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Species' responses along environmental gradients on different spatial scales

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SPECIES RESPONSES ALONG ENVIRONMENTAL GRADIENTS ON DIFFERENT SPATIAL SCALES

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"Research is the process of going up alleys to see if they are blind[1]." All alone, I would have ended up in many seemingly blind alleys, without realising that in fact, it wasn't so - the way out was just entirely different from what I expected! Therefore, I would like to thank all of the following persons, including those I might have forgotten to mention by name, for helping me to successfully make my way out of the alleys:

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[1] Bates, Marston (1950): The nature of natural history. Scribner, New York

IV

It's time to begin, isn't it?
No more time for second-guessing or going back to sleep.

I might get a little bit bigger, but then, I'll admit, I'm just the same as I was, so I want you to understand, I'm never changing who I am!

Lyrics changed after "It's time to begin" by Imagine Dragons and "Defying gravity" from the Wicked Soundtrack

Dedication

Für Opa.

Und alle, die an mich glaubten.

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Summary

The abundance of species on Earth varies greatly – while some occur all over the globe, others can only exist in very distinct regions. Trying to explain the reasoning behind the temporal and spatial variation in the commonness and rarity of species has a long history in ecology and yet, many pieces are still missing to complete the puzzle.

Presently, the world's ecosystems are subjected to unprecedented rates of change, with the chief anthropogenic threats being habitat destruction, pollution and climate change. In order to understand how the environmental changes influence the distribution patterns of species, and to have a chance to predict their reactions to a changing environment, it becomes vital to identify what governs their distribution today.

This thesis investigates species' responses to changing environmental gradients and asks in how far niche characteristics can be used to predict species' range sizes at different spatial scales. We worked with herbaceous species from semi-natural grasslands as well as deciduous forests, focusing especially on their reactions to abiotic conditions (soil pH, nutrients and light). At first, species' response to specific environmental factors were characterised as increasing or decreasing along an environmental gradient. Later on, more sophisticated measures utilising the niche concept were used, and we calculated niche breadth, position (optima) or tolerance limits of species for different environmental factors. These were related to species' reactions to nutrient pollution, range size or threat level to identify generalist or specialist species, with the assumption that species being able to utilise wider ranges of resources or resources being more common, are themselves more common. Alternatively to this gradient approach, species' niche breadth was calculated using a co-occurrence approach, where species that have many different neighbours (large turnover index between sample plots) are the common ones.

To begin with, we were interested in the importance of species' responses for their occurrence patterns under environmental change. We found that both nitrogen and phosphorus pollution are reasons for the change in abundance of many grassland species and observed the same patterns over a spatial as well as a temporal gradient, re-affirming the reasoning behind space-for-time substitutions.

Next, we investigated the relationship between niche breadth and range size. It has been assumed that methodological artefacts and biases (e.g. sampling or phylogenies) are the main reason for their correlations. However, we could show that although unequal sampling enhances the relationship, it is not the main cause, as we found a significant niche breadth-range size relationship even after correcting for these biases. Combining all the results that we gathered on different niche characteristics as predictors of range size, we draw the following conclusions:

1) Combining the niche breadth of species with their niche position and the availability of suitable habitats into one parameter called "available niche breadth" was the best predictor of range size across different spatial scales. However, the data needed to calculate the available niche breadth is severely lacking.

2) Species niche breadth or tolerance limits of soil pH are good-working alternatives to predict species' rarity when the available niche breadth cannot be calculated.

3) Using the co-occurrence based estimate to predict the range size of species works well, and is very useful, since many relevés without environmental measurements are available.

In conclusion, we could show that the breadth of resources used by species (especially regarding soil pH), as well as their tolerance limits, are reliable predictors for their rarity and commonness across different spatial scales. Furthermore, we believe that the niche properties generated in this study can provide guidelines for conservation decisions, especially concerning the selection of suitable habitats for the reintroduction of species. This is a particularly important task to preserve the world's biodiversity in today's ever changing environments.

Zusammenfassung

Die Häufigkeit verschiedener Arten auf der Erde unterliegt einer hohen Variabilität – während einige Arten überall verbreitet sind, kommen andere nur sehr kleinräumig vor. Die Suche nach einer Erklärung für diese unterschiedlichen Muster in der zeitlichen sowie räumlichen Verbreitung von Arten hat Ökologen seid jeher beschäftigt. Es fehlen jedoch auch heute noch Teile zur Fertigstellung dieses Puzzles.

Die Ökosysteme der Welt unterliegen derzeit einem nie da gewesenem Wandel, allen voran bedingt durch Habitatzerstörung, Umweltverschmutzung und den Klimawandel. Um zu verstehen, wie Arten auf diese sich verändernden Bedingungen reagieren, und um eine Möglichkeit zu haben, Voraussagen über die Reaktionen von Arten zu treffen, ist es unerlässlich zu verstehen, was die momentane Verbreitung der Arten steuert.

Aus diesem Grund beschäftigt sich diese Arbeit mit den Reaktionen von Arten entlang sich ändernden Umweltgradienten und geht der Frage nach, inwieweit Nischeneigenschaften in der Lage sind, die Gebietsgröße („range size") von Arten vorherzusagen. Diese Arbeit konzentriert sich vor allem auf krautige Arten des naturnahen, trockenen Grünlands sowie der Laubwälder, mit einem besonderen Fokus auf die Reaktionen dieser Arten auf abiotische Umweltparameter (Boden pH, Nährstoffe und Licht). In einem ersten Schritt beschreiben wir die Reaktion einer Art auf einen bestimmten Umweltfaktor durch die Änderung ihrer Häufigkeit bei Änderung des Faktors. Dann verwenden wir Messungen, die das Nischenkonzept nutzen. Verschiedene Nischencharakteristika, wie Nischenbreite, Nischenposition (Optimum) oder auch Toleranzgrenzen der Arten werden für unterschiedliche Umweltparameter ermittelt. Durch die Verknüpfung dieser Parameter mit der Gebietsgröße oder Gefährdung (z.B. Rote Liste-Daten) von Arten können Umweltspezialisten und -generalisten identifiziert werden. Hier ist die Annahme, dass die Arten, die eine größere Zahl von Ressourcen nutzen können oder Arten, die Ressourcen nutzen, die häufig sind, häufiger sind als Arten, die nicht dazu in der Lage sind. Neben der Methode der Berechnung von Nischencharakteristika entlang von Umweltgradienten, beschäftigen wir uns auch mit der Nischenberechnung mittels der direkten Nachbarpflanzen einer Zielart. Hier gilt, dass seltene Arten mit wenigen und häufige Arten mit vielen unterschiedlichen Arten gleichzeitig auftreten.

Im ersten Teil der Arbeit interessieren uns die Reaktionen von Arten auf veränderte Umweltbedingungen infolge des Klimawandels. Hier konnten wir zeigen, dass sowohl die Zunahme von Stickstoff als auch Phosphat im Boden der Grund für die Häufigkeitsveränderung vieler

Arten war. Außerdem zeigte sich, dass Arten gleichermaßen entlang eines räumlichen sowie zeitlichen Gradienten reagierten, was die Anwendung von Raum-statt-Zeit-Daten (space-for-time substitutions) stützt.

Es wurde viel diskutiert, ob methodische Probleme der Hauptgrund für den Zusammenhang der Gebietsgröße einer Art mit ihrer Nischenbreite ist. Wir konnten jedoch zeigen, dass ungleiche Probennahme den Zusammenhang zwar verstärkt, aber nicht die alleinige Ursache ist – auch bei gleicher Probengröße für alle Arten fanden wir einen signifikanten Zusammenhang der Gebietsgröße mit der Nischebreite und -position. Fasst man alle Ergebnisse, die wir über den Zusammenhang der Gebietsgröße einer Art mit ihren Nischencharakteristika gewonnen haben zusammen, kann man diese Schlussfolgerungen ziehen:

1) Wird die Nischenbreite einer Art mit ihrer Nischenposition sowie der Verfügbarkeit von passenden Habitaten in einen Parameter (Verfügbare Nischenbreite) zusammengefasst, so erweist sich dieser Parameter als der beste für die Vorhersage über die Seltenheit einer Art. Die Daten, die für diese Berechnung nötig sind, sind allerdings kaum verfügbar.

2) Nischenbreite sowie die Toleranzlimits basierend auf Boden pH sind gute Alternativen zur Vorhersage der Gefährdung von Arten, wenn die Datengrundlage nicht zur Berechnung der Verfügbaren Nischenbreite reicht.

3) Die Berechnung basierend auf dem gemeinsamen Vorkommen mit anderen Arten funktioniert ebenfalls gut und ist vor allem deswegen sinnvoll, weil eine Menge Vegetationsaufnahmen zur Verfügung stehen, diese jedoch nicht mit Umweltdaten verknüpft sind.

Zusammenfassend konnten wir zeigen, dass die Breite an bestimmten Ressourcen, die eine Art nutzen kann, sowie ihre Toleranzlimits im Bezug auf Umweltfaktoren, gute Vorhersagen über die Seltenheit von Arten in einem Gebiet zulassen. Außerdem sind wir der Meinung, dass die Nischencharakteristika aus dieser Studie Leitlinien für den praktischen Naturschutz sein können, vor allem dann, wenn es um die Wiedereinbürgerung von Arten geht. Dies ist gerade in der heutigen Zeit der globalen Umweltveränderungen eine sehr wichtige Aufgabe, um die Biodiversität des Planeten zu erhalten.

Chapter 1

Introduction

Rare and common species and their range sizes in Germany.
Left (from top to bottom)*:* Caltha palustris *(20.04.2014),* Holcus mollis *(02.07.2013) and* Phyteuma nigrum *(12.06.2013).*
Middle (from top to bottom)*:* Platanthera chloranta *(18.06.2013) and* Lunaria annua *(20.04.2014).*
Right (from top to bottom)*:* Pedicularis palustris *(12.06.2014),* Pulsatilla vulgaris *(26.06.2009) and* Lysimachia nemorum *(19.06.2012).*
All pictures taken by A. Pannek, distribution maps taken from Bettinger et al. (2013)

General introduction

The explanation of the distribution and abundance of species on Earth as well as the analysis of species-environment relationships have always been a central issue in ecology, the science relating organisms to their environment (Guisan & Zimmermann, 2000; Hoef & Boveng, 2007). Indeed, plant species' responses along environmental gradients have attracted the interest of vegetation scientists for a long time (Ferrer-Castán *et al.*, 1995), with renewed attention in recent years. This is not surprising, because, apart from its prime importance as a research tool in autecology (Guisan & Zimmermann, 2000), the knowledge about the requirements of species is vital in times of global change. Detailed information on the responses of single species can be used, for example, in conservation biology when managing biodiversity, allowing to find previously unknown populations or to define suitable areas for reintroductions or translocations (Barry & Welsh, 2002; Guisan *et al.*, 2006; Townsend, 2006; Richardson & Whittaker, 2010). Species' requirements are of interest also in species invasion studies (Franklin, 2011) as well as for global change forecasts (Araujo & New, 2007). Moreover, without knowing the ecological optima and limits of species, it is not possible to predict how the ongoing changes in our environment will influence the distribution and dynamics of species. The old puzzle of ecology of "why one species ranges widely and is very numerous, and another allied one has a narrow range and is rare" (Darwin, 1859) has not sufficiently been answered so far, with many uncertainties remaining (Gaston, 2009). This thesis aims to shed some light onto this topic.

Niches – the most influential concept in ecology[2]
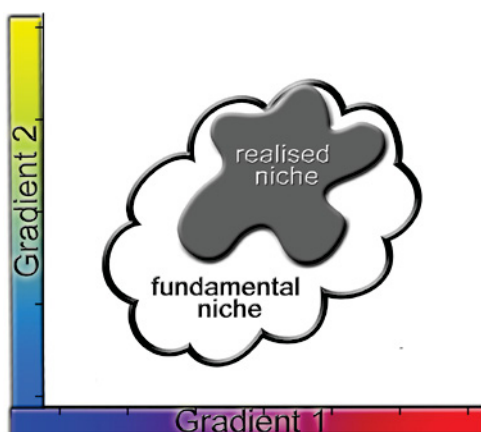
Figure 1.1 *Graphical explanation of the fundamental and realised parts of the niche sensu Hutchinson (1957).*

The niche concept has re-emerged over the past decade as a major focus in the ecological, conservational and global change literature (Sax *et al.*, 2013), since it offers a way of characterizing central ecological features of species (Brown, 1995; Beaugrand & Helaouet, 2008), which are often used in species distribution models (SDM). Although the concept of the niche is used in many ecological studies, it is still regarded as one of the "most confusing but yet important topics in ecology" (Root, 1967), and in a recent review it has even been entitled "the dark matter of ecology" (Turnbull, 2014). The most in-

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[2] Clavel *et al.* (2010)

fluential definition of the niche comes from Hutchinson (1957), stating that the niche of a species is a n-dimensional hypervolume of ecological variables among which a species is able to maintain a viable population. One can divide the niche into its fundamental part, describing the basic requirements and tolerances of a species, and the realised response in the presence of competition, which can actually be observed in nature (Figure 1.1; Hutchinson, 1957).

Even though the concept of the niche appears to be straightforward, the calculation of niche characteristics is not simple. The niche includes different features that can potentially be measured, especially the niche breadth or niche width, describing the range of resources a species is able to exploit (Brown, 1984), and the niche position, defining the optimum (or optima) in the response curve of a species. Statistical artefacts, however, can bias the calculation of these characteristics. First, when sampling, common species are usually found more often than rare ones, which might lead to an overestimation of the niche breadth of common species, simply because by chance, these are detected in more different habitats (Gaston, 1994b). Second, when comparing different species with each other, it is assumed that closely related species are more similar than distantly related ones and therefore, when working with species, appropriate statistics should be used to correct for phylogeny (Harvey, 1996). Only few studies have paid attention to these biases (e.g. Burgman, 1989; Kolb *et al.*, 2006; Luna & Moreno, 2010).
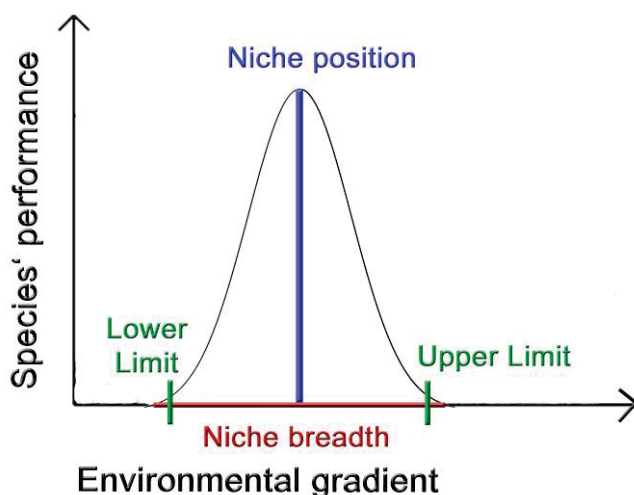
Figure 1.2 *Niche characteristics most often used in this thesis: Niche position (blue), niche breadth (red) and limits (green).*

The niche characteristic most often calculated and used is the optimum of a species (Figure 1.2, blue line; ter Braak & Looman, 1986; Entling *et al.*, 2007; Peppler-Lisbach, 2008), most likely because it is usually easy to estimate from measurements, can be replaced by indicator values when no measurements are available (e.g. Ellenbergs indicator values for Europe; Ellenberg *et al.*, 2001; Lawesson, 2003) and generally has been shown to be ecologically important (Bartelheimer & Poschlod, 2014). Niche breadth (Figure 1.2, red line), is another parameter often encountered, as it describes the range of resources a species can utilise (e.g. Williams *et al.*, 2006; Botts *et al.*, 2013; McCauley *et al.*, 2014).

Equally important, but often neglected, is the threshold of existence, or limit, of a species (Figure 1.2, green line). Limits can be critical for understanding species needs, as they offer information on the minimum or maximum requirements / tolerances of a species concerning a specific resource (Ficetola & Denoël, 2009). This is especially crucial for the conservation of species in changing environments (see below), since the gradual shifts in abiotic conditions we are currently experiencing (Dubuis *et al.*, 2013) may lead to situations where the tolerance limits of species are exceeded (Loreau *et al.*, 2001). Furthermore, a clumping of the limits at a specific point along the environmental gradient indicates whether all or a majority of species react in a similar way to the studied factor (Dale, 1988). The question whether the limits of species clump (meaning that species drop out or appear simultaneously) or whether they are independent of each other is in the centre of an old controversy between the community-unit hypothesis suggesting that limits are clumped at specific points along the gradient (Clements, 1916), and the individualistic hypothesis claiming independent distributions of upper and lower limits along the gradient (Gleason, 1926). Of course, there are more possible patterns than those two and a negative answer to one hypothesis does not necessarily imply support for the other (Shipley & Keddy, 1987; Minchin, 1989).

Responses and niches in the face of global change

Changes in the planet's biotic environment have always substantially affected its biodiversity (Chown & Gaston, 2008). However, the world's ecosystems are presently subjected to unprecedented rates of change, mainly due to an increasing domination of all ecosystems by humans (Vitousek, 1994; Pimm *et al.*, 1995; Sala *et al.*, 2000; Loreau *et al.*, 2001). The chief anthropogenic threats responsible for the current extinction crisis are habitat loss, habitat fragmentation, pollution and climate change (Sala *et al.*, 2000; Millennium Ecosystem Assessment, 2005). These also form the background for the necessity to model the future responses of species and for the renewed interest in the niche theory that had almost been forgotten in the late 1970ies and 80ies (Wiens *et al.*, 2009).

Habitat alterations have been recognised as the main driver of plant species decline in Central Europe. The destruction is mainly caused by the conversion of natural ecosystems to agricultural and urban lands, leading to a loss of natural habitats and to habitat fragmentation (Honnay & Jacquemyn, 2007). Among others, these transformations in land use create barriers for species movements. It has even been stated that many species now live in "island-like conditions" (Holt, 1990). For many already endangered species, this is especially crucial,

since they often have low dispersal abilities and are not able to cross the large distances necessary to reach the next suitable habitat space (Honnay *et al.*, 2002). It is predicted that habitat loss will go on and remain to be the most dominant threat, as the transformation of natural landscapes is not showing any indication of slowing down (Baillie *et al.*, 2004).

Another key factor in environmental change is the increasing amount of nutrients being released into the ecosystems, especially of nitrogen and phosphorus as macro-nutrients, the availabilities of which are still rising (Vitousek, 1994; Bobbink *et al.*, 1998; Falkowski *et al.*, 2000; Galloway *et al.*, 2008). Another factor is the concentration of greenhouse gases in the atmosphere. The CO_2 concentration, for example, already exceeds the pre-industrial levels by about 40% (Intergovernmental Panel on Climate Change, 2014). This, together with the raise of other greenhouse gases (e.g. methane), has resulted in a general change in climate, with rising temperatures, modified precipitation regimes and differences in other means and variances of climate (Thuiller, 2007).
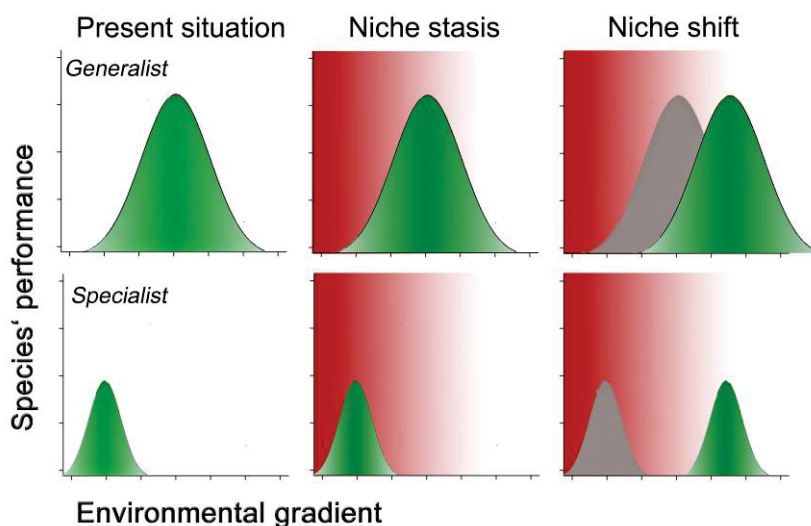
Figure 1.3 *In the face of climate change (red background), species can respond either by staying where they are (niche stasis) or by shifting their niches. In both cases, generalists (upper panels) have a higher chance of "finding" suitable habitats than specialists (lower panels) due to their larger niches.*

Whether species will be able to avoid extinction in the face of the previously mentioned global changes, depends on their response patterns. One hypothesis claims that the niche of a species will remain relatively stable over time and space (niche stasis; Peterson *et al.*, 1999; Ozinga *et al.*, 2009). In a changing environment, this would mean that the suitable habitat space for many species is drastically reduced. For species with small niches, this might mean that, in currently occupied areas, suitable habitats will no longer be available (*cf.* Figure 1.3, niche stasis). Under the assumption of niche conservatism, however, species should be able to track the changes via niche shifts (Wiens & Graham, 2005; Lenoir & Svenning, 2015). Here as well, broader-niched species have an advantage compared to smaller-niched ones, because the extent of the necessary shift is smaller (*cf.* Figure 1.3, niche shift). For a review on the processes of niche shift and stasis, see Pearman *et al.* (2008). Moreover, rare species

are often habitat specialists and slow dispersers, making it even harder for them to find suitable habitat patches and to reach these patches in highly fragmented landscapes (Thuiller *et al.*, 2005; Dullinger *et al.*, 2012; Casazza *et al.*, 2014). However, as the environmental changes are occurring more rapidly than any natural processes observed in the history of the Earth (Vitousek, 1994; Tilman & Lehman, 2001; Smart *et al.*, 2006), it is unknown which species will be able to shift fast enough or alternatively will have enough adaptive ability to survive in the novel situation. Species not able to react accordingly therefore face the risk of extinction. The consequences this will have on ecosystem functioning and services remain uncertain (Foley *et al.*, 2005; Smart *et al.*, 2006). Therefore, understanding how these drivers have led and are still leading to biodiversity loss and what actions can be taken to mitigate these effects are among the most important tasks of ecology today (Chown & Gaston, 2008).

Macroecology

One way of increasing the understanding of the consequences of environmental change and of broadening the knowledge of ecology is to use the macroecological perspective of taking "one step back for a distant view" (Brown, 1995).

Macroecology, as a research area in ecology, is concerned with detecting and explaining relationships between the distribution of species and their environment, searching for explanations of both the abundances of single species at local sites and of the variation in species' range sizes across the globe (Gaston & Blackburn, 1999). Macroecology differs from most other ecological research in that way that it considers broad spatial and temporal scales with an emphasis on the analysis of shapes and

Figure 1.4 *Number of macroecological studies published in each year between 1989 and 2014. Data from a search of the Web of Science for all journal articles including the term "macroecol*"on 06.01.2015.*

boundaries of statistical patterns (Brown, 1995; Gaston & Blackburn, 2000).

Although the idea of macroecological research dates back to the beginning of the nineteenth century (Smith *et al.*, 2008), it can be considered a recent field in ecology (Gaston & Blackburn, 2000); only in 1989, the term "macroecology" was introduced by Brown and

Maurer (1989). The authors formally described the top-down approach used by macroecolo-gists to develop an understanding of the ecological world. Overall, the field is still gaining in importance (Figure 1.4), since only large-scale research adequately addresses many of the im-portant conceptual and applied issues in ecology (Brown, 1999). Due to the unprecedented ways modern humans are changing the world, macroecological studies present an ideal way to address key global change issues, since these cannot be sufficiently tackled by small-scale ecological experiments (Brown, 1995; Kerr *et al.*, 2007; Smith *et al.*, 2008). Indeed, the scales used in macroecology largely preclude the application of manipulative experiments, while natural experiments can be explored to study macroecological patterns (Gaston & Blackburn, 2000). Therefore, to address the problems of environmental change and decreasing biodiver-sity, it is worthwhile to apply studies that sacrifice the precision of small-scale experiments in order to see the bigger picture behind (Brown, 1995), which is exactly the reason for the in-creasing interest in macroecological research today.

The disadvantage of macroecological studies with its broad scales and non-experimental ap-proaches is similar to that of any observational study: cause and effect are not easy to disen-tangle (Brown, 1995). The solution, however, is to test whether the patterns change when the conditions change. In other words, spatial relationships should be consistent in time if they are true (Kerr *et al.*, 2007). Interestingly, many ecological patterns that are expressed over time are also observed over space (Blackburn *et al.*, 1998), as illustrated in Figure 1.5. Moreover, the patterns that are most important on large spatial scales are also those most relevant on large temporal scales (Willis & Whittaker, 2002).

Figure 1.5 *Strength of the influence of different biotic and abiotic factors on species distribution depending on scale (cf. Willis & Whittaker, 2002; Pearson & Dawson, 2003).*

In general, broad-scale patterns are mostly influenced by climatic factors, while edaphic patterns play major roles for the regional to local distribution of species (Brändle & Brandl, 2001; Pearson & Dawson, 2003). Emerging from these findings is the insight that great varieties of macro- and micro-environmental factors over different spatial and temporal scales determine where a species occurs (Willis & Whittaker, 2002; Gaston & Fuller, 2009). Although there is growing agreement that edaphic factors are essential for a detailed prediction of species occurrences (Bertrand *et al.*, 2012; Dubuis *et al.*, 2013; Thuiller, 2013; Beauregard & de Blois, 2014), many species distribution models still rely solely on climate variables, often because of a limited availability of edaphic variables over broader scales (Bertrand *et al.*, 2012; Dubuis *et al.*, 2013).

A toolbox for studying species' responses

Regression techniques for relating species' responses to environmental conditions

Currently, there is no best practice for modelling the environmental niche of species (Austin, 2007), but many methods have been proposed (for reviews, see Guisan & Zimmermann, 2000; Elith *et al.*, 2006; Leathwick *et al.*, 2006). Among these, regression techniques are most often applied to characterise the relationship between species and their environment. In the simplest case, the regression coefficient can be taken as an indicator for the increase or decrease of species' abundance along a gradient. However, in changing environments, it is even more informative to learn not only about the species' general responses, but also about their tolerances and limits.

The traditional linear regression approach is based on the assumption of Gaussian response curves along environmental gradients (Gauch & Whittaker, 1972; Whittaker *et al.*, 1973; Austin, 1985; Austin & Meyers, 1996). In the last decades, however, counter-evidence was gathered and scientists started to agree that unimodal responses of species to environmental gradients are rare and that the realised niche may have various shapes (Minchin, 1989; Austin & Meyers, 1996; Bio *et al.*, 1998; Oksanen & Minchin, 2002). Therefore, alternative modelling procedures that can cope with this non-linearity of responses have become popular. The most prominent ones are Generalised Linear Models (GLM), which provide several useful statistical features (Lawesson & Oksanen, 2002), as well as Generalised Additive Models (GAM; Hastie & Tibshirani, 1987), as their non-parametrical extension, or Huisman-Olff-

Fresco (HOF) models (Huisman *et al.*, 1993), as a parametric answer to complex species' responses.

Statistical analyses of the non-parametric models, however, are highly challenging. Standard tools are only available for parametric models, and GAMs have so far only been interpreted visually (Lawesson & Oksanen, 2002; Heikkinen & Mäkipää, 2010). Furthermore, GAMs struggle with the problem of over-fitting, which is a huge drawback for their usage. The HOF models, first introduced by Huisman *et al.* (1993) as a set of five hierarchical models with increasing complexity, form a compromise between the extremes. Although not as flexible as GAMs, they provide the opportunity of calculating ecologically important parameters (e.g. optima, niche breadths, limits) and of statistically testing for the shapes of the response curves (e.g. Lawesson & Oksanen, 2002). In a recent paper, Jansen and Oksanen (2013) expanded these models to encompass seven different types (eHOF), from simple linear responses to bimodal skewed ones, keeping the balance of a good data fit *vs.* an ecological interpretability of the models and providing a straightforward way of analysing species niches (Jansen & Oksanen, 2013).

Space-for-time substitutions

Another approach in ecology that as well uses the spatial variation of environmental factors across sites is the so called "space-for-time substitution". Although initially used for the study of succession, this approach has increasingly been applied to infer potential effects of anthropogenic factors on natural ecosystem dynamics (Pickett, 1989; Fukami & Wardle, 2005). While the best technique for learning about the impacts of environmental change would be to compare historical datasets with more recent ones, pre-impact records with environmental measurements from known locations are sparse or non-existent. Therefore, other methods need to be considered, one of them being the space-for-time substitution. Here, distant sites differing with respect to a factor of interest (such as nitrogen deposition), but otherwise similar environmental conditions, are compared to infer about the effects of this factor. The approach has, for example, been used to examine the biological impact of acid deposition (Pickett, 1989) or nitrogen deposition (Stevens *et al.*, 2010), and has generally been widely applied for studying long-term phenomena in ecology (Pickett, 1989). One drawback when using space-for-time substitutions is that it is not possible to control for non-target variables (Stevens *et al.*, 2009; 2011). Moreover, without a validation with data using other methods, it remains unclear whether the patterns found really reflect what has been happening in the past (Johnson & Miyanishi, 2008; Walker *et al.*, 2010).

Resource based and co-occurrence based methods
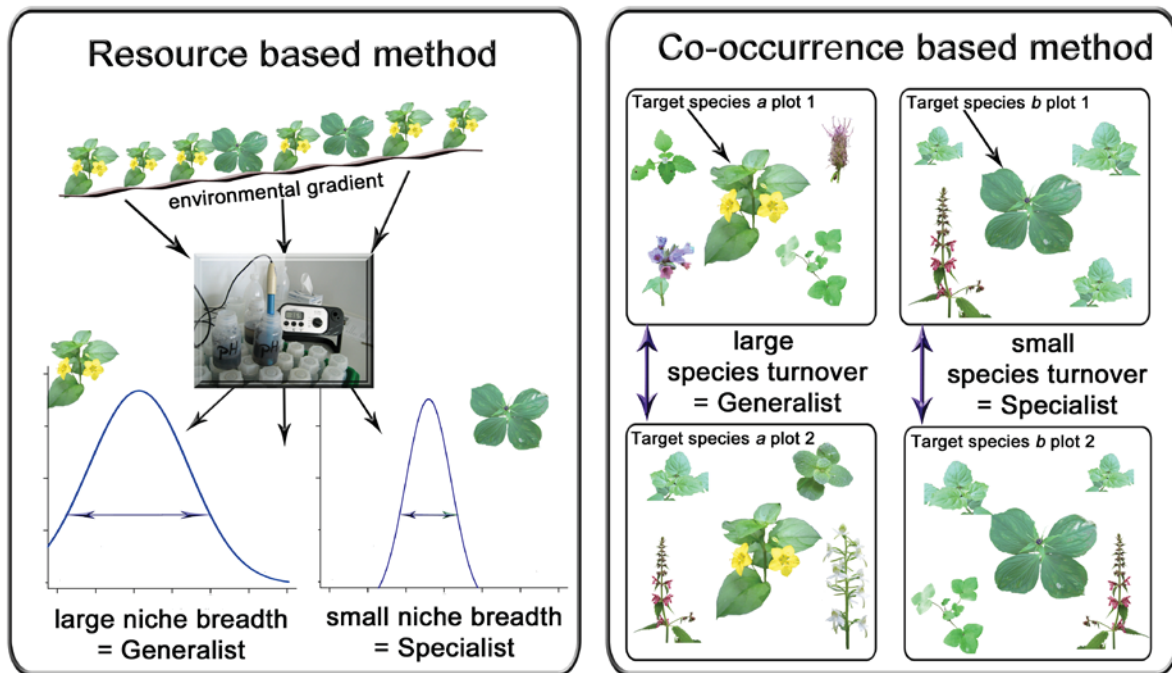
Figure 1.6 *Graphical explanation of the resource based and co-occurrence based methods of estimating species' niches. The resource based method determines niche breadth as the response of a species along environmental and resource gradients (e.g. soil pH or light), while the co-occurrence method calculates the niche breadth based on the co-occurrence of species, using a turnover index among plots. This method assumes that generalists co-occur with many different species, while specialists will likely be associated with few specific neighbours.*

Traditionally, niches were quantified based on measurements of species' performance along environmental gradients, describing the range of resources a species can exploit (Whittaker, 1956; Underwood, 1978; Krebs, 1994). When a species is able to utilise many different resources or resource states, it can be regarded as a generalist, the opposite being true for specialists (Figure 1.6; Brown, 1984). For example, Wamelink *et al.* (2014) for the Netherlands found that, while *Agrostis canina* tolerates a wide range of pH values (= generalist), *Allium oleraceum* has specific demands on soil pH (= specialist). In a study about niche breadths of breeding birds in Britain, species were classified as specialists or generalists depending on the number of differing habitat types they occurred in (Gregory & Gaston, 2000).

All techniques of studying species responses introduced so far are based on the quantification of resources. This traditional approach, however, has the drawback that there is a myriad of direct and indirect environmental variables to choose from that could be of relevance for the species. Their final selection often depends on expert insight and awareness of ecological processes as well as on the measurability (or general availability) of the factors in question (Austin & Meyers, 1996; Fridley *et al.*, 2007). Moreover, a species can theoretically be a spe-

cialist on the measured gradient, but a generalist on all non-measured ones (Gaston *et al.*, 1997; Clavero & Brotons, 2010). However, species only occur at sites with conditions that they are adapted to, and all species occurring with them are adapted to occupy similar niches. There is thus no random collection of species at any given site, but an assemblage at a site is characteristic for the conditions present (Bell, 2001). Another option is therefore the calculation of niches based on co-occurrence data, which was proposed by Fridley *et al.* (2007) as an alternative of calculating niches without an a-priori selection of an environmental gradient underlying the distribution pattern. Here, it is assumed that, over a certain number of sample plots, a generalist species occurs with many different species while a specialist has only few direct neighbours (Figure 1.6). Therefore, a turnover-index among plots can be used to measure the extent of habitat specialisation (Fridley *et al.*, 2007). This has the advantage that no environmental measurements are needed. Moreover, the multidimensionality of niches is taken into account (Fridley *et al.*, 2007; Manthey *et al.*, 2011).

In the end, no matter the precise choice of methodology, there is agreement that it is important to obtain realistic pictures of the responses of species, because a failure to do so is one of the causes for inefficient predictions of species' distribution, which is of huge practical concern (Austin & Meyers, 1996). Even though niches are "frustrating" (Turnbull, 2014), they are a central part of ecology and therefore a continuous effort should be maintained to quantify and better understand them.

Species' responses and niches in relation to measures of rarity

About 70% of all plant species on Earth are estimated to be endangered (Baillie *et al.*, 2004), and therefore more prone to extinction than more common species (Pimm *et al.*, 1988; Gaston, 1994b). To improve the effectiveness of conservation efforts, a better understanding of the needs of species is required (Baillie *et al.*, 2004). One way of doing so is to relate species' niche characteristics to measurements of endangerment, to be able to understand how species react to specific environmental gradients and changes in their environment. Here, our first expectation (Figure 1.7a) was that a species with a higher level of endangerment according to the IUCN Red List criteria for threatened species (IUCN, 2012) would have a smaller niche than a non-endangered species. Using these criteria has the advantage of getting a confirmation of how tolerant species with different levels of threat are in relation to specific environmental factors.
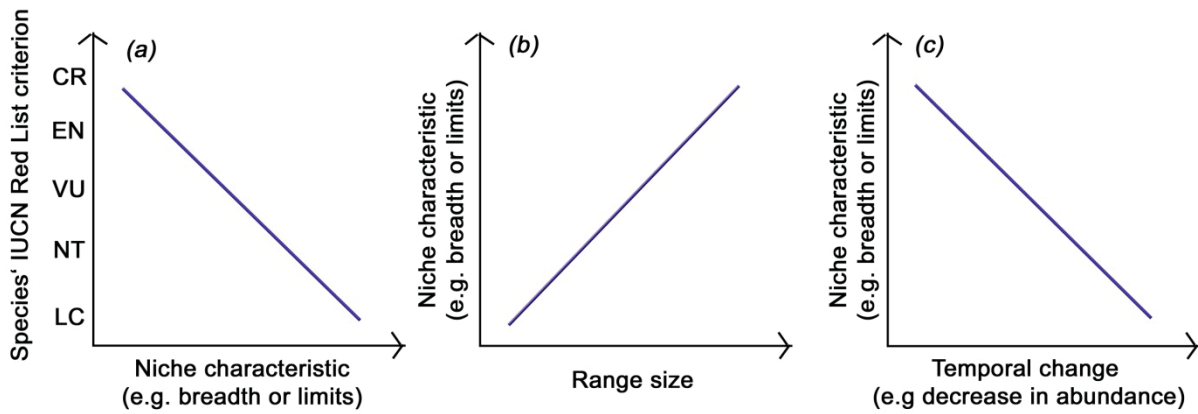
Figure 1.7 *Expected relationships between measured niche characteristics of species and* (a) *species' IUCN Red List criteria (CR = critically endangered, EN = endangered, VU = vulnerable, NT = near threatened, LC = least concern),* (b) *their range size, or* (c) *their temporal change in range size.*

Not all species occurring in a region can be found everywhere. In fact, there are widely and narrowly distributed species and ones in-between, with a fundamental question of macroecology asking for the reasons behind these variations in range sizes. Range size can be estimated in two ways: either as "extent of occurrence", being the area which lies within the outermost geographical limits (e.g. longitude to latitude) over which a species can be found, or as the "area of occupancy", quantifying the area within the geographical limits where a species is actually present (e.g. counting grid cells). In contrast to the extent of occurrence, the area of occupancy does not consider the parts of a species' range that are uncolonised or unsuitable (Gaston, 1991). While both measures have their merits, the area of occupancy is the measure of choice in most ecological and conservation studies, because it is a more accurate representation of the spatial abundance of a species (Gaston, 1994a; Blackburn *et al.*, 2006).

The reasoning behind the use of range size as an indicator of a species' threat level is that, according to Brown (1984), species being able to utilise a wider range of resources should be more widespread than species being specialised on specific resources (Figure 1.7b). Moreover, range size has been recognised as a strong predictor of the extinction risk of species, playing a key role in categorising species according to the IUCN Red List of threatened species (IUCN, 2012). Range size measures are available for different spatial scales. In this thesis, we use estimates from the Weser-Elbe region (Cordes *et al.*, 2006), Lower Saxony (Garve, 2007), Germany (Bettinger *et al.*, 2013) as well as Europe (Hultén & Fries, 1986). This has the huge advantage that we are able to examine which environmental variable might be most important for specific species on different spatial scales.

Instead of using range size *per se*, it is also possible to calculate the change in range size (range contraction or expansion) a species underwent in the past and to relate this measure to the niche characteristics of species (Figure 1.7c). Here, it is possible to either apply old distribution maps and compare them to newer ones or, for specific areas, use expert opinions on the increase or decrease of species' ranges over time.

Open questions

Considering all plant species in the world, about a third are classified as "rare" (Dirzo & Raven, 2003), being characterised by restricted geographic ranges, small ecological niche breadths and small population sizes (Gaston, 1994b). Understanding the requirements of species is therefore of obvious relevance for biodiversity conservation (Rannap *et al.*, 2009). However, even with the awareness that rare species will be affected the most by the changing environment, knowledge about ecological optima and tolerances of single species is still largely missing. Moreover, there is a cavalcade of niche characteristics available, with different methods for extracting them. Here, studies are necessary to provide guidelines on which environmental factors are most relevant, i.e. which niche characteristics best determine the rarity or commonness of species.

In how far the rarity and vulnerability of species to environmental changes is related to or explained by their life-history traits is another field of research with many open questions remaining (but see for example Verheyen *et al.*, 2003; Suding *et al.*, 2005). Even in fields where much research has been conducted, e.g. regarding the relationship between niche breadth and range size of species (for reviews, see Gaston *et al.*, 2000; Borregaard & Rahbek, 2010; Slatyer *et al.*, 2013), definite answers are still missing, mostly because of the challenge of successfully overcoming methodological biases and disentangling possible explanations.

In addition, from an applied point of view, it seems to be unwise to base all predictions of a species' future distribution on climate data alone (see, for example, Thuiller *et al.*, 2005), while factors being more important at the regional or local level, like edaphic variables, are mostly being neglected. Whereas climate models might be able to predict the broad future ranges of species, they are not able to predict where exactly a species will occur due to missing small-scale information, especially about soil factors (Coudun *et al.*, 2006).

General thesis framework and objectives

Summarizing the above, it becomes clear that our ecosystems are undergoing drastic changes affecting species' distributions. This thesis aims to examine species requirements, niche characteristics in relation to (changing) environmental gradients and the relation of niche parameters to species' range sizes or their rarity. Studies were conducted in two habitat types, both being heavily influenced by ongoing environmental changes: semi-natural grasslands and deciduous forests (see Chapter 2).

In particular, the major objectives of this thesis are to

1) *study the importance of species' responses for their occurrence patterns under environmental change and examine the reliability of space-for-time substitutions,*

2) *determine whether specific life-history traits are correlated with the species' susceptibility to environmental changes,*

3) *examine how well resource based estimates of niche characteristics are related to the species' range sizes, and which role statistical artefacts play in the calculation of species' niche characteristics,*

4) *study the feasibility of working with expert-selected environmental gradients and their correlation with indirect estimations of species' niches, and*

5) *examine whether optima are the parameters of choice or whether marginal habitats (limits) might be better predictors of range size than measured optima or indicator values*

Aims and outline of this thesis

After a brief introduction to the study habitats in *Chapter 2*, with the following set of research articles, I present the result of macroecological studies aimed at answering the objectives outlined above. The articles presented in *Chapters 3 to 7* use data from different spatial scales and, in the case of *Chapter 3*, from different time periods (Figure 1.8). Since they have been published in or are submitted for publication to international, peer-reviewed journals, they can be read independently from each other. In the following, a short overview of the studies is provided.

Figure 1.8 *Graphical overview of the five research articles included in this thesis concerning their spatial and temporal scales.*

The reasoning behind space-for-time substitutions is that macroecological patterns that are true over time should also be reflected in spatial patterns, i.e. differences across space. In *Chapter 3*, we compare the effects of nitrogen (N) deposition on the temporal increase or decrease of species with spatial patterns of species' abundance in relation to N deposition in semi-natural grasslands. While the temporal dataset encompasses data on the species composition from two regions (Germany and the Netherlands) over time periods of 67 and 71 years, respectively, the spatial dataset includes vegetation data from 10 countries within the Atlantic biogeographic region of Europe along an N-deposition gradient. A correlation of the results from these two independent datasets enables us to examine the reliability of space-for-time substitutions. Moreover, we were interested in revealing the different contributions of N-deposition, different forms of N and phosphorus availability on the decline or increase of species in semi-natural grasslands.

In *Chapter 4*, we test one of the most prominent macroecological patterns: the correlation between niche breadth and range size of species. The data originates from two regions in Germany - the Weser-Elbe region in the northwest of the country and the Bavarian Alps in the southeast. Considering the sampling and phylogenetic bias, we asked whether the species' niche breadth and niche position with respect to soil pH and light are related to their range

size over different spatial scales (regional to European). Moreover, we generated a measure that combines niche breadth and position with the availability of suitable habitat space, the "available niche breadth". We then tested over which scales the measured niche characteristic had the strongest impact on the commonness of species.

It has been criticised for some time that the traditional approach of estimating species' niches along gradients is biased due to the expert knowledge required to select suitable gradients. A new method circumvents this problem by calculating niches from co-occurrence data of species. In *Chapter 5*, we asked to what extent the resource based and co-occurrence based methods provide comparable results and in which way they are influenced by methodological biases. We compared niche characteristics for the same set of species based either on gradient data (niche position and breadth for pH and light and additionally available niche breadth for pH) or a co-occurrence. Here, generalists were expected to tolerate a wider range of environmental values and at the same time co-occur with many different species, the opposite being true for specialists.

Species distribution models (SDM) generally consider only climate data for their predictions of the future ranges of species. Yet, for an accurate forecast, edaphic factors need to be considered as well. Due to the ongoing changes in the environment, it is questionable whether optima are of largest interest for species survival or whether limits are more significant, because habitat loss may force species to live in ecologically marginal environments. In the opinion paper in *Chapter 6*, we argue the case for the need of better soil data in relation to plant occurrences. We use soil data from deciduous forests (soil pH) and dry calcareous grasslands (phosphorus availability) to calculate measured optima and species limits and test them as alternative niche characteristics for predicting the range sizes or threat levels of species.

When niches are determined, they are more often based on indicator values than on measurements. However, indicator values only offer the possibility to calculate optima for species, which, as we argued in Chapter 6, might become less important in environments undergoing global changes. Therefore, *Chapter 7* deals with the calculation of pH limits for deciduous forest species in two regions of Lower Saxony. Next to comparing different ways of calculating limits and their consistency across regions, we correlated them with range size to estimate the relative importance of limits *vs*. optima for the prediction of commonness and rarity of

species. Moreover, a boundary clumping of limits is being investigated to get an idea of community responses.

Chapter 8 serves as a synthesis with a brief prospect – it draws together some of the themes of the preceding chapters and gives an outlook at future research. *Chapter 9* contains all appendices

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Chapter 2

Study habitats

Top: *Traditional management of grasslands in the Weser-Elbe region. Picture taken form the family-collection of Herbert & Inge Helmke. Photographer and date unknown.*
Left: *Angela in a dry calcareous grassland. Picture taken by J. Müller, 12.06.2014.*
Right: *Deciduous forest dominated by* Alnus glutinosa *in the Weser-Elbe region (A. Pannek, 17.06.2013)*

Characterisation of studied habitats

Historically, the climate in Central Europe with its warm summers and cold winters favoured the development of forests, while grasslands were relatively rare (Sammul *et al.*, 2003), and largely confined to sites where various kinds of physical disturbance disfavoured the growth of woody plants (Pärtel *et al.*, 2005a). Still, grasslands in Central Europe have existed since millions of years, although their extent has varied greatly over time (Pärtel *et al.*, 2005a). During the periods when forests had their highest cover, grasslands were found only in refugial areas where conditions (edaphic as well as climatic) were not suitable for forest growth (Ellenberg, 1988). Today, the present climate and land-use history together have formed complex landscapes as a mosaic of different vegetation types (Jongman, 2002), accompanied by a continuing reduction of the area of natural habitats, primarily caused by changes induced by the increasing human population and its demands (Vitousek, 1994). Therefore, semi-natural grasslands and semi-natural forests are at present mainly found in locations unsuitable to agriculture (hilly terrain, shallow soils, etc.; Pärtel *et al.*, 2005c).

Forests

Forest environments offer a habitat that buffers the extremes in weather conditions, like temperature or exposure to wind (Ellenberg, 1996). They cover about 37% of the land surface of the European Union (Barbati *et al.*, 2011). The proportion of forested land in Germany is 30% (Wulf, 2003), in Lower Saxony 24.3% (Niedersächsisches Ministerium für den ländlichen Raum, 2004), but only 9.8% in the Weser-Elbe region (Wulf & Kelm, 1994) (Figure 2.1 a-c), which is thus one of the most sparsely wooded regions of the country (Wulf & Kelm, 1994). Generally, forests are considered to be among the most valuable ecosystems in terms of the provision of ecosystem goods and services (Thuiller, 2007).

In Germany, 60% of the woodlands are composed of coniferous forest and only 40% of deciduous forest, even though the latter represents the potential natural vegetation throughout the country except the highest mountains (Federal Ministry of Food, Agriculture and Consumer Protection, 2011). The reason for the dominance of coniferous forest is that especially *Picea abies* is an undemanding species and therefore intensively used for timber production in large monocultures all over the country (Härdtle *et al.*, 2004a).

Figure 2.2 gives an overview over the most common semi-natural forest types in the north of Germany.

Figure 2.2 *Characteristics of typical forest types regularly encountered in the north of Germany (cf. Härdtle et al., 2004a; Niedersächsisches Ministerium für Ernährung, Landwirtschaft, Verbraucherschutz und Landesentwicklung, 2010; Drachenfels, 2011; Federal Ministry of Food, Agriculture and Consumer Protection, 2011). All pictures taken by A. Pannek in summers 2012-2014.*

Fagus sylvatica **forests** form the potential natural vegetation in large parts of Central Europe, as *Fagus* acts as a strong competitor to most other tree species on dry to moist and acidic to base-rich soils. Light-levels at the forest floor are usually low, as the canopy intercepts a high proportion of the light. Of all wooded areas in Germany, about 15% are *Fagus*-dominated, which is about 74% of the deciduous forest area.

Quercus **forests** are mostly composed of *Q. robur* and *Q. petraea,* both very long-lived trees, often together with *Carpinus betulus*. They can be found on dry to wet, base-rich or acidic soils. In contrast to beech forests, the canopy is more open, allowing the growth of relatively light-demanding species in the understorey. Around 6% of the woodlands in Germany and 18% of the deciduous forest area are covered by oak forests.
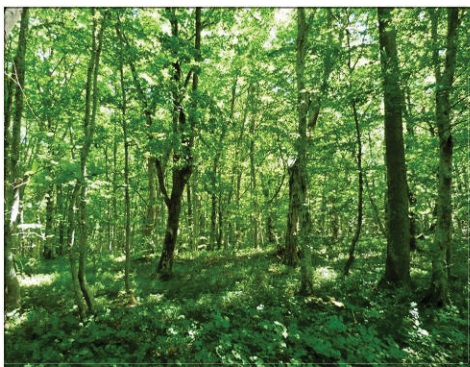
Different types of **mixed deciduous forests** are (in varying combinations) composed of e.g. *Acer* sp., *Fraxinus excelsior* and *Ulmus* sp. As they are mostly confined to very nutrient-rich sites, they have become rare due to their conversion to agricultural land. In the lowlands of northern Germany, alder-ash forests with *Fraxinus* and *Alnus glutinosa* are still relatively widespread on wet, fertile soils along creeks.

Coniferous forests, in the north of Germany usually planted, are dominated by *Picea abies* and/or *P. sylvestris,* two undemanding species growing on different kinds of soils. These forests are intensively used for timber production. More natural coniferous forests are only found at the highest elevations in the Harz Mountains (spruce) and on extremely acid soils on dry sand or in the margins of bog (pine).

There are two main types of **swamp forests** on very wet, periodically inundated soils: one with *Alnus glutinosa* on nutrient-rich, base-rich to moderately acidic soils, and a second type with *Betula pubescens* and *Pinus sylvestris* on nutrient-poor and highly acidic soils, often with *Sphagnum* sp. in the understorey.

Even though the herb layer in temporal forest ecosystems represents only 1% of the forest biomass, it encompasses 90% of its plant biodiversity (Gilliam, 2007) and has been in the focus of naturalists since ancient times, mostly for the purpose of food supply or because of medical properties of specific species (e.g. *Allium ursinum* in Germany) (Whigham, 2004; Düll & Kutzelnigg, 2011). More recently, it has attracted the attention also of ecologists, the more so as forests are especially susceptible to the threats of environmental change, because they are often found in areas with a high population density of humans, associated with an increased land use change, fragmentation, pollution and impact of invasive species (Nilsson & Ericson, 1997).
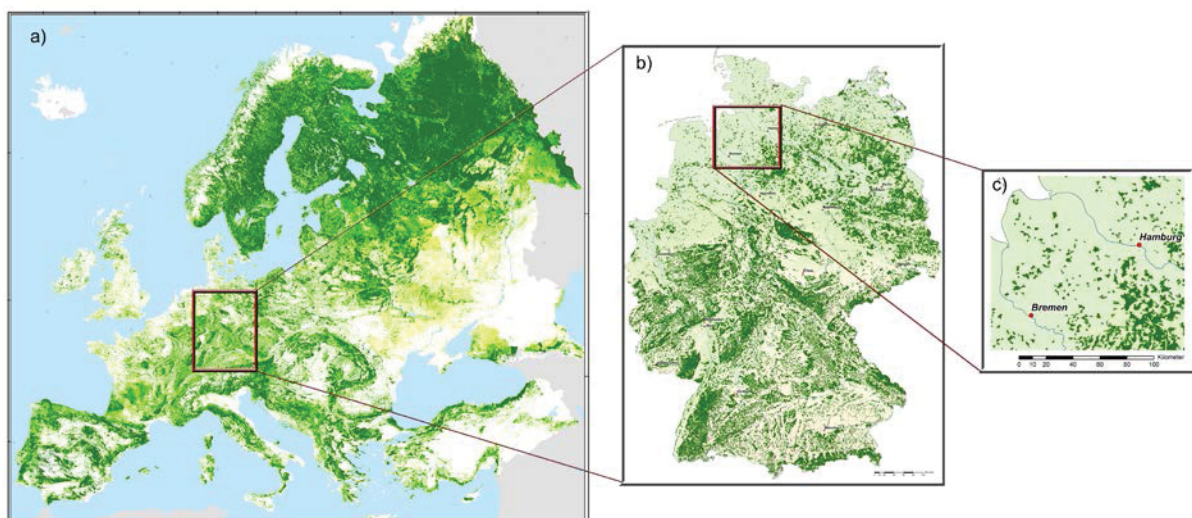
Figure 2.1 *Forest cover in a) Europe, b) Germany and c) the Weser-Elbe region. Figures adapted from The European Forest Institute (Kempeneers et al., 2011) and Bundesamt für Kartographie und Geodäsie (2014).*

Especially increasing fragmentation (Graae & Sunde, 2000; Honnay *et al.*, 2002b), going along with a higher isolation and decreasing size of the forest patches, is a major challenge for many forest species. The reason for this is the limited dispersal ability of many taxa: typical forest understorey species mostly disperse unassisted, are transported by ants or rely on vegetative reproduction (Bierzychudek, 1982; Wulf & Kelm, 1994). This low dispersal ability of many ancient forest species (species charactersing a long continuous forest history, sensu Hermy *et al.*, 1999) is largely due to the fact that, in former times, forests naturally covered large areas and therefore no long-distance dispersal was required to reach neighbouring space that was suitable for establishment (Nilsson & Ericson, 1997). Nowadays, the limited dispersal ability of many forest species is problematic, since the predicted northwards shift of species and vegetation zones due to rising temperatures might be severely hampered by the strong fragmentation of forest landscapes in Europe (Parmesan *et al.*, 1999; Honnay *et al.*, 2002a). This has, for example, already been observed for herbaceous species in the lowland

forests of France (Bertrand *et al.*, 2011), but is also an important issue in the lowlands of north-western Germany, with its highly fragmented forest cover (Kolb & Diekmann, 2004, 2005).

Soil pH and nutrient availability

Soil conditions are one of the most important factors governing the growth of plants (Thomas & Packham, 2007). Soil pH, for example, is among the main determinants of the distribution of species in an area, because acidity affects a multitude of other edaphic factors and influences especially the nutrient availability, which in turn may affect plant growth and survival (Diekmann, 2003; Tyler, 2003; Dubuis *et al.*, 2013). In the Weser-Elbe region, where most of the fieldwork for this thesis was conducted, the soils are predominantly acidic. In fact, only about 5% of today's forest soils in the area are base-rich (Wulf & Kelm, 1994). Here, there is a high positive inter-correlation between soil pH, nutrient availability and groundwater level, with dry soils being nutrient-poor and acidic and moist to wet soils being base- and nutrient-rich (Wolter & Dierschke, 1975; Härdtle *et al.*, 2004f). Geologically, the bedrock largely consists of a ground moraine with a mixture of sand, loam and clay formed by depositions from the last glacial period (Saale-glaciation; ca. 200.000 - 100.000 years ago; Wulf & Kelm, 1994). Today's soils of the area originate mainly from the

Figure 2.3 *Distribution patterns of* Phyteuma spicatum *(left) and* Phyteuma nigrum *(right) in the Weser-Elbe Region. Distribution maps adapted from Cordes et al. (2006), pictures taken by J. Müller (*P. spicatum*; 29.05.2011) and A. Pannek (*P. nigrum*; 12.06.2013).*

depositions of two moraines (Drenthe-1 and -2) with different composition (especially regarding clay and calcium carbonate contents). This difference in the raw soil materials is one reason for the specific distribution patterns of some forest species found in the area (Wulf, 1992). For example, *Phyteuma nigrum* grows only on soils originating from the Drenthe-1 moraine, while *Phyteuma spicatum* and *Hepatica nobilis* are found exclusively in areas covered by soils originating from Drenthe-2 (Figure 2.3; Cordes *et al.*, 2006).

Figure 2.4 Galium odoratum. *Picture taken by A. Pannek (03.05.2014).*

In Central Europe, plant species diversity is lower under acidic than under more base-rich conditions (Ellenberg, 1996; Diekmann & Lawesson, 1999; Dupré & Ehrlén, 2002; Ewald, 2003; Härdtle *et al.*, 2004a). Therefore, the soil acidification caused by the atmospheric deposition of nitrogen and sulphur (Umweltbundesamt, 2004; Bernhardt-Römermann & Ewald, 2006; de Vries *et al.*, 2007) is a potential problem for many species. An acidification of woodland soils has been shown among others by Falkengren-Grerup (1989), who compared the pH values of a large number of forest sites in South Sweden between two different time periods. She found significantly lower soil pH in 1984/85 compared to 1949-1970. Acidification has the consequence that the conditions become too acidic for the establishment and long-term survival of many forest plant species (Falkengren-Grerup & Tyler, 1993). The increasing aluminium availability following from decreasing soil pH (at and below pH 4.3) results in toxic concentrations for many taxa (Schulze *et al.*, 2005; Poschenrieder *et al.*, 2008). Even though the deposition of acidifying substances has decreased since about 1980 in 86% of the area of Germany, the critical loads are still being exceeded (Niedersächsisches Ministerium für Ernährung, Landwirtschaft, Verbraucherschutz und Landesentwicklung, 2010; Umweltbundesamt, 2011), causing sensitive species, like *Galium odoratum* (Figure 2.4), to gradually disappear from acidified forest sites (Falkengren-Grerup, 1986; Falkengren-Grerup & Tyler, 1992; Dierschke, 2013).

In contrast to the acidifying substances, N deposition rates are estimated to further rise in the 21st century (Dentener *et al.*, 2006; Intergovernmental Panel on Climate Change, 2014), with considerably higher deposition loads to the forest understorey than the surroundings due to the large intercepting surface area of the canopy (Niedersächsisches Ministerium für Ernährung, Landwirtschaft, Verbraucherschutz und Landesentwicklung, 2010). In Austria, for example, critical loads for nitrogen are exceeded in 94% of the forested area (Obersteiner & Offenthaler, 2006). In addition to N deposition, also the abandonment of litter removal for livestock farming and a shift in forest management from coppice and coppice-with standards to "high forest" during the last decades has further increased the nitrogen level of the soils (Glatzel, 1991; Federal Ministry of Food, Agriculture and Consumer Protection, 2011; Jantsch *et al.*, 2013). As a result, the requirements of many species might no longer be met

under the changed conditions. Therefore, the species composition is bound to change, with stress-tolerant species being outcompeted by more competitive ones being able to grow more efficiently under more fertile conditions. This floristic turnover to more nutrient-demanding species, resulting in a general homogenisation across sites, has been observed in many studies (e.g. Cordes *et al.*, 2006; Diekmann, 2010; Hédl *et al.*, 2010; Reinecke *et al.*, 2011; Umweltbundesamt, 2011; Verheyen *et al.*, 2012; Heinrichs *et al.*, 2014).

Light

Figure 2.5 *Sun flecks in a forest in the Weser-Elbe region. Picture by A. Pannek, 22.06.2012.*

Next to the soil conditions, the light environment is the second important factor for the growth and distribution of plants. In the understorey vegetation of forests, light availability is highly variable, as the canopy cover controls the quality, quantity, spatial and temporal variation of the light (Jennings *et al.*, 1999). On the one hand, radiation changes between the seasons because of foliage development and leaf fall.

On the other hand, even in summer, sun flecks (Figure 2.5) add to a high small-scale spatial heterogeneity of light (Härdtle *et al.*, 2004a). Interestingly, even among species generally occurring in closed forests (sensu Schmidt *et al.*, 2011), shade tolerance varies considerably. Whereas, for example, *Cardamine amara* has an Ellenberg light value of 7, *Oxalis acetosella* has a score of only 1, with most other species typical for deciduous forests having in-between values (Ellenberg *et al.*, 2001). Due to the increased N availability (causing the leaf area especially of *Fagus sylvatica* to increase, Leuschner, 2010) and increasing proportion of high-grown forest, light availability at the forest floor decreases. This results in a reduction of species richness due to the decline of the more light-demanding species, as it has been reported for the Weser-Elbe and the Harz regions in Germany (Diekmann, 2010; Heinrichs *et al.*, 2014). Winners of this environmental change are e.g. *Rubus idaeus* and *R. fruticosus,* both being shade-tolerant and nitrophilous (Diekmann & Dupré, 1997; Härdtle *et al.*, 2004a).

Semi-natural grasslands

Figure 2.6 *Species-rich calcareous grassland on Öland (Sweden). Picture by A. Pannek, 12.06.2014.*

Semi-natural grasslands are an important component of European landscapes (Stevens *et al.*, 2009), with their origin rooted in the forests of former times: forest gaps or open woodlands were the original habitats of many species now regarded as grassland species (Nilsson & Ericson, 1997; Dierschke & Briemle, 2002).

The climate of open grasslands is much different from that of the buffered forest interior. Trees do no longer intercept light, which means that there is a much higher intensity of direct radiation. Moreover, the variability of environmental conditions (e.g. with respect to temperature or wind) is higher in grasslands than in forests, which also influences the soil conditions: in summer, the soil is much warmer and in winter much colder than in the forest interior (Ellenberg, 1996). Data on how much area is occupied by semi-natural grasslands in Germany is largely missing, mainly because of a lack of a precise differentiation between different kinds of grasslands (Hopkins, 2009). In 2012, 13.36% of the country was covered by grasslands (here defined as vegetation dominated by grasses and other non-woody plants and generated by human usage), which is 5% less than in 2003. Reasons for this decline are mainly the intensification of farming, grassland abandonment and increased biogas production (Bundesamt für Naturschutz, 2014). In Europe, the grassland area (Figure 2.7) has decreased by 12% over the last decades. Here, the reasons for the change include altered management practices, drainage and nitrogen deposition (European Commission, 2008).
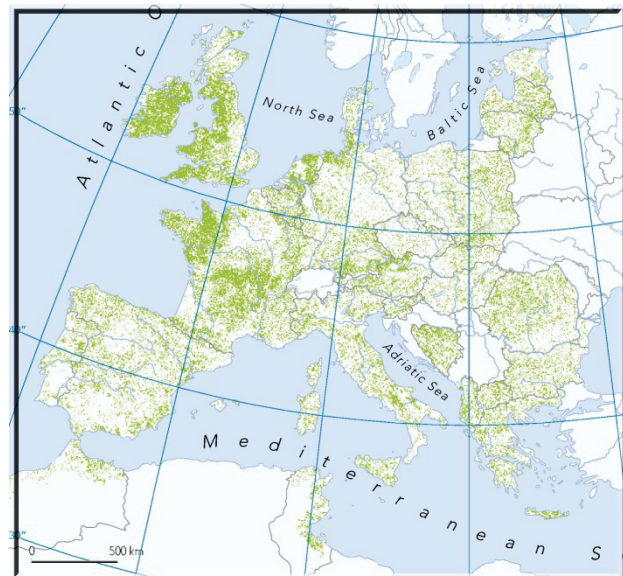
Figure 2.7 *Grassland cover of Europe. Here, grasslands are broadly defined by the EUNIS habitat classifications (Päivinen et al., 2001; EEA, 2014b) as "grasslands and lands dominated by forbs, mosses or lichens" (Schuck et al., 2002; Davies et al., 2004). Map adapted from EEA (2014a).*

Soil variables and light
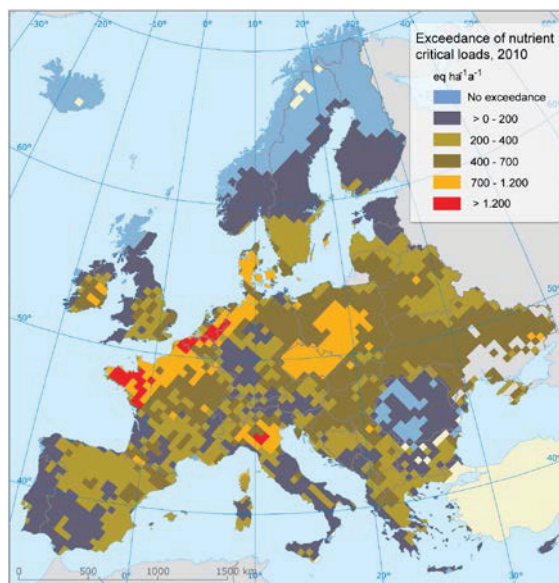
Figure 2.8 *Exceedance of critical loads in Europe in 2010. Figure adapted from EEA (2011).*

The availability of nutrients is one of the most important abiotic factors determining species composition in semi-natural grasslands (Bobbink *et al.*, 2003). In general, eutrophication, especially the increasing availability of nitrogen and phosphor in natural and semi-natural ecosystems, is one of the most severe threats to biodiversity in Europe, since it increases primary production and thereby decreases biodiversity, mainly via changes in the competitive relationships between species (Tamm, 1991). A measure of the amount and effect of deposited air pollutants is the so-called "critical load", which defines a deposition level below which no harmful effects are expected to occur to the ecosystems (Bobbink *et al.*, 2003; Bobbink, 2004; Burns *et al.*, 2008). At present, these loads are widely exceeded (Figure 2.8). In fact, in 2004, only 4% of the measured deposition loads in Germany were below this critical threshold (Umweltbundesamt, 2011). Across the globe, the planetary boundaries, defining a safe operational space for humanity, are also transgressed for nitrogen and phosphorus (Rockström *et al.*, 2009; Steffen *et al.*, 2015).

Between 1860 and 2002, the global production of reactive N increased from c. 15 to 210 Tg N year^{-1} (Galloway *et al.*, 2008), and is still expected to rise (Intergovernmental Panel on Climate Change, 2014), mostly because of growing energy and food demands (Galloway & Cowling, 2002). The availability of P has been amplified by 400% due to human activities (Falkowski *et al.*, 2000). Since both N and P are limiting nutrients, their increase likely influences ecosystems at all levels of their organization (Vitousek, 1994), although the consequences are said to be largest in the northern temperate zone (Sala *et al.*, 2000). Adding nutrients to grasslands leads to a shift from belowground competition for resources to aboveground competition for light (Tilman & Lehman, 2001). Grassland species are generally light-demanding, although some of them can also grow in open woodlands. There is therefore a huge concern regarding the shift in competition for light, because under this scenario, management is necessary for smaller-statured species to not become outcompeted by taller ones (Dierschke & Briemle, 2002).

Moreover, the deposition of N is often in the form of ammonia, the oxidation of which by nitrifying bacteria can further accelerate soil acidification (Bakker & Berendse, 1999; Roem & Berendse, 2000), even though depositions of sulphuric oxides have declined over the last decades and are now stable (Berge *et al.*, 1999; NEGTAP, 2001; EEA, 2014c). Generally, while ammonium is the dominant N form in more acidic soils, nitrate predominates under neutral to calcareous conditions (Bartelheimer & Poschlod, 2014). Since not all species are able to utilise all N sources equally well (Falkengren-Grerup & Lakkenborg-Kristensen, 1994; Falkengren-Grerup, 1995), a decrease in pH due to acidification is often accompanied by a shift of the dominant N form, which highly impacts species richness and composition (Stevens *et al.*, 2010). Generally, the combined effects of acidification and eutrophication are especially pronounced in habitats in which the soils are already relatively acidic and not well buffered, which is the case in acidic grasslands (Ellenberg, 1996; Stevens *et al.*, 2011), and may lead to a decline of characteristic grassland species adapted to low nutrient and high light availabilities (Ellenberg, 1996).

Management

Figure 2.9 *Grazing Konik horses in the Cuxhavener Küstenheide – a successful example of traditional management for the protection of species-rich areas. Picture by A. Pannek, 18.09.2007.*

Not only have the environmental conditions of many semi-natural grasslands changed, but also the area of these grasslands, especially in North-western Europe including Germany, has declined (Hopkins, 2009; Bundesamt für Naturschutz, 2014). This poses a huge problem, since a wide variety of plants, invertebrates and birds nowadays confined to European temperate grasslands are endemic and in need of protection (Bobbink *et al.*, 2003; Pärtel *et al.*, 2005c). The main reason for the areal decline of grasslands is the land use change over the last decades (Nilsson & Ericson, 1997; Jongman, 2002; Hejcman *et al.*, 2013). Interestingly, this includes two contrasting processes: on the one hand the abandonment of farming especially on low-productive land, and, on the other hand, land use intensification with the conversion of near-natural habitats into arable land exposed to fertilisation and intensive farming. In fact, many natural grasslands have been destroyed due to increased grazing from domesti-

cated livestock, herbicides or fertiliser applications (Watkinson & Ormerod, 2001). To stop the conversion of species-rich to species-poor grasslands, traditional grazing or hay making can be employed (Nilsson & Ericson, 1997; Reier *et al.*, 2005; Borer *et al.*, 2014). A successful example of using extensive grazing for nature conservation purposes in the Weser-Elbe region is the LIFE project "Cuxhavener Küstenheiden" (Figure 2.9; Niedersächsischer Landesbetrieb für Wasserwirtschaft, Küsten- und Naturschutz, 2009). The reason that these more traditional types of management practices work so well is that the animals establish open space and light for smaller-statured species, by this enabling them to persist. Moreover, the removal of biomass is essential to maintain nutrient-poor conditions, especially considering the steady N deposition to which these grasslands are subjected (Intergovernmental Panel on Climate Change, 2014).

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Chapter 3

Spatial gradient in nitrogen deposition affects plant species frequency in acidic grasslands

Pannek, A., Duprè, C., Gowing, D.J.G., Stevens, C.J. & Diekmann, M.
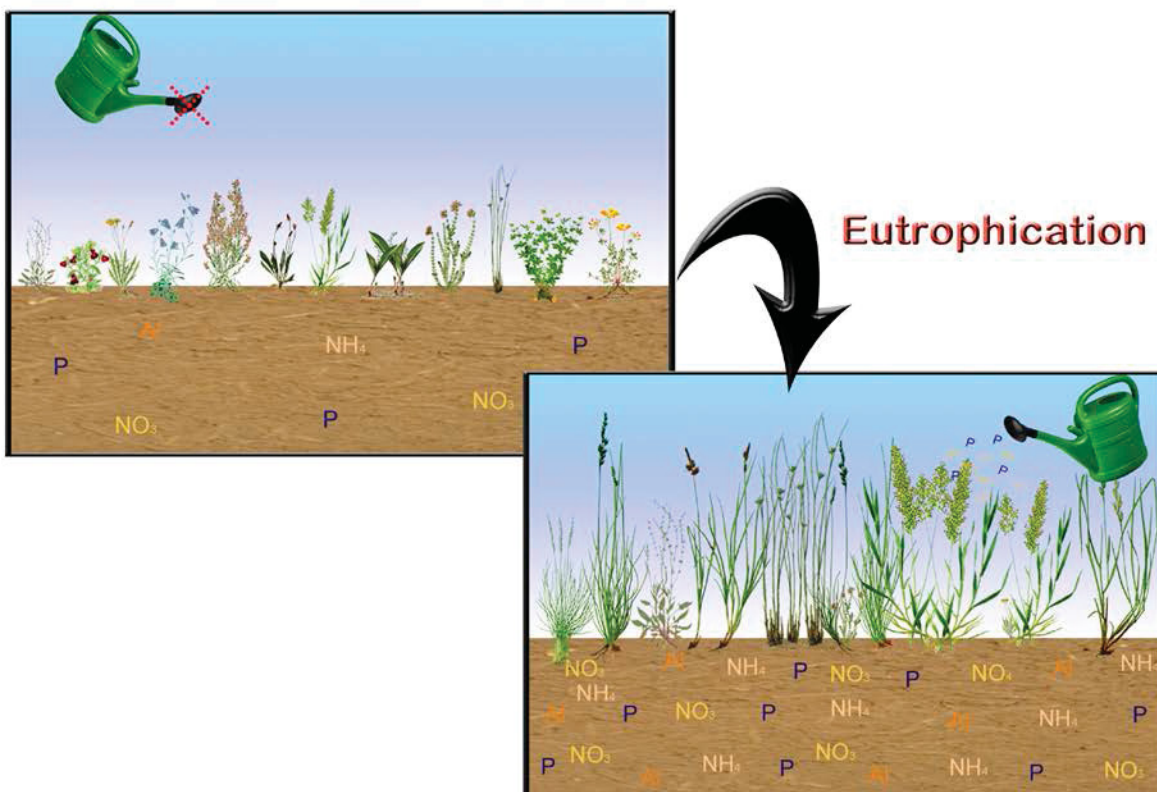
Eutrophication

Picture of the title page shows the expected (and often observed) change from a species-rich meadow to a species poor grassland due to eutrophication effects

Abstract

Anthropogenic eutrophication impacts ecosystems worldwide. Here, we use a vegetation dataset from semi-natural grasslands on acidic soils sampled along a gradient in Northwestern Europe to examine the response of species frequency to nitrogen (N) deposition, controlling for the effects of other environmental variables. A second dataset of acidic grasslands from Germany and the Netherlands containing plots from different time periods was analysed to examine whether the results of the spatial gradient approach coincided with temporal changes in the abundance of species.

Out of 44 studied species, 16 were affected by N deposition, 12 of them negatively. Soil pH and phosphorus (P) influenced 24 and 14 species, respectively, predominantly positively. Fewer species were related to the soil contents of NO_3^- or NH_4^+, with no significant differences between the number of positive and negative effects. Whereas the temporal change of species was unrelated to their responses to pH, species responding negatively to N deposition, soil P and NO_3^- showed a significant decline over time in both countries. Species that were negatively affected by high N deposition and / or high soil P, also showed a negative temporal trend and could be characterised by short stature and slow growth.

The results confirm the negative role of N deposition for many plant species in semi-natural acidic grasslands. The negative temporal trends of species sensitive to high N deposition and soil P values clearly show a need for maintaining low soil nutrient status and for restoring the formerly infertile conditions in nutrient-enriched grasslands.

Keywords

Introduction

Anthropogenic eutrophication, albeit stimulating to plant growth, has plenty of negative impacts worldwide (Güsewell, 2004; Galloway *et al.*, 2008). Nitrogen (N), for example, although essential for life on Earth (Galloway & Cowling, 2002), is forecast to be among the three major drivers of the on-going change in biodiversity (Sala *et al.*, 2000). The main reason for this is that, between 1860 and 2002, the global production of reactive N has increased from c. 15 to 210 Tg N year^{-1} (Galloway *et al.*, 2008), mostly as a consequence of increasing energy and food demands (Galloway & Cowling, 2002). This value is predicted to multiply about 2.5-fold by the year 2050 (Tilman *et al.*, 2001).

Generally, many ecosystems are N-limited and characterised by species specifically adapted to N-poor conditions (Vitousek *et al.*, 1997; Bobbink *et al.*, 1998). A general effect of N addition is that competitive species are favoured, thereby reducing the number of species that can coexist in the community (Falkengren-Grerup, 1995; Bobbink *et al.*, 1998; Roem & Berendse, 2000; Stevens *et al.*, 2010b). Another factor influencing species composition is the ratio of the deposition of nitrate (NO_3^-) vs. ammonium (NH_4^+) (Bobbink *et al.*, 2003 and references therein). Not all species are able to use these N sources equally well (Fangmeier *et al.*, 1994; Falkengren-Grerup, 1995; Ellenberg *et al.*, 2010), and it is likely that the dominance of species under certain conditions is in part due to species-specific differences in the uptake of different N forms (Weigelt *et al.*, 2005). Therefore, it is important to differentiate between NO_3^- and NH_4^+ when investigating the effects of N in the soil (Bobbink *et al.*, 1998). NH_4^+ deposition, for example, can cause local acidification near the plant roots, as the uptake of NH_4^+ mostly takes place in exchange for hydrogen ions. An increase in NH_4^+ deposition thus causes a general change in the base status of the soil (Roelofs *et al.*, 1996; Bobbink *et al.*, 2003; Horswill *et al.*, 2008), especially by mobilizing metals, mainly aluminium, one of the most potentially toxic elements for plants (Falkengren-Grerup, 1995). In contrast, NO_3^- uptake is associated with higher energy costs for the plants, but can counteract the acidification (Tamm, 1991 and references therein).

Different ways of studying the impact of N deposition and additions to ecosystems are available. One is via experimental fertilisation (e.g. Morecroft *et al.*, 1994; Phoenix *et al.*, 2012), where a pre-decided amount of the target nutrient is added to test plots over a given time. This approach has the advantage of being highly controllable, but it is unclear how representative such experiments are: in many cases, high amounts of nutrients are used over a relatively

short time span, while in unmanipulated conditions, low amounts of nutrients have been deposited over decades (Dupré *et al.*, 2010). Another way of studying deposition effects is to examine temporal trends by comparing historical with more recent data (for example, Blake *et al.*, 1999; Bennie *et al.*, 2006). A limitation to this method is the paucity of permanent plots, but an alternative is to use large amounts of data for the same regions from different time periods (Dupré *et al.*, 2010; Diekmann *et al.*, 2014). Finally, it is possible to use spatial gradients in N deposition as a space-for-time substitution (e.g. Stevens *et al.*, 2010b; Vallano & Sparks, 2013). This approach has the drawback that there is no control of non-target variables that may differ across the gradient, like climate, site morphology or other environmental drivers, which might prevent trends from being readily identified (Stevens *et al.*, 2009; 2011e).

In our study, we use a spatial gradient approach to examine the effects of N deposition on the frequency of individual species of vascular plants in semi-natural grasslands on acidic soils. Along with other types of semi-natural grasslands, these are an important component of temperate European landscapes (Stevens *et al.*, 2009), being characterised by traditional management (extensive grazing or hay production) over a long period of time, with limited application of fertilisers compared to intensively managed grasslands (Ellenberg, 1952; Ellenberg *et al.*, 2010). These grasslands currently are projected to be among the ecosystems that are most sensitive to global change (Fangmeier *et al.*, 1994; Sala *et al.*, 2000), which is a concern to nature conservation since they support such a wide variety of plant, invertebrate and bird species, many of which are rare and endangered (Bobbink *et al.*, 2003).

As previously mentioned, studies along spatial gradients face the problem of confounding factors that may distort the relationship between species occurrence and N deposition. Among the most important factors is phosphorus (P,) the availability of which has been amplified by about 400% by human activities (Falkowski *et al.*, 2000) and has been hypothesised to be as important for ecosystems as N addition (e.g. Wassen *et al.*, 2005). While the input of P into terrestrial ecosystems from weathering as well as the atmosphere is usually low (about $0.2 - 2$ kg P ha^{-1} yr^{-1}), large amounts of P are added to agricultural land by means of fertilisers (Newman, 1995; Bennett *et al.*, 2001). The availabilities of N and P in the soil are directly linked: with increased N availability, plants are able to produce more phosphatase, thereby being able to take up more P from the soil and increasing the rate of P cycling (Vitousek *et al.*, 2010; Marklein & Houlton, 2012). Studies over the past ten years have shown that P may play an important role for changes in species richness (Wassen *et al.*, 2005; Ceulemans *et al.*,

2011, 2013). Soil pH also is of large significance for the local distribution of plants (Schuster & Diekmann, 2003) and affects the availabilities of both N and P as well as the ratio between NO_3^- and NH_4^+. In grasslands on weakly buffered, already relatively acidic soils, acidification may be a major problem in terms of species diversity (Bobbink *et al.*, 2010). Although the anthropogenic emission of sulphur (SO_2) which was the major driver of soil acidification, has steadily declined over the last decades (Berge *et al.*, 1999), the process continues with the atmospheric deposition of N appearing to be an important factor (Stevens et al. 2010b). A third factor that has to be taken into account as co-variable of the relationship between species frequency and N deposition is grassland management in the form of grazing or mowing. Large areas of semi-natural grasslands have disappeared as a result of the cessation or reduction of management, and for those grasslands that are still managed sufficiently, the increased input of N is likely to have both a direct influence by changing the nutrient status of the soil and an indirect effect by altering the competitive relationships between species (Janssens *et al.*, 1998; Bennett *et al.*, 2001; Ellenberg *et al.*, 2010; Peñuelas *et al.*, 2012).

The main aim of our study was to disentangle the effects of N deposition on species frequency from those of confounding factors on a large spatial scale. Furthermore, we intended to verify our results by examining whether species that were positively or negatively related to varying N deposition along the spatial gradient were the same as those that showed an increase or decrease, respectively, over the past 70 years as revealed by Dupré et al. (2010). In addition, we aimed to correlate the species' responses to specific life-history traits. In contrast to previous studies (Stevens et al. 2010a, 2011a, b), we do not focus on total species richness, but on the responses of individual species, because only by doing so, it is possible to make predictions at the species level.

Materials & Methods

In this study, we worked with two data sets from semi-natural grasslands on acidic and nutrient-poor soils, characterised by species such as *Agrostis capillaris*, *Festuca ovina, Galium saxatile, Luzula campestris, Nardus stricta* and *Potentilla erecta* (Ellenberg, 1952; Stevens *et al.*, 2011e). Both data sets originate from material obtained in the framework of the BEGIN-project (*cf.* Stevens *et al.*, 2011b). The first data set includes recent vegetation data sampled along a spatial gradient in N deposition, while the second one comprises historical as well as more recent plots from Germany and the Netherlands compiled from the literature (*cf.* Dupré

et al., 2010). In the following, we give a short overview on how the data sets were collected and what they contain.

Spatial gradient data set

Field sampling
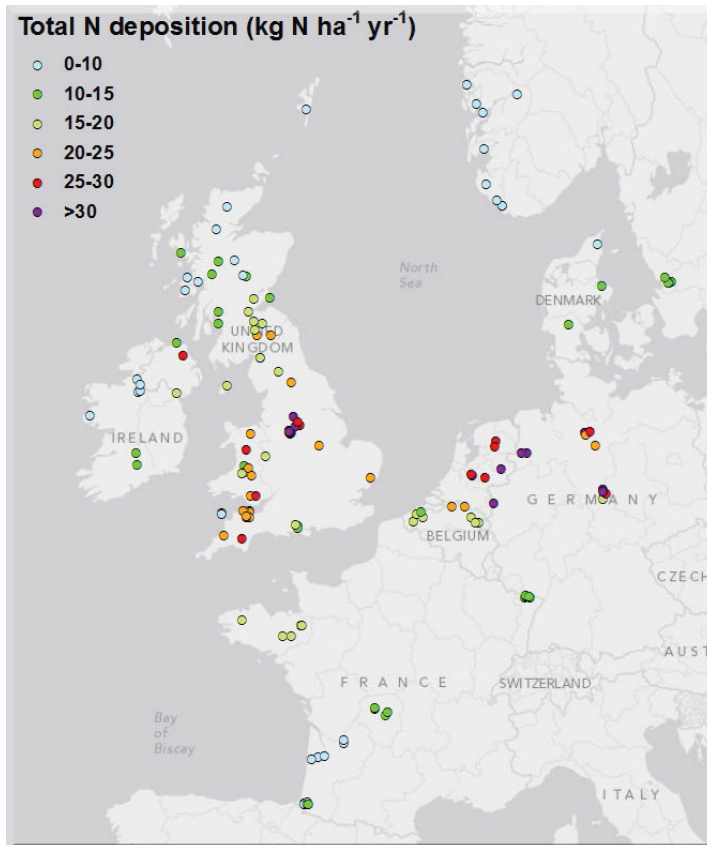
Figure 3.1 *Map of the location of the 153* Violion caninae *grasslands surveyed in the Atlantic biogeographic region of Europe. For each study site also the annual level of nitrogen deposition is given.*

Between May and September in 2002/03 and 2007, 153 acidic grasslands of the *Violion caninae* alliance were surveyed in 10 countries within the Atlantic biogeographic region of Europe, encompassing Belgium, Denmark, France, Germany, Great Britain, Ireland, Isle of Man, the Netherlands, Norway and Sweden (Figure 3.1). Although the vegetation sampling in the three study years extended over several months, it is unlikely that this distorted the data analysis because the acidic grasslands consist almost exclusively of perennial species that are visible over the completely growing season. The sites were selected to cover the range of N deposition over Northwestern Europe (Figure 3.1). To ensure the sampling of comparable sites across countries, five of 13 pre-defined indicator species (monocots: *Agrostis capillaris*, *Carex pilulifera*, *Danthonia decumbens*, *Deschampsia flexuosa*, *Festuca rubra / ovina* aggregates, *Luzula campestris* s.l., *Nardus stricta*; dicots: *Calluna vulgaris, Campanula rotundifolia, Galium saxaile, Polygala* sp., *Potentilla erecta*; bryophyte: *Rhytidiadelphus squarrosus*), which typically have a high constancy in the community, had to be present at each surveyed site. Stevens et al. (2011a) used a DCA analysis and showed that, despite the large geographical range of sample plots, there were no marked differences in community composition between the sites surveyed in the different countries. In addition, all grasslands had been unfertilised for at least 17 years and were extensively managed by grazing. Areas in the grassland sites that

were strongly affected by humans or animals or appeared to belong to other vegetation types were avoided. Within each sampling area (1 ha), five 4 m^2 plots were randomly selected and all vascular plants and bryophytes identified to the species level; species cover was estimated by eye using the Domin scale (Rich *et al.*, 2005). Overall, the data set includes 335 vascular plants, of which 44 (13%) were finally selected for this study (for selection criteria, see below). In each plot, general site descriptions were made and soil samples collected. Meteorological data were obtained for all sites from the European Space Agency's Monitoring Agriculture with Remote Sensing (MARS) unit (Monitoring Agricultural Resourses (MARS), 2009) for 10-year averages (1996-2006): Mean annual maximal daily temperature ranged from 6.8 to 18.8 °C, mean annual minimal temperature from 0.6 to 10.2 °C and mean annual rainfall from 498 to 1971 mm.

Laboratory analysis

Two topsoil samples from 0-10 cm below the litter layer were taken in each plot, bulked and thoroughly mixed to ensure homogeneity. In the laboratory, the samples were air-dried, roots and stones removed and the remaining soil ground to < 2 mm before analysis. Soil pH was measured in a 1:5 mixture of soil:de-ionised water. Nitrate (NO_3^-) and ammonium (NH_4^+) were analysed with two different methods: 68 samples from the UK were leached with 1M KCl (Ministry of Agriculture, Fisheries and Food, 1986) and analysed using ion chromatography. Other samples were shaken with 0.4M NaCl and analysed with an auto analyser. Stored soil samples from the UK were re-analysed with ion chromatography to ensure the comparability of both methods. An Olsen extraction with subsequent colorimetric determination was used to analyse plant available phosphorus (P) (Ministry of Agriculture, Fisheries and Food, 1986). For more details on field and laboratory methods, see Stevens et al. (2010b; 2011b).

Deposition models

To estimate the N deposition at each site, the best available deposition model was used, resulting in varying models depending on the country. Smaller resolution national models were used wherever possible: Germany (Gauger *et al.*, 2002), Great Britain (Smith *et al.*, 2000; NEGTAP, 2001) and the Netherlands (van Jaarsveld, 2004 and references therein), whereas the European Monitoring and Evaluation Programme (EMEP)-based Integrated Deposition Model (IDEM) (Pieterse *et al.*, 2007) was applied in all other countries. All models used similar approaches to estimate deposition and comparisons between models revealed that, for most regions, results from national approaches and IDEM were comparable. Differences were

found in areas with considerable variation in altitude. In all of these areas, national models were used. For all models, four-year averages (2000-2003) were calculated to provide a more robust estimate of long-term N input.

Historical data set

The historical data set is based on a time-series approach and covers a temporal gradient from 1940 to 2007 (Germany) and from 1936 to 2006 (Netherlands) with species occurrence data from acid grasslands of the *Violion caninae* community type (for details see Dupré *et al.*, 2010). In Germany, 392 plots were sampled and 390 species detected, while in the Netherlands, 144 plots were surveyed and 247 species found. Instead of cover scores, presence/absence values of species were used for the analysis, because different authors had used different survey methods and cover-abundance scales, and converting the data to presence/absence records ensures comparability.

Life-history data of species

To attempt to explain the responses of species to the spatial variation in N deposition, topsoil pH and soil P availability as well as to their change over time, we compiled literature data on some life-history traits of our study species that we assumed to be relevant to their reactions. We were able to gather information on the maximum height (cm), minimum height (cm), relative (seedling) growth rate (RGR; maximum day^{-1}) and seed mass (mg) from the Ecological Database of the British Isles (Fitter & Peat, 1994) as well as on specific leaf area (SLA; mm^2 mg^{-1}) from the LEDA Traitbase (Kleyer *et al.*, 2008). Some other traits of interest, like the N or P contents of the leaves, were not available for a sufficient number of species to warrant statistical tests.

Data analysis

To standardize the two data sets, *Luzula campestris* and *L. multiflora* were aggregated into *L. campestris* agg., and *Festuca rubra* and *F. ovina* into *Festuca rubra / ovina* agg., since they were not distinguished from each other in one of the datasets. The nomenclature of vascular plants follows Wisskirchen and Haeupler (1998).

For the spatial gradient data set, we started building general linear models (GLMs) for all species having relative frequencies between 10 % and 100 % across all plots. For each species, we built multiple models, including total N deposition, soil P, pH, NH$_4$$^+$ and NO$_3$$^-$ as well as further confounding factors related to geography and climate (latitude, longitude, alti-

tude, radiation and annual rainfall; see Appendix 3.3 in Chapter 9) and management (coded as 0 = not regularly grazed, 1 = low grazing intensity, 2 = medium grazing intensity and 3 = high grazing intensity). In the analysis, we excluded mean annual potential evapotranspiration, mean maximum daily temperature and mean minimum daily temperature because of multi-collinearity (see Appendix 3.2 in Chapter 9). Species abundance served as a dependent variable, and a Poisson distribution was used for all model runs. Backwards stepwise elimination of non-significant terms was used to find the minimal adequate model for each species. To test whether species were influenced predominantly negatively or positively by a given factor, chi-square analysis was used. In a second step, one-variable models were built for the same set of species, using general linear mixed-effects models (GLMMs). The abundance of species was again used as a dependent variable and, with separate model runs for each variable, total N deposition, soil P, pH, NH_4^+ or NO_3^- as a fixed explanatory factors. "Country" served as a random variable to account for the non-independency of measurements within the same country, relating to the differences in abiotic factors (geography, climate) and management intensity between the countries, applying Poisson distributions. For the historical data set, we used general linear models (binomial distribution) to regress the presence/absence of those species that were also present in the spatial analysis against the year of the survey. These regressions were performed separately for Germany (44 species) and the Netherlands (34 species) (see Appendix 3.1 in Chapter 9).

For relating the species responses to N deposition and other variables along the spatial gradient to the observed changes in species presence or absence in the historical data set, we used the regression coefficients resulting from the one variable GLMM-models for the spatial gradient (β total N deposition, β soil P [log-transformed], β pH, β NH_4^+ [log-transformed] and β NO_3^- [log-transformed]) and from the historical models (β year, separately for Germany and the Netherlands) as estimates of the strength and direction of the effects of variables on the occurrence of species (*cf.* Dupré & Ehrlén, 2002). In general, positive β-values denote positive responses and negative values negative responses to the variable in question. We used the β-coefficients of all species, irrespective of whether the regressions were significant or not. We did so because we were mainly interested in the relative effect of each factor on the frequency of the species, and because we aimed to increase the number of data points.

To examine whether species with different life-history traits were affected differently by N deposition and the main co-variables, we used the β-values from the above analysis and re-

lated them in separate models to the selected life-history traits. We furthermore built a full model with the β-values of total N deposition, soil P and pH as well as year as dependent variables and the life-history traits as explanatory variables, using stepwise backwards elimination for each variable to obtain a minimal adequate model. However, as the results were basically the same as for the single models, we decided to report the results only of the single analyses. All statistical tests were conducted using R, version 3.0.2 (R Developmental Core Team, 2013) and the lme4-package for GLMM-analyses (Bates *et al.*, 2011).

Results

Across all plots along the spatial gradient, N deposition values ranged from 2.4 to 43.5 kg N ha^{-1} yr^{-1} (Figure 3.1), pH-values from 3.69 to 5.72, and plant available phosphorus (P) from < 0.01 to 86.41 mg P kg^{-1} soil, NO$_3$$^-$ in the soil varied between < 0.01 to 171.95 mg N kg^{-1} and NH$_4$$^+$ from < 0.01 to 305.26 mg N kg^{-1}. For a correlation matrix of the environmental variables, see Appendix 3.2 (Chapter 9).
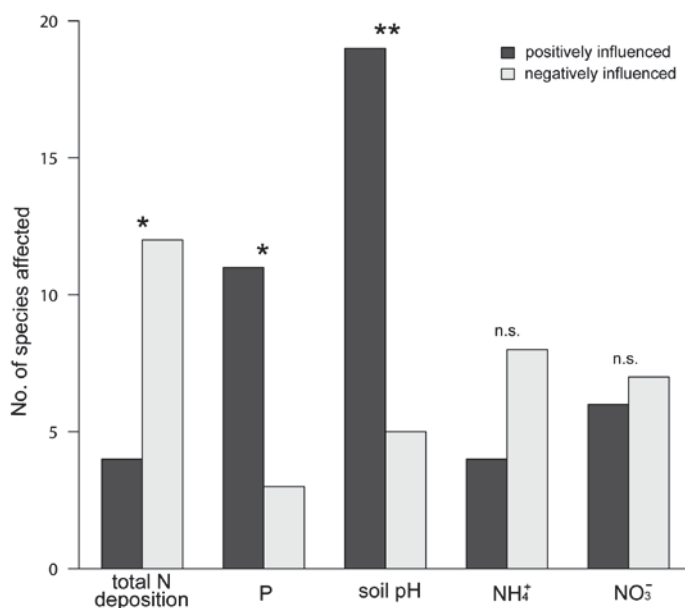
Figure 3.2 *Number of species influenced positively (dark bar) or negatively (light bar) by either total nitrogen (N) deposition, available phosphorus in the soil (P; log-transformed), soil pH, and the contents of soil ammonium (NH$_4$$^+$; log-transformed) and nitrate (NO$_3$$^-$; log-transformed), as summarized from the linear models given in Appendix 2.3 (Chapter 8). Asterisks indicate significant differences between the numbers of species affected positively or negatively at P < 0.01 (**) or P < 0.05 (*). 'ns' denotes non-significance.*

The GLM analyses (Table 3.1 and Figure 3.2) revealed that, out of the 44 studied species, 16 (55%) responded significantly to N deposition, with most of them (75%) being negatively affected ($\chi^2 = 4.00$, $P = 0.046$). In total, the abundances of 14 species (32%) were significantly related to available P, predominantly (11 *vs.* 3) in a positive way ($\chi^2 = 4.57$, $P = 0.033$). More than half of the species showed a (marginally) significant response to soil pH, again mostly in a positive way ($\chi^2 = 8.17$, $P = 0.004$). Somewhat lower proportions of species responded significantly to the NH$_4$$^+$ or the NO$_3$$^-$ contents of the soil (27% and 30%, respectively), with no pronounced differences between the number of negative and positive effects (NH$_4$$^+$: $\chi^2 = 1.33$, $P = 0.248$; NO$_3$$^-$: $\chi^2 = 0.08$, $P = 0.782$).

Table 3.1 *Species responses to total nitrogen deposition (N_{dep}; in kg N ha^{-1} yr^{-1}), available phosphorus in the soil (P; mg P kg^{-1}, log-transformed), soil pH, soil ammonium content (NH$_4^+$; kg N ha^{-1} yr $^{-1}$, log-transformed) and soil nitrate content (NO$_3^-$; kg N ha^{-1} yr $^{-1}$, log-transformed) in 153 plots of acidic grasslands, as analysed in general linear models. The regression coefficients and P values as well as the effects of further co-variables (see Methods) are found in Appendix 3.3 (Chapter 9). "+" indicates positive and "–" negative relationships at P < 0.05, parentheses indicate that the estimates were marginally significant (0.05 < P < 0.10). N = number of occurrences.*

Species	N	N_{dep}	P	pH	NH$_4^+$	NO$_3^-$	R^2
Achillea millefolium L.	53	(−)		+		+	0.23
Agrostis capillaris L.	151						0.28
Agrostis stolonifera L.	21						0.51
Anthoxanthum odoratum L.	100	−				+	0.31
Calluna vulgaris (L.) Hull	87	−	−				0.27
Campanula rotundifolia L.	38	−	−	+			0.58
Carex nigra (L.) Reichard	27						0.41
Carex panicea L.	50	−		−		−	0.21
Carex pilulifera L.	90					−	0.28
Cerastium fontanum Baumg.	57		+	+			0.34
Convallaria majalis L.	15		+	+			0.32
Cynosurus cristatus L.	15	+	+	+			0.51
Danthonia decumbens (L.) DC.	81	−		+			0.41
Deschampsia flexuosa (L.) Trin.	80			−			0.30
Erica tetralix L.	17					−	0.21
Festuca ovina / rubra agg.	142		(+)		(+)		0.12
Galium saxatile L.	114			−			0.22
Hieracium pilosella L.	46						0.46
Holcus lanatus L.	77		+	+	−		0.28
Holcus mollis L.	30		(+)	+			0.15
Hypochaeris radicata L.	51			+			0.39
Juncus effusus L.	41	+					0.38
Juncus squarrosus L.	34			(−)			0.16
Leontodon autumnalis L.	16		+		−		0.50
Leontodon hispidus L.	23				(−)	−	0.43
Lotus corniculatus L.	46	(−)		+	−		0.35
Luzula campestris agg.	148		+	+	−		0.31
Molinia caerulea L. (Moench)	62				(+)	−	0.22
Nardus stricta L.	82	+					0.21
Plantago lanceolata L.	51			+		+	0.38
Poa pratensis agg.	32			(+)			0.17
Polygala serpyllifolia Host	31	(−)	−			−	0.31
Potentilla erecta (L.) Raeusch.	116	−					0.17
Ranunculus acris L.	24			+		(+)	0.23
Ranunculus repens L.	22			+			0.38
Rumex acetosa L.	75		+	+	−	+	0.32
Rumex acetosella L.	50	+			(−)	+	0.60
Succisa pratensis Moench	30	−		+			0.43
Trifolium pratense L.	24		+	+			0.40
Trifolium repens L.	52		+				0.33
Vaccinium myrtillus L.	63			−	+		0.40
Vaccinium vitis-idaea L.	13	−				−	0.83
Veronica chamaedrys L.	74			+	+		0.30
Veronica officinalis L.	96	−			−		0.32

Only in four of the studied species, were no significant effects of any of the main variables on their occurrence detected. Among the co-variables, latitude and longitude had by far the largest importance (see Appendix 3.3 in Chapter 9), reflecting the differences in floristic composition along the spatial gradient. The average R^2 of the GLM models for the species was 0.34, meaning that there was a relatively high proportion of unexplained variation.

Among the 12 species of *Poaceae* analysed, some responded positively to N deposition (*Cynosurus cristatus*, *Nardus stricta*), others negatively (*Anthoxanthum odoratum*, *Danthonia decumbens*; Table 3.1). Soil P had a positive effect on six grass species (50%), while the remaining graminoids were unaffected by P. All dwarf shrubs except *Vaccinium myrtillus* showed a negative response to N deposition and / or NO_3^-, and *Calluna vulgaris* was in addition affected negatively by high P availability. There were no consistent patterns among the dicot herbaceous species, but it was notable that a majority of them were favoured by high soil pH. Finally, it was remarkable that the two *Trifolium* species (*T. pratense* and *T. repens*) were unaffected by N variables, but positively influenced by P.

Regression analysis of the β-values showed a positive correlation between the changes in species' frequency over the years and the responses to N-deposition loads (Figures 3.3a, b), suggesting that species declining over time were predominantly sensitive to high N deposition. The response to soil available P also proved to be important for the species' incidence over time, with a temporal increase in species growing better in P-rich environments (Figures 3.3c, d). In contrast, there was no effect of the responses of species to soil pH on their temporal trends (Figures 3.3e, f).The response to soil NH_4^+ content also had no influence on the change in abundance of species over time (Figures 3.3g, h). In contrast, species being favoured by a high NO_3^- concentration in the soil increased in abundance over the years, both in Germany (Figure 3.3i) and in the Netherlands (Figure 3.3j).
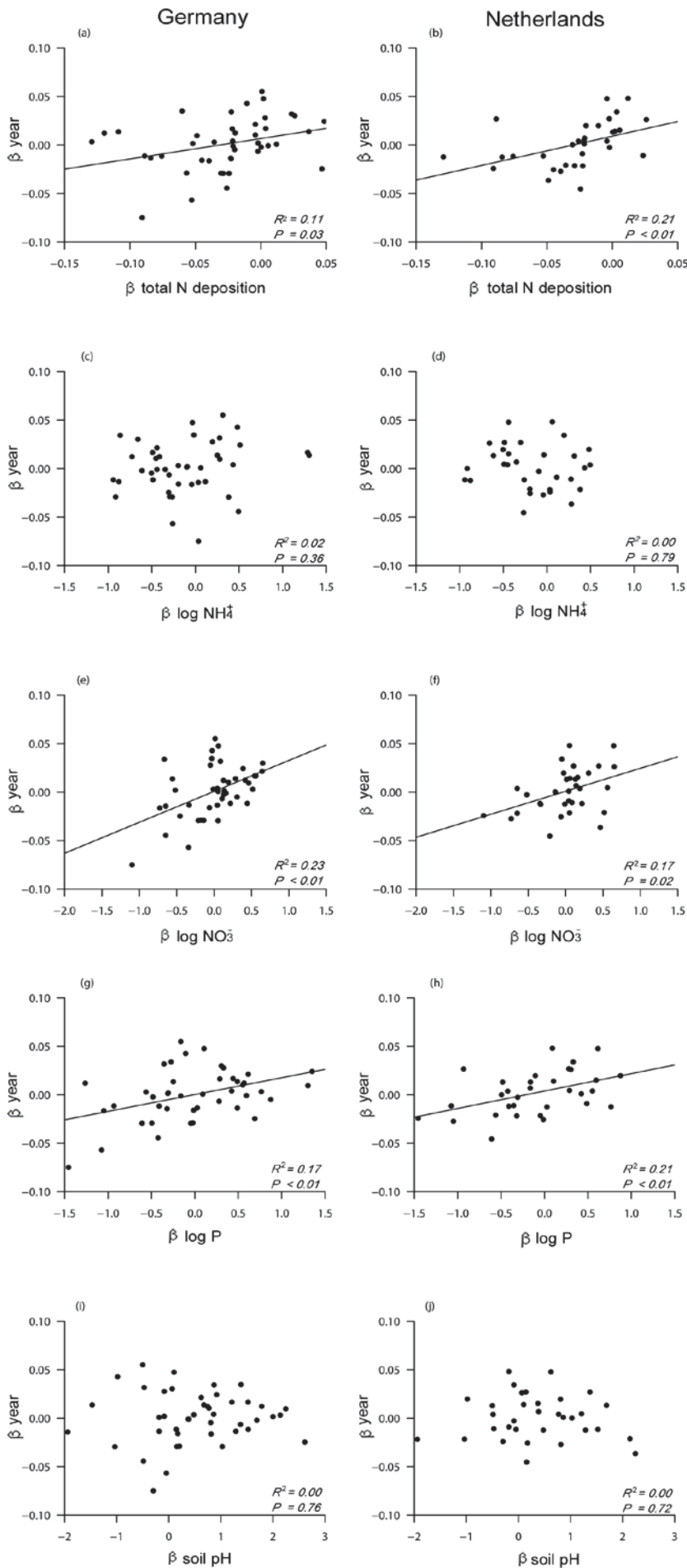
Figure 3.3 *Relationship between β year (extracted from the temporal data set, see Table 2) and β total N deposition, β log P, β soil pH, β NH_4^+ and β NO_3^-, shown separately for Germany and the Netherlands. For Germany, n = 44 for total N deposition, soil pH, NH_4^+ and NO_3^-, and n = 42 for log P; for the Netherlands, n = 34 for total N deposition, soil pH, NH_4^+ and NO_3^-, and n = 33 for log P. R^2 and P values are given in each panel.*

The analysis of life-history traits (Table 3.2) showed that the maximum height of a plant had no influence on its response to any of the variables (all $P > 0.05$). Minimal plant height, however, was negatively related to the β-coefficients for N deposition, while it was unrelated to the species' responses to soil P and pH. Relative growth rate of the species revealed to be the most important life-history trait for the frequency of species in relation to the studied environmental factors. Species with relatively high growth rates tended to be the beneficiaries of increased N deposition, and they were also superior competitors in plots with high levels of available P. Moreover, we found species with a high relative growth rate to be favoured by less acidic soil conditions (Table 3.2). Species with higher specific leaf area tended to be favoured by higher soil P. Furthermore, species with a high seed mass and a large minimum height in Germany and species with a high relative growth rate in the Netherlands increased or tended to increase in occurrence over the years.

Table 3.2 *Relationship between the β coefficients extracted for all species from the single generalised linear mixed models (spatial gradient data: β total N deposition - β N_{dep}, β log P, β pH, and temporal data: β year) and some life history traits, analysed separately for a) Germany and b) the Netherlands. The traits include minimum height (cm; log-transformed), relative growth rate (RGR; maximum day^{-1}), seed mass (mg; log-transformed) and specific leaf area (SLA; mm^2 mg^{-1}). For significant relationships (in bold) and marginally significant relationships (in italics), R^2 and P values are shown. The directions of all relationships were positive.*

	β N_{dep}		β P		β pH		β year	
	R^2	P	R^2	P	R^2	P	R^2	P
a) Germany								
log min height ($n = 36$)	0.14	**0.023**						
RGR ($n = 30$)	0.12	*0.059*	0.27	**0.003**	0.15	**0.036**		
log seed mass ($n = 43$)					0.12	0.021	0.10	**0.042**
SLA ($n = 37$)			0.09	*0.051*				
b) Netherlands								
log min height ($n = 26$)	0.23	**0.012**					0.26	**0.008**
RGR ($n = 23$)			0.41	**0.001**	0.13	*0.088*	0.15	*0.064*

Discussion

The aim of this study was to use a spatial gradient approach to examine the effects of N deposition on the frequency of vascular plant species in acidic grasslands, taking confounding factors into account. We also aimed to test whether the patterns found along the spatial gradient correspond to changes in species abundance observed in a time-series analysis.

We found that more than a third of the studied species responded significantly to N deposition, predominantly in a negative way. The results correspond to previous studies by Stevens et al. (2010a, 2011a, b) who found a negative effect of N deposition on the total species rich-

ness of vascular plants across the same gradient. It is unlikely that a statistical artefact causes this main result, because a large number of co-variables, including geographic and climatic variables as well as other soil factors, were taken into account in the analysis. Among these co-variables, P also had a strong effect on species occurrence; N and P together influenced the frequency of 59% of the study species, a higher proportion than observed by Ceulemans et al. (2011). Whereas those authors showed that 30% of the species responded negatively to P but only 8% to N, we found a higher proportion of species being affected by N than by P. In contrast to their finding (Ceulemans *et al.*, 2011; 2014), the effect of P was predominantly positive. Interestingly, only few species reacted in the same way in the data sets. This suggests that the location of the data and the selection of species used in an analysis play important roles, and that results for individual species in our and other studies should be interpreted with caution. There is no conclusive evidence yet that either N or P is the more important environmental driver in acidic grasslands, we rather conclude that both have marked effects on species frequencies in grassland communities and that their relative importance may be context-dependent. While N deposition had predominantly negative impacts on species, the responses to P can be positive for many, which corresponds to the results of Güsewell (2004), who concluded that the effects of P on species varied from case to case. Overall, we agree with the statement of Ceulemans et al. (2013; 2014) that, for securing high levels of biodiversity, both N and P levels have to be managed, because the outcome of an increase in both nutrients would invariably be the disappearance of many smaller species due to competitive exclusion (Olde Venterink *et al.*, 2003 and references therein). Next to the absolute values of N and P, also their relative availability in the soil, as reflected in the N:P ratio, plays an important role for plants' reactions, and is among others being influenced by the increased atmospheric N deposition. The change in the N:P-ratio of the soil has in turn an effect on the nutrient status of the plants, thereby influencing their physiological responses, which then affects herbivores and decomposers (Güsewell, 2004).

We also analysed the responses of species to different forms of N in the soil. Most attention has so far been given to NH_4^+ (e.g. Lucassen *et al.*, 2003; van den Berg *et al.*, 2005), which at higher concentrations is generally assumed to lower photosynthetic rates, to inhibit the growth of plants (Falkengren-Grerup & Lakkenborg-Kristensen, 1994 and references therein), and to cause local acidification (e.g. Tamm, 1991). Correspondingly, in our study, eight species showed a negative, but only four species a positive, response to NH_4^+. Whereas Bobbink et al. (2003) found no direct link between NH_4^+ concentrations and the decline in species diversity,

NH_4^+ had a negative influence on the incidence of rare species in a study by Kleijn *et al.* (2008). Generally, NH_4^+ prevails in very acidic soil, while in more base-rich soils, NO_3^- is the dominant N-form. However, N deposition occurs as both NH_4^+ and NO_3^-, with NO_3^- often being the more dominant form. Studies on the preferences of species or species groups relative to the uptake of different N-forms are equivocal (Falkengren-Grerup & Lakkenborg-Kristensen, 1994; Falkengren-Grerup, 1995; Gilliam, 2006; Ashton *et al.*, 2010). In our study, an equal amount of species responded positively or negatively to NO_3^-.

In addition, more than half of the species showed a significant response to soil pH, with most species' frequencies increasing with increasing pH. Although all plants in acidic grasslands have to be adapted to relatively acid soils, only a few species tolerate or ecologically prefer the very low values of pH 4 or below (e.g. *Deschampsia flexuosa*, *Galium saxatile*, *Vaccinium myrtillus*). Generally, dicot herbaceous plants are favoured by more base-rich soil conditions.

The comparison of species responses along the spatial gradient with the temporal changes in species abundance reveals clear patterns that are consistent across countries. Species showing a negative response to high N deposition have decreased over time (e.g. *Anthoxanthum odoratum* and *Potentilla erecta*; Dupré et al. 2010). The same was true for some taxa being negatively affected by both high N deposition and high P availability (*Calluna vulgaris, Campanula rotundifolia*). In contrast, species indifferent to N deposition, for example *Agrostis capillaris*, *Galium saxatile* and *Deschampsia flexuosa*, have increased over the past decades (Dupré et al. 2010). Whereas our results showed no systematic relation between the change in species abundance over the years and their response to NH_4^+, species increasing over time were predominantly those that tolerate or prefer high NO_3^- concentrations in the soil (such as *Rumex acetosa* and *R. acetosella)*, whereas species with a negative response to high NO_3^- concentrations, like the dwarf shrubs *Erica tetralix* and *Vaccinium vitis-idaea*, have declined. These results correspond to the experiments done by Nordin *et al.* (2001), showing that plants adapted to N-rich environments are often better able to use NO_3^- than species adapted to N-poor soils. Surprisingly, there was no decline over time of species being negatively related to soil pH in the surveyed grasslands, although pH was the most important soil variable in the models and it has been postulated that N deposition is often associated with acidification (Stevens *et al.*, 2010a), which is a major driver of diversity loss (Sala *et al.*, 2000). Generally, the results support the use of a spatial gradient approach as a space-for-time substitution.

The positive or negative responses of species to the concentrations or additions of specific nutrients are not only physiological reactions, but also an effect of interspecific competition being altered by changing nutrient levels in the soil. For example, species with a high N-efficiency, such as N_2-fixing species (for example, in our data set, *Lotus corniculatus*), decline with increasing N, while relatively nitrophilous species (such as *Cynosurus cristatus*) increase (Gilliam, 2006; Skogen *et al.*, 2011). The same may apply to species associated with mycorrhiza such as Ericaceae: while these are generally known to be superior competitors on soils with low nutrient supply, they have been found to decline in areas with high N deposition or P availability (Treseder, 2004; Gilliam, 2006), most likely because of a change in the costs and benefits for supporting mycorrhizal fungi (Ceulemans *et al.*, 2011). The competitive relationships between species may also be altered by changing management, with an abandonment of management often having similar short-term effects on species frequency as nutrient addition. Although current management was taken into account in the models, we cannot exclude that in some areas there were strong differences in management in the past and that there is a legacy of former land use in the present-day species composition. This may also apply to anthropogenic nutrient additions: although none of the sites to our knowledge had been fertilised for 17 years prior to the observations, we cannot exclude that some of them received N and / or P in earlier periods.

The importance of interspecific competition is also reflected in the examination of the responses of species with different life-history traits: taller species and those with higher growth rates benefited most from higher nutrient conditions. This is plausible because, if nutrients are in sufficient supply, plant growth is enhanced, light becomes limiting and smaller as well as slower-growing species are being overshadowed and outcompeted. Similar results were reported by Suding et al. (2005), who found that species of the lower canopy were more likely to go extinct due to fertilisation than species of the upper canopy, because of increased competition for light. Newman (1973) stressed that even a small difference in initial height can give a species a significant advantage in shoot competition. Below-ground, species can occupy distinct niches by varying in rooting depth or using different forms of nitrogen, while in competition for light, the tallest and fastest-growing species will consistently be the winner, which explains the low diversity under high nutrient conditions and why the height of plants has repeatedly been found to be an important factor for the response of species to eutrophication (e.g. Pennings *et al.*, 2005; Bobbink *et al.*, 2010).

Conclusion

During the past decades, semi-natural grasslands throughout the world have suffered greatly from habitat destruction and deterioration. Apart from altered management (both too intensive and abandonment), the addition of nitrogen, which is commonly the limiting nutrient in these grasslands, is hypothesised to contribute to this change. The predominantly negative responses of species to N deposition and the coincidence of responses to spatial and temporal gradients found in this study support the significant negative role of N deposition in acidic grasslands. The results give strong evidence for the power of descriptive approaches (both spatial gradient and temporal gradient analyses) for elucidating the effects of environmental drivers on the species composition of semi-natural vegetation. At the same time, the role of P relative to the role of N needs to be studied in more detail and also in other grassland types. Our results also stress a continued need for environmental measures and restoration efforts to preserve and improve the quality of the remaining grasslands.

Supplemental Material

Supplemental Material for this article can be found in the Appendix (Chapter 9):

Appendix 3.1 Species included in the study based on their occurrences in the temporal gradient dataset in Germany and the Netherlands

Appendix 3.2 Correlation matrix of all variables considered for the linear models in the spatial gradient dataset.

Appendix 3.3 Species' responses obtained in the GLM analysis of the spatial gradient dataset.

Appendix 3.4 Mean values of environmental factors in the spatial gradient dataset for each country.

Acknowledgements

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Chapter 4

Resource-based determinants of range sizes of forest vascular plants in Germany

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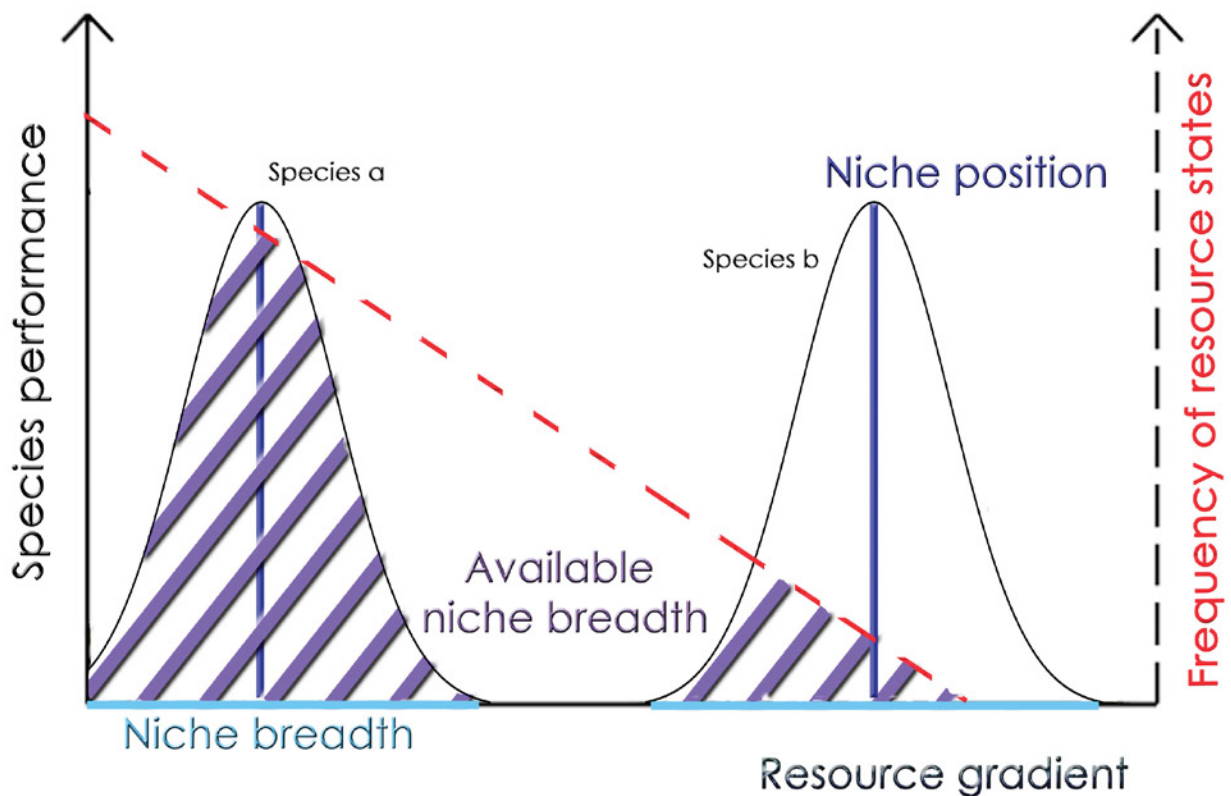
Picture on the title page shows the calculation of the "available niche breadth", a concept in-
troduced in this Chapter

Abstract

Aim Examining whether niche breadth, niche position and a compound measure of the two variables contribute to explain the range sizes of forest vascular plants.

Locations Deciduous forests in two regions of Germany, the Weser-Elbe region and Bavarian Alps.

Methods We compiled range size data for vascular plant species (30 in Weser-Elbe region, 35 in the Bavarian Alps) on regional, national and continental scales by determining the area of occupancy (number of occupied grid cells) in both regions, Germany and Eurasia. Estimates of realised niche breadth and niche position (ecological optimum) for soil pH and light were based on measurements in 46 sites for all species. Frequency distributions of pH values on regional and national scales served to calculate the "available niche breadth", i.e., niche breadth values corrected for the different availabilities of pH values in the region and country.

Results Regional range size in the Weser-Elbe region increased with increasing niche breadth for both soil pH and light and with decreasing pH niche position. pH niche breadth was positively correlated to national range size in the Weser-Elbe region and to Eurasian range size in the Bavarian Alps. In the latter region, all other relationships with range size were (partly marginally) non-significant. Available niche breadth was generally closer related to the regional and national distribution of species in both regions than either niche breadth or position alone.

Main conclusions Niche breadth and position performed well as predictors of range size only for soil pH and in the Weser-Elbe region, which shows more homogeneous environmental conditions than the Bavarian Alps. If the frequencies of different ranges of pH values can be quantified, the calculation of available niche breadth for soil pH appears to be a promising approach for assessing the possible effects of niche variables on the range sizes of species.

Keywords Abundance-range size relationship · Available niche breadth · Deciduous forest · Niche breadth · Niche position · Phylogenetically independent contrasts

Introduction

The positive interspecific relationship between the range size and abundance of species is one of the most general and robust patterns in ecology, as it has been documented for various taxa, diverse habitats and different spatial scales (e.g. Brown, 1984; Hanski *et al.*, 1993; Gaston *et al.*, 1997; Heino, 2005). The mechanisms governing this pattern, however, remain elusive (Heino, 2005), and at least thirteen hypotheses have been put forward (*cf.* Borregaard & Rahbek, 2010). Four of these recognize the importance of statistical artefacts (especially the underestimation of range size of species with lower abundance), while the others refer to biological explanations.

One explanation for the positive relationship between abundance and range size across species is Brown's (1984) niche (or resource) breadth hypothesis, stating that species able to exploit a wide range of resources are expected to occur over large areas and in high densities. The idea of a positive relationship between niche breadth and commonness at different spatial scales is immediately appealing: for example, most generalist plant species in Central Europe are relatively common, while habitat specialists are often rare and threatened. However, the evidence for this relationship is not unequivocal (Gregory & Gaston, 2000; Heino & Soininen, 2006 and references therein). A major problem associated with many studies is that common species are generally encountered more often than rare ones, causing the niche breadth estimates for common species to be larger than for rare ones, which in turn leads to an artificial positive correlation between niche breadth and range size or abundance (Burgman, 1989; Hanski *et al.*, 1993; reviewed in Gaston *et al.*, 1997). Although this problem is often acknowledged, it is rarely accounted for (but see for example Burgman, 1989; Kotze *et al.*, 2003; Kolb *et al.*, 2006), causing many studies to be invalid or at least difficult to interpret (Gregory & Gaston, 2000).

A related, and also intuitively appealing, theory is the niche availability or niche position hypothesis (Hanski *et al.*, 1993), emphasizing that range size and abundance of species are determined by their niche position along environmental gradients. It predicts that species utilising common resources are common as well, whereas species specialised on rare habitats are also rare (Hanski *et al.*, 1993; Gregory & Gaston, 2000). Again, the existing evidence is not conclusive, although more studies appear to support (e.g. Gregory & Gaston, 2000; Heino & Soininen, 2006) than contradict (e.g. Kotze *et al.*, 2003) the niche position hypothesis. In par-

ticular, there is a lack of evidence for the impact of both niche variables on the local abundance of species (e.g Brändle & Brandl, 2001; Marsden & Whiffin, 2003).

Although the concept of the *n*-dimensional niche (Hutchinson, 1957) is impossible to make operational in everyday research (Colwell & Futuyma, 1971), vascular plants offer a suitable study system in the sense that they all need to take up water and nutrients from the soil and to capture enough light for photosynthesis. Therefore, the niche breadth and position with respect to edaphic factors and light are likely to contribute to the commonness of plant species. In our study, we want to examine this by using two environmental variables that are comparatively easy to quantify for a larger number of sites and species, soil pH and light. Soil acidity is known to be of large significance for the regional and local distribution of plants (Schuster & Diekmann, 2003). Its relationship to the general nutrient status of forest soils is complex, with high-pH soils being more fertile in lowlands with Pleistocene loose sediments (Kolb *et al.*, 2006), but markedly infertile in limestone and dolomite mountains (Ewald, 2005). The local distribution patterns of forest plants are also known to be strongly affected by light availability (Schuster & Diekmann, 2005). We focus on larger spatial scales (range size) and test the relationship between range size and niche estimates in two regions with contrasting environments in terms of the homogeneity of topography and climate. As the relative importance of soil variables (but also light) for the range sizes of species decreases with increasing spatial scale - mainly due to the higher variation in temperature climate across large geographic gradients (Pearson & Dawson, 2003)-, niche breadth and niche position for soil pH and light are expected to show a weaker correlation with range size in regions with more heterogeneous climatic conditions. To avoid statistical artefacts due to different sample sizes for common and rare species, environmental data were obtained by subsampling the same number of sites for all species; to our knowledge, this is one of the first studies explicitly doing so.

If both niche breadth and position contribute to explaining the distribution of species, it is likely that a combination of the two would show an even better relationship with range size than either of the variables alone. This can be achieved by a multiple model including both variables (see for example Heino & Soininen, 2006), or by a compound measure in which the niche breadth of a species is corrected for the different availabilities of habitats that form part of the species' niche. The calculation of such a measure, in the following called "available niche breadth", is illustrated in Figure 4.1a: Species ideally show a Gaussian response curve along environmental or resource gradients. If the niche breadths of two species are the same,

but their niche positions not, their commonness is likely to differ if the abundance of resource states varies along the gradient. We predict species 1 to be more abundant than species 2, because its response curve better matches the higher frequency of low resource values. If, for example, a species has a relatively large pH niche breadth but is lacking from very acid soils, it is likely to have a small range size in those regions that only or predominantly offer low-pH sites.

Our main expectations were the following: (1) The range sizes of species should be affected both by niche breadth and niche position, with a closer relationship in the region with more homogeneous climatic conditions (Weser-Elbe region); (2) available niche breadth as a compound measure of niche breadth and niche position should be more closely related to the range size of species than the single variables.

Material & Methods

Study area and species

Data material was compiled from two regions in Germany, one in the north, the other in the far south. The Weser-Elbe region is located in North-Western Germany (Figure 4.2) and characterised by a geologically and topographically relatively uniform landscape. Being predominantly covered by agricultural land, woodlands occupy only 9.8% of the area (Kelm, 1994) and consist mostly of managed, near-natural deciduous forest and planted coniferous forest. In contrast, the Bavarian Alps are a hotspot of geodiversity in terms of relief (rough terrain ranging from 450 to 2,963 m a.s.l.) and geology (alpine folded mountains with highly variable bedrock composition). 53% of the region is covered by forest comprising submontane deciduous, mixed montane and subalpine coniferous types, with remnants of old growth stands (Ewald, 2001).

In order to confine the species sample to a reasonably cohesive ecological unit (*cf.* Brown, 1984), we considered only herbaceous forest plants with a preference for growing in closed forests or forest edges and gaps (according to Schmidt *et al.*, 2011). Species occurrence data and local environmental information for the study sites were compiled from the database BERGWALD (GIVD ID EU-DE-002, Ewald, 2012) and from published sources (Wulf, 1992; Heinken, 1995) as well as a new survey carried out during summer 2011 for the Weser-Elbe region. In both regions, the data sets encompassed the complete spectrum of forest communities on mineral soils. All sample plots represented forest sites with homogeneous topography

and species composition. Data sampling followed a phytosociological approach (Braun-Blanquet, 1964): in each plot (average size: c. 500 m^2 in the Weser-Elbe region and 144 m^2 in the Bavarian Alps) all vascular plants were recorded separately for the tree, shrub and field layers for which also their total cover degrees were estimated. In total, 46 sites were included for each species, and if abundance and environmental data for a given species were available for a larger number of sites, 46 of these were randomly selected. In the Weser-Elbe region with a relatively poor flora, information was occasionally available for less than 46 sites so that we needed to add own survey data. For this, regional flora maps (Küver, 1999; Cordes *et al.*, 2006; A. Kolb pers.com.) were consulted to identify additional occurrences of the species in question. For the more common species, we randomly selected and visited as many sites as necessary to reach the total number of 46; for the rarer taxa, all additional sites were visited. Sufficient information was finally available for 30 species in the Weser-Elbe region and for 35 species in the Bavarian Alps (see Appendix 4.1 in Chapter 9; nomenclature according to Wisskirchen & Haeupler, 1998).

Range size was defined as area of occupancy within a given area (Gaston *et al.*, 1997), which is more commonly used in and works better for most ecological studies than the extent of occurrence (Gaston, 1994; Blackburn *et al.*, 2006), because it is an estimate of the area over which a species is actually found. On the regional scale, range size for the Weser-Elbe region was estimated from the flora atlas for this region (Cordes *et al.*, 2006) as the number of occupied grid cells (in total 1,109), each having a size of about 2.8 km × 2.8 km. On this rather fine scale, gaps in the distribution of species may be the result of insufficient mapping rather than a reflection of true absence. However, the flora of the Weser-Elbe region is among the best known in Germany, where particular efforts were carried out to search for rare species and to map previously under-sampled areas. The regional range size for the Bavarian region was estimated from distribution maps provided by the "Botanischer Informationsknoten Bayern" (http://www.bayernflora.de), as the number of occupied quadrants (c. 40 km^2) in the Bavarian Alps (in total 133). On the national scale, range size information was obtained from the FloraMap database (http://www.floraweb.de), which divides Germany into 3,071 grid cells of an extension of 10.0' longitude and 6.0' latitude (c.130 km^2, depending on its location in Germany). In addition, a very crude measure of continental (Eurasian) range size was estimated from the Atlas of North European Vascular Plants (Hultén & Fries, 1986) as the number of occupied grid cells extending over 10° longitude and 10° latitude in Europe, Asia and North Africa (in total 105, each c. 760,300 km^2, depending on its location on the globe). Only

13 of the 54 study species also grow outside this area, and across all species, Eurasian range size was highly positively correlated with global range size (if measured in the same way as European range size but including all continents) ($r_s = 0.98$, $P < 0.001$, $n = 46$).

Niche measurements

As all species and environmental data were recorded in the field under natural conditions, the niche measures refer to the realised niches of the species, and we will not make any inference on fundamental niches. Most of the literature on abundance-range size relationships and their underlying causes is based on the realised measures of niches and realised species distributions. For reasons of brevity, we will hereafter use the general term niche instead of realised niche.

Soil pH was measured in $CaCl_2$ solution with a glass electrode according to standard procedures. Light availability values at the forest floor were obtained in an inverse way as '100% - total canopy cover' in percent. To test whether this visual estimate was a good proxy for light, we collected additional canopy cover and light intensity data across 101 sites in deciduous forests of the Weser-Elbe region. Light intensity was measured under overcast sky as photosynthetic photon flux density of photosynthetically active radiation ($\mu mol\ s^{-1}m^{-2}$; Li-Cor Quantum Photometer), simultaneously in the plot and in the open (averages of 15 seconds) and expressed as a relative percentage value. There was a high positive correlation between measured light intensity at the forest floor and estimated canopy cover ($r_s = 0.78$, $P < 0.001$).

For the calculation of niche breadth, first the niche gradients were divided into equally spaced intervals, namely steps of 0.2 units for pH and of 5% units for light. Then the percentage occurrence of each species in each interval was calculated to account for the different number of plots in each interval, by dividing the number of plots containing the species by the total number of plots in the interval (Kolb *et al.*, 2006). Niche breadth (NB) was calculated on a 0-1 scale according to the formula

$$NB = \frac{\left(\sum I_{ij}\right)^2}{n\sum \left(I_{ij}^2\right)} \qquad (1)$$

as described by Økland (1986). In this equation, I is the percentage occurrence of a species i in an interval j and n the total number of intervals along the gradient. For the calculation of the niche position of species, we regressed the percentage occurrence of the species in each interval on the interval value. The species' niche position (NP) with respect to soil pH and

light was then determined as the mode of the polynomial regression (*cf.* Kolb *et al.*, 2006) (the optima of the solid lines in Figure 4.1a).
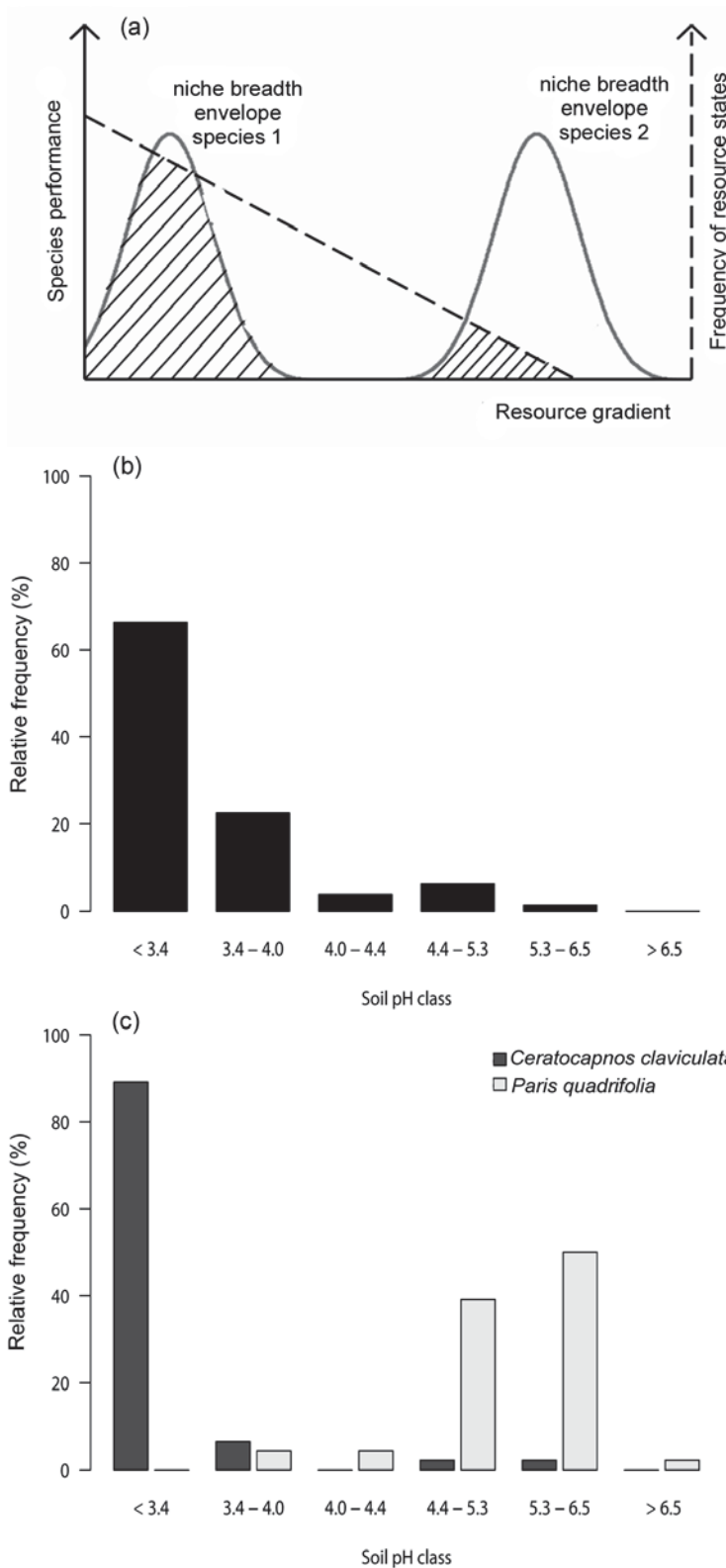
Figure 4.1 *(a) Calculation of the compound measure of niche breadth and niche position: the "available niche breadth" (hatched area) corresponds to the overlap between the area below the solid line, representing the niche breadth as species performance along the resource gradient, and the area below the dashed line, being the relative frequency of different resource states at a specific spatial scale; (b) frequency distribution (%) of pH values of forest soils in the lowlands of Lower Saxony, divided into classes (see Table 1); (c) relative frequencies (%) of* Ceratocapnos claviculata *(dark grey, 683 grid cells occupied) and* Paris quadrifolia *(light grey, 65 grid cells occupied) in the above-given classes of soil pH in the Weser-Elbe region.*

For the calculation of available niche breadth, a species' NB value was multiplied with a correction factor (CF, between 0 and 1), expressing the commonness of the different resource states that the species is able to exploit (represented by the dashed line in Figure 4.1a). This

requires information on the frequency distribution of different resource states. For soil pH we extracted such data from the National Forest Inventory of Germany (Bundesministerium für Ernährung, Landwirtschaft und Forsten, 1996) both for the two regions (North-West German lowlands, Bavarian Alps) and the whole of Germany (national). The National Forest Inventory divides Germany into 1,800 grid squares of 8 km × 8 km, in which, at a random forest location, information about structure, species composition and environment is collected and stored in a national database. The frequency distribution of soil pH values (Table 4.1) shows that, in the Weser-Elbe region, niche availability is highest at low pH values and decreases linearly towards higher values.

Table 4.1 *Frequency distribution (in %) of pH values of forest soils in Germany, in the lowlands of Lower Saxony and in the Bavarian Alps (see Methods) (Bundesministerium für Ernährung, Landwirtschaft und Forsten, 1996). For comparability with our own measurements, the pH values were converted from values measured in KCl to their equivalent values measured in CaCl₂, according to Conyers & Davey (1988).*

Soil pH range	Germany ($n = 1741$)	Lower Saxony ($n = 80$)	Bavarian Alps ($n = 65$)
< 3.4	27.8	66.2	15.4
3.4 - 4.0	48.5	22.5	18.5
4.0 - 4.4	8.9	3.7	7.7
4.4 - 5.3	5.2	6.3	6.2
5.3 - 6.5	5.2	1.3	41.4
> 6.5	4.4	0	10.8

As these percentage values were available only for larger pH ranges and not for the 0.2 units, the CF had to be determined in a simplified way. For the Weser-Elbe region (hereafter abbreviated as WE), we applied the linear function:

$$CF = a + b * NP_i ,$$ (2)

where NP is the niche position for pH of species i. The two parameters a and b can be estimated by assuming that CF = 1 if NP equals the lowest pH value measured in the region (2.36), and that CF = 0 if NP equals the highest value (7.0). Thus, by solving $1 = a + b * 2.36$ and $0 = a + b * 7.0$, the correction factor on the regional scale was calculated with the equation $CF = 1.5036 - (0.2155 * NP_i)$.

For the Bavarian Alps (BA) and on the national scale, values did not show a linear increase or decrease along the pH gradient (Table 4.1); here, we applied a quadratic equation:

$$CF = a + b * NP_i + c * NP_i^2 ,$$ (3)

and estimated the parameters (a, b and c) and the CF in a similar manner as described for the linear equation.
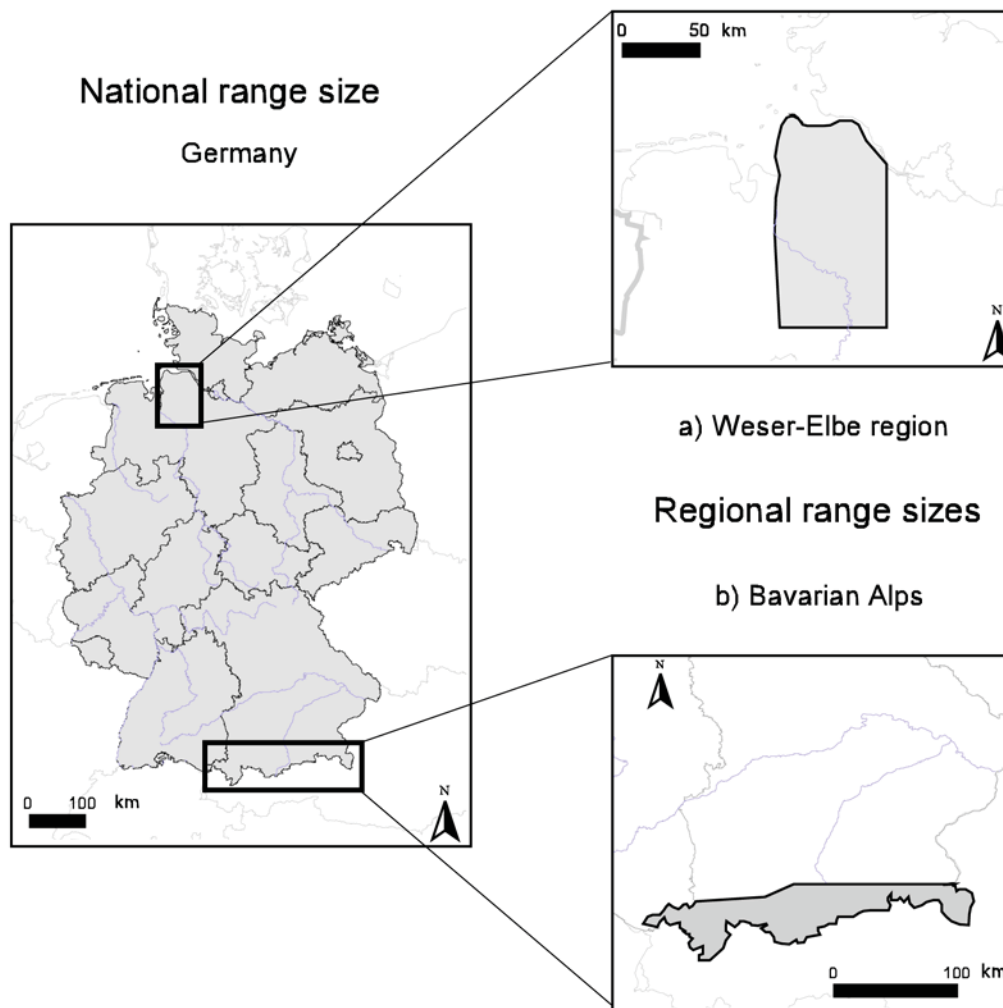
Figure 4.2 *Geographic areas for which the species data on national range size (Germany) and regional range sizes (Weser-Elbe region and Bavarian Alps) were calculated.*

Statistical analysis

The abundance measures of species were related to the corresponding values of niche variables, separately for soil pH and light. As some of the variables did not meet the assumptions for parametrical tests, we first carried out data transformations and then multiple linear regressions with the range measures as dependent variables and niche breadth and niche position as explanatory variables. However, as no interactions between NB and NP were found to be significant and the NB and NP for light were highly significantly correlated in one of the regions (resulting in multicollinearity), we finally applied Spearman rank correlation.

Additionally, we took the relatedness of species into account by calculating phylogenetically independent contrasts (PIC). To achieve this, first a phylogenetic tree of the studied species was built (Durka & Michalski, 2012) and contrasts calculated using the *CAIC* (Comparative Analysis by Independent Contrasts) package (Purvis & Rambaut, 1995; Orme *et al.*, 2009)

and the "crunch" algorithm for continuous variables with branch lengths scaled in million years (Durka & Michalski, 2012). For polytomies in the tree, only one contrast per node was calculated. The relationship between the PICs for range sizes and the PICs for the niche variables was then analysed by Spearman rank correlation using the "cor.table" function with the "contrasts" option of the *picante* package (Purvis & Rambaut, 1995 and references therein; Kembel *et al.*, 2010). All analyses were performed with the program R, version 2.13.1 (R Developmental Core Team, 2011).

We will present the results of cross-species and PIC analyses, as both may yield biologically informative results (*cf.* Blackburn & Gaston, 1998; Luna & Moreno, 2010).

Results

The smallest and largest realised pH niche breadths (NB) were observed in *Dryopteris carthusiana* (0.28) and *Adoxa moschatellina* (0.63) for WE, and in *Blechnum spicant* (0.37) and *Hieracium murorum* (0.67) in BA. The NB for light was highest in *Moehringia trinervia* (0.79, WE) and *Paris quadrifolia* (0.74, BA), and lowest in *Mercurialis perennis* (0.17, WE) and *Maianthemum bifolium* (0.35, BA). Across the 11 species sufficiently frequent in both regions, the regional niche breadths for both pH and light were unrelated to each other ($P > 0.28$). Among the species with the lowest niche positions (NP) for soil pH in both regions were *Dryopteris carthusiana*, *D. dilatata* and *Rubus idaeus*, showing optima on highly acidic soils (< pH 4.3). In WE, *Brachypodium sylvaticum*, *Cardamine flexuosa* and *Paris quadrifolia* showed a NP on particularly base-rich soils with pH = 6.6. In BA, with a higher proportion of calcareous soils, some taxa showed even higher NP (*Salvia glutinosa*: 7.7, *Hepatica nobilis*: 7.6, *Veronica urticifolia*: 7.5). The pH niche positions of species occurring in both data sets tended to be positively correlated with each other ($r_s = 0.55$, $P = 0.077$, $n = 11$). The pH niche positions of species were significantly positively correlated with Ellenberg's R indicator values (WE: $r_s = 0.44$, $P = 0.034$, $n = 23$; BA: $r_s = 0.70$, $P < 0.001$, $n = 27$). With respect to light availability, *Ceratocapnos claviculata* had an optimum at 62% in WE, whereas most other species had optima at considerably darker conditions (often only 2%). The same pattern was observed in BA, where few species attained NP for light equal to or slightly larger than 50% (*Galium anisophyllon*, *Lycopodium annotinum* and *Stellaria nemorum*). There was no correlation between the NP for light across regions ($r_s = -0.29$, $P = 0.392$) or between NP and Ellenberg's indicator values for light (WE: $r_s = 0.16$, $P = 0.417$, $n = 29$; BA: $r_s = 0.10$, $P = 0.583$, $n = 34$).

Table 4.2 *Relationship between regional / national range sizes and (realised) niche variables for soil pH and light (expressed as 100% full light minus canopy cover) of species, calculated from the original species data (Spearman rank correlation) for the Weser-Elbe region (n = 30) and the Bavarian Alps (n = 35). a) niche breadth, b) niche position, c) available niche breadth. Significant values are bolded, marginally non-significant values in italics.*

a) Niche breadth

	Weser-Elbe region		Bavarian Alps	
	r_s	P	r_s	P
pH				
Regional range size	**0.39**	**0.031**	*0.32*	*0.063*
National range size	**0.68**	**<0.001**	0.25	0.141
light				
Regional range size	**0.46**	**0.012**	-0.04	0.799
National range size	0.19	0.315	-0.12	0.492

b) Niche position

	Weser-Elbe region		Bavarian Alps	
	r_s	P	r_s	P
pH				
Regional range size	**-0.75**	**<0.001**	-0.14	0.413
National range size	-0.29	0.120	-0.24	0.168
light				
Regional range size	0.17	0.374	0.09	0.590
National range size	-0.05	0.760	0.21	0.220

c) Available niche breadth

	Weser-Elbe region		Bavarian Alps	
	r_s	P	r_s	P
pH				
Regional range size	**0.79**	**<0.001**	0.25	0.166
National range size	**0.63**	**<0.001**	*0.32*	*0.058*

In the cross-species analysis of the WE data we found a positive correlation between the NB for soil pH and national (r_s = 0.68, P < 0.001) as well as regional range size (r_s = 0.39, P = 0.031, both n = 30; Table 4.2, Figure 4.3). For BA there was only a tendency of a positive relationship between regional range size and the NB for pH (r_s = 0.32, P = 0.063, n = 35). Eurasian range size was significantly related to niche breadth only in the Bavarian data set (WE: r_s = 0.32, P = 0.406, n = 30; BA: r_s = 0.47, P = 0.011, n = 28). With respect to light, the only significant relationship was found for species in WE where regional range size increased with increasing niche breadth (r_s = 0.46, P = 0.012; Table 4.2, Figure 4.3).

In the analysis of phylogenetically independent contrasts (PIC), the significant relationships remained about the same (see Appendix 4.2 in Chapter 9). Notable is the tendency for a nega-

tive correlation between national range size and the NB for light in BA (r_s = -0.30, P = 0.084).

The regional range sizes of the studied species decreased with increasing NP for pH in WE (r_s = -0.75, $P < 0.001$), but not in BA (r_s = -0.14, $P = 0.413$; Table 4.2, Figure 4.3). In both regions, there were weak tendencies for the same negative relationship also for national range size, meaning that species confined to high-pH soils tended to be less widespread than acidipyhtic species. The NP for soil pH was unrelated to the Eurasian range sizes of species (WE: $r_s = 0.11$, $P = 0.568$ $n = 30$; BA: $r_s = -0.02$, $P = 0.935$, $n = 28$). In all cases, the NPs of species along the light gradient were uncorrelated with range size. The results of the PIC analysis coincided well with the cross-species analysis (see Appendix 4.2 in Chapter 9).

Available niche breadth (the compound measure of niche breadth and niche position) showed a strong positive correlation with regional ($r_s = 0.79$, $P < 0.001$) and national range size ($r_s = 0.63$, $P < 0.001$; Table 4.2, Figure 4.3) in WE. In BA, in contrast, there was only a (relatively weak) indication of available niche breadth being correlated with national, but not regional, range size. The PIC analyses show the same patterns, but here the relationship between national range size and available niche breadth for pH in BA was significant. The superior performance of available niche breadth compared to niche breadth and position on the regional scale in WE is illustrated in Figs. 4.1b and c, showing the frequency distribution of pH values in forests of the Weser-Elbe region and the contrasting responses of two species to soil pH. *Ceratocapnos claviculata* has a narrow niche breadth (0.32), but as its niche position (2.6) coincides well with the pH range with the largest frequency on the regional scale, the available niche breadth value is relatively high, corresponding to the high number of occupied grid cells in the region (683). In contrast, *Paris quadrifolia* has a larger niche breadth (0.44), but is confined to high-pH soils (niche position = 6.6), resulting in a low value for available niche breadth that reflects the regional rarity of the species (65 grid cells occupied).
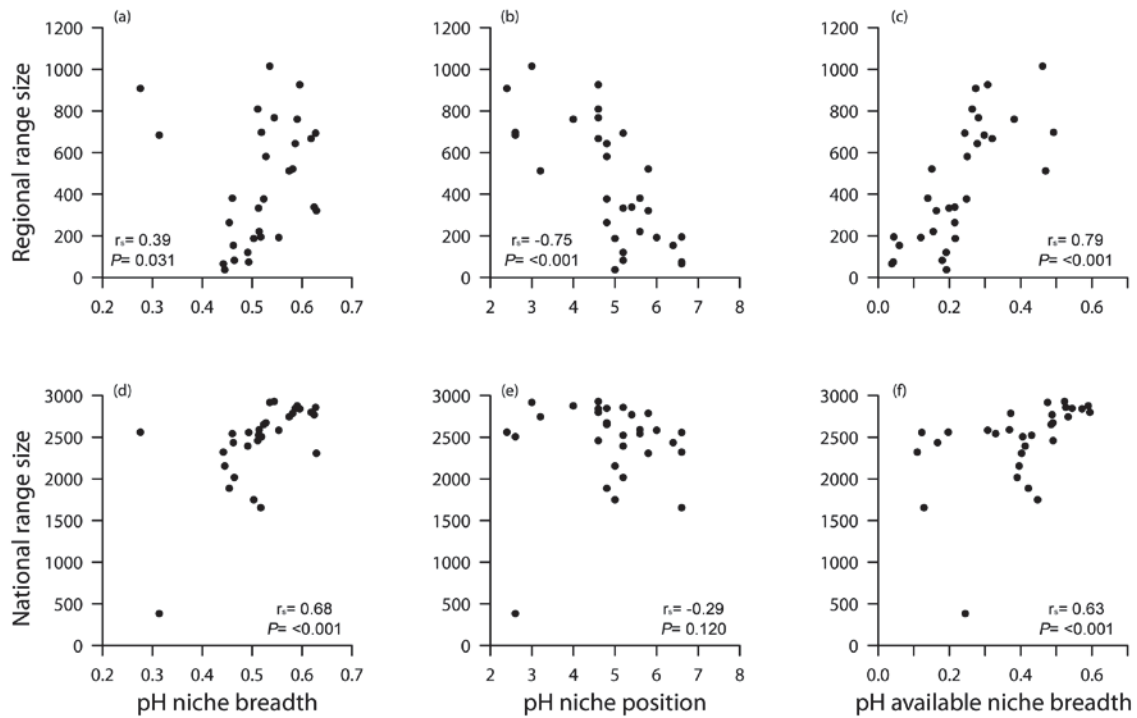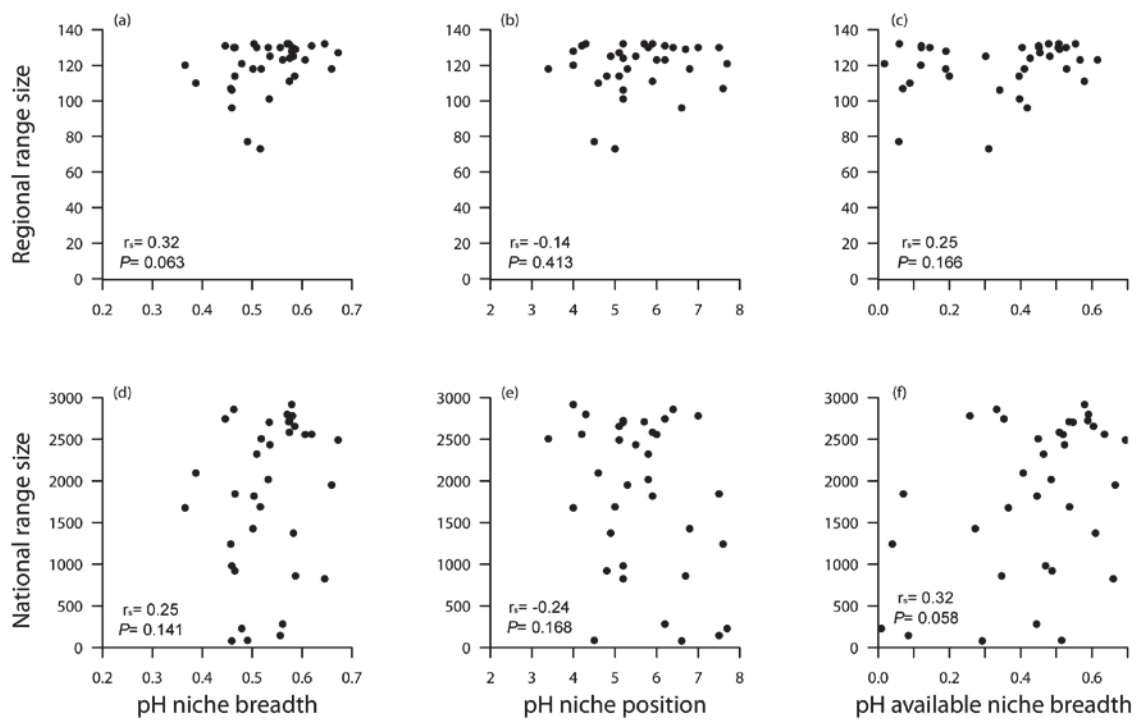
Figure 4.3 *Relationship between regional / national range sizes and (realised) niche (niche breadth, niche position and available niche breadth) for soil pH, calculated from the original species data for a) the Weser-Elbe region (n = 30) and b) the Bavarian Alps (n = 35). Spearman correlation coefficients (r_s) as well as P values are given in each panel (cf. Table 4.2).*

Discussion

The results of the study only partly met our expectations: the niche variables for soil pH in the Weser-Elbe region were in several cases correlated to the range sizes of species, whereas hardly any significant relationships emerged for light in WE and for both environmental factors in the Bavarian Alps. Available niche breadth performed better than niche breadth or niche position alone. In accordance with most other studies comparing cross-species analyses and phylogenetic independent contrasts (e.g. Gaston *et al.*, 1997; Kotze *et al.*, 2003), we found that the results did not fundamentally differ. In the following, we discuss the scale-dependence of environmental predictors of range size, the reasons for the lack of a close relationship between range size and the niche variables for light, and the different performance of niche variables found for the two regions. The discussion concludes by reflecting on the preconditions for a successful application of the available niche breadth.

The importance of niche variables for the large-scale distribution of species has been shown by some studies (e.g. Thompson *et al.*, 1998; Heino, 2005; Heino & Soininen, 2006), but challenged by others (see review in Gaston *et al.*, 1997; Gregory & Gaston, 2000). One of the reasons for this diversity of outcomes is the difficulty of defining and measuring niches, which by definition are multidimensional (Hutchinson, 1957). Moreover, the importance of different variables for the distribution of species is expected to differ between regional and national, or global, scales, reflecting the scale dependence of the relationships between range size and its different predictors, and thus also of the importance of different hypotheses about abundance-range size relationships (Brändle & Brandl, 2001; Pearson & Dawson, 2003; Köckemann *et al.*, 2009; Borregaard & Rahbek, 2010). In fact, on smaller spatial scales, soil parameters are expected to be among the major predictors of plant species distribution, while towards larger scales climate becomes increasingly important (Pearson & Dawson, 2003; Köckemann *et al.*, 2009 and references therein). Accordingly, the importance of soil pH and especially of light for range size is likely to decrease with increasing spatial extent.

A striking example for this scale dependence is *Ceratocapnos claviculata.* This acid-tolerant species is common in WE, despite its narrow pH niche breadth. Although also Germany as a whole has more acidic than base-rich forest sites (Table 4.1), *C. claviculata* is nationally rare, because of its strictly oceanic distribution caused by pronounced frost sensitivity (continentality value of 1, Ellenberg *et al.*, 2001; Voss *et al.*, 2012). The species thus has a narrow climatic niche breadth that, on the national scale, overrules the soil-related niche. In

general, the niche variables may have higher explanatory power on the regional compared to the national or continental scales, as species may not have the same responses to environmental factors across their whole distribution range. Even if the fundamental response is stable, the realised response may not, due to changing competitive relationships with other species, which was most likely the reason for the weak correlation of NBs across species between WE and BA. However, species' responses to edaphic factors are generally known to be relatively constant (Ellenberg *et al.*, 2001; Diekmann, 2003), which is especially true for soil pH: many species are strictly acidophytic (confined to acid soils) or calciphytic (only found on basic soils) across their entire European range.

Overall, the niche variables for pH were superior to light in terms of the relationship with the range size of forest plants. Since pH (and nutrients) as below-ground resources and light as above-ground resource are both among the major determinants of the local distribution of plants (Schuster & Diekmann, 2003; Schuster & Diekmann, 2005), the relatively poor performance of light - also reflected by the lack of a significant correlation between the niche position for light and Ellenberg's L indicator values - is unexpected. In the light of our test results, it appears to be unlikely that this is caused by an insufficient accuracy of canopy cover as (inverse) surrogate for light availability. A general problem may be that our study considered only forest plots with forest specialists (*sensu* Schmidt *et al.* 2011, see Methods), which by definition have similar ecological responses to light (despite possible differences in their fundamental niches), resulting in a relatively short light gradient. In contrast, the study plots comprised a wide range of soil-pH, which thus appears to play a more important role for the distribution patterns of the examined plant species than light availability. In addition, the response of species to light in the field is also dependent on its edaphic environment: for example, on moister soils, some species may be able to tolerate lighter conditions as they are able to compensate higher transpiration rates by water uptake. Thus, within the range of light availabilities offered in forests, the light niche of species will partly depend on their responses to soil factors and is unlikely to have any effect on range size.

It was obvious that the niche variables performed reasonably well in the Weser-Elbe region, but not in the Bavarian Alps. The latter region is much more diverse in terms of climate and topography (strong differences between altitudinal belts, slope aspects and landforms), but also bedrock geology (*cf.* Schmidtlein & Ewald, 2003). In addition, there is a larger variation in soil conditions: the calcareous soils in BA often have extremely steep vertical pH-gradients

within the same profile and high lateral within-plot variation of humus depth and stone con-
tent (Ewald, 1999). This means that, in the Bavarian Alps, the species experience a wider set
of conditions (*cf.* Boulangeat *et al.*, 2012) over a small area than in the Weser-Elbe region,
and that the realised niche is more difficult to quantify and to 'reduce' to any variable such as
pH or light. Consequently, most forest species in BA considered in this study are also widely
distributed throughout the region, resulting in a much smaller variation in regional range size
compared to WE.

Available niche breadth, the compound measure of niche breadth and position, showed in two
(in the PIC three) out of four cases a significant relationship with the range sizes of species
and thus turned out to be a better predictor than the single variables. Intuitively, this makes
sense to us, because - everything else being equal - species with a broad ecological amplitude
and an ecological preference for widespread habitats are likely to have larger range sizes than
species with a narrow amplitude and specificity to rare habitats. The predictive ability of
available niche breadth would fail if it were associated with a low competitive or dispersal
ability - or other traits negatively affecting species distribution, for which, however, there is
no evidence. Thus, to evaluate the generality of niche variables as determinants of range size,
more studies are needed that use measured environmental variables, are based on equal-sised
data sets for all species, and additionally examine the relationship between the niche variables
of species and their corresponding life history attributes, especially in cases where niche
breadth or position fail.

The scarcity of data on frequency distributions of environmental variables so far may render
the calculation of available niche breadth values difficult, but the increasing number of moni-
toring programmes on large spatial scales will improve the data basis for such calculations.
Examples are the ICP Forest Project (http://icp-forests.net/) for Europe and the Forest Inven-
tory and Analysis (FIA) Program of the U.S. Forest Service (http://www.fia.fs.fed.us/), the
results of which will enable the future calculation of available niche breadth measures for
other environmental variables than soil pH. If niche breadth or position are calculated relative
to the proportion or identity of habitat types occupied by species (see, e.g. Thompson *et al.*,
1998; Cowley *et al.*, 2001), vegetation or habitat maps will also help to determine available
niche breadth estimates.

Supplemental Material

Additional Supporting Information can be found in the Appendix (Chapter 9):

Appendix 4.1 Plant species included in the study with information on environmental data, range sizes and niche variables

Appendix 4.2 Relationship between regional / national range sizes and (realised) niche variables for soil pH and light, calculated from the phylogenetically independent contrasts

Acknowledgements

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Chapter 5

Comparing resource based and co-occurrence based methods for estimating species' niche breadth

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under revision
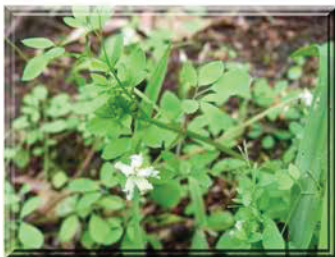
Top left: *Light conditions at the forest floor as an important resource based gradient (Picture taken on 22.06.2012 by A. Pannek)*

Bottom right: *Co-occurring species at the forest floor (Picture taken on 20.06.2012 by A. Pannek)*

Top right & bottom left: *The troublemakers of this study:* Ceratocapnos claviculata *(bottom)* and Dryopteris carthusiana *(top). Both pictures taken on 19.06.2012 by A. Pannek.*

Abstract

Questions Examining the responses and co-occurrence patterns of 30 herbaceous forest plant species sampled altogether in 302 plots, we asked whether the niche estimates of rare and common species are affected by the different sample sizes for these species, and whether the resource based niche estimates coincide with the values obtained with the co-occurrence based approach.

Location Deciduous forests in north-western Germany

Methods We compare the classical method of determining niche breadth as the response of a species along environmental resource gradients (here soil pH and light availability) with a recently introduced method based on the co-occurrence of a target species with other species, using the Jaccard and Multi-Simpson index for turnover calculations.

Results The total frequency of the species in the data set had a strong effect on the niche breadth estimates in the resource based methods, with species with higher frequencies having larger niches. In contrast, co-occurrence based niche breadth was independent of sample size. When calculating the niche breadth estimates for equal numbers of plot occurrences for all species, none of the methods resulted in significant differences between common and rare species. Soil pH niche breadth and co-occurrence based niche breadth were unrelated to each other, whereas light niche breadth and soil pH niche breadth corrected for the different frequencies of pH values in the region were positively correlated with the co-occurrence based estimates. Species richness, increasing with increasing soil pH, was negatively correlated with niche breadth.

Conclusions As the co-occurrence method is not distorted by varying plot frequencies, it offers a reliable alternative for extracting species niches from vegetation surveys even if no environmental data is available. The gradient approach however remains important, as it provides additional information about measured niche characteristics (e.g. optima, breadth) along these gradients, which is of particular importance in various fields of applied ecology.

Keywords

Introduction

To counteract biodiversity loss as a result of habitat destruction and climate change (e.g. Sala *et al.*, 2000), one of the most important tasks of ecologists is to examine which species are most vulnerable to these transformations of their environment. An indicator of a species' susceptibility to current environmental threats is its position along a specialist-generalist gradient (Slatyer *et al.*, 2013), as the specialisation of a species can be viewed as a trade-off between how efficient it is to use a given level of a resource, and in how far it can exploit the range of different resources (Colwell & Futuyma, 1971; Boulangeat *et al.*, 2012). The extent of ecological specialisation can thus be regarded as a key trait for predicting the decline or increase in species (Clavel *et al.*, 2010; Ozinga *et al.*, 2013). One measure of ecological specialisation is the so-called "niche", a versatile concept in ecology, which in its broadest sense describes the suite of (environmental) conditions at which a species thrives. The most widespread definition was provided by Hutchinson (1957), who stated that the niche of a species is a measure of the n-dimensional space of resources needed for its long-term survival.

There is a wide range of methods for the estimation of niche characteristics of species (Slatyer *et al.*, 2013), all having their advantages and disadvantages. In the classic approach, niches are determined based on the responses of species along environmental gradients (e.g. Whittaker, 1956; Underwood, 1978). With respect to one particular factor, the niche breadth can be described as the range of values along the gradient that a species is able to utilise (Brown, 1984), while the niche position reflects the point along the gradient at which the species is most likely to occur, i.e., has its optimum. Niche breadth and niche position can also be combined into the measure of "available niche breadth", which, for a given region, takes into account the varying availabilities of different resource states (Pannek *et al.*, 2013). A species has a large available niche breadth only if it is capable of utilising a wide range of resources and, in addition, if these resources are also realised in the area. The classic approach has the drawback that the researcher's choice of factors considered for niche determination is often based on expert knowledge and on the availability of environmental information, whereas gradients that are more relevant for species occurrence might be overlooked (Austin & Meyers, 1996; Fridley *et al.*, 2007). Moreover, a species can be a generalist on the measured gradient but a specialist in its response to other, non-measured variables (Gaston *et al.*, 1997; Clavero & Brotons, 2010).

A novel approach introduced by Fridley *et al.* (2007) circumvents the above problems by looking at the co-occurrence patterns of species in vegetation matrices, where habitat generalists and specialists are defined based on the number of species with which a target species co-exists. This method relies on the assumption that a generalist will co-occur with many different species, whereas a specialist will tend to have only few neighbours. As a consequence, the turnover of species across plots can be used to measure the extent of habitat specialisation (Fridley *et al.*, 2007). Inspired by the original work of Fridley *et al.* (2007), some methodological modifications were proposed to overcome potential bias in the choice of turnover measures (Manthey & Fridley, 2009; Zelený, 2009; Botta-Dukát, 2012), and several studies have applied the co-occurrence approach for a broad range of research questions (e.g. Albert *et al.*, 2010; Chabrerie *et al.*, 2010; Zelený *et al.*, 2010; Abadie *et al.*, 2011; Manthey *et al.*, 2011; Boulangeat *et al.*, 2012; Fajmonová *et al.*, 2013; Wasof *et al.*, 2013).

This study aims at comparing the resource based method and the co-occurrence method by calculating niches for the same set of herbaceous forest species. For the resource based method, we selected soil pH and light availability at the forest floor as our main environmental factors of interest. In Central Europe, soil acidity is one of the best predictors for the occurrence of vascular plants (Schuster & Diekmann, 2003), because it is closely correlated with other soil variables, notably the availability of several nutrients and the concentration of toxic elements like aluminium (Falkengren-Grerup, 1995; Peppler-Lisbach & Kleyer, 2009). Soil pH thus represents a complex gradient in nutrient status and also has the advantage to be easy to measure, and indeed there is more species-related information available for pH than for any other soil variable. Light availability, on the other hand, is a key limiting factor for species in the forest understory (Ellenberg *et al.*, 2010) and known to affect the local distribution of forest herbs (Schuster & Diekmann, 2005).

One problem inherent to many studies on species' niches is that the estimation of niche breadth is often confounded by a sampling bias (reviewed in Gaston *et al.*, 1997) that arises when more plots (and therefore more data points) are available for common species than for rare ones. This bias has only exceptionally been corrected for (but see for example Burgman, 1989; Boulangeat *et al.*, 2012). However, adequate information on the effects of this potential bias is largely missing. Therefore, we created and analysed two types of data sub-sets: the first type consisted of matrices with the same number of plot occurrences for all species irrespective of their frequency in the total data set. For the second type, all plot occurrences of a

species were considered for the estimation of niche characteristics, i.e., the matrices of the common species included more plots than those of the rare species.

More specifically, we wanted to answer the following questions:

(1) Do the varying numbers of plot occurrences of rare and common species have an effect on the niche breadth estimates?

(2) Do the resource based and co-occurrence based methods give similar estimates of niche breadth?

(3) Do differences in plot species richness along the environmental gradients affect the results of the two approaches?

Material and Methods

Study area and data set

Field work was conducted in semi-natural deciduous forests located in the Weser-Elbe region of North-western Germany. The area is relatively uniform in terms of climate, geology and topography, and the landscape is at present primarily covered by agricultural land. Woodlands occupy only 9.8% of the area (Kelm, 1994) and consist of both deciduous forest and planted coniferous forest, with most of the woodland being managed.

The data set used for the analysis consists of 302 sample plots of an average size of c. 400 m^2. The majority of plots (227) were compiled from different literature sources (Wulf, 1992; Heinken, 1995), but additional plots were collected during the growing seasons of 2011 and 2012. The plots cover the whole spectrum of forest communities on mineral soils present in the lowlands of northern Germany. Sampling followed a phytosociological approach (Braun-Blanquet, 1964), meaning that all plots were placed in forest sites with a high degree of ho-mogeneity in terms of topography and species composition. In each plot, all vascular plants were recorded, soil samples taken for chemical analysis and the canopy cover estimated by eye (see Pannek *et al.*, 2013). The pH-values (2.36 to 7.00, measured in a $CaCl_2$ solution with a glass electrode according to standard procedures) covered the whole range of soil acidity found in forest soils of this region (*cf.* Bundesministerium für Ernährung, Landwirtschaft und Forsten, 1996). Light availability at the forest floor was expressed as '100% - canopy cover', which has been shown to be a reliable proxy for measured light availability (Pannek *et al.*, 2013). These relative light values ranged from 1 to 80%, with a mean of 20%.

For the statistical analysis, we selected all herbaceous forest plant species that show a preference of growing in closed forests or in forest edges and gaps (according to Schmidt *et al.*, 2011), and that were present in at least 46 out of the 302 sample plots (in total 30 species). The number of 46 sites represents a compromise between the wish to maximize the number of plot occurrences for each species and the need to include also rare species. As all species and environmental data were collected in the field under natural conditions, the niche estimates refer to the realised (ecological) niches of species, and no conclusions can be drawn from the results as to the species' fundamental (physiological) niches.

Calculation of niche breadth and niche position

For the determination of niche breadth (NB), the environmental gradients were divided into equally spaced intervals of 0.2 units for soil pH and 5% units for light. We then calculated the percentage occurrence of each species in each interval. To account for the varying frequency of plots along the environmental gradients, the number of plots in each interval containing the species was divided by the total number of plots in that interval, thereby obtaining a percentage occurrence of each species in each interval (Kolb *et al.*, 2006). Then, NB was calculated on a 0-1 scale according to the following equation (Økland, 1986):

$$NB = \frac{\left(\sum I_{ij}\right)^2}{n \sum \left(I_{ij}^2\right)}$$

(1)

where I is the percentage occurrence of a species i in an interval j, while n is the total number of intervals along the gradient.

The niche position (NP) describes the optimum (highest likelihood of occurrence) of a species along an environmental gradient. NP was determined as the mode of the polynomial regression line of the response of the species along the environmental gradients (see Kolb *et al.*, 2006).

For the calculation of the available niche breadth (ANB) for soil pH, the NB of each species i was multiplied by a correction factor (CF, ranging from 0 to 1):

$$ANB_i = NB_i * CF_i$$

(2)

The CF takes into account the commonness of the different resource states in an area that a species is able to exploit. The forests in the Weser-Elbe region grow predominantly on low-pH soils, and the abundance of forest sites decreases with increasing pH (*cf.* Bundesministerium für Ernährung, Landwirtschaft und Forsten, 1996). Therefore, we applied a linear function to determine the CF:

$$CF = a + b * NP_i$$
(3)

Here, NP is the niche position for pH of species i. To estimate the parameters a and b, it was assumed that CF = 1 if NP equals the lowest measured pH value in the area, while CF = 0 if NP equals the highest measured value. For more details on the calculations of CF and ANB, see Pannek *et al.* (2013).

Estimation of niche breadth based on the co-occurrence approach

For the calculation of co-occurrence values we generally followed the approach described in Fridley *et al.* (2007). However, we replaced additive partitioning, which has originally been used as turnover index, with two alternative measures of beta diversity (for the bias of additive partitioning see Zelený, 2009): the mean Jaccard dissimilarity of plot pairs and the Multiple Simpson index proposed by Baselga *et al.* (2007). Both indices are relatively robust against positive skewness of plot richness distributions, i.e., when species occur more often in species-poor than in species-rich plots (for more details on the behaviour of different beta diversity indices in the context of co-occurrence based niche modelling see Manthey & Fridley, 2009). Since the Multiple Simpson index of Baselga *et al.* (2007) is influenced by sample size we used a randomization technique, where 20 plots from the plot × species matrix containing a focal species are randomly chosen for the calculation of co-occurrence values, thereby keeping total plot frequency constant across species. For each species, we applied this randomization 100 times and used the average value (R code is provided in Appendix S1 of Manthey & Fridley, 2009).

Statistical analysis

In a first step, two data sets were created from the original material. One data set consisted of matrices of a constant number of 46 plots for each of the species (i.e. 30 matrices, in the following referred to as *equal frequency data set*) to obtain equal sample sizes for all, both common and rare, taxa (*cf.* Pannek *et al.*, 2013). This was achieved by randomly selecting 46 plots out of all plots containing the target species. The second data set again consisted of 30 matrices (one for each species), but in contrast to the first data set all plots with a target spe-

cies were considered in the matrix, thereby resulting in much larger data tables for the common than for the rare species (further on referred to as *varying frequency data set*).

In a next step, we calculated all niche measures for each species using the methods described above, separately for the *equal frequency data set* and the *varying frequency data set*. We finally compared the results from the different methods of assessing niche characteristics. Since the variables were not normally distributed, Spearman rank correlations were applied in all analyses using the program R (v. 3.0.2, http://www.r-project.org/; R Foundation for Statistical Computing, Vienna, AT).

Results

The number of sampled plots for each species ranged from 210 for *Oxalis acetosella* to 46 for *Paris quadrifolia* (mean = 100 plots). The varying species frequency had a strong influence on the niche breadth estimates of the resource based method when using all plots with the target species. Species with a higher frequency in the data set showed a significantly larger niche breadth than rare species (Table 5.1).

Table 5.1 *Relationship between different estimates of niche breadth and the total frequency of species in the vegetation data set of 302 plots. The niche breadth estimates were based either on all plots in which the species occurred (*varying frequency data set, *left columns) or on a constant number of 46 plots including the target species (*equal frequency data *set; right columns). Results of Spearman correlation tests are given (significant values bolded), n = 30 in all cases.*

| | Estimate based on | | | |
| | all plots | | 46 plots | |
Niche breadth estimator	r_s	P	r_s	P
Soil pH	**0.863**	**<0.001**	0.321	0.084
Light availability	**0.559**	**0.001**	0.114	0.547
Available niche breadth for soil pH	0.301	0.106	0.315	0.090
Jaccard index	0.217	0.249	0.092	0.628
Multiple Simpson index	0.230	0.222	0.092	0.628

This was true both for soil pH and for light. In contrast, the number of occurrences did not have a positive effect on the available niche breadth for pH. The co-occurrence based estimates of niche breadth were independent of the number of sampled plots. When using the *equal frequency data set* with equal numbers of plot occurrences for all species, the niche breadth estimates were found to be independent of the total frequency of species (Table 5.1), i.e. there was no longer a systematic difference in the calculated niche breadths for rare and common species.

The difference between the estimates of pH niche breadth based on the two data sets becomes
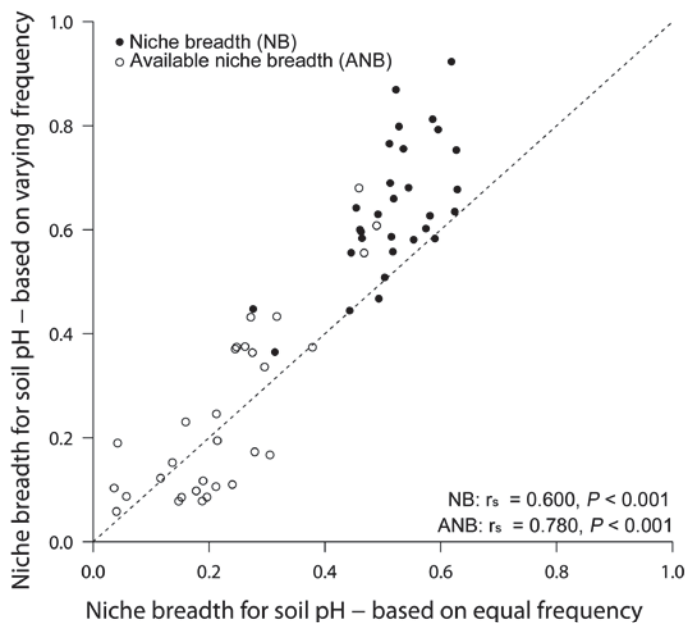
obvious in Figure 5.1, where the values derived from the *varying frequency data set* were consistently higher than those obtained from the *equal frequency data set*. This did not apply for the available niche breadth values being scattered around the x = y diagonal. Furthermore, the estimates for available niche breadth were much smaller (mean: 0.23) than those for niche breadth (mean = 0.52).

Figure 5.1 *Comparison of niche breadth estimates for soil pH, calculated either on the basis of all plots in which the species occurred (*varying frequency data set*) or using a constant number of 46 plots including the target species (*equal frequency data set*). Results are shown for niche breadth (NB, ●) and available niche breadth (ANB,○). n = 30 species. The dashed line represents the diagonal with y = x.*

The two niche estimates based on co-occurrence matrices, the Jaccard index and the Multiple Simpson index, were highly positively correlated with each other, both when using all plots (r_s = 0.94, P < 0.001) and when considering a constant number of 46 plots per species (r_s = 0.94, P < 0.001, all n = 30; Figure 5.2).

Figure 5.2 *Relationship between the two co-occurrence based (species similarity) estimates of niche breadth, Jaccard index and Multiple Simpson index, based on a constant number of plots for all species (equal frequency data set; n = 30).*
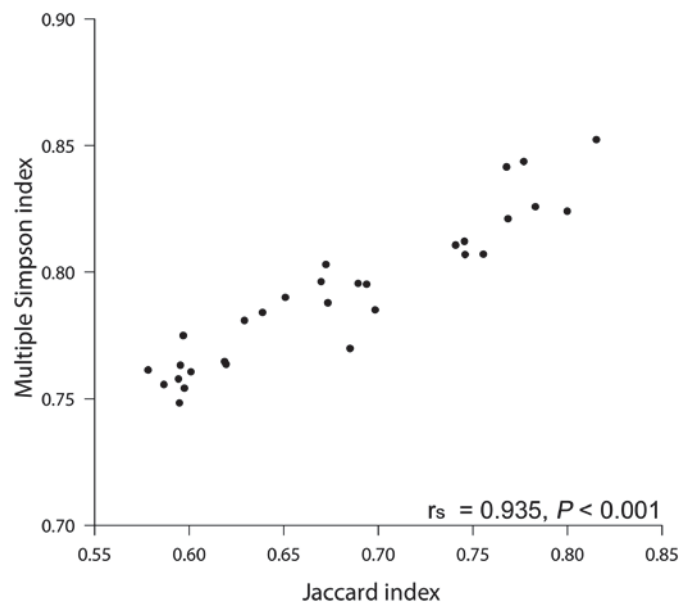
The resource based niche breadth for soil pH was uncorrelated with the species co-occurrence based estimate of niche breadth (*equal frequency data set*, Figure 5.3a; results are shown for the Jaccard index, but those for the Multiple Simpson index were almost identical). Two species behaved as outliers, *Dryopteris carthusiana* and *Ceratocapnos claviculata*, having high Jaccard indices between 0.75 and 0.8, but low niche breadths for soil pH of around 0.3. In

contrast, the available niche breadth for soil pH was highly positively correlated with the co-occurrence based estimate (Figure 5.3b). Here, no outlier species could be identified. The same was true for the correlation between the niche breadth for light and the Jaccard index (Figure 5.3c). Values for the calculated niche breadths for all species from the *equal* and *varying frequency datasets* are given in Appendix 5.1 in Chapter 9.

The mean species richness of plots including the different target species ranged from 10 for *Ceratocapnos claviculata* to 28 for *Carex remota* (mean = 22). In general, plot richness increased with increasing soil pH ($R^2 = 0.42$, $P < 0.001$). There were significant negative correlations between plot richness and the niche estimates for light availability, available niche breadth for soil pH and both co-occurrence based measures (Table 5.2), meaning that species with small niche breadths occurred predominantly in plots with high species richness. Only for the pH niche breadth, no significant correlation with plot richness was observed (Table 5.2).

Table 5.2 *Relationship between different estimates of niche breadth and mean species richness of plots containing the target species. The niche breadth estimates were based on a constant number of 46 plots including the target species (*equal frequency data set*, see Table 5.1). Results of Spearman correlation tests are given (significant values bolded), n = 30 in all cases.*

Niche breadth estimator	r_s	P
Soil pH	-0.084	0.658
Light availability	**-0.661**	**<0.001**
Available niche breadth for soil pH	**-0.646**	**<0.001**
Jaccard index	**-0.874**	**<0.001**
Multiple Simpson index	**-0.817**	**<0.001**

Discussion

In this paper, we aimed at comparing the classic resource based approach of measuring niches with the more recent, indirect approach of estimating niches from co-occurrence matrices of species. We will discuss the results along the three research questions outlined in the introduction.

The importance of the number of plot occurrences for niche breadth estimations of rare *vs.* common species has been a topic of debate for some time (see review in Gaston *et al.*, 1997). Evidence from studies correcting for this bias statistically (e.g. Burgman, 1989; e.g. Kolb *et al.*, 2006; Reif *et al.*, 2010) indicates that the species' niche breadths based on many sites are generally larger than estimates based on fewer sites. This fact may render studies not correcting for this bias invalid or hard to interpret (Gregory & Gaston, 2000), although in the past decade, researchers increased their efforts to control for sample size (Slatyer *et al.*, 2013).

This study suggests that the effect of sample size is considerable: Regarding the niche estimates for soil pH and light, the values were positively related to the number of plot occurrences of species, i.e. more common species had systematically wider niches than rare species. This pattern disappeared for the measure of available niche breadth for pH, because here the commonness or rarity of species is not only explained by their niche breadth, but also by their niche position (optima), taking into account whether the resource states preferred (or best tolerated) by species are themselves common or rare (resource availability hypothesis, see e.g. Gaston *et al.*, 1997; Gregory & Gaston, 2000). The available niche breadth thus captures niche breadth and niche position in one composite value.

In contrast, the co-occurrence based approach appears to be unbiased (or only weakly biased) with regard to the number of plots sampled for each species. This is, at least partly, due to the randomization technique already implemented in the original method invented by Fridley *et al.* (2007), which ensures that all focal species obtain the same plot representation and which has also been applied in other studies using the co-occurrence approach (e.g. Abadie *et al.*, 2011; Boulangeat *et al.*, 2012). In general, species with a very high frequency in a given dataset will inevitably co-occur with most other species and thus, are estimated as generalists. However, empirical evidence from the analysis of different datasets shows that, below a certain threshold, this positive correlation between frequency and niche breadth tends to disappear (e.g. Fridley *et al.*, 2007; Manthey *et al.*, 2011 and unpublished work).

The fact that species with a preference for species-rich communities on base-rich soils had lower turnover rates compared to species from species-poor communities on acidic soils also reflects the specific nature of the co-occurrence approach – it scales the environment according to the diversity of existing communities and not by any "traditional" scaling of environmental factors. This relates to the discussion about the advantages and disadvantages of direct *vs.* indirect ordination, in that the direct approach might "miss" the most important gradients or scales them inappropriately while indirect methods might be based on unrealistic assumptions about species-environment relationships (see Ejrnæs, 2000 and references therein for further discussions on this topic).
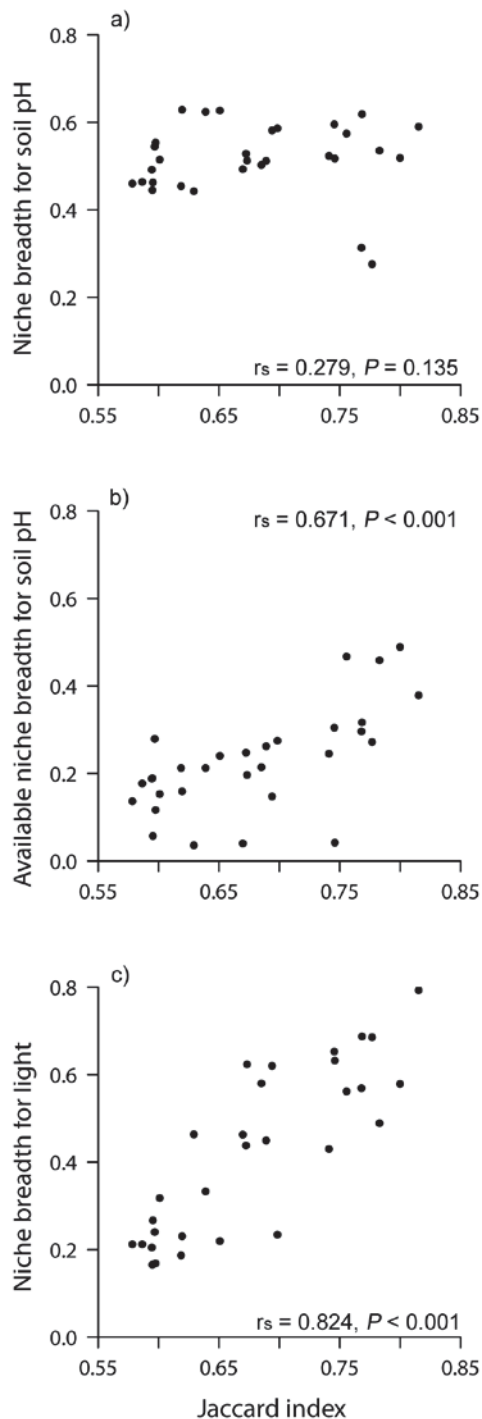
Figure 5.3 *The Jaccard index as predictor of three resource based estimates of niche breadth: a) niche breadth for soil pH, b) available niche breadth for soil pH, c) and niche breadth for light. For all species (n = 30), a constant number of plots including the target species were used in the analyses (equal frequency data set).*

Overall, when keeping the number of plot occurrences of species constant, the resource based approach (for light and the available niche breadth for soil pH) and the co-occurrence based approach resulted in niche breadth estimates that were positively correlated. Surprisingly, there was no significant correlation between the soil pH niche breadth and the Jaccard index. This finding is best explained by the behavior of two species, the herb *Ceratocapnos claviculata* and the fern *Dryopteris carthusiana*. These are confined to a narrow range along the soil pH gradient (low-pH sites), translating into a narrow pH niche breadth. In the study area of the Weser-Elbe region, however, they are omnipresent in forests wherever the soil pH is adequately low, which is the case in a majority of plots (*cf.* Bundesministerium für Ernährung, Landwirtschaft und Forsten, 1996). Consequently, the turnover rates of co-occurring species, also being determined by the heterogeneity of other environmental drivers such as soil moisture or the level of disturbance, are high, resulting in a multitude of species that co-occur with *C. claviculata* and *D. carthusiana*. Whereas the resource based approach reflects that the two species are specialised with regard to their pH niche, the co-occurrence based method emphasizes their broad amplitudes relative to other niche axes. That species can be classified differently with the direct *vs.* indirect approach was already predicted by Manthey *et al.* (2011). Interestingly, the co-occurrence based estimates coincided with those for the available niche breadth for pH.

Here, the correction for the availabilities of different resource states inherent to the measure causes the two species *C. claviculata* and *D. carthusiana* to attain relatively high values de-

spite their restricted soil pH niche. Thus, the available niche breadth captures the "niche" better than pH niche breadth without a correction.

For light, no adjustment of the niche breadth estimate was possible, because no data for the frequency distribution of different light values in forests are available for the study area (or any area). However, across species, the niche breadth estimates for light were highly positively correlated with the co-occurrence based estimates.

Except for soil pH, the niche breadths of species were negatively correlated with the mean species richness of plots in which the species occurred. At the same time, plot species richness increased with soil pH. This means that species preferring base-rich sites had narrower niche breadths than those confined to more acidic sites. These observations are interesting for two reasons. First, the higher species richness of more base-rich soils runs counter to the generally higher availability of acidic habitats in the region (Bundesministerium für Ernährung, Landwirtschaft und Forsten, 1996), which would suggest a larger species pool of acidophilous species (Pärtel, 2002). However, Ewald (2003) already hypothesised that the low number of acidophilous (forest) species in Central Europe can be explained by Pleistocene range contractions causing the extinction of many acidophilous species, because acid soils were rare when the refugial areas of plants were at their minimum (but see also Peet *et al.*, 2003 for a contradicting case). Second, the observation that a majority of forest species on base-rich soils showed narrow niche breadths supports the hypothesis of MacArthur (1972) that the realised niche decreases when the species pool and the number of species in a community increase. This effect of species packing, i.e. narrower niches at base-rich sites with higher densities of species optima, has also been shown for forest species in Denmark (Lawesson & Oksanen, 2002). The finding of narrow niches in species-rich communities further suggests that base-rich sites in the study region - compared to acidic sites - are more homogeneous in terms of other important site conditions. This would translate into lower species turnover rates at base-rich sites in the co-occurrence approach.

Conclusions

Whether a species is a generalist or a specialist plays an important role for its predicted response to climate change, and we agree with the opinion of Abadie *et al.* (2011) that an accurate assessment of species specialisation is essential. Both approaches tested in this study have their strengths and weaknesses. While it has been argued by Wasof *et al.* (2013) that the co-

occurrence approach relies too much on the biotic components of the niche, the resource based approach has been criticised because a lack of pattern can always be explained by the multi-dimensional nature of the niche: the measured gradient might simply not be relevant for the system or species studied (Colwell & Futuyma, 1971; Gregory & Gaston, 2000). Furthermore, our results suggest that the direct approach may suffer from unusual behaviours of species and from the distorting effect of the varying number of occurrences. If, however, the measured gradient is important and scaled appropriately, a sufficient number of observations is sampled also for rare species and the niche breadth is corrected for the frequency of different resource states, the direct approach works well and has the advantage of being more "real". In general, this study supports the use of the co-occurrence method as a reliable alternative for extracting species niches from vegetation surveys even if no environmental data is available. Both approaches are complementary with respect to the resulting information. On the one hand, the co-occurrence method provides a measure of realised niche breadth that integrates all drivers of species composition in a given ecosystem. The direct approach, on the other hand, measures niche breadth only along selected gradients but provides additional information about species optima along these gradients, which is of particular importance in various fields of applied ecology.

Supplemental Material

Additional Supporting Information can be found in the Appendix (Chapter 9):

Appendix 5.1 Calculated niche breadth values for all species used in the study from the *equal* as well as *varying frequency datasets*

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Chapter 6

*Know your limits -
the need for better data on species' responses
to soil variables*

Diekmann, M., Michaelis, J. & Pannek, A.

under revision

Abstract

Even though habitat destruction and change in terms of an altered edaphic environment is the main factor behind the decline of plant species in Central Europe, species distribution modelling has largely focused on climatic variables and their significance for future species ranges. In this study, we argue that more attention should be paid to soil variables and to the responses of species along soil gradients. Examples from deciduous forests and calcareous dry grasslands show that response optima and especially response limits relative to soil pH and phosphorus availability are more closely related to the range sizes and threat levels of species than the traditionally applied Ellenberg indicator scores, and that species assumed to have similar preferences show considerable, ecologically relevant differences in their thresholds. There is an urgent need for collecting more and better soil data and for analyzing the relationships between the spatial distribution of plant species and edaphic variables, in order to identify optimal and marginal habitats of species as a pre-requisite for their successful conservation.

Zusammenfassung

Obwohl Habitatzerstörung und der vor allem durch edaphische Veränderungen hervorgerufene Verlust an geeigneten Lebensräumen als wichtigste Ursachen für das Verschwinden von Pflanzenarten in Mitteleuropa gelten, beschäftigen sich Modelle zur zukünftigen Verbreitung von Pflanzen vornehmlich mit dem Einfluss von Klimafaktoren und Klimawandel. Bodenfaktoren und den Reaktionen von Pflanzen entlang von Bodengradienten sollte daher größere Aufmerksamkeit geschenkt werden. Beispiele aus Laubwäldern und Kalkmagerrasen belegen, dass die Optima und speziell Grenzwerte von Arten in Bezug auf den Boden-pH und die Verfügbarkeit von Phosphor enger mit der Verbreitung und Gefährdung der Arten korreliert waren als die Zeigerwerte von Ellenberg, die traditionell zur Charakterisierung der Ökologie der Arten herangezogen werden. Arten mit ähnlichen Optima unterschieden sich zum Teil deutlich in ihren Grenzwerten, die wiederum einen signifikanten Einfluss auf die Verbreitung der Arten hatten. Wir sehen es als dringend erforderlich an, in größerem Umfang Bodendaten zu erheben und die Reaktionen der Arten entlang von edaphischen Gradienten zu analysieren, um sowohl die Optimal- als auch Marginalstandorte von Arten im Hinblick auf deren erfolgreichen Schutz besser charakterisieren zu können.

Keywords

Over the last years, species distribution models (SDM) have become increasingly popular in ecology, especially in the framework of climate change research. SDM relate the distribution of organisms to a suite of environmental predictors, most often on large spatial scales and by primarily using climatic variables (Guisan & Thuiller, 2005). These models allow to determine the relative importance of different factors for the distribution of species, thereby enabling us to, for example, predict the responses of species to environmental change and to identify areas not yet occupied that might be suitable for the species in the future. Even though it has since long been recognised that many range limits of species are closely related to specific values of climatic variables, notably temperature (e.g. Iversen, 1944), more quantitative approaches have emerged only about 10-15 years ago when new modelling techniques and large climate data bases became available (Elith *et al.*, 2006). The popularity of SDM in ecology is reflected in the recent exponential increase in the number of publications on the topic. A search in the *Web of Science* on December 16, 2014, resulted in 1513 findings of papers using the term "species distribution models", about 2/3 of which published over the past three years.

Hardly any of the above publications integrate variables other than climatic. Among the few exceptions are recent papers by Coudun *et al.* (2006), Bertrand *et al.* (2012), Chambers *et al.* (2013), Dubuis *et al.* (2013) and Beauregard and de Blois (2014). They give credit to edaphic variables by acknowledging their value in SDM, but still centre on the importance of climatic drivers for the distribution of species. While this appears to be a logical approach for climate change research acting on a global level, it is not meaningful on more regional or local scales. In fact, from a viewpoint of a plant ecologist and conservation biologist, the strong focus on climate is unsatisfactory, because the main causes of species loss in most regions of the world are habitat loss and habitat change. In Germany, these two processes, often caused or accompanied by the addition of nutrients due to e. g. atmospheric deposition and fertilisation, are the most important factors behind the decline of vascular plant species (Korneck *et al.*, 1998). At the global scale, the addition of nitrogen and phosphorus to ecosystems has been identified as a process where the planetary boundary of what the Earth can tolerate - without facing unacceptable environmental changes - has been exceeded (Rockström *et al.*, 2009; Steffen *et al.*, 2015). The distribution of many plant species especially in regions with a low climatic and topographic heterogeneity is mainly a function of bedrock and soil conditions. In the lowlands of North-western Germany, for example, the absence of many calciphilous species (such as the orchids *Orchis militaris* and *O. morio*; Garve, 2007) is caused by the scarcity of lime-rich,

high-pH soils and not by any climatic factor, as these species show an extent of occurrence far beyond the region. Furthermore, the dramatic decline of many stress-tolerant species with a low competitive ability is caused by eutrophication and competitive exclusion, not climate change. This means that, while the future movement of species due to climate change will be prompted and in parts be controlled by climatic variables, establishment in new areas will also be strongly affected by the availability of suitable sites (apart from being dependent on the species' dispersal capacities).

A main reason for disregarding soil variables in SDM is data shortage. Whereas many climatic variables can easily be extracted from climate data portals such as WorldClim (e.g. Hijmans *et al.*, 2005 http://www.worldclim.org), soil variables vary on much smaller spatial scales, and their sampling involves time-consuming field work and often expensive laboratory measurements. The few available soil data have often been obtained using different methods with regard to, for example, sampling depth or chemical analysis, which further complicates comparability and interpretation. Therefore, measurements of important environmental drivers in terms of soil variables have in most cases been replaced by an indirect assessment of habitat quality by means of indicator values. These quantify the ecological behaviour of species integrated over time, instead of reflecting conditions at a specific moment. In Europe, one widely used system of indicator values is that of Ellenberg *et al.* (2001), who developed indicator scores for three climatic factors (light, temperature and continentality) and four edaphic factors (soil moisture, reaction [pH], nitrogen and salt). These indicator values have been widely and successfully used in ecological research (Diekmann, 2003) and are indispensable in historical studies when environmental measurements for the past are not available. However, a drawback for the application of indicator values in SDM is that they are not easily transformed to real values (Wamelink *et al.*, 2005). Another general problem consists in the risk to obtain biased results when using mean indicator values for the interpretation of ordinations of vegetation data (Zelený & Schaffers, 2012). More importantly, indicator values describe the response optima of species relative to environmental variables in the field, but do not include any information on response limits. In the same way as the large-scale geographic distribution of species is limited by climatic variables, their small-scale distribution is limited by soil variables: it is a valid assumption that there are many edaphic physiological thresholds beyond which species are not able to survive (for soil pH, see Falkengren-Grerup & Tyler, 1993). In the field, species are further affected by competition. We know very little about these species limits, which is alarming as many species already at present are forced to live in

environments that do not offer optimal conditions, but rather represent marginal habitats. If climate change prompts a movement of species towards the north, most areas in the new potential range will not offer edaphically optimal conditions, but rather marginal habitats just sufficient to enable the species to survive.

In this paper, we argue that knowledge about species limits is crucial not only for improving the quality and predictive power of SDM, but is highly important also in the context of practical nature conservation. Plant re-introductions may fail if the requirements and responses of the target species are not taken into account and unsuitable sites are selected. We also argue that parameters derived from species' response curves are an important tool for the interpretation of vegetation data, and that measurements obtained from large regional data sets can be superior to Ellenberg values that in many cases do not properly reflect the species' ecological responses across the whole of Central Europe. More specifically, this study aims (1) to show that the range size – being an essential variable in SDM – and the threat status of species are better explained by response limits than by optima, especially when the latter are estimated based on indicator values, (2) to demonstrate that response limits may differ considerably also between species considered to have very similar ecological optima, and (3) to examine in how far the differentiation of the vegetation is more closely related to response optima than to Ellenberg values.

Data sets and methods

Response models of species were constructed with data sets from two habitat types focusing on two different edaphic gradients. Data set 1 included 1460 sample plots of deciduous forests from the lowlands of North-western Germany, complemented by values of soil pH representing a complex-gradient in nutrient status (Michaelis *et al.*, unpubl. data). The pH was measured in a $CaCl_2$-solution, or measured in H_2O or KCl and later transformed to pH ($CaCl_2$). The data set comprises the full range of forest types found in the study region. Analyses were carried out exclusively with herbaceous species that show a preference of growing in closed forests or forest edges (Schmidt *et al.*, 2011) and that had a minimum frequency of 10 occurrences, altogether 61 species.

Data set 2 included vegetation samples of dry calcareous grasslands in the sub-atlantic, hilly regions of North-western Germany (Niedersachsen). To avoid confounding management effects, plots were only retained if the sites were still grazed or mown and not abandoned, and if

there was no evidence of recent fertilisation. In total 125 sample plots and 60 species were used for the analysis. In each of these plots, soil samples were collected and analysed in the laboratory. Whereas soil pH was consistently high in these grasslands and only plays a minor role for the differentiation of the vegetation, one of the critical factors affecting the occurrence of many dry grasslands species is the availability of nutrients, especially phosphorus (P). P contents were determined with flow-injection analysis after extraction with ammonium lactate (for more details, see Diekmann *et al.*, 2014).

The regional range size of species was determined as area of occupancy by counting the number of occupied grid squares in the lowlands (forests) and uplands (dry grasslands) of the federal states of Niedersachsen and Bremen based on topographical maps (Garve, 2007). The threat level of the species was obtained from the red list of vascular plants for the same region (Garve, 2004).

Species response curves relative to either soil pH or P were calculated with Huisman-Olff-Fresco (HOF) modelling based on hierarchical logistic regression using the R package eHOF, version 1.3 (Jansen & Oksanen, 2013; R Developmental Core Team, 2013). These models distinguish seven types of curves, from a simple linear to a bimodal skewed response. For each species, the HOF approach selects the best fit out of the pre-determined model types. The species optimum of the selected response curve is defined as the value along the gradient where the species has its highest probability of occurrence or, in case of a plateau response, at the midpoint of the plateau. To determine the species limits with regard to soil pH or P, we calculated those points of the HOF model response curves where the probability of occurrence reaches 0.05. Two examples of response curves are shown in Figure 6.1. Species with optimum curves can have two limits (a lower and an upper), while no limits are defined for those species where the response curve never falls below $p = 0.05$. More details on data sets and modelling procedures can be obtained from the authors.

The ecological relevance of the species' response optima and limits *vs.* Ellenberg scores was assessed by relating all variables to range size by means of simple linear regression. For data set 1, only the lower pH limits were considered, because the large majority of herbaceous forest specialists prefer base-rich sites and reach a (likely physiological) threshold at the lower end of the pH gradient, i.e. on moderately acid or highly acid soils, but not at the upper end. In contrast, the dry grassland species in data set 2 mostly showed upper P limits, probably

predominantly caused by competition. Differences for optima, limits and Ellenberg scores be-
tween red list categories were tested with Analysis of Variance. All statistical analyses were
carried out with the programme package R (R Developmental Core Team, 2013). The compo-
sitional variation of the vegetation of both deciduous forests and dry grasslands was analysed
with Detrended Correspondence Analysis (DCA) using the 'decorana' function of the
VEGAN package in R (Oksanen *et al.*, 2015).
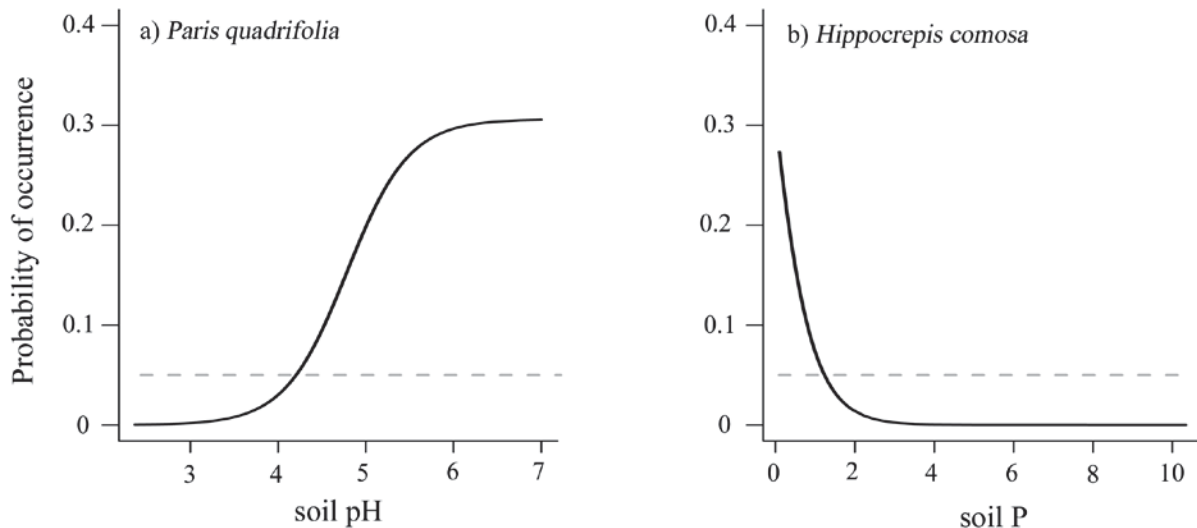
Figure 6.1 *Two examples of HOF models showing the responses of* Paris quadrifolia *along the soil pH gradient in deciduous forests (left) and* Hippocrepis comosa *along the soil P gradient in dry calcareous grasslands (right). The dotted grey line shows the probability of occurrence = 0.05 and its intersection with the response curve corresponds to the lower limit (pH) or upper limit (P).*

Results

For the deciduous forest species, range size (no. of occupied grid cells) decreased with an in-
creasing Ellenberg R score, i.e., species with an indicated higher pH optimum were less wide-
spread (Figure 6.2). The range size of dry grassland species was positively correlated with the
Ellenberg N score, meaning that species with higher nutrient demands were more common
than species tolerant of low nutrient availability. When using measured optima instead of in-
dicator values, identical relationships were obtained, but with higher (forests) and lower
(grasslands) R^2. The same effects on range size were also found for the measured lower limits
for soil pH (negative) and upper limits for soil P (positive), but here both R^2 exceeded those
for the indicator scores.
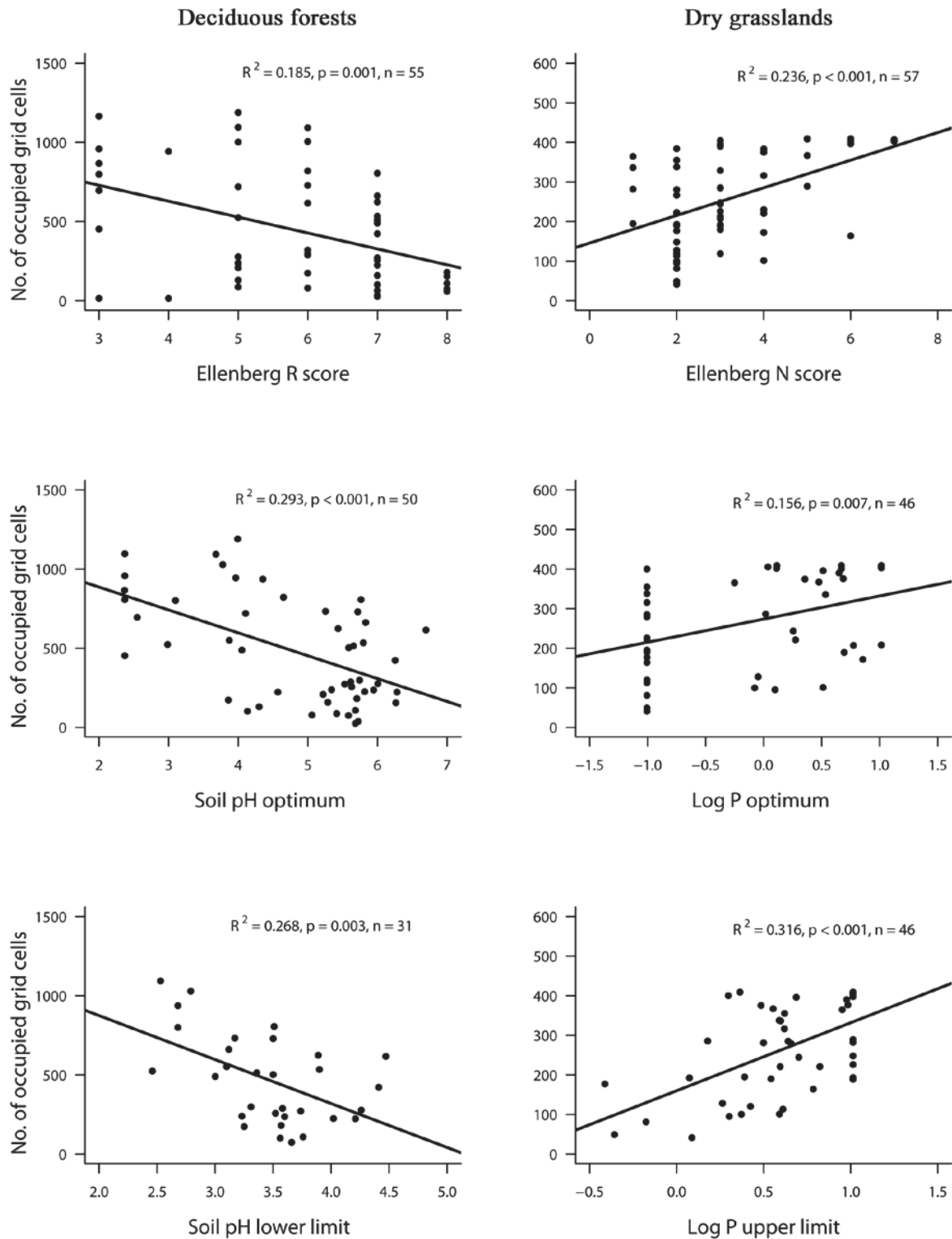
Figure 6.2 *Relationship between range size and ecological responses of species along edaphic gradients in deciduous forests (soil pH; left) and dry calcareous grasslands (log-transformed soil P; right) in North-western Germany. The upper panels show Ellenberg scores, the panels in the middle measured optima, and the lower panels measured lower and upper limits, respectively.*

Figure 6.3 shows that dry grasslands species assessed to have similar optima relative to nutrient availability differ in their ecological behaviour as reflected by their range size. For the 15 species with an identical Ellenberg N score of 2, the no. of occupied grid cells increased with an increasing upper limit for soil P, meaning that the species most tolerant of low P availability and/or those being least competitive had the smallest range size.

The seven species with the lowest upper P limits are all considered as threatened or near-threatened. Optima and upper limits for P were positively correlated ($r = 0.460$, $p = 0.036$, $n = 41$), showing that the Ellenberg scores fail to differentiate between species that differ in their ecological responses.

Figure 6.3 *Relationship between range size and the upper limit for soil phosphorus (P, log-transformed) of 15 species of dry calcareous grasslands, which all have an Ellenberg N score of 2 and thus are assessed as being very similar in their preference of low nutrient availability.*

Corresponding to the results shown in Figure 6.2, deciduous forest species with higher Ellenberg R scores tended to be more threatened than those with lower scores (Figure 6.4). This pattern became more pronounced for the measured pH optima and was especially striking for the measured lower limits for pH. For the dry grasslands, threatened species showed significantly lower Ellenberg N scores than species of least concern, whereas there was no significant difference in P optima between red list categories. In contrast, the differences of upper P limits between threat categories were slightly more pronounced than those for the Ellenberg scores.

The main gradients in species composition for both habitat types were captured by Detrended Correspondence Analysis. The scores of deciduous forest species along DCA axis 1 were significantly related to the Ellenberg R scores (Figure 6.5). The relationship between DCA scores and pH optima was even closer, while the linear regression of ordination scores on the lower pH limits showed a much lower R^2. For the dry grasslands, the measured P optima performed best among the three species response variables for explaining the variation in DCA scores for axis 1, followed by the upper P limits and the Ellenberg N scores.
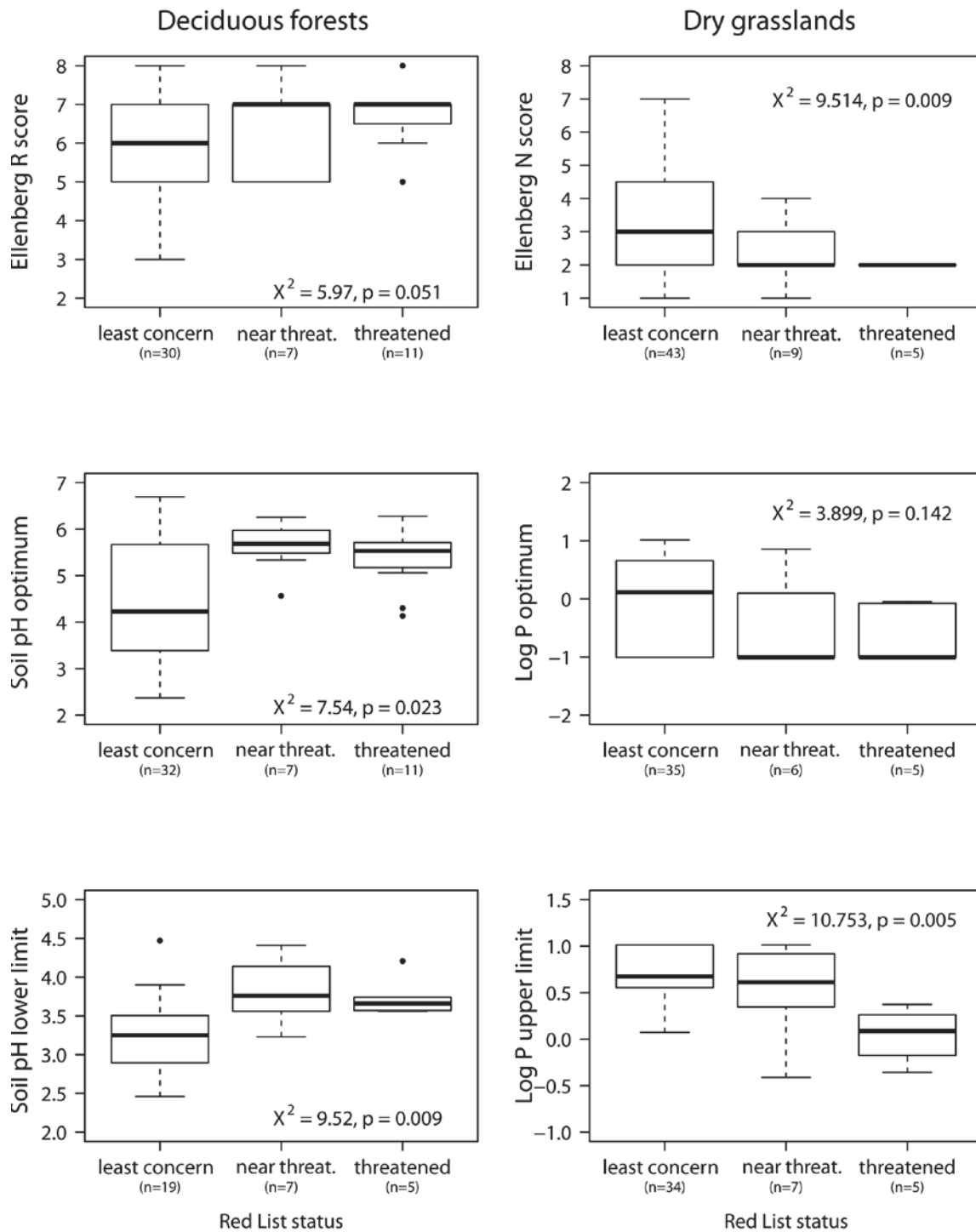
Figure 6.4 *Differences between species' threat categories (red list status) in Ellenberg scores (upper panels), measured optima (middle panels) and measured limits (lower panels) for soil pH in deciduous forests (left) and for soil P in dry calcareous grasslands (right) in North-western Germany. The statistical results refer to Kruskal-Wallis tests.*

Discussion

The results of the exemplary analyses can be summarised as follows: first, measured response limits performed consistently better than Ellenberg scores in explaining the range size and threat status of species. Second, the limits were also related to the range sizes of those species

that were considered having the same optima with respect to a specific environmental factor. And third, measured optima were superior to measured response limits and Ellenberg scores in explaining the variation of vegetation data. We will first try to shortly interpret the results and then discuss what these mean with respect to our initial hypotheses.

Even though the species' optima and limits were significantly related to each other in both habitat types, they differed in their ability to explain the regional range size of species. Overall, response limits were more closely related to the area of occupancy and the threat status of species than both indicated and measured optima. This means that many species (or their populations) do not or no longer occur in preferred environments, but are confined to habitats with less favourable or even marginally favourable conditions. Several forest specialists, such as *Hepatica nobilis*, prefer high-pH and moderately moist soils and face the problem that base-rich forest sites in the North-west German lowlands are generally also relatively wet and therefore not particularly suitable. Such species do not have – and perhaps never had – sites in the region that would represent an optimal environment. Similarly, many dry grassland species lack sites with optimal conditions, especially where nitrogen deposition and / or the addition of phosphorus, often accompanied by reduced management, lead to an increase in taller-growing, more competitive species (Diekmann *et al.*, 2014). The importance of phosphorus-deficient soils is reflected in Figs. 6.3 and 6.4, showing that the species with the lowest upper P limits (such as *Euphrasia officinalis*, *Helictrotrichon pratense* and *Hippocrepis comosa*) were also the least widespread and most threatened ones. At least on a regional scale, the distribution of plant species appears to be more closely related to the extreme ends of the species' response curves than to their optimum positions.

The differentiation of the vegetation as reflected by the position of species scores in the DCA ordination was best explained by the measured optima. This is not surprising, because the ordination scores represent the locations of the realised-niche positions of species and not their niche boundaries (Wasof *et al.*, 2013). Unexpected was that the measured optima also outperformed the Ellenberg scores, which indicates that, on a regional scale, measurements and response curves based on measurements may describe the ecological behaviour of species better than expert-based indicator values and their averages. Similar results were found by e.g. Diekmann and Falkengren-Grerup (1998) and Gégout *et al.* (2003).

Being aware that the extent of this study is limited and that the results must be considered as preliminary, we nonetheless conclude the following:

(1) At least in regional vegetation studies, species optima derived from measurements of soil variables show a higher explanatory power than indicator values. They also have the advantage to represent true values that can be compared between regions, ecosystems and species without the need for transformation. Studies on niche characteristics (such as niche breadth and position) of plants have often been based on indirect assessments of species' behaviour and turnover along gradients (e.g. Fridley *et al.*, 2007; Wasof *et al.*, 2013), which often involves analytical problems and a lack of transferability to field conditions. A direct approach might contribute to make studies on ecological niches more realistic.

(2) When aiming to predict the potential or future distribution of plant species – especially on a regional scale – measured response optima AND limits need to be considered. The importance of edaphic variables for predicting plant distributions has already been emphasised by Thuiller (2013) and put in practice by, for example, Dubuis *et al.* (2013) and Beauregard and de Blois (2014). Rare species were shown to have narrower habitat preferences in terms of soil parameters than common species (Wamelink *et al.*, 2014). As already noted, a practical problem is the shortage of available environmental data. Another drawback is the high spatial heterogeneity of most soil variables that makes it difficult to integrate these variables in SDM models on a coarse spatial resolution (Thuiller, 2013). The problem can partly be rectified by using units on a much smaller spatial scale such as classical sample plots. Another possible solution was offered by Bertrand *et al.* (2012) who used an indirect estimation of soil pH for 1 km^2 grid cells based on the species composition and the modelled response of species to pH. While response optima and limits summarize the species' behaviour and will not directly be entered into SDM models relying on primary site-based data, they are invaluable for the interpretation of modelling results. It is likely that climate-only models will fail especially for those species that have narrow niches in terms of soil variables, while they are expected to work better for edaphic generalists. For example, the general prediction of a climate change-induced shift of highly base-demanding species towards the north in Scandinavia needs to be modified by taking into account the relative scarcity of high-pH soils in northern Europe and the relatively high lower pH limits of many species in Central Europe (Ewald, 2003).
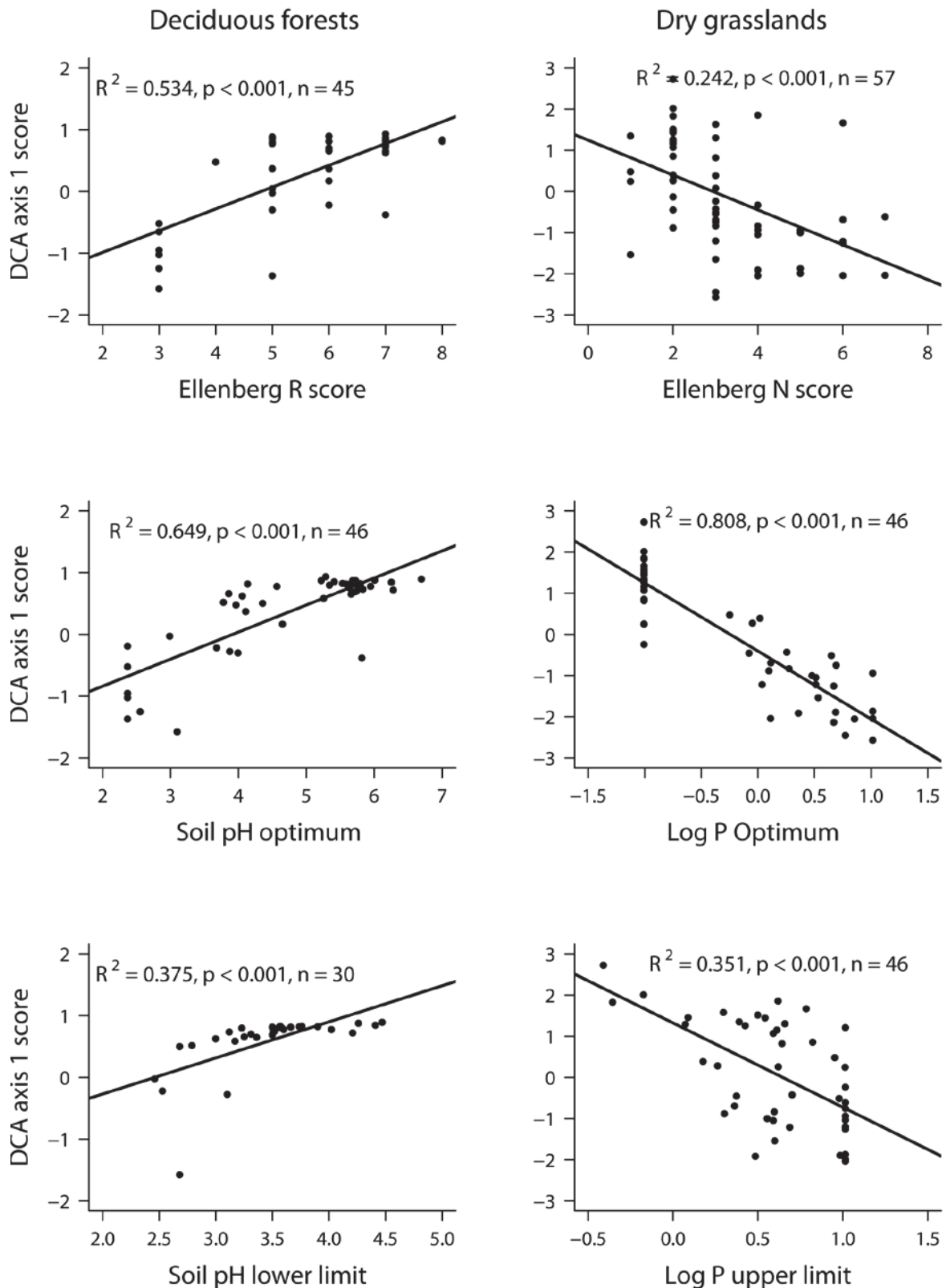
Figure 6.5 *Relationship between the species scores along DCA axis 1 and ecological responses of species along edaphic gradients in deciduous forests (soil pH; left) and dry calcareous grasslands (log-transformed soil P; right) in North-western Germany. The upper panels show Ellenberg scores, the panels in the middle measured optima, and the lower panels measured lower and upper limits, respectively.*

For predictions of plant distributions in climatically relatively homogeneous regions, information on species responses to edaphic variables is crucial, as shown by Kelly *et al.* (2014) in a study on invasive plants.
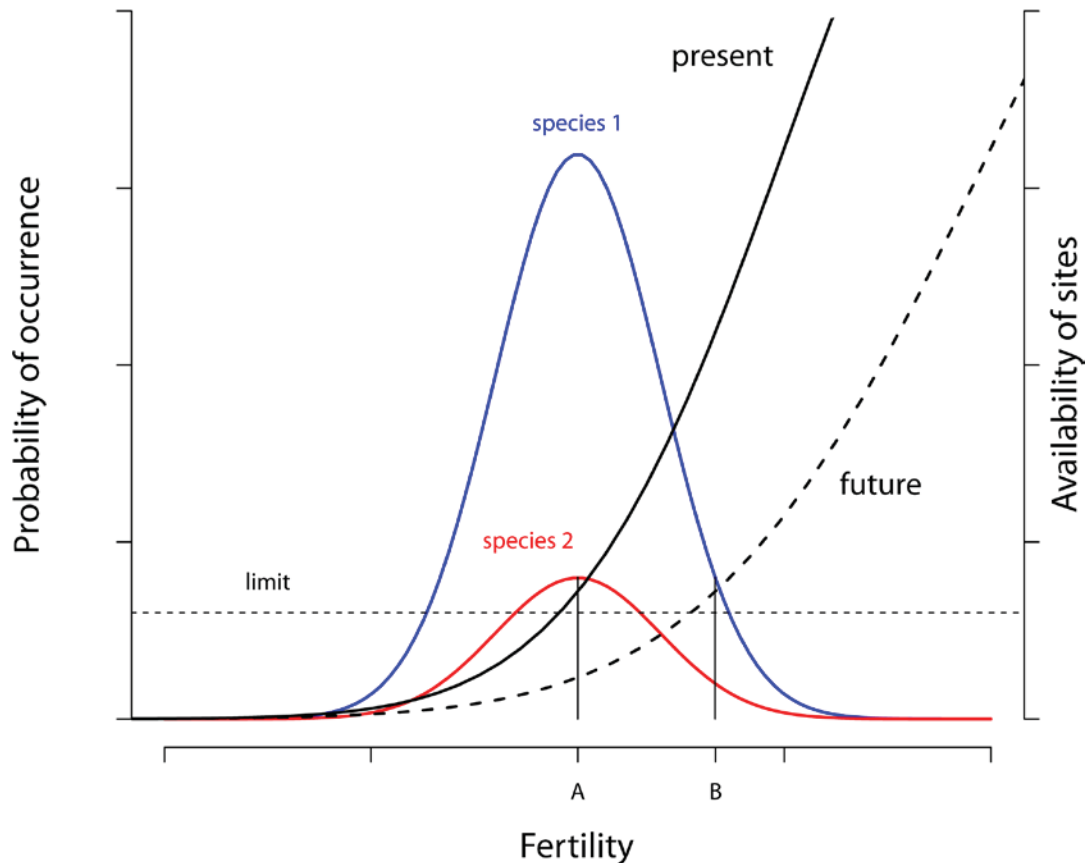
Figure 6.6 *Model of species response (colored optimum curves) under scenarios of increasing fertility (black exponential lines). A species is able to persist in an environment if its response curve exceeds a probability of occurrence (limit) at a point where enough sites with a suitable fertility are available. In the example, species 1 and 2 have the same optima, but differ in their abundance and limits. At point 'A' representing current conditions, both species can persist because the number of sites with an optimal fertility is sufficiently large. Point 'B' describing a future scenario of increased fertility is beyond the threshold of species 2, but still allows species 1 to persist.*

Our results suggest that response optima and Ellenberg scores both perform reasonably well, but do not succeed to differentiate between species with highly similar preferences but diverging limits (Figure 6.3). On a course spatial scale such as a topographic grid cell, there is often a close agreement between occurrence and the general ecological behaviour of species, which is reflected in many flora maps documenting the importance of bedrock types for the distribution of acidophilous *vs.* calciphilous species (Bettinger *et al.*, 2013). Within these broadly defined groups of plants, however, limits appear to work better than optima. If the landscape in Central Europe becomes increasingly homogenised due to the omnipresent processes of land use intensification and eutrophication, limits will likely gain even a higher importance. This is depicted in Figure 6.6 showing the responses of

two species along a fertility gradient under a scenario of increasing nutrient availability. Species with identical optima but different overall abundances and limits are expected to respond differently to future eutrophication. Thus, the optima of species may just give a rough indication of their ecological behaviour in changing ecosystems.

(3) Knowing that edaphic species thresholds matter and that at the same time edaphic limits are not yet quantified for most species and variables is alarming, because the conservation of species will depend on a thorough understanding of the ecological niches of species and where these are met, now and in future. Given the long tradition of vegetation science in Central Europe and in other parts of the world, with hundreds of thousands of plots being available, we still know little about the species' niches and especially their limits. In our opinion, we need:

    a. To carry out more measurements of edaphic variables, especially of pH and nutrient contents or availabilities, both in vegetation plots and in a systematic manner across regions. More standardised procedures for these measurements would be desirable.

    b. To use these data to model the species' response curves and their variation across different biogeographical regions in order to determine optima and limits, both for single variables and for combinations of variables. The latter will help us to quantify the niches of species, being a difficult but central task of ecology (Turnbull, 2014).

    c. To examine the relationship between the spatial distribution and responses of species to identify the most critical factors for the persistence of plant populations, and to incorporate this knowledge into predictions of future range sizes. Ultimately, detailed knowledge about the edaphic pre-conditions for the survival of plants will be crucial for the conservation of species as well as for a successful re-establishment of populations at restored sites. We especially need to know the response limits beyond which the species are no longer able to survive.

Acknowledgements

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Chapter 7

Ecological significance of soil pH limits

for forest vascular plants

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submitted
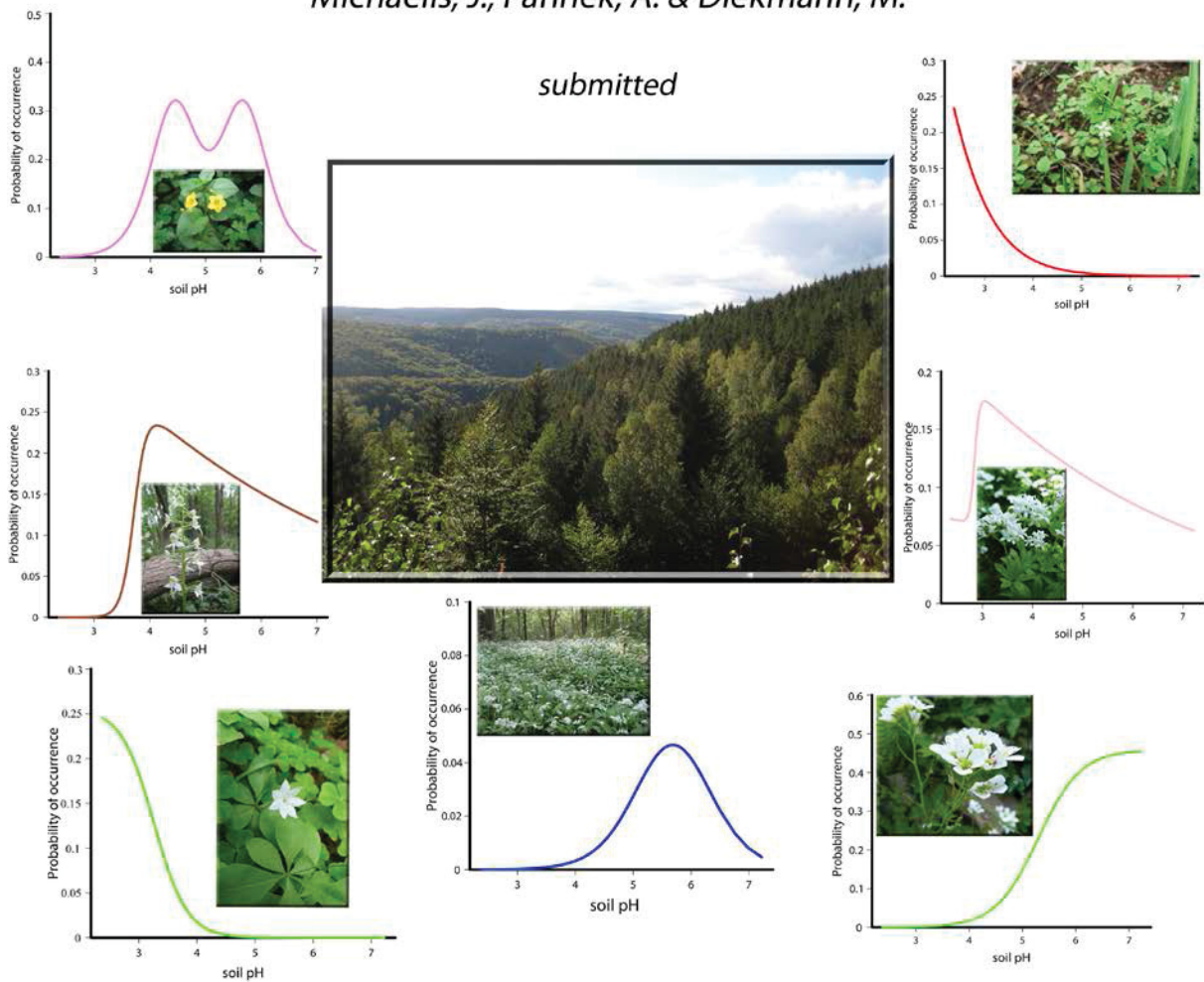
Species' reactions to soil pH, modelled with eHOF. From the top left to the top right:
Lysimachia nemorum *(19.06.2012)*, Platanthera chloranta *(18.06.2013)*, Trientalis europaea
(13.06.2014), Allium ursinum *(08.05.2010)*, Cardamine amara, Galium odoratum *(both
03.05.2014)* and Ceratocapnos claviculata *(19.06.2012). All pictures taken by A. Pannek*

Abstract

Although edaphic factors are known to play a major role in explaining plant distributions, knowledge about the responses of species to soil variables is scarce. In the framework of species distribution modelling and plant conservation, these responses are usually expressed as optima or indirectly assessed by indicator values. However, habitat loss and degradation may force species to live in ecologically marginal environments, i.e. close to their physiological or ecological limits. Here we used Huisman-Olff-Fresco models to examine the species responses of forest vascular plants along a soil pH gradient in two regions of northern Germany with a particular focus on rare species. Optima and limits were then related to regional range size, change in range size over the past decades and threat level.

Lower pH limits showed an aggregation around pH 4 and were consistent across regions, whereas upper pH limits were not clumped and not significantly correlated between regions. Soil pH affected range size, as species being intolerant of acid soils were less widespread than less sensitive taxa. In the lowlands, species with relatively high lower pH limits had also decreased more over time and were more threatened than species able to grow on very acid soils. Lower limits were more closely related to range size and rarity than optima, and it is argued that they in most cases represent the physiological thresholds of species instead of being determined primarily by competition. The results reinforce the importance of soil variables for the occurrence of plant species and suggest that limits may be better predictors of current and future species distributions than optima.

Keywords

Introduction

The study of plant species' responses along environmental gradients and research exploring the consequences of environmental change for the occurrence of species are essential for informed conservation decisions. Therefore, the quantification of species niches is considered to be of fundamental importance both for basic and applied vegetation ecology (Økland, 1992; Sala *et al.*, 2000; Rushton *et al.*, 2004). Whilst the impact of climate change on species distributions and biodiversity has been in the focus of many publications since 1990 (e.g. Graham & Grimm, 1990; Walther *et al.*, 2002; Thuiller *et al.*, 2005), the CBD mentions four other main threats to biodiversity, one of which is habitat loss and soil degradation (Secretariat of the Convention on Biological Diversity, 2010). In fact, habitat destruction has already been called the "leading cause of species extinction" by Pimm and Raven (2000).

Although edaphic factors are known to have a major influence on the occurrence of plants, species distribution models are most often run with climatic variables only (e.g. Huntley *et al.*, 1995; Araújo *et al.*, 2011; Engler *et al.*, 2011; Thuiller *et al.*, 2011). Coudun *et al.* (2006) and Bertrand *et al.* (2012) recently showed that the inclusion of soil variables significantly improved the quality of distribution models for two tree species in France. For *Quercus pubescens*, these variables did not only contribute significantly to the definition of niche space, but also enabled the model to find corridors and refugia for the species in the face of climate change (Bertrand *et al.*, 2012). The scepticism of many authors against climate-only models thus seems to be justified (Lafleur *et al.*, 2010; Austin & Van Niel, 2011).

A concern for using soil variables in species distribution models, and for their use as predictive tool for local conservation measures, is the lack of soil data, which are scarce because site-specific sampling involves time-consuming field work and laboratory measurements. The few available soil data have often been obtained by applying different methods of sampling or chemical analysis, further complicating comparability and interpretation. Therefore, field measurements of important environmental drivers have in most studies been replaced by an indirect assessment of habitat quality by means of indicator values. These quantify the ecological behaviour of species integrated over time, instead of reflecting conditions at a specific moment. In Europe, one widely used system of indicator values is that of Ellenberg *et al.* (2001), who developed indicator scores for three climatic factors (light, temperature and continentality) and four edaphic factors (soil moisture, reaction [pH], nitrogen and salt). Despite their great usefulness and common application (for a review concerning Ellenberg's indicator

values see Diekmann, 2003), indicator values have some drawbacks. One problem is the difficulty to transform the scores to physical numbers, which usually introduces a large amount of uncertainty (Wamelink *et al.*, 2005). In many situations, real numbers representing measurements are preferable and in some cases inevitable, for example when calculating critical loads or assessing the suitability of a specific site for a target species.

Species' response curves along measured environmental gradients are usually characterised by their optima and amplitudes (e.g. ter Braak & Looman, 1986; Peppler-Lisbach, 2008b), which allow the comparison between different species. Although response curves have earlier been regarded as usually being either sigmoid or Gaussian (Whittaker, 1956; Gauch, 1982), they can adopt different forms (Minchin, 1989; Økland, 1990), and more recent studies have used statistical techniques that are able to cope with non-Gaussian responses, like Generalised Additive or Huisman-Olff-Fresco (HOF) models. These are assumed to give more realistic results (Hastie & Tibshirani, 1987; Huisman *et al.*, 1993) than the traditional Gaussian models. Generally, these modelling approaches may produce three kinds of useful outputs. First, they allow an easy calculation of niche characteristics; second, they enable us to predict the probability with which a species is present at a specific site along the measured gradient; and third, they give a possibility to predict the suitability of a site for a species, for example in the framework of species distribution modelling or in reintroduction trials.

With ongoing habitat destruction and land use changes, ecosystem restoration is crucial to stop further biodiversity loss. In fragmented landscapes, the reintroduction of rare and dispersal-limited species is an important restoration measure that has become common practice in nature conservation (Godefroid *et al.*, 2011). The reestablishment of species, however, often fails, probably caused by poor site selection due to insufficient knowledge about the requirements and responses of the target species with respect to soil factors and about the extent of the ongoing environment changes (Maschinski & Haskins, 2012). From a conservation point of view, the quantification of responses especially of endangered species to soil variables such as moisture, pH and nutrients is urgently needed to assess the match between species presence and site conditions of extant populations, and to improve the success rate of future reintroductions.

As habitat degradation is one of the main threats to biodiversity, many species already at present – and increasingly so in the future – may be forced to live in environments that are closer

to their physiological or ecological limits than to their optima. If this is true, the optima of species' response curves, as reflected e.g. in Ellenberg indicator values, may be less relevant for practical conservation measures than the species' minima and maxima or threshold values with a defined probability of occurrence. These limits define marginal habitats in which species are just able to survive, whereas, beyond these limits, the species no longer meet their basic physiological needs or become outcompeted. An aggregation of limits of many species in a plant community might indicate that these are determined by physiological constraints rather than by biotic interactions. In that case, the limits are likely to be more stable across larger spatial scales than optima known to sometimes vary between different regions (Diekmann, 1994; Gustafsson, 1994; Wasof *et al.*, 2013). Stable response limits of species across regions would facilitate the interpretation of species distribution models. The ecological relevance of species limits *vs.* species optima can be tested by correlating both with measures of range size, local abundance or the level of threat. A suitable variable for analyzing these relationships is soil pH that usually shows a close correlation to several other soil factors (Peppler-Lisbach, 2008a).

In this study, we examined the response of forest vascular plants along the soil pH gradient in Germany, being particularly interested in the ecological significance of pH limits. The main research questions were:

1) Where are the lower and upper pH limits of species, and are these aggregated along the pH gradient, i.e., is there "boundary clumping"?

2) Are the pH limits of species consistent across different regions?

3) Are the pH limits correlated with the species' regional range size, threat level and temporal change in range size?

4) Are the relationships for limits stronger than those for the species' optima?

Methods

Study area & species

The study was carried out in two distinct geographical regions in Germany, the North German lowlands and the Central German Upland Range, hereinafter referred to as "lowlands" and "uplands". Data were compiled from several published sources (Gönnert, 1989; Wulf, 1992; Heinken, 1995; Mast, 1999; Pflume, 1999; Brand, 2000; Pollmann, 2000; Huntke, 2002; Rüther & Peppler-Lisbach, 2007; Pannek *et al.*, 2013) and, for the lowlands, additionally from an own survey carried out in summer 2013 that served to enlarge the data set, especially for rare plant species. In total 1470 plots were available from the lowlands (897 plots from the literature), while the data set for the uplands comprised 1437 plots.

Species data for the lowlands were collected in the area between the regions Westmünsterland and Westmecklenburgisches Seenhügelland (see Figure 7.1) (Meynen & Schmithüsen, 1959). Here, the soils are mostly acidic podsols or secondary podsols and cambisols on more base-rich sites. The landscape is flat to slightly undulating, with elevations varying mostly between 10 and 40 m a.s.l. Today, the region is predominantly used for agriculture, with forests covering on average 14% of the area. The woodland consists mainly of coniferous plantations, while deciduous forests are largely confined to the scarce base-rich forest sites.

Figure 7.1 *Map of Germany with contour lines of the federal state boundaries. The study area is mainly situated in Lower Saxony. The black part marks the sampling area for lowland data, the region for the upland sample data is marked in white.*

Upland data were mainly collected in the regions Niedersächsisches Bergland, Osnabrücker Hügelland and the Harz mountains (see Figure 7.1) (Meynen & Schmithüsen, 1959). Compared to the lowlands, the uplands have a higher geodiversity in terms of relief, bedrock and soils. Elevation in most parts ranges from 50 to 500 m a.s.l., but reaches up to 1141 m a.s.l. in the Harz. The soil conditions in this region are highly diverse, including both very base-poor

sandstones and lime-rich soils. Agriculture in the uplands was less intensive in the past than in the lowlands, and therefore a larger area (32%; Niedersächsisches Ministerium für den ländlichen Raum, 2004) is still covered by forests.

In order to confine the species sample to a reasonably cohesive ecological unit, we considered only herbaceous taxa with a preference of growing in closed forests or forest edges in the lowlands (group K1.1 and K1.2 according to Schmidt *et al.*, 2011), overall 61 species. In the uplands, 17 of these species are also found in more open habitats and assigned to group K2.1. The nomenclature follows Haeupler and Schönfelder (1988).

Chemical analysis

In each plot of the 2013 survey, mixed soil samples were collected from the upper soil layer and pooled. Each sample was air-dried to constant mass and passed through a 2-mm sieve. For pH measurements, 10 g of soil and 25 ml of $CaCl_2$ buffer solution were mixed for 90 minutes, after which pH was analysed with a standard glass electrode. A sub-sample was also measured in KCl buffer solution and in H_2O to enable us to convert the pH data from the literature to standardised values of pH_{CaCl_2}. We followed the procedure proposed by Conyers and Davey (1988) using regression equations for the conversion of pH values: $pH_{H_2O} = 0.933 * pH_{CaCl_2} + 0.694$ (R^2 = 0.92, P < 0.001, N = 72) and $pH_{KCl} = 1.05 * pH_{CaCl_2} - 0.092$ ($R^2 = 0.99$, P < 0.001, N = 72), see Appendix 7.1 in Chapter 9.

Modeling species response & niche boundaries

Species' response curves relative to soil pH were modeled with hierarchical logistic regression in the statistical software environment R (R Developmental Core Team, 2013), using the package eHOF, version 1.3 (Jansen & Oksanen, 2013). The Huisman-Olff-Fresco (HOF) models were first introduced by Huisman *et al.* (1993) as a set of five hierarchical models with increasing complexity. Recently Jansen and Oksanen (2013) expanded them to encompass seven different types, from simple linear to bimodal skewed responses (see Figure 7.2). The HOF modelling approach selects the best fit out of the pre-determined model types for each species, using statistical information criteria and bootstrapping to stabilize the model choice. A minimum of 10 occurrences for each species is required (Jansen & Oksanen, 2013).

A species' optimum is defined as that value along the gradient where the species has its highest probability of occurrence or, in case of model III (plateau response), at the midpoint of the plateau. No single optimum can be calculated for bimodal models. The eHOF package also allows to calculate species tolerance limits, according to Heegaard (2002) defined as those values where the response drops to "exp(-1/2)" of the top. These so-called Central Borders are calculated separately for the left and right hand side of the optimum (LowCB and UppCB).
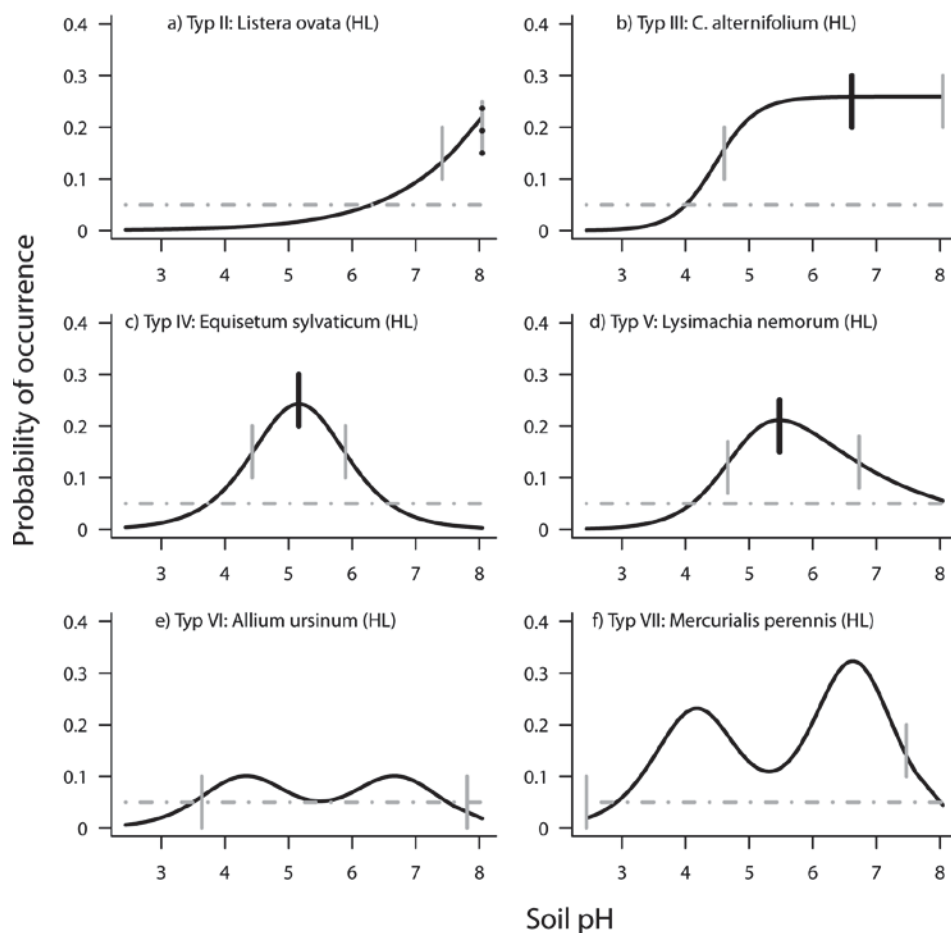
Figure 7.2 *Example of HOF models of types II-VII showing the responses of species along the pH gradient in the uplands (cf. Jansen & Oksanen, 2013). None of the species complied with model I. a) Type II: monotonic sigmoid curve with an optimum at the extreme left or right of the gradient (Chrysosplenium alternifolium), b) Type III: monotonic sigmoid with a plateau, c) Type IV: unimodal symmetric response, d) Type V: unimodal skewed response, e) Type VI: bimodal with more or less symmetric optima, f) Type VII: bimodal with asymmetric optima. Black vertical solid lines describe the position of the optima as calculated for each model (not available for bimodal responses), grey vertical solid lines denote the upper and lower central borders, respectively. The dotted grey line corresponds to a probability of occurrence of y = 0.05, and its intersection(s) with the response curve marks the lower and / or upper limits.*

We calculated another set of upper and lower pH limits as those points where the response curve of the HOF models reaches a probability value of 0.05. We did so in order to quantify the broad range of conditions a species tolerates, without taking into account extreme and outlier values that often encompass the whole range of pH values found in a region. The threshold of 0.05 might seem arbitrary, but corresponds to the classical significance threshold in sta-

tistical tests and allows including also some of the rarer species in the analysis. A probability threshold of 0.1 as suggested by Austin and Smith (1990) would have excluded a large number of more uncommon species and made it difficult to analyze the relationship between limits and measures of threat status (see below). The limits with a probability value of 0.05 are in the following called 0.05 limits or LowLim and UppLim, for the left- and right-hand side of the response curve, respectively. Not in all cases both limits, or even one, could be calculated, for example if species were too rare to reach the 0.05 mark or if the probability of occurrence at the lower or upper extreme of the pH gradient did not fall below 0.05 (see Figure 7.2).

Determination of conservation status and range size

The threat level status of the species was obtained from the red list of vascular plants in Lower Saxony and Bremen (Garve, 2004). In the lowlands, 41 species were classified as least concern, eight as near-threatened, ten as vulnerable and two as endangered. In the uplands, 56 out of 61 species were classified as least concern, two as vulnerable and three as endangered. For data analysis, the threat level categories were coded contrasting to the red list as "0" for least concern, "1" for near-threatened, "2" for vulnerable and "3" for endangered species.

Regional range size and temporal change in frequency were determined using a 1:25000 Ordnance Survey map (Garve, 2007). This floristic map covers the area of Lower Saxony and Bremen and is divided into 473 grid cells (11 km x 11 km). Regional range size, defined as area of occupancy (*cf.* Gaston *et al.*, 1997), was determined by counting the number of occupied grid squares over the inventory period 1982-2003. We did so separately for the lowlands (360 grid cells) and the uplands (113 grid cells). To determine the temporal change in range size, we compared the number of occupied grid cells for the period 1982-2003 with the corresponding number for the period before 1981.

To standardize the temporal change relative to the overall frequency (separately for the two regions), the number of 'extinctions' (no. of grid cells occupied until 1981 but lost in recent times) of each species was divided by the number of all grid cells occupied until 1981, multiplied by 100. The number of 'establishments' was calculated by dividing the number of recently occupied grid cells by the number of all grid cells occupied until 1981, again multiplied by 100. By subtracting the percentage decrease from the percentage increase, we calculated the overall temporal change in range size. Although we worked on a rather course spatial scale, gaps in the distribution of species may be due to insufficient mapping, especially in former times (before 1981), rather than reflecting true absence (for a quality assessment see

Garve, 2007). Therefore, a second approach for determining the temporal change in range size was used for parts of the lowlands, the Weser-Elbe region, the flora of which is among the best known in Germany (Cordes *et al.*, 2006). Here, a particular effort was carried out to search for rare species and to map previously under-sampled areas. The flora gives an estimation of population trends for the region based on expert opinion for the reference period from 1935 to 2004, which we used as a proxy for the trends of species in the whole lowland area. Unfortunately, no comparable information was available for the uplands.

Statistical analysis

Not all species reached the required minimum frequency so that pH limits and optima were finally calculated for 54 species in the lowlands and for 56 species in the uplands. First, we quantified the boundary clumping of the species for the two types of limits (central borders and 0.05 limits) using Morisita's Index (MI). In a null model where range boundaries are randomly scattered across a given set of sites, the index value is expected to be about 1.00. A value greater than 1.00 indicates that range boundaries are more clumped than expected and vice versa. In addition, we used chi-square analysis to test whether there were significant deviances of range boundaries from the null model (Hoagland & Collins, 1997). To examine possible shifts of species behavior between the lowlands and uplands of Germany, upper and lower limits from both regions were correlated to each other. Furthermore, the measures of species' frequency in northern Germany (threat level, range size, temporal change in range size) were correlated with the pH optima and limits. Unless otherwise stated, Spearman's rank correlation was applied in all analyses, using the statistical program R, version 3.0.2 (R Developmental Core Team, 2013).

Results

None of the 54 species in the lowlands and 56 species in the uplands followed a type I response in the HOF models, meaning that all species were affected by soil pH. In the lowlands, the predominant model shapes were plateau (type III) and (optimum) unimodal curves (type IV & V), shown by 48% and 36% of all species, respectively. In the uplands, 36% of the species showed unimodal and 29% plateau-like responses. Among the plateau species, the probability of occurrence increased with increasing pH, except for *Convallaria majalis, Maianthemum bifolium, Pteridium aquilinum, Senecio sylvaticus* and *Trientalis europaea* in the lowlands, *Oxalis acetosella* in the uplands and *Ceratocapnos claviculata* in both regions. Monotonic responses played a minor role in both regions (9% in the lowlands, 13% in the up-

lands), whereas bimodal curves were obtained for 7% and 23% of the species, respectively. In both regions, most of the unimodal and bimodal responses were skewed.

In a first analysis, we compared the two differently calculated limits (central borders and 0.05 limits, see methods) with each other. LowLim and UppLim were significantly positively correlated with the LowCB and UppCB, respectively, both in the lowlands (lower: $r_s = 0.73$, $N = 31$; upper: $r_s = 0.86$, $N = 15$) and in the uplands (lower: $r_s = 0.56$, $N = 40$; upper: $r_s = 0.79$, $N = 20$, all $P < 0.001$). Across all species, we found a significant aggregation of the limits in the lowlands. Lower and upper limits were strongly clumped at pH values between 4 and 4.5 (Morisita Index [MI] = 1.67; $\chi^2 = 39.21$, $P < 0.001$), mainly caused by a large number of species having their lower limits in this pH range (Figure 7.3).
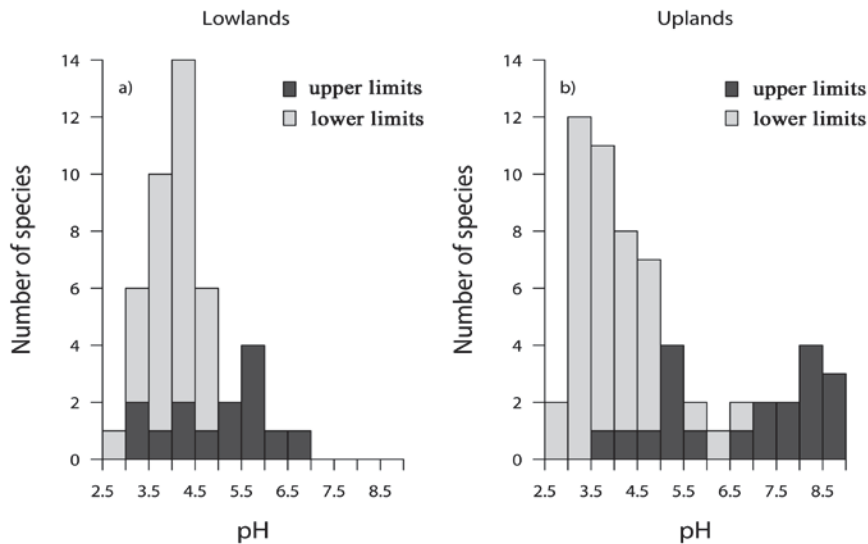
Figure 7.3 *Barplots showing the positions of the species' pH limits along the soil pH gradient. Light grey bars indicate lower limits, whereas dark grey bars show upper limits, separately for lowlands (left) and uplands (right).*

In the uplands, the main aggregation of LowLim and UppLim shifted towards more acidic values between pH 3 and 4 (MI = 1.55; $\chi^2 = 35.33$, $P < 0.001$), again mainly explained by a clumping of LowLim values. Significant aggregations were also found for the central borders of both regions, which can be explained by the large number of species (showing response curves of type II and III) having their UppCB in the highest pH interval recorded in the regions. As this describes a statistical artefact rather than an ecological pattern, we repeated the calculations for the CB excluding the last pH interval. The results for the lowland CB were similar to the lower and upper limits, with the main clustering of species at pH values between 4 and 4.5 (MI = 1.15; $\chi^2 = 22.18$, $P = 0.008$). In the uplands, no significant aggregation of LowCB and UppCB was found (MI = 1.06; $\chi^2 = 16.65$, $P = 0.119$). As the 0.05 limits showed the most distinct patterns, all further analyses were done with LowLims and UppLims only.

A comparison of LowLim and UppLim between lowlands and uplands showed that the LowLims of most species remained constant across regions (Figure 7.4). However, some species shifted their LowLims towards more base-rich conditions in the lowlands compared to the uplands (e.g. *Stachys sylvatica* with pH 2.47 *vs.* 3.51). In contrast, *Paris quadrifolia,* showed a LowLim of pH 4.21 in the lowlands but a value of 5.30 in the uplands. Despite the high r_s value (0.9), no significant correlation between lowlands and uplands was found for the UppLims, an effect of the low sample size ($N = 7$). In the uplands, five species showed a shift to limits on clearly more base-rich sites (e.g. *Dryopteris dilatata* from 5.74 to 7.92 or *Melica uniflora* from 5.52 to 7.97), which is not surprising considering the much higher frequency of calcareous, high-pH soils in this region.
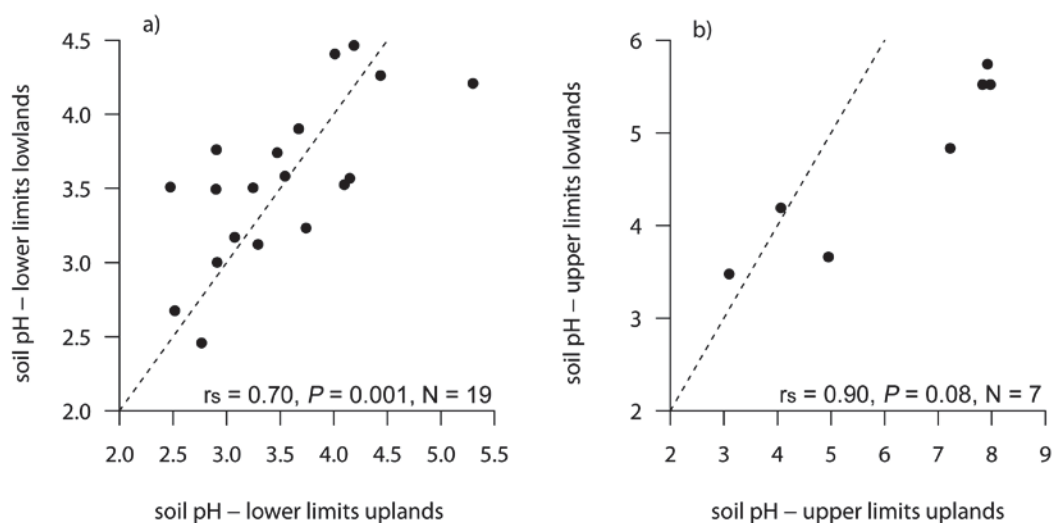
Figure 7.4 *Correlation between the (a) lower pH limits and (b) upper pH limits of the studied species between lowlands and uplands. Spearman rank correlation coefficients (r_s), P values and sample sizes (N) are given in each panel. The dashed line corresponds to the y=x diagonal.*

In the lowlands, the LowLim of species were significantly positively correlated with their threat level, i.e., species confined to more base-rich soils were more threatened than species able to tolerate more acidic soils (Table 7.1). There was no such trend in the uplands. In both regions, species with low LowLim values had larger range sizes than more base-demanding species. Interestingly, none of the measures of rarity, range size or change in range size was significantly related to the UppLim of species (Table 7.1). No correlation could be calculated between the UppLim in the uplands and the threat level, since all species for which sufficient data points were available were of least concern. In both regions, no significant relationship was found between the temporal change in regional range size and the LowLim. The expert assessment of the population trends of species in the lowlands, in contrast, indicated a decline of species not able to tolerate low pH values.

Table 7.1 Correlations of lower limits, upper limits and optima of species for soil pH with measures of species frequency in northern Germany (threat level, range size and temporal change in range size either based on counts of formerly and currently occupied grid cells, or based on expert opinion (only for the lowlands)). Spearman rank correlation coefficients (r_s) as well as P values and sample sizes (N) are given, with significant values in bold. Analyses were carried out separately for lowlands and uplands.

	Lower Limits			Upper Limits			Optimum		
	r_s	P	N	r_s	P	N	r_s	P	N
Lowlands									
Threat level	**0.54**	**0.002**	**31**	0.31	0.262	15	**0.34**	**0.016**	**50**
Regional range size	**-0.55**	**0.001**	**31**	-0.47	0.081	15	**-0.46**	**<0.001**	**50**
Change in regional range size	0.03	0.885	31	0.17	0.550	15	-0.12	0.404	50
Expert-based change in frequency	**-0.51**	**0.004**	**31**	-0.30	0.275	15	**-0.32**	**0.023**	**50**
Uplands									
Threat level	0.24	0.131	40	NA	NA	NA	0.14	0.383	43
Regional range size	**-0.56**	**<0.001**	**40**	0.18	0.445	20	-0.01	0.957	43
Change in regional range size	-0.15	0.357	40	-0.29	0.216	20	-0.09	0.576	43

The optima of species in the uplands were on average 1.3 pH units higher than those in the lowlands, mainly caused by the different pH maxima (7.22 in lowlands, 8.04 in uplands). Corresponding to the results for the LowLim values, species optima in the lowlands were positively correlated with their threat level (Table 7.1): Species having their optima on more base-rich soils were rarer than species having their optima on more acidic soils. Range size and temporal change in range size (based on expert assessment) were negatively correlated with the optima of species in the lowlands. The correlation coefficients for the above optima were throughout lower than those for the 0.05 limits. For the uplands, no significant correlations were found. In both regions, the optima for soil pH were highly positively correlated with the reaction values of Ellenberg (lowlands: $r_s = 0.60$, $P < 0.001$, $N = 45$; uplands: $r_s = 0.66$, $P < 0.001$, $N = 40$).

Discussion

Previous studies about species responses along pH gradients used a set of five hierarchical types of curves that were not able to model bimodal behaviors of species (e.g. Lawesson, 2003; Pakeman *et al.*, 2008; Peppler-Lisbach, 2008b). Our results based on the extended set of HOF models demonstrated that this extension of model types is important: in the uplands, 23% of the species showed a bimodal response (Figure 7.2e and f). The upland forests are characterised by a high geological diversity and by relatively nutrient-poor conditions both on low-pH soils (such as oligotrophic brown earth on acidic sandstone) and high-pH soils (such as dry and infertile rendzina on limestone). Thus, in this region there is only a relatively weak correlation between soil pH and nutrient availability, and the bimodal response of at least some species might be caused by competitive interactions in that these species are outcompeted from the intermediate pH range where fertility is high and fast-growing, tall herbs are abundant. In the lowlands with a much shorter pH gradient and a closer relationship between soil pH and nutrient availability, the number of species with bimodal responses is accordingly lower. Here, we furthermore found a remarkably high number of plateau responses, corresponding to the findings of Peppler-Lisbach (2008b) who concluded that this is due to the rather short pH gradient: in the North German lowlands, few forest soils exceed pH values of 6.0 which has the consequence that many species do not reach their potential upper pH limits. Austin (2007) argued that environmental gradients should clearly exceed the upper and lower limits of species occurrence to determine species response curves, but this requirement is in many cases unrealistic (*cf.* Hájková *et al.*, 2008). Most gradients in an ecosystem do not span the entire range of possible values, but include only one of the extreme ends of the gradient,

such as the lower pH end in our study of deciduous forests. Although parameters estimated from such *incomplete* species responses might not be useful in the modeling of the entire *potential* species niche, they are still valuable in describing regional patterns in species response and distribution, and in identifying species limits at the complete side of the gradient. Care must be taken especially when optima or amplitudes are calculated, as they may be heavily biased when the full gradient of possible values is not realised. Accordingly, the optima of species in the uplands with a large pH range were much higher than those in the lowlands.

Limits are likewise biased if the gradient is incomplete, such as the upper limit in the lowlands. However, the acidic extremes were comparable in both regions (pH minimum: 2.37 in lowlands and 2.40 in uplands) and represent the lowest pH values generally realised in forests in Germany. The lower limits thus were more stable across regions and independent of the overall gradient length.

The fundamental Grinnellian niche is determined by suitable abiotic conditions only (Grinnell, 1917; Pulliam, 2000; Guisan & Thuiller, 2005), and many authors argue that information on its properties can only be derived from single-species greenhouse experiments in which biotic interactions are excluded. Statistical models based on observational field data include competition (Malanson *et al.*, 1992; Guisan & Zimmermann, 2000; Austin, 2002) and may only yield insight into the realised niche *sensu* Hutchinson (1957). The boundary clumping at pH values between 3.5 and 4.5 (lowlands) and between 3.0 and 4.0 (uplands) was mainly caused by the strong aggregation of lower limits. Previous studies by, for example, Andersson (1992) and Falkengren-Grerup and Tyler (1993) have identified this pH range (3.2 - 4.3) as a physiological threshold for several forest vascular plants. They found a significant drop in growth rate and establishment for 13 species also analysed in the present study, caused by high H^+ concentrations and Al toxicity leading to reduced nutrient absorption, degenerated cell walls and changes in root structure. It is unlikely that the lower limits are induced by negative biotic interactions, as highly competitive species usually have a high nutrient demand and are incapable of growing on low-pH soils with low nutrient availability (Ellenberg, 1996; Crawley, 2009). As already suggested by Austin and Smith (1990), the observed, i.e. realised, limits of species in the field can be congruent with their physiological tolerances. We believe that the lower limits in our study reflect the physiological thresholds of a major part of the species in the community.

In contrast, the upper limits do not show a strong aggregation pattern along the gradient. Neither do they contribute much to the clumping at values between pH 3.0 and 4.5, nor do they form a maximum at higher pH levels. This indicates that the upper limits of most species are determined by biotic interactions rather than by physiological limitation. The lower soil pH limits were strongly positively correlated between the two regions, which supports the interpretation that these limits represent physiological thresholds for most species. Even though also the fundamental limits might differ slightly due to interacting abiotic factors, e.g. pH and soil moisture (Pakeman 2008), they are probably more consistent than parameters of the response curves that are also influenced by biotic interactions (Diekmann & Lawesson, 1999).

The lower limits of species were good predictors of threat level and regional range size in the lowlands where acidic soils dominate. Here, accordingly, species appear to be less common the more base-demanding they are. Species optima show a similar pattern, but with a weaker correlation. The significant relationship between the expert-based change in frequency and lower limits (and optima) indicates a decline of species intolerant to low pH values, as observed already by Falkengren-Grerup (1986). With respect to the threat level, the lower limits again showed a clearer pattern than the optima. In the uplands with their higher diversity of soils and higher proportion of base-rich sites, the only significant correlation was found between the lower pH limit and regional range size, suggesting that acid-tolerant species also here are more widespread. In contrast, the upper limits of species were unrelated to all measures of range size or frequency. This may partly be attributed to the low number of replicates, but also indicates that the observed upper limits are ecologically less meaningful.

Conclusions and further outlook

Our results suggest a large ecological importance of lower soil pH limits of species: these appeared to be relatively stable across regions and were more closely related to range size, threat level and population decline than optima. More generally, the study confirms the importance of soil parameters for plant species distribution. However, even though soil pH is the edaphic factor most frequently measured in vegetation studies, data are scarce especially for many rare species, and for the large majority of soil factors information is lacking even for more common species. Hence, there is an urgent need for more data and for compiling a comprehensive database of species responses relative to soil variables. If we want to predict future plant distributions under different climate change scenarios, we have to extend climate only-models to incorporate information on the regional variation of soil factors and the responses of plant

species to these factors. The identification of suitable sites is also crucial for plant conservation, for example in the framework of habitat restoration and species reintroductions. If better edaphic data became available in various regions it would be possible to compare species optima and limits to test the consistency of these parameters across different areas. This would also facilitate the distinction between physiological thresholds and competition-induced limits.

Supplemental Material

Additional Supporting Information can be found in the Appendix (Chapter 9):

Appendix 7.1 Linear regression of pH values of the same soil samples measured in H_2O, $CaCl_2$ and KCl. The regression equation was used to convert all pH data to standardised values of pH_{CaCl_2}.

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Chapter 8

Synthesis

„*When you have eliminated the impossible,
whatever remains, however improbable, must be the truth!*"

Left side: Stachys sylvatics *in a deciduous forest patch (19.06.2012, A.Pannek)*
Right site: Ranunculus *sp. in a dry grassland area (12.06.2014, A.Pannek)*
Quote: Doyle, Arthur Conan (1890): Sherlock Holmes, The Sign of the Four

Putting the pieces together

Today's biodiversity is facing unprecedented rates of loss. To aid the struggling species and to prevent them from decline or extinction, there is an urgent need to understand and correctly predict their environmental requirements. In this thesis, I studied the responses and niche characteristics of single species in two different ecosystems – deciduous forests and semi-natural grasslands – by using a large-scale perspective that offers deeper insights compared to more small-scale approaches (Brown & Maurer, 1989; Lawton, 1994). In contrast to many other studies, the environmental data are based on actual measurements (especially of edaphic factors) instead of on indicator values. This has been encouraged for plant ecological studies (Austin & Meyers, 1996; Lawesson & Oksanen, 2002; Wamelink *et al.*, 2002; Diekmann, 2003). In practice, however, indicator values or other indirect estimations prevail, mostly because of money and time constraints. Moreover, I was primarily concerned with the reactions of single species instead of plant communities, because previous studies have shown that species respond individually to environmental changes (e.g. Davis *et al.*, 2005; Lavergne *et al.*, 2010). In the following, I will synthesise the results gained in this thesis and further discuss the findings.

Species' responses under environmental change

Even though continuous efforts are being taken to decrease the nutrient inputs, the critical loads as well as planetary boundaries of nitrogen and phosphorus for our ecosystems are exceeded (Galloway *et al.*, 2008; Steffen *et al.*, 2015). In the past four decades, numerous papers focused on the consequences of nutrient depositions to ecosystems, especially in semi-natural grasslands (BassiriRad, 2015). While many studies showed that species richness declines with increasing N-deposition (e.g. Haddad *et al.*, 2000; Stevens *et al.*, 2004; Wesche *et al.*, 2012; Field *et al.*, 2014), there still is a lack of studies focussing on the effects on single species, although only these can reveal possible changes on species composition (Wiens *et al.*, 2009).

The effects of nutrient inputs can be studied with three complementary methods, namely (1) experiments, (2) temporal gradients and (3) spatial gradients (space-for-time substitutions). Since nutrient addition experiments are usually impossible over larger scales, temporal gradients (i.e. using historical *vs.* more recent data; Blake *et al.*, 1999; Bennie *et al.*, 2006; Dupré *et al.*, 2010) or spatial gradients (i.e. using relevés along an area differing in nutrient deposition loads; Fukami & Wardle, 2005; Stevens *et al.*, 2011; Field *et al.*, 2014), are often the methods

of choice to study the impacts of atmospheric nutrient additions. It is generally assumed that spatial gradients reflect the changes that have occurred over time, although prior to our study (Chapter 3), no one directly compared the results gained from both approaches. In fact, the interpretations of space-for-time substitutions were heavily criticised, because the risks of incorrect results are supposed to be high (Chytry *et al.*, 2014). In Chapter 3, we tested if the same species are increasing/decreasing along a spatial as well as a temporal gradient of nutrient input, following the thought of Kerr *et al.* (2007) that spatial relationships should be consistent in time if they are true. Indeed, we could show that this is the case, as the reactions of the species were the same along the temporal and spatial gradient (Figure 3.3). Especially the levels of N and P had negative effects on species' abundances. These two nutrients have been suggested for quite some time as the main drivers of species' decline in acidic grasslands, as both are potentially limiting and their addition changes the competition-structure among species (see below) (Vitousek *et al.*, 2010). Surprisingly, most studies have so far only dealt with the effects of N (Morecroft *et al.*, 1994; Jefferies & Maron, 1997; Gilliam, 2006; Horswill *et al.*, 2008; Maskell *et al.*, 2010), although more recently some studies also examined possible effects of phosphorus additions (Gilbert *et al.*, 2009; Falk *et al.*, 2010; Ceulemans *et al.*, 2011; 2014). In our study, no single nutrient could be detected to be the main driver of species decline. In fact, we believe that both N and P have context-depending impacts, which is in agreement with the results obtained by Ceulemans *et al.* (2013) and Helsen *et al.* (2014). Generally, ecologists should consider the effects of multiple key elements together (Elser *et al.*, 2007), instead of focussing only on single nutrients, since the addition of any limiting nutrient can drastically change the dominance structure in an ecosystem (Vitousek *et al.*, 1997). However, no matter which nutrient is the main cause for the decline of species, management is necessary to negate the inputs and to preserve and improve the quality of the remaining grasslands.

The identification of plant species that consistently increase or decrease in abundance as a reaction to nutrient additions would be strong predictors for changing environmental conditions. However, in a comparison of the reactions of our study species to the levels of available phosphorus with those obtained by Ceulemans *et al.* (2011; 2014), we found that for example *Achillea millefolium*, *Cerastium fontanum*, *Succisa pratensis* and *Trifolium pratense* showed contrasting responses – species that decreased in abundance under higher P-levels in our study increased in their study and the other way around. Contrasting responses of species where also detected by Pennings *et al.* (2005), who observed that only six of their 20 study

species reacted consistently across experiments. This suggests that the origin of the data as well as the selection of species used in an analysis play a huge role for the outcome of a study and that the results of single species need to be interpreted with caution.

Traits, however, seem to be more consistent predictors of species' reactions than species' identity and have been proposed as likely parameters for better understanding ecological communities. Therefore, we were interested if specific life-history traits are correlated with species' susceptibility to environmental change. In our study, species declining in response to increased levels of N and P were often small and slow growing (Table 3.2), which is in agreement with the results obtained by Pennings *et al.* (2005) and Diekmann and Falkengren-Grerup (2002), who also identified species height as an important predictor of their reactions to nitrogen input. In fact, slow-growing species are outcompeted unless they have some adaptation allowing them to either tolerate low light conditions or otherwise escape the competition (Pärtel *et al.*, 2005; Hautier *et al.*, 2009). This poses quite a bit of a problem, since resource-conservative traits (e.g. a slow growth and small stature) are characteristic of typical semi-natural grassland species (Graham & Hutchings, 1988; Tamm, 1991; Sammul *et al.*, 2003). Consequently, these are also the ones disappearing due to the shift from belowground to aboveground competition, when no management actions to preserve these species are being taken.

Niche characteristics as determinants of range size

In Chapter 3, we showed that the changes in the abundance of species are dependent on the current state of the environment, with loser and winner species being the same over space and time. Species with both low abundance and small range size have often been considered to be the great losers of past and recent global environmental change (Rooney *et al.*, 2004; Clavel *et al.*, 2010; Devictor *et al.*, 2010), because this double jeopardy makes them highly vulnerable to stochastic effects and localised catastrophes (Lawton, 1994). In fact, range size is one of the most important criteria for classifying the threat status of a species (IUCN, 2012), and it becomes even more important in the face of widespread habitat destruction and other global changes, since the factors determining species' ranges also affect their capacity of reacting to changes in the environment. Therefore, one of the most prominent macroecological questions is which mechanism can best explain species' range size. We explored this question in Chapters 4, 5 and 7.
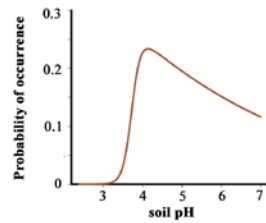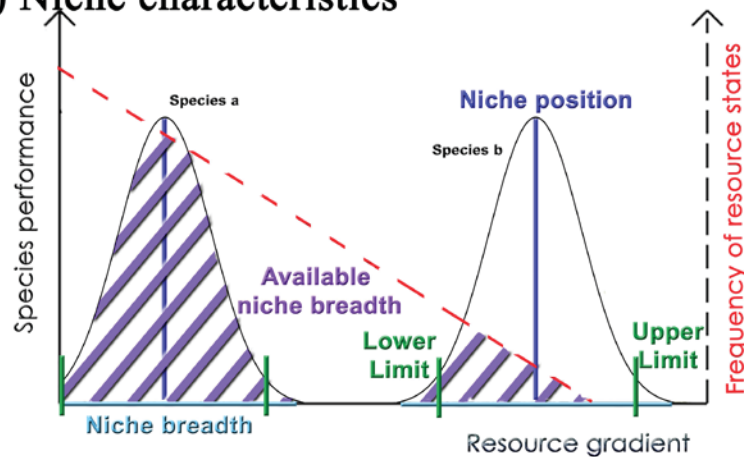
Figure 8.1 *I) Overview of the methods used for calculating niches with A) the resource based method and B) the occurrence based method. II) Summary of the niche characteristics calculated in this thesis for the resource based method, namely available niche breadth (violet; compound measure out of niche breadth, niche position and the frequency of resource states), niche breadth (dark blue), niche position (light blue) and upper and lower limits (green).*

Step 1: Know your methods

In this thesis, two different approaches of estimating niches were used: a "traditional" one, based on a direct gradient analysis using environmental measurements (Figure 8.1 and Chapters 4 to 7) , and a rather new one, based on an indirect estimation using species co-occurrence data (Chapter 5). Both the gradient approach as well as the co-occurrence methods have already been applied elsewhere (Austin & Gaywood, 1994; Coudun & Gégout, 2005; Zelený, 2009; Albert *et al.*, 2010; Heikkinen & Mäkipää, 2010; Cachovanová *et al.*, 2012; Wasof *et al.*, 2013). So far, however, no study compared the results of these different approaches for explaining the ranges of species or enquired how the approaches cope with the specific strengths and weaknesses known to accompany the calculations of species' niches.

Studies seeking to relate the niche breadth of species to their range size are often confounded by artefacts influencing the calculation of niche characteristics, making it difficult to discern the evidence for or against it. For one, phylogenetically related species are thought to be more

similar due to a shared ancestor (Felsenstein, 1985; Harvey, 1996) and therefore do not constitute independent data points in the analyses (Blackburn, 2004). For this reason, in Chapter 4, we applied a phylogenetically controlled comparative method in addition to working with the uncorrected cross-species analysis. Thereby, we could show that also in our study, ancestry had no influence on the outcome of the relationship between niche breadth and range size. This is in agreement with almost all of the results found in the literature (e.g. Gaston *et al.*, 1997; Dennis *et al.*, 2000; Cowley *et al.*, 2001; Brändle *et al.*, 2002; Kotze *et al.*, 2003; McCauley *et al.*, 2014), indicating that phylogenies play no or only a very minor role for determining the relationship between niche characteristics and range size.

Another bias is caused by unequal sampling of the studied species: If more plots are sampled for common than for rare species, niche breadth is likely to be greater for common ones simply by chance (Burgman, 1989), resulting in a positive relationship between range size and niche breadth. In Chapter 4, we therefore used the same number of plot occurrences per species and showed that niche breadth and position were good predictors of species' range sizes also with an equal sampling size for all species (Table 4.2). This suggested that sampling is not the main reason for the relationship between niche characteristics and range size. However, using this approach, we only "bypassed" the sampling bias, not knowing anything about its potential magnitude. In fact, while this sampling bias has been widely acknowledged to influence the niche breadth-range size relationship (Brown, 1984; Gaston *et al.*, 1996; Selmi & Boulinier, 2004), the strength of the potential bias has not yet been quantified. Moreover, all existing evidence only applies to the gradient approach and not to the co-occurrence approach, where such questions simply have not yet been tackled. To answer this question, in Chapter 5, we therefore compared the two approaches with respect to the sampling bias. Interestingly, while the estimates obtained from the gradient approach were highly biased, this was not the case for the co-occurrence results (Table 5.1), at least partly because of a randomisation process inherent to the method (Fridley *et al.*, 2007). When the sampling bias was corrected for (using equal plot occurrences for all species, *cf.* Chapter 4), the niche breadth estimates of both methods were highly comparable (Figure 5.3). Due to the significant influence of the number of sampled plots on the niche parameters for the gradient method, however, we agree that caution has to be taken. The reason for this is that when neglecting to address this bias, studies definitely become hard to interpret (Gregory & Gaston, 2000).

Taken together, neither the phylogenies of species nor the unequal sampling is causing the relationship between niche characteristics and range size in this study. While we

agree that the sampling bias increases the strength of the relationship, there must be some other pattern generating the link. Thus, this demonstrates that the niche breadths-range size relationship is not an artefact but a fact, which is in agreement with a recent review from Slatyer et al. (2013), which too shows a consistent relationship between niche breadth and range size, independent from possible biases or spatial scales.

Apart from the two potential artefacts and biases mentioned above, one encounters additional challenges when calculating niche characteristics. For one, the selection of a particular gradient is often based on expert knowledge, but this gradient may not be of actual relevance for the species studied (Köckemann *et al.*, 2009). This could therefore lead to an incorrect ranking in species' niche breadth (Lawesson & Oksanen, 2002). The reason for this is that a species can theoretically be a specialist on the measured gradient, but be a generalist on other, non-measured ones (Colwell & Futuyma, 1971). However, as both direct and indirect niche breadth estimates were significantly correlated in our study (Figure 5.3), we believe that the environmental gradients, although selected based on data availability and expert knowledge, indeed reflect a correct ranking of species' niche breadth. Moreover, this correlation also disproves the notion that the co-occurrence niche breadth estimate relies too much on the biotic component of the niche (Wasof *et al.*, 2013), since in our case, it was significantly correlated with two environmental gradients (light and pH; Figure 5.3).

Comparing the two approaches to estimating niches, the co-occurrence method seems at a first glance to be the holy grail of niche research. It is not biased in regard to sampling size, and literally millions of relevés are available in the form of vegetation surveys (Schaminée *et al.*, 2011), which can be used. More and more of them are even becoming available online through different database-projects, like the Global Index of Vegetation-Plot Databases (http://www.givd.info) or the Botanical Information and Ecology Network (http://bien.nceas.ucsb.edu/bien). Moreover, the lack of a relationship between the predictor variable and range size cannot be due to the fact that an environmental variable unimportant for the study organism has been studied, as it could be the case when working with the gradient approach. However, as an indirect method, no predictions regarding the actual requirements of species are possible – the estimates cannot be transformed to real values. Moreover, for predicting suitable locations for reintroductions, measured environmental data are indispensable.

Step 2 – Work with old friends

Having eliminated the possibility of artefacts/biases as the main reason for the positive relationship between range size and niche measurements in the previous section, we still have to discuss two prominent biological explanations for differing range sizes between species: Niche position and niche breadth. While the niche position hypothesis of Hanski *et al.* (1993) predicts that species using common resources are common as well, Brown (1984) argued for the niche breadth hypothesis: Generalists should occur over a larger geographical area than specialists, because they are able to exploit a wider range of resources. These intuitively appealing theories have been discussed, tested and analysed in many studies (Gregory & Gaston, 2000; Williams *et al.*, 2006; Laube *et al.*, 2013; McCauley *et al.*, 2014) and books (Brown, 1995; Gaston & Blackburn, 2000). Still, we know remarkably little about the relative importance of the different explanations and a general consensus on their predictive power remains elusive.

The positive correlation between both niche breadth/position and range size in our study (*cf.* Figure 4.3) confirms the assumption of Gaston *et al.* (1997) that the explanations are not mutually exclusive. Gouveia *et al.* (2014) argue that a combination of factors outperforms single parameters, because they describe different aspects of the species' niche. This is in agreement with theory, since already Gaston *et al.* (2000) proposed that most likely not "the one" mechanism exists for the explanation of the niche character- range size hypothesis, but a multitude of them with specific explanations applying at larger and some at smaller spatial scales. This was also a reason for introducing the concept of the "available niche breadth" in Chapter 4. In the concept of the available niche breadth, species with broad ecological amplitudes and ecological preferences for widespread habitats are likely to have larger range sizes than species with a narrow amplitude and specificity to rare habitats. Overall, we found that our measure of available niche breadth was better correlated to range size than the single variables (*cf.* Appendix 8.1 in Chapter 9). Interestingly, this was not only true in a comparison with the measured niche characteristics, but also for the co-occurrence estimate. The reason for this is that with the correction of the availability of resources, the available niche breadth captures the niche of species with specific soil-related distribution patterns better than an assessment without this correction. It also explains why our measure of available niche breadth was so successful in predicting range sizes: For one, it combines niche breadth and position, which both explain a different part of the pattern. Second, it also includes the available habitat space

for each species in a given region, which is of utmost importance for a precise prediction of how large the range size can be.

In summary, while both niche breadth and position were good predictors of range size, the co-occurrence approach worked equally well. Available niche breadth, as a compound measure however, was superior in predicting the range sizes of species.

Interlude: The curious case of *Ceratocapnos claviculata*

One species that tended to behave differently from most others was the herb *Ceratocapnos claviculata*. For example, in Chapter 4, its niche breadth and position estimates did not fit into the range-size pattern found for all other species (Figure 4.3d-f). In Chapter 5, *C. claviculata* had a high turnover of neighbouring species (= large niche breadth) but a small niche breadth for soil pH (Figure 5.3a). However, using the available niche breadth, in both cases, the former outlying tendencies vanished. The reason for this is that *C. claviculata* has a small soil pH niche

Figure 8.2 *National (Germany; Bettinger et al., 2013) as well as regional (Weser-Elbe region; Cordes et al., 2006) distribution of the forest herb* Ceratocapnos claviculata. *Picture taken by A. Pannek (19.06.2012).*

breadth, but is still very common in the North-western German Lowlands (see Fig 8.2: regional distribution), since it mostly grows on acidic soils, which in turn are quite common there. Moreover, as reflected in its oceanic distribution (national distribution pattern; Figure 8.2), it is dependent on relatively mild winters. The species is therefore only sparsely distributed over the rest of Germany, although this pattern may change, as *C. claviculata* appears to be favoured by global environmental change, specifically by the increases in temperature and by the higher nutrient loads in its habitat (Lethmate *et al.*, 2002; Pollmann & Lethmate, 2006; Voß, 2014). However, when the climate matches (reason for its broad distribution in NW Germany), *C. claviculata* is a specialist only with respect to its soil requirements; on all other environmental axes, it is a generalist. For this reason, the herb has many neighbouring species and is regarded as a generalist via the co-occurrence assessment in the Weser-Elbe region.

This behaviour is in the gradient approach only captured by the available niche breadth, with its correction of the high availabilities of forest soils with low-pH values in the Weser-Elbe region.

This shows that species utilising resources that are common in an area can be widespread even with a seemingly small niche breadth. This is consistent with the results from Gregory and Gaston (2000), who confirmed for breeding birds in Britain that species utilising resources that are more common in a specific community tended to be widespread. Markham (2014) demonstrated as well that rare species are occupying uncommon niches, while the common ones were found under conditions that are more widespread. What is regarded as rare and common, however, can very much depend on the scale, as this example clearly shows. A regional specialist can be a generalist at a national scale and vice versa. However, it is important that species with "unusual" reactions, like it at first seemed to be the case with *C. claviculata,* are not instantly dismissed, as species that are exceptions to general patterns present unique opportunities for understanding what is going on in nature (Brown, 1999).

Step 3 – Make new acquaintances

Especially nowadays, where the world's biota face manifold threats, reliable predictions of present and future range sizes of species, and therefore of their commonness or rarity, are of importance. Even though niche breadth or niche position of species are quite often and, as we have seen, successfully used as parameters for explaining range sizes, especially the use of niche position (=optima) might be outdated due to the ongoing changes in our landscapes (e.g. habitat destruction, nutrient pollution). In fact, humans are modifying the ecosystems more and more and as a consequence, it could be that in 50 to 100 years, the suite of environmental factors that species have evolved in might no longer be present (Tilman & Lehman, 2001). From this, it follows that for many species, "optimal" habitats might no longer exist. In this case, knowledge about factors that describe the range of environmental conditions that a species is able to tolerate will be much more important, for example for making informed management decisions or for maximising the success of reintroductions, than restricted knowledge about their optima.

An alternative to the work with species optima, which are further constrained by different biotic interactions as well as the species pool of a region (Hájková *et al.*, 2008), are therefore the minimal requirements of species – their limits or tolerance thresholds. Although already more than two decades ago, Falkengren-Grerup and Tyler (1993) realised that envi-

ronmental limits will be of importance in the future, we are not aware of any other study dealing with limits in plants. For animals, a few papers working on upper thermal limits are available (e.g. Calosi *et al.*, 2008; Peck *et al.*, 2009; Gouveia *et al.*, 2014), because this limit is inherently linked to species' survival in warmer environments and therefore to the threat of environmental warming (Gaston *et al.*, 2009).

Generally, it is assumed that one extreme of a gradient is physically stressful, while the other one is biologically stressful (Brown *et al.*, 1996). It follows that one hand of the gradient side might indicate a fundamental limit, while the other indicates a realised one mainly based on competitive interactions (sensu the definitions of realised and fundamental niches of Hutchinson, 1957). In our studies dealing with limits in vascular plants (Chapters 6 and 7), we investigated both a lower limit (soil pH in deciduous forests) as well as an upper limit (phosphorus availability in dry calcareous grasslands), which are the main environmental factors governing species' abundance in their respective ecosystems. In the case of soil pH, the lower limit would be the physiological stressful one, while at the upper limit, competition determines the survival of species. Evidence for this theory is the clumping of lower pH limits at a value of about 4.0-4.5 (Fig 7.4). This is exactly the range where aluminium becomes toxic (Falkengren-Grerup, 1986; Balković *et al.*, 2014) and therefore describes a physiological limit for many plants. With respect to phosphorus availability, we have seen that species that are able to tolerate higher levels are more common than species that are less tolerant (Figure 6.2). The reason for this is that they are able to out-compete the typical grassland species adapted to low nutrient conditions (see discussion about species reactions to nutrient pollution further above). Therefore, the upper P limit is of importance for the prediction of range size, since it decides about the "success" of species in the face of nutrient pollutions.

A clear advantage of using limits as predictors of range size instead of niche breadth or position is the fact that they are independent from the realised length of the environmental gradient in an area. As long as one side of the gradient is sufficiently covered, the limit can be calculated and no corrections for the bias of differing gradient lengths have to be made. While we believe that our lower limit (soil pH) will be quite stable across spatial scales, since it describes a fundamental limit, we are uncertain if this is also true for the upper limit (P availability). The reason for this is that the competition-limit might change depending on the presence or absence of specific species in the community.

Taken together, the fact that limits of two environmental factors in two different eco-systems were successful predictors of species' range sizes and threat levels and often showed to be superior to optima or Ellenberg indicator scores (cf. Chapter 6 and 7) confirms that species limits are indeed interesting alternative predictor variables, which should be considered more often in future studies.

Step 4 – Be spoilt for choice

Comparisons of species niche characteristics with range size can be found in Chapter 4, 6 and 7 of this thesis. In Chapter 4, we started with correlating niche breadth, niche position and the available niche breadth with species' range sizes. Here, the available niche breadth was a better predictor of species rarity than the single values. In a next step (Chapter 5, data shown in Appendix 8.1), the indirect measure of niche breadth via the co-occurrence approach had about the same predictive power of species rarity on a regional level than available niche breadth. On the national level, however, available niche breadth was superior, most likely because in the co-occurrence approach, biotic interactions play a major role for the distribution of species. In Chapter 7, limits and niche position were compared to the range sizes of forest species. Here, limits were by far the better predictors of range size than niche position. The same was true for the grassland species in Chapter 6. Which parameter is thus "the best" to reliably estimate the range size of species?

NICHE BREADTH AND POSITION, two easy-to-calculate niche parameters, worked well in predicting species range sizes, with niche breadth being more important than niche position, especially on larger scales. The drawback here is that specific species with unusual distribution patterns (*cf. Ceratocapnos claviculata*) may behave as outliers and cause spurious patterns in the analysis. Moreover, caution has to be taken as the number of sampled plots per species influences these measures.

When the data for the calculation of the AVAILABLE NICHE BREADTH exist, this can be recommended as the parameter of choice. The reason for this is that it showed to be a very reliable predictor of range size and that it coped very well with area-specific distribution patterns of species. Moreover, it provided reliable predictions on regional as well as national scales. The drawback, however, is the data availability. Even for an often-used measure like soil pH, the data availability of the distributions of pH-values in a given area is very sparse. For other

environmental variables, this data is practically non-existent, which at the moment severely limits the application of available niche breadth as a predictor of species' range size.

The **CO-OCCURRENCE APPROACH** forms a good alternative when no environmental measurements, but only species relevés, are available, although the predictions seem to be only reliable in the area where the data were collected. The reason for this is that competitive effects and local characteristics (e.g. many plots with low soil pH values in our area) heavily influence the co-occurrence of species and these are changing over spatial scales. Therefore, predictions on national scales are not reliable if the data come from a limited regional survey (Appendix 8.1). A big advantage, however, is the independence of the number of sampled plots per species, making it easier to include rare species in an analysis.

The use of species **LIMITS** may be another promising approach. In some cases (low soil pH), they even represent physiological limits, describing the border of the realised as well as of the fundamental niche. Here, biotic interactions are irrelevant and the limits should be stable across spatial scales. The stability of upper limits will depend on the comparability of competitive strength and co-occurring species across regions. Interestingly, limits calculated on a regional scale also showed to be very good predictors of national range sizes (Appendix 8.1). In how far they are even able to predict the ranges across larger scales, how comparable they are across regions or how well different kinds of limits generally perform, remains to be seen.

What's next?

Most predictions on current and future distributions of species are primarily based on climatic conditions (Pearson & Dawson, 2003; Early & Sax, 2014; Gouveia *et al.*, 2014), and we agree with the notion of Corlett and Westcott (2013) that this is quite a "naïve assumption". As we have seen, soil parameters are of equal importance for determining species' distributions. Notwithstanding this realisation (e.g. Stanton-Geddes *et al.*, 2012), actual studies working with soil variables are rare (but see Dubuis *et al.*, 2013; Thuiller, 2013; Beauregard & de Blois, 2014), even though habitat specialisation can be a better predictor of range size than climate (Botts *et al.*, 2013). Moreover, Coudun *et al.* (2006) showed that including soil pH in species distribution modelling improves the quality of predictions compared to climate-only models. The reason for this is that soil pH acts as a local filter by predicting occurrences at finer resolutions, which is also the reason why our predictors are good at the regional and national levels, but scaled further up, no correlations with range size were found. Therefore, we

agree with the assessment of Pearson and Dawson (2003) that climate and soil act at different spatial scales and therefore are very well suited for a combined prediction effort. While the climate layer predicts whether an area is generally suited to contain a species, the soil layer acts as a filter to allow detailed predictions of where a species can or cannot grow due to the basic nature of the soil (see Dubuis *et al.*, 2013 and compare Figure 8.2). Still, studies combining this information are largely missing. For reliable predictions of where a species might occur in the future, however, they are vital.

One reason for the shortage of edaphic factors (e.g. soil acidity, nutrient status or water availability) in species distribution models is that such data are simply lacking. This is not only true for Germany, but for Europe as a whole (de Vries *et al.*, 2007). Although gaining this data is both time- and money-consuming, it is the only possibility of obtaining sufficient material for modelling species responses to several abiotic factors and for ecologically testing their significances for the commonness and rarity of species. It is exactly this know-how of species' niche breadth and limits that can be informative in translocation studies, because it is known that the failure of many of these trials is due to the lack of knowledge of species' requirements (Maschinski & Haskins, 2012; Chauvenet *et al.*, 2013). In this thesis, we could provide some niche characteristics for forest as well as grassland species. For these species, our results can be guidelines for selecting sites with conditions where they have an increased chance of survival instead of basing the translocations on expert opinion alone.

As per definition, the niche is an n-dimensional hypervolume (Hutchinson, 1957). Still, most approaches work only with one dimension at a time. The reason for this is that, even though some methods (e.g. GAMs) are able to cope with interactions, the outputs cannot easily be interpreted and analysed. For the HOF models, it would as well be interesting to have the possibility to model interacting factors. Here, further statistical research is needed to make it possible for ecologists to calculate multidimensional niches. At the moment, the only possibility of capturing the multidimensionality of niches is the use of indirect approaches, like the co-occurrence method or similar methods, although there it is not known, which (a-)biotic factors interact and are the most important ones for the distribution of species.

Whichever approach is used to calculate niche characteristics, the problem of suitable predictions remains complex, mainly because an establishment will depend on multiple driving factors (Anderson, 2013). However, efforts to increase data availability, modelling with predictors operating at different scales as well as advances in statistical techniques, will make sure

that much improved predictions about which species are likely to be most affected by habitat change or environmental pollution will be possible, which is of uppermost importance from an applied or conservation perspective.

Another area to tackle in more detail in niche research is the shift of species' niche parameters across regions as well as the stability of niche characteristics as range size predictors across larger spatial scales. Here, a major question is whether there is one niche characteristic that provides to be a reliable predictor of range size not only in one but in many countries, and across different ecosystems. Although we expect our limits to be quite stable, we do not know yet how they would fare in such a broad-scale comparison in contrast to the generally used niche parameters or how much the results will vary depending on the edaphic factor studied. Here, more studies are needed to provide this generality and answer which parameter is best to use for tackling global change issues across larger scales.

Conclusion

In his paper from 1999, Brown observed that nature reveals its secrets only very reluctantly. This is very much true in macroecology, where some questions have been asked for a long time, with only partial answers found so far. Darwin posed one of these questions in 1859, asking for the reasoning behind the rarity and commonness of species. Even then, he believed this question to be of highest importance, with its answer being connected to the welfare of "every inhabitant of this world". This study offers further puzzle pieces for providing an explanation for this pattern, as we could show here that especially the breadth of resources used as well as the environmental tolerance limits of species play important roles for their distributions. Furthermore, we believe that the niche properties generated during this study can be used to get one-step closer to explaining why some species are rare and others are common, while at the same time providing new insights and guidelines for conservation decisions, being especially important in today's ever changing environments.

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Chapter 9

Appendices
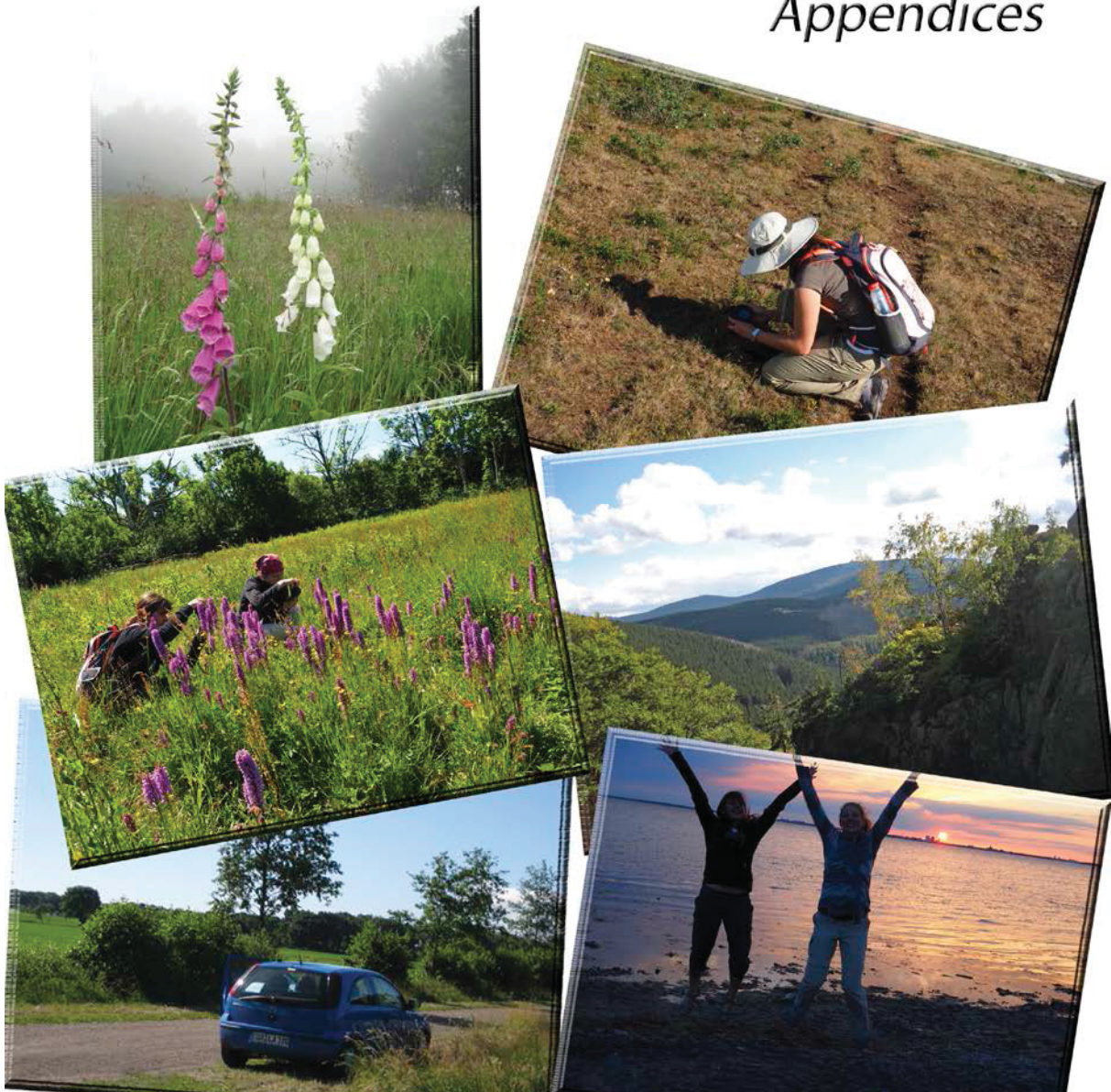
Appendix 3.1

Species included in the study based on their occurrence in the temporal dataset (indicated with an x) in Germany and the Netherlands.

Species	Germany	Netherlands
Achillea millefolium L.	x	x
Agrostis capillaris L.	x	x
Agrostis stolonifera L.	x	
Anthoxanthum odoratum L.	x	x
Calluna vulgaris (L.) Hull	x	x
Campanula rotundifolia L.	x	
Carex nigra (L.) Reichard	x	x
Carex panicea L.	x	x
Carex pilulifera L.	x	x
Cerastium fontanum Baumg.	x	x
Convallaria majalis L.	x	
Cynosurus cristatus L.	x	
Danthonia decumbens (L.) DC.	x	x
Deschampsia flexuosa (L.) Trin.	x	x
Erica tetralix L.	x	x
Festuca ovina / rubra agg.	x	x
Galium saxatile L.	x	x
Hieracium pilosella L.	x	x
Holcus lanatus L.	x	x
Holcus mollis L.	x	
Hypochaeris radicata L.	x	x
Juncus effusus L.	x	x
Juncus squarrosus L.	x	x
Leontodon autumnalis L.	x	x
Leontodon hispidus L.	x	
Lotus corniculatus L.	x	x
Luzula campestris agg.	x	x
Molinia caerulea L. (Moench)	x	x
Nardus stricta L.	x	x
Plantago lanceolata L.	x	x
Poa pratensis L.	x	x
Polygala serpyllifolia Host	x	x
Potentilla erecta (L.) Raeusch.	x	x
Ranunculus acris L.	x	
Ranunculus repens L.	x	
Rumex acetosa L.	x	x
Rumex acetosella L.	x	x
Succisa pratensis Moench	x	x

Species	Germany	Netherlands
Trifolium pratense L.	x	
Trifolium repens L.	x	x
Vaccinium myrtillus L.	x	
Vaccinium vitis-idaea L.	x	
Veronica chamaedrys L.	x	
Veronica officinalis L.	x	x

Appendix 3.2

Correlation matrix of the environmental variables considered for the GLM analysis of the spatial gradient dataset, including: total N deposition, P (log-transformed), topsoil pH, NO_3^- (log-transformed), NH_4^+ (log-transformed), longitude, latitude, altitude (log-transformed), mean annual rainfall, management, mean annual potential evotranspiration (mean annual pot. evotransp.), mean maximum daily temperature, mean minimum daily temperature and radiation index. Spearman correlation coefficients are given.

	Total N deposition	P (log)	Topsoil pH	NO_3^- (log)	NH_4^+ (log)	Longitude	Latitude
Total N deposition	1.000	-0.038	-0.454	-0.058	0.145	0.151	-0.283
P (log)	-0.038	1.000	-0.133	0.144	0.272	-0.204	-0.003
Topsoil pH	-0.454	-0.133	1.000	-0.048	-0.376	0.181	-0.133
NO_3^- (log)	-0.058	0.144	-0.048	1.000	0.324	-0.085	0.051
NH_4^+ (log)	0.145	0.272	-0.376	0.324	1.000	-0.190	0.105
Longitude	0.151	-0.204	0.181	-0.085	-0.190	1.000	-0.141
Latitude	-0.283	-0.003	-0.133	0.051	0.105	-0.141	1.000
Altitude (log)	0.247	0.228	-0.328	0.335	0.483	-0.235	-0.118
Mean annual rain	-0.347	0.081	0.096	0.106	0.233	-0.169	0.348
Management	0.143	0.118	-0.328	0.140	0.283	-0.201	0.153
Mean annual pot. evotransp.	0.138	0.013	0.161	-0.007	-0.103	0.140	-0.884
Mean max daily temperature	0.303	-0.077	0.196	-0.150	-0.251	0.212	-0.916
Mean min daily temperature	0.082	0.062	0.091	-0.076	-0.106	-0.318	-0.731
Radiation index	0.080	0.002	0.149	0.064	-0.045	0.279	-0.563

	Altitude (log)	Mean annual rainfall	Management	Mean annual pot. evotransp.	Mean max daily temp.	Mean min daily temp.	Radiation index
Total N deposition	0.247	-0.347	0.143	0.138	0.303	0.082	0.080
P (log)	0.228	0.081	0.118	0.013	-0.077	0.062	0.002
Topsoil pH	-0.328	0.096	-0.328	0.161	0.196	0.091	0.149
NO_3^- (log)	0.335	0.106	0.140	-0.007	-0.150	-0.076	0.064
NH_4^+ (log)	0.483	0.233	0.283	-0.103	-0.251	-0.106	-0.045
Longitude	-0.235	-0.169	-0.201	0.140	0.212	-0.318	0.279
Latitude	-0.118	0.348	0.153	-0.884	-0.916	-0.731	-0.563
Altitude (log)	1.000	-0.057	0.120	0.114	-0.072	-0.083	0.023
Mean annual rain	-0.057	1.000	0.139	-0.343	-0.446	-0.140	-0.253
Management	0.120	0.139	1.000	-0.109	-0.222	-0.074	-0.137
Mean annual pot. evotransp.	0.114	-0.343	-0.109	1.000	0.805	0.727	0.550
Mean max daily temperature	-0.072	-0.446	-0.222	0.805	1.000	0.714	0.533
Mean min daily temperature	-0.083	-0.140	-0.074	0.727	0.714	1.000	0.399
Radiation index	0.023	-0.253	-0.137	0.550	0.533	0.399	1.000

Appendix 3.3 Species responses (spatial gradient data set) to total nitrogen deposition (N_{dep}; in kg N ha^{-1} yr^{-1}), available phosphorus in the soil(P; mg P kg^{-1}, log-transformed), soil pH (pH), and the soil contents of ammonium (NH_4^+; kg N ha^{-1} yr^{-1}, log-transformed) and nitrate (NO_3^-; kg N ha^{-1} yr^{-1}, log-transformed), longitude of the site (Long), Latitude (Lat), Altitude (Alt), radiation index (Rad), Management intensity (Manage., coded as a factor with 4 levels with varying grazing intensity from 0 = no grazing to 3 = high intensity), mean annual rainfall (Rain, in mm) Regression coefficients (Coef, with the direction of the effect) and significance values (P) for each variable as well as the R^2-value of the final model are shown. The analyses were carried out with general linear models with a Poisson distribution. N = number of occurrences in the dataset.

Species	N	N_{dep} Coef	N_{dep} P	P Coef	P P	pH Coef	pH P	NH_4 Coef	NH_4 P	NO_3 Coef	NO_3 P	Long Coef	Long P	Lat Coef	Lat P	Alt Coef	Alt P	Rad Coef	Rad P	Manage. Coef	Manage. P	Rain Coef	Rain P	R^2
Achillea millefolium L.	53	-0.04	0.07			0.8	0.02			0.43	0.04	0.06	0.03											0.23
Agrostis capillaris L.	151											-0.03	0	0.04	0					0.09	0.01			0.28
Agrostis stolonifera L.	21											-0.34	0	0.19	0.01					-1.2	0	-2.66	0.09	0.51
Anthoxanthum odoratum L.	100	-0.03	0.01							0.29	0.01	-0.07	0	0.07	0					-0.31	0			0.31
Calluna vulgaris (L.) Hull	87	-0.03	0.01	-1.05	0							-0.44	0	0.05	0									0.27
Campanula rotundifolia L.	38	-0.08	0.02	-0.9	0.01	1.14	0.01					0.07	0	0.25	0	0.89	0.01	-1.22	0.07	0.2	0.09			0.58
Carex nigra (L.) Reichard	27									-0.69	0	-0.19	0	0.3	0							3.53	0.01	0.41
Carex panicea L.	50	-0.06	0.01			-1.88	0																	0.21
Carex pilulifera L.	90									-0.46	0	0.08	0	-0.09	0									0.28
Cerastium fontanum Baumg.	57			0.92	0.03	1.39	0							0.18	0			-1.61	0	0.16	0.01			0.34
Convallaria majalis L.	15			3.54	0	1.8	0.01					-0.12	0.08									4	0.07	0.32

Species	N	N_dep Coef	N_dep P	P Coef	P P	pH Coef	pH P	NH₄ Coef	NH₄ P	NO₃ Coef	NO₃ P	Long Coef	Long P	Lat Coef	Lat P	Alt Coef	Alt P	Rad Coef	Rad P	Manage. Coef	Manage. P	Rain Coef	Rain P	R²
Cynosurus cristatus L.	15	0.12	0	2.61	0	2.22	0					-0.37	0			-1.97	0	-2.21	0.02					0.51
Deschampsia flexuosa (L.) Trin.	80					-0.95	0					0.12	0					-0.83	0.06					0.3
Erica tetralix L.	17									-1.15	0													0.21
Festuca ovina / rubra agg.	142			0.3	0.05			0.17	0.08					-0.02	0.05					0.12	0.01	-0.58	0.1	0.12
Galium saxatile L.	114					-0.52	0					0.04	0	0.08	0	0.39	0.01							0.22
Hieracium pilosella L.	46											0.19	0	-0.25	0							3.12	0.01	0.46
Holcus lanatus L.	77			1.02	0.01	0.92	0	-0.44	0.04			-0.12	0											0.28
Holcus mollis L.	30			1.43	0.06	0.99	0.03									1.16	0.04	-1.51	0.06					0.15
Hypochaeris radicata L.	51					0.83	0.01							-0.14	0	-1.02	0							0.39
Juncus effusus L.	41	0.07	0									-0.28	0	0.18	0.01	-0.75	0.03			0.44	0.01	-2.23	0.08	0.38
Juncus squarrosus L.	34					-0.86	0.05					-0.15	0.01							-0.59	0.03			0.16
Leontodon autumnalis L.	16			1.74	0.03			-1.89	0					0.38	0							3.95	0.02	0.5
Leontodon hispidus L.	23							-0.67	0.06	-0.52	0.05	-0.3	0							-0.59	0.04			0.43
Lotus corniculatus L.	46	-0.04	0.07			1.13	0	-0.53	0.03			-0.1	0	0.08	0.02									0.35
Luzula campestris agg.	148			0.7	0.01	0.81	0	-0.44	0			0.04	0											0.31
Molinia caerulea L. (Moench)	62							0.77	0.07	-0.77	0									-0.41	0.06			0.22
Nardus stricta L.	82	0.03	0.01									0.06	0	0.06	0.09	0.78	0							0.21

Species	N	N_{dep} Coef	N_{dep} P	P Coef	P P	pH Coef	pH P	NH_4 Coef	NH_4 P	NO_3 Coef	NO_3 P	Long Coef	Long P	Lat Coef	Lat P	Alt Coef	Alt P	Rad Coef	Rad P	Manage. Coef	Manage. P	Rain Coef	Rain P	R^2
Plantago lanceolata L.	51					2.14	0			0.38	0.06	-0.08	0.01	0.08	0.03									0.38
Poa pratensis agg.	32					0.94	0.07							0.2	0	1.42	0.02							0.17
Polygala serpyllifolia Host	31	-0.05	0.06	-1.14	0.03					-0.59	0	-0.08	0.06	-0.15	0									0.31
Ranunculus acris L.	24					2.03	0			0.52	0.07			0.19	0							-4.78	0.02	0.23
Ranunculus repens L.	22					2.29	0					-0.07	0.08	0.15	0.01							4.76	0.01	0.38
Rumex acetosa L.	75			0.96	0.01	0.68	0.01	-0.35	0.1	0.6	0			0.17	0									0.32
Rumex acetosella L.	50	0.04	0					-0.55	0.09	0.68	0	0.2	0	-0.22	0	-1.1	0					5.34	0	0.6
Succisa pratensis Moench	30	-0.07	0.04			1.18	0.01					-0.17	0	0.12	0.01					-1.11	0			0.43
Trifolium pratense L.	24			1.91	0.01	2.68	0					-0.14	0.01					-2.1	0.04	0.43	0.08			0.4
Trifolium repens L.	52			1.43	0									0.13	0	0.53	0.08			0.61	0	2.06	0.05	0.33
Vaccinium myrtillus L.	63					-1.17	0	0.86	0.04					0.11	0.01	1.11	0.01			-0.48	0.01			0.4
Vaccinium vitis-idaea L.	13	-0.21	0					2.1	0	-0.46	0.01	0.33	0			-1.24	0							0.83
Veronica chamaedrys L.	74					2.16	0									1.14	0.05					-3.19	0.08	0.3
Veronica officinalis L.	96	-0.05	0.03					-0.93	0.02			0.14	0			1.58	0							0.32

Appendix 3.4

Means and standard deviations (sd) of environmental variables in the spatial gradient dataset given for each country, including: total nitrogen deposition (N deposition; in kg N ha^{-1} yr^{-1}), available phosphorus in the soil (P; mg P kg^{-1}), soil pH, the soil contents of ammonium (NH$_4^+$; kg N ha^{-1} yr^{-1}) and nitrate (NO$_3^-$; kg N ha^{-1} yr^{-1}), radiation index, mean annual rainfall (mm), altitude and management (coded as a factor from 0 = no grazing to 3 = high grazing intensity). N = number of plots analysed in each country. For more detailed information, see Stevens *et al.* (2011).

Country	N	N deposition		P		soil pH		NH$_4^+$		NO$_3^-$	
		mean	sd	mean	sd	mean	sd	mean	sd	mean	sd
Belgium	9	18.13	2.85	8.96	5.89	4.92	0.39	27.96	19.76	0.38	0.82
Denmark	3	11.60	2.68	11.48	4.48	4.58	0.16	12.09	7.61	3.12	3.69
France	25	12.78	3.22	14.94	6.64	5.23	0.28	27.38	14.27	23.20	30.66
Germany	12	29.82	8.29	13.02	3.91	4.57	0.16	18.85	17.66	16.06	24.51
Great Britain	73	20.61	8.17	18.59	15.70	4.33	0.40	72.76	49.61	17.01	20.47
Ireland	10	11.66	6.90	14.53	6.50	4.86	0.48	60.57	94.98	4.44	3.55
Isle of Man	1	18.63	NA	10.43	NA	4.00	NA	53.16	NA	62.03	NA
Netherlands	7	31.42	5.63	15.09	11.22	4.55	0.37	15.21	9.58	1.62	1.17
Norway	9	7.30	1.66	20.04	8.71	4.68	0.29	113.42	62.32	68.75	70.88
Sweden	4	11.70	0.14	7.93	2.20	4.77	0.28	12.51	4.88	2.24	1.56

Country	N	Radiation index		Annual Rainfall		Altitude		Management	
		mean	sd	mean	sd	mean	sd	mean	sd
Belgium	9	0.63	0.00	813.64	42.37	32.11	25.34	0.33	0.71
Denmark	3	0.55	0.01	752.93	64.32	38.33	33.71	1.33	1.15
France	25	0.65	0.12	970.44	237.55	237.56	188.10	0.56	0.82
Germany	12	0.60	0.02	653.24	117.16	280.75	315.43	1.33	0.98
Great Britain	73	0.45	0.28	970.12	299.96	268.56	141.39	1.84	0.78
Ireland	10	0.42	0.25	819.61	188.77	177	112.69	1.30	0.67
Isle of Man	1	0.77	NA	878.60	NA	587	NA	1.00	NA
Netherlands	7	0.61	0.01	861.77	49.18	18	12.66	0.14	0.38
Norway	9	0.54	0.15	1623.72	396.40	159.89	171.77	1.33	0.50
Sweden	4	0.51	0.07	1031.55	23.70	68.50	7.68	1.25	0.50

Appendix 4.1

Plant species included in the survey for the a) Weser-Elbe region, b) Bavarian Alps. Information is provided for the mean values and ranges of soil pH and light (expressed as 100% full light minus canopy cover) in the study sites, range size as area of occupancy (number of occupied grid cells in the regions [Weser-Elbe flora atlas by Cordes *et al.* (2006), Bavarian flora at http://www.bayernflora.de], in Germany [FloraMap database at http://www.floraweb.de] and in Eurasia [Atlas of North European Vascular Plants by Hultén and Fries (1986); for some species no data were available]), niche breadth and niche position for soil pH and light, and available niche breadth (the compound measure of niche breadth and niche position) for soil pH at the regional and national scale. The sample size for all species was $n = 46$.

a) Elbe-Weser region

Scientific name	Soil pH		Light		Range size			Niche breadth		Niche position		Available pH niche breadth	
	mean	range	mean	range	regional	national	Eurasian	pH	light	pH	light	regional	national
Adoxa moschatellina L.	4.97	2.7	4.85	24	320	2,307	60	0.629	0.231	5.8	2	0.163	0.403
Anemone nemorosa L.	4.98	3.57	5.59	44	693	2,860	19	0.627	0.219	5.2	2	0.243	0.527
Athyrium filix-femina (L.) Roth	4.35	3.67	5.54	14	644	2,848	78	0.586	0.235	4.8	2	0.278	0.544
Brachypodium sylvaticum (Huds.) P. Beauv.	5.08	3.57	13.46	49	74	2,557	47	0.493	0.463	6.6	25	0.043	0.123
Cardamine flexuosa With.	5.02	3.5	24.11	79	194	1,654	21	0.517	0.632	6.6	55	0.045	0.129
Carex remota L.	5.15	3.67	4.85	29	380	2,541	25	0.461	0.212	5.6	2	0.139	0.33
Carex sylvatica Huds.	5.06	2.25	4.65	24	121	2,394	24	0.491	0.205	5.2	5	0.191	0.413
Ceratocapnos claviculata (L.) Lidén	3.02	2.92	44.13	90	683	38	5	0.314	0.569	2.6	62	0.297	0.245
Circaea lutetiana L.	5.03	2.85	13.89	74	332	2,523	32	0.513	0.624	5.2	25	0.199	0.431
Dryopteris carthusiana (Vill.) H. P. Fuchs	2.99	3.24	27.63	64	908	2,560	30	0.276	0.686	2.4	42	0.274	0.197
Dryopteris dilatata (Hoffm.) A. Gray	3.56	3.54	19.3	59	697	2,509	14	0.519	0.579	2.6	52	0.492	0.405
Festuca gigantea (L.) Vill.	5.06	2.85	7.96	49	337	2,767	35	0.624	0.333	5.4	7	0.215	0.488

Scientific name	Soil pH		Light		Range size			Niche breadth		Niche position		Available pH niche breadth	
	mean	range	mean	range	regional	national	Eurasian	pH	light	pH	light	regional	national
Geum urbanum L.	4.89	2.35	5.07	29	768	2,928	33	0.544	0.24	4.6	2	0.282	0.523
Hedera helix L	4.16	3.6	14.52	69	926	2,839	23	0.595	0.652	4.6	17	0.308	0.572
Impatiens noli-tangere L..	5.01	3.26	6.91	49	221	2,590	50	0.515	0.318	5.6	7	0.155	0.368
Lamium galeobdolon (L.) L. s.str.	4.94	2.35	4.24	14	264	1,884	14	0.454	0.187	4.8	2	0.215	0.422
Lysimachia nemorum L.	4.97	2.54	19.57	79	187	1,751	14	0.503	0.581	5	27	0.217	0.447
Maianthemum bifolium (L.) F. W. Schmidt	3.93	3.38	15.61	84	511	2,744	42	0.574	0.562	3.2	22	0.47	0.533
Mercurialis perennis L.	5.05	3.01	3.7	14	37	2,153	24	0.445	0.166	5	5	0.192	0.396
Milium effusum L.	4.44	3.37	9.46	39	377	2,653	56	0.523	0.43	4.8	5	0.248	0.486
Moehringia trinervia (L.) Clairv.	3.93	3.47	25.17	74	761	2,874	42	0.59	0.793	4	52	0.381	0.59
Oxalis acetosella L.	4.42	3.47	19.78	74	667	2,798	46	0.619	0.687	4.6	42	0.32	0.594
Paris quadrifolia L.	5.22	3.29	12.17	54	65	2,324	42	0.443	0.463	6.6	25	0.038	0.11
Polygonatum multiflorum (L.) All.	4.78	3.38	9.04	49	581	2,675	24	0.528	0.438	4.8	7	0.25	0.49
Rubus idaeus L.	3.69	3.53	16.09	59	1,016	2,917	59	0.535	0.489	3	15	0.462	0.476
Sanicula europaea L.	5.1	2.25	4.98	29	82	2,017	26	0.464	0.212	5.2	2	0.18	0.39
Stachys sylvatica L.	5.07	2.96	18.46	69	522	2,785	32	0.582	0.62	5.8	27	0.15	0.272
Stellaria holostea L.	4.55	3.43	9.2	44	809	2,458	30	0.512	0.45	4.6	2	0.265	0.491
Viola reichenbachiana Jord. ex Boreau	5.14	2.25	4.04	19	192	2,582	17	0.553	0.169	6	2	0.119	0.308

b) Bavarian Alps

Scientific name	Soil pH		Light		Range size			Niche breadth		Niche position		Available pH niche breadth	
	mean	range	mean	range	regional	national	Eurasian	pH	light	pH	light	regional	national
Anemone nemorosa L.	5.71	4.55	26.48	97	130	2,860	19	0.463	0.614	6.4	33	0.452	0.333
Blechnum spicant (L.) Smith	3.92	4.11	22.09	97	120	1,677	34	0.366	0.611	4	20	0.12	0.366
Brachypodium sylvaticum (Huds.) P. Beauv.	5.82	4.55	27.02	84	123	2,557	47	0.606	0.57	6	12	0.616	0.519
Carex alba Scop.	5.67	3.69	27.13	79	123	284	NA	0.561	0.609	6.2	11	0.567	0.444
Carex digitata L.	5.83	4.15	20.89	59	118	1,427	24	0.502	0.591	6.8	2	0.411	0.273
Dryopteris carthusiana (Vill.) H.P. Fuchs	5.00	4.22	23.04	84	131	2,560	43	0.619	0.66	4.2	10	0.121	0.636
Dryopteris dilatata (Hoffm.) A. Gray.	4.28	4.14	22.2	79	118	2,509	14	0.519	0.603	3.4	30	0.189	0.449
Dryopteris filix-mas (L.) Schott	5.06	4.29	22.46	79	101	2,703	57	0.535	0.611	5.2	5	0.397	0.547
Epilobium montanum L.	5.07	3.87	28.17	84	124	2,724	36	0.576	0.56	5.2	17	0.427	0.588
Fragaria vesca L.	5.55	3.76	32.76	84	132	2,707	51	0.573	0.487	5.7	36	0.555	0.536
Galium anisophyllon Vill.	6.06	3.69	39.24	87	96	80	NA	0.459	0.593	6.6	54	0.419	0.292
Galium odoratum (L.) Scop.	5.19	4.2	16.15	44	125	2,434	40	0.536	0.446	5.5	5	0.482	0.524
Galium rotundifolium L.	4.46	3.85	21.09	56	114	918	18	0.465	0.682	4.8	2	0.2	0.489
Gymnocarpium dryopteris (L.) Newman	4.99	4.07	26.96	84	118	1,953	70	0.659	0.451	5.3	15	0.529	0.666
Hepatica nobilis Schreb.	6.12	3.63	26.39	84	107	1,244	14	0.458	0.655	7.6	5	0.07	0.04
Hieracium murorum L..	4.84	4.6	24.74	79	127	2,492	NA	0.672	0.582	5.1	9	0.454	0.695
Hordelymus europaeus (L.) Harz	4.94	3.88	20.09	49	106	978	16	0.459	0.48	5.2	2	0.341	0.47
Luzula luzulina (Vill.) Racib.	4.17	3.74	29.09	84	77	87	NA	0.491	0.638	4.5	45	0.058	0.515
Luzula pilosa (L.) Wild	4.88	4.28	29.87	79	114	2,655	32	0.586	0.553	5.1	42	0.395	0.605

Scientific name	Soil pH		Light		Range size			Niche breadth		Niche position		Available pH niche breadth	
	mean	range	mean	range	regional	national	Eurasian	pH	light	pH	light	regional	national
Lycopodium annotinum L.	4.68	4.79	29.39	69	125	1,372	66	0.583	0.421	4.9	52	0.302	0.611
Maianthemum bifolium (L.) F.W. Schmidt	5.7	4.09	32.57	96	131	2,744	42	0.446	0.353	6.2	33	0.45	0.353
Melica nutans L.	6.19	3.68	27.61	89	130	1,847	46	0.446	0.355	7.5	28	0.122	0.071
Mycelis muralis (L.) Dumort.	5.37	4.04	21.5	56	130	2,779	24	0.581	0.636	7	5	0.404	0.258
Oxalis acetosella L.	4.86	4.28	24.2	94	132	2,798	46	0.57	0.62	4.4	25	0.06	0.595
Paris quadrifolia L.	5.65	4.55	29.43	97	130	2,324	42	0.509	0.738	5.8	37	0.505	0.464
Polystichum aculeatum (L.) Roth ex Mert.	5.78	4.45	17.91	39	129	859	44	0.587	0.456	6.7	2	0.51	0.347
Prenanthes purpurea L.	4.83	4.05	24.22	84	132	827	NA	0.645	0.615	5.2	5	0.479	0.66
Rubus idaeus L.	4.81	4.21	24.74	97	128	2,917	89	0.58	0.6	4	25	0.191	0.579
Salvia glutinosa L.	5.92	3.98	25.89	79	121	227	NA	0.48	0.641	7.7	10	0.017	0.01
Sanicula europaea L	5.47	4.11	19.61	49	130	2,017	26	0.533	0.543	5.8	7	0.528	0.485
Senecio ovatus Willd.	5.21	4.46	22.37	59	132	1,818	43	0.504	0.562	5.9	15	0.507	0.446
Stellaria nemorum L.	4.34	4.18	29.91	79	110	2,094	21	0.387	0.562	4.6	50	0.089	0.408
Veronica montana L	4.72	4.04	19.07	42	73	1,689	12	0.516	0.551	5	2	0.31	0.538
Veronica urticifolia Jacq	5.96	4.53	24.41	79	130	147	NA	0.556	0.715	7.5	7	0.145	0.085
Viola reichenbachiana Jord. ex Boreau	5.62	4.12	23.02	84	111	2,582	17	0.575	0.655	5.9	10	0.579	0.5

Appendix 4.2

Relationship between regional / national range sizes and (realised) niche variables for soil pH and light (expressed as 100% full light minus canopy cover) of species, calculated from the phylogenetically independent contrasts (PIC, Spearman rank correlation for contrasts) for the Weser-Elbe region and the Bavarian Alps. a) niche breadth, b) niche position, c) available niche breadth. Significant values are bolded, marginally non-significant values in italics.

a) Niche breadth

	Weser-Elbe region		Bavarian Alps	
	r_s	P	r_s	P
pH				
Regional range size	**0.39**	**0.032**	**0.37**	**0.029**
National range size	**0.67**	**<0.001**	0.20	0.246
light				
Regional range size	0.30	0.107	-0.16	0.366
National range size	0.13	0.497	*-0.30*	*0.084*

b) Niche position

	Weser-Elbe region		Bavarian Alps	
	r_s	P	r_s	P
pH				
Regional range size	**-0.53**	**0.003**	-0.15	0.413
National range size	-0.06	0.734	-0.19	0.272
light				
Regional range size	0.13	0.517	0.08	0.648
National range size	-0.13	0.494	0.05	0.796

c) Available niche breadth

|	Weser-Elbe region		Bavarian Alps	
	r_s	P	r_s	P
pH				
Regional range size	**0.59**	**<0.001**	0.19	0.276
National range size	**0.5**	**0.006**	**0.41**	**0.016**

Appendix 5.1

Calculated niche breadth values for all species used in the study, either using the *varying frequency dataset* with all available plots per species or the *equal frequency dataset* with 46 data points per species. Values are given for the direct gradient approach as: soil pH, available niche breadth for soil pH (ANB), light availability (Light), as well as for the co-occurrence approach as Jaccard index (Jaccard) and Multiple Simpson index (multi Sim). Nomenclature follows Wisskirchen & Haeupler (1998).

Species	*varying frequency dataset*					*equal frequency dataset*				
	Soil pH	ANB	Light	Jaccard	Multi Sim	Soil pH	ANB	Light	Jaccard	Multii Sim
Adoxa moschatellina L.	0.677	0.230	0.427	0.624	0.767	0.629	0.160	0.231	0.620	0.764
Anemone nemorosa L.	0.753	0.110	0.595	0.691	0.798	0.627	0.240	0.219	0.651	0.790
Athyrium filix-femina (L.) Roth	0.813	0.364	0.689	0.732	0.803	0.586	0.275	0.235	0.698	0.785
Brachypodium sylvaticum (Huds.) P. Beauv.	0.467	0.058	0.564	0.673	0.797	0.493	0.040	0.463	0.670	0.796
Cardamine flexuosa With.	0.558	0.190	0.661	0.729	0.802	0.517	0.042	0.632	0.746	0.807
Carex remota L.	0.600	0.152	0.839	0.673	0.786	0.461	0.137	0.212	0.578	0.761
Carex sylvatica Huds.	0.630	0.078	0.609	0.648	0.778	0.491	0.188	0.205	0.594	0.758
Ceratocapnos claviculata (L.) Lidén	0.365	0.336	0.516	0.773	0.840	0.314	0.296	0.569	0.768	0.842
Circaea lutetiana L.	0.690	0.086	0.651	0.662	0.790	0.513	0.196	0.624	0.673	0.788
Dryopteris carthusiana (Vill.) H. P. Fuchs	0.448	0.432	0.723	0.784	0.844	0.276	0.272	0.686	0.777	0.844
Dryopteris dilatata (Hoffm.) A. Gray	0.660	0.608	0.778	0.806	0.842	0.519	0.489	0.579	0.800	0.824
Festuca gigantea (L.) Vill.	0.635	0.106	0.558	0.660	0.790	0.624	0.212	0.333	0.639	0.784
Galium odoratum (L.) Scop.	0.596	0.087	0.294	0.599	0.759	0.462	0.058	0.267	0.595	0.763

Species	varying frequency dataset					equal frequency dataset				
	Soil pH	ANB	Light	Jaccard	Multi Sim	Soil pH	ANB	Light	Jaccard	Multi Sim
Geum urbanum L.	0.681	0.173	0.571	0.643	0.782	0.544	0.279	0.240	0.597	0.775
Hedera helix L.	0.793	0.167	0.736	0.733	0.811	0.595	0.305	0.652	0.746	0.812
Impatiens noli-tangere L.	0.586	0.086	0.427	0.631	0.768	0.515	0.153	0.318	0.601	0.761
Lamium galeobdolon (L.) L. s.str.	0.642	0.246	0.651	0.670	0.792	0.454	0.213	0.187	0.619	0.765
Lysimachia nemorum L.	0.508	0.195	0.577	0.671	0.774	0.503	0.214	0.581	0.685	0.770
Maianthemum bifolium (L.) F. W. Schmidt	0.602	0.555	0.475	0.753	0.809	0.574	0.467	0.562	0.756	0.807
Mercurialis perennis L.	0.556	0.117	0.161	0.601	0.748	0.445	0.190	0.166	0.595	0.748
Milium effusum L.	0.869	0.370	0.753	0.737	0.811	0.523	0.245	0.430	0.741	0.811
Moehringia trinervia (L.) Clairv.	0.583	0.374	0.632	0.788	0.846	0.590	0.379	0.793	0.815	0.852
Oxalis acetosella L.	0.923	0.433	0.867	0.765	0.822	0.619	0.317	0.687	0.769	0.821
Paris quadrifolia L.	0.444	0.103	0.528	0.627	0.782	0.443	0.036	0.463	0.629	0.781
Polygonatum multiflorum (L.) All.	0.798	0.375	0.604	0.721	0.806	0.528	0.248	0.438	0.672	0.803
Rubus idaeus L.	0.756	0.680	0.739	0.795	0.836	0.535	0.459	0.489	0.783	0.826
Sanicula europaea L.	0.583	0.098	0.455	0.620	0.780	0.464	0.178	0.212	0.587	0.756
Stachys sylvatica L.	0.627	0.078	0.796	0.661	0.784	0.582	0.148	0.620	0.694	0.795
Stellaria holostea L.	0.765	0.376	0.843	0.727	0.808	0.512	0.262	0.450	0.689	0.796
Viola reichenbachiana Jord. ex Boreau	0.581	0.122	0.188	0.586	0.756	0.553	0.117	0.169	0.597	0.754

Appendix 7.1

Linear regression of pH values of the same soil samples measured in H_2O, $CaCl_2$ and KCl. The regression equation was used to convert all pH data to standardised values of pH_{CaCl_2}.
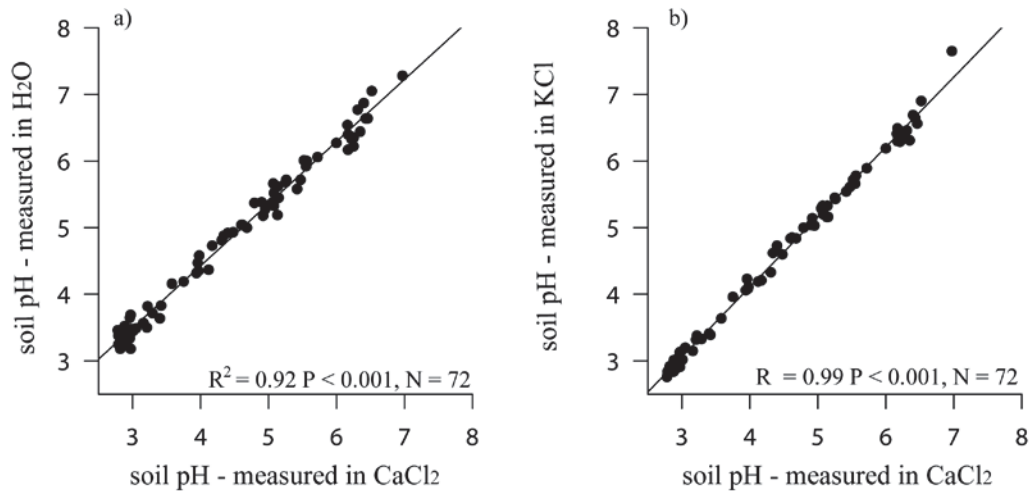
Appendix 8.1

Summary of all niche parameters used in the studies (Chapters 4-7) for the estimation of range size across different spatial scales. Since in Chapter 4 and 6/7 different measures of regional range sizes were used (dependent on the area the data was acquired from), two different regional range sizes are used in this comparison. For more information on the calculation of the niche parameters, as well as the data behind the range size estimations, see the Chapters indicated in the specific column. Significant values are in bold, marginal significant ones in italics.

	Regional range size (Weser-Elbe region)			Regional range size (Lowlands Lower Saxony)			National range size (Germany)			More info in Chapter
	r_s	P	n	r_s	P	n	r_s	P	n	
Niche breadth *(for soil pH)*	**0.39**	**0.031**	30	**0.56**	**0.005**	23	**0.68**	**<0.001**	30	4
Niche position *(for soil pH)*	**-0.75**	**<0.001**	30	**-0.53**	**0.008**	23	-0.29	0.120	30	5
Available niche breadth *(for soil pH)*	**0.79**	**<0.001**	30	**0.65**	**<0.001**	23	**0.63**	**<0.001**	30	4 & 5
Lower limit *(for soil pH)*	*-0.33*	*0.066*	*30*	**-0.55**	**<0.001**	30	**-0.57**	**0.001**	30	6 & 7
Niche breadth *(co-occurrence based)*	**0.65**	**<0.001**	30	**0.64**	**<0.001**	23	0.3	0.108	30	5

References

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