.e. areas of high uncertainty when climatic factors alone are included in the model), to generate a basis for larger-scale forest management under climate change (i.e. evaluate climatic conditions under which the management of species may be especially important in order to reduce overly strong competition for ecologically or economically important species), to better plan the assisted migration of migration limited species that are important for either economic or biodiversity reasons (i.e. transplant them to areas that are becoming suitable, but that are currently out of reach for these species to migrate to), or to improve the efficiency of management strategies to contain the spread and population growth of invasive species. In conclusion, the insight provided on processes affecting large-scale species distributions and their implementation in species distribution models can assist in assessing and maintaining ecosystem goods and services.

### ***6.4 Areas of future research***

In order to make conclusive scientific and management decisions, one may do the following: (1) conduct experiments to validate the findings from the models and to gain more insight into the processes involved, (2) develop or adapt methods to better estimate the uncertainty of complex models, (3) investigate the effect of niche stasis on responses of species distributions, and (4) investigate if one does good or harm if one assists species migration.

First, in order to obtain more insight on the relative importance of biotic interactions and climatic constraints, as well as on the direction of biotic interactions along climatic gradients, one should carry out experiments that can be linked to large-scale species distribution models instead of simply analysing observational data. For instance, to disentangle the small-scale processes comprised in biotic predictors (e.g. positive and negative species interactions, species management, local soil and climate conditions), one could conduct frost and drought experiments with two competing species replacing each other along altitudinal or other ecological gradient (i.e. testing to what degree physiological tolerances and biotic interaction determine the distribution of species along environmental gradients). Such experiments would allow for the assessment of the direction of biotic

interactions when evaluating competition effects in species pairs along experimental conditions that mimic large-scale environmental gradients. Such insights from careful experimental design combined with the power of large observational datasets would add considerably to our understanding of range restrictions in plants.

Second, quantifying uncertainty in models and projections is a crucial task and not yet sufficiently considered in ecological global change studies. Assessing uncertainty is, however, a complex task. On the one hand, global change scenarios and projections cannot, by definition, be easily compared with observational data due to the enormous scales involved and the lack of relevant historical data. On the other hand, it is ethically unacceptable to carry out full-scale validation experiments, e.g. by allowing invasive species to spread over a large landscape for the sake of model validation. Nevertheless, the need for model evaluation and uncertainty assessment is growing, especially as models become increasingly more complex, e.g. hybrid models, inherently containing more uncertainty than simple models (Midgley *et al.*, 2006; Thuiller *et al.*, 2008). The now frequently used model averaging and ensemble methods are claimed to be a first step in the direction of quantifying a model's effect on the variability in its projections. This may, however, only be the relevant if the assessed models depict reality to a sufficient degree. To assess a full suite of uncertainty effects in model projections is a huge task requiring thousands of simulations, even for computationally simple methods, such as SDMs. For more complex models, it can be virtually impossible. For simple SDM-derived methods, Bayesian statistics has the potential to directly incorporate uncertainty elements from partial processes into more complex model projections. The effect of parameter uncertainty, for instance, could be examined in a Bayesian framework with emphasis on the derivation of the Bayesian distributions of unknown quantities given some measurements, which would not only account for natural variability but also for parameter uncertainty (Kitanidis, 1986).

Third, the assumption of niche stasis should be further investigated. Acknowledging the ongoing research on niche stasis, it would be important to further investigate the stability of the fundamental niche, particularly at different ontogenetic stages. Knowledge on the magnitude of fundamental niche-stasis would improve our risk assessment during climate change. Of prime importance is, firstly, an improved understanding of the fundamental niche of a given species, which would improve our estimates of a species' ability to adapt to new conditions. Further knowledge on the capacity to adapt (i.e. niche adaptation vs. stasis) will improve our understanding of the degree to which migration to suitable habitats is a prerequisite over adaptation to changing conditions. Species with stable niches (i.e. no adaptation possible) are under higher pressure to migrate and success will be dependent on whether or not they are dispersal limited (e.g. Skov & Svenning, 2004; Wiens & Graham, 2005), where dispersal limitation will result in extinction (e.g. Foden *et al.*, 2007). Species

with less stable niches, on the other hand, may be able to persist locally by adapting to the current climate by modifying their physiology or seasonal behaviour (e.g. Zavaleta *et al.*, 2003; Wiens & Graham, 2005). Thus, alpine plant species, which are restricted to northward and upward migration, that have pronounced functional flexibility and high levels of genetic plasticity (i.e. an unstable niche) would be more likely to persist during climate change than other alpine species that lack such characteristics (Larcher, 2003). New insight into niche conservatism would further improve trait-based risk evaluations that aim at preventing species invasions by detecting species that have yet to become highly invasive, but that have the potential to do so. In situations where species and ecosystems are not static over time, invasive species may rapidly evolve in the new habitats as a result of fluctuations or shifts. Yet, native species may also adapt under the pressure of invaders (Cox, 2004), which would have a large impact on the success of invasions. Further, the effect of the (in)stability of the ontogenetic niches on large-scale species distributions should be further examined. From the field of population biology, it is known that juveniles may be more vulnerable to adverse abiotic and biotic conditions than adults (Bazzaz, 1996). Ontogenetic niche differences are well studied for many animal species (Olson, 1996; Sillett & Foster, 2000; Kanda & Fuller, 2004). However, literature on ontogenetic niche differences in plants is scarce (Harper *et al.*, 1965; Hobbs & Mooney, 1985; Ellenberg, 1992; Miriti, 2006). If ontogenetic niche differences in plants are also detected along climatic gradients, i.e. by detecting a separation of the actual distribution of adult tree species and the regeneration limit of seedlings during climate change, it would be necessary to add a dynamic component to static and dynamic models in order to improve model projections. This could be done by intersecting the niche of all ontogenetic stages with climate in order to more accurately project the effect of range retractions or expansions induced by climate change.

Fourth, one should more broadly discuss if migration of (plant) species should be assisted or not. Currently, transplanting migration limited native species within a continent is a widely accepted solution to prevent them from going extinct. However, whether or not transplanting dispersal limited species into areas they never would have reached by themselves is beneficial or harmful to the environment remains a controversial issue. The effect of deliberately transplanting ecologically or economically important species may be similar to the effect of unintentionally introducing alien species that become invasive in their introduced environment. To elucidate the effect of transplanting dispersal limited species into a new environment, one could simulate the different trajectories of areas that are not yet reached by dominant dispersal limited species, i.e. compare communities with and without the introduction of dispersal limited species. It is, however, difficult to foresee how the outcome should be judged. To what degree humans should attempt to primarily reduce the drivers versus the effects of human induced global change remains an ethical question.

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## 7 Appendix paper - Climatic extremes improve predictions of spatial patterns of tree species

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### 7.1 Abstract

Understanding niche evolution, dynamics, and the response of species to climate change requires knowledge of the determinants of the environmental niche and species range limits. Mean values of climatic variables are often used in such analyses. In contrast, the increasing frequency of climate extremes suggests the importance of understanding their additional influence on range limits. Here, we assess how measures representing climate extremes (i.e., interannual variability in climate parameters) explain and predict spatial patterns of 11 tree species in Switzerland. We find clear, although comparably small, improvement (+20% in adjusted  $D^2$ , +8% and +3% in cross-validated True Skill Statistic and area under the receiver operating characteristics curve values) in models that use measures of extremes in addition to means. The primary effect of including information on climate extremes is a correction of local overprediction and underprediction. Our results demonstrate that measures of climate extremes are important for understanding the climatic limits of tree species and assessing species niche characteristics. The inclusion of climate variability likely will improve models of species range limits under future conditions, where changes in mean climate and increased variability are expected.

**Keywords** climate change, ecological niche, generalized additive model, geographic range, species distribution models

## 7.2 Introduction

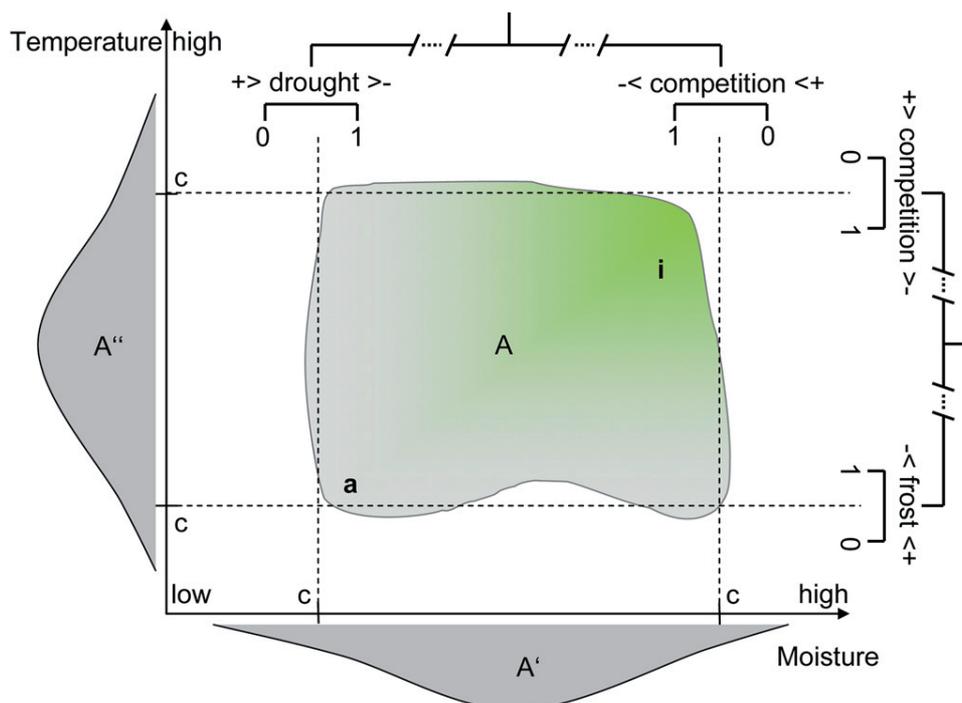
The understanding of the principles and mechanisms that shape distribution patterns has long been a focus in biogeographical, ecological, and evolutionary research. The ecological niche concept, coined and initially developed by Grinnell (1), is the foundation for our understanding of the processes that shape the geographical distributions of species (2). Conceptual clarifications with regards to using the concept for the explanation of species ranges have been presented by several authors (3, 4). Climatic variables are often used to predict biogeographical patterns (5), and considerable effort has been put into improving methods to describe the response of species along climate gradients (6–8). These methods of species distribution or niche modeling are frequently used for conservation management (9–12), prediction of the likely effects of global change (13–16), and, increasingly, assessment of niche characteristics in the study of niche evolution (17–20). These studies in general use monthly or annual climatic means to analyze species distribution patterns. To date, little attention has been paid to the question of how climatic extremes, i.e., the long-term, interannual variation around mean values, could help to explain species distributions. There are two major reasons that highlight the importance of including climatic variability in niche analyses and models. First, ongoing climate change not only affects means but also extremes (21). Second, niche evolution often results in changes of the stress tolerance of evolving clades (22, 23). Thus, both adaptation and possible future response of species to climate are certainly affected by extremes in addition to means.

On a more fundamental level, the question is what aspects of climate actually determine the “climate response” of plant species. The expected effects of climate extremes are diverse. At the range limit of species, source-sink dynamics likely exert strong influence (3, 24–26). In sessile organisms like plants, extremely adverse climate can constrain regeneration and impact range limits through increased mortality (27). Extremely favorable climate, in contrast, might allow unusually high reproductive success or the advance of range limits, especially when such effects occur over several years. The observed effects of severe heat and drought illustrate such range contractions at the trailing edge of species ranges. Such effects are visible by the dieback of Scots pine (*Pinus sylvestris* L.) in the warmest part of the dry valleys of the European Alps and increased diebacks in conifers in western North America (28) that are likely caused by recent warming and increased drought. Ongoing climate change impacts species phenology (29), individual growth (30), and ecosystem dynamics (31, 32). In addition, species have experienced recent range shifts (33–35), some of which are clearly induced by climatic extremes (36), whereas other responses seem more gradual (37). In particular, climatic extremes can be responsible for dieback at the trailing edge of species distributions (38).

These examples illustrate the potential importance of including climatic variability into analyses and models.

Climate variability alone likely does not explain the climatic response of species very well. Rather, variability may complement a species' response to mean climate, which summarizes complex mechanisms that are not directly expressed in a fitted response curve. For instance, under optimal temperature or moisture conditions, climatic variability or extremes could have relatively little effect on species, whereas the effect of variability is likely severe where mean temperature or water availability is closer to physiological tolerances. In contrast, under conditions in which warm temperatures and abundant moisture are favorable for growth, the effects of competition (on abundance, reproductive success, etc.) may outweigh the direct effects of climate. For example, a species' range might in some areas be directly limited by physiological tolerance to low temperatures, whereas in other areas with relatively warm climate, the range limit is caused not by an excess of heat, but by competition (refs. 39 and 40 and Fig. 1). Thus, gradients of mean climate likely integrate both physiological constraints (effected at certain climatic extremes) and the gradual competitive replacement of one species by another (41).

Here, we examine whether climatic extremes help to explain patterns of tree species distributions compared with using climatic means alone. We tested whether this effect is stronger when interactions between means and extremes are modeled. We report tests using data from 12,328 forest plots in Switzerland, where climatic extremes and long-term means were calculated for each plot for a 47-year period by using daily climate estimates. We developed generalized additive models (GAMs) for each of 11 abundant tree species to test our hypotheses. The effects of extreme climatic events were analyzed by using specific approaches based on extreme value statistics (42). Frequencies of extreme events are, however, sensitive to the mean and even more to the variability of climatic variables at a given location (43, 44). Thus, adding as predictor variables indices of extreme events to models that include mean values would confound the effects of mean and variability. Therefore, we used the standard deviation of monthly climate variables to express information on extremes additional to that on means. Collinearity problems were therefore much reduced, because measures of variability are less correlated with means than are extremes expressed as quantiles or absolute extremes. Our long-term temporal variability measures are also fundamentally different from variability parameters available in the Worldclim dataset (45), because these measures capture intraannual variability calculated from long-term monthly means. We focus on interyear variability in extremes. If our hypotheses are supported, inclusion of climatic extremes might help to forecast effects of climate change and assess adaptive niche evolution.



**Fig. 1.** Conceptual graph explaining possible effects of climatic and biotic constraints of species niches (A) with its effects on range limits along simple gradients of climatic means. The response shape typically fitted by regression-type models along gradients of mean climates is given as unimodal curves. Additionally, we illustrate the likely more local (with respect to ecological and spatial gradients) effect of extremes and biotic interactions as causal drivers of a reduction in the mean response along the same mean gradient. Zone a of the observed distribution in environmental space thus may represent areas where a species occurs close to the fundamental niche, whereas zone i does not give an indication of fundamental niche constraints, and the distribution may then be rather constrained by biotic interactions.

## 7.3 Materials and Methods

### 7.3.1 Tree Distribution Data

We used data from two forest inventory periods in Switzerland, which were sampled during the years 1983–1985 (NFI1) and 1995–1997 (NFI2) on a regular 1-km grid. In total, we had 12,328 plots available where species presence and absence for >50 species was derived from basal area estimates. The inventory records a total of >50 tree species, of which we selected 11 species for modeling. The selected species are (i) sufficiently abundant, (ii) belong to two different functional groups [broadleaf deciduous: *Fagus sylvatica* L., *Acer pseudoplatanus* L., *Fraxinus excelsior* L., *Quercus petraea* (Mattuschka) Lieblein, *Q. robur* L., *Sorbus aria* (L.) Crantz, *Betula pendula* Roth; needleleaf evergreen: *Picea abies* (L.) H. Karsten, *Abies alba* Miller, *Pinus sylvestris* L., *P. cembra* L.], and (iii) cover the full elevational gradient available in Switzerland from 180 m above seal level (a.s.l.) to the

treeline situated at  $\approx 2,450$  m a.s.l. in the dry interior valleys. Additional details regarding the forest inventory data are given in SI Appendix.

### 7.3.2 Climate Predictor Data

We generated a climate predictor set containing long-term (1961–2006) averages of monthly, seasonal, or annual predictors and standard deviations of the mean values representing extremes. These estimates were derived at a spatial resolution of 100 m by using the DAYMET algorithm (64). We used data from automated weather stations ( $>180$  for temperature;  $>350$  for precipitation provided by MeteoSwiss) and a 100-m digital elevation model from the Swiss National Office of Topography. DAYMET generates output for daily average, minimum, and maximum temperature and precipitation. Additionally, we calculated potential evapotranspiration, and moisture index, which is the difference between precipitation and potential evapotranspiration (65). For the methods for deriving these two variables, see ref. 66. Additional to these climate predictors, we added slope and topographic position to the lists of evaluated predictors. More information on the derivation of the climate predictors is given in SI Appendix, and high and low mean and standard deviations of the selected climate variables are presented in Fig. S1 in SI Appendix.

Extreme climatic events are best analyzed by using specific approaches based on extreme value statistics (42). Frequencies of extreme events are, however, sensitive to the mean and even more to the variability of climatic variables at a given location (43, 44). Thus, adding extreme event indices as predictor variables to a model including the mean values would confound the effects of mean and variability. Therefore, we chose standard deviations as expressions of extremes in combination with means. We did this for three additional reasons, namely: (i) single-day or rare extremes are very difficult to assess or detect, and even more so to spatially extrapolate. Standard deviations that include the likelihood of extreme events are much easier to extrapolate and to measure. (ii) We do not know exactly what period is relevant regarding extremes for each individual species. They are different in size and age, and the relevant period of sensitivity may change. Thus, a measure of variability (in combination with means) is more likely to capture the general likelihood of extreme events relevant to individual species than do single few observations. Variability can be calculated quite accurately from the whole time series. (iii) There is a high correlation between mean and extremes (percentiles). Thus, adding both means and percentiles as expressions of extremes would result in severe collinearity problems when fitting models.

For our model exercise with the selected tree species we chose two climatic variables, namely: (i) average winter temperature (TAWI: December, January, February), and (ii) average summer moisture index (MISU: June, July, August). TAWI ( $^{\circ}\text{C}$ ) expresses winter cold limitations, whereas MISU (mm) expresses water availability and levels of drought stress. For these two variables, we calculated both means and standard deviations. Additionally, we added slope and

topographic position (66). The six selected variables show very low correlations on average (0.254), and only two variables correlate  $>0.5$  (mean and SD of MISU: 0.73).

### 7.3.3 Statistical Analyses

We chose GAMs as implemented in the R package *mgcv* (67). This is a flexible, nonparametric method for calibrating the species response to topo-climatic predictors, which allowed us to additionally test the effect of interactions between means and standard deviations by using smooth terms built with tensor products (68). In *mgcv*, the degrees of smoothing are selected by internal cross-validations. All variables were entered in the default mode, and three models were finally calibrated for each species. The first used all selected variables except the two standard deviations, whereas the second included the two standard deviations. The third used interaction terms from tensor product smoothed terms of the respective mean and standard deviations (MISU and TAWI), instead of adding the two variables separately.

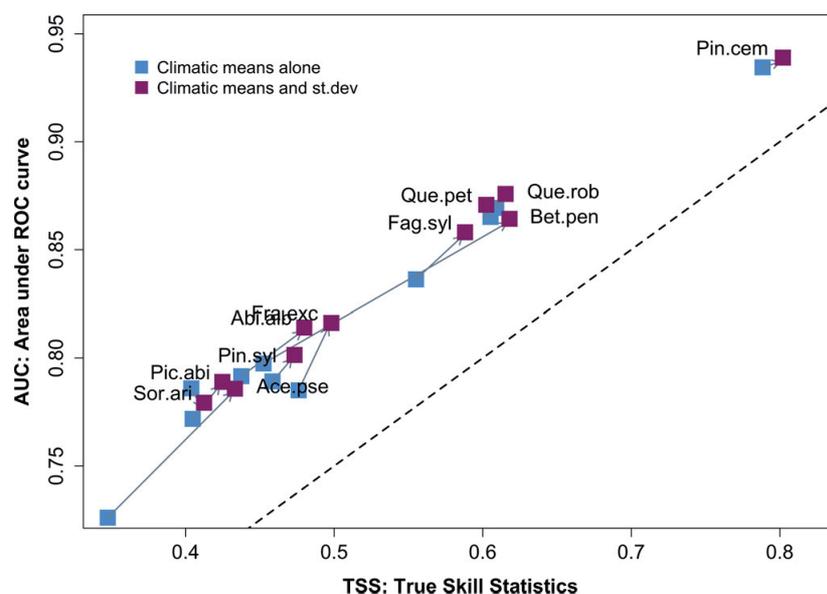
All models were 10-fold cross-validated and model performance of calibrated and cross-validated models was analyzed by calculating the adjusted  $D^2$  (see ref. 5), threshold-maximized TSS (46) and AUC (69), which allows assessment of model accuracy independent of thresholds. The model improvement when adding extremes in addition to means was tested in two ways. First, we performed an ANOVA using a  $\chi^2$  test for checking the significance of the improvement in calibration strength. Second, we tested the improvement in model quality by applying a paired Wilcoxon test to the model evaluation values (TSS, AUC) of all species' models with means only against all species' models with means and extremes. The first (ANOVA) test allowed us to evaluate the individual improvement of models, whereas the second (Wilcoxon) test allowed us to evaluate the overall improvement of the predictive power of the models. All analyses were performed in the statistical environment R (70).

## 7.4 Results

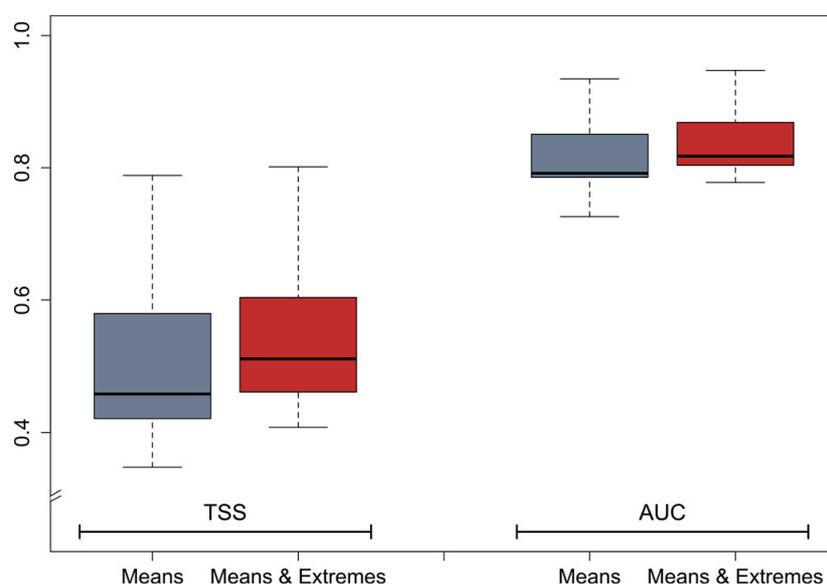
We found a significant improvement (ANOVA,  $\chi^2$  test; see Table S1 in SI Appendix) in the calibration of the nonparametric GAMs of species distributions when using climatic variability as predictors compared with using average climate variables alone (Fig. 2). The fit of models for the 11 species, as measured by the True Skill Statistic (TSS) (46) from 10-fold cross-validation, was better when we included variables representing both climate means and extremes [ $0.548 \pm 0.036$  (mean  $\pm$  SE)] than when only climate means were represented ( $-0.040 \pm 0.038$ ), a significant difference (two-tailed Wilcoxon signed rank test,  $V = 0$ ,  $P = 0.001$ ). This improvement was also true when we evaluated model fit with area under the receiver operating characteristics curve (AUC) (variables representing mean and extremes:  $0.843 \pm 0.016$ ; mean only:  $-0.025 \pm 0.017$ ;  $V = 1$ ,  $P =$

0.002; Fig. 3 and Table S2 in SI Appendix). The results were similar when we included the interaction of variables representing climatic means and extremes instead of only adding climatic extremes variables. We observed again a significant improvement of each model in an ANOVA test compared with using climatic means alone (Fig. S1 in SI Appendix). The overall improvement in cross-validated model performance was significant (TSS: interactions of variables representing means and extremes:  $0.561 \pm 0.034$ ; mean only:  $-0.052 \pm 0.038$ ;  $V = 0$ ,  $P = 0.001$ ; AUC: interactions of mean and extreme variables:  $0.848 \pm 0.015$ ; mean only:  $-0.030 \pm 0.015$ ;  $V = 0$ ,  $P = 0.001$ ). Adjusted  $D^2$  increased by 20%, whereas TSS and AUC increased by 8% and 3%, respectively. However, when comparing the two versions of implementing extremes into models, we found that in 4 (*Acer pseudoplatanus*, *Pinus sylvestris*, *Quercus robur*, and *Betula pendula*) of the 11 species no significant improvement was reached in the ANOVA tests (Fig. S1 in SI Appendix). Only the overall improvement in cross-validated model accuracies was significant (TSS: interactions of mean and extreme variables:  $0.561 \pm 0.034$ ; no interaction of mean and extreme variables:  $-0.012 \pm 0.036$ ;  $V = 8$ ,  $P = 0.024$ ; AUC: interactions of mean and extreme variables:  $0.848 \pm 0.015$ ; no interaction of mean and extreme variables:  $-0.006 \pm 0.016$ ;  $V = 9$ ,  $P = 0.032$ ).

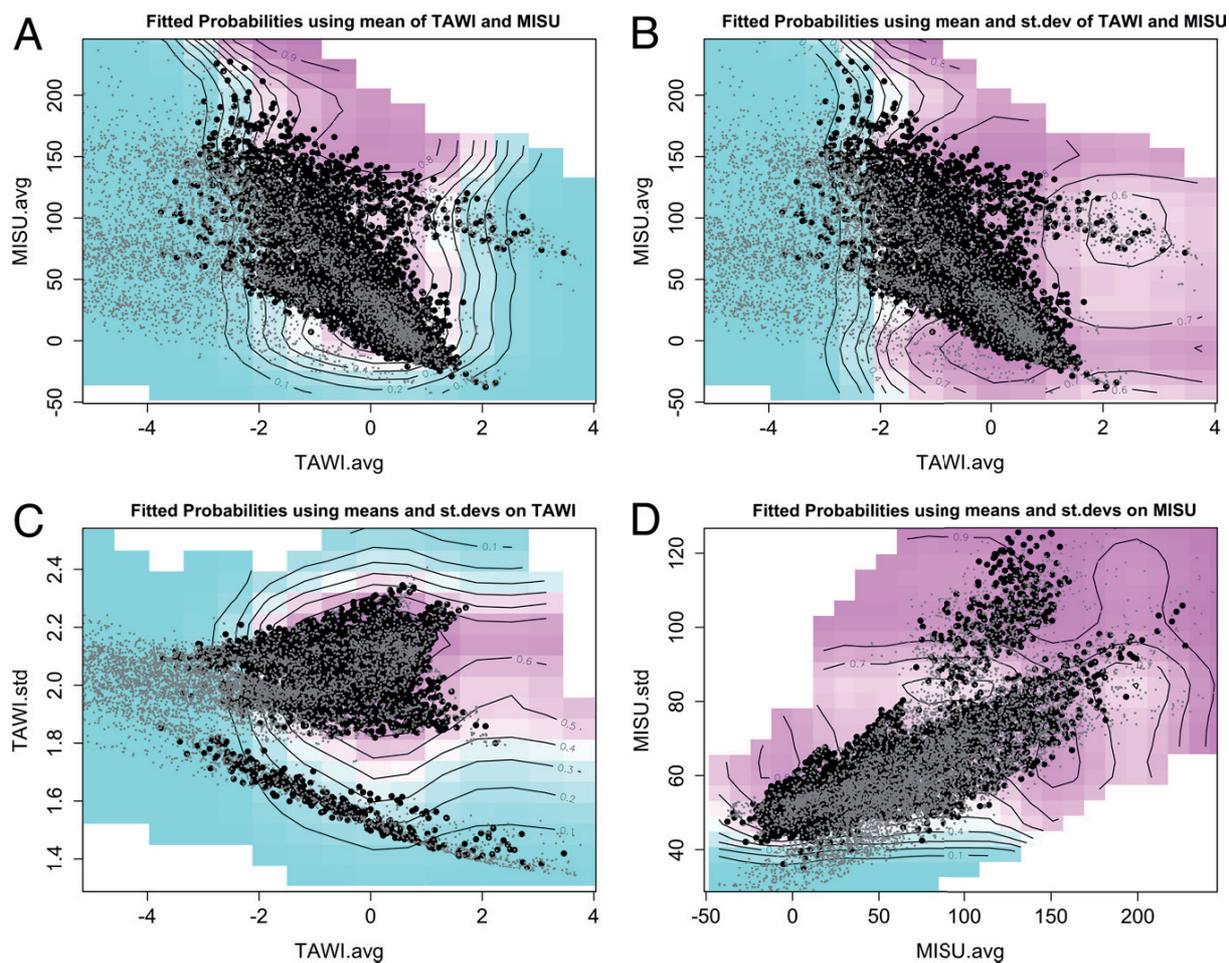
When adding variables representing extremes to models using climatic means for predicting spatial patterns of tree species, we note a shift in the probability space of *Fagus sylvatica* (Fig. 4). The species becomes less limited toward warmer temperatures and the limitation toward cold temperatures depends less on water availability (Fig. 4B). In the geographic space, adding variables representing extremes translates into a correction of predictions from the model using means only, especially in the dry and Mediterranean (Southern) parts of Switzerland (Fig. 5 A and B) for *F. sylvatica*. Including climate variability in the models of *Abies alba* (Fig. 5 C and D) increases prediction probabilities in the comparably moist climates of central and western Switzerland and further reduces the spatial distribution in the southern part of the Alps and in the central valleys with comparably dry climates. Presence/absence information for all tree species is given in Fig. S2 in SI Appendix; results for all 11 species are given in Fig. S3 in SI Appendix.



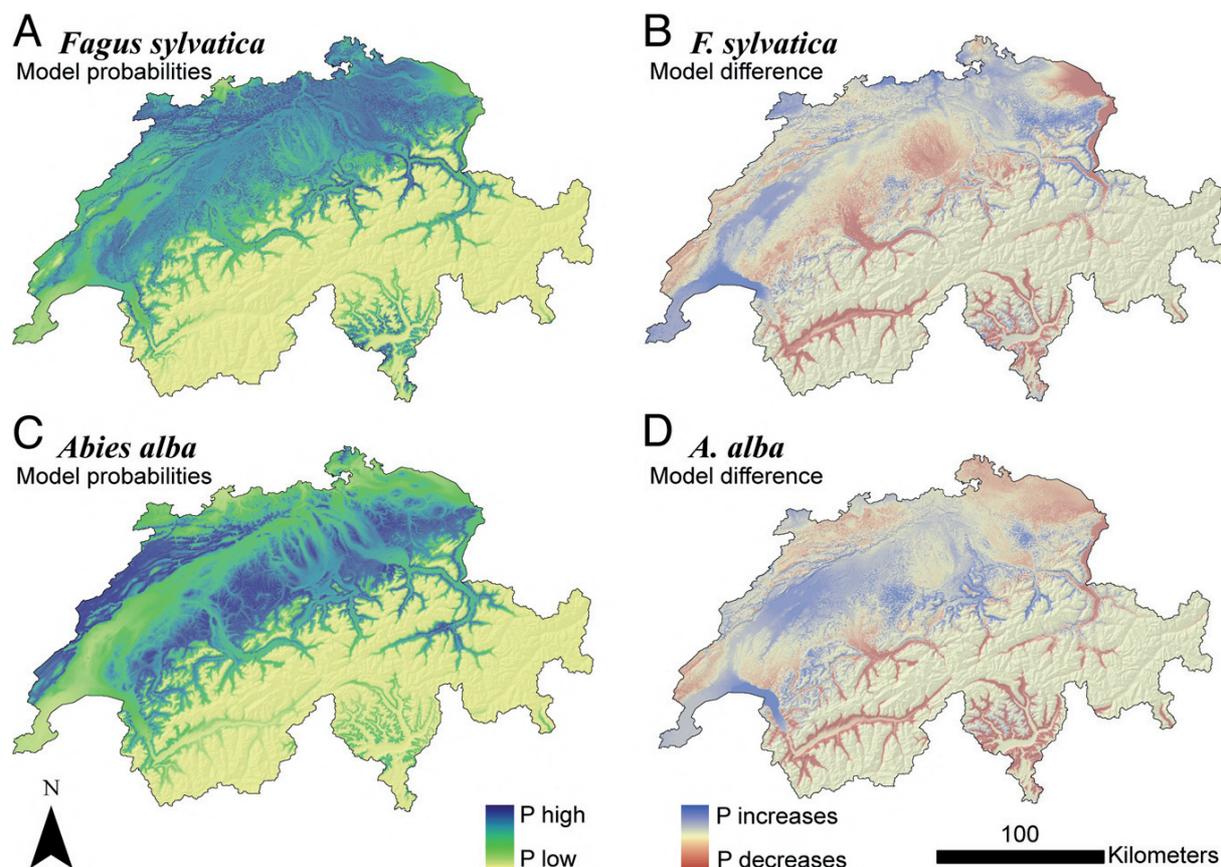
**Fig. 2.** Comparison of 10-fold cross-validated model performance (TSS, AUC) when using climate means (light blue) vs. means and extremes (purple) climate predictors in GAMs predicting the spatial patterns of 11 tree species. Species names are abbreviated, and the full names are given in Table S1 in SI Appendix. With the exception of *P. abies*, all species more or less clearly increase their predictive capacity.



**Fig. 3.** Comparison of the influences of two tested predictor types in nonparametric GAMs using 10-fold cross-validated model performance (TSS, AUC) for 11 tree species. When adding measures of extremes to mean climatic predictors (maroon), the average model performance and the accuracy of the least performing models increase compared with using only climatic means (steel blue).



**Fig. 4.** Predicted probabilities for *F. sylvatica* along major climate gradients. (A and B) Illustration of fitted probabilities for *F. sylvatica* when using only mean climate predictors (A) compared with using means and standard deviations without statistical interaction term (B). (C and D) The probabilities from the model using means and standard deviations are plotted against TAWI.avg and TAWI.std (C) and against MISU.avg and MISU.std (D). Light gray and black dots represent all plots and plots where *F. sylvatica* is present, respectively. Blue and magenta represent low and high model probabilities, respectively, as indicated by the contour lines.



**Fig. 5.** Effect of adding climatic extremes on predicted spatial patterns. (A and C) Simulated probabilities of *F. sylvatica* (A) and *A. alba* (C) from GAMs using climatic means and extremes as predictors with no statistical interactions added. (B and D) The effect of adding extremes calculated as the difference between predicted probabilities of the more complex model using means and extremes and the model using means alone. Red and blue colors indicate the forcings of the standard deviations as predictors to decrease and increase the probabilities of the species models in A and C compared with the simple model consisting of climatic means alone.

## 7.5 Discussion

Our analyses reveal that complementing mean climate predictors with variables that represent climate extremes yields an improvement in the predictive power of species distribution models. The improvement is small compared with the model using climatic means only and specifically corrects spatial predictions compared with using climate means alone. This small improvement is partly in agreement with early investigations regarding explanations of distribution range patterns in trees and other plants. Larcher and Mair (47) observed that absolute climatic extremes alone are incapable of explaining the northern range limits of (climate constrained) Mediterranean oak species. They argued that average (winter) temperatures are more suitable for explaining northern range limits. We found, however, that adding climatic variability helps to explain such range limits. Another example involves

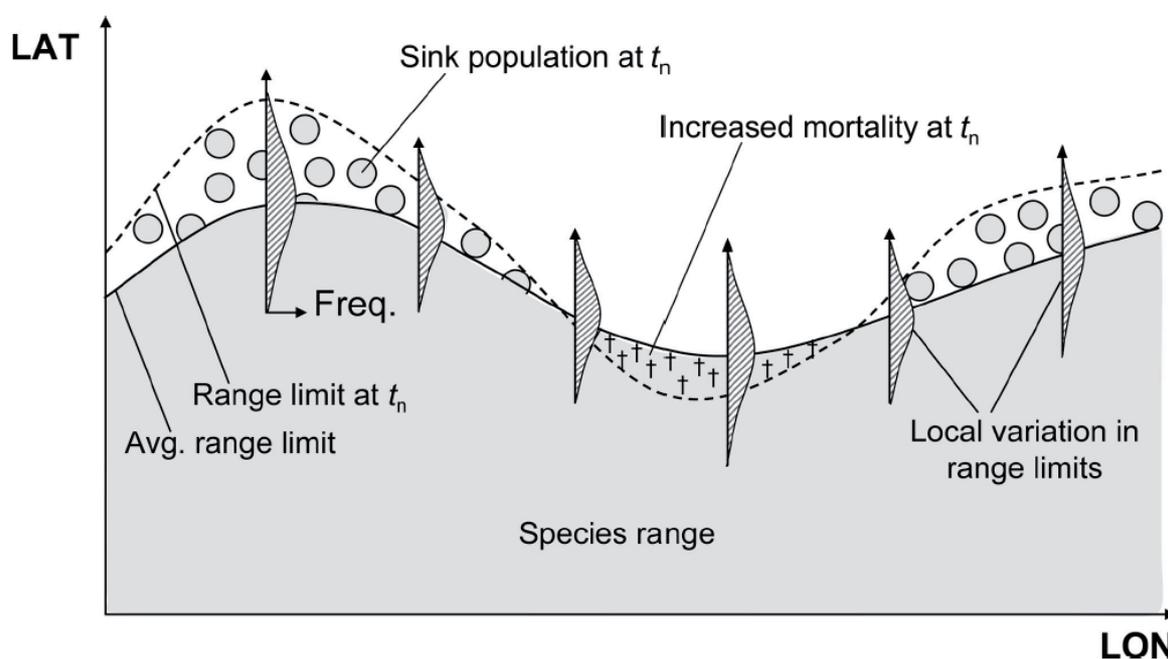
the quest for a climatic explanation of the upper treeline worldwide. Current explanations focus on average climate predictors (48), and the best model based on a global dataset of mountain treeline temperatures reveals a strong relationship between treeline and average summer temperatures (49, 50). However, no explanation that we examined included additional effects of climate variability.

The effect of extremes and means are not easy to separate because of the high correlation between mean values and percentiles as measures of extremes. We expect that higher frequency or severity of extremes affect range margins in plants. Clear evidence exists that severe climate extremes influence plant demographic processes, such as growth (30, 32), regeneration (51), and mortality (38, 52, 53). However, it is not immediately evident from these studies that the observed responses affect range limits directly. Such processes may simply result in strong source-sink dynamics at range edges, with the range limit resulting from complex and multiple interactions (24, 54). For example, there may be strong mortality patterns after dry or cold years in tree saplings, but even a complete failure of recruitment in particularly adverse years may not impact the species range limit, but instead primarily affect age structure and source-sink dynamics (55, 56). The demographic signal of extreme adverse and favorable events may lead to both positive (range expansion, regeneration) and negative (range contraction, mortality) effects locally. The resulting patterns of overall range limits may well reflect climatic means (Fig. 6). However, when the variability around means is very high, then a species may not be able to compensate in good years the losses that occur during adverse years. Climate variability, in addition to means, then clearly affects range limits.

The association of range margin and climatic mean may not hold when climatic extremes occur with a skewed frequency distribution where the mean slowly shifts in a single direction, as during current, ongoing climatic change (57). In this situation mortality and regeneration are increasingly affected by climatic extremes rather than by means (28, 38, 58). Thus, projections of species responses to climate change might benefit from calibrating models to both climate means and extremes (expressed as variability). This addition could be especially important for forecasting the trailing edge of shifting ranges (59). Evaluation of the differences in forecasts that are based on climate means and variables representing extremes could contribute to better assessment of forecasting uncertainty. In our example with *F. sylvatica* and *A. alba*, a reduction in predicted probability at the warm end of the current distribution occurred when adding variables representing climatic extremes to the model calibration. The challenge remains to cover sufficient climatic variability during sampling to span the range of climatic variation that is expected in the future. Ongoing climate change, however, could also reduce the sensitivity of species distribution patterns to climatic extremes. Such reduced sensitivities, specifically with regards to tree growth, have been observed repeatedly in the recent past (60, 61), and climate change is a likely explanation (62).

The effects of climatic extremes on limiting species distributions are likely important when climate means shift geographically and when variability changes. The daily climate surfaces we used

may have smoothed climatic extremes, causing us to overlook patterns of truly extreme events. The same could also occur because of the limited temporal span of the climate data. First, such limitations are difficult to overcome, because we used a contemporary method to generate daily climate surfaces. Second, we performed initial tests to use absolute extremes instead of means, which did not improve the model fits. Third, the size of the available time window to analyze extremes over a large area is potentially problematic. Trees are long-lived and their stress tolerance differs among life stages. More information on stress tolerance at different life stages would enhance our ability to optimize analyses to the relevant time window. Other effects that reduce the sensitivity of species distributions to climate fluctuations include human influence through forest management and the possibility that observed distributions may not be in equilibrium with current climate (63). In our dataset, we assume a strong effect of forest management on the Swiss Plateau for *Picea abies*. For most forests of dry interior valleys we expect little to no effect from management on the elevational ranges of the species we considered. Finally, we believe that some of the limitations identified in our analysis of large-scale observational data can only be overcome by experiments. Ideally, such complementary analyses combine the power of large observational datasets with the insights of careful experimental design.



**Fig. 6.** Possible effects of climate variability at range margins. This graph illustrates that climatic means may sometimes explain the general range limit, whereas climatic extremes may rather influence local sink populations and extinctions ( $t_n$ ). However, strong climatic variability at range margins may lead to asymmetric effects, and thus influence range limits additional to means.

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## *7.8 SI Appendix*

Additional Supporting Information may be found at:

[http://www.pnas.org/cgi/data/0901643106/DCSupplemental/Appendix\\_PDF](http://www.pnas.org/cgi/data/0901643106/DCSupplemental/Appendix_PDF)



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