The long-term legacy of historical land cover changes

Patterns and dynamics in herb-layer species richness in deciduous forests of the Prignitz region (NE Germany)

Ph.D. Thesis
Jens Kolk

Title figure: Excerpt of the Schmettau-Map (Signatur: Kart. L 5420) showing the forest distribution around 1780 AD of parts of the study area. Used with permission of the Staatsbibliothek zu Berlin - Preußischer Kulturbesitz.

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General introduction

Land cover changes are among the most important threats to biodiversity and lead to major declines in species richness and compositional diversity in ecosystems (Sala et al. 2000, Fischer & Lindenmayer 2007). Human-induced land cover changes incorporate the reduction, fragmentation and isolation of natural or semi-natural habitats and of species populations within those habitats. Dramatic recent land-cover changes have been registered worldwide (Hansen et al. 2013). For example, over the last decades we saw a steep decline of the area of tropical rainforest with those primary forests being converted to arable land or palm tree plantations (Wearn et al. 2012). While there are massive recent land cover changes in many regions of the world, the land cover in the north-western European Lowland has been relatively stable, although the land use has become more intense. Here, the alteration from an almost entirely forested landscape to today's cultural landscape occurred a lot earlier: Historical man-made land-cover changes could be dated back to more than 3,000 years when permanent agriculture was well established over Europe (Kaplan et al. 2009). Since then the area of deciduous forest dramatically declined. The highest rate of deforestation of deciduous forests was reached from 1500 to 1850 (Kaplan et al. 2009). Furthermore, in those times many remaining deciduous forests have been converted into fast-growing coniferous forests, which have comparably low biodiversity (Felton et al. 2010). The landscape change was largely completed by the end of the 19th century (Darby 1956, Hermy & Verheyen 2007, Kaplan et al. 2009) and only remnants of deciduous forest remained.

The historical land cover changes in the north-western European Lowland were obviously dramatic and those changes could have left a long-term legacy that still affects present-day biodiversity. We know that species often react with a delay to environmental changes (Hanski & Ovaskainen 2002, Grau et al. 2003, Lunt & Spooner 2005, Hermy & Verheyen 2007, Kuussaari et al. 2009). A delay can especially be expected in species communities that only slowly respond to changing environmental conditions (Eriksson 1996, Jackson & Sax 2010). Compared with (most) animal groups, plants tend to persist longer when conditions change as many of them are long-lived, build seed banks and are able to reproduce asexually (Cronk 2016). For instance, many forest herbs have clonal organs, which enable them to persist up until several hundred years and more even when sexual reproduction is interrupted (Inghe & Tamm 1985, Verheyen et al. 2003 a, Collard et al. 2010, De Witte & Stöcklin 2010). On the other hand most forest specialists have a low recovery rate and the colonization of newly established forest habitats may take up to centuries (Honnay et al. 2002, De Frenne et al. 2011, Jamoneau et al. 2011). Therefore, there is reason to believe that today's species richness and composition of forest herb layer plant communities may still be shaped by the dramatic land cover changes that occurred in the past.

Below I will first describe which patterns of species richness have been found in forest herb-layer plant communities of the north-western European Lowland and how they may be linked to the past. Then I address how more recent species richness dynamics may be determined by land cover changes that occurred decades to centuries ago. I conclude with the main objectives of my thesis. Afterwards, the study area and the outline of the thesis chapters will be presented.

A link to the past - Patterns of herb layer species richness and composition

A consequence of the historical landscape change is that today's deciduous forests in landscapes of the north-western European Lowland basically consist of a small number of remnants that have now continuously been forested for at least 200 years and can be considered "ancient forests" (Wulf 1997) and of deciduous forests that have been established later on former agricultural land ("post-agricultural forests"). The different habitat continuity and land use history of todays forest patches is a key to the understanding of effects of historical land cover changes on present day species richness.

Habitat continuity appears to be an important factor that determines species richness in forests and other stable habitats. It has been observed that habitats with long habitat continuity often have higher species richness than more recently established habitats (e.g. Johansson et al. 2008, Norden et al. 2014, but see Kolb & Diekmann 2004, Fenton & Bergeron 2008). For one this phenomenon could be explained with different recent environmental conditions between older and more recently established habitats. For example, post-agricultural forests could only be stocked on poor soils that few species are adapted to or ancient forests may per se be more structured and provide more niches for different plant species. However, herb-layer species richness was often compared between ancient and post-agricultural forest stands that were located in the same region or even next to each other and in stands that were managed with comparable intensity (e.g. Graae 2000, Dumortier et al. 2002, Hermy & Verheyen 2007, Svenning et al. 2009, De Sanctis et al. 2010, Brudvig & Damschen 2011). Among almost all those studies species richness was higher in ancient forests. Furthermore, some species were significantly more abundant in ancient forests and can act as ancient forest indicator species (Wulf 1997, 2003, Honnay et al. 1998, Hermy et al. 1999).

While the relationship of species richness and land use history is long known, more knowledge on the actual explanation of this pattern has been accumulated lately. By the theory of island biogeography (Mac Arthur & Wilson 1967) species richness in habitat patches is dependent on the area and degree of isolation of a patch and species extinctions and colonizations are in equilibrium. In habitats that experienced historical land cover changes species richness is still dependent on the area and isolation of a patch, but on that of the past and not (or not only) on that of the present. Here, species extinctions and colonizations are not in equilibrium. A historically larger and better-connected habitat patch may exhibit more species than predicted by its current area and isolation. The species community exhibits an "extinction debt" (Tilman et al. 1994). In contrast, newly established habitat patches or existing patches whose area and connectivity recently increased have less species than predicted and the community exhibits a "colonization credit" (Baeten et al. 2010, Jackson & Sax 2010) (Fig. 1).

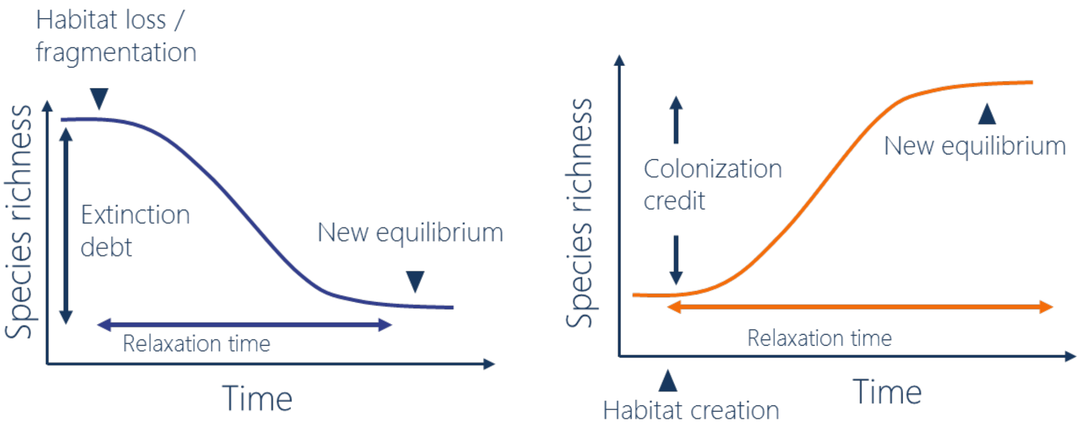

Fig. 1. Model of extinction debt (left) and colonization credit (right). Before a habitat loss / habitat creation or extension, species richness is in quasi-equilibrium with the environmental conditions of a habitat patch. When the habitat alteration event occurs, species richness does not change instantly, but gradually changes during the relaxation time until finally a new quasi-equilibrium is reached. During the relaxation time the species community exhibits an extinction debt and colonization credit, respectively.

Extinction debts and colonization credits may not only be induced by land cover changes, but also any other environmental changes, like climate change (Talluto et al. 2017). However, habitat loss and fragmentation are among the most important causes of species extinctions, and habitat loss is often gradual (Tilman et al. 1994, Fischer & Lindenmayer 2007). Species populations in remaining habitat remnants may persist for a prolonged time but they are doomed to extinction in the future because of increasing competition from the edges, reduced population sizes and disrupted connectivity (Hanski & Ovaskainen 2002, Hylander & Ehrlen 2013). Extinction debts have been found in ancient forest plant communities in Belgium (Piessens & Hermy 2006, Vellend et al. 2006) and Sweden (Paltto et al. 2006). All three studies have in common that the ancient forest area loss in those regions (Paltto et al. 2006 c. 26% loss, Piessens & Hermy 2006 and Vellend et al. 2006 c. 75% loss) was indeed dramatic but the remaining share of ancient forests on the total forested area was still higher than in many other European regions where often only small fractions (> 90% loss) of ancient deciduous forest remained (Honnay et al. 1998, Graae 2000, De Frenne et al. 2011). Such regions represent highly fragmented or highly transformed landscapes (Adriaens et al. 2006, Cousins 2009) in terms of deciduous forest area. Currently there are no specific studies on extinction debts in forest herb-layer communities in highly transformed landscapes but for grassland plant communities it was revealed that species richness was not dependent on past landscape patterns, i.e. the extinction debt had been paid off quickly (Cousins 2009).

While fragmented remnants may hold more species than expected from their actual area and connectivity, recently established habitats may have less species than expected. The community then exhibits a colonization credit that is depleted over time when species immigrate (Jackson & Sax 2010). Colonization credits have been found in plant communities of calcareous grasslands (Piqueray et al. 2011 a) and wet heathlands (Cristofoli et al. 2010) but forest herb-layer communities have not been investigated yet although colonization of forest plants is generally a well-studied topic (e.g. Flinn & Vellend 2005, Orczewska 2009 a, Baeten et al. 2009 a). The slow colonization of forest herb species suggests a colonization credit in post-agricultural forests because species may not have reached a newly established forest patch. Further, colonization success is hampered by subpar environmental conditions (e.g. Verheyen & Hermy 2001, Baeten et al. 2009 a). In this respect it is interesting to notice that several studies found that herb-layer species richness in post-agricultural forests was still dependent on the form and intensity of the former agricultural land use (e.g. Dupouey et al. 2002, Kopecky & Vojta 2009), i.e. previous land use could influence the magnitude of a colonization credit.

Recent species richness dynamics and how they may be shaped by the past

Recently many resurvey studies have been conducted on forest herb-layer plants with most studies finding that species richness both increased and decreased in the last decades, i.e. there have been recent species richness dynamics (Vellend et al. 2013, Bernhardt-Römermann et al. 2015). Recent species richness dynamics have been attributed to recent environmental changes such as changes in management (Amatangelo et al. 2011, Durak, 2012, Kopecký et al. 2013), increased atmospheric depositions of acidifying and eutrophicating substances (Jantsch et al. 2013, Dirnböck et al. 2014, Reinecke et al. 2014), the invasion of exotic species (Lysik 2008, Rooney & Rogers 2011, Johnson et al. 2014) and climate warming (Lenoir et al. 2010, Bai et al. 2011, De Frenne et al. 2013).

In all those studies land use history and historical land cover changes were not specifically considered. However, extinction debts and colonization credits pay off gradually, i.e. a payment of an extinction debt should lead to species richness decrease and an payment of a colonization credit should lead to a species richness increase over time. Therefore there is reason to believe that payments of extinction debts and colonization credits could have a share on recent species richness dynamics and there may be interactions with the effects from recent environmental changes. However, an actual payment of an extinction debt has currently only been proven for Southern Wisconsin forest understory plants (Rogers et al. 2009) where the enviromental and spatial conditions were not totally comparable to the situation in the European lowlands. A payment of a colonization credit has only been predicted in space-for-time studies where older post-agricultural forests had more specialists than younger forests (Jacquemyn et al. 2001, Heráult & Honnay 2005).

Except in areas where none or very little ancient forest is left, for example in the Netherlands, remnants of ancient forests and post-agricultural forests can be found together within potential dispersal distance of forest plants or at least within one landscape. In this situation it is possible that both extinction debts in ancient forest communities and colonization credits in post-agricultural forest communities exist. By theory, differences in species richness between ancient and post-agricultural forests should then become smaller when the extinction debt is being paid and/or the colonization credit is being depleted over time. Although this theory has been tested for alluvial forests in a very fragmented landscape in Belgium (Baeten et al. 2010) and in Sweden (Kokarēviča et al. 2016) both with a negative result, there is reason to believe that in a landscape where ancient and post-agricultural forests occur within potential dispersal distance and are comparable in their environmental conditions (including tree species composition) species richness in ancient and post-agricultural forests would approximate over time.

Objectives

The overarching goal of my thesis is to improve the understanding of the long-term legacies of historical land cover changes on forest herb-layer species richness.

I specifically aim to

- determine patterns of herb layer species richness of deciduous forests in a landscape where massive historical land cover changes occurred
- analyze recent species richness dynamics in herb-layer plant communities and link those dynamics to recent environmental changes and land use legacies

Study area

The study was conducted in the Prignitz region in north-western Brandenburg, Germany (4217 km², 52°42'N – 53°23'N, 11°15'E – 12°43'E). The mean annual temperature is about 8.0°C and the mean annual precipitation is between 550 and 650 mm (Krumbiegel & Schwinge 1991). The Prignitz-region exhibits many small to medium sized deciduous forest patches in different patch configurations; e.g. solitary patches within large arable fields, ancient and post-agricultural patches adjacent to each other; and with different patch ages. Therefore it represents a landscape configuration that is typical for many other north-western European lowland regions. Besides large Scots-Pine plantations (78% of total forest cover), which were not investigated in this study, the main forest types are deciduous and mixed forests with oak and beech and alder forests (18.8% of total forest cover). Figure 2 shows the current distribution of ancient and post-agricultural deciduous forest patches in the study area. A detailed description of the land use history of the study area is provided in the Methods section of Chapter 2.

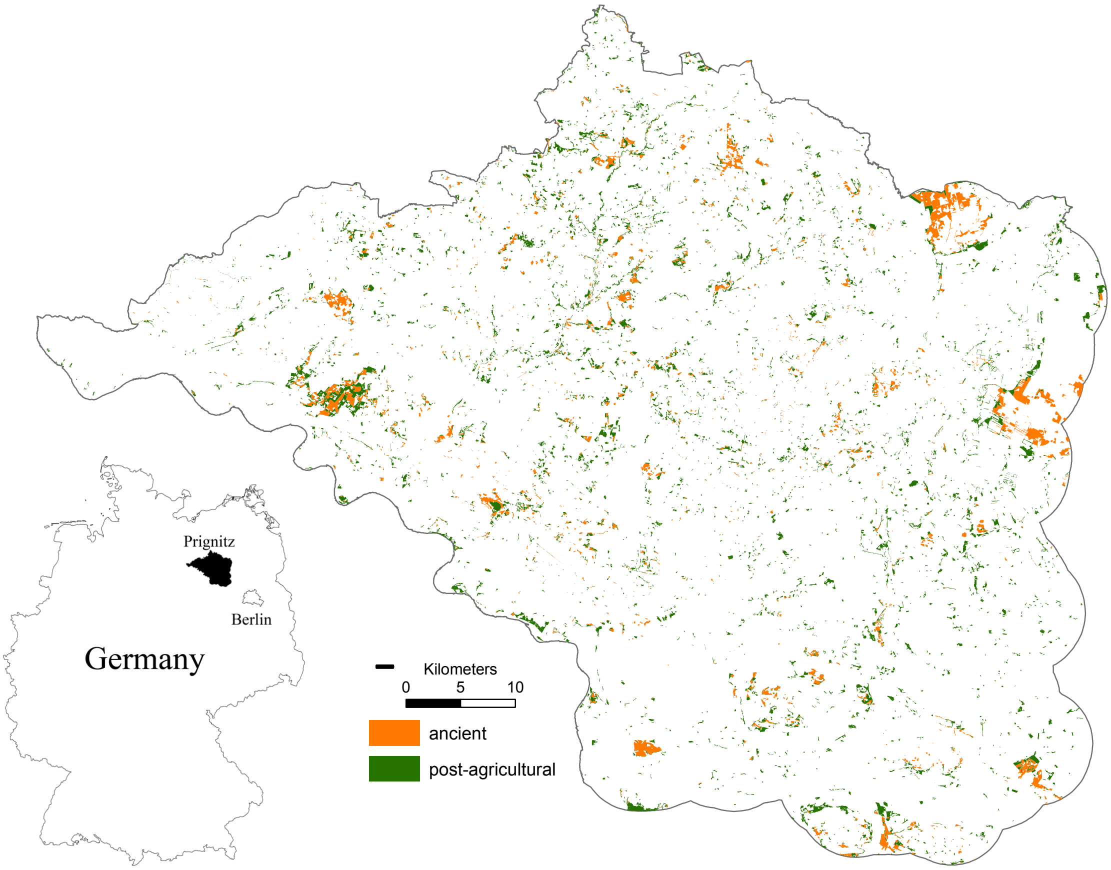

Fig. 2. Location of the study area (left) and present distribution of ancient and post-agricultural deciduous forest patches.

Outline of the study

The thesis consists of 5 chapters, which represent five individual research papers. The first three Chapters contribute to the first objective and the Chapters 4 and 5 contribute mainly to the second objective.

Chapter 1: *"Plant species richness of very small forests related to patch configuration, quality, heterogeneity and history"*

In this chapter we analyze multiple environmental factors that likely constitute species richness of understory plants in small deciduous forests remnants. The aim is to determine the relative contribution of the factor land use history on species richness in comparison to patch configuration, patch heterogeneity and patch quality. For this analysis we compiled existing data of plant species occurrences and environmental parameters in the forests of the Prignitz and used a hierarchical partitioning approach to analyze the data.

Chapter 2 *"Herb layer extinction debt in highly fragmented temperate forests – completely paid after 160 years?"*
Here, we assess the influence of historical land cover changes in ancient forest remnants by modelling present herb-layer species richness dependent on the patch configuration, i.e. patch area and connectivity, around the year 1780 and in 2014. The aim was to determine whether species richness was still dependent on historical patch configuration, which would indicate a persistent extinction debt.

Chapter 3 *"Colonization credit of post-agricultural forest patches in NE Germany remains 130-230 years after reforestation"*
Chapter 3 is the complement of Chapter 2, here we assess post-agricultural forests of different age and analyze whether the herb-layer plant community exhibits a colonization credit and how soil conditions and patch connectivity potentially influence its magnitude using the ancient forest patches as a baseline.

Chapter 4 *"Paying the colonization credit: Converging plant species richness in ancient and post-agricultural forests in NE Germany over five decades"*
This chapter extends the results from the Chapters 2 and 3 and examines both, potential extinction debt in ancient forest remnants and colonization credit in post-agricultural forests using a resurvey approach in plots that were originally surveyed in the 1960ies. With this data we actually quantify species richness dynamics during the last five decades and link those dynamics to historical land cover changes.

Chapter 5 *"Initial site conditions and interactions between multiple drivers determine herb-layer changes over five decades in temperate forests"*
Chapter 5 is dedicated to the effects of more recent environmental changes on species richness dynamics. Multiple regional and global drivers and their interactions are assessed and linked to local site conditions. For this paper we used a subset of the same resurvey data that was used in Chapter 4.

Chapter 1: Plant species richness of very small forests related to patch configuration, quality, heterogeneity and history

Monika Wulf & Jens Kolk

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1.1 Abstract

Questions: (i) Is the plant species richness related to patch configuration, quality, heterogeneity and history in very small forest patches? (ii) Is there a similar effect of patch configuration, quality, heterogeneity and history on all plant species or does it vary for different plant species groups? (iii) Does the importance of patch configuration, quality, heterogeneity and history vary for the plant species richness between patch size classes?

Location: Prignitz region, western part of Brandenburg, Germany

Methods: Plant species lists for 183 forest patches (0.08-12.7 ha) were compiled. We conducted a hierarchical partitioning analysis to test which of the four patch variables, configuration, quality, heterogeneity and history explained most of the variance in plant species richness and richness of various plant species groups.

Results: Irrespective of patch size classes, species richness is mainly predicted by patch quality and heterogeneity. In particular, generalists are primarily affected by the soil moisture and nutrient level, and specialists additionally by patch heterogeneity and history. A higher historical habitat quality together with long habitat continuity led to an increase in forest specialists and geophytes in all patches. In the >5 ha patches only the historical habitat quality account for a significant increase in the number of species with short-distance dispersal capacity and all species. Regardless of the patch size, the number of locally infrequent species increased significantly with historical habitat quality. The effect of patch configuration is negligible, except for the space-filling trees and shrubs considering all patches.

Conclusions: Our more comprehensive statistical approach shows in general that all complex variables have an effect on species richness, what should be considered in prospective studies. The fact, that patch heterogeneity and quality are the main predictors

for species richness, indicates that the very small forest patches covered a range of manifold structured patches and growing on sites with various conditions. We assumed that the century-old tradition of private ownership smallholder social structure is the main reason for the variability in stand structure and species assemblages resulting in uniqueness of each patch. Since the number of locally infrequent plant species increases significantly with historical habitat quality we suggested particularly this variable as important to consider in prospective studies on the decline of infrequent plant species.

1.2 Introduction

Several studies have been carried out on relationships between species richness and various plot or patch-based variables in temperate deciduous forests (e.g., Honnay et al. 1999 a, Jacquemyn et al. 2001, Kolb & Diekmann 2004, De Sanctis et al. 2010). Four complex variables, namely patch configuration (e.g., area, connectivity), patch quality (e.g., pH, soil types), patch heterogeneity or diversity (e.g., number of biotope types) and patch history (e.g., ancient or recent forest) were considered as potentially important variables for species richness. Most of the authors confirmed the well-known positive species-area relationship (e.g., Zacharias & Brandes 1990, Grashof-Bokdam 1997, Godefroid & Koedam 2003), while Lawesson et al. (1998) found a negative relationship. The explanatory variables for species richness vary from region to region. Some studies revealed patch configuration (Butaye et al. 2001, Petit et al. 2004) or patch configuration and patch history (Graae 2000, De Sanctis et al. 2010) as the most important variables for species richness. Other authors found patch quality to be the best predictor for species richness (Honnay et al. 1999 a, Dupré & Ehrlen 2002, Kolb & Diekmann 2004). Patch heterogeneity was found to be a major determinant for species number by Honnay et al. (1999 a), while Dumortier et al. (2002) found the major determinants to be patch heterogeneity along with forest area and forest age. The variability of these results can mainly be explained by three facts: (i) nearly all studies considered only two or three of the four complex variables, (ii) the considered independent variables differed between the studied regions, and (iii) the sizes of the studied forest patches covered a large range, between <0.1 ha and 8,000 ha.

A high variability in patch size between studied regions matters because patch area and patch heterogeneity may be highly correlated; however, only a few authors have considered both variables in their models of species richness (e.g., Honnay et al. 1999 a, Dumortier et al. 2002, Jamoneau et al. 2012). Further important aspects may be the patch history in term of habitat/patch continuity and historical patch connectivity. Only some authors provide information on whether their investigated forest patches are either ancient sites (habitat continuity >200 years) or recent sites (habitat continuity usually distinctively <200 years). For central Europe, this is essential to know because ancient and recent forests may have quite different species assemblages (Honnay et al. 1999 a, De Sanctis et al. 2010). The occurrence of plant species or particular species groups may be determined by the extent of patch connectivity several decades or centuries before today as demonstrated by Dzwonko & Loster (1989) and by van Ruremonde & Kalkhoven (1991). Thus, actual data on patch configuration may fail to sufficiently explain the species richness of forest patches. Other authors mentioned, in the context of patch history, that small forest patches in Europe are often remnants of one-time large forest areas (e.g., Grashof-Bokdam 1997), but studies to determine whether this variable affects species richness have not been carried out. The exclusion of this variable cannot be justified when studying ancient small forest remnants of former larger forest areas. This lack of justification stems from the fact that they may contain more plant species than expected for three reasons: (i) the species richness has been established over a long period that is most likely long enough for colonisation by short-distance dispersed plant species (e.g., auto- and myrmecochores) as demonstrated by Dzwonko & Loster (1989), (ii) small forest remnants are usually embedded in an agricultural matrix and therefore are not attractive for recreation seekers, and (iii) small forest remnants are not attractive for forestry, which reduces disturbances to the patch (Lawesson et al. 1998). Moreover, it is well-known that populations of herbaceous forest species may survive for decades or centuries even after sites are altered towards more unfavourable conditions as long as the plant populations have not become extinct (Vellend et al. 2006). Hence, today small forest remnants may act as valuable refuges for several plant species, in particular for true forest plant species.

In addition to the "remnant aspect", we assume that the historical habitat quality of former larger forest areas is also important for species richness today. By historical habitat quality we mean the forest vegetation types in former times and their specific species pools. None of the former studies considered the historical habitat quality of the former larger forest areas simply because such data usually do not exist. We assume a forest patch remnant once embedded in a larger species-rich forest to be richer in plant species today than a forest patch remnant of a formerly large forest area that was species-poor. For the studied region we have a historical forest vegetation map from c. 1800 published in Wulf & Rujner (2011) from which we can derive this information.

There is no consensus on what constitutes a "small forest" in the scientific community. Many studies with a focus on small forests considered patch sizes over a large range between less than one hectare to more than one hundred hectare (e.g., Lawesson et al. 1998, Dumortier et al. 2002). In fact, forest patches in central Europe are often less than

50 ha in size (FAO 2010, Schmithüsen & Hirsch 2010). Privately owned forests are usually very small. Approximately 50% of the European small forests (excluding the Russian Federation) are privately owned (Schmithüsen & Hirsch 2010), and it is expected that the number of privately owned forest areas will increase in the future (Wiersum et al. 2005). According to Wiersum et al. (2005) the private owners of the small forests are highly interested in maintaining their forest areas for the protection of natural resources (e.g., air and water) or for contribution towards biodiversity (e.g., animals and plants). Therefore, small forests should be included in the focus on maintaining and enhancing the biodiversity of temperate deciduous forests.

Prior studies revealing a positive species-area relationship (e.g., Grashof-Bokdam 1997, Godefroid & Koedam 2003) appear to disregard small forests as valuable contributors to biodiversity perhaps based on the relatively low number of species compared to larger forest patches, which are more likely to maintain or enhance species diversity. However, a large part of the European landscape is covered by small forests of only a few hectares in size on average. Detailed data published by Schmithüsen & Hirsch (2010) demonstrated that 61% of all private forest holdings in Europe have areas <1 ha and 86% of all holdings belong to the size classes of up to 5 ha, while only 13% are in the size classes from 6 to 50 ha. Thus, we can state that most of all small private owned forests in Europe are not larger than five hectares, and for that reason we focus in the paper on very small forest patches.

Compared to other studies we include all four types of complex explanatory variables (configuration, quality, heterogeneity and history of patches) in the models to predict various dependent variables, as opposed to using only two or three explanatory variables. Furthermore, we use more than one variable per complex variable and calculate the independent contribution of each variable over all possible models using hierarchical partitioning. Last but not least, we concentrate on very small forest patches rather than on all of the more or less small forest patches in a given landscape that have a wide size range. With this approach we hypothesize (i) that patch configuration, quality, heterogeneity and history are of importance for plant species richness in very small forest patches, (ii) that patch configuration, quality, heterogeneity and history have different effects on richness of all plant species and species groups of growth and life form, frequency, habitat preference and dispersal potential, and (iii) that importance of patch configuration, quality, heterogeneity and history for the richness of plant species groups depends on the patch size class.

1.3 Materials and methods

Study area

The Prignitz region (52°50’N - 53°20’N, 11°30’E - 12°30’E) is located in northeastern Germany (Fig. 1.1) and covers c. 320,000 ha (Wulf 2004 a). The region has a mild climate with a mean annual temperature of c. 8.0 °C and annual variation in air temperature ranges from 17.5-18.5 °C. The mean annual precipitation is between 550 and 650 mm (Krumbiegel & Schwinge 1991). Ground moraines consisting of sand and loam, as well as glacio-fluvial sand deposits are prevalent (Stackebrandt et al. 1997). The main soil types are Eutric Cambisols (70%), while Haplic Stagnosols and Haplic Gleysols together cover c. 22% of the total land surface (IUSS Working Group WRB 2006). The natural forest communities are various beech and oak stands that belong to the Querco-Fagetea (Passarge 1966) and cover c. 15% of the actual forest area, whereas all other forest communities are mainly dominated by *Pinus sylvestris*. Today most forest patches in the Prignitz region are relatively small islands embedded in a matrix of arable fields and grasslands. Many of them are remnants of former large forest areas (c. 200 years ago).

Fig. 1.1. Location of the Prignitz region (localization of the studied 183 forest patches see Appendix 1.1).

Floristic survey and selection of forest patches

Lists of vascular plant species for 386 forest patches were compiled between 1995 and 2000 (Wulf 2004 a). Before sampling, we conduced lists of plant species from publications by Fischer (1958, 1963, 1970, 1978) for each forest patch to check for the actual occurrences of these plant species. Each forest patch was sampled twice by walking along transects (c. 10-20 m wide) to get a complete list as possible. We assumed the sampling effort to be very high (≥ 90% of all typical forest plants) since we found generally most of all plant species and even sometimes more infrequent plant species in several patches than mentioned in the publications by Fischer (1958, 1963, 1970, 1978). The lists include plant species belonging to deciduous forests and related shrub communities, coniferous forests and related heaths as well as communities of perennial herbs and shrubs near forests as defined in Ellenberg et al. (1992).

From the 386 patches we selected 183 patches with sizes between 0.1 ha and 12.7 ha. The value of 12.7 ha is the mean patch size of all 386 patches and is set as upper threshold. All patches with a size less than this threshold were defined as ‘very small forest patches’. In order to have a balanced number of patches among the size classes, we used the two classes of ≤5 ha (n = 98; 43 remnant and 55 non remnant) and 5.1 – 12.7 ha (n = 85; 50 remnant and 35 non remnant).

All vascular plant species were grouped according to their growth form, frequency, habitat preference, dispersal potential and life form. The growth form (tree, shrub or herb species) and the number of true forest species (forest specialists) and non-forest species (generalists) follows Ellenberg et al. (1992). The frequency was defined after Fischer (1963). He distinguished the plant species into very rare (1-5 localities), rare (6-25 localities), moderately frequent (26-100 localities), frequent (>100≤500 localities) and common species (>500 localities). We defined infrequent species as those with ≤25 localities. The dispersal potential (long- and short-distance dispersal potential) is determined according to the categories in Frey & Lösch (1998). Auto-, baro- and myrmecochorous species are assumed to have a potential for short-distance dispersal, while anemo-, endo- and epizoochorous species are assumed to be potentially dispersed over long distances. The life form (geo-, hemicrypto- and therophyte) follows Raunkiaer (1937). Because fewer than three plant species belong to the chamaephytes, this species group was excluded from statistical analysis.

Explanatory variables

We choose four complex variables (i) patch configuration, (ii) patch quality, (iii) patch heterogeneity and (iv) patch history as independent variables. Each comprises two or more single explanatory variables.

(i) Patch configuration involved the patch area, the Patton shape index, and the distance to the other forest patches for all 183 selected patches. The patch area was derived from recent orthophotos. Some patches of less than 5 ha and all patches less than 0.25 ha were redrawn and measured using GIS-software. The Patton-shape index is a measure of the area-perimeter relationship of patches and can be seen as a measure of microenvironments (Honnay et al. 1999 a). The index value was calculated using the formula $\mathrm{P}/200(\sqrt{\pi}\,\mathrm{A})$ with P = patch perimeter in meters and A = patch area in ha. Values for the perimeter were calculated with the ArcView extension X-Tools (DeLaune 2000). A high shape-index reflects a high number of micro-climatic gradients.

We used Hanski's incidence function model (Hanski 1994) (Equation 1) to calculate the patch connectivity of all focal patches (the 183 plots) to all other forest patches (including the other focal patches) in the study area.

Equation 1) Incidence function model: $S_i = \sum_{j \neq i} \exp\left(-\alpha d_{ij}\right) A_j^b$

with α as the scaling effect of distance, d the distance in meters, A as the area in square meters (of each target patch) and b as the scaling effect of area. We used an α of 0.002 as proposed by Verheyen et al. (2004) and Herault & Honnay (2005). This value represents a dispersal distance of 500 m (1/ α is the average migration distance (Moilanen & Nieminen 2002)). The scaling factor b was set to 0.5 as recommended by Moilanen & Nieminen (2002) and De Sanctis et al. (2010). The distance d was calculated by using the ArcGis-function "generate near table". This function calculates the edge to edge distance from the focal patch to every patch within a specified distance. We set the maximum search distance to 5000 m to keep the calculation time low (at distances above 5000 m the connectivity-values become very small).

(ii) Patch quality was defined in terms of nutrient and water levels at five levels for mineral soil, but five water and six nutrient levels for the humus layer, respectively. The information on nutrient and water level were taken from maps of the forest inventory (scale 1:10,000, Kopp & Schwanecke 1994). Nutrient level for mineral soils were defined as very low (poor, coded as 1), low (relatively poor), moderate (medium level of nutrients), high (relatively rich) and very high (rich, coded as 5). Water level for mineral soils were distinguished into dry (coded as 1, fresh (frequently inundated), moist, wet (permanent moist) and swamp sites (coded as 5). For the humus layer nutrient level were defined as very low (coded as 1), low, relatively low, moderate, high and very high (coded as 6), and the water level as dry (coded as 1), relatively fresh, fresh, moist and wet (coded as 5).

We combined both the nutrient and water level for the mineral soil and the humus layer (coded as 1 to 5 = fairly low or dry to very high or wet, respectively) into one weighted nutrient and water level for each patch because levels were correlated (Pearson correlation coefficients of 0.69 and 0.57, respectively). The proportion of area that each nutrient and water level covered in a patch was multiplied with the coded nutrient and water level. The maximum value (500) was set to 100, and values for each patch were adjusted to the value of 100.

(iii) Patch heterogeneity was expressed in term of the number of different forestry site units and number of structuring elements. Forestry site units mean the maximum number of sub-patches with different nutrient and water levels for the mineral soil or the humus layer within a patch. The number of structuring elements was gathered by Wulf (2004) during field work. She recorded the occurrence of very old (>150 yrs) and old (>80 <150 yrs) tree species, very old or old stumps, ramparts with old tree species and boulders or clearance cairns within or at the edge of forest patches. We used the number of different structuring elements per patch for analyses.

(iv) Patch history involved two independent variables. First, we use the digitised historical Schmettau map (scale 1: 50,000 from 1767 to 1787) and the map of the Prussian government (scale 1:25,000 from c. 1880) to check whether a forest patch is a remnant of a former larger forest area or not and coded the information as 1 and 0, respectively. Because all remnants are ancient forest (habitat continuity >200 yrs) one can also say that remnants are ancient (n = 93) and all other patches are recent forests (n = 90).

Second, we used a map of historical forest communities for estimating the historical patch quality published in Wulf & Rujner (2011). They distinguished 17 forest communities ranging from species rich to species-poor, depending on the number of characteristic species ("Kennarten") usually occurring in the forest community. Based on the species richness of these historical forest communities we create three categories of historical patch quality; low (coded as 1) if there was no forest in the historical time, medium with <30 characteristic species (codes as 2, e.g. beech forests with *Frangula alnus* and oak-forests with *Agrostis capillaris*) and high with >50 characteristic species (coded as 3, e.g., ash forests with *Aegopodium podagraria* and beech-forests with *Mercurialis perennis*). We then constructed a buffer zone of three km around each of the 183 forest patches and checked the occurrence of historical forest communities. If at least one of the forest communities classified as rich occurred in the 3 km buffer zone around a patch the 'historical patch quality' of this patch was classified as species-rich (coded as 3). A buffer zone of three km was chosen to limit overlaps with other forest patches and to consider the much larger extension of forest patches at historical time.

Statistical analysis

To check of significant differences between means of plant species groups we used an unpaired t test. We applied 'hierarchical partitioning' (Chevan & Sutherland 1991) to measure the improvement in fit that each of the variables contributed to the fit of the total model. For each variable the averaged independent- and joint-contribution over all models (combination of all explanatory variables) were calculated (MacNally 1996). The joint-contribution is the contribution of a variable that is already represented by other variables (MacNally 2000). All calculations were performed with the statistical package R, version 2.15.0 (R Development Core Team 2012).

We used the function "hier.part" from the R-package "hier.part" (Walsh & MacNally 2012) to calculate the independent and joint contribution of the explained variance in the complete model for the nine variables (Table 1.2). The Poisson distribution was set as a GLM-link-function and the log-likelihood was taken as a goodness of fit measure. Model conditions of the full models were checked graphically. The independent contributions of variables to the complete model were tested for significant differences to the Null-model using a randomisation test with 1000 repeats (function "rand.hp" of R-package "hier.part"). The function was adapted to a significance level of p=0.05. The calculation was performed for all response variables (total species richness, richness of the species groups growth and life form, frequency, habitat preference and dispersal potential), explanatory variables (patch configuration, quality, heterogeneity and history) within the two patch size groups and for all 183 patches.

1.4 Results

Species richness of small forest remnants

The mean number of plant species in the patches is c. 31. Seventy per cent of all species occurred in the herb-layer and c. 15% each in the shrub-layer and the tree-layer. The mean numbers of herb species and of several species groups were higher in the ≤5 ha patches, while the mean of woody and infrequent species number is higher in the ≥5 ha patches. However, the differences in means are significant in only three cases. The mean number of generalists and therophytes is significantly higher in the ≤5 ha patches, while the mean number of tree species is higher in the >5 ha patches (Table 1.1).

Table 1.1. Mean number of species in species groups within the two patch size classes and in all patches.

	≤5 ha (n = 98)	5.1 to 12.7 ha (n = 85)	p-value of differences between means	All (n = 183)
All species	31.8 ± 1.4	30.6 ± 2.0	p = 0.610	31.3 ± 1.2
Growth form				
Tree species	4.4 ± 0.3	5.3 ± 0.3	p = 0.027*	4.8 ± 0.2
Shrub species	4.3 ± 0.3	4.6 ± 0.4	p = 0.430	4.5 ± 0.2
Herb species	23.1 ± 1.1	20.7 ± 1.5	p = 0.178	22.0 ± 0.9
Frequency				
Infrequent species	8.7 ± 0.6	9.2 ± 0.8	p = 0.627	9.0 ± 0.5
Habitat preference				
Forest specialists	12.5 ± 0.6	12.6 ± 1.0	p = 0.920	12.6 ± 0.6
Generalists	11.8 ± 0.6	8.0 ± 0.7	p = 0.002***	9.5 ± 0.4
Dispersal potential				
Short-distance dispersal	6.1 ± 0.3	5.8 ± 0.5	p = 0.543	5.9 ± 0.3
Long-distance dispersal	5.7 ± 0.3	5.4 ± 0.5	p = 0.627	5.6 ± 0.3
Life form				
Geophytes	5.8 ± 0.3	5.5 ± 0.4	p = 0.157	5.7 ± 0.3
Hemicryptophytes	13.1 ± 0.7	11.5 ± 0.9	p = 0.157	12.4 ± 0.5
Therophytes	2.8 ± 0.1	2.4 ± 0.2	p = 0.047*	2.6 ± 0.1

Relationship between number of all species or species in species groups and patch variables

Total species number and of nearly all species groups depend mainly on patch quality and patch heterogeneity. Generalists and therophytes depend only on patch quality. Additionally, the number of tree species is affected by patch size and the number of shrub species by inter-patch distance. The number of trees, forest specialists, species with short-distance dispersal capacity and geophytes depend significantly on patch history, too. This is also true for the infrequent species, but only historical habitat quality is important and patch size also plays a significant role for them. The number of herbs, species with long-distance dispersal ability and hemicryptophytes are only determined by patch quality and patch heterogeneity (Table 1.2).

Most of the herb-species are hemicryptophytes (mean 12.4) and geophytes (mean 5.7), while therophytes are the least abundant (mean 2.6). The number of geophytes increases with patch quality, heterogeneity and history. Hemicryptophytes appear more often in forest patches with higher moisture and nutrient level and with more structuring elements.

Relationship between all species or richness of species groups and patch variables in the two patch size classes

Irrespective of the size classes, patch quality and heterogeneity are the most important explanatory variables for species richness or richness of various plant species groups in all forest patches (Table 1.3). This is generally also true for both size classes, but it is striking for the ≤5 ha patches that both variables of patch quality, but exclusively structuring elements of patch heterogeneity determining the number of several species groups. In contrast, for the >5 ha patches both variables of patch heterogeneity but nearly only the nutrient level of patch quality are important for the number of many species groups.

Regardless of the patch size, patch history explains species richness for almost half of the different species groups. This statement is true only for species with short-distance dispersal capacity in both patch size classes, while patch history also is important for geophytes in the >5 ha patches. Patch configuration is by far the least important variable, and plays a role only for woody and infrequent species considering all patches. However, patch size is important for most species groups in the ≤5 ha forest patches (Table 1.3 and Appendix 1.2).

Table 1.2. Independent contributions of explanatory variables to the species number of all species and the species groups. Left of the slash: percentage of contribution; right of the slash: z-score of randomisation test; * = significant at α = 0.05.

	All species	**Growth form**			**Frequency**	**Habitat preference**		**Dispersal potential**		**Life form**		
		Trees	Shrubs	Herbs	Infrequent plant species	Forest specialists	Generalists	Short-distance dispersal	Long-distance dispersal	Geophytes	Hemicrypto-phytes	Thero-phytes
Patch configuration												
Patch size	2.5 / 0.0	**14.2 / 3.4***	10.1 / 1.6	0.6 / -0.5	**7.0 / 2.3***	3.4 / 0.3	3.1 / 0.3	0.5 / -0.5	2.0 / -0.3	0.6 / -0.4	0.8 / -0.4	2.6 / -0.3
Patton-shape index	1.8 / -0.1	1.7 / -0.4	4.5 / 0.3	1.4 / -0.2	3.5 / 0.9	2.0 / -0.1	0.9 / -0.4	1.5 / -0.1	0.4 / -0.6	1.7 / -0.1	1.5 / -0.3	0.9 / -0.6
Inter-patch distance	3.2 / 1.1	1.1 / -0.1	**9.2 / 2.5***	2.7 / 0.6	2.6 / 0.8	2.1 / 0.5	2.9 / 0.1	2.5 / 0.4	2.0 / 0.1	4.2 / 1.5	2.7 / 0.5	0.6 / -0.7
Patch quality												
Moisture level	**11.9 / 6.4***	6.6 / -0.1	4.2 / 0.8	**20.7/ 11.0***	**10.1 / 6.3***	**9.6 / 5.6***	**39.7/11.4***	**11.1 / 5.4***	**25.4 / 8.8***	**15.6 / 9.6***	**21.4 / 9.8***	**38.2/5.5***
Nutrient level	**43.0 / 17.1***	**19.4 / 4.5***	**30.8/8.4***	**45.8/17.0***	**49.1/21.6***	**39.5/17.6***	**44.7/12.7***	**43.3/13.8***	**41.5/12.4***	**35.0/15.8***	**50.0 / 16.5***	**44.3/6.0***
Patch heterogeneity												
Structuring elements	**20.8* / 9.8***	**33.3/11.5***	**16.7/4.6***	**16.7 / 6.6***	**13.4 / 6.3***	**22.0/10.9***	5.5 / 1.1	**17.0 / 6.3***	**16.7 / 4.5***	**18.7/10.0***	**15.9 / 5.4***	3.3 / -0.1
Forestry site units	**6.0 / 2.7***	**7.1 / 2.9***	**14.4/3.8***	3.7 / 1.4	**6.1 / 3.5***	**6.6 / 3.6***	0.5 / -0.5	**4.8 / 2.1***	6.8 / 1.6	**5.3 / 3.1***	3.6 / 1.0	1.5 / -0.4
Patch history												
Forest remnant	4.6 / 1.2	**8.6 / 2.8***	3.8 / 0.4	3.5 / 0.8	3.0 / 1.2	**6.6 / 2.3***	1.0 / -0.4	**10.0 / 3.1***	2.0 / 0.0	**8.2 / 2.8***	1.7 / 0.0	4.6 / -0.1
Historical habitat quality	**6.0 / 1.7***	**8.0 / 2.3***	6.3 / 1.0	4.8 / 1.4	**5.1 / 2.1***	**8.4 / 3.2***	1.7 / -0.1	**9.4 / 3.0***	3.3 / 0.5	**10.7 / 3.7***	2.6 / 0.2	4.1 / 0.0

Table 1.3. Effects of complex variables on species groups in forest patches of different size classes and all forest patches. Black = all variables of the complex variable are significant. Grey = only one variable of the complex variables is significant. conf = patch configuration; qual = patch quality; het = patch heterogeneity and hist = patch history.

Patch size classes	≤5 ha				5.1 – 12.7 ha				all			
All species	conf	qual	het	.	.	qual	het	hist	.	qual	het	hist
Growth form												
Tree species richness	conf	qual	het	.	.	qual	het	.	conf	qual	het	hist
Shrub species richness	.	qual	.	.	.	qual	het	.	conf	qual	het	.
Herb species richness	conf	qual	het	.	.	qual	het	.	.	qual	het	.
Frequency												
Infrequent species	conf	qual	het	.	.	qual	het	.	conf	qual	het	hist
Habitat preference												
Forest specialists	.	qual	het	.	.	qual	het	.	.	qual	het	hist
Generalists	conf	qual	.	.	.	qual	.	.	.	qual	.	.
Dispersal potential												
Short-distance dispersal	.	qual	het	hist	.	qual	het	hist	.	qual	het	hist
Long-distance dispersal	conf	qual	.	.	.	qual	het	.	.	qual	het	.
Life form												
Geophytes	.	qual	het	.	.	qual	het	hist	.	qual	het	hist
Hemicryptophytes	conf	qual	.	.	.	qual	het	.	.	qual	het	.
Therophytes	.	qual	.	.	.	.	.	.	.	qual	.	.
Sum of black variables	.	10	.	.	.	4	8	1	.	10	7	4
Sum of grey variables	7	2	7	1	.	7	2	2	3	2	3	2

1.5 Discussion

Overall richness of all species and species groups

Our results show, that all explanatory variables are important for the overall species richness and for the richness of species groups, and confirmed our first hypothesis. The mean number of all species and all species groups, however, is higher in the ≤5 ha patches, except for woody and infrequent species, but the result is not significant. This result did not confirm the results of several other studies on relatively small forest patches in the temperate region (e.g., Peterken & Game 1984, Zacharias & Brandes 1990, Grashof-Bokdam 1997). However, we sampled only plant species usually occurring in forests and forest-related habitats and we had a focus on very small patches. The results may have been more comparable to other studies supporting the species-area relationship if all plant species had been considered and the size range of patches had been larger (e.g., Grashof-Bokdam 1997, Godefroid & Koedam 2003). On the other hand, it is likely that larger forest patches are more affected by forest management than smaller patches. Lawesson et al. (1998) found a negative relationship between species number and area for Danish forests due to the intensive management of coniferous stands and drainage of the forests. These events caused a higher disturbance frequency and a reduction of habitats suitable for plant species adapted to near-natural forest communities. Indeed, in our larger forests there are larger parts of coniferous stands and better connections to roads in order to facilitate forest management.

In the context of the theory by MacArthur & Wilson (1967), it was often assumed that area is a surrogate for habitat diversity (patch heterogeneity), and several studies support this assumption (e.g., Honnay et al. 1999 a, b; Dumortier et al. 2002). In that case patch heterogeneity (habitat diversity) leads to an increase in species number. We also found patch heterogeneity to be an important variable in predicting the total species number, but with regard to the patch size classes, patch quality is more important. In particular, the nutrient level delivers an independent contribution of c. 50% considering all plant species and herb species, which is consistent with the results of Dupré & Ehrlen (2002) and Kolb & Diekmann (2004). However, patch heterogeneity played a major role in explaining the variance in species richness, while the number of structuring elements explained more than the number of forestry site units. This is an unexpected result because, for example, Dumortier et al. (2002) find the number of habitat types to be significant predictors of species number. One explanation may be that other authors used only the number of habitat types as a 'habitat or patch heterogeneity' variable, while we used an additional variable. A further aspect may be that structuring elements are spatially more fine-scaled than forestry site units, and therefore have a stronger effect on spatially small-scaled species occurrences within patches (Mölder et al. 2008).

We found only a minor effect of patch configuration on species richness, which is in contrast to Butaye et al. (2001), Petit et al. (2004) and De Sanctis et al. (2010). This is quite surprising because we include three variables, and at least one of them usually gives a significant result in the other regions. It could be assumed that our data set of very small forest patches has a range of values that is too small to show a differentiating effect. In fact, the range of all three patch configuration variables is large enough to expect significant results, as demonstrated by other studies on small forest patches, e.g., Jacquemyn et al. (2001), and Petit et al. (2004). However, two-third of the investigated forest patches had a neighbour within the 200 m radius, and this distance is clearly below those that were assumed to have an isolating effect. While Mikk & Mander (1995) set 3 km as the threshold, other authors find 500 m or 200 m to be the maximum distance to allow colonisation of plant species from one patch to another (van Ruremonde & Kalkhoven 1991, Grashof-Bokdam 1997, Butaye et al. 2001). Our results are further confirmed by Dupré & Ehrlen (2002) and Kolb & Diekmann (2004) who found patch configuration negligible but habitat quality as highly important for species incidence.

Patch history or land use history in terms of 'habitat continuity' (c. ≥ 200 years) was found to be relevant for species richness in forest patches by De Sanctis et al. (2010). Several other studies have shown that ancient forests contain more plant species or true forest plant species than recent forests (e.g., Peterken & Game 1984, Lawesson et al. 1998). This conclusion supports our results because we found the status 'forest remnant' affected the species richness. However, it is also manifest that patch history is of importance for more plant species (groups) and for all species (see below).

Richness of plant species groups in relation to patch variables

In accordance with our second hypothesis, we found different effects of the explanatory variables on richness of all plant species and species groups. There are only a few tree and shrub species but many herb species on our lists whose incidences are determined by a moisture gradient. We assumed therefore, that the richness of shrub- and tree species depend mainly on the nutrient level, while the richness of herb species is predicted by both the moisture and nutrient levels. Several of the shrub species produces palatable seeds for birds and other animals. These animals are able to bridge long distances. Therefore, it is likely, that the number of shrub species is affected by inter-patch distance. This assumption is supported by findings of Grashof-Bokdam (1997) who found an increased number of zoochorous species with increasing connectivity.

The infrequent plant species also depend more on patch quality, but patch heterogeneity is likely important. In all patches the infrequent plant species depend also on patch size and historical patch quality. If patch heterogeneity is seen as surrogate for patch size, these results fit those of Zacharias & Brandes (1990), who found rare (= endangered or infrequent) plant species more often in larger forests. The authors considered the chance to have more undisturbed sites in a larger forest as a chance for rare species to survive. Here we suggest that small ancient forests are also refuges for infrequent plant species. These forests are more or less exclusively privately owned and, due to their small size, have not been managed for several decades. Owners used only single trees from time to time. Additionally, the forests are often completely surrounded by agricultural land. Thus, people cannot reach the patches via roads or footpaths.

The fact that forest specialists are more affected by patch heterogeneity than generalists is not surprising. It is also consistent the number of small scale suitable habitats forest specialists will increase with increasing patch heterogeneity. In contrast, generalists are able to growth on sites with less specific site conditions and were mainly affected by both the moisture and the nutrient level (Dupré & Ehrlen 2002; De Sanctis et al. 2010).

Species with short- and long-distance dispersal potentials show similar patterns with respect to patch quality and patch heterogeneity, but species with low dispersal capacities are strongly affected by the patch history, too. It is well-known that species with short-distance dispersal potentials require several decades or even centuries colonising new isolated habitats (Vellend et al. 2006).

In our study, many geophytes, hygro- and several mesomorphs (plants with soft shadow leafs and with no specific adapted leafs with regard to the soils water balance and gas exchange, respectively) belong to the forest specialists and species with short-distance dispersal capacities. Thus, they are expected to behave like these species groups (Table 1.3). Hermy et al. (1999) found a higher number of geophytes in ancient forests. Herault et al. (2005) found geophytes more abundant on base-rich soils. This is quite well reflected by our results because we found these species groups significantly more often on ancient sites with a high historical patch quality. However, Hermy et al. (1999) also report a higher number of hemicryptophytes in ancient forests, which contrasts with our results. This is because many of our non-forest species are hemicryptophytes (60%). We found a significantly higher number of generalists in the ≤5 ha forest patches than in the >5 ha patches (Table 1.2), which might mask differences in species composition between patches with different histories. Since smaller forest patches are more sensitive to edge effects, e.g. higher light flux to the ground at the edges, it is likely that generalists are more common in smaller patches where these conditions occurred. Therophytes are wide-spread annual species, and their occurrence is mainly affected by patch quality but, as expected, not as much by other specific patch features.

Richness of plant species groups in relation to patch variables with regard to patch size classes

We cannot fully confirm our third hypothesis, since we obtained the most significant results when patch size classes were ignored and found a comparable number of significant results for both patch size classes. In the ≤5 ha patches, however, configuration deliver significant results for several species groups, while the number of forestry site units doesn't play any role. In contrast, number of forestry site units are important for many species groups and some species groups depend also on the historical patch quality in the >5 ha patches. Obviously, the number of site units fits better to the species number of some species groups than the 'quality of site units' (= moisture and nutrient level). This demonstrates that, in some cases, patch heterogeneity is more important than patch quality or is of equal importance (Honnay et al. 1999a, b).

It is likely that patch configuration is more important for plant species in the ≤5 ha patches than >5ha patches due to abiotic or direct biological edge effects. These edge effects e.g. favoured species adapted to higher light flux to the ground. Among the group of generalists and species with long-distance dispersal capacity are many species adapted to higher light availability, which is in accordance with other studies, e.g. Murcia (1995) and Honnay et al. (1999a, b).

The historical patch quality reveals for us the unexpected result that it played a larger role for the >5 ha patches than for the ≤5 ha patches. During our field survey we often found, even in <1 ha ancient forest patches, several true forest species. For example, the smallest forest remnant (ancient patch) is only 0.1 ha large but hosts 28 plant species. Smaller patches are perhaps more exposed to changes in environmental conditions caused by various measures in the surrounding agricultural land during the past decades. Drainage of grasslands and fertilisation of arable fields may have led to more concordant nutrient and water levels among all small forest patches, and this may mask the effects of the historical patch quality on plant species richness (Honnay et al. 1999 b). Another explanation may be the fact, that very small patches are simply too small to maintain viable populations (Honnay et al. 2005).

Historical habitat quality gives significant results for species with short-distance dispersal capacity and geophytes in the >5 ha patches. Several of our infrequent plant species belongs to these groups. We suggest, as found by Zacharias & Brandes (1990), that populations of such species have better chances to survive in larger forest patches than in smaller patches. However, even if not significant, there are many higher independent contributions of historical patch quality for several species groups in the ≤5 ha sized patches, too (Appendix 1.2). This is also true for infrequent plant species. Their number is significantly higher ($F = 6.9$; $df = 1$; $p = 0.0097^{**}$) in patches with high historical habitat quality (12.1 ± 1.8) compared to those with low historical habitat quality (7.7 ± 0.6).

1.6 Conclusions

We included more potential predictors than other studies and applied a hierarchical partitioning analysis to calculate the independent contributions of all combinations of all explanatory variables to explain the variance over all models. This comprehensive approach shows in general that all complex variables have an effect on species richness. That even within a restricted size range many variables affecting the species number of forest patches stresses the relevance of considering them all for further studies at the landscape scale.

The fact, that patch heterogeneity and quality are the main predictors for species richness, indicates that the very small forest patches covered a range of manifold structured patches and growing on sites with various conditions. We know, that our studied region is characterised by private owned small hold structures. The use of forest patches was different from owner to owner, resulting obviously in a high variability of the forest patches with respect to their stand structure and species composition. Since the number of locally infrequent plant species increases significantly with historical habitat quality we suggested particularly this variable as important to consider in prospective studies on the (potential) decline or even extinction of infrequent plant species.

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Chapter 2: Herb layer extinction debt in highly fragmented temperate forests – completely paid after 160 years?

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2.1 Abstract

The time-delayed extinction of plant species following habitat fragmentation is a well-known phenomenon in ecology. The length of the relaxation time until this ‘extinction debt’ is paid (i.e., until extinctions cease) depends on the ecosystem, species group and extent of fragmentation. Studies of grassland ecosystems have revealed that plant extirpations after fragmentation can occur rapidly when the degree of fragmentation is high. Studies of extinction debt in highly fragmented forests, however, are lacking. In this study, we evaluated the existence of an extinction debt in the Prignitz, Brandenburg, Germany, where 94% of the semi-natural forests have vanished since 1780. We surveyed the herb-layer species of 104 forest patches and fitted species richness as a function of the historical and present-day patch configurations. Models including the present-day habitat area and connectivity explained the present day species richness better than models including historical patch-configuration variables. There was no significant effect of the historical habitat area on the present day species richness. However, the effect of historical patch connectivity on the richness of forest specialists with short-distance dispersal potential was significant when excluding present-day habitat area from the models and habitat quality and heterogeneity were used as covariables. The extinction debt has largely been paid after approximately 160 years of relaxation time which contrasts with previous studies of temperate forests that have found extinction debts persisting 120 to 225 years after fragmentation. We demonstrate that extinction debts in temperate forests may be paid off more rapidly if the degree of fragmentation is high.

2.2 Introduction

Habitat destruction and fragmentation are among the most important threats to biodiversity (Sala et al. 2000, Sax & Gaines 2003). Although the most dramatic land-cover changes in Central Europe occurred centuries ago (especially when forests that had been more or less continuous were cut for agriculture (Darby 1956)), there are several indications that historical land-cover changes still affect present-day species richness and community composition (Kuussaari et al. 2009). Land-cover changes can cause a time-delayed loss of species in ecological communities, which is known by the term ‘extinction debt’ (‘ED’) (Tilman et al. 1994). Given that species richness was in equilibrium before the habitat destruction event, species will eventually go extinct until the species richness reaches a new quasi-equilibrium. At this time, the ED has finally been paid. The time span from the destruction event until the ED is paid is termed the relaxation time (Kuussaari et al. 2009). Determinations of the magnitudes of an ED and the detection of the processes that influence the magnitudes of ED are important tasks in ecology (Sutherland et al. 2013).

ED has been detected for various species groups and habitats at several spatial scales (Dullinger et al. 2012 (mountain plants), Lira et al. 2012 (small mammals), Brudvig & Damschen 2011 (pine woodlands), Kuussaari et al. 2009 (review, listing 32 papers where an ED was found)). However, to date, only a few studies have been published for plants of temperate deciduous forests (Paltto et al. 2006, Piessens & Hermy 2006 (in parts); Vellend et al. 2006). This paucity of studies is surprising because forest herbs are often clonal and are able to persist without sexual reproduction for many decades (Inghe & Tamm 1985, Cain & Damman 1997). Thus, a delay in changes in species richness in response to habitat fragmentation could be particularly pronounced in forest ecosystems.

For grassland plants, there are studies with conflicting results. Several authors have found strong evidence for the existence of an ED following habitat fragmentation (Lindborg & Eriksson 2004, Piqueray et al. 2011 b), while others did not find any ED (Adriaens et al. 2006, Cousins et al. 2007, Oster et al. 2007). In a meta-study, Cousins (2009) noted that, in grassland studies that verified an ED, patches had retained greater than 10% of the target habitat, whereas no evidence for an ED was observed in studies in which patches retained less than 10% (‘highly transformed landscape’).

For plant communities of temperate deciduous forests, Paltto et al. (2006) (Sweden), Piessens & Hermy (2006) (Belgium) and Vellend et al. (2006) (UK and Belgium) have verified occurrences of an ED. In these studies, the forest covers decreased moderately by 26% in approximately 120 years (Paltto et al. 2006) and by approximately 75% in approximately 210 to 225 years (Piessens & Hermy 2006, Vellend et al. 2006). However, there are many regions in Central Europe where the extent of forest area loss was substantially higher (Honnay et al. 1998, Graae 2000, see also De Frenne et al. 2011). To date, it remains unknown as to whether or not and for how long an ED exists in such highly transformed landscapes. Our objective was to investigate ED in a region where forest area loss was greater than 94% over approximately 200 years. The answers to the questions of whether the ED has been paid or not have broad implications for conservation (Kuussaari et al. 2009, Wearn et al. 2012, Vellend & Kharouba 2013). In scenarios with an enduring ED, conservation actions can focus on stopping or slowing down extinction processes. If there is no ED, other conservation actions may be more appropriate.

Many studies on ED use historical and present-day patch configuration to model present-day species richness (Kuussaarri et al. 2009). However, species richness also depends on the habitat quality and habitat heterogeneity (Honnay et al. 1999 a, Dumortier et al. 2002, Wulf & Kolk 2014). The omission of these environmental factors may lead to false conclusions: A weak, but true habitat-loss-induced ED may remain undetected, or a non-existent ED may be erroneously confirmed although in fact correlations of patch configuration with environmental factors are the reason for significant results. Here, we aim to study the effects of including environmental variables when quantifying the ED.

Species do not respond to land-use changes in the same way. Several studies have revealed that forest specialists are prone to fragmentation effects (Dupré & Ehrlen 2002, Kolb & Diekmann 2004, Jamoneau et al. 2011, Rodríguez-Loinaz et al. 2012) and are overall more dependent on patch configuration than generalists (Dupré & Ehrlen 2002, Kimberley et al. 2014). Specialists often have slow metapopulation dynamics, i.e. a high persistence and limited dispersal abilities, which may support delayed extinctions (Vellend et al. 2006, Hylander & Ehrlén 2013). The analysis of trait-defined groups that represent species with slow metapopulation dynamics can give further knowledge about which specialists contribute most to an ED. A precondition is that the considered trait attributes make species respond to the spatial configuration of habitats because only then such species can constitute an ED induced by area loss and fragmentation. It has been shown that in forest ecosystems clonal species, species with low numbers of seeds per ramet and species with a short-distance dispersal potential are especially dependent on patch configuration and that such species also have low rates of colonization and a high level of persistence (Dupré & Ehrlen 2002, Kolb & Diekmann 2005, Kimberley et al. 2014).

Hence, we hypothesize that a) the historical habitat area and degree of patch connectivity are better predictors for present-day species richness than present-day habitat area and patch connectivity and, in consequence, that the ED has not been paid; b) forest specialists contribute more to an ED than generalists; c) specialists with an extensive clonal growth, a low seed production and a short distance dispersal potential are most highly influenced by the historical patch configuration.

2.3 Material and methods

Study area

Our study was conducted in the Prignitz region (4217 km², 52°42'N – 53°23'N, 11°15'E – 12°43'E), which is located in the western portion of the federal state of Brandenburg, North-Eastern Germany (Fig. 2.1).

Fig. 2.1. Location of the study area in Prignitz, Brandenburg, Germany.

The region has an overall flat terrain with elevations ranging from 10 to 150 meters locally and is mainly subject to intensive agricultural land use. The primary soil types are Eutric Cambisols, Haplic Stagnosols and Haplic Gleysols that have developed on glaciofluvial sand deposits and loamy ground moraines (Stackebrandt et al. 1997). The mean annual temperature is 9.2°C. The mean annual precipitation is 574 mm (DWD 2014, Kyritz weather station). The primary forest types are large, Scots-pine (*Pinus sylvestris*)-dominated plantations, deciduous or mixed forests with oak (*Quercus robur*) and beech (*Fagus sylvatica*), and alder forests (*Alnus glutinosa*). The deciduous and mixed deciduous forests cover 18.8% of the total forested area, while the coniferous forests contribute 78.3% (see Appendix 2.2 for the proportions of specific deciduous forest types). The area of the deciduous forest patches ranges from approximately 0.3 ha to 275 ha. The majority of the patches are less than two ha in size. These patches are often scattered within large agricultural fields.

Land-use history

Comparisons of historical and present-day patch configurations require comprehensive data on land-use history. We used the historical Schmettau map created from 1767 to 1787 at a scale of 1:50 000 (hereafter, 1780) and the Prussian government map created from 1875 to 1915 at a scale of 1:25 000 (hereafter, 1880) to derive the forest distribution during these time periods. The forest patch configuration in 1780 was used in our species richness models (sections 2.5 and 2.7). The forest distribution in 1880 was used to identify ancient forest patches, i.e. those that have been continuously forested since 1780, and as an intermediate stage for determining the land-use changes. During the Schmettau period, the deciduous and coniferous forest stands were not clearly separated. However, Bratring (1804) stated that a proportion of approximately 22% of the forested land cover was coniferous forests. We used the location names provided in the Schmettau map that likely indicate coniferous tree species (e.g. 'Kien-', 'Fichten-', or 'Theerofen') and treated those areas as coniferous forests. The Prussian government map distinguished three categories of forested areas: 'deciduous forest', 'coniferous forest' and 'mixed forest'. For the area calculations, we added 50% of the area of mixed forests to the deciduous forests. To obtain the present day forest cover, we analyzed recent 1:25 000 scale topographical maps in combination with data from a statewide habitat survey (LUA 1995). We intersected the forest distributions of the three periods using ArcGIS 10 to determine the changes in forest cover between 1780 and the present-day (see Fig. 2.2 for separate maps for each period).

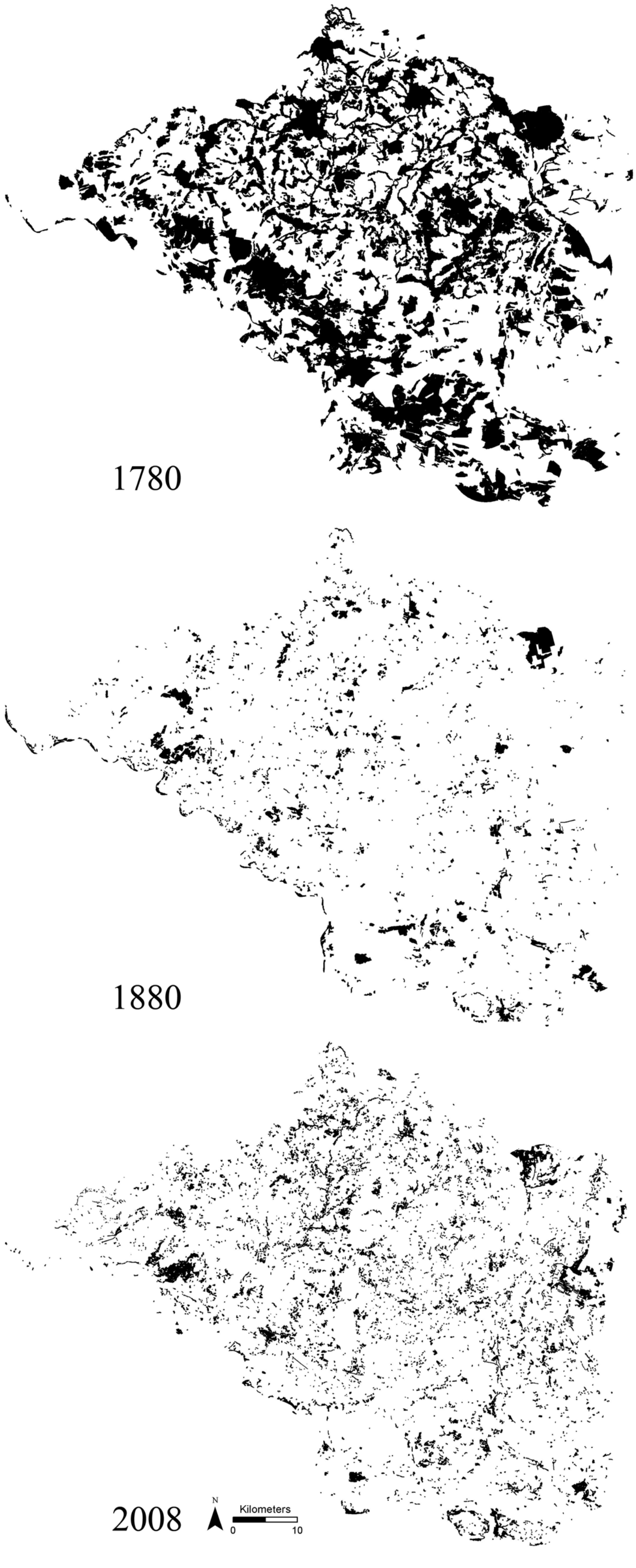

Fig. 2.2. Extent of deciduous forests in the Prignitz region in NW Brandenburg, Germany, in the years 1780, 1880 and 2008.

Our data indicate a massive loss of forest area between 1780 and 1880. In 1780, the total deciduous forest area was 124 293 ha. This area decreased to approximately 9375 ha by 1880 (92.4% loss). These forests were mainly converted to agricultural land and coniferous forest plantations. At present, deciduous forests cover 19 901 ha, representing a gain of 10 841 ha of deciduous forest through afforestation. However, the remaining ancient forest area was 7230 ha; thus, 1830 ha of ancient deciduous forests were lost between 1880 and the present-day. In total, the loss of ancient deciduous forests amounted to 94.2% of the 1780 area within approximately 230 years. From 1780 to the present-day, the median size of an individual deciduous forest patch decreased from 7.6 ha to 1.8 ha to 1.0 ha. In contrast, the number of patches increased from 1075 in the Schmettau period to 1459 in the Prussian period and rose to 5964 in the year 2008. Hence, the vast majority of the loss of deciduous forest area occurred during the first period examined (from 1780 to 1880), while the degree of fragmentation increased remarkably between 1880 and the present-day.

Patch selection

Forest patches that fit our study aim had to be largely ancient and deciduous (allochthonous coniferous stands rarely constitute a habitat for forest specialists). Therefore we only included patches where the majority share was deciduous. From this selection, we further only used patches whose ancient deciduous forest share was more than 33%. Moreover, we only included patch sizes from 0.5 to 25 ha into our 'patch pool' in order to keep the sample size high and the fieldwork manageable. We used a stratified random sampling for the selection of 110 ancient forest patches (out of a pool of 178 suitable ancient patches) for our field survey. As strata, we used the area of deciduous forest (five subclasses, Appendix 2.1) and the main forest community types, based on Hoffmann & Pommer (2005), which are connected to nutrient and water availability (Appendix 2.2). Community types were assigned to a patch when the areal extent of the community type in the patch was at least 1000 m^2. This means that there could be more than one forest community type per patch. The numbers of patches in each area class (Appendix 2.1) and the numbers of patches with a specific forest community type (Appendix 2.2) were not evenly distributed. To ensure that less frequent forest types would be represented in the study, we calculated probability weights for each class combination and used these weights for the random sampling of patches. Six patches were omitted after fieldwork because they were either strongly affected by other land use types (cemetery, park, archaeological site) or the area was restricted and thus inaccessible. The total habitat area of the 104 remaining patches was 65 643 ha in 1780 and 561 ha in 2008 representing a total loss of 99.2%. The median of the habitat area in a patch was 742 ha in 1780 and 2.8 ha in 2008. The habitat loss within a patch ranged from 57.1% to 99.9%. The habitat loss was under

90% in only seven patches. The mean deciduous forest cover within a buffer zone of 1000 m surrounding each patch was 47.2% in 1780 and 4.6% in 2008, thus connectivity had decreased for all 104 patches.

Species richness

We recorded all vascular plant species in the herb layer (≤ 1 m, tree saplings were excluded) by walking 20-m wide transects. We surveyed the whole deciduous forest area of a patch, i.e. the transect length depended on the deciduous forest area of a patch. We included the species growing at the within-forest edges and the species at the inner patch edges, i.e., all species growing inside of the outermost tree line. We excluded coniferous stands, clear-cut areas and areas where there was no clearly visible tree-layer. The species growing in mixed forests were included when the deciduous component was dominant. To include both spring and summer species, we performed two field campaigns, from mid-April to May 2013 and from June to August 2013, respectively.

We determined the species richness per patch for several species groups: (a) all species, (b) forest specialists, i.e., species restricted to the closed forest environment (species of category 1.1 in the list of Schmidt et al. 2011), (c) species that are not forest specialists (hereafter called ‘generalists’, i.e., species that grow in forests as well as in open environments (categories 2.1 and 2.2 in Schmidt et al. 2011), those that grow at forest edges (category 1.2 in Schmidt et al. 2011) and those that are not included in the list), and (d) within the specialists the trait groups of extensive clonals, species with few seeds per ramet and species with short-distance dispersal potential.

We defined extensive clonals as specialists with ≥ 2 offspring shoots per parent plant per year. The trait data was acquired from the CloPla database (Klimešová & de Bello 2009). To identify specialists with few seeds per ramet, we used the mean number of seeds per ramet from the LEDA traitbase (Kleyer et al. 2008) and classified all specialists with a seed number below the median (<154 seeds per ramet) as specialists with few seeds per ramet. Specialists with a short-distance dispersal potential were defined as those belonging to the dispersal mode groups 1, 2 and 3 (representing species with a dispersal distance up to 15 m) from Vittoz & Engler (2007). Dispersal mode data was mainly taken from Müller-Schneider (1986) and, in addition, from Jäger & Werner (2005) and the floraweb database (Floraweb 2014).

Present day and historical patch configuration

We performed a comparison of the present and historical patch configurations to detect the ED, e.g., Lindborg & Eriksson (2004). To characterize the present day and historical patch configurations, we employed two variables: habitat area and patch connectivity. The historical habitat area was the forest area of the patch in 1780. The present day habitat area was the area dominated by deciduous tree species, i.e., the area in which we recorded the plants in the fields. The variables were log (1+x)-transformed to obtain a more equal distribution what enables us to detect underlying patterns more clearly. We calculated the patch connectivity based on the percent of habitat area within a buffer zone of 1000 m surrounding the recorded area of the patch. For the historical connectivity, we calculated the percentage of deciduous forest area in 1780 relative to the total buffer area. For the present day connectivity, we only included the patches that contained ancient forest stands with an area of at least 1000 m^2. We did not consider purely post-agricultural forests because these habitats cannot be assumed to hold any source populations of forest specialists yet.

There are numerous opinions on how to calculate connectivity and on how to choose an appropriate buffer distance (Molainen & Nieminen 2002; Calabrese & Fagan 2004). We choose a buffer distance of 1000 m, which is a commonly used distance for forest plant-specific studies (Kolb & Diekmann 2004, Endels et al. 2007, Bergès et al. 2013), because most forest plants have a maximum dispersal distance that is < 1000 m (Thomson et al. 2011). We did not use Hanski's incidence function model (Hanski 1998) because Moilanen & Nieminen (2002) reported problems with using this measure for highly fragmented habitats. In our study, we compared highly fragmented (present-day) forest patches with nearly continuous (1780) forest patches. The present day and historical connectivity was log (1+x) transformed for analysis to obtain a more equally distribution of values.

Habitat quality and habitat heterogeneity

To characterize habitat quality, we collected soil samples in September 2013. Five samples (within a distance of 1 m) were collected from a sampling depth of 10 cm (after litter removal) at the most base-rich spot of each patch (following the approach of Kolb & Diekmann (2004)). The expected species richness in temperate forests is highest on base-rich sites, which are also often close to groundwater (Härdtle et al. 2003). Hence, the most base-rich portion of a patch is best suited for predictions of species richness. This spot was determined visually based on expert knowledge of the plant species' indicator values for soil chemistry (Ellenberg et al. 2001). We mixed all five soil samples from a patch together. Afterwards, we immediately weighed the samples, air-dried the samples and weighed them again to determine the soil moisture content. After sieving (2-mm mesh), the samples were analyzed for total carbon and nitrogen by the dry combustion method (ISO 10694 and ISO 13878). In addition, we calculated the C/N ratio from the percentages of total carbon and total nitrogen. We determined the contents of phosphorus and potassium per 100 g soil using the double calcium lactate method at pH 3.6, with potassium and phosphorus determined photometrically. To determine the content of calcium (-orthophospate) per 100 g soil we used an extractant solution of ammonium acetate in combination with acetic acid and hydroxypropionic acid. We measured the magnesium content per 100 g soil by atom absorption spectrometry after extraction with a calcium chloride solution. The soil pH was determined in 0.01 M calcium chloride using a glass electrode (ISO 10390). All soil variables were log-transformed to meet assumptions of normality. To reduce the number of variables, we performed a principal component analysis with varimax rotation using the ‘principal’ function in the Psych R package (Revelle 2013). The first three axes represented 84% of the total variance in soil variables. The first axis was positively correlated with soil moisture, nitrogen and carbon supply (‘moisture-axis’). The second axis was positively correlated with pH and calcium availability (‘soil pH-axis’).The third axis was positively correlated with the phosphorus and potassium (‘P-availability-axis’) contents of the soils (Appendix 2.3).

We evaluated habitat heterogeneity by assessing four variables: subpatch diversity, geological diversity, topographical heterogeneity and edge effect. The subpatch diversity reflects the man-made diversity of the patches. In the field, we differentiated each patch into homogeneous subpatches based on the composition and structure of the woody layers. We then used the area of each subpatch to calculate the Shannon diversity per patch. For geological diversity, we aggregated information from geological maps into twelve substrate types (Appendix 2.4). We determined the substrate-type area per patch and calculated the Shannon diversity per patch. To measure topographical heterogeneity, we determined the range in elevation based on a digital elevation model (resolution 25 m; height accuracy ± 2 m). The range values were log (1+x)-transformed for analysis to obtain a more equally distribution of values for a better interpretation of the results. Lastly, the edge effect variable was defined as the total edge length (including both the outer edge of the habitat area and within-patch edges (e.g., forest tracks or aisles)) divided by the perimeter of a theoretical circular patch constructed with the same habitat area. We used this calculation to decouple the edge length from the habitat area of the patches. The variable edge effect was log-transformed before analysis to approximate a symmetric distribution.

Data analysis

First, we conducted a correlation analysis to investigate the relationships between the historical and present-day patch configuration variables and the habitat quality and heterogeneity variables. Next, we compared statistical models to explain species richness that included the historical habitat area and connectivity against models that included the present-day habitat area and connectivity. We assumed that, if the historical model does explain the variation in present day species richness better than the present day model, then the herb layer plant community in our forest patches exhibits an ED. If the present day model performs better, we assume that the ED has been paid. For modelling, we first considered generalized linear models (GLM) with a Poisson error distribution. Subsequently, we checked for overdispersion and, in that case, we instead used a negative binomial model (GLM-NB) (following Lindén & Mantyniemi (2011)). The GLM-NB models were fitted using the R-function "glm.nb" from the MASS package (Venables & Ripley 2002).

In a first step, we fitted models without the addition of the habitat quality and habitat heterogeneity variables. Then, we looked for the best combination of habitat quality and habitat heterogeneity variables to explain species richness. For this purpose, we fitted models for all possible variable combinations and selected the model that contained only significant predictors and had the lowest AIC-value. This was our basic model. We then added the variables for the historical habitat area and historical patch connectivity to the basic model to determine the influence of the historical patch configuration in combination with present day habitat quality and heterogeneity variables on species numbers (historical model). For the present day model, we added the variables for the present-day habitat area and patch connectivity to the basic model. We compared the AIC-values of the historical and present day models and assumed that the model with the lowest AIC-value best explained species richness.

Finally, to assess the combined effects of the historical and the present day area and connectivity, we created another model that included the significant patch configuration variables in addition with the habitat quality and habitat heterogeneity variables of both the historical model and the present-day model (combined model). These three models (historical, present day and combined) were compared to the basic model by performing likelihood-ratio tests to determine if there were significant differences. For the negative binomial models, we used the adapted likelihood-ratio test 'anova.negbin' from the MASS package (Venables & Ripley 2002). We created models for the total number of species in the herb layer, for the numbers of forests specialists and generalists, and for each of the specialists groups. All predictor variables were standardized to a mean = 0 and an SD = 1 to facilitate the interpretation of the parameter estimates (Schielzeth 2010). All of the analysis steps were performed using R, version 3.0.2 (R Core Team 2013).

2.4 Results

We identified 374 herb-layer plant species in the 104 forest patches, with a mean number of 71.8 per patch (SD = 30.5; range 25-150). Sixty-five (17.3%) of these species were forest specialists (16.9 per patch; SD = 8.0; range 1-35), while 309 (82.7%) were generalists (55 per patch; SD = 25.1; range 20-120).

The correlation analysis (Table 2.1) revealed only marginal correlations of the habitat quality and heterogeneity variables with the historical patch configuration variables. Historical patch connectivity correlated weakly and negatively with topographical heterogeneity. Correlations between present-day patch configuration variables and habitat quality and heterogeneity were more distinct, especially for present-day habitat area.

Table 2.1. Pearson correlation between patch configuration variables and habitat quality and heterogeneity variables. Significance: * $0.01 < P \leq 0.05$; ** $0.001 < P \leq 0.01$; *** $P \leq 0.001$.

	Area 1780	Connectivity 1780	Area 2008	Connectivity 2008
Edge effect	0.03	0.01	0.58^{***}	0.05
Moisture	0.09	0.07	-0.10	0.12
Soil pH	-0.01	0.01	0.12	0.22^{*}
P-Availability	0.07	0.03	-0.41^{***}	-0.01
Subpatch-diversity	0.04	0.06	0.52^{***}	-0.01
Substrate-diversity	0.10	0.05	0.31^{***}	0.01
Topographical heterogeneity	-0.20	-0.33^{***}	0.49^{***}	-0.32^{***}

The models that included the present-day patch configuration variables generally explained species richness better than the models including the historical patch configuration variables (Table 2.2). For both, the historical and the present-day models, the inclusion of habitat quality and –heterogeneity variables leaded to lower AIC-values, i.e. to models with a better fit. The AIC-values of the historical models did not differ significantly from those of the basic models.

The models revealed only a weak relationship between the historical patch configuration and the present day species richness (Table 2.3). In the models without the habitat quality and heterogeneity variables we found no significant effects of the historical patch connectivity and area on present-day species richness. When including the additional habitat quality and heterogeneity variables the results indicate a significant effect of the historical patch connectivity on the richness of specialist species. The historical patch connectivity also had a significant effect on the richness of specialists with short-distance dispersal potential. There was no significant effect of the historical habitat area on any species richness variable. The AIC-values of the combined models for specialists and short-dispersing specialists were only slightly lower than the AIC-values of the model including the present-day patch configuration alone (Table 2.2). In these models, the historical patch connectivity was no longer a significant predictor variable. Including historical patch connectivity also did not alter the significance of the other patch variables either (Table 2.3). All of the present-day models indicated a strong influence of habitat area on species richness (Table 2.3). The present-day patch connectivity was not significant in any model. Furthermore, there was a strong influence of habitat quality on species richness. Species richness increased with increasing soil moisture and nitrogen availability (PCA-axis 1) and decreasing P-availability (PCA-axis 3), but was not influenced by soil pH (PCA-axis 2). In contrast, the richness of generalists was only dependent on P-availability. Habitat heterogeneity in terms of the subpatch diversity, geological diversity and topographical heterogeneity was only significant in the historical and basic models, with few exceptions. Habitat heterogeneity in terms of the edge effect was more influential. In particular, the edge effect significantly influenced the richness of generalists and was also influential in the model for all herb species.

Table 2.2. AIC-values of models of species richness as a function of the historical and the present day patch configurations. Models that included patch configuration were tested against the model without patch configuration by performing a likelihood-ratio-test. Config. = Patch configuration, Env. = Habitat quality and heterogeneity variables. Significance: * 0.01 < P ≤ 0.05; ** 0.001 < P ≤ 0.01; *** P ≤ 0.001.

Species richness of	Config. only 1780	Config. only 2008	Env. without config.	Env. with config. 1780	Env. with config. 2008	Env. with conn. 1780, area 2008
All herbs	1000.0	895.1	912.1	913.6$^{n.s.}$	867.8***	
Herb specialists	733.9	652.3	670.9	670.1$^{n.s.}$	638.0***	637.2***
Herb generalists	954.3	873.9	880.9	882.5$^{n.s.}$	849.2***	
Few seeds per ramet	598.7	540.4	555.6	556.8$^{n.s.}$	535.5***	
Short-distance dispersal	633.2	568.7	587.9	586.8$^{n.s.}$	563.0***	562.2***
Extensive clonals	576.2	501.3	473.1	474.8$^{n.s.}$	451.4***	

Table 2.3. Results of the regression models of forest herb species richness in 2013 against patch configurations (in 1780 and 2008), habitat quality and habitat heterogeneity. The first row of each group provides the model results without the inclusion of patch configuration variables. The second row provides the model with the historical patch configuration variables only. The third row provides the model with the present day variables only. The fourth row includes the model with the historical patch configuration and additional habitat quality and heterogeneity variables. The fifth row includes models with present day patch configuration and additional habitat quality and heterogeneity variables. The sixth row includes the model with the present day habitat area and the historical patch connectivity. For each model, the standardized regression coefficients and significance are shown. x = Parameter not in model, significance: * 0.01 < P ≤ 0.05; ** 0.001 < P ≤ 0.01; *** P ≤ 0.001.

Richness of	Area	Connectivity	Moisture	Soil pH	P-avail.	Subpatch diversity	Geological diversity	Topog. heterogen.	Edge effect
All herbs	x	x	0.08^{*}	x	-0.15^{***}	0.08^{*}	x	x	0.22^{***}
1780	$-0.03^{\text{n.s.}}$	$0.05^{\text{n.s.}}$	x	x	x	x	x	x	x
2008	0.34^{***}	$0.02^{\text{n.s.}}$	x	x	x	x	x	x	x
1780	$-0.02^{\text{n.s.}}$	$0.05^{\text{n.s.}}$	0.07^{*}	x	-0.15^{***}	0.08^{*}	x	x	0.23^{***}
2008	0.23^{***}	$0.03^{\text{n.s.}}$	0.06^{*}	x	-0.08^{**}	$0.02^{\text{n.s.}}$	x	x	0.13^{***}
Herb specialists	x	x	0.18^{***}	x	-0.21^{***}	0.11^{*}	0.07^{*}	0.07^{*}	0.11^{**}
1780	$-0.02^{\text{n.s.}}$	$0.06^{\text{n.s.}}$	x	x	x	x	x	x	x
2008	0.37^{***}	$0.00^{\text{n.s.}}$	x	x	x	x	x	x	x
1780	$-0.03^{\text{n.s.}}$	0.09^{*}	0.18^{***}	x	-0.21^{***}	0.09^{*}	0.08^{*}	0.11^{**}	0.10^{**}
2008	0.29^{***}	$-0.01^{\text{n.s.}}$	0.17^{***}	x	-0.13^{**}	$0.04^{\text{n.s.}}$	$0.04^{\text{n.s.}}$	$-0.00^{\text{n.s.}}$	$0.01^{\text{n.s.}}$
Conn. 1780, area 2008	0.27^{***}	$0.03^{\text{n.s.}}$	0.16^{***}	x	-0.13^{***}	$0.06^{\text{n.s.}}$	$0.05^{\text{n.s.}}$	$0.03^{\text{n.s.}}$	$0.01^{\text{n.s.}}$
Herb generalists	x	x	x	x	-0.11^{**}	x	x	x	0.28^{***}
1780	$-0.03^{\text{n.s.}}$	$0.05^{\text{n.s.}}$	x	x	x	x	x	x	x
2008	0.33^{***}	$0.03^{\text{n.s.}}$	x	x	x	x	x	x	x
1780	$-0.02^{\text{n.s.}}$	$0.06^{\text{n.s.}}$	x	x	-0.11^{**}	x	x	x	0.28^{***}
2008	0.21^{***}	$0.04^{\text{n.s.}}$	x	x	-0.05^{*}	x	x	x	0.17^{***}
Few seeds / ramet	x	x	0.19^{***}	x	-0.22^{***}	0.10^{*}	0.09^{*}	0.14^{**}	x
1780	$-0.05^{\text{n.s.}}$	$0.04^{\text{n.s.}}$	x	x	x	x	x	x	x
2008	0.36^{***}	$-0.01^{\text{n.s.}}$	x	x	x	x	x	x	x
1780	$-0.04^{\text{n.s.}}$	$0.09^{\text{n.s.}}$	0.18^{***}	x	-0.22^{***}	$0.09^{\text{n.s.}}$	0.09^{*}	0.09^{***}	x
2008	0.26^{***}	$0.00^{\text{n.s.}}$	0.15^{**}	x	-0.13^{*}	$0.04^{\text{n.s.}}$	$0.05^{\text{n.s.}}$	$0.05^{\text{n.s.}}$	x
Short distance dispersal	x	x	0.20^{***}	x	-0.21^{***}	0.12^{*}	0.10^{*}	0.15^{**}	x
1780	$-0.03^{\text{n.s.}}$	$0.06^{\text{n.s.}}$	x	x	x	x	x	x	x
2008	0.40^{***}	$-0.02^{\text{n.s.}}$	x	x	x	x	x	x	x
1780	$-0.04^{\text{n.s.}}$	0.12^{*}	0.19^{***}	x	-0.22^{***}	0.10^{*}	0.10^{*}	0.19^{***}	x
2008	0.30^{***}	$-0.03^{\text{n.s.}}$	0.16^{**}	x	-0.12^{*}	$0.06^{\text{n.s.}}$	$0.05^{\text{n.s.}}$	$0.04^{\text{n.s.}}$	x
Conn. 1780, area 2008	0.28^{***}	$0.04^{\text{n.s.}}$	0.15^{**}	x	-0.12^{*}	$0.05^{\text{n.s.}}$	$0.05^{\text{n.s.}}$	$0.07^{\text{n.s.}}$	x
Extensive clonals	x	x	0.22^{***}	x	-0.21^{***}	0.09^{*}	0.08^{*}	0.08^{*}	0.10^{*}
1780	$-0.00^{\text{n.s.}}$	$0.05^{\text{n.s.}}$	x	x	x	x	x	x	x
2008	0.36^{***}	$0.01^{\text{n.s.}}$	x	x	x	x	x	x	x
1780	$-0.01^{\text{n.s.}}$	$0.08^{\text{n.s.}}$	0.22^{***}	x	-0.22^{***}	$0.07^{\text{n.s.}}$	0.08^{*}	0.12^{**}	0.09^{*}
2008	0.28^{***}	$-0.00^{\text{n.s.}}$	0.21^{***}	x	-0.14^{**}	$0.04^{\text{n.s.}}$	$0.05^{\text{n.s.}}$	$0.02^{\text{n.s.}}$	$0.00^{\text{n.s.}}$

2.5 Discussion

Present-day patch configuration predicts species richness better than historical patch configuration

Our study on examining the ED in highly fragmented forests revealed contrary results to studies conducted in less fragmented areas from Paltto et al. (2006), Piessens & Hermy (2006) and Vellend et al. (2006). The present-day species richness was largely determined by the present-day patch area, in combination with habitat quality. Hence, our data does not support the hypothesis of an ED for herb layer plant species after approximately 160 years of relaxation time. Our results are in line with studies that have examined highly fragmented grasslands (Berglund & Jonsson 2005, Bagaria et al. 2012) and with the review study of Cousins (2009). Cousins (2009) noted that, in grassland studies that reported an ED, the patches still retained greater than 10% of the original target habitat. In contrast, the studies conducted in highly transformed landscapes did not report any evidence of an ED. The fragmentation of forest patches in our study region was very dramatic. Our investigated patches retained only approximately 0.8% of the area that was present in 1780 and the degree of connectivity had decreased considerably. Across our entire study region, 94.2% of the ancient forest area had been transformed. The vast majority of the deciduous forest area was lost by 1850 (Wulf et al. 2010). Hence, the relaxation time in our study area was approximately 160 years. This time span is within those of other ED studies that have examined temperate forests who are approximately 120 years in Paltto et al. (2006) and approximately 210 to 225 years in Piessens & Hermy (2006) and Vellend et al. (2006). We conclude that the main reason for the complete payment of the ED is the truly massive loss of habitat and the reduced level of connectivity rather than a long relaxation time.

Historical patch connectivity affects forest-specialist richness

The species richness of all herbs and of the generalists was not dependent on the historical patch configuration, but we detected an effect of the historical patch connectivity on the species richness of the specialists. We only found this effect in the models that included the additional habitat quality and heterogeneity variables. The effect was also marginal in the combined models, i.e. when historical connectivity was included to the model with the present-day habitat area (Table 2.3). These results suggest that the inclusion of the additional habitat quality and heterogeneity variables had an influence on the significance, i.e. the strength of the relationship of historical patch connectivity with present-day species richness. When looking at the correlation analysis (Table 2.1) it can be seen that correlations of the habitat quality and heterogeneity variables with the historical patch connectivity are weak to non-existent. However, there was one variable, the topographical heterogeneity, that showed a weak, though significant negative correlation with historical patch connectivity. Unfortunately, we cannot explain why the historical patch connectivity should be smaller in regions with a high topographical heterogeneity. One could imagine that in regions with a high topographical heterogeneity soils are less suitable for agriculture. According to our maps, this was not the case for our study area. To test whether topographical heterogeneity is the crucial variable that lets historical patch connectivity become significant, we fitted a model for specialist species richness without topographical heterogeneity, but all other variables. In this case the historical connectivity was no more significant (Appendix 2.5). However, we also fitted models omitting other, less correlated variables (e.g. soil moisture) and in several of these models the historical connectivity also turned non-significant (Appendix 2.5). Thus, we assume that the main reason for the significance of historical patch connectivity is that the inclusion of the habitat quality and heterogeneity variables reduces the amount of unexplained variation in the models, which means that the true, though weak effects of historical connectivity become more important relative to the total unexplained variation. Although the reason for the weak correlation between topographical heterogeneity and historical patch connectivity remains obscure and the effects of correlations in general seem to be small in our study, our study demonstrates that historical effects on species richness may be masked by environmental patch attributes. Considering environmental conditions in the examination of extinction debts should therefore be standard in future studies.

Our results suggest that forest specialists contribute more to the ED than generalists because the richness of forest specialists was still dependent on the historical patch configuration (although only in one model combination), while the richness of generalists was not. The results also support the well-known influence of patch configuration on forest specialists, in contrast to generalists (Rodríguez-Loinaz et al. 2012, Kuussaari et al. 2009, Petit et al. 2004). However, because the ED has largely been paid now the specific contributions of the specialists and generalists to the ED cannot be quantified anymore.

We detected a significant relationship between specialist species richness and historical patch connectivity, but not historical habitat area. It is unlikely that there was never an ED associated with habitat loss. In the present-day models, habitat area was the most important factor for explaining species richness, and the amount of habitat loss was very high. We expect that the ED associated with habitat loss was quickly paid off. Connectivity has not dropped as dramatically as habitat area and the majority of habitat fragmentation occurred after the reduction in forest area. A massive area of habitat had been lost by 1850, while the increase in the number of patches (i.e., the degree of fragmentation) primarily occurred from 1880 to 2013. Bommarco et al.

(2014) noted the importance of historical connectivity over a historical area with respect to delayed extinctions. These authors reported a connection between the richness of grassland species and the level of historical connectivity, but not the area of the historical habitat. Nevertheless, the determination of the actual importance of fragmentation vs. area loss for ED remains an open question. Unfortunately, it was not possible to extend our study to a region with either a lower amount of area loss or a higher degree of connectivity. Such a comparison could provide more detail concerning the relationships of losses of connectivity and area to species extinctions in deciduous forests.

Extinction debt in forest-specialist groups

The present-day models always explained the present-day species richness of the specialists groups better than the historical models. Nevertheless, the historical connectivity influenced the richness of specialists with a short-distance dispersal potential (at least in the models that did not include present-day habitat area). This result partly confirms our hypothesis concerning the contribution of trait groups to the ED and is in accordance with the results of Vellend et al. (2006). However, the authors included species with short distance dispersal potential to a broader group of species with “slow metapopulation dynamics” which also includes other traits (see Verheyen et al. (2004) for details). For the groups of specialists with extensive clonal growth or few seeds per ramet, we did not observe the hypothesized relationship between species richness and historical patch configuration. In the literature, persistence traits are seen as crucial to experiencing delayed extinctions (Hylander & Ehrlén 2013). It has been shown that clonals are more sensitive to forest area loss than to connectivity (Lindborg et al. 2012). As discussed above (sections 4.1 and 4.2), area loss was very high; thus, probably the delay for the extinction of clonals was shorter than the delay for species with short-distance dispersal potential and many clonals vanished rapidly after habitat destruction. The same rapid extinction may be true for specialists with few seeds per ramet because according to Saar et al. (2012) this trait influences both, the dispersal abilities and persistence abilities of a species. Species with few seeds have often large seeds that may enhance the persistence of a small population that is not connected to others, because species with large seeds are more competitive in (within-patch) recruitment and do cope better with temporal poor conditions after germination (Lonnberg & Eriksson 2013, Leishman 2003).

Implications for forest conservation

Our study demonstrates that, even in a stable environment such as that of forests, an ED can be completely paid within 160 years of relaxation time if the loss of area is extremely high. These findings demonstrate the urgency for conservation actions with respect to ED following forest fragmentation. Currently, the species richness of the ancient forest remnants in the Prignitz region is in a state of equilibrium with the present day patch configuration. We could thus conclude that any conservation actions are superfluous. This would be too hasty of a conclusion though. We were surprised to find that the present day-patch connectivity played no role in determining species richness. However, in many other studies examining extinction debt, there was also no reported effect of present-day connectivity but was an effect of historical connectivity (e.g., Lindborg & Eriksson 2004, Bommarco et al. 2014). If the richness of forest specialists in a patch does not benefit from the surrounding ancient forest cover (and thus other populations of forest specialists), we must assume that the metapopulation functioning has been disrupted (Jamoneau et al. 2012). If metapopulation functioning is disrupted, environmental changes can more easily lead to local extinctions (Honnay et al. 2005). Species are also unable to recolonize patches, and there are no source populations for the colonization of recently established forest patches. For forest specialists, especially those with a low dispersal potential, it will require a long time (if ever) before new populations eventually emerge (Butaye et al. 2001). In colonization processes, patch isolation is more crucial than area loss in hampering colonization of new areas (Peterken & Game 1984). Increasing connectivity would thus largely increase the chances of species colonization in post-agricultural forests and of recolonizations in ancient forests. However, the benefits from increasing connectivity require a long time before they are realized and an ED may already be paid by the time conservation actions are finally effective. Hence, we also stress the need for active introductions of forest specialists to gain more time for conservation actions to take effect.

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Chapter 3: Colonization credit of post-agricultural forest patches in NE Germany remains 130-230 years after reforestation

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3.1 Abstract

In many temperate regions worldwide, a large portion of deciduous forest grows on former agricultural land, while a smaller portion is ‘ancient’ forest on sites with no historical record of agricultural land use. The differences in species diversity between ancient and post-agricultural forests have been well documented. However, in regions where forest fragmentation occurred only a few centuries ago, it remains unclear whether these differences are due to an extinction debt in ancient forests (i.e., a delay in local species extinction), a colonization credit in post-agricultural forests (i.e., species are yet to colonize a patch), or both. Additionally, our knowledge on how soil conditions and landscape configuration interact with species’ traits to determine the colonization credit is limited. Here, we surveyed ancient and post-agricultural forest patches in NE Germany to quantify the magnitude of the colonization credit and identify its determinants. The colonization credit in an average forest patch amounted to 4.7 forest specialist species and ranged up to 9 species in highly isolated patches. In contrast, we found more species than predicted in patches better connected to ancient forests. The colonization credit was not smaller in older patches than it was in younger ones. Species with a low dispersal potential and a low seed output contributed most to the colonization credit. Our study demonstrates that in a landscape where the extinction debt has already been paid and only a small fraction of ancient forest is left, the recovery of forest specialist diversity in post-agricultural forests may take several centuries.

3.2 Abbreviations

DP	Dispersal potential
SM	Seed mass
SPR	Seeds per ramet
OPP	Offspring shoots per parent plant

3.3 Introduction

Across the temperate regions of eastern North America and Europe, forests have been cleared for agriculture over recent centuries or even millennia, respectively, leaving behind only a small fraction of their original extent (Darby 1956, Whitney 1994). After agricultural abandonment, the land has become reforested in many places, so that today, most forests are on former agricultural land (Hermy & Verheyen 2007). There is reason to assume that these historical land use cover changes affect the plant species diversity today because plants are expected to exhibit delayed responses to forest fragmentation and reforestation (Eriksson 1996, Jackson & Sax 2010). On the one hand, forest patches that have experienced substantial area loss and fragmentation during recent centuries are likely to exhibit an ‘extinction debt’ (Tilman et al. 1994, Vellend et al. 2006) and can be expected to lose species in the future. On the other hand, forest patches that were established after agricultural abandonment are likely to exhibit a ‘colonization credit’, i.e. they have less species than comparable ancient forest patches and will gain species over time (Baeten et al. 2010, Jackson & Sax 2010). The colonization of post-agricultural forests by forest plants has been intensively studied (Flinn & Vellend 2005, De Frenne et al. 2011), though rarely in terms of a colonization credit. Patch colonization has been mostly viewed from a species perspective, i.e. in terms of colonization success of single species. For instance, migration rates from ‘ancient’ forest stands (those with no historical record of agricultural land use; Hermy & Verheyen 2007) into immediately bordering post-agricultural stands have been calculated, and they indicate a slow colonization by many typical forest plant species (Matlack 1994, Orczewska 2009 b, Brunet et al. 2012). Additionally, colonization success in isolated post-agricultural forest patches has been quantified, e.g., using the regression coefficients of the logistic regression of species occupancy against patch area and connectivity (Dupré & Ehrlén 2002, Honnay et al. 2002, Kolb & Diekmann 2005) or using the ratio of the percent occupancy in post-agricultural over ancient forest (Bellemare et al. 2002, De Frenne et al. 2011). In all the cited studies, the colonization ability of the individual species was set in relation to species life-history traits. Across studies and regions, small, perennial forest herbs with few and heavy seeds and unassisted seed dispersal have proved to be slow colonizers (see also Verheyen et al. 2003 a).

Studies on the recovery of post-agricultural forests from a patch perspective (i.e., in terms of species diversity) are also numerous, though less accurate in methodology and with controversial results. Most studies examining the richness of typical forest plants have found a reduced richness in post-agricultural compared to ancient forests (Peterken & Game 1984, Matlack 1994, Lawesson et al. 1998, Vellend 2004, Brudvig & Damschen 2011), although the observed difference may become small or insignificant with increasing age (Bellemare et al. 2002) and in regions with acidic soils and small species pools (Graae 2000, Jacquemyn et al. 2001). However, in regions where forest clearance and fragmentation occurred only a few centuries ago, it remains unclear to what extent the observed differences in species richness between ancient and post-agricultural forests can be attributed to an extinction debt in forest remnants or a colonization credit in afforestations (Piqueray et al. 2011 a). Early empirical evidence indicates that an extinction debt in ancient forest remnants may persist for more than a century (Paltto et al. 2006, Vellend et al. 2006) due to the ability of many forest plants to survive without sexual reproduction for many decades (Inghe & Tamm 1985, Cain & Damman 1997). Species sentenced to extinction will, however, never colonize new patches. The simple difference in species richness between ancient and post-agricultural forests may thus overestimate the number of species yet to colonize a patch.

The plant species richness of a forest patch is the result of multiple determinants, including soil conditions, habitat heterogeneity within the patch, connectivity to other patches and patch shape (Kolb & Diekmann 2004, Gonzalez et al. 2010, Jamoneau et al. 2011). All these determinants may confound differences in species richness between ancient and post-agricultural forests if they differ systematically between these two forest types. Including these determinants as covariables in the quantification of the colonization credit is therefore essential. For instance, soil productivity in post-agricultural forest patches may be higher than in ancient patches because sites for agriculture were not chosen at random (Flinn and Vellend 2005). Univariate tests for differences in species richness as conducted in several of the studies mentioned above may therefore be misleading, unless the remnant and recent sites are paired and directly adjacent (Brudvig et al. 2013). Such a study would necessarily exclude isolated patches that are not in close vicinity to a similar ancient patch.

While the determinants of species richness in forest patches in general are well known, the drivers of the colonization credit in post-agricultural forests remain rather elusive. Existing knowledge on the effects of soil conditions, landscape configuration and time since reforestation is limited and inconsistent. Although several of the more recent studies used soil characteristics as a covariable when analyzing the effect of forest continuity on species richness (Vellend 2004, Hérault & Honnay 2005, Brudvig & Damschen 2011), they did not consider any interactions in their models. There are, however, indications in studies that have conducted separate analyzes for several regions. The richness deficit in post-agricultural forests may be greater on moist, base-rich soils (Peterken & Game 1984, Graae 2000, Jacquemyn et al. 2001). In an analysis of data from ten different regions, Vellend (2003) showed that the relative difference in species richness between ancient and post-agricultural forests increases with a decreasing cover of ancient forest in the landscape. In contrast, De Frenne et al. (2011) found that the recovery of post-agricultural forests across 18 regions was not affected by the cover of ancient forest. Finally, although it seems to be a matter of course that the species richness of post-agricultural forests approaches that of ancient forest with increasing forest age, not all studies have found a positive relationship between richness and age, particularly if the afforestations were isolated (Peterken & Game 1984, Wulf 2004 b, Brunet et al. 2011).

In this study, we aimed to quantify the colonization credit in post-agricultural forest patches based on the species richness values predicted by ancient forest patches in which the extinction debt has largely been paid. Our main objective was to investigate how soil conditions, patch configuration and patch age affect the magnitude of the colonization credit and how these effects interact with species life-history traits. Specifically, we tested the following hypotheses:

H1 The post-agricultural forest patches exhibit a colonization credit, i.e., they have fewer forest specialist species than ancient forests of comparable soil conditions, habitat heterogeneity and patch configuration.
H2 The colonization credit is larger in small and strongly isolated patches that were only recently forested.
H3 The colonization credit is larger on moist, base-rich sites.
H4 The effects of soil conditions, patch configuration and patch age on the colonization credit depend on the plant species' ability to colonize (i.e., to disperse to and establish in) new patches.

3.4 Material and methods

Study region and land-use history

We conducted the study in the 4100 km² Prignitz region (52°42'N – 53°23'N, 11°15'E – 12°43'E) in the northwestern part of the federal state of Brandenburg, Germany (Appendix 3.1.1). The climate is sub-oceanic with a mean annual temperature of 9.1°C. Monthly temperatures range between 0.5°C in the coldest and 18.5°C in the warmest month. Mean annual precipitation ranges between 533 mm and 676 mm (DWD 2014). The terrain is generally flat or undulating, with elevations ranging from 10 m a.s.l. to local peaks of 150 m a.s.l. The prevalent geological substrates are sandy to loamy glacial deposits as well as glacio-fluvial sands (LBGR 2008, 2009). From these, mostly cambisols developed, often combined with gleysols and stagnosols (IUSS Working Group WRB 2006, LBGR 2007).

The land-use history of the Prignitz region can be traced back to the second half of the 18th century. We intersected topographical maps from three time periods: the so-called Schmettau map from 1767-1787 (hereafter 1780) at a 1:50,000 scale (Wulf & Groß 2004); the map of the Prussian Government from 1879-1902 (hereafter 1880) at 1:25,000; and recent topographical maps from 2008 at 1:25,000 (see Appendix 3.3 for details). Around 1780, c. 32% of the Prignitz region was covered by forest, mainly with deciduous, autochthonous tree species (Wulf & Rujner 2011). Since then, c. 71% of the original forested area was cleared for agriculture and another 25% was converted into allochthonous pine (*Pinus sylvestris*) forests, mainly between 1780 and 1880. At the same time or later, however, afforestations with deciduous tree species occurred, mostly in small patches. The deciduous forest cover today amounts to c. 5% and consists of mostly small, isolated patches with a median size of 1.4 ha (Appendix 3.1.1). More than one-third of these stands (c. 36%) are ancient, i.e., continuously forested since 1780. Approximately 20% are old (not forested in 1780, but continuously forested since 1880), and c. 45% are recent (not forested in 1880, but afterwards afforested). Although land-cover changes were associated with site conditions (Wulf et al. 2010), today, the entire range of forest communities of the Prignitz region (ranging from species-rich alder and ash forests on wet sites over oak-hornbeam forest on moist, relatively nutrient-rich soils to species-poor oak forests on dry, sandy sites; Appendix 3.2.1) is still present in all three forest continuity types.

Patch selection

Out of the 3318 forest patches in the Prignitz region (forested area > 0.5 ha), we selected 104 ancient and 110 post-agricultural forest patches for our study. The patches had to fulfill the following four criteria: (1) The share of deciduous stands had to be ≥ 50%; (2) the patch had to be located at least 5 km away from the border of the study region to allow reliable connectivity calculations; (3) the patch size had to be at most 25 ha, which is the maximum size that allows a single researcher to survey a patch within one long day; (4) the patch had to match one of the following age class definitions: A forest patch was defined as ‘ancient’ if at least one third of the deciduous forest area was continuously forested since 1780; as ‘old’ if the patch had no ancient part and if at least one third of the deciduous forest area was continuously forested since 1880; as ‘recent’ if 100% of the forest area was afforested after 1880. These criteria left us with 1022 patches that could be selected. We then applied a stratified random sampling to obtain a uniform distribution across five patch size classes (of equal width on a log scale) and the main forest communities, which correspond to different levels of nutrient and water availability (Appendix 3.2.1). A patch was assumed to represent a certain forest community when this patch contained at least 1000 m^2 of that community. Patches strongly affected by other land-use types (pasture, cemetery, park etc.) or located in former military areas were excluded from the survey. The final sample of post-agricultural forest patches comprised 34 old and 76 recent patches.

Plant species recording

For each patch, we compiled a list of all herbaceous vascular plant species by walking along parallel transects with a width of 20 m. Only stands dominated by deciduous trees were included. The border of the patch area was defined as the line connecting the inner stem bases of the edge trees, i.e., inner fringes as well as plants growing along trails, ditches, etc. within the patch were included. The patches were visited twice, in spring (April-May) and in summer (June-July) 2013. For data analysis, we retained only forest specialist species, i.e. species that are closely tied to closed forest habitats (category 1.1 in the German forest species reference list of Schmidt et al. 2011).

Patch characterization

Apart from land-use history, plant species richness in temperate forest patches is largely determined by three groups of variables: soil conditions, habitat heterogeneity within the patch and patch configuration within the surrounding landscape (Kolb & Diekmann 2004, Jamoneau et al. 2011). We quantified each of these groups by three variables (see Appendix 3.4 for details and Appendix 3.2.2 for correlations among variables). Soil conditions were assessed by taking soil samples in the most base-rich part of a patch (Kolb & Diekmann 2004) as indicated by the plant species’ indicator values for soil reaction (Ellenberg et al. 2001). The most base-rich part of a patch is best suited to predict species richness because species richness in temperate forests is highest on base-rich sites (Härdtle et al. 2003). Species richness may be underestimated when patches assumed base-rich contain also nutrient-poor soils. In this case, variables of habitat heterogeneity (see below) will contribute to predicting species richness. The number of measured soil variables was reduced to three dimensions be means of principal components analysis (Appendix 3.4). After varimax rotation, the first component was highly correlated with Nt (r = 0.97), Ct (0.96), water content (0.94) and Mg (0.81). We will refer to it as PC1.productivity. The second component was highly correlated with pH (r=0.93), Ca (0.82) and CN-ratio (-0.78). We will refer to it as PC2.pH. The third component was highly correlated with P (r=0.93) and thus will be referred to as PC3.P.

Habitat heterogeneity was quantified by topographical heterogeneity (HH.topo; the range in elevation within a patch), geological heterogeneity (HH.geol; the Shannon diversity of different geological substrates within a patch) and man-made structural heterogeneity (HH.stru). For the latter, we divided each patch into homogeneous subpatches with a uniform overstory composition and structure. The area proportions of the different subpatches were used to calculate a Shannon index of structural heterogeneity.

We assessed the patch configuration within the landscape with the variables ‘habitat area’, ‘connectivity’ and ‘edge length’. Habitat area refers to the part of the patch that was dominated by deciduous trees, where we recorded the plant species. Pure coniferous stands were not regarded as habitat because most of the forest specialist plants considered here do not or only very rarely occur in coniferous forests (Schmidt et al. 2011). If they are frequently found there they will have a much larger habitat area available in the region (Appendix 3.1.1) and will contribute little to the colonization credit anyway. We measured connectivity with the incidence function model derived from Hanski (1994): $C_j = \sum_{j \neq i} A_j^b \times \mathrm{e}^{-\alpha d_{ij}}$, where C_i is the connectivity of patch i, A_j is the habitat area of patch j and d_{ij} is the edge-to-edge distance between patches i and j. The calibration parameters α and b were set to 0.002 m^{-1} and 0.5, respectively (Moilanen & Nieminen 2002, Verheyen et al. 2004). The edge length of a patch as a measure of shape complexity comprises all inner fringes, including the edge of the habitat area as well as trails, rides etc. To make edge length independent of area, we divided it by the potential minimum edge a patch can have, i.e., the perimeter of a corresponding circular patch.

Data analysis

We quantified the colonization credit and its determinants at two levels. At the first level, we took all forest specialist species into account. At the second level, we differentiated between species groups defined by life-history trait attributes. To colonize forest patches, plant species face two main challenges: (a) they must disperse over relatively long distances and (b) after arrival, they must establish a viable population. We used, therefore, two traits related to dispersal, dispersal potential (DP; Vittoz & Engler 2007) and the number of seeds per ramet (SPR; Eriksson & Jakobsson 1999), and two traits related to establishment, seed mass (SM; Moles & Westoby 2004) and the number of offspring shoots per parent plant (OPP; Stöcklin 1992). All traits were measured with three categories (low, intermediate, high). Only species of the low or high category were used for analysis to enhance the contrast between species groups (Table 3.1).

Table 3.1. Life-history traits used to differentiate between species groups when quantifying the colonization credit and its determinants.

Trait	Categories [a]	Data source	Missing values (%)
Dispersal potential (DP)	**low** (dispersal types 1 and 2 as defined by Vittoz and Engler 2007, see Appendix 3.5) high (types 5 and 6)	Mostly Müller-Schneider (1986) and recent empirical studies (see Appendix 3.5)	0
Seeds per ramet (SPR)	**few** (≤ 56; lower third of species ranks) many (> 346; upper third of species ranks)	Kleyer et al. (2008)	20
Seed mass (SM)	low (≤ 0.36 mg; lower third of species ranks) **high** (> 2.72 mg; upper third of species ranks)	Kleyer et al. (2008) Hintze et al. (2013)	3
Offspring shoots per parent plant (OPP)	none (< 1 offspring shoot per year) **several** (≥ 2 offspring shoots per year)	Klimešová and de Bello (2009)	0

[a] Categories printed in bold face are expected to contribute most to the colonization credit.

At both levels, we quantified the colonization credit and its determinants as follows: First, we modeled species richness as a function of soil conditions, patch heterogeneity and patch configuration using only the subset of ancient forest patches. In a related study (Kolk & Naaf 2015), we found no effect of historical (1780) patch connectivity and patch area on current species richness. We may therefore assume that any extinction debt due to forest fragmentation has already been paid and species richness is in equilibrium with the current patch configuration. Before modeling, habitat area, edge length and HH.topo were log-transformed and connectivity was sqrt-transformed to achieve approximate symmetry of frequency distributions. All patch attributes were standardized to mean = 0 and sd = 0.5 to facilitate the interpretation of the parameter estimates (Schielzeth 2010). To model species richness as a function of patch attributes, we used general linear models (LM) at the first level and linear mixed models (LMM) at the second level. It was possible to assume a Gaussian error distribution because the residuals were approximately normally distributed. The predictive quality of these models was assessed by leave-one-out cross-validation and the resulting root mean squared error of prediction.

Then, we used these models to predict species richness in old and recent forest patches. The difference between the predicted and observed species richness represents an estimate for the colonization credit of each patch. Next, we modeled the colonization credit as a function of soil conditions, patch configuration and patch age (old vs. recent) to identify its determinants. For this purpose, the predictor variables were again standardized to mean = 0 and sd = 0.5, based only on the subset of post-agricultural patches. Finally, we characterized the magnitude of the colonization credit by the fitted values of average patch attribute values (as an estimate of a typical colonization credit in the Prignitz region) and the range of the fitted values (as an estimate for the variation of the colonization credit in the Prignitz region).

At the second level, a life-history trait (one at a time) was added as a categorical predictor to the models together with its interactions with all other predictor variables. For this purpose, we replicated the dataset with regard to all variables except species richness, which contained values for both levels of the categorical predictor. Patch identity was used as a random effect to account for the paired data structure. This approach allowed us to examine two things at the same time: (a) which species groups contribute most to the colonization credit and (b) how the effect of patch attributes on the colonization credit changes depending on species attributes.

In all modeling procedures, we applied the following protocol to find the best model: First, we fitted a full model with all potential predictors and checked for model assumptions. If needed, a variance structure was defined to account for variance heterogeneity using the ‘weights’ argument in the R function lme() for LMM (Pinheiro et al. 2014). Quadratic terms were added where it seemed appropriate. Second, the best model was found by fitting a model for all possible subsets of predictors and choosing the one with the lowest AICc among those models, in which all predictors contributed significantly ($P \leq 0.05$) based on an F-test on the marginal sums of squares, and in which the assumptions of variance homogeneity could be met.

3.5 Results

Species richness and patch attributes in ancient and post-agricultural forest patches

Overall, we found 71 forest specialist species in the surveyed patches. In ancient forest patches, we found a total of 65 specialist species, of which 7 were not recorded in any post-agricultural forest patch. In post-agricultural forest patches, we found a total of 64 specialist species, of which 6 were not recorded in any ancient forest patch. The average number of specialists found in ancient patches (17) was slightly higher than in post-agricultural patches (14), but the ranges were almost equal (1 – 35 and 2 – 35 in ancient and post-agricultural patches, respectively).

Patch attributes were generally similar between ancient and post-agricultural forest patches in terms of median and standard deviation (Appendix 3.2.3). The variation in PC1.productivity was significantly higher in post-agricultural patches, while the covered range of values was still rather similar. Ancient forest patches had on average a higher connectivity than post-agricultural patches.

The most important patch attribute in determining species richness in ancient forest patches was habitat area, which yielded the highest regression coefficient in all models (Table 3.2). Soil conditions were also important in most models. Species richness increased with soil productivity and soil pH, while it decreased with P availability. For all species and some species groups, patch connectivity predicted the highest species numbers at mean connectivity values. Habitat heterogeneity and edge length affected only the richness of particular specialist groups. The normalized root mean squared error of prediction ranged between 13.6% and 15.5% (Table 3.2).

Table 3.2. Results of modelling forest specialist species richness in ancient forests as a function of soil conditions, habitat heterogeneity, patch configuration and life-history traits (n = 104). Given are the group means (intercept) and standardized regression coefficients. Asterisks indicate significance against zero (n.s. $P > 0.05$, * $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$) based on t-tests. Significant differences between groups are indicated by lower-case letters. RMSE: root-mean-square error of prediction, Norm. RMSE: root-mean-square error normalized by the range of observed values.

	All forest specialists	Low (L) vs. high (H) dispersal potential	Few (F) vs. many (M) seeds per ramet	Low (L) vs. high (H) seed mass	None (N) vs. several (S) offspring shoots per parent plant
RMSE	4.6	2.3	2	1.7	1.9
Range	1; 35	0; 16	0; 14	0; 12	0; 12
Norm. RMSE (%)	13.6	14.1	14.2	14.2	15.5
Intercept	17.6 ***	L 6.8 *** ^{a}	F 5.9 *** ^{a}	L 5.5 *** ^{a}	N 5.3 *** ^{a}
		H 7.2 *** ^{a}	M 4.4 *** ^{b}	H 5.3 *** ^{a}	S 5.3 *** ^{a}
PC1.productivity	4.4 ***	L 3.2 *** ^{a}	1.2 ***	L 1.5 *** ^{a}	N 0.3 $^{n.s.}$ ^{a}
		H 1.5 ** ^{b}		H 0.1 $^{n.s.}$ ^{b}	S 2.5 *** ^{b}
PC1.productivity^2		L -2.3 * ^{a}			
		H 0.4 $^{n.s.}$ ^{b}			
PC2.pH	2.4 *	0.8 *			N 0.2 $^{n.s.}$ ^{a}
					S 1.1 ** ^{b}
PC3.P	-3.1 **	-1.2 **	-0.8 **		-0.8 **
HH.geol				L -0.3 $^{n.s.}$ ^{a}	
				H 0.7 * ^{b}	
HH.stru		0.9 *	F 1.4 ** ^{a}	0.7 *	0.7 *
			M 0.2 $^{n.s.}$ ^{b}		
HH.topo		L 0.0 $^{n.s.}$ ^{a}			
		H -0.9 * ^{b}			
Habitat area	10.6 ***	4.2 ***	2.9 ***	2.8 ***	2.8 ***
Connectivity					0.8 *
Connectivity^2	-2.9 ***	-1.1 **		L -0.8 * ^{a}	N -0.7 $^{n.s.}$ ^{a}
				H 0.1 $^{n.s.}$ ^{b}	S -1.5 *** ^{b}
Edge length				0.9 *	
Edge length^2				-2.0 **	

Magnitude of the colonization credit and its determinants

The colonization credit of an average post-agricultural forest patch amounted to 4.7 species (Table 3.3). Fitted values ranged between -6 and 9 species. Fifteen patches (13.6%) exhibited a negative fitted value, suggesting that these patches had been colonized by more species than predicted. The magnitude of the colonization credit depended mainly on patch connectivity. The colonization credit increased with decreasing connectivity, but leveled off when connectivity became lower than average (Fig. 3.1). At high values of connectivity, the colonization credit was negative. Further, the colonization credit increased with increasing edge length. Neither soil conditions, habitat area nor patch age had a significant effect on the colonization credit.

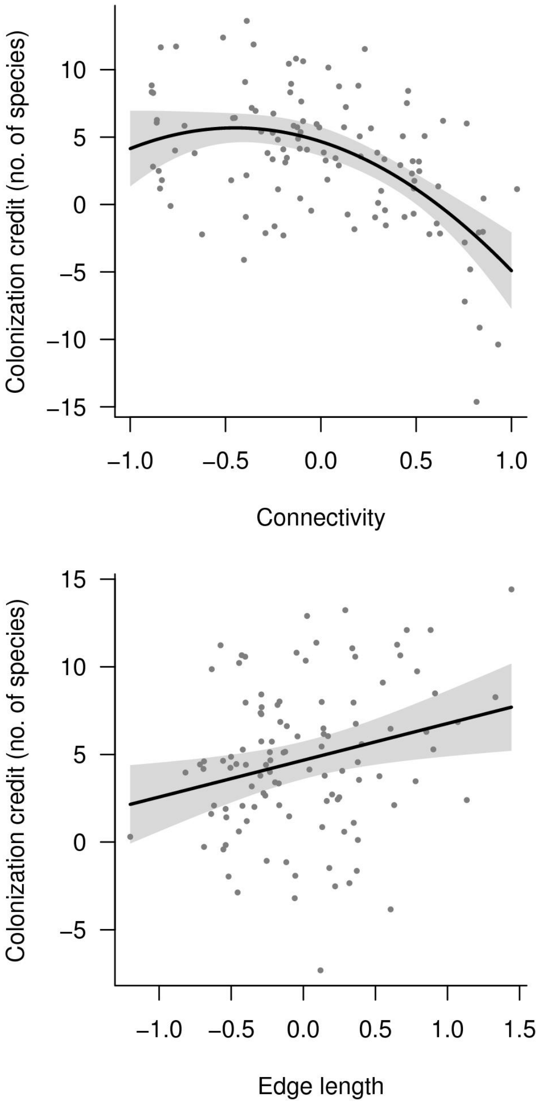

Fig. 3.1. Visualization of the partial effects of patch connectivity and edge length on the magnitude of the colonization credit as resulting from the model including all forest specialists presented in Table 3. The gray band represents the 95% confidence range.

Table 3.3. Results of modelling the colonization credit in post-agricultural forest patches as a function of soil conditions, patch configuration, patch age and life-history traits ($n = 110$). Given are the group means (intercept and patch age) and standardized regression coefficients. Asterisks indicate significance against zero ($^{\text{n.s.}}$ $P > 0.05$, * $P \le 0.05$, ** $P \le 0.01$, *** $P \le 0.001$) based on *t*-tests. Significant differences between groups are indicated by lower-case letters.

	All forest specialists	Low (L) vs. high (H) dispersal potential	Few (F) vs. many (M) seeds per ramet	Low (L) vs. high (H) seed mass	None (N) vs. several (S) offspring shoots per parent plant
Intercept	4.7 ***	see patch age	F 1.7 *** ^{a} M 1.1 *** ^{b}	1.4 ***	N 0.5 ** ^{a} S 1.3 *** ^{b}
PC1.productivity		L 1.6 *** ^{a} H 0.4 $^{\text{n.s.}}$ ^{b}			N -0.5 $^{\text{n.s.}}$ ^{a} S 1.6 *** ^{b}
PC1.productivity^2		L -3.2 *** ^{a} H 0.8 $^{\text{n.s.}}$ ^{b}			
PC2.pH					
PC2.pH^2			F 1.7 ** ^{a} M 0.0 $^{\text{n.s.}}$ ^{b}		
PC3.P				0.5 *	
PC3.P^2			-0.8 *		
Habitat area			0.9 ***		
Connectivity	-4.5 ***	L -1.7 *** ^{a} H -0.5 $^{\text{n.s.}}$ ^{b}	F -2.1 *** ^{a} M -0.9 *** ^{b}	-0.9 ***	
Connectivity^2	-5.1 ***	-1.6 ***	-1.2 **	-1.0 *	N -0.3 $^{\text{n.s.}}$ ^{a} S -2.4 *** ^{b}
Edge length	2.1 *	0.9 ***		0.9 ***	
Edge length^2				-2.3 ***	
Patch age old		L 2.8 *** ^{a} H 1.7 *** ^{b}			
recent		L 2.8 *** ^{a} H 0.7 * ^{c}			

The colonization credit was significantly influenced by three of the four life-history traits studied (Table 3.3). Seed mass had no significant effect on the colonization credit (Appendix 3.1.4). Species with a low DP exhibited a larger colonization credit than species with a high DP. This difference was greater in recent than in old forest patches due to the low colonization credit of the species with high DP in recent forests (Appendix 3.1.2). Furthermore, DP interacted with the effects of connectivity and PC1.productivity. The negative effect of connectivity was significantly stronger in species with a low DP. In the case of weak dispersers, the effect of PC1.productivity on the colonization credit was significant and on average positive, but unimodal, i.e., with a maximum colonization credit between mean and highest productivity values (Appendix 3.1.2).

The colonization credit was also larger in species with few rather than many SPR. The negative effect of connectivity and the quadratic effect of PC2.pH were stronger or only significant in species with a low seed output (Table 3.3; Appendix 3.1.3). Finally, the colonization credit was significantly larger in species with extensive clonal growth. Species with several OPP showed an increasing colonization credit with increasing PC1.productivity and a maximum colonization credit at mean connectivity (Appendix 3.1.5).

3.6 Discussion

Significance of the colonization credit

Despite rather similar raw species richness values in ancient and post-agricultural forest patches in terms of mean and range, we found a highly significant colonization credit in post-agricultural forests. Our results are, therefore, in accordance with earlier studies that have observed fewer species in post-agricultural than in ancient forests (Hermy & Verheyen 2007). In addition, however, our results demonstrate that comparing raw species richness values between forest types may lead to an underestimation of the colonization credit. Moreover, we can be sure not to have overestimated the colonization credit because we may assume that no extinction debt has to be paid in ancient forest patches.

A species deficit of c. 5 species in an average forest patch may appear relatively small at first glance. It may, however, increase up to 9 species in highly isolated patches with a complex shape. Given that we found 71 forest specialist species in the entire region and only an average of 17 specialist species per ancient forest patch, the magnitude of the colonization credit appears substantial.

A remarkable result of this study is that the number of species in post-agricultural forest patches may exceed that of comparable ancient patches when connectivity is high (negative colonization credit). This finding implies that living conditions for forest specialists may be better in post-agricultural forests than in ancient forests. In fact, several observational or experimental studies that compared the performance of ancient forest specialists between ancient and post-agricultural stands found a similar or even better performance in post-agricultural stands (Endels et al. 2004, Graae et al. 2004, Verheyen & Hermy 2004), although contrary findings exist as well (Vellend 2005, Baeten et al. 2009 a). In the search of what those better living conditions in post-agricultural patches might be, we discovered that some tree species that are associated with productive soils (*Alnus* spp., *Prunus padus*, *Ulmus glabra*) were more dominant in post-agricultural forest patches than in ancient ones, whereas some tree species often associated with less productive soils (*Betula pendula*, *Fagus sylvatica* and *Quercus robur*) were more dominant in ancient patches (according to rough field estimates of population sizes, see Appendix 3.2.4). Thus, although similar ancient and post-agricultural patches both may provide productive soils somewhere in the patch, it might be that post-agricultural patches contain on average a larger portion of these species-rich habitats. Additional data would be needed to test this assumption, but if it should apply the true colonization credit could be even higher than estimated here.

Determinants of the colonization credit

Patch configuration

In accordance with our second hypothesis, the colonization credit increased with patch isolation in all but one model. Specifically, species with a low DP and few SPR were affected by isolation. Only for small connectivity values, the negative effect was missing. This indicates that beyond a certain degree of isolation (i.e., a connectivity value of c. 78, roughly corresponding to a habitat area of 1 ha within a 1000 m buffer; Appendix 3.1.6), patch colonization may completely fail or at least occur independent of the nearest source populations. Although anticipated, these results are not trivial. Our connectivity measure is largely based on the area of surrounding ancient forest fragments. De Frenne et al. (2011) also used the area of ancient forest in the landscape to explain the recovery rate of forest herbs in post-agricultural forests. In 18 different studies from throughout Europe, they found no significant effect of the ancient forest area, not even on the group of small perennial herbs with heavy seeds, the group most likely to consist of species with a low DP and seed output (Verheyen et al. 2003 a). In contrast, Vellend (2003) found a strong impact of ancient forest cover in the landscape on the relative difference in species richness between ancient and recent forests. The cover of ancient deciduous forest in our study region is lower than in all or most of the regions covered by De Frenne et al. (2011) and Vellend (2003). Additionally, the distance to the closest ancient forest remnant (median 542 m) is larger in our study than in other studies that have observed a lower forest species richness in isolated compared to non-isolated post-agricultural stands (Jacquemyn et al. 2003, Brunet et al. 2011). Thus, our results demonstrate that even in a landscape with very little ancient forest left, the connectivity to these ancient forest remnants is still a crucial determinant for the colonization of post-agricultural forest patches.

In contrast to our expectations, habitat area had hardly any effect on the colonization credit except for the model accounting for SPR, where the colonization credit increased slightly with habitat area (independent of SPR). According to our second hypothesis, we had expected to find a larger colonization credit in small patches because diaspores from a specific source habitat are more likely to reach patches with a large extent. Only few other studies have addressed the effect of patch area on the difference in species richness between ancient and post-agricultural forests. These have found either an increasing difference in richness with area (Jacquemyn et al. 2001) or no interaction between patch age and area (Vellend 2004). It appears that patch area is not a major determinant of the colonization credit, at least not in the sense of our hypothesis.

Even more contrary to our expectations, patches with a complex shape exhibited a larger colonization credit than patches with a compact shape. We had expected that patches with a long edge in relation to their area would be easier to colonize because the probability of diaspores reaching a patch increases with edge length (Pfenning et al. 2004). In their review of species responses to habitat fragmentation, Ewers & Didham (2006) state that patches with a complex shape are consistently colonized more frequently than compact patches. In contrast, Cousins & Aggemyr (2008) found that the shape of secondary grassland patches on former arable fields was not associated with species richness. No study, however, has documented a hampering effect of shape complexity on patch colonization. We found a reasonable explanation for this result, which assumes a size effect: In patches with a large ecotone area, species richness and therefore the absolute differences between predicted and observed richness values may be large. We repeated our analysis, this time quantifying the colonization credit as relative difference between predicted and observed species richness values. Edge length had no significant effect in this model (Appendix 3.2.5).

Patch age

Although anticipated, old forest patches did not exhibit a smaller colonization credit than recent forest patches. For species with a high DP, the colonization credit was even greater in old forest patches than it was in recent ones. As there is no sensible reason why a colonization credit should increase with patch age, we must assume that patch age is confounded with another determinant of the colonization credit. The most obvious potential factor was former land use. While some studies have found a significant influence of former land-use on the magnitude of richness differences between ancient and post-agricultural forests (Wulf 2004 b), others have not (Brudvig & Damschen 2011). In our dataset, most of the old forest patches (91%) had been formerly used as arable fields, whereas the majority of recent patches (61%) had been formerly used as grassland. To see if former land use was responsible for the missing (all specialists) or unexpected effect (low vs. high DP) of patch age, we refitted these two models, using only those patches that had formerly been used as arable fields (31 old and 30 recent patches). The results were almost the same as with the whole dataset (Appendix 3.2.6). Thus, former land use could not explain the missing or unexpected patch age effect.

We also looked for associations with other patch attributes and found that PC1.productivity had significantly higher values in recent forests (Wilcoxon rank sum test: $W = 618$, $P < 0.001$). If PC1.productivity were responsible for the effect of patch age, we should observe a negative effect of PC1.productivity on the colonization credit because the colonization credit should be larger in old, less productive patches than in recent, more productive patches. In fact, however, the effect of PC1.productivity on the colonization credit was either missing (all specialists) or unimodal with a maximum colonization credit on more productive sites (species with a low DP, see below).

Thus, we still must conclude that the colonization credit is not reduced in old patches compared to recent patches, despite the fact that patch age is confounded with former land use and productivity. This evokes the question of whether the colonization credit in post-agricultural forest patches will ever be repaid. Most studies investigating isolated post-agricultural forest patches have found an increase in forest specialist richness with patch age. In some of these studies, the forest cover in the study region was relatively high (> 10%; Matlack 1994, Jacquemyn et al. 2001, Hérault & Honnay 2005), though it was rather low in others (<10%; Lawesson et al. 1998, Jamoneau et al. 2011). There is scant evidence for the failure of a time effect on species richness in post-agricultural forests (Peterken & Game 1984, Brunet et al. 2011). In central Lincolnshire, UK, an intensively cultivated region with a total woodland cover of only 5.6%, Peterken & Game (1984) could not discern an increase in forest specialist richness with patch age. They tested this in post-agricultural forest patches originating between 1600 and 1947. In addition to their findings, our study strengthens the notion that the recovery of forest specialist richness on former agricultural land may take several centuries if the degree of isolation is high.

Soil conditions

Soil conditions did not affect the colonization credit of all forest specialists, but was important for some specialist groups. As hypothesized, the colonization credit increased with site productivity (species with several OPP) or was at least highest at sites with a productivity value above the regional mean (species with a low DP). With these results, our study provides some empirical evidence from a patch perspective for what is known already from a species perspective. Most ancient forest species across Europe, which are known to be clonal and strongly dispersal-limited (Verheyen et al. 2003 a), prefer moderately moist to moist sites with an intermediate pH and N availability, thus fairly productive sites (Hermy et al. 1999).

Effects of dispersal and establishment abilities

In accordance with our fourth hypothesis, three of the four life-history traits affected the magnitude of the colonization credit and influenced at least some of the effects of the patch attributes. However, only the two dispersal related traits (DP and SPR) showed the anticipated effects. The colonization credit was significantly larger in species that are not adapted to long distance dispersal and that produce only few seeds. The effect of patch connectivity was particularly strong in these species groups. Additionally, the effect of PC1.productivity interacted with DP as discussed above.

In contrast, the two establishment-related traits were either insignificant for the magnitude of the colonization credit (SM) or showed effects opposed to those expected (OPP). Plant species with extensive clonal growth showed, in fact, a larger colonization credit than species with little or no clonal growth. This would be no surprise if the group of species with several offspring shoots per year consisted mainly of species with a low DP and/or few SPR. Slow-colonizing forest herbs have often been characterized as clonal with few and heavy seeds (Dupré & Ehrlén 2002, Verheyen et al. 2003 a, Kolb & Diekmann 2005). There was, however, no significant association between OPP and DP or SPR as indicated by Fisher's exact test ($P = 0.916$ and $P = 0.804$, respectively). We also tested for associations between SM and DP and SPR and found that species with light seeds exhibited a high DP significantly more often than expected ($P = 0.024$) and produced many seeds ($P \leq 0.001$). It is well established that small seed size is often associated with higher seed production (Westoby et al. 2002). We can thus assume that a facilitating effect of maternal provisioning in large seeds on colonization success, if present at all, was counterbalanced by a small seed output and low dispersal ability (Thomson et al. 2011), resulting in no significant effect of SM on the colonization credit. In conclusion, our results suggest that neither the provision of nutrients nor extensive clonal growth is important for colonizing new forest patches. Instead, the dispersal of diaspores across the agricultural matrix appears to be the crucial step.

3.7 Conclusions

Our study demonstrates that in a landscape where only a small fraction of deciduous ancient forest cover is left, isolated post-agricultural forest patches can exhibit a colonization credit for more than 130 to 230 years after establishment. Where connectivity to ancient forest remnants is very low, this colonization credit may increase up to 9 species, which corresponds to more than half of the average forest specialist richness found in ancient patches. Species with a low DP and a low seed production contribute most heavily to the credit. Given such a slow recovery from agricultural land-use, potential threats posed by a rapidly changing environment must be reassessed. Both source populations in ancient forest remnants as well as recently founded populations in post-agricultural patches may suffer from climate change (De Frenne et al. 2013), eutrophication due to nitrogen deposition (Verheyen et al. 2012) or the invasion of exotic species (Essl et al. 2012). In the face of these threats, relying on forest specialists to eventually colonize the post-agricultural forest patches may not be adequate. Instead, active conservation measures may be necessary. Planting hedgerows could be one measure to create new habitats for forest plants and increase connectivity between forest patches. It is, however, not certain that hedgerows effectively assist forest specialists to migrate between patches (Liira and Paal 2013). We argue that active introductions of forest plant species should be taken into account (Thomaes et al. 2014).

In addition, our study shows that, within two centuries, well connected post-agricultural forest patches may be colonized by even more forest specialists than comparable ancient patches. Thus, another effective measure to favor forest plant populations and reduce local extinction risks would be to extend existing ancient forests by establishing new adjacent or nearby forest stands (Brunet et al. 2011).

3.8 Acknowledgements

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Chapter 4: Paying the colonization credit: Converging plant species richness in ancient and post-agricultural forests in NE Germany over five decades

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4.1 Abstract

Massive historical land cover changes in the Central European lowlands have resulted in a forest distribution that now comprises small remnants of ancient forests and more recently established post-agricultural forests. Here, land-use history is considered a key driver of recent herb-layer community changes, where an extinction debt in ancient forest remnants and/or a colonization credit in post-agricultural forests are being paid over time. On a regional scale, these payments should in theory lead toward a convergence in species richness between ancient and post-agricultural forests over time. In this study, we tested this assumption with a resurvey of 117 semi-permanent plots in the well-studied deciduous forests of the Prignitz region (Brandenburg, NE Germany), where we knew that the plant communities of post-agricultural stands exhibit a colonization credit while the extinction debt in ancient stands has largely been paid.

We compared changes in the species richness of all herb layer species, forest specialists and ancient forest indicator species between ancient and post-agricultural stands with linear mixed effect models and determined the influence of patch connectivity on the magnitude of species richness changes. Species richness increased overall, but the richness of forest specialists increased significantly more in post-agricultural stands and was positively influenced by higher patch connectivity, indicating a convergence in species richness between the ancient and post-agricultural stands. Furthermore, the richness of ancient forest indicator species only increased significantly in post-agricultural stands. For the first time, we were able to verify a gradual payment of the colonization credit in post-agricultural forest stands using a comparison of actual changes in temporal species richness.

4.2 Introduction

Land cover changes have been identified as a key driver of biodiversity changes (Sala et al. 2000, Fischer & Lindenmayer 2007). Even land cover changes that occurred long ago and have long ceased can still influence current species occurrence and species richness (overview in Kuussaari et al. 2009, Jackson & Sax 2010).

For example, species richness in a habitat fragment that was part of a much bigger habitat area in the past might still be higher than predicted from its current size and degree of isolation because species often react with a delay to environmental changes (Lindborg & Eriksson 2004, Helm et al. 2006, Paltto et al. 2006, Dullinger et al. 2012, Cronk 2016). As a consequence, a species community exhibits an 'extinction debt' (Tilman et al. 1994). The relaxation time, i.e., the time until the extinction debt is paid off with species loss, is largely dependent on the magnitude of land cover changes and may take up to centuries (Paltto et al. 2006, Vellend et al. 2006, Cronk 2016). On the other hand, a habitat that has recently been established can have a deficit in species due to the slow or even interrupted colonization of species from other suitable habitats. Such habitats are said to exhibit a 'colonization credit' (Hanski 2000, Jackson & Sax 2010).

We recently tested the presence of an extinction debt in forest remnants with no historical record of agricultural land use ('ancient forests') in the Prignitz region in NE Germany (Kolk & Naaf 2015). In the highly fragmented ancient forests of this region, the extinction debt has essentially been paid 160 years after major deforestation has stopped. This outcome is further supported by the results of a subsequent resurvey study in ancient forest stands in the Prignitz region, in which we found no decrease in species richness independent of site conditions (Naaf & Kolk 2016). In another parallel study in the Prignitz region (Naaf & Kolk 2015), we investigated forests that were established after the year 1880 on former agricultural land ('post-agricultural forests') and found an existing colonization credit, i.e., a deficit in the species richness compared to the species richness predicted for similar ancient forests. This deficit was largest for the group of forest specialists and greater when post-agricultural forests were less well-connected to adjacent ancient forest patches. This indicates that the distance to potential source populations is a crucial factor in the recovery rate of species richness in post-agricultural forests (Jacquemyn et al. 2003, Brunet et al. 2011). The limited colonization success of forest specialists (Orczewska 2009 b, Brunet et al. 2012) is the main reason why ancient forests generally have higher numbers of forest specialists (Hermy & Verheyen 2007, Svenning et al. 2009) than comparable post-agricultural forests, as well as specific ancient forest indicator species (Wulf 1997, Honnay et al. 1998, Hermy et al. 1999). However, under the precondition that ancient and post-agricultural forests are located in the same region, i.e., have the same potential species pool and are exposed to comparable environmental conditions, the species richness of ancient and post-agricultural forests should become more similar over time because specialists from adjacent ancient forests subsequently colonize post-agricultural forest patches and thus reduce the colonization credit.

Although an increasing similarity in species richness is predicted by theory, rarely has any study examined whether species richness indeed converges. There are space-for-time studies that have found more forest specialists in older than in younger post-agricultural forests (Jacquemyn et al. 2001, Heráult & Honnay 2005), but there are also studies showing that this was not the case (Peterken & Game 1984, Brunet et al. 2011). A problem in such studies is that species richness differences could also be attributed to differences in the environmental conditions independent from land-use history. Furthermore, the method used in these studies can only detect a difference in species richness but no direction of change, i.e., a possible convergence in species richness can only be predicted but not proven. While space-for-time studies have often been conducted, only three resurvey studies of forest plants have been conducted that address legacies from past land cover changes.

Rogers et al. (2009) resurveyed forest stands in southern Wisconsin and found that the extinction debt in ancient forest remnants has been paid since the 1950s; the magnitude of which is dependent on the surrounding landscape configuration. However, the spatial situation in the Wisconsin area is different from that in Central Europe insofar that there were no recently established forests in the region. Until now, a direct comparison of the development of species richness in ancient and post-agricultural forests has only been performed by Baeten et al. (2010) for understory plant communities in Belgium and by Kokarēviča et al. (2016) for communities in boreo-nemoral forests of Latvia. Although expected, both studies found no convergence in species richness and composition between ancient and post-agricultural stands after 30 years and 100 years, respectively. In case of the Belgian study (Baeten et al. 2010), it remains unclear how severe the historical land cover changes and their legacies in present species occurrences in the region really were and to what extent different environmental conditions in ancient and post-agricultural stands have led to the persistence of differences. In the boreo-nemoral forests of Latvia (Kokarēviča et al. 2016), the spatial and temporal situation was different from the development in most central European forests. The authors compared unmanaged deciduous forests with adjacent spontaneously emerged forests of Spruce and Birch on abandoned farmland. The environmental conditions in such emerging forests appear to remain plainly different (more light available on ground, different tree species composition) from the conditions in the established forests for more than 100 years.

With this study, we aim to directly compare species richness changes in environmentally comparable ancient and post-agricultural forests in a single study system by conducting a resurvey of semi-permanent plots in the Prignitz region that were initially surveyed more than five decades ago.

We hypothesize that

- The species richness of post-agricultural forests approaches that of ancient forests as the colonization credit is paid
- The payment of the colonization credit is mainly driven by an increase in forest specialists and ancient forest indicator species
- Species richness increases more in post-agricultural forests that are better connected to surrounding ancient forests.

4.3 Materials & Methods

Study area and land-use history

We conducted the study in forest patches that are situated in the Prignitz region (52°42“N – 53°23“N, 11°47“E – 12°37“E, 2800 km^2) in the northwestern part of the federal state of Brandenburg, Germany (Fig. 4.1). The climate is sub-oceanic with a mean annual temperature of 9.1°C and a mean annual precipitation of between 533 and 676 mm (DWD 2014). The study area is largely flat with elevations ranging from 10 m a.s.l. to 150 m a.s.l. locally. The prevalent geological substrates are sandy to loamy glacial deposits as well as glacio-fluvial sands (LBGR 2008, 2009). From these substrates, mostly Cambisols, often combined with Gleysols and Stagnosols, have developed (LBGR 2007, IUSS Working Group 2014). The study area is mainly subject to intensive agricultural land use. The forest structure consists of many small deciduous and mixed-forest patches surrounded by agricultural land and of several large coniferous forest areas mainly stocked with Scots pine (*Pinus sylvestris*). Adjacent to or included in these coniferous plantations are smaller stands of native deciduous tree species.

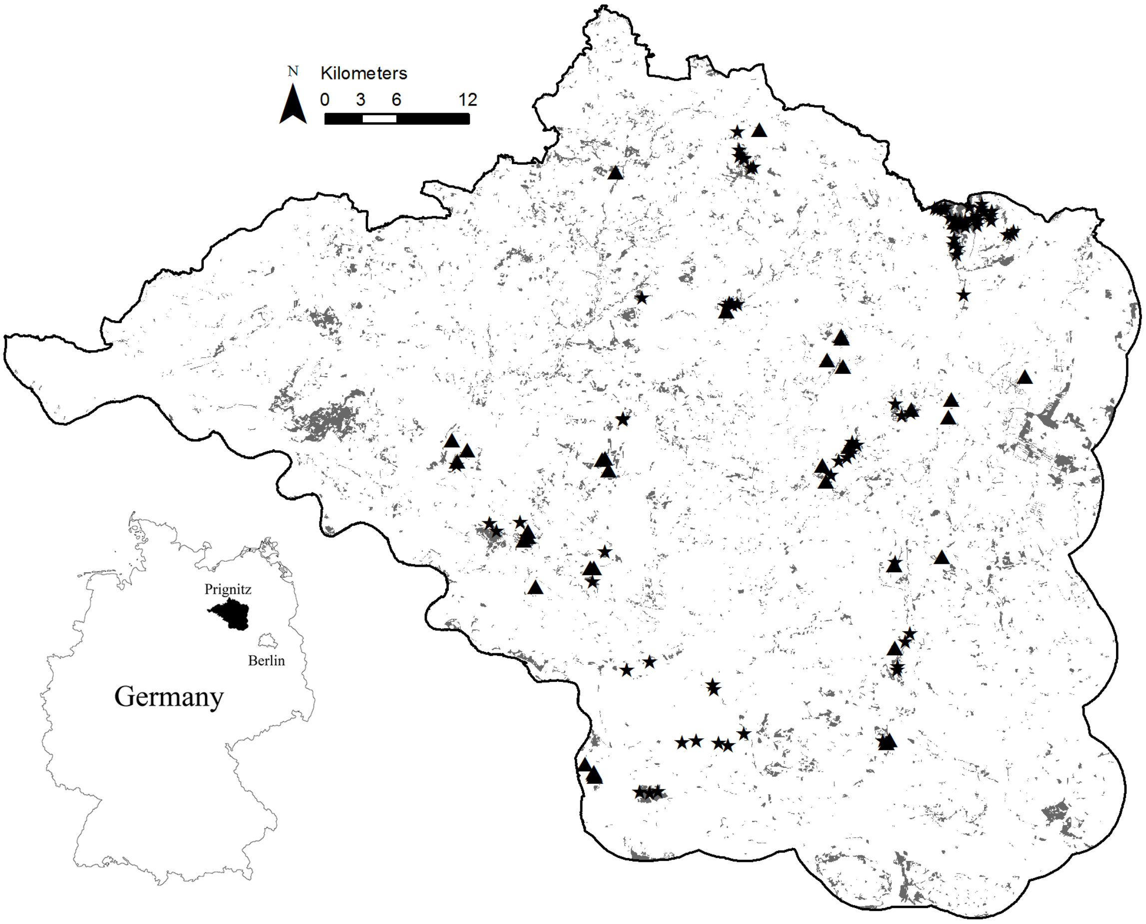

Fig. 4.1. Location of the study area in the Prignitz region in northeastern Germany, showing the distribution of the deciduous forests; stars = plots in ancient stands, triangles = plots in post-agricultural stands.

We analyzed and described the land-use history of the Prignitz region in more detail in previous studies (Kolk & Naaf 2015, Naaf & Kolk 2015). We found a massive loss in deciduous forest cover of approximately 92% over the period from 1780 to 2008. However, the main period of conversion was until 1880. Subsequently, the remaining patches became more fragmented, but the loss in area largely stopped (Wulf & Rujner 2011, Kolk & Naaf 2015). The ancient forest remnants constitute one third of the current deciduous forest cover. Despite the massive forest area loss and fragmentation, afforestation with deciduous tree species has occurred on former agricultural land, mainly until the beginning of the 20th century (Wulf 2004 b). At present, such forests constitute two thirds of the deciduous forest cover. The forest distribution in the second half of the 20th century remained largely constant (IFS 1960, Wulf 2004 b).

Relocation and plot selection

During the 1950s and early 1960s (hereafter, 1960), the regional forest authorities conducted a thorough survey of the site conditions and vegetation in all state-owned forests of the Prignitz region. The surveyors dug more than 2000 pits to investigate soil layer structure and soil moisture (IFS 1960). Soil chemistry was not analyzed except for very few selected pits that not conformed to the selection criteria for our resurvey (see below). The soil pits had a size of ca. 1 × 2 m and the soil material was stored directly besides the pit, i.e. the pit area had a maximum size of approximately 3 × 3 m. Either during the soil survey or directly afterwards, the surveyors recorded all tree species as well as all vascular plants and epigeic mosses in the shrub and herb layers in a 20 × 20 m^2 plot around each soil pit (IFS 1960).

From the pool of 2000 plots, we preselected plots that consisted mainly of native deciduous tree species and with a stand stage beyond the pole wood stage for relocation (196 plots). After relocation we found 119 plots to be suitable for a resurvey. For all 119 plots either the actual pit was found (79 plots) or the location of the pit was found somewhat accurately (<30 m) with the help of distance information from provided hand sketches and by comparing the tree species composition (40 plots). Eighty-three plots were located in ancient forest stands, and 36 plots were situated in post-agricultural forest stands. The remaining 77 plots were not selected for the following reasons: a) For 29 plots the pit was found but the vegetation was strongly disturbed (e.g. large canopy gaps, deep trails or original stand entirely replaced); b) for 12 plots the pit itself or an indication for the position of the pit was not found at all c) for 36 plots the pit location was not searched in detail because the stand was obviously not suitable for a resurvey (e.g., clear-cut area, purely coniferous stands, area not accessible).

The studied forests cover a broad range of environmental conditions and corresponding forest types, ranging from stands dominated by *Alnus glutinosa* and *Fraxinus excelsior* on moist soils to mesic stands with *Carpinus betulus* or *Fagus sylvatica* and stands dominated by *Quercus robur* on dry, sandy soils (Fig. 4.2). We chose to keep all of the plots and not to select a specific forest type, which would have resulted in too few plots. To be able to compare the development of species richness between ancient and post-agricultural stands, the environmental conditions need to be tested for differences in their mean and variability. This is particularly important, as our design is unbalanced, and the range of site conditions covered by the smaller group of post-agricultural forest stands could be smaller only by chance. We compared the environmental conditions in terms of the light availability and soil conditions. For this purpose, we took hemispherical photos under overcast conditions in the summer of 2014 using the HemiView system (DeltaT Devices, Burwell, UK) to determine the proportion of visible sky (‘VisSky’) above the plots (detailed methodology in

Appendix 4.1). To assess the soil conditions, we measured the soil water content in the topsoil in % vol. using a time-domain reflectometry field probe (TDR); twelve measurements were collected per plot at a depth of 0-10 cm in April 2013 and April 2014, and the arithmetic mean of these values was calculated. We further collected and pooled eight soil samples per plot (0-10 cm depth) in September 2014 and determined the total carbon, total nitrogen, phosphorus, potassium, magnesium and calcium contents and the pH($CaCl_2$) in the laboratory and calculated the C/N ratio (detailed methodology in Appendix 4.1).

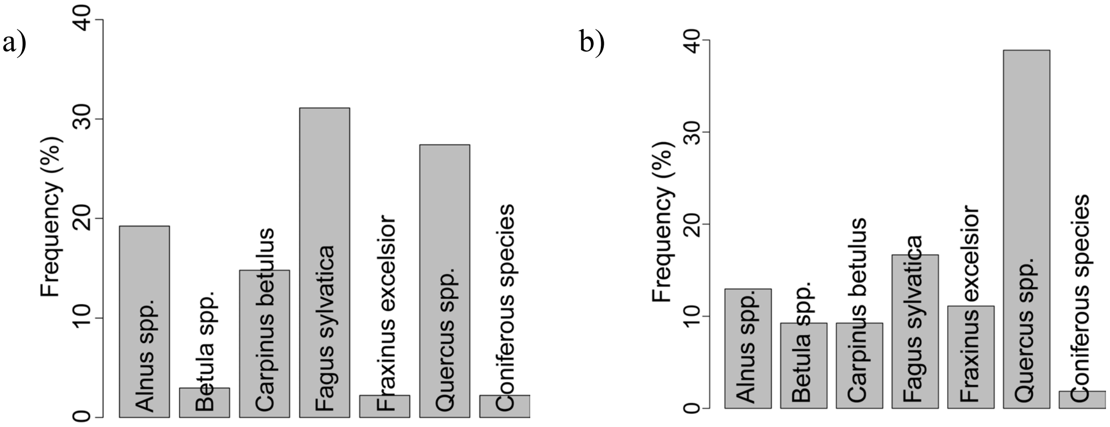

Fig. 4.2. Distribution of dominant tree species (here defined as species with more than 15% cover in the plots) in terms of their percent share in ancient plots (a) and post-agricultural plots (b).

We tested for differences between the ancient and post-agricultural stands in terms of their mean, minimum, maximum and variance using permutation tests (Manly 2007) with the t-value, minimum, maximum and F-value, respectively, as the test statistics and 1000 permutations. The soil variables (soil moisture, Ca, Mg, K, N_{TOTAL}, P, C_{TOTAL}, pH, and C/N ratio) were log-transformed and aggregated using a principal component analysis (PCA). We used the first three axes for the analysis, which represent 88.0% of the total variance. The first PCA axis (PCA_{FERT}) represented soil fertility, uniting Ca, Mg, K, N_{TOTAL} and C_{TOTAL} (48.8% of the total variance), the second axis (PCA_{ACID}) mainly represented acidity (C/N ratio and negative pH value, 30.4% of the total variance), and the third axis (PCA_{PHOS}) represented the phosphorous content, explaining 8.8% of the total variance. We conducted the tests by first including all 119 plots and then subsequently excluding a single plot from either the ancient or post-agricultural group that had the lowest minimum or the highest maximum in the environmental variable that was the most significantly different. We then repeated the tests with the reduced dataset until there were no more significant differences between the selected environmental variables at a $\alpha \leq 0.10$ level. In the end, two plots from the ancient forest group, those with highest values in PCA-Axis 3 (i.e. highest phosphorous content) were removed so that 36 plots in the post-agricultural stands and 81 plots in the ancient stands remained. The means, minima, maxima and standard deviations of this dataset are given in Table 4.1.

Vegetation resurvey

In 1960, the species were recorded once in each plot between mid-May and mid-October. We resurveyed species composition in the plots at a similar phenological state as in the original survey by including a correction for the earlier beginning of the growing season in 2014 compared with 1960 (Walther et al. 2002) with an analysis of cumulative degree hours (details in Appendix 4.1). Between April and July, the vegetation ran between 6 and 30 days ahead of 1960. The resurvey date was adapted to this shift. For practical reasons the plots were not always visited in the same order as in the original survey and not always on the exact corresponding day, but still at a comparable phenological state. Plots that had been initially surveyed in October were resurveyed already in late summer in 2014. In addition, we checked for the persistence of species that are likely to be no longer visible in autumn in October 2014. Of the doubtful occurrences, 85% could still be verified, although sometimes with lower cover, i.e. in terms of presence-absence the autumn and summer aspects of the two different recording periods were largely comparable.

Identically to the initial survey in 1960, we used a plot size of 400 m^2 and recorded all vascular plants and epigeic mosses in the herb layer but not those growing in or directly beside the remnant of the soil pit. We excluded the juveniles and saplings of trees because these were not systematically sampled in 1960. We further excluded very early spring ephemerals (*Gagea* spp.; *Anemone ranunculoides*) as these were mostly missed even by the surveys originally done in (later) spring.

Table 4.1. Comparison of means, minima, maxima and standard deviations of light availability and soil conditions between ancient (ANC) and post-agricultural (PA) plots.

Environmental variable	Mean with standard error		Minimum		Maximum		Standard deviation with standard error	
	ANC	PA	ANC	PA	ANC	PA	ANC	PA
VisSky[a]	0.09±0.01	0.11±0.01	0.03	0.04	0.28	0.25	0.04±0.00	0.04±0.00
PCA_{FERT}[b]	0.09±0.25	-0.20±0.29	-3.49	-2.82	6.29	3.98	2.25±0.18	1.79±0.21
PCA_{ACID}[c]	-0.03±0.18	0.08±0.29	-3.30	-4.69	3.31	3.61	1.61±0.13	1.77±0.21
PCA_{PHOS}[d]	0.07±0.09	-0.15±0.16	-1.38	-14.07	2.63	1.70	0.84±0.07	0.98±0.11

[a] Proportion of visible sky (light availablility), [b] PCA axis 1 (soil fertility), [c] PCA axis 2 (soil acidity), [d] PCA axis 3 (soil phosphorous content), for explanations see Material & Methods section "Relocation and plot selection"

Data analysis

We tested for changes in the species richness of all herb-layer plants and forest specialists, i.e., species that belong to category 1.1 (‘largely restricted to closed forests’) of the forest plant species list of Schmidt et al. (2011) and for changes in the richness of (regional) ancient forest indicator species. Ancient forest indicator species represent species that predominantly occur in ancient stands in the study area. These were determined from the species distribution data from our previous investigations in the study area (Kolk & Naaf 2015, Naaf & Kolk 2015) (details in Appendix 4.1). To test whether species richness became more similar between the ancient and post-agricultural stands over time, we used generalized linear mixed models (GLMM) with land-use history (ancient vs. post-agricultural), year (1960 vs. 2014) and their interaction as the fixed factors. For changes in the richness of all species, we used the lme function in the nlme package in R (Pinheiro et al. 2015) under the assumption of a Gaussian error distribution (identity link). We used a linear model with Gaussian error distribution because species richness approximately followed a normal distribution and using a Poisson error distribution indicated overdispersion due to the high variation in species numbers. For changes in the species richness of forest specialists and ancient forest indicator species, we used the glmer function in the lme4 package in R (Bates et al. 2015) with a Poisson error distribution (log link).

Because each plot was included twice, i.e., in 1960 and 2014, we used plot identity as a random effect in all models. We further included patch identity (identity of the forest patch in which a plot is located) as a second random effect to account for possible spatial autocorrelation. Subsequently, we compared the models with and without patch identity using likelihood-ratio tests and selected the best and most parsimonious model. We then checked graphically for homoscedasticity and the normality of the residuals and for the normality of the random effects.

To test whether the magnitude of the increase in species richness in post-agricultural stands and, for comparison, in ancient stands, was dependent on the connectivity to adjacent ancient forest patches, we first calculated the absolute difference (Δ) in species numbers for the specialists and the ancient forest indicator species from 1960 to 2014 for the ancient and post-agricultural plots and modelled this Δ as a function of patch connectivity and land-use history (ancient vs. post-agricultural) with a linear mixed model (lme function in the nlme package in R (Pinheiro et al. 2015)). Patch identity was included as a random effect in this model. The patch connectivity was calculated with Hanski’s incidence function model (Hanski 1994): $C_i = \sum_{j \neq i} A_j^b \cdot e^{-\alpha d_{ij}}$,

where C_i is the connectivity of patch i, A_j is the habitat area of patch j and d_{ij} is the edge-to-edge distance between those patches. Alpha (α) and b are calibration parameters and were set to 0.002 m^{-1} and 0.5 in accordance with Moilanen &

Nieminen (2002) and Naaf & Kolk (2015). We calculated distances within a radius of 5000 m and only included forest patches that may act as potential source populations, i.e., only deciduous forest parts and mixed forest parts that have a higher share of deciduous tree species. We further only included patches that exhibit at least a 1000 m^2-share of ancient forest. The patch connectivity measure was sqrt-transformed and scaled to mean = 0 and sd = 1 for the statistical modelling.

Finally, we analyzed changes in the occurrence of single species, i.e., we identified winner and loser species. This information will be used as supporting information to interpret the overall changes in species richness. We modelled changes in the occurrence of single species with the glmer function (Bates et al. 2015) with a binomial error distribution (logit link), using the Laplace approximation, Wald Z-test and BOBYQA algorithm (details in Appendix 4.1). We only selected species with more than ten occurrences in either 1960 or 2014. All statistical analyses were conducted using R, version 3.1.2 (R Core Team 2014).

4.4 Results

The overall species richness increased significantly from 1960 to 2014 in both ancient and post-agricultural stands. The interaction with land-use history was not significant (Fig. 4.3a). The same overall increase was apparent in the group of forest specialists (Fig. 4.3b); however, here, species richness increased significantly more in post-agricultural stands than in ancient stands (Fig. 4.3b). The interaction term was not significant for the changes in the richness of ancient forest indicator species (Fig. 4.3c). However, while the mean number of ancient forest indicator species in the ancient stands remained ± constant, the number of species increased significantly (but only just) in post-agricultural stands (Fig. 4.3c). Additional information on model coefficients and included random effects are provided in Appendix 4.2.

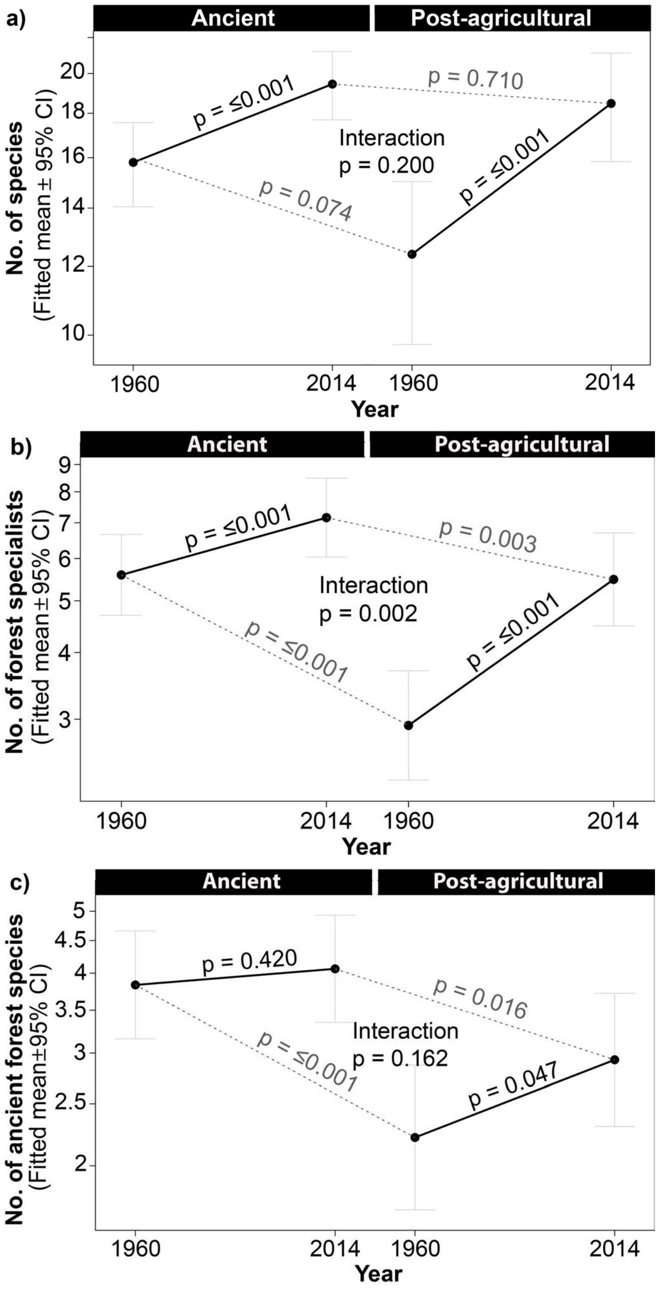

Fig. 4.3. Changes in the richness of all species (a), forest specialists (b) and ancient forest indicator species (c) in the herb layer of the plots in the ancient and post-agricultural stands between 1960 and 2014. The p-values derived from the generalized linear mixed models are presented.

Table 4.2. Model results of the differences in species richness from 1960 to 2014 dependent on land-use history (ancient vs. post-agricultural) and connectivity for forest specialists and ancient forest indicator species. Intercept and the coefficient of connectivity were tested against zero with a t-test, separately for ancient and post-agricultural stands. The difference between the two groups was also tested against zero with another t-test.

	Δ specialists			Δ ancient forest indicator species		
	Coefficient	t-value	p-value	Coefficient	t-value	p-value
Intercept						
Ancient	2.58	4.42	≤0.001	0.81	1.85	0.068
Post-agricultural	4.36	4.10	≤0.001	0.91	1.30	0.197
Ancient vs. post-agricultural	1.78	1.56	0.123	0.10	0.14	0.887
Connectivity						
Ancient	0.27	0.43	0.670	0.43	0.99	0.327
Post-agricultural	1.93	1.78	0.079	-0.09	-0.13	0.895
Ancient vs. post-agricultural	1.66	1.37	0.173	-0.52	-0.67	0.506

Patch connectivity had no significant effect on the magnitude of species richness changes at the $\alpha = 0.05$ level (Table 4.2). However, patch connectivity was almost significant in the group of specialists in post-agricultural stands, with p=0.079, whereas connectivity was far from being significant in ancient stands, with p=0.670 (Table 4.2, Fig. 4.4). Patch connectivity was not significant for changes in number of ancient forest indicator species (Table 4.2).

Among the 36 winners, 20 species were overall winners, 10 species were winners only in ancient stands and six species were winners only in post-agricultural stands; of these, three species were completely new (Table 4.3). Among the overall winners, only one species (*Carex pilulifera*) was an ancient forest indicator species. In contrast, four of the six species that were winners only in post-agricultural stands were ancient forest indicator species. Seven out of the nine loser species were losers only in the ancient stands, while one loser species was an overall loser and the other species was a loser only in the post-agricultural stands (Table 4.3).

Table 4.3. (Next page) List of species with either a significant increase or decrease in their probability of occurrence in the ancient and post-agricultural stands from 1960 to 2014. Given separately are the absolute and relative frequencies in 1960 and changes in frequencies (in brackets) for ancient and post-agricultural plots with significance indicators and the p-value of the interaction term.

Species	Ancient stands		Post-agricultural stands		Interaction	Characteristics	
	Frequency	Relative frequency	Frequency	Relative frequency	p-value	AFS[a]	Forest affinity[b]
Overall winners							
Agrostis capillaris	3(+6)**	3.7(+200%)	2(+6)***	5.6(+300%)	0.480	.	.
Athyrium filix-femina	29(+12)*	35.8(+41%)	2(+8)*	5.6(+400%)	0.148	.	SPEC
Atrichum undulatum	8(+13)***	9.9(+163%)	2(+3)*	5.6(+150%)	0.556	.	.
Brachypodium sylvaticum	13(+2)*	16.0(+15%)	1(+4)***	2.8(+400%)	$\leq$0.001	.	SPEC
Carex acutiformis	7(+4)***	8.6(+57%)	2(+3)***	5.6(+150%)	0.861	.	.
Carex elongata	4(+3)**	4.9(+75%)	1(+3)*	2.8(+300%)	0.857	.	SPEC
Glechoma hederacea	23(+10)*	28.4(+43%)	5(+7)***	13.9(+140%)	0.053	.	.
Hedera helix	3(+13)***	3.7(+433%)	3(+11)***	8.3(+367%)	0.465	.	SPEC
Impatiens parviflora	6(+45)***	7.4(+750%)	1(+19)***	2.8(+1900%)	$\leq$0.001	.	SPEC
Juncus effusus	2(+8)*	2.5(+400%)	3(+5)***	8.3(+167%)	0.944	.	.
Lysimachia vulgaris	9(+7)***	11.1(+78%)	4(+2)*	11.1(+50%)	0.588	.	.
Molinia caerulea	8(+4)*	9.9(+50%)	4(+2)*	11.1(+50%)	0.508	.	.
Poa trivialis	6(+15)***	7.4(+250%)	5(+4)*	13.9(+80%)	0.042	.	.
Polytrichum formosum	11(+10)*	13.6(+91%)	1(+5)*	2.8(+500%)	0.242	.	.
Rubus fruticosus agg.	12(+11)*	14.2(+92%)	7(+8)*	19.4(+114%)	0.645	.	.
Rumex sanguineus	2(+6)$^{N/A}$	2.5(+300%)	0(+2)$^{N/A}$	#	N/A	.	SPEC
Carex pilulifera	12(+6)$^{N/A}$	14.8(+50%)	0(+7)$^{N/A}$	#	N/A	AFS	.
Circaea lutetiana	13(+10)$^{N/A}$	16.0(+77%)	0(+6)$^{N/A}$	#	N/A	.	SPEC
Dicranum scoparium	0(+6)$^{N/A}$	#	2(+2)$^{N/A}$	5.6(+100%)	N/A	.	.
Dryopteris filix-mas	9(+9)$^{N/A}$	11.1(+100%	0(+5)$^{N/A}$	#	N/A	.	SPEC
Winners (ancient)							
Anemone nemorosa	26(+13)*	32.1(+50%)	2(+1)$^{n.s.}$	5.6(+50%)	0.418	AFS	SPEC
Calamagrostis epigeios	1(+11)***	1.2(+1100%	4(+1)$^{n.s.}$	11.1(+25%)	0.002	.	.
Carex remota	1(+10)***	1.2(+1000%	1(+1)$^{n.s.}$	2.8(+100%)	$\leq$0.001	AFS	SPEC
Cirsium oleraceum	6(+8)***	7.4(+133%)	7(-2)$^{n.s.}$	19.4(-29%)	0.004	.	.
Dryopteris carthusiana	21(+15)*	25.9(+71%)	4(+4)$^{n.s.}$	11.1(+100%)	0.658	.	.
Galium palustre	3(+4)*	3.7(+133%)	2(+2)$^{n.s.}$	5.6(+100%)	0.600	.	.
Humulus lupulus	5(+4)*	6.2(+80%)	5(+3)$^{n.s.}$	13.9(+60%)	0.733	.	.
Moehringia trinervia	13(+15)*	16.0(+115%	13(+6)$^{n.s.}$	36.1(+46%)	0.626	.	SPEC
Polygonatum multiflorum	1(+9)***	13.6(+82%)	4(+2)$^{n.s.}$	11.1(+50%)	0.168	.	SPEC
Stachys sylvatica	16(+7)*	19.8(+44%)	4(+3)$^{n.s.}$	11.1(+75%)	0.743	.	SPEC
Winners (Post-agricultural)							
Agrostis stolonifera	8(-3)$^{n.s.}$	9.9(-38%)	1(+4)*	2.8(+400%)	0.009	.	.
Geranium robertianum	19(-4)$^{n.s.}$	23.5(-21%)	4(+2)***	11.1(+50%)	0.269	.	.
Luzula pilosa	24(-2)$^{n.s.}$	29.6(-8%)	3(+6)***	8.3(+200%)	$\leq$0.001	AFS	SPEC
Maianthemum bifolium	26(+6)$^{n.s.}$	32.1(+23%)	3(+6)***	8.3(+200%)	0.006	AFS	SPEC
Milium effusum	44(+7)$^{n.s.}$	54.3(+16%)	5(+6)*	13.9(+120%)	0.308	AFS	SPEC
Scrophularia nodosa	3(+0)$^{n.s.}$	3.7(±0%)	1(+6)***	2.8(+600%)	0.297	AFS	.
Overall losers							
Ajuga reptans	14(-7)*	17.3(-50%)	8(-6)***	22.2(-75%)	0.202	AFS	.
Losers (ancient)							
Deschampsia cespitosa	67(-17)**	82.7(-25%)	15(+0)$^{n.s.}$	41.7(±0%)	0.027	.	.
Deschampsia flexuosa	35(-15)**	43.2(-43%)	15(+0)$^{n.s.}$	41.7(±0%)	0.063	.	.
Festuca gigantea	38(-16)**	46.9(-42%)	9(+4)$^{n.s.}$	25.0(+44%)	0.011	.	SPEC
Mycelis muralis	13(-8)*	16.0(-62%)	3(+2)$^{n.s.}$	8.3(+67%)	0.012	.	.
Poa nemoralis	22(-19)***	27.2(-86%)	5(-1)$^{n.s.}$	13.9(-20%)	$\leq$0.001	.	SPEC
Vaccinium myrtillus	12(-5)**	14.8(-46%)	4(-1)$^{n.s.}$	11.1(-25%)	0.166	AFS	.
Veronica chamaedrys	15(-13)***	18.8(-87%)	5(+0)$^{n.s.}$	13.9(±0%)	0.002	AFS	.
Losers (Post-agricultural)							
Veronica officinalis	6(-1)$^{n.s.}$	7.4(-17%)	4(-2)***	11.1(-50%)	0.079	.	.

a AFS = Ancient forest indicator species

b Affinity to forest based on data from Schmidt et al. 2011, SPEC = specialist (category 1.1 ('largely restricted to closed forests'))

* Significance: $0.01 < P \leq 0.05$. ** Significance: $0.001 < P \leq 0.01$. *** Significance: $P \leq 0.001$. N/A; #: Statistical model/part of model was not applicable because species was not present in 1960.

4.5 Discussion

Our results revealed that the richness of forest specialist plant species converged between ancient and post-agricultural stands over the last five decades due to a higher increase in forest specialists in post-agricultural stands. Under consideration of our former studies (Naaf & Kolk 2015, 2016), we are therefore able to quantitatively verify a theoretically predicted payment of a colonization credit in post-agricultural forest plant communities for the first time using a temporal approach. Although the effect of patch connectivity was not significant in any of the species richness models, we have reason to believe that patch connectivity plays an important role in the colonization of post-agricultural forests by forest plant species and for the payment of the colonization credit.

Overall increase in species richness

Species richness did not only increase in the post-agricultural stands but also overall from 1960 to 2014. We observed this increase in all three species groups, although the differences were not significant for the ancient forest indicator species in the ancient forest stands. A first suggestion for the reason of the overall increase could be that the investigators in 1960 were less accurate or less skilled in plant identification and therefore recorded fewer species. Although we cannot fully exclude this possibility, it cannot account for the observed pattern alone. Many winner species are rather common and easy to recognize in the field, for example, *Athyrium filix-femina, Carex sylvatica, Glechoma hederacea, Hedera helix* and *Polygonatum multiflorum*. Another possible factor might be a general observer bias due to the repeated sampling. In such cases, more species may be found because the species that occurred in the first survey are already known and additional species are unintentionally searched for more intensively (Lepš & Hadincová 1992). While we cannot falsify or quantify a possible observer bias, an increase in plant species richness in temperate forests has by no means been generally found in resurvey studies (Bernhardt-Römermann et al. 2015).

We recently investigated the effect of recent environmental changes on changes in species richness in ancient forest stands of the Prignitz region (Naaf & Kolk 2016). We see these changing environmental conditions to be the main factor that led to the overall changes in species richness. While there were differences between the stands occurring on acidic and on base-rich soils, an overall trend toward increased shading and nutrient availability as well as a decrease in soil moisture was observed. This development has also been found in many other studies (Baeten et al. 2009 b, Keith et al. 2009, Verheyen et al. 2012) and is considered to be a main factor in temporal diversity changes in European forest plant communities, i.e., increases or decreases

(Bernhardt-Römermann et al. 2015). At first sight higher shading and lower soil moisture should lead to lower species richness (Ling 2003, Baeten et al. 2009 b, Vockenhuber et al. 2011). However, the situation in the Prignitz forests appears to be more complex (Naaf & Kolk 2016). On one hand, some light-demanding species may have decreased in occurrence due to increased shading, and indeed, the increase in species richness was stronger in sites with a less pronounced decrease in light availability (Naaf & Kolk 2016). On the other hand, there was an increase in mesophilic species on formerly wet sites, while the species adapted to wet conditions also persisted (Naaf & Kolk 2016). In addition to local environmental changes and interactions with the initial site conditions, the invasion of alien species, especially *Impatiens parviflora* and *Prunus serotina*, directly increased the herb layer species richness (Table 4.3; Naaf & Kolk 2016). It is important to note that while we only analyzed ancient forest stands in our previous study, the results are most likely also applicable to the post-agricultural stands, which exhibit environmental conditions comparable to those of ancient forest stands (Table 4.1 and Materials & Methods section 4.3).

Species richness increased more in post-agricultural stands

Despite the overall increase in species richness, we observed a significant convergence in forest specialist richness in ancient and post-agricultural stands, which cannot be explained by any observer bias or overall environmental changes. The significantly higher increase in forest specialists in post-agricultural stands and the fact that the richness of ancient forest indicator species only significantly increased in post-agricultural stands indicates that a part of the colonization credit in the post-agricultural stands has been paid since 1960. The winner / loser analysis (Table 4.3) revealed that several of the exclusive winners in the post-agricultural forest were ancient forest indicator species (four out of six). We see this as an indication that colonization by species from surrounding ancient forest stands was responsible for the reduction in the colonization credit in post-agricultural stands. In addition, immigration of ancient forest indicator species from nearby hedgerows may be a factor (McCollin et al. 2000, Petit et al. 2004). Our result is supported by Vellend (2003), who found that the amount of ancient forest cover loss influenced the recovery rate of species richness in post-agricultural forests. Further, Baeten et al. (2010) attribute the absence of a convergence in the species richness of ancient and post-agricultural forests to the dramatic loss of source populations of ancient forest indicator species, among other factors. While the importance of the total amount of surrounding forest habitat independent of the patch age should not be underestimated (see De Frenne et al. 2011), the distance to and the amount of ancient forest habitat seem to be very important in the recovery of species richness in post-agricultural forests (Peterken & Game 1984, Dzwonko & Loster 1992, Matlack 1994; Singleton et al. 2001, Flinn & Vellend 2005). This will be further addressed in the section after the next.

While it is likely that a reduction in the colonization credit in the post-agricultural stands led to the convergence of species richness, we found, however, that loser species were predominantly only losers in ancient stands (seven out of nine, Table 4.3). Ostensibly, the cause of this could be an extinction debt in the ancient stands that is still yet to be paid. However, we can largely exclude this: on one hand, we found the extinction debt to be paid by 2014 (Kolk & Naaf 2015) as well as found an overall increase in species richness in the ancient stands (Naaf & Kolk 2016, Fig. 4.3); on the other hand, many of the loser species (e.g., *Deschampsia cespitosa*, *Deschampsia flexuosa*, *Poa nemoralis*, *Vaccinium myrtillus*) are associated with soils with poor nutrient supply and suffered from the increasing nutrient availability in the Prignitz forests (Naaf & Kolk 2016). The fact that these species are only losers in ancient stands is rather a matter of the fact that these species have never been abundant in post-agricultural stands (e.g., *Mycelis muralis*, *Poa nemoralis*, *Vaccinium myrtillus*, *Veronica chamaedrys*, Table 4.3).

Differential development of environmental conditions

We assume that the overall increasing species richness can be attributed to more recent regional environmental changes (see section "Overall increase in species richness"), but this cannot explain the higher increase of forest specialists and ancient forest indicator species in post-agricultural stands. Different management might be a factor, but we have no indications of a different forest management in ancient and post-agricultural stands based on regional forest authorities and field experience.

With our study design, we aimed to keep differences in the environmental conditions between ancient and post-agricultural stands overall comparable. Further, in a previous study, Wulf (2004b) compared different soil chemistry parameters between ancient and post-agricultural forests in the same region. None of the chemistry parameters were significantly different between ancient and post-agricultural plots and soil chemistry parameters were similar to the values we measured in 2014. While this was largely the case for today's environmental conditions it could be possible that environmental conditions developed differently in post-agricultural forest stands than in ancient forest stands as a legacy of former land use. For instance, the plant available phosphorous may have decreased in post-agricultural stands (e.g. De Schrijver et al. 2012) or carbon and nitrogen contents may have increased (e.g. Thomaes et al. 2012) while they remained constant in ancient forest stands. Such a different development in soil chemistry could have led to different species richness development.

From the original survey we have few data on the environmental conditions in 1960 and therefore cannot track possible changes until today. However, post-agricultural forests were at least in a pole-wood-stage in 1960 and we know that most post-agricultural forests in the region were established before the beginning of the 20th century. Thus, they had some time to mature and to reduce soil phosphorous content and accumulate carbon and nitrogen. Furthermore, we previously found that the magnitude of the colonization credit in post-agricultural stands was independent from soil conditions of the patch (Naaf & Kolk 2015).

In sum, we conclude that for our studied forests, other than for the forests in the studies of Baeten et al. (2010) and Kokarēviča et al. (2016), environmental limitation (Verheyen et al. 2003 b, Baeten et al. 2009 b) seemed to play a minor role for the species richness differences between ancient and post-agricultural stands and that rather dispersal limitation has been responsible for the different species richness development.

Effect of patch configuration / connectivity

In our previous study on colonization credits (Naaf & Kolk 2015), we found that the colonization credit largely persisted, regardless of the forest patch age. Post-agricultural forests that were established between 1780 and 1880 exhibited a colonization credit that was similar to the colonization credit in stands that were established after 1880 because these were largely isolated. In the present study, however, post-agricultural stands were often situated directly adjacent to ancient stands. Flinn & Vellend (2005) and Flinn & Marks (2007) state that post-agricultural forests that are closer to ancient forests have a higher level of diversity. Forest specialists are often slow in colonizing newly established patches (Flinn & Vellend 2005, Orczewska 2009 b) and, depending on the degree of isolation (Brunet et al. 2011), it may take up to centuries until a patch is ‘fully’ colonized (Flinn & Vellend 2005). However, forest specialists are able to colonize adjacent stands much faster (Butaye et al. 2001, Brunet et al. 2012). Spatial configuration along with a higher age of the post-agricultural stands of the Prignitz could also be the reason why our main result differs from the findings of Baeten et al. (2010), who observed a decrease in species richness that was independent of land-use history, i.e., they found no payment of a colonization credit. Unfortunately, Baeten et al. (2010) provide no information on the spatial distribution of the forest stands they studied. We did this by including patch connectivity in the models for the differences in the numbers of forest specialists and ancient forest indicator species between 1960 and 2014 (Δ in species richness). In combination with our previous study (Naaf & Kolk 2015), we have observed indications of a positive effect of patch connectivity for the payment of the colonization credit, although the effect of patch connectivity was not significant at a α

≤ 0.05 level (p = 0.079) in the Δ in species richness models (Table 4.2, Fig. 4.4). We assume that this effect is in reality even more pronounced than it is represented by the statistical output because in our previous study (Naaf & Kolk 2015), we were able to show that the colonization credit (not the payment of the colonization credit) was lower in better connected post-agricultural stands. Therefore, it seems likely that the difference in species numbers was already small in 1960 in the best-connected post-agricultural stands, i.e., the additional increase in species richness after 1960 was comparably small. Another point could be that our connectivity measure overestimates the connectivity as it is perceived by the forest specialists because we included patches with a minimum ancient forest area of 1000 m^2. This area might be too small to act as a habitat for ancient forest indicator species. However it can be expected that ancient forest indicator species extend their population area to directly adjacent post-agricultural stands within a few decades (Jacquemyn et al. 2003, Brunet et al. 2012) and also very small forest patches can exhibit high numbers of forest specialists (Wulf & Kolk 2014). Finally, the fact that the connectivity effect hardly misses significance may be due to the relatively low number of observations (36 plots).

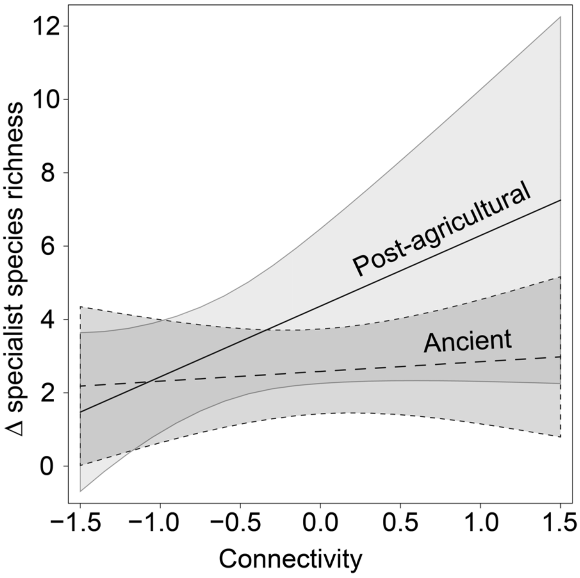

Fig. 4.4. Prediction of the potential gain in specialist species numbers (Δ species richness) from 1960 to 2014 dependent on the patch connectivity in ancient and in post-agricultural stands. The patch connectivity measure has been sqrt-transformed and scaled to mean = 0 and sd = 1; grey shades are showing the 95% confidence intervals.

While we can assume that there is an effect of patch connectivity on the number of specialists that colonize post-agricultural stands, there was no effect on the magnitude of colonization by ancient forest indicator species (Table 4.2). It is unlikely that the colonization of post-agricultural stands by ancient forest indicator species is not dependent on the distance to and the amount of ancient forest habitat around the post-agricultural stands. One explanation could be the relatively low numbers of ancient forest indicator species in the plots. Such low numbers can only lead to subtle changes from 1960 to 2014. Those small changes may be dependent on patch connectivity but a larger number of samples would be needed to statistically verify the effect. In addition, the result becomes clearer when considering the fact that the number of ancient forest indicator species did not always increase but also decreased. The reason for the decrease is contingent on changes in the environmental conditions and their interactions with the initial site conditions (Naaf & Kolk 2016). Further investigations of the interactions between environmental changes and legacy effects of former land use on a large time-scale could provide more insight into the crucial factors of long-term extinction and immigration processes (Perring et al. 2016).

4.6 Conclusions

We have shown a recovery of the herb-layer species richness from agricultural land use over the last five decades, thus colonization credits in post-agricultural forests can be paid off. This recovery resulted from the colonization of forest specialists and ancient forest indicator species. In consideration that many areas that are now stocked with ancient forest were likely also under agricultural land use at some point in historic times, for example during the medieval periods (Williams 2000, Kaplan et al. 2009, Etienne et al. 2013), the observed payment of the colonization credit implies that post-agricultural forests may become ancient-forest-like in terms of species richness and -composition in the future. Our result highlights the importance of land-use history as an influencing factor of recent species richness changes, although the major land cover changes had already occurred in the 18th and 19th century. Neglecting land-use history in resurvey studies may lead to incorrect conclusions regarding the “real” importance of recent environmental drivers. Our study shows that the interactions between recent environmental changes and land-use legacies seem to play an especially important role in current forest plant community assemblages and species richness development and should be a focus of forthcoming studies.

4.7 Acknowledgements

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Chapter 5: Initial site conditions and interactions between multiple drivers determine herb-layer changes over five decades in temperate forests

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5.1 Abstract

The resurvey of forest plant communities some decades after the first survey has become a valued approach to determine long-term responses in species diversity and composition to various anthropogenic environmental drivers, such as management changes, excess nitrogen deposition, or overabundant deer populations. However, little is known about the effects of initial site conditions, such as soil acidity or soil moisture, on these long-term responses and how multiple drivers interact with each other in affecting herb layer diversity and composition. Moreover, the extent to which local changes in canopy cover and composition may mimic or counterbalance effects of regional or global drivers is largely unexplored. Here, we resurveyed herb layer vegetation plots in northeastern Germany after more than five decades. Our main objectives were (1) to determine the effects of initial site conditions, here soil pH buffer range, on herb layer and environmental changes; (2) to disentangle the effects of presumed regional and global drivers from local changes in canopy density and composition; and (3) to identify interactions between environmental drivers in affecting species diversity and composition. We observed significant changes in species diversity and environmental conditions, mostly in dependence on the initial site conditions. Species richness increased only at moderately acidic to base-rich sites, while floristic distinctiveness (beta diversity) generally decreased but decreased significantly stronger on base-rich than on acidic sites. The indicated environmental changes comprised increased shading (particularly on acidic sites), a decrease in soil moisture, acidification (only on initially moderately acidic to base-rich sites), eutrophication (only on acidic sites), an increase in browsing pressure and more continental climatic conditions, probably in terms of increased summer drought (on well-drained sites only). The presumed regional/global environmental changes could not be explained by local changes in canopy composition. The herb layer responses were affected by several important interactions among the drivers. The floristic homogenization was more pronounced the stronger the eutrophication signal, but only on (moderately) acidic sites, while the homogenization occurred independent of any eutrophication on base-rich sites. The environmental change indicators for soil acidity and nitrogen availability showed opposing effects on temporal species turnover and a positive interaction, pointing to atmospheric deposition as the most important driver. Our study demonstrates that both initial site conditions and interactions between different drivers should be taken into account in resurvey studies to broaden our understanding of plant community responses to environmental changes.

5.2 Abbreviations

AlFe	aluminum and aluminum-iron buffer range
BA	browsing attractiveness
BETA	floristic distinctiveness (beta diversity)
CatEx	cation-exchange buffer range
FC	floristic continentality
FT	floristic temperature
LQ	litter quality
mF, mR, mN	mean Ellenberg values for moisture (F), soil reaction (R) and nutrient availability (N)
RR	log response ratio
SCA	shade-casting ability
SiliCar	silicate and carbonate buffer range
SPEC	forest specialist richness
SR	species richness

5.3 Introduction

An increasing awareness that anthropogenic environmental changes affect biodiversity and species distributions worldwide (Pereira et al. 2012) has stimulated interest among ecologists in observing and documenting species shifts and in relating them to drivers of environmental change (Dornelas et al. 2014, Grytnes et al. 2014). Resurveys of biological communities after several years or decades before have become a valued approach to identify species extirpations, immigrations and turnover (Vellend et al. 2013). Resurveys after several decades are particularly relevant for communities with long-lived, slow-responding species, such as the herb layer of temperate forests (Bernhardt-Römermann et al. 2015). During the past decade, the number of resurvey studies in temperate forests has increased substantially. According to these studies, the most important drivers for changes in herb-layer diversity and composition in temperate forests are (a) changes in canopy cover and composition due to changes in management or succession (e.g., Amatangelo et al. 2011, Durak 2012, Kopecký et al.

2013, Van Calster et al. 2008); (b) atmospheric deposition of acidifying and eutrophicating substances (e.g., Dirnböck et al. 2014, Jantsch et al. 2013, Reinecke et al. 2014, Sebesta et al. 2011); (c) changes in deer densities that lead to an altered browsing pressure on palatable plants (e.g., Bernhardt-Römermann et al. 2015, Hédl et al. 2010, Jenkins et al. 2014, Wiegmann & Waller 2006); and (d) the invasion of exotic species (e.g., Johnson et al. 2014, Lysik 2008, Rooney & Rogers 2011). Species shifts in response to climate warming have also been observed, particularly in terms of elevational shifts in mountain or subalpine forests (Bai et al. 2011, Lenoir et al. 2010). In lowland forests, a general trend towards 'thermophilization' seems to exist (De Frenne et al. 2013), although this signal is often weak or not significant yet (Bertrand et al. 2011, Jantsch et al. 2013) and is masked or even reversed by changes in microclimate (De Frenne et al. 2013).

Meta-analyses across resurvey studies from the whole temperate forest biome in Europe have revealed some general trends in environmental changes and associated herb layer responses but also substantial differences among studies and regions (Bernhardt-Römermann et al. 2015, Dirnböck et al. 2014, Verheyen et al. 2012). For instance, there is a general trend towards a denser canopy, resulting from the abandonment of traditional management practices such as coppicing and cattle grazing and the conversion into high forests with less intensive management (Kopecký et al. 2013, Verheyen et al. 2012). However, several resurvey studies also report an increase in canopy openness due to natural and anthropogenic disturbances (e.g., Durak 2010, Smart et al. 2014, Von Oheimb & Brunet 2007). There is also a general trend towards eutrophication, i.e., an increased frequency and abundance of competitive, nitrogen-demanding species (Bernhardt-Römermann et al. 2015, Verheyen et al. 2012). However, the eutrophication signal was not found in all studies and regions despite substantial amounts of accumulated nitrogen deposition (e.g., Cornelis et al. 2007, Hédl 2004, Naaf & Wulf 2011).

The reasons for the different outcomes among resurvey studies are manifold. One important factor that determines vegetation response to environmental changes is initial site conditions, such as soil nutrient status (Reinecke et al. 2014), soil moisture (Woods et al. 2012) or canopy structure and composition (Amatangelo et al. 2011). However, only few studies so far have directly analyzed the effect of initial site conditions in their resurvey. For instance, Verstraeten et al. (2013) found significant temporal changes in species composition and diversity in forest stands on neutral sites but not on acid sites. However, it remained unclear whether this difference was due to ecological reasons or due to sample size differences (27 vs. 16).

The outcome of a resurvey may also depend on the coaction of several drivers. To disentangle the effects of different simultaneously acting drivers is often difficult (Naaf & Wulf 2011, Wiegmann & Waller 2006). In particular, it is necessary to separate the effects of regional/global drivers from local changes in canopy structure and composition (Bernhardt-Römermann et al. 2015). For instance, the eutrophication signal is often attributed to atmospheric nitrogen deposition but may often be explained by shifts in tree species composition and associated changes in light regime and litter quality (Verheyen et al. 2012). Shifts in tree species composition may also change the microclimate within a forest stand and produce either cooler or warmer conditions that may counteract or mimic macroclimate warming (De Frenne et al. 2013, Stevens et al. 2015). Additionally, a denser canopy could lead to the loss of light-demanding species. If these species are at the same time acid-tolerant the observed species losses could erroneously be interpreted as response to a reduced soil acidity (Diekmann 2003). A clear distinction between local and regional effects has rarely been achieved in resurvey studies so far.

Moreover, drivers may interact with each other, i.e., the effect of one driver may depend on the magnitude or direction of another driver. For instance, a general perception is that excess nitrogen deposition leads to a loss of species diversity (Bobbink et al. 2010, Gilliam 2006). Empirical evidence from European temperate forests showed, however, that the competitive exclusion of N-efficient forest specialists by nitrophilous generalists is temporarily impeded by a gradual canopy closure (Verheyen et al. 2012). Thus, one interaction could be, for instance, that eutrophication leads to a dominance of nitrophilous species at the expense of N-efficient species, but only at sites, where canopy density did not increase. Although several resurvey studies consider several of the drivers mentioned above, their interactions in driving changes in species diversity and composition have never been analyzed explicitly.

Here, we resurveyed herb layer vegetation plots more than five decades after the first survey. The plots are scattered across the Prignitz region in northeastern Germany, which has experienced several regional to global environmental changes, including the lowering of the groundwater table, increased deer abundances, atmospheric deposition of sulfur and nitrogen and climate change. The plots cover a broad range of soil conditions in terms of acidity and moisture.

Our main objectives were, first, to determine the effects of initial site conditions on (a) changes in species diversity and composition and (b) changes in environmental conditions; second, to disentangle the effects of presumed regional and global drivers from local changes in canopy density and composition; and third, to identify interactions between environmental drivers in affecting species diversity and composition.

We expected, for instance, to find more pronounced changes in species diversity on the initially most base-rich and at the same time most species-rich sites. We hypothesized stronger eutrophication effects on initially acidic, nutrient-poor sites; stronger acidification effects on poorly buffered soils; and a stronger drainage effect on initially wet sites. We also expected that presumed global change signals, such as thermophilization or eutrophication would partly result from local changes in tree species composition. Finally, we anticipated significant interactions among the drivers, e.g., between nitrogen deposition and changes in canopy density.

5.4 Materials and Methods

Study area and regional environmental changes

We conducted the study in the Prignitz region (52°45'N – 53°22'N, 11°47'E – 12°37'E; 2800 km²) in north-eastern Germany (Appendix 5.1). The climate is suboceanic to subcontinental, which is reflected by the common occurrence of both (sub-)oceanic and (sub-)continental floristic elements (Fischer 1970). The mean annual temperature is 9.1°C with monthly temperatures ranging between 0.5°C in the coldest and 18.5°C in the warmest month. Mean annual precipitation ranges between 533 mm and 676 mm (reference period 1981-2010; DWD 2014). The terrain is generally flat or undulating, with elevations ranging from 10 m a.s.l. to local peaks of 150 m a.s.l. The prevalent geological substrates are sandy to loamy glacial deposits as well as glacio-fluvial sands (LBGR 2008, 2009). From these, mostly cambisols developed, often combined with gleysols and stagnosols (LBGR 2007). The landscape is intensely cultivated for agriculture. The forest cover amounts to 26%, of which approximately four-fifth are allochthonous pine stands. Deciduous forest occurs mostly as relatively small isolated patches (min = 0.5 ha, median = 1.4 ha, mean = 4.1 ha, max = 876.2 ha) surrounded by either arable fields or pine plantations.

Over the past five decades, the region has experienced several environmental changes that need to be considered: (a) In many lowland parts of the Prignitz region, extensive drainage measures were taken after 1960 to lower the groundwater table and improve site conditions for agri- and silviculture (Stengel 2002) (Appendix 5.2.1). (b) Deer abundances and, thus, most likely, browsing pressure have strongly increased over the last four decades (Appendix 5.2.2). This is particularly true for roe deer (*Capreolus capreolus* L.) which is by far the most abundant deer species in the region. (c) Nitrogen deposition rates have been exceeding the threshold for nitrogen deposition effects on herb-layer biodiversity (10-15 kg $ha^{-1}yr^{-1}$ according to Bobbink et al. 2010) for more than three decades (Appendix 5.2.3). Sulphur deposition was high (>40 kg $ha^{-1}yr^{-1}$) in the 1980s and has since decreased below 10 kg $ha^{-1}yr^{-1}$. However, soil acidification may still occur given that the larger part of the nitrogen deposition is in the form of NH_4^+. (d) The climate has become significantly warmer over the last five decades, i.e., the mean annual temperature has increased by 1.0 to 1.5°C, and the growing season has been extended by 23 to 32 days. At the same time, summer precipitation has significantly decreased in parts of the region so that the ratio of potential evapotranspiration over precipitation has significantly increased (Appendix 5.2.4).

Old and new survey

In the 1950s, the regional forest authorities conducted extensive site investigations in all state-owned forests of the Prignitz region. The site investigators established approximately 2000 site investigation pits within this region (approximately one per 14.6 ha forest) during the period from 1958 to 1960 to analyze the soil profile (IFS 1960, 1961). At each soil profile, they not only recorded the profile characteristics but also the plant species composition in a, 20 x 20 m square around the pit. The cover of all vascular plant species and easily identifiable epigeic mosses in the herb, shrub and tree layers was estimated on a seven-degree combined cover-abundance scale: 1 (cover <1%, 1-5 individuals), 2 (cover ≤1%, 5-20 individuals), 3 (cover >1 and ≤5% and 5-20 ind. or cover ≤5% and, 20-100 ind.), 4 (cover ≤5% and >100 ind. or cover 5-25% and any number of ind.), 5 (cover 25-50%), 6 (cover 50-75%), 7 (cover 75-100%). The exact location of each site investigation pit was marked in a forestry map at scale 1:10,000 and in a hand-drawn sketch with exact distances in meters from forest roads, forest edges or drainage ditches (Appendix 5.3).

From the original dataset, we selected those plots that had a tree layer dominated by native, deciduous tree species, a stand age beyond the pole wood stage and that were located, even today according to aerial photographs, in deciduous forest stands. This resulted in 188 plots worth for relocation (indeed, most of the plots were located in allochthonous pine stands). At the majority of the corresponding sites (63%), the original site investigation pit was still recognizable by its characteristic shape (Appendix 5.3); thus, the original plot position could exactly be determined. At another 30% of sites, the original pit was no longer visible (mostly moist to wet sites), but the distances provided on the hand-drawn sketches, together with the tree species composition, allowed us to relocate the plots with an error of <30 m. The remaining 7% of plots could not be reliably relocated. For the present study, we selected 82 plots from the relocated plots that met the following criteria: (a) They still exhibited a similar (though matured) deciduous stand as the original stand, i.e., no stand-replacing management actions had taken place; (b) they showed no sign of strong recent disturbance, natural or due to forest management activities; and (c) they were located in ancient forest stands, i.e., with a habitat continuity of at least 230 years according to our reconstruction of the regional land cover history (Kolk and Naaf, 2015). The latter two criteria should ensure a strong species-environment relationship and therefore a good indicative quality of the vegetation.

In 2014, we recorded the cover-abundance of all vascular plant species and easily identifiable epigeic mosses separately for the herb, shrub and tree layers with the same seven-degree scale used by the original site investigators. This cover-abundance scale is relatively coarse and thus robust towards subjective cover estimation. To maximize the comparability between the two surveys, we applied the following rules (cf. Van Calster et al. 2008): First, seedlings of shrub and tree species were ignored because their abundance depends mostly on the seed output of the surrounding mother trees, which is highly variable. We kept, however, woody species that have their main cover in the herb layer, such as *Hedera helix*, *Vaccinium myrtillus* or *Rubus* spp. We ignored also plants growing on the dug-out material of the original pit because they indicate different site conditions. Second, we surveyed the plot at a similar phenological stage as the original investigators did. To achieve this, we corrected for differences in the proceeding of the growing season between 1960 and 2014 using cumulative degree hours (CDH). These govern the phenology of many herbaceous species, particularly in spring (Lindsey & Newman 1956). Modeling CDH thresholds as a function of years since 1960 indicated that phenology between April and July in 2014 ran between 6 and 30 days ahead compared with 1960 (Appendix 5.4).

Quantification of environmental change

The only environmental driver that could be directly quantified was change in canopy cover and composition. The tree and shrub layer influences the herb layer in two ways: it governs the light availability through its density and it affects the availability of nutrients through its litter quality (Wulf & Naaf 2009). As a measure of light availability, we calculated the shade-casting ability (SCA) as cover-weighted average of the tree and shrub species' shade-casting ability scores listed in Appendix 5.6.1 (Verheyen et al. 2012). Similarly, we quantified the litter quality (LQ) as cover-weighted average of the tree and shrub species' litter quality scores (Appendix 5.6.1; Verheyen et al. 2012). These scores range from 1 (low shade-casting ability/decomposition rate) to 5 (high shade-casting ability/decomposition rate). For a few tree species, litter quality scores were not available. The average litter quality of a plot was only included in the analyses when the cover proportion, for which a litter quality score was available, was at least 75%. This was true for 74 plots. The change in shade-casting ability and litter quality over time was quantified as log response ratio (RR), e.g., $RR_{SCA} = \log(SCA_{2014}/SCA_{1960})$. This has the advantages that the magnitude of change can be compared among variables measured at different scales and that the change can be tested against zero with linear models (e.g., Rogers et al. 2009). The log response ratio was also used to quantify the change in other variables over time (see below). To make the log response ratios approximate a normal distribution and to improve their comparability, we transformed and scaled the underlying variables as described in Appendix 5.5.

For all other environmental drivers, no measured data existed for both time periods. Therefore, we used the change in herb layer species composition together with independent expert knowledge on the species-environment relationships as indicator for environmental changes. We applied abundance-weighted mean Ellenberg values (Ellenberg et al. 2001) for soil moisture (mF), soil reaction (mR) and nutrient availability (mN). Ellenberg values indicate a species' habitat preference and range from 1 (very dry/acidic/nutrient-poor conditions) to 9 (very wet/alkaline/nutrient-rich conditions). Mean Ellenberg values are an acknowledged tool in temperate Europe to assess site conditions (Diekmann 2003) and have been frequently used in resurvey studies to indicate environmental changes. A valid indicator value for F, R and N was available for 87%, 65% and 81% of the species. Mean Ellenberg values were only included in the analyses when they were based on at least 2 species, which yielded 80, 81 and 80 plots for mF, mR and mN, respectively.

In a similar way, we calculated a mean browsing attractiveness (BA) based on the browsing attractiveness scores provided by Ellenberg (1988). These scores indicate a species' susceptibility to browsing by row deer and range from 1 (not browsed at all) to 5 (heavily browsed). We excluded species that are known to be highly tolerant of browsing/grazing or are even favored when frequently browsed, i.e., species with a cutting tolerance of ≥ 7 according to Briemle & Ellenberg (1994). Thus, the browsing attractiveness index can be assumed to reflect browsing pressure. A browsing attractiveness score was available for 76% of all vascular plants. Mean browsing attractiveness values were only included in the analyses, when they were based on at least two species, which yielded 81 plots.

Finally, we used species distribution data to derive two measures indicative of climate change: floristic temperature (FT) and floristic continentality (FC). Floristic temperature is the ratio of species with a southern distribution over species with a northern distribution. A species' distribution was classified as southern if it was described as 'Mediterranean' in the regional flora by Fischer (1963) or as 'southern-temperate' in the moss flora by Smith (2004). Similarly, floristic continentality is the ratio of species with a (sub-)continental distribution over species with a (sub-)oceanic distribution. A species' distribution was classified as '(sub-)continental' if it was described as 'continental' or 'subcontinental' in the flora by Fischer (mosses with a (sub-)continental distribution did not occur). A species' distribution was classified as (sub-)oceanic if it was described as 'oceanic' or 'suboceanic' in the flora by Fischer or Smith.

For all herb layer indicator variables we calculated the change over time as log response ratio as for shade-casting ability and litter quality. An overview on all environmental change variables is given in Table 5.1. The collinearity of all environmental change variables was generally low (Appendix 5.6.2) with two exceptions: a strong correlation between change in mR and change in mN ($r = 0.74$), which was no surprise because R and N values are known to be strongly correlated (e.g., Diekmann et al. 1999); and a moderate correlation between change in mR and change in floristic temperature ($r = 0.52$), which results from the fact that acid tolerant species have often their main distribution in the boreal zone (Fischer 1963).

Table 5.1. Overview on variables used in data analysis. For all variables except temporal floristic turnover the change over time is quantified as log response ratio (RR).

Environmental changes

- *Canopy change variables*
  - Change in shade-casting ability (RR_{SCA})
  - Change in litter quality (RR_{LQ})
- *Environmental change indicators*
  - Change in mean Ellenberg value for soil moisture (RR_{F})
  - Change in mean Ellenberg value for soil reaction (RR_{R})
  - Change in mean Ellenberg value for nutrient availability (RR_{N})
  - Change in browsing attractiveness (RR_{BA})
  - Change in floristic temperature (RR_{FT})
  - Change in floristic continentality (RR_{FC})

Changes in herb layer diversity and composition

- Change in total species richness (RR_{SR})
- Change in forest specialist richness (RR_{SPEC})
- Change in floristic distinctiveness (RR_{BETA})
- Temporal floristic turnover

Initial site conditions

- Soil pH buffer range
  - Aluminum and aluminum-iron buffer range (AlFe)
  - Cation-exchange buffer range (CatEx)
  - Silicate and carbonate buffer range (SiliCar)

Changes in herb layer diversity and composition

To assess the impact of environmental changes on herb layer diversity and composition, we used four variables (Table 5.1): change in total species richness (RR_{SR}), change in the richness of forest specialists (RR_{SPEC}), change in the average floristic dissimilarity of a plot to all other plots, i.e., its floristic distinctiveness (RR_{BETA}), and temporal floristic turnover. Total species richness is the number of all plant species recorded in a plot. The richness of forest specialists comprises only typical forest interior species that would not survive in open habitats and do not mainly occur beneath canopy gaps or at forest edges according to the reference list of Schmidt et al. (2011). Because forests represent essentially the habitat for forest specialist plants, we were particularly interested to determine how environmental changes affect the performance of this species group. The floristic dissimilarity among plots was quantified with the Lennon dissimilarity, which ignores differences in species richness and thus measures real spatial turnover (Lennon et al. 2001). The resulting floristic distinctiveness can be regarded as a measure of beta diversity but at the same time refers to one specific plot so that it can be related to other plot-based variables (Naaf & Wulf 2010). To measure the temporal floristic turnover, we again used the Lennon dissimilarity to quantify the amount of species replacement over time.

Initial site conditions

The surveyed sites comprised a wide range of soil conditions, particularly in terms of soil pH, which is known to reflect the nutritional status of soils and thus governs plant establishment and growth (Härdtle et al. 2004). Particularly, the pH(H_2O) threshold of 4.2 between the aluminum and the cation-exchange buffer range seems to be crucial for the performance of many forest plants (Falkengren-Grerup & Tyler 1993). Therefore, we categorized the sites according to their buffer range (*sensu* Ulrich 1991). Because soil pH had not been measured in 1960, we used the relationship between soil pH measured in 2014 and mR to assign the plots to the buffer ranges. To measure soil pH, eight soil samples (0-10 cm) were taken in each plot in September, then pooled, air-dried and sieved (2 mm). Soil pH was then determined in a 0.01 M $CaCl_2$ solution with a glass electrode following ISO 10390. The pH(H_2O) buffer thresholds provided by Ulrich (1991) were first translated into pH($CaCl_2$) thresholds using a published regression model (Reuter et al. 2008) and then into mR thresholds based on the regression of mR on pH($CaCl_2$) values (Fig. 5.1). Plots were then assigned to buffer ranges based on mR in 1960. This resulted in 33 plots in the aluminum or aluminum-iron buffer range (AlFe), 22 plots in the cation-exchange buffer range (CatEx) and 27 plots in the silicate or carbonate buffer range (SiliCar). These three categories differed not only in terms of buffer capacity and soil pH but also in terms of other environmental conditions, species richness and tree species composition (Tables 5.2 and S3), demonstrating the usefulness of this categorization.

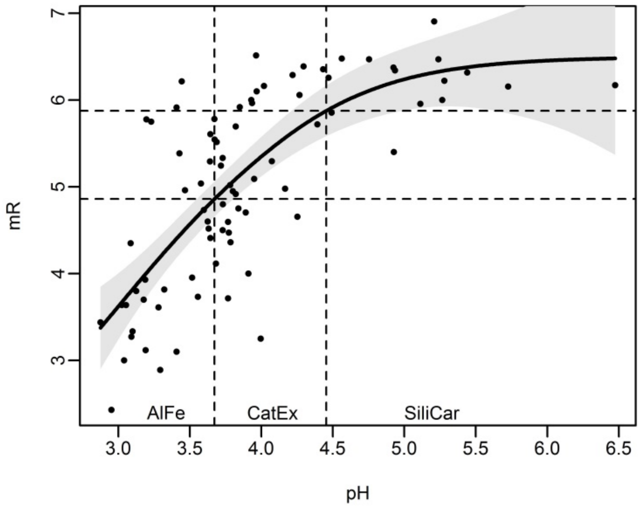

Fig. 5.1. Regression of mean Ellenberg values for soil reaction (mR) in 2014 against measured pH($CaCl_2$) based on a penalized thin plate regression spline (function gam in R package mgcv; Wood 2006). The shaded area represents the 95% confidence band. The vertical and horizontal dashed lines mark the thresholds between the aluminium or aluminium-iron buffer range (AlFe), the cation-exchange buffer range (CatEx) and the silicate or carbonate buffer range (SiliCar). Note that despite the scatter ($R^2 = 0.56$), most of the plots are assigned correctly to the buffer ranges with mR values.

Table 5.2. Differences in initial environmental conditions and species richness between the buffer range categories in 1960, based on a Kruskal-Wallis test followed by a post-hoc multiple comparison among groups according to Dunn (1964). Given are group means with standard errors in parentheses. Different small letters indicate significant differences between groups. AlFe = aluminum and aluminum-iron buffer range; CatEx = cation-exchange buffer range; SiliCar = silicate and carbonate buffer range.

	AlFe (n = 33)	**CatEx** (n = 22)	**SiliCar** (n = 27)	**Kruskal-Wallis chi^2**	**df**	***p***
Canopy variables						
Shade-casting ability	3.05 (0.17) ^{a}	3.86 (0.23) ^{b}	3.01 (0.07) ^{ab}	9.0	2	0.011
Litter quality	1.43 (0.12) ^{a}	2.11 (0.23) ^{a}	3.34 (0.19) ^{b}	32.1	2	<0.001
Herb-layer indicator variables						
Mean Ellenberg F (soil moisture)	5.56 (0.08) ^{a}	5.63 (0.08) ^{a}	6.37 (0.14) ^{b}	26.3	2	<0.001
Mean Ellenberg R (soil reaction)	3.96 (0.12) ^{a}	5.40 (0.07) ^{b}	6.37 (0.06) ^{c}	71.0	2	<0.001
Mean Ellenberg N (nutrient availability)	4.28 (0.12) ^{a}	5.40 (0.07) ^{b}	6.14 (0.06) ^{c}	66.0	2	<0.001
Browsing attractiveness	2.59 (0.06) ^{a}	2.63 (0.06) ^{ab}	2.78 (0.07) ^{b}	10.0	2	0.007
Floristic temperature	0.40 (0.06) ^{a}	0.85 (0.08) ^{b}	3.44 (0.93) ^{c}	49.1	2	<0.001
Floristic continentality	0.10 (0.01) ^{a}	0.21 (0.03) ^{b}	0.35 (0.05) ^{b}	30.1	2	<0.001
Herb layer species richness						
Total species richness	13.5 (0.9) ^{a}	17.7 (1.2) ^{b}	18.1 (0.9) ^{b}	12.3	2	0.002
Forest specialist richness	6.0 (0.6) ^{a}	9.8 (1.0) ^{b}	7.0 (0.7) ^{ab}	9.0	2	0.011

Data analysis

Effects of initial site conditions on change over time

We tested all log response ratios for their dependence on the initial buffer range, with either linear mixed models (LMM) or simple linear models using generalized least squares (GLS). Some plots were located within the same larger forest patch and thus might behave more similar than plots of different forest patches. To account for the nested data structure, we tested if adding the forest patch as random effect to the full model significantly improved model fit based on a likelihood-ratio test (Zuur et al. 2009). In case the random effect improved model fit, we proceeded with LMM, otherwise we used GLS. In both cases, we added a constant variance function to the model to allow the residual variance to differ between buffer ranges (Pinheiro and Bates 2000). For LMM and GLS, we used the functions *lme* and *gls*, respectively, in the nlme package (Pinheiro et al. 2014) in R version 3.1.1 (R Core Team, 2014). The effect of buffer range was tested with a likelihood ratio test using ML estimation of parameters. If buffer range had a significant effect, we conducted pairwise comparisons of means with a Tukey's post-hoc test using the function *glht* of the R package multcomp (Hothorn et al. 2008). Similarly, we also tested whether temporal floristic turnover depended on the buffer range.

Effects of canopy change variables on environmental change indicators

To determine the extent to which environmental changes indicated by the herb layer are the result of local changes in canopy cover and composition rather than regional or global drivers, we modeled the environmental change indicators as a function of canopy change variables. Only those log response ratios that indicated a significant change over time were included. Initial buffer range and its interaction with the canopy change variables were added as potential predictors to determine whether the canopy effects depend on initial site conditions. We used again either LMM or GLS as explained above. The global model was simplified by first testing and, if necessary, excluding the interaction with buffer range based on a marginal *F* test (Pinheiro & Bates 2000). The buffer range main effect was then tested in the same way and, if necessary, excluded. The significance of all remaining effects will be reported.

Effects of environmental changes on changes in herb layer diversity and composition

We modeled the four variables referring to changes in herb layer diversity and composition as a function of environmental change variables to (a) determine the relative importance and (b) identify significant interactions among environmental drivers. As potential predictors we included all environmental change variables that indicated a significant change over time with one exception. As will be shown in the Results section, the change in floristic temperature does apparently neither reflect the recent climate warming nor is it significantly associated with a change in canopy density. Because it is unclear what this factor is actually representing, change in floristic temperature was excluded from this analysis.

The predictors were centered and standardized to make parameter estimates comparable and to allow the interpretation of main effects in the presence of interactions (Schielzeth 2010). We also considered initial buffer range and its interactions with the environmental change variables as potential predictors to test, whether the environmental change effects on the herb layer composition depend on initial site conditions. Again, we chose to use either LMM or GLS as explained above, but finally always used GLS.

Because the number of main effects and their pairwise interactions would have been too large to be included in a global model, we started with a preliminary global model containing only the main effects and their interactions with buffer range. Then, we tested all pairwise interactions between environmental change variables as well as their second-order interaction with buffer range in models containing always only one pair of environmental change variables and buffer range as predictors. Interaction terms that were significant at the 10% level were then added to the preliminary global model to build the final global model.

We fitted models for all possible subsets of predictors, but allowed only a maximum of seven terms to ensure that there are at least ten plots for each term (Harrell 2001). Among all potential candidate models we selected those with a $\Delta AIC_C \leq 2$ (Burnham & Anderson 2002) and then applied full model averaging on this set of models using the function *model.avg* in the R package MuMIn (Barton 2015). For each model term in the average model, we calculated an importance value as the sum of the Akaike weights over all of the component models in which the term appeared. This importance value ranges between 0 and 1, with a value of 1 indicating that a model term appears in all component models. The effect of any predictor or interaction will be reported and interpreted whose averaged coefficient was significantly different from zero or whose relative importance was ≥ 0.5, indicating that it occurs in the most important component models.

To assess the extent to which changes in herb layer diversity and composition can be explained by changes in environmental conditions, we calculated R^2 values for both the full average model (R^2_{TOT}) and a similar average model whose component models contain only (if anything) buffer range as predictor. The difference between these two

R^2 values is interpreted as the amount of explained variance that can be uniquely attributed to the environmental change variables (R^2_{ENV}).

5.5 Results

Effects of initial site conditions on changes in species diversity and composition

Both total species richness and forest specialist richness generally tended to increase over time, but significantly increased only on sites in the SiliCar buffer range and the CatEx and SiliCar buffer ranges, respectively (Fig. 5.2). The average increase in species richness on sites in the SiliCar buffer range was 7.1 and 4.4 species, respectively. Specialist richness on sites in the CatEx buffer range increased on average by 0.9 species. Floristic distinctiveness decreased significantly on all sites but significantly more on sites in the SiliCar than in the AlFe buffer range while sites in the CatEx buffer range took an intermediate position. Despite the general increasing trend in species richness, the loss of floristic distinctiveness was mostly due to the local loss of initially less common species rather than the spread of initially very common species (Appendix 5.6.4). The mean temporal turnover in species composition amounted to 29.1 ± 2.0%, meaning that on average more than every forth but less than every third species had been replaced by another species. The magnitude of turnover did not differ between the initial buffer range categories ($\chi^2 = 0.85$; df = 2; $p = 0.655$).

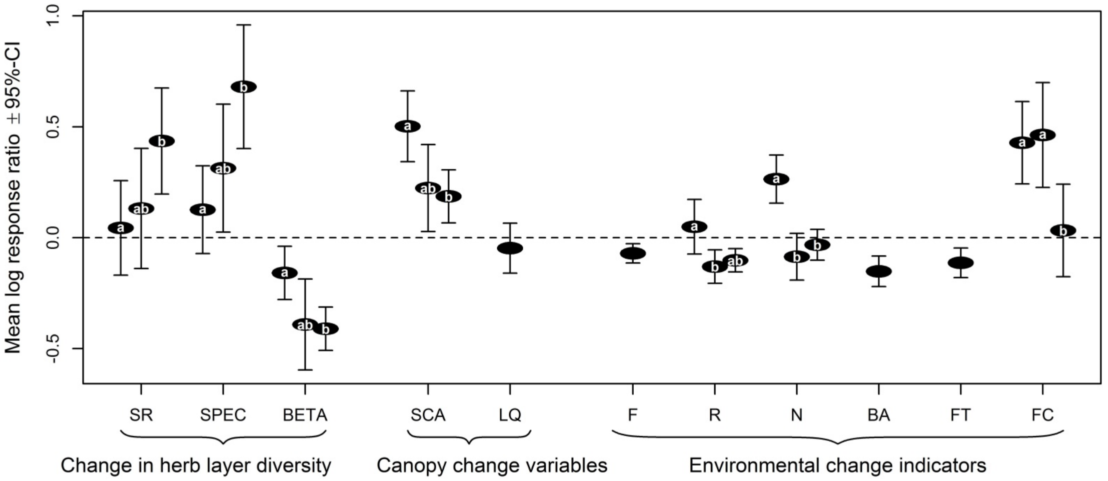

Fig. 5.2. Changes over time in total species richness (SR), forest specialist richness (SPEC), floristic distinctiveness (BETA), canopy shade-casting ability (SCA) and litter quality (LQ), mean Ellenberg values for soil moisture (F), soil reaction (R) and soil nutrient availability (N), mean browsing attractiveness (BA), floristic temperature (FT) and floristic continentality (FC). Presented are the mean log-response ratios ± 95% confidence interval, separately for each initial buffer range category (from left to right: aluminum or aluminum-iron buffer range, cation-exchange buffer range, silicate or carbonate buffer range) when the initial buffer range category had a significant effect on the log-response ratio (see main text). Significance of differences between buffer range categories is indicated by lower-case letters.

Effects of initial site conditions on environmental changes

The shade-casting ability of the canopy increased significantly on all sites, but significantly stronger on sites in the AlFe than in the SiliCar buffer range (Fig. 5.2). This increase in shade-casting ability resulted from (a) the decrease in cover of some tree species with a less dense canopy, especially *Quercus robur* but also *Betula pendula* (on acidic sites) and *Alnus* spp. and *Fraxinus excelsior* on base-rich sites (Appendix 5.6.3); and (b) the increase in cover of some strongly shading species, especially *Fagus sylvatica* but also *Carpinus betulus*, *Prunus serotina* (on acidic sites) and *Ulmus* spp. (on base-rich sites). Independent of initial site conditions, litter quality did not change over time (Fig. 5.2). Mean Ellenberg F (soil moisture), browsing attractiveness and floristic temperature decreased significantly on all sites. While mR (soil reaction) did not change on sites in the AlFe buffer range, mN (nutrient availability) significantly increased on these sites. In return, mR decreased significantly on sites in the CatEx or SiliCar buffer range, while mN did not change here. Floristic continentality significantly increased on sites in the AlFe or CatEx buffer range, but not on sites in the SiliCar buffer range (Fig. 5.2).

Effects of canopy change variables on environmental change indicators

Because litter quality did not change over time, we included only change in shade-casting ability to explain changes in herb layer indicator variables. Effects of the change in shade-casting ability were generally weak and not significant (Appendix 5.6.5). Any interactions with initial buffer range did not occur.

Effects of environmental changes on changes in herb layer diversity and composition

Approximately 25% of the variation of the change in species richness (RR_{SR}) could be uniquely attributed to the environmental change variables (Table 5.3). Species richness increased most where there were less pronounced decreases in light availability (RR_{SCA}), soil moisture (RR_F) and soil acidity (RR_R; Fig. 5.2). Moreover, the change in mN (RR_N) had a weak negative but non-significant effect on RR_{SR}, i.e., species richness tended to increase most where nutrient availability increased least or even decreased. Any important interactions among environmental change variables or with initial buffer range did not occur.

The richness of forest specialists increased most where floristic continentality increased most (Table 5.3). Otherwise, the modeling results for the change in forest specialist richness (RR_{SPEC}) were similar to those for RR_{SR}. Instead of the weak negative effect of RR_N, the change in floristic continentality (RR_{FC}) had a significant positive effect here.

The variation of the change in floristic distinctiveness (RR_{BETA}) that could be uniquely attributed to the environmental change variables was approximately 30%. The only predictor that had a significant effect on RR_{BETA} was RR_N (Table 5.3). This effect depended on the initial buffer range: although it was significantly negative on sites in the AlFe buffer range and even more negative on sites in the CatEx buffer range, it was close to zero on sites in the SiliCar buffer range (Fig. 5.3). Although this interaction lacked strong significance, it occurred in all candidate models (Table 5.3). It indicates that on sites in the AlFe or CatEx buffer range, the loss of floristic distinctiveness was most pronounced where mN increased most (Figs. 5.3a and b). On sites in the SiliCar buffer range, floristic distinctiveness generally decreased independent from RR_N (Fig. 5.3c). Furthermore, the effect of RR_N was slightly modified by an interaction with RR_F (Table 5.3, Fig. 5.3). While this interaction was not significant in the average model, it had an importance value > 0.5, indicating that the negative effect of RR_N on RR_{BETA} was strongest where soil moisture decreased most.

Table 5.3. Effects of environmental change variables on changes in species diversity and composition as resulting from generalized least squares regression analyses. The estimates are average standardized regression coefficients resulting from full averaging over all candidate models with a $\Delta AIC_C \leq 2$. Given are the unconditional standard errors (SE), the z and p value of the test against zero, the importance value (Imp.; see main text), the variance explained by the complete average model potentially including also initial buffer range as predictor (R^2_{TOT}), the variance that is uniquely explained by the environmental change variables (R^2_{ENV}), the number of candidate models (Cand.) and the sample size (n; varying due to missing values). Intercepts, buffer range main effects and effects with an importance value < 0.5 are not shown (see Appendix 5.6.6 for the complete version). See Table 1 for explanations of response and predictor names.

Response	**Predictors**	**Estimate**	**SE**	***z***	***p***	**Imp.**	R^2_{TOT}	R^2_{ENV}	**Cand.**	***n***
RR_{SR}	RR_{SCA}	-0.248	0.060	4.082	0.000	1.00	0.292	0.247	9	78
	RR_F	0.133	0.055	2.361	0.018	1.00				
	RR_R	0.241	0.080	2.967	0.003	1.00				
	RR_N	-0.084	0.102	0.819	0.413	0.54				
RR_{SPEC}	RR_{SCA}	-0.129	0.055	2.321	0.020	1.00	0.391	0.242	4	79
	RR_F	0.064	0.062	1.036	0.300	0.66				
	RR_R	0.166	0.048	3.364	0.001	1.00				
	RR_{FC}	0.180	0.055	3.192	0.001	1.00				
RR_{BETA}	RR_F	-0.021	0.031	0.680	0.496	0.58	0.384	0.299	2	78
	RR_N	-0.165	0.050	3.221	0.001	1.00				
	CatEx*RR_N	-0.177	0.109	1.602	0.109	1.00				
	SiliCar*RR_N	0.152	0.092	1.613	0.107	1.00				
	RR_F*RR_N	0.039	0.040	0.969	0.332	0.58				
Temporal turnover	RR_F	-0.015	0.017	0.871	0.384	0.68	0.300	0.299	12	78
	RR_R	-0.075	0.028	2.668	0.008	1.00				
	RR_N	0.056	0.029	1.871	0.061	1.00				
	RR_R*RR_N	0.051	0.017	2.961	0.003	1.00				

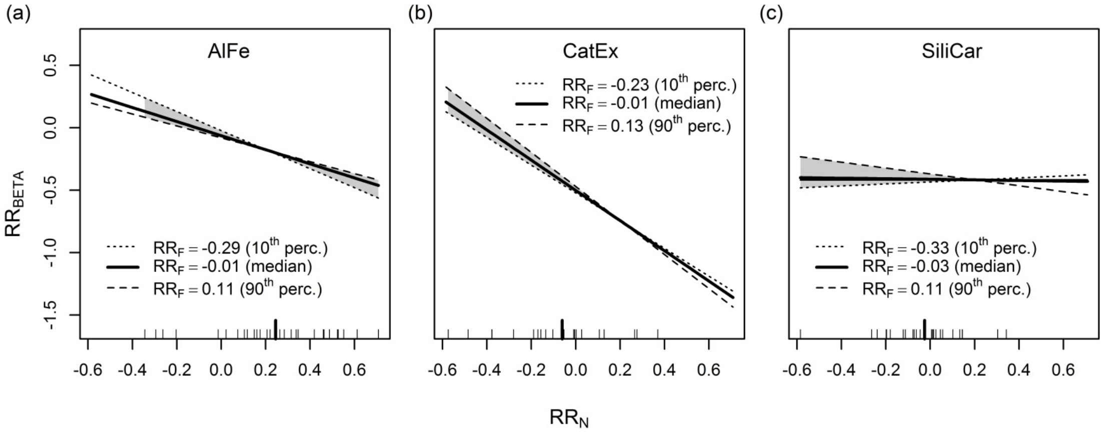

Fig. 5.3. Interaction between the changes in mean Ellenberg N (RR_N) and F (RR_F) and initial buffer range categories in affecting the change in floristic distinctiveness (RR_{BETA}). Regression lines represent partial effects of RR_N on RR_{BETA} for different levels of RR_F according to the corresponding model presented in Table 3. The shaded area between regression lines indicates the range of RR_N values actually observed in the respective buffer range category. Rugs on the abscissa present the observed RR_N-values with their mean indicated as thicker and longer line. AlFe = aluminum and aluminum-iron buffer range; CatEx = cation-exchange buffer range; SiliCar = silicate and carbonate buffer range.

Finally, approximately 30% of the variation in temporal turnover could be uniquely attributed to the environmental change variables (Table 5.3). The degree of temporal turnover was mainly determined by the opposing effects of RR_R and RR_N (with borderline significance) and their positive interaction (Table 5.3, Fig. 5.4). The negative effect of RR_R was enhanced when mN decreased, while the positive effect of RR_N was enhanced when mR increased. Thus, temporal turnover was highest when both mR and mN either strongly decreased (e.g., on sites in the AlFe or SiliCar buffer range) or strongly increased (e.g., on sites in the AlFe buffer range; Fig. 5.4c). When mN strongly increased or mR strongly decreased, turnover was generally high and more or less independent of RR_R or RR_N, respectively (Figs. 5.4a and b). The turnover was low when changes in mean Ellenberg values were small to moderate or had an opposed sign. In addition, RR_F had a weak negative, but non-significant effect on temporal turnover (Table 5.3), indicating that turnover tended to be higher where the decrease in soil moisture was more pronounced.

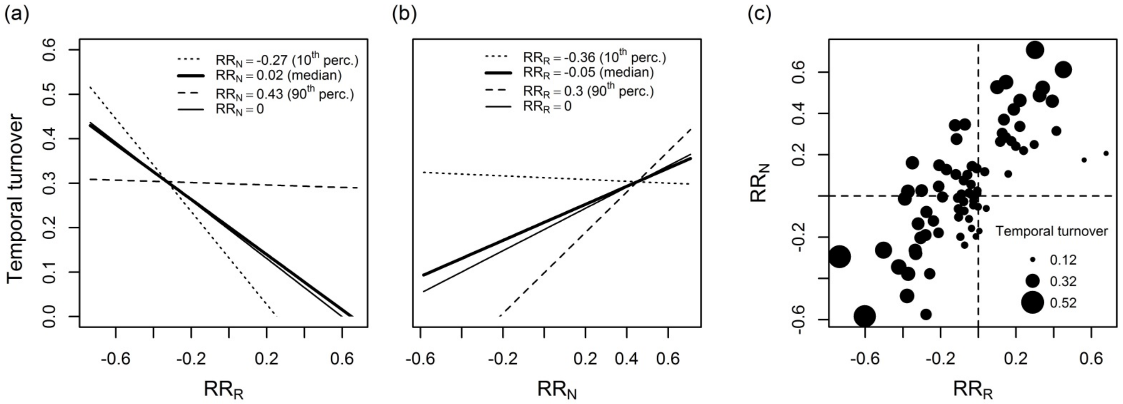

Fig. 5.4. Interaction between the changes in mean Ellenberg R (RR_R) and N (RR_N) in affecting temporal species turnover. The regression lines in panels (a) and (b) present the partial effects of RR_R and RR_N, respectively, on temporal turnover for different levels of RR_N and RR_R, respectively, according to the corresponding model presented in Table 3. Panel (c) shows the fitted values of temporal turnover for the observed RR_R and RR_N values.

5.6 Discussion

Initial site conditions matter

We observed significant changes in both herb-layer species diversity and environmental conditions over the past five decades, and most of these changes depended significantly on the initial buffer range. Species richness increased most at more base-rich sites, which also exhibited a higher initial species richness in 1960. Additionally, the decrease in floristic distinctiveness at these sites was highest. Although sites with a higher initial species richness have a higher potential for diversity changes, other resurvey studies found diversity changes to be independent of habitat type and initial richness (Vanhellemont et al. 2014, Woods et al. 2012). Thus, the differences in the magnitude of diversity changes among the buffer range categories could also be attributed to contrasting environmental changes among the three buffer range categories (see below).

While the magnitude of temporal species turnover was similar in all buffer range categories, changes in species composition still differed qualitatively among buffer range categories, as indicated by the herbaceous environmental change indicators for soil reaction, nutrient availability and continentality. Mean Ellenberg R (soil reaction) decreased most on sites initially in the CatEx buffer range, which are known to be most sensitive to acidification (Baeten et al. 2009 b, Van Calster et al. 2007). It did not change at the initially most acidic sites, which are well buffered against further acidification (Thimonier et al. 1994, Van Calster et al. 2007). In contrast, the eutrophication signal (increase in mN) was largely restricted to the most acidic sites, which were also the initially most nutrient-deficient sites (Table 5.2; Härdtle et al. 2004). Although a stronger eutrophication signal on nutrient-deficient sites can be expected (Gilliam 2006) it has so far been rarely reported (but see Reinecke et al. 2014; Sebesta et al. 2011). The majority of resurvey studies found similar or even more pronounced increases in mN on calcareous or moderately acidic sites compared to acidic sites (e.g., Lameire et al. 2000, Thimonier et al. 1994, Verstraeten et al. 2013).

Floristic continentality increased markedly only on sites in the AlFe or CatEx buffer range, i.e., on sites that are less moist and less influenced by groundwater than sites in the SiliCar buffer range. The increase in floristic continentality was mostly due to the loss of several (sub-)oceanic species, such as *Deschampsia flexuosa*, *Fragaria vesca*, *Galium odoratum* or *Gymnocarpium dryopteris*, whereas only two (sub-)continental species markedly increased in frequency, *Calamagrostis epigejos* and *Impatiens parviflora* (Appendix 5.6.4). It could well be that the former suffer from the enhanced dryness during summer (Appendix 5.2.4), which is less perceptible on sites close to the groundwater.

Although the canopy became denser on all sites, the decline in the weakly shading *Quercus robur* was most pronounced on sites in the AlFe buffer range, where it had been the dominant tree species in 1960 and was largely replaced by the strongly shading *Fagus sylvatica* in 2014 (Appendix 5.6.3). The decline of *Quercus spp.* is a commonly observed phenomenon in temperate forests across Europe (e.g., Amar et al. 2010, Kwiatkowska 1994, Vanhellemont et al. 2014) and has been attributed to the abandonment of traditional management forms such as grazing and coppicing (Hédl et al., 2010, Von Oheimb & Brunet 2007). *Quercus spp.* fails to regenerate beneath a closed canopy and in competition with more shade-tolerant species such as *F. sylvatica* and *Carpinus betulus* (Vera 2000). In the Prignitz region, forests were used for wood pasture still at the beginning of the 20th century (Wulf 2004 b).

Some of the indicated environmental changes were independent from the initial buffer range. A decrease in mF (soil moisture) was expected as a result of drainage measures (Appendix 5.2.1), however we had expected to find a more pronounced decrease on sites in the SiliCar buffer range which comprised originally also the most wet sites (cf. Lameire et al. 2000, Maděra 2001). A reason for the relatively small decrease in mF might be that several wetland plants, although they locally declined in abundance, were able to persist because they are rather long-lived and/or clonal, such as *Carex acutiformis*, *Iris pseudacorus* or *Phalaris arundinacea* (Appendix 5.6.4). For instance, *I. pseudacorus* is known to be capable of growth in dry sandy soils, although it usually occurs on continuously wet sites (Sutherland 1990).

Browsing attractiveness decreased independent of initial buffer range. Because attractive and non-attractive plants occur on all sites independent of soil pH (no rank correlation between browsing attractiveness and soil pH: $r_s = 0.048$, $p = 0.671$, $n = 81$), increased deer densities can be assumed to exert a higher browsing pressure on attractive plants in all buffer ranges.

The general decrease in floristic temperature was unexpected and obviously does not reflect the increase in mean annual temperature over the last five decades (Appendix 5.2.4). One might expect that the species composition in the herb layer reflects more directly the microclimatic conditions that are determined by canopy density (De Frenne et al. 2013). A decrease in floristic temperature in response to an increasing canopy density has, for instance, been observed in the Milovice Wood in SE Czech Republic (Hédl et al. 2010) or the Göttinger Wald in Central Germany (Heinrichs et al. 2012). However, here, the decrease in floristic temperature was not significantly related to the increase in shade-casting ability (Appendix 5.6.5). Instead, there was a significant correlation between the change in floristic temperature and changes in mR (Appendix 5.6.2), thus the decrease in floristic temperature might result from acidification and from the success of acid-tolerant species with a Nordic distribution, such as *Maianthemum bifolium*, *Oxalis acetosella* and *Polytrichum formosum* (Appendix 5.6.4).

Changes in canopy structure complement regional or global drivers

In contrast to our expectations, the environmental changes indicated by the herb layer were unrelated to changes in canopy cover and composition. The litter quality remained similar over time because, although the tree species with a decreasing and increasing cover differ in their shade-casting ability, they have a similar litter quality. For instance, *Fagus sylvatica* and *Quercus robur* both have a score of 1. As litter quality did not change over time, it cannot account for the observed changes in mR and mN. Shade-casting ability significantly increased over time and could therefore theoretically account for the observed changes in herb-layer indicator variables. We had expected that particularly the indicator variables related to climate would respond to changes in shade-casting ability. An increase in floristic continentality could result, when the canopy opens up and the microclimate in the forest interior becomes less well buffered against changes in temperature and humidity (Bauhus & Bartsch 1995). However, in our study, the canopy became denser and changes in floristic continentality were unrelated to changes in shade-casting ability. Additionally, the change in floristic continentality showed no important correlation with any other environmental change variable (Appendix 5.6.2). We, therefore, assume that the increase in floristic continentality indeed reflects the increased macroclimatic continentality in terms of summer drought (Appendix 5.2.4).

The change in shade-casting ability was also unrelated to any other environmental change indicator. We therefore assume that the corresponding environmental changes indicated by the herb layer, i.e., decreasing soil moisture, acidification, eutrophication and enhanced browsing pressure, reflect indeed the corresponding regional or global drivers. The local changes in canopy structure and composition complement these large-scale drivers by regulating mainly light availability.

Drivers of changes in herb layer diversity and composition and their interactions

The most pronounced change in the herb layer was the increase in species richness on base-rich sites. An increase in species richness has frequently been found in other resurvey studies (e.g., Baeten et al. 2009 b, Naaf & Wulf 2010, Vanhellemont et al. 2014) and seems to occur as often as a decrease across studies from temperate Europe (Bernhardt-Römermann et al. 2015). It was, however, unexpected for us to see that it could only insufficiently be explained by the indicated environmental changes. The effects of the changes in shade-casting ability, mF and mR on the changes in total and forest specialist richness were significant, but according to their sign the observed environmental changes (decreased light availability, decreased soil moisture and higher soil acidity) should have caused a decrease in species richness, rather than an increase. That is, the observed environmental changes counteracted an increase in species richness, which still increased due to an unobserved driver. The assumption that another driver is at work is also supported by the fact that less than 25% of the variance of the change in total species richness could be uniquely attributed to the environmental change variables. The only environmental change variable with a positive effect on the change in forest specialist richness was change in floristic continentality, indicating that the richness of forest specialists increased most where floristic continentality increased most. Indeed, some (sub-)continental species increased markedly in frequency, such as *Cirsium oleraceum*, *Impatiens parviflora*, *Maianthemum bifolium* or *Ranunculus lanuginosus* (Appendix 5.6.4). However, floristic continentality increased most on sites initially in the AlFe or CatEx buffer range, whereas species richness increased most on sites in the SiliCar buffer range. Thus, the changed climatic conditions only partly explain the increase in species richness.

A ‘driver’ that may seem likely under these circumstances is that we recorded plant species occurrences more accurately than the original site investigators. Although we cannot exclude this possibility, we do not believe that the observed increase in species richness results from differences in sampling intensity alone. According to the scientists of the regional forest authorities, the site investigators in 1960 were very skilled in plant identification, which can also be judged from the fact that they recorded mosses. Additionally, the species that increased markedly in frequency were mostly relatively common forest plants that are easy to identify and difficult to overlook (Appendix 5.6.4).

Although the true driver must remain unclear, we want to speculate about two mechanisms for the increase in forest specialist richness. First, two alien forest specialists, *Impatiens parviflora* and *Prunus serotina,* which were almost absent in 1960, invaded many plots (Appendix 5.6.4). The expansion of *I. parviflora* into the forest interior during recent decades has been observed in numerous locations (Hédl et al. 2010, Jantsch et al. 2013, Lysik 2008, Naaf & Wulf 2011). The therophyte seems to benefit from disturbances by forest management activities (Chmura & Sierka 2007). Although our selected plots showed no signs of strong recent disturbance, most plots probably experienced some disturbance over the last half century. The invasion of *P. serotina* is probably promoted by strong propagule pressure from nearby invaded *Pinus sylvestris* plantations (Jagodziński et al. 2015).

Second, mesophilic forest specialist plants (e.g., *Circaea lutetiana*, *Hedera helix*, *Milium effusum*, *Oxalis acetosella*) have become more competitive on formerly wet sites (i.e., mostly on sites in the SiliCar buffer range) due to either drainage or enhanced summer drought or both. Increased deer abundances might have facilitated this colonization process. At the same time, the wetland species that are typical for these forests, but are mostly not restricted to forest habitats (and therefore do not count for forest specialist richness) have persisted on these sites (e.g., *Carex acutiformis*, *Geum rivale*, *Iris pseudacorus*, *Lycopus europaeus*). This increase in forest specialist richness on formerly wet sites does not stand in contrast to the observed positive effect of change in mF on changes in species richness (Table 5.3), indicating that species richness should have decreased where soil moisture decreased. This positive effect refers probably to originally more mesic sites that have become too dry to support some mesophilic forest plants. The persistence of wetland plant species for one or several decades after lowering of the groundwater table with the simultaneous expansion of more mesophilic forest plant species has also been observed in an alder swamp in Central Germany (Fischer 1993) and in floodplain forests in SE Czech Republic (Maděra 2001). In these studies, however, mF decreased markedly due to changes in species' cover. As we do not have exact information on the extent of drainage measures in our study region, we cannot fully reveal the importance of hydrological changes for the observed shifts in species diversity and composition.

The spread of two common mesic forest specialists, *Milium effusum* and *Oxalis acetosella*, can also explain the loss of floristic distinctiveness on moist to wet sites initially in the SiliCar buffer range (Figs. 5.2 and 5.3). Both species occurred in more than half of the plots in 1960 and then increased in frequency (Appendix 5.6.4). Species that tolerate a broad soil moisture and acidity range such as those mentioned have a great potential to homogenize communities (Naaf & Wulf 2010). Even the spread of species with a high allegiance to the surveyed habitats can result in floristic homogenization, as has been observed in floodplain forests in southern Wisconsin (Johnson et al. 2014). Together, these findings demonstrate that a homogenization of communities not necessarily implies a floristic degradation.

On sites initially in the AlFe and CatEx buffer range, the change in floristic distinctiveness was mainly determined by the change in mN. This suggests that the floristic homogenization was caused by the spread of nitrophilous species in response to nitrogen deposition. However, only two nitrophilous species, *Urtica dioica* and *Rubus idaeus*, were already sufficiently common in 1960 to have a homogenizing effect through their slight increase in frequency (Appendix 5.6.4). Some other nitrophilous species, e.g., *Galium aparine*, increased as well in frequency, but were less common in 1960 and therefore had a differentiating effect. The negative effect of the change in mN on the change in floristic distinctiveness is probably more due to the loss of some plant species known to prefer less fertile sites and which were initially common but then decreased in frequency, particularly on sites in the AlFe buffer range (e.g., *Deschampsia flexuosa*, *Poa nemoralis*, *Vaccinium myrtillus*). This is also supported by the weak negative effect of the change in mN on the change in total species richness (Table 5.3). According to the nitrogen homogeneity hypothesis (Gilliam 2006), the reduced spatial heterogeneity in nitrogen availability due to excess nitrogen deposition will increase the compositional similarity among sites. However, few studies so far were able to link the observed homogenization to the eutrophication of formerly oligotrophic sites (Hülber et al. 2008, Reinecke et al. 2014). In a large-scale resurvey study of 41 forest vegetation plots scattered across Europe, Dirnböck et al. (2014) found that the cover of oligotraphent species decreased the more nitrogen deposition exceeded the critical load for eutrophication effects. However, a significant homogenization was only found in 17 plots and the magnitude was not related to the exceedance of the critical nitrogen load. In a resurvey of nutrient-deficient temperate Scots pine forests after 45 years, Reinecke et al. (2014) observed the strongest decrease in beta diversity at the most oligotrophic sites where the decrease in oligotraphent species richness (particularly lichens) had been most pronounced. Together with the findings of these studies, our results suggest that the loss of oligotraphent species in response to nitrogen deposition is more important for the homogenization of communities than the spread of nitrophilous species.

Another oligotraphent and initially common species is *Deschampsia cespitosa*, which prefers moist soils. The marked decline in the frequency of this species on sites in the AlFe buffer range explains, why the negative effect of the change in mN on the change in floristic distinctiveness was enhanced when mF decreased most. Whether this species suffered more from excess nitrogen or decreased soil moisture is unclear.

The environmental changes not only caused changes in species diversity but also marked temporal species turnover. The contrasting effects of the changes in mR and mN and their interaction indicate that atmospheric deposition of both acidifying and eutrophicating substances is the main driver for this turnover. Under natural conditions, i.e., before the agricultural and industrial revolutions, soil acidity and soil fertility in temperate forests were largely coupled: acidic soils had low nutrient availability and neutral soils had high nutrient availability (e.g., Härdtle et al. 2004). Additionally, the plants' preferences or tolerances for nutrient availability and soil acidity are largely coupled (e.g., Diekmann et al. 1999). However, atmospheric deposition tends to dilute this acidity-fertility relationship: While the deposition of sulfur oxides and reduced nitrogen (ammonia) causes acidification, the deposition of both reduced and oxidized nitrogen causes eutrophication (Bobbink et al. 2010). In this resurvey, temporal species turnover was strongest when either the acidifying effect (e.g., on sites initially in the CatEx buffer range) or the eutrophying effect (e.g., on sites initially in the AlFe buffer range) was predominant. Under the effect of acidification, the decrease in soil pH led to local losses of acid-intolerant species (such as *Aegopodium podagraria*, *Festuca gigantea*, *Galium odoratum*) and local gains of acid-tolerant species (such as *Carex pilulifera*, *Dryopteris carthusiana*, *Polytrichum formosum*). This resulted in a decrease in mR and a high species turnover. The simultaneous decrease in mN was merely due to the correlation between Ellenberg R and N values rather than a decrease in nitrogen availability. Under the effect of eutrophication, the increase in nitrogen availability led to local gains of nitrophilous species (such as *Galium aparine*, *Urtica dioica*) and local losses of oligotraphent species (such as *Deschampsia flexuosa*, *Holcus mollis*, *Vaccinium myrtillus*). This resulted in an increase in mN and a high temporal turnover. The simultaneous increase in mR was merely due to the correlation between Ellenberg R and N values rather than an increase in soil pH. A similar increase in mR as a result of increasing mN has been found by other researchers, mostly on acidic sites (Thimonier et al. 1992, Reinecke et al. 2014, Verstraeten et al. 2013) and even when topsoil acidification was evident from pH measurements (Van Calster et al. 2007). However, the former phenomenon of decreasing mN as a result of decreasing mR has, to our knowledge, not yet been reported, although Diekmann et al. (1999) observed a decrease in some 'nitrophilous', acid-intolerant species.

5.7 Conclusions

First, the results of this study show that herb layer plant communities in the Prignitz region are responding to several interacting environmental change drivers. The indicated drivers, in order of decreasing importance, are atmospheric deposition of acidifying and eutrophicating substances, a decrease in soil moisture, likely due to drainage, a decrease in light availability due to the increased dominance of strongly shading tree species, a more continental climate in terms of summer drought, and the expansion of some exotic species. These drivers were at least partly responsible for the observed temporal species turnover, the increase in species richness and the floristic homogenization of communities. Although the significant decrease in browsing attractiveness might reflect an enhanced browsing pressure due to increased deer abundances, this driver did not contribute to explain changes in species diversity and temporal turnover. Indirectly, however, the increased deer abundances may have contributed to changes in species diversity by facilitating plot colonization through seed dispersal and effects of soil disturbance.

Second, initial site conditions, such as pH buffer range or soil moisture, should be taken into account when changes in species diversity and composition in relation to environmental changes are analyzed. Here, all three buffer range categories showed distinct changes in one or several variables.

Third, interactions between different drivers should likewise be considered, as they can broaden our understanding of how plant communities respond to environmental changes. Here, the interaction between the changes in mN (nutrient availability) and mR (soil reaction) clearly indicates that atmospheric deposition is the main driver for the temporal species turnover.

Although species richness generally increased, several of the observed changes are undesirable from a conservation point of view, such as the decline of some oligotraphent species on initially nutrient-poor sites, the spread of some nitrophilous species on these sites, the decline of acid-intolerant species on weakly buffered soils, the decline of some mesophilic forest species due to summer drought on well-drained sites, the impending decline of wetland species on sites initially close to the groundwater, and the invasion of two exotic species. Given the regional to global scale of the responsible drivers, only some of these changes might be counteracted by forest management. For instance, the closing of drainage ditches would allow wetland plants to recover and might prevent the loss of species sensitive to summer drought. The promotion of tree species with a high leaf litter quality, such as *Carpinus betulus* or *Tilia cordata*, instead of *Fagus sylvatica* could inhibit further acidification on weakly buffered soils.

Finally, we should bear in mind that the changes in species diversity and composition observed in this study (like in many other resurveys) are not representative for the entirety of deciduous forest in the landscape, but rather for semi-natural, relatively mature forests that are managed at low intensity. Sooner or later, these forests will experience severe disturbances, may it be through storm damage, fungal disease or management activities. Disturbance may reverse some trends observed here, such as increased shading and a decrease of less shade-tolerant species, and may enforce others, such as the invasion of exotic or nitrophilous species.

5.8 Acknowledgements

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General Discussion

In this final section the results of the Chapters 1 to 5 are used to discuss the impact of land use history and associated historical land cover changes on recent patterns and dynamics of herb-layer species richness in deciduous forests.

In the first section of this General discussion I assess, which species groups were affected by land use history in general and discuss how legacies from historical land cover changes may still be influencing recent species richness dynamics and today's species richness. In the second section I summarize how species richness patterns and dynamics are shaped by the environmental conditions and discuss the role of environmental legacies from historical agricultural land use. In the third section the role of recent and historical patch configuration and historical land cover changes for species richness patterns and dynamics in ancient and post-agricultural forests is assessed.

Response of species groups to land use history and associated historical land cover changes

Overall species richness

It is long known that ancient and post-agricultural forests differ in their herb-layer species richness and species composition (Rackham 1980, Peterken 1981, Peterken & Game 1984, Dzwonko & Loster 1989, van Ruremonde & Kalkhoven 1991). In following studies it was found that species richness in ancient forests is often still determined by the larger area and better connectivity that the forests had in historical times (Bellemare et al. 2002, Svenning et al. 2009, De Sanctis et al. 2010). For post-agricultural forests it was revealed that dispersal and to a lesser extent recruitment limitation lead to a delayed colonization of species (e.g. Singleton et al. 2001, Baeten et al. 2009 a, Butaye et al. 2001, Brunet et al. 2012).

In accordance to those previous studies we showed that land use history in terms of forest age was a significant predictor of species richness (Table 1.2). This result gives first hints for legacies of historical land cover changes because in the study area the land cover did not change substantially since the historical forest transformations and historical forest area loss did only occur in ancient forests, while post-agricultural forests have been newly established. This means that for our study forests with a different land use history (ancient vs. post-agricultural) do also represent different historical land cover changes. In addition to the significance of land use history for species richness, the historical habitat quality, a variable that is based on the reconstruction of the historical forest types in the year 1780, was also a significant predictor of present day species richness (Table 1.1).

Specialists vs. Generalists

Supposed legacies of historical land cover changes should be most pronounced in groups of species that only slowly adapt to changing environmental conditions. Accordingly we showed that richness of species with a high bound to forests (forest specialists) was significantly dependent on land use history in terms of forest age, while richness of generalists was not. Our finding is supported by numerous studies (e.g. Graae 2000, Dumortier et al. 2002, Svenning et al. 2009, De Sanctis et al. 2010) but there is also one example where generalist numbers decreased in post-agricultural stands with increasing patch age (Brunet et al. 2011). This finding is most likely attributed to a substantial increasing in shading in the first decades of the establishment of a forest patch, which was not the case here. The post-agricultural forest patches in our study area do persist longer and while we also found increased shading over the last decades (Chapter 5), it seems that this effect was independent from land use history and more akin to changes in forestry practices and overall environmental conditions (Chapter 4; Chapter 5).

Species in life-history trait groups

The compilation of (sub)-groups of species based on their life-history traits reveals further insight on how land use legacies may act on present day species richness. First, we found that species with short-distance dispersal potential were dependent on land use history, while species with long-distance dispersal capacities were not (Table 1.1, Table 1.3). This connection is easy to understand because species with short-distance dispersal capacities are directly dependent on patch connectivity and degree of fragmentation, which changed dramatically in history in the study area, and those species also take longer to colonize a newly established forest patch in general (Dzwonko & Loster 1989, Grashof-Bokdam 1997, Verheyen et al. 2006). It was therefore no surprise that species with short distance dispersal capacities were the group of species that were most dependent on land use legacies in both, ancient and post-agricultural forests among all other groups (Chapter 2; Chapter 3). In post-agricultural forests they contributed most to the colonization credit and in ancient forests they were the only group of species that were significantly dependent on historical patch connectivity.

Second, extensive clonals and geophytes (most forest geophytes have the ability to reproduce vegetatively), were dependent on land use history, i.e. those species were significantly more abundant in ancient forests than in post-agricultural forests (Table 1.1, Table 1.3; Fig. 4.3). Clonal species are highly dependent on habitat area and prone to area loss (Lindborg et al. 2012). They are also slow colonizers but have the ability to persist for a prolonged time when connectivity is interrupted. It is therefore likely that clonal species would depict long-term legacies. In our study, an effect of historical land cover changes could only be shown for post-agricultural forests where extensive clonals contribute substantially to the colonization credit (Chapter 3) but not for ancient forests, although we predicted that clonal species would especially be responsible for an extinction debt in ancient forests due to their prolonged persistence (Chapter 2). In this respect, we have shown that the contribution to the colonization credit in post-agricultural forests was most likely not due to the clonal ability itself, i.e. due to environmental limitation, but due to the limited inter-patch dispersal abilities of clonal species which insists that land use legacy effects were not especially pronounced in clonal species (Chapter 3).

In sum we can conclude that the difference in herb-layer species richness between ancient and post-agricultural forest can be attributed to the forest specialists and especially to species that only have short distance dispersal capabilities. It is therefore highly likely that patch configuration and either the historical fragmentation and decline in area in the ancient forests, the establishment of post-agricultural forests or both factors are main factors for species richness differences and the different species richness development over time. But also different environmental conditions, which could stem from the different land use history of ancient and post-agricultural forests, sensu "environmental legacies", could be responsible for species richness differences.

The role of recent environmental conditions and environmental legacies from historical land use for species richness patterns and dynamics

Several studies indicate that soils in forests on former agricultural land may still represent the conditions before the forest was established (Koerner et al. 1997, Verheyen et al. 1999, Dupouey et al. 2002, Blondeel et al. 2018, but see Compton & Boone 2000, Flinn et al. 2005). For example, the P-level of soils in post-agricultural forests is often higher than the level in ancient forests due to the former agricultural land use (De Schrijver et al. 2012, Baeten et al. 2009 a). Biodiversity is often higher under P-limitation (Schelfhout et al. 2015) and this could mean that environmental limitation may be a more severe factor for species richness in post-agricultural forests, especially for forest specialists. In general species richness in all groups was to a substantial amount determined by the local environmental conditions, especially positively by soil moisture and nutrient supply, but also negatively by P-availability (Table 1.1; Table 2.1; Chapter 3; Chapter 5), i.e. the environmental conditions were important and legacies can principally be expected. Also changes in environmental conditions, like increased atmospheric deposition, increased shading and a decrease in soil moisture (Chapter 5) over the last decades, were the main factor for the joint species richness changes in both, ancient and post-agricultural forests (Chapter 4). We found that many environmental factors interact with the initial site conditions of a patch. For example, species richness increased dependent on decreasing acidification but only on initially moderately acidic to base-rich sites (Fig. 5.2). This means that different initial site conditions could be another factor to explain species richness differences and different species richness dynamics, for instance, when the range of environmental conditions is reduced due to former agricultural land use.

However, we showed that environmental legacies could at best partly explain the differences in species richness. With one exception the effects of the environmental conditions on species richness were similar in all herb-layer species groups, e.g. the environmental conditions did not affect richness of specialists and generalists differently, and the effects were similar among ancient and post-agricultural forests (Chapter 1 to Chapter 3). Only soil-pH was a significant predictor of species richness of all species (but not in groups) in the post-agricultural forests, but not in the ancient forests. A possible interaction of the soil-pH with land use history determining species richness cannot be fully excluded but we explain this result with the different analysis methods we used in the studies in Chapter 2 and 3 (single pH-variable vs. pch-Axis) because we showed that the environmental conditions were comparable in ancient and post-agricultural forests, i.e. largely independent from the land use history of a patch (Table 4.1). We further covered a broad range of different forest stands with different dominant tree species and different site conditions in all individual studies, i.e. all studies also covered a wide range of initial site conditions. Finally, the environmental conditions were no significant predictor for the overall magnitude of the colonization credit in post-agricultural forests (however, in some groups, see Chapter 3) and while we could not test this, it appears that the time-span since the agricultural land use ended was long enough so that soil conditions in post-agricultural forests did approximate to soil conditions in ancient forests already by the time of the initial survey in the 1960ies (Chapter 4).

In conclusion we can assume that different environmental conditions in ancient and post-agricultural forests were not the main factor for species richness differences between ancient and post-agricultural forests and also no major limiting factor for species richness recovery in post-agricultural forests. The result further shows that the land use prior to the establishment of the post-agricultural forest (specifically arable land or grassland) played a minor role for present-day herb-layer species richness in our study (see also Chapter 3).

The role of recent and historical patch configuration for species richness patterns and dynamics

Overall importance of patch configuration

In contrast to the fundamental theory of island biogeography (Mac Arthur & Wilson 1967) and many field studies (e.g. Butaye et al. 2001, Petit et al. 2004, De Sanctis et al. 2010) recent patch area and connectivity were, with the exception of infrequent species, no significant predictor for species richness when we studied species richness patterns in both, ancient and post-agricultural forests (Table 1.1). This could either mean that patch configuration was generally not important in the study area, which is unlikely, or that species richness was still (at least partly) determined by historical patch configuration. We showed that the latter is true; because when we analyzed ancient and post-agricultural forest stands separately (Table 2.3; Table 3.2) species richness in all groups was significantly determined by recent patch area. Recent connectivity was also important, but largely only in post-agricultural forests. On the other hand, historical connectivity was important for specialist species richness in ancient forests but recent connectivity was not important. Those diverging results insist that the influence of both, recent and historical patch configuration was and still is different in ancient and post-agricultural forests and that those differences ultimately led to today's species richness differences.

Patch configuration in ancient and post-agricultural forests

In ancient forests we showed that the extinction debt had been largely paid, meaning that the influence of historical land cover changes on today's species richness was only marginal and species richness was in quasi-equilibrium. The almost complete payment of the extinction debt was an unexpected result in the light of previous studies who found persistent extinction debts in the forest herb-layer community (Paltto et al. 2006, Piessens & Hermy 2006, Vellend et al. 2006) but can be explained with the in comparison more dramatical historical changes, i.e. the very high area loss and fragmentation in a comparably short time period (see further Chapter 2, Section 5).

Nevertheless we found last signs for legacies of the historical land cover changes and for an associated extinction debt but they were all comparably weak. For one, infrequent species (less than 25 localities out of 183 forest patches (≤ 13%)) were significantly dependent on historical habitat quality (Table 1.1), which suggests a connection of species "rarity" to historical land cover changes. A high number of infrequent species is a sign that species (meta)-populations are at their extinction threshold in the sense of Hanski & Ovaskainen (2002) and those species are often responsible for extinction debts (Ewers & Didham 2006, Kuussaari et al. 2009) because few individuals from a previously much larger population may persist for a prolonged time. We did not test for changes of infrequent species numbers in our models because richness of infrequent species was only dependent on historical habitat quality and not on land use history, but in the analysis of winner and loser species, exclusive loser species in ancient forests were not infrequent (the least abundant was found in 14% of all patches) but rather abundant (Table 4.3). Then, as a last glimpse of an extinction debt, we found that richness of specialists and species with short-distance dispersal capabilities was still dependent on historical patch connectivity (but not on historical area), while recent patch connectivity was not important (Table 2.3). This result implies two things: First, from the reconstruction of the land use history we know that the extensive habitat fragmentation occurred after the massive reduction in forest area, i.e. the relaxation time in terms of habitat fragmentation was shorter than for the area loss, which explains why historical patch connectivity still affected species richness while historical patch area had no effect at all. Second, it is safe to say that today's connectivity between ancient forest patches of the Prignitz is largely interrupted (Table 2.3; Table 4.2, Fig. 4.4). Our results for ancient forests mean that the reasons for species richness differences are largely to be found in the post-agricultural forests which could be validated with the finding of a colonization credit of up to 9 species (Chapter 3; Chapter 4).

The analyzed post-agricultural forests in the Prignitz were established after the massive decrease in forest area, and about 70% of the analyzed patches have been established after 1880, i.e. the time-span for species to colonize a patch and establish a viable population and pay off the colonization credit, was shorter than the time a species "had to persist" in ancient forests to account for an extinction debt. But, it seems that relaxation time was not the only important factor for the lower species richness in post-agricultural forests because then the colonization credit in younger forests should be always higher and there should be more forest specialists in older forests, respectively (Jacquemyn et al. 2001, Hérault and Honnay 2005, Jamoneau et al. 2011). In our analysis the magnitude of colonization credit was not significantly higher in younger forests (Chapter 3) but on the other side we saw that the colonization credit was reduced over the last decades (Chapter 4). This result sounds like a contradiction at first but this contradiction can be solved when focusing on connectivity. It appears that connectivity obscured the effect of patch age and relaxation time, because our data suggests that the connectivity of many forest patches was totally interrupted which means that the colonization credit would never pay off, irrespective of patch age (Chapter 3, Section 6). On the other hand, in well-connected post-agricultural forests the colonization credit was lower, or we even found more species that predicted by the present day area and connectivity (Fig. 3.1).

In the resurvey study (Chapter 4) we then specifically focused on those better-connected forests, as a payment of colonization credit could not be expected in highly isolated forests. In those forests we found a mean colonization credit of 1.5 species in the group of forest specialists (Fig. 4.3), which was lower, than the average colonization credit of 4.7 specialists that we found in post-agricultural forests we studied in Chapter 3. The colonization credit was still significant in 2014 but in 1960 it was more than twice as high and amounted to 2.7 species. Thus we showed that the colonization credit had been actually paid off since 1960 and that species richness in ancient and post-agricultural forests did approximate (Fig. 4.3). As predicted, the colonization credit has been paid off due to a higher increase of forests specialists and ancient forest indicator species in post-agricultural forests, while number of all species increased in both forest types equally (Table 4.2, Fig. 4.3). Connectivity was important for this recovery; though only at a significance level of $P = 0.10$ (p-value of 0.079); and our models predicted that species richness in highly connected post-agricultural forests would fully approximate or even (theoretically) exceed species richness of ancient forests (Fig. 4.4).

With the verification of an approximation of species richness between ancient and post-agricultural forests we have shown that it is theoretically possible that newly established forests could become similar to ancient forests in their species richness and composition. The preconditions for this development are the availability of source populations from remaining ancient forests and comparable environmental conditions. However, it could take many decades until an approximation starts and supposedly centuries until most of the forest specialists that persist in the ancient forest patches of the area have colonized a newly established forest patch. This is a time-scale that exceeds the scope of typical conservation measures and programs. Furthermore, it has to be considered that a full “reconstruction” of the forest plant species diversity to a state before the large deforestation took place seems impossible and it is also highly unlikely to stop or counterbalance species extinctions in forests that still exhibit an extinction debt, at least in areas with highly fragmented forests and in areas where the fragmentation occurred long ago.

Conclusions

We showed that present-day species richness patterns were still shaped by historical land cover changes that ranged back to more than a century. Land use legacies especially act on richness of forest specialists and species with short-distance dispersal capabilities and especially in post-agricultural forests. In those forests the magnitude of colonization credit and its gradual payment was determined by patch connectivity and corresponding dispersal limitation. Environmental legacies from historical agricultural land use could not explain species richness differences but present-day environmental conditions and recent environmental changes were the most important factor for overall species richness patterns and an overall species richness dynamics.

Summary

Over the last years there is an increasing awareness that historical land cover changes and associated land use legacies may be important drivers for present-day species richness and biodiversity due to time-delayed extinctions or colonizations in response to historical environmental changes. Historically altered habitat patches may therefore exhibit an extinction debt or colonization credit and can be expected to lose or gain species in the future. However, extinction debts and colonization credits are difficult to detect and their actual magnitudes or payments have rarely been quantified because species richness patterns and dynamics are also shaped by recent environmental conditions and recent environmental changes.

In this thesis we aimed to determine patterns of herb-layer species richness and recent species richness dynamics of forest herb layer plants and link those patterns and dynamics to historical land cover changes and associated land use legacies. The study was conducted in the Prignitz, NE-Germany, where the forest distribution remained stable for the last ca. 100 years but where a) the deciduous forest area had declined by more than 90 per cent (leaving only remnants of "ancient forests"), b) small new forests had been established on former agricultural land ("post-agricultural forests"). Here, we analyzed the relative importance of land use history and associated historical land cover changes for herb layer species richness compared to recent environmental factors and determined magnitudes of extinction debt and colonization credit and their payment in ancient and post-agricultural forests, respectively.

We showed that present-day species richness patterns were still shaped by historical land cover changes that ranged back to more than a century. Although recent environmental conditions were largely comparable we found significantly more forest specialists, species with short-distance dispersal capabilities and clonals in ancient forests than in post-agricultural forests. Those species richness differences were largely contingent to a colonization credit in post-agricultural forests that ranged up to 9 species (average 4.7), while the extinction debt in ancient forests had almost completely been paid. Environmental legacies from historical agricultural land use played a minor role for species richness differences. Instead, patch connectivity was most important. Species richness in ancient forests was still dependent on historical connectivity, indicating a last glimpse of an extinction debt, and the colonization credit was highest in isolated post-agricultural forests. In post-agricultural forests that were better connected or directly adjacent to ancient forest patches the colonization credit was way smaller and we were able to verify a gradual payment of the colonization credit from 2.7 species to 1.5 species over the last six decades.

Deutschsprachige Zusammenfassung

In den vergangenen Jahren reift immer mehr die Erkenntnis, dass historische Landnutzungsveränderungen und deren Folgewirkungen einen wichtigen Einfluss auf die heutige Artenvielfalt und Biodiversität haben können. In Habitaten, deren Landnutzung und Fläche sich in historischer Zeit verändert hat kann aufgrund von verzögerten Aussterbe- und Einwanderungsprozessen eine erhöhte oder verringerte Artenvielfalt vorliegen, die nicht den heutigen Umweltbedingungen entspricht. Es liegen Aussterbeschulden oder Einwanderungs- bzw. Kolonisierungskredite vor, welcher über die Zeit mit Artverlusten oder Zugewinnen von Arten bezahlt werden. Aussterbeschulden oder Einwanderungskredite und deren Bezahlung sind schwierig zu ermitteln, da einerseits Informationen zu historischen Landnutzungsveränderungen oft fehlen und andererseits auch heutige Umweltfaktoren einen wichtigen Einfluss auf die Artenvielfalt haben.

Das Ziel dieser Arbeit war es die heutigen Muster der Artenvielfalt von Waldbodenpflanzen in Laub- und Mischwäldern und deren Veränderungen über die letzten 60 Jahre zu ermitteln und diese Muster im Hinblick auf historische Landnutzungsveränderungen zu untersuchen. Das Studiengebiet umfasst große Teile der Prignitz (Brandenburg und angrenzende Teile von Sachsen-Anhalt), ein Gebiet, dessen Waldanteil sich in den letzten 100 Jahren kaum verändert hat, in dem sich jedoch seit dem Ende des 19ten Jahrhunderts der Anteil historisch alter Wälder (ohne historische nachgewiesene agrarliche Nutzung) um mehr als 90% reduziert hat, während an anderer Stelle wenige neue Wälder auf vorigen Agrarflächen etabliert wurden. Im Rahmen dieser Studie wurde zunächst die Artenvielfalt und deren aktuelle Veränderung in historisch-alten Wäldern und neu etablierten Wäldern untersucht und verglichen. Um den Einfluss von historischen Landnutzungsveränderungen auf die Artenvielfalt zu ermitteln, wurde die historische und heutige Vernetzung der Waldflächen analysiert, die Umweltbedingungen in historisch-alten Wäldern und neu etablierten Wäldern verglichen und der Umfang und die Bezahlung der Aussterbeschulden und der Kolonisierungskredite ermittelt.

Die Arbeit zeigt, dass historische Landnutzungsveränderungen die heutige Artenvielfalt noch immer beeinflussen. Obwohl die heutigen Umweltbedingungen in historisch-alten und neu etablierten Wäldern vergleichbar waren, war die Gesamtartenzahl in historisch-alten Wäldern signifikant höher und in diesen Wäldern wurden insbesondere mehr Waldspezialisten und sich nur über kurze Enfernung ausbreitende Pflanzenarten gefunden. Die Unterschiede in den Artenzahlen sind vor allem auf einen Kolonisierungskredit in neu etablierten Wäldern zurückzuführen, während die Aussterbeschulden in historisch-alten Wäldern weitgehend bezahlt wurden. Der Kolonisierungskredits war am höchsten in isoliert gelegenen Waldflächen und belief sich auf bis zu 9 Arten (im Mittel 4,7). Der Kolonisierungskredit in besser

vernetzten und in direkt an historisch-alten Wäldern angrenzenden Flächen war deutlich geringer. In diesen Wäldern konnte eine Verringerung des Kolonisierungskredites von im Mittel 2,7 zu 1,5 Arten über die letzten sechs Jahrzehnte nachgewiesen werden.

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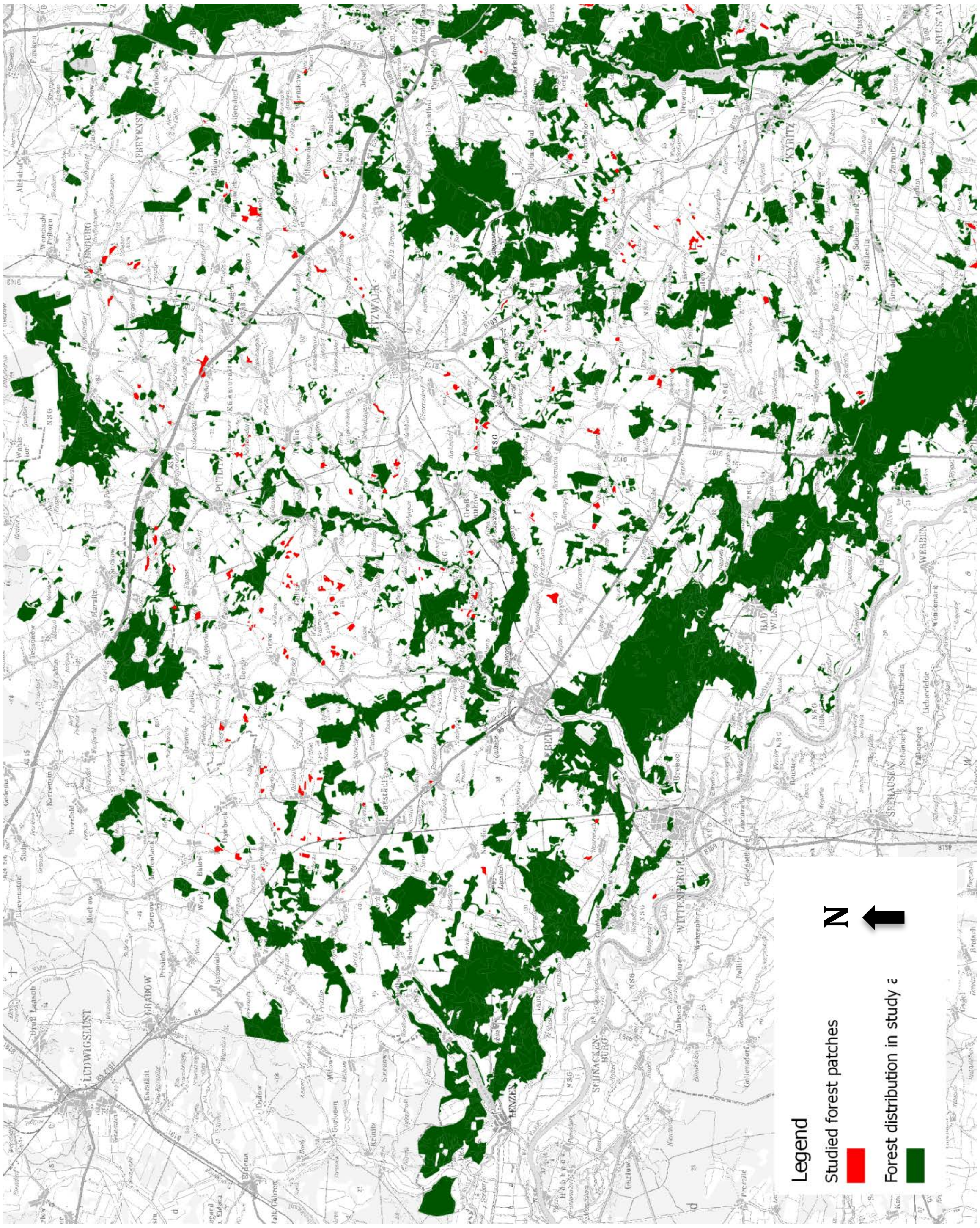
Appendix 1



Appendix 1.1. Studied forest patches and forest distribution in the study area (Prignitz, Germany). Map scale: 1: 600000

Appendix 1.2. Independent contributions of explanatory variables to the species number of all species and the species groups.
Left of the slash: percentage of contribution; right of the slash: z-score of randomisation test; * = significant at α = 0.05.
Significant results are in bold letters.

≤5 ha forest patches	**All species**	**Growth form**			**Frequency**	**Habitat preference**		**Dispersal potential**		**Life form**		
		Trees	Shrubs	Herbs	Infrequent plant species	Forest specialists	Generalists	Short-distance dispersal	Long-distance dispersal	Geophytes	Hemicryptophytes	Therophytes
Patch configuration												
Patch size	**16.5 / 2.6***	**15.6 / 1.7***	11.2 / 0.1	**14.1 / 2.3***	**14.5 / 2.8***	10.2 / 1.3	**14.1 / 1.8***	4.5 / 0.2	**23.1 / 3.1***	3.3 / -0.2	**17.8 / 3.4***	18.4 / 1.2
Patton-shape index	1.0 / 0.0	10.2 / 1.0	2.0 / -0.4	-0.2 / -0.2	-0.1 / -0.6	-0.2 / -0.5	0.9 / 0.1	-0.1 / -0.3	-0.7 / -0.4	-0.9 / -0.4	-0.5 / -0.3	0.5 / -0.6
Inter-patch distance	2.0 / -0.3	0.7 / -0.6	15.4 / 1.0	1.1 / -0.4	2.2 / -0.2	0.7 / -0.5	2.5 / -0.3	0.7 / -0.5	0.7 / -0.6	5.3 / 0.4	0.4 / -0.5	0.9 / -0.6
Patch quality												
Moisture level	**21.2 / 6.5***	4.7 / -0.1	5.0 / -0.2	**34.5 / 9.9***	**15.0 / 4.8***	**18.8 / 5.4***	**46.5 / 9.2***	**21.0 / 5.2***	**39.1 / 7.1***	**26.2 / 7.1***	**36.5 / 9.7***	**32.0 / 4.1***
Nutrient level	**36.4 / 7.5***	**19.0 / 1.7***	**33.0 / 1.8***	**33.7 / 8.0***	**45.5 / 10.8***	**35.1 / 8.2***	**27.6 / 6.0***	**39.6 / 9.1***	**22.9 / 4.3***	**27.9 / 5.1***	**32.9 / 8.1***	**28.7 / 3.4***
Patch heterogeneity												
Structuring elements	**15.0 / 2.8***	**32.0 / 5.2***	6.4 / -0.1	**10.5 / 2.2***	**13.4 / 2.6***	**20.9 / 3.8***	1.0 / -0.3	**16.1 / 3.0***	7.0 / 0.8	**15.7 / 2.5***	7.8 / 1.3	2.6 / -0.3
Forestry site units	0.6 / -0.6	4.9 / 0.3	17.0 / 0.6	0.7 / -0.6	0.6 / -0.6	0.5 / -0.7	4.4 / 0.0	0.3 / -0.7	1.0 / -0.6	1.8 / -0.4	1.2 / -0.4	9.7 / 0.3
Patch history												
Forest remnant	3.0 / 0.0	6.3 / 0.6	3.4 / -0.4	2.5 / 0.0	3.2 / 0.3	5.9 / 0.8	1.6 / -0.5	**10.6 / 1.8***	2.8 / -0.2	9.4 / 1.3	1.8 / -0.4	4.5 / -0.2
Historical habitat quality	4.3 / 0.3	6.6 / 0.6	6.6 / -0.1	3.1 / 0.2	5.8 / 1.0	8.2 / 1.4	1.4 / -0.4	7.4 / 1.3	4.1 / 0.1	11.4 / 1.5	2.0 / -0.2	2.6 / -0.5

>5.0 ha forest patches	**All species**	**Growth form**			**Frequency**	**Habitat preference**		**Dispersal potential**		**Life form**		
		Trees	Shrubs	Herbs	Infrequent plant species	Forest specialists	Generalists	Short-distance dispersal	Long-distance dispersal	Geophytes	Hemicryptophytes	Therophytes
Patch configuration												
Patch size	1.8 / -0.1	1.5 / -0.3	4.4 / 0.7	1.4 / -0.1	1.5 / 0.0	1.2 / -0.3	1.5 / -0.3	0.8 / -0.4	0.9 / -0.6	0.6 / -0.5	2.0 / 0.0	2.9 / -0.4
Patton-shape index	4.2 / 0.2	8.6 / 0.8	6.4 / 0.7	2.9 / -0.2	6.2 / 1.0	4.5 / 0.1	0.7 / -0.6	4.0 / 0.1	1.2 / -0.6	2.9 / -0.1	3.4 / -0.1	0.9 / -0.6
Inter-patch distance	2.8 / 0.2	1.6 / -0.2	6.4 / 1.0	2.4 / 0.0	2.8 / 0.1	2.5 / 0.3	2.0 / 0.5	3.4 / 0.2	1.6 / -0.2	3.5 / 0.6	2.6 / 0.0	0.5 / -0.7
Patch quality												
Moisture level	6.1 / 1.2	6.8 / 0.7	4.3 / 0.3	8.3 / 1.6	**7.8 / 2.1***	5.5 / 1.0	**20.3 / 2.2***	5.1 / 0.5	**11.6 / 2.3***	**9.3 / 2.8***	7.1 / 1.3	15.7 / 1.1
Nutrient level	**39.9 / 7.8***	**26.3 / 3.5***	**32.4 / 5.0***	**43.1 / 7.5***	**52.4 / 10.9***	**40.3 / 6.4***	**44.8 / 4.3***	**37.9 / 6.4***	**48.5 / 7.3***	**38.6 / 9.0***	**46.8 / 7.6***	21.5 / 0.9
Patch heterogeneity												
Structuring elements	**20.8 / 5.5***	**32.5 / 7.8***	**23.1 / 6.2***	**17.6 / 3.8***	**13.5 / 3.1***	**21.0 / 5.4***	10.3 / 0.7	**15.3 / 3.0***	**19.4 / 2.8***	**20.6 / 6.0***	**17.3 / 3.2***	1.7 / -0.5
Forestry site units	**8.9 / 3.2***	4.4 / 0.9	7.3 / 1.6	**9.9 / 3.2***	**6.1 / 3.0***	**9.1 / 3.9***	10.0 / 0.8	**11.6 / 3.3***	**11.4 / 3.0***	**5.3 / 3.0***	**11.6 / 3.0***	17.6 / 1.5
Patch history												
Forest remnant	6.2 / 1.1	7.9 / 1.2	6.0 / 1.0	5.6 / 0.7	3.4 / 0.3	6.4 / 1.1	3.9 / -0.1	8.5 / 1.3	2.0 / -0.2	**7.2 / 1.7***	3.9 / 0.3	11.6 / 0.2
Historical habitat quality	**9.4 / 1.8***	10.4 / 1.5	9.7 / 1.4	8.7 / 1.6	6.3 / 1.0	9.5 / 1.6	6.6 / 0.3	**13.3 / 2.0***	3.5 / 0.2	**12.1 / 2.6***	5.3 / 0.6	27.6 / 1.3

Appendix 2

Appendix 2.1

Numbers of selected patches in area classes with class thresholds as it was used for stratified random sampling.

threshold area for groups in ha	threshold area in log m^2-scale	total number of patches	selected number of patches
0.81	8.99	22	19
2.20	9.99	54	29
5.99	10.99	54	26
16.28	11.99	33	24
25.00	12.42	15	15

Appendix 2.2

Main forest community types in the Prignitz region, based on Hoffmann and Pommer (2005).

Forest community type	Site conditions	Share of deciduous forest area[a]	share of selected community types
Alder forest (*Alnus glutinosa*)	Permanently wet, primarily nutrient-rich, organic soils (fenland)	16.6	8.8
Ash-alder forest	Wet, nutrient-rich, mineral soils	2.1	6.6
Birch-oak(-hornbeam) forest with *Molinia caerulea*	Moist, nutrient-poor soils (sand with groundwater influence)	7.4	12.1
Oak-hornbeam forest with *Stachys sylvatica*	Moist, base-rich soils (loam with groundwater influence)	1.5	3.3
Oak forest with Agrostis capillaris	Dry, sandy, nutrient-poor soils	44.1	42.9
Beech forest with *Maianthemum bifolium*	Nutrient-poor soils without groundwater influence	28.4	26.4

[a] Forest-type proportions were calculated on the basis of 178 ancient forest patches in the study area which were used as the pool for stratified random sampling. , The information on the forest community types was only available for approximately 45% of the deciduous forest area. This discrepancy results in a level of uncertainty in the true forest-type proportions. After gaining further knowledge from our field campaign, the share of oak-hornbeam forests is likely higher in reality.

Appendix 2.3

Results of the principal component analysis (with varimax rotation) of the soil variables. Given are the standardized loadings of the principal components, i.e. the correlations between the soil variables and the principal components. Eigenvalues of the components are given in parentheses.

	PC1 (39%)	PC2 (29%)	PC3 (16%)
Moisture	0.89	0.19	0.11
C/N ratio	0.30	-0.77	0.16
Calcium	0.52	0.81	-0.05
Phosphorus	0.03	-0.21	0.84
Potassium	0.32	0.03	0.77
Magnesium	0.62	0.65	0.12
pH	0.06	0.92	-0.11
Carbon	0.96	-0.14	0.20
Nitrogen	0.96	0.05	0.18

Appendix 2.4

Substrate types for geological diversity.

1) Peat or moor mud over sand
2) Peat or moor mud over till or silt
3) Peat or moor mud; undifferentiated
4) Moor-till
5) Sand; dry
6) Gravel-sand
7) Weak humus-rich sand
8) Humus-rich sand
9) Weak loamy, gravel-sand
10) Loamy sand
11) Fine sand or silt
12) Not classified

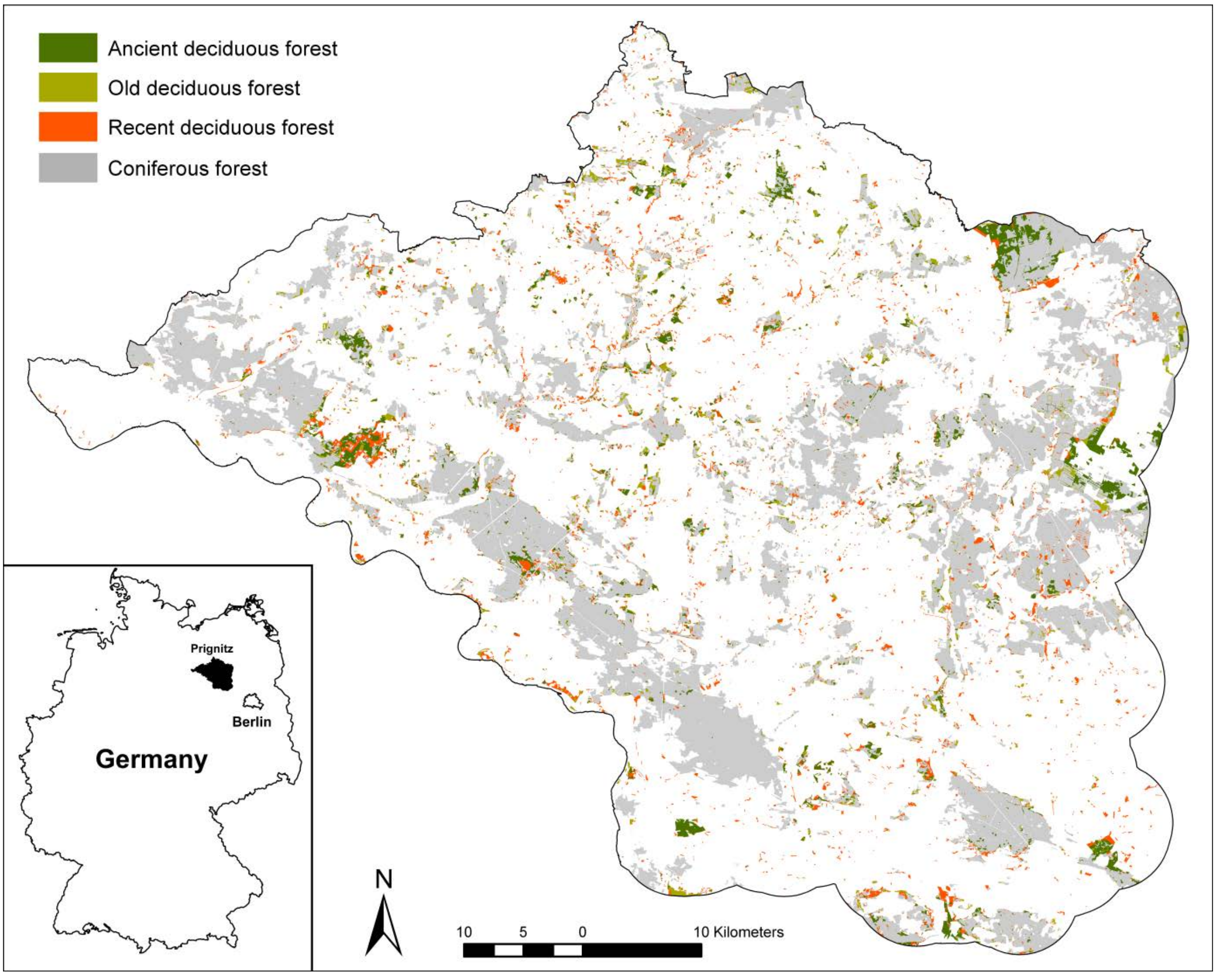
Appendix 2.5

Standardized regression coefficient and significance of historical patch connectivity in species richness models when excluding selected habitat quality and habitat heterogeneity variables from the models. Variables that were already dropped in the model selection process (see method section 2.3, subsection: "Data Analysis") are indicated with an "x". Here, the regression coefficient and significance are equal to the main results (Table 2.3).

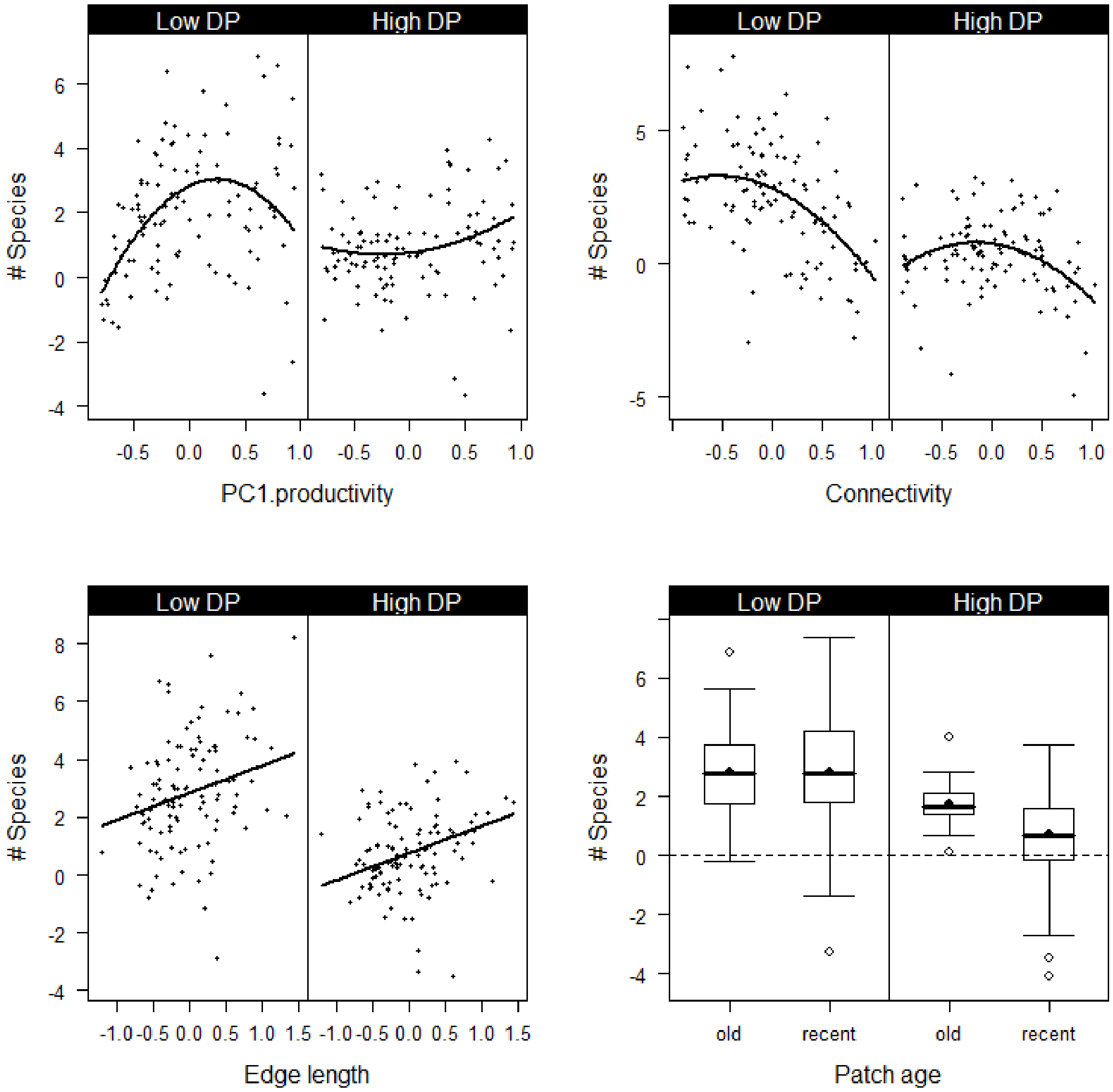
Omitted variable	Models for specialist species richness	Models for species richness of specialists with short-distance dispersal potential
Moisture	$0.07^{n.s.}$	0.12*
Soil pH	x	x
P-availability	$0.07^{n.s.}$	0.12*
Subpatch diversity	0.11*	0.12*
Geological diversity	$0.05^{n.s.}$	$0.11^{n.s.}$
Topographical heterogeneity	$0.05^{n.s.}$	$0.06^{n.s.}$
Edge effect	0.10*	x

Appendix 3

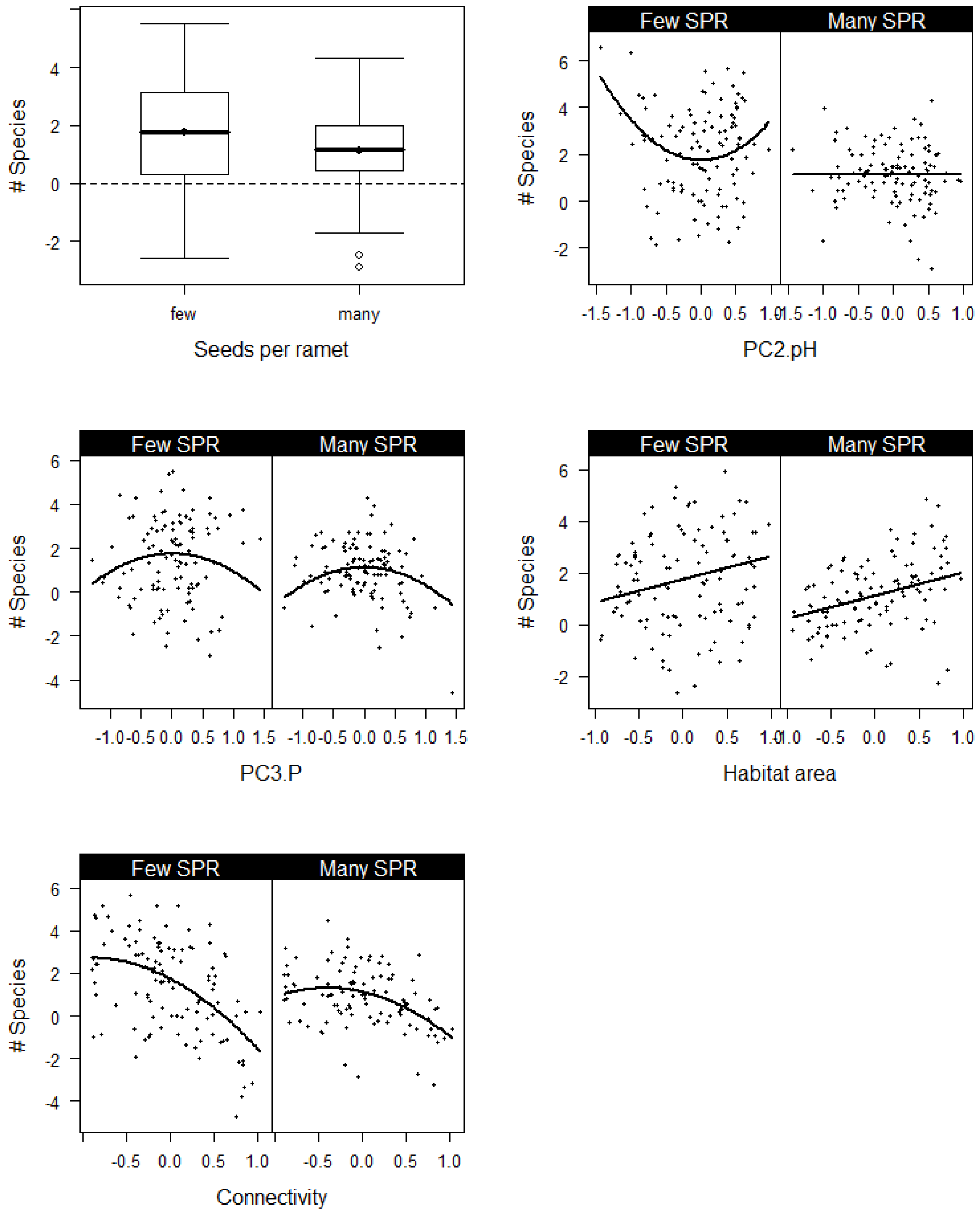
Appendix 3.1 - Supplementary figures for Chapter 3



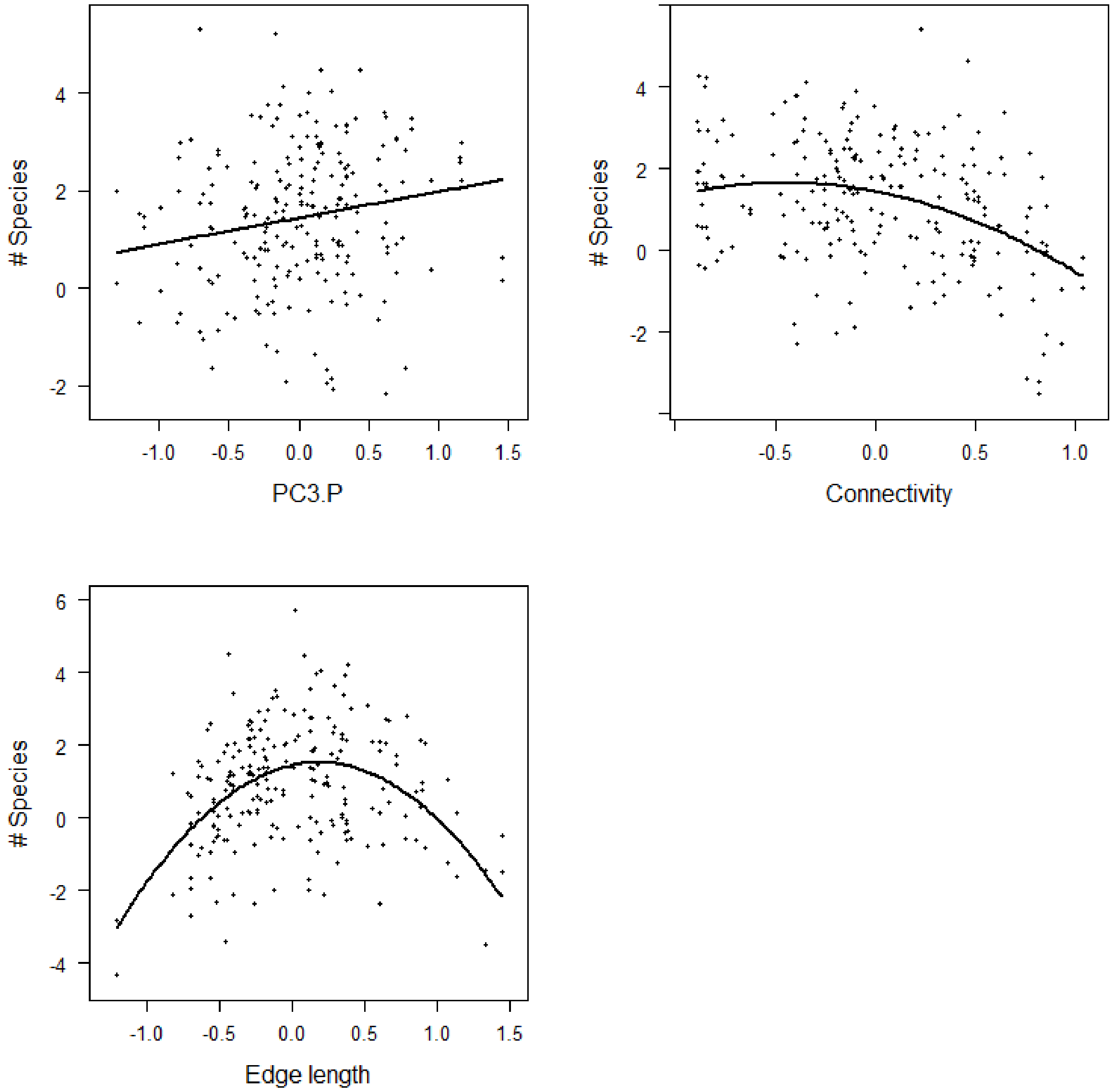
Appendix 3.1.1. Distribution of ancient, old and recent deciduous forest in the study region (see Chapter 3 for explanation).



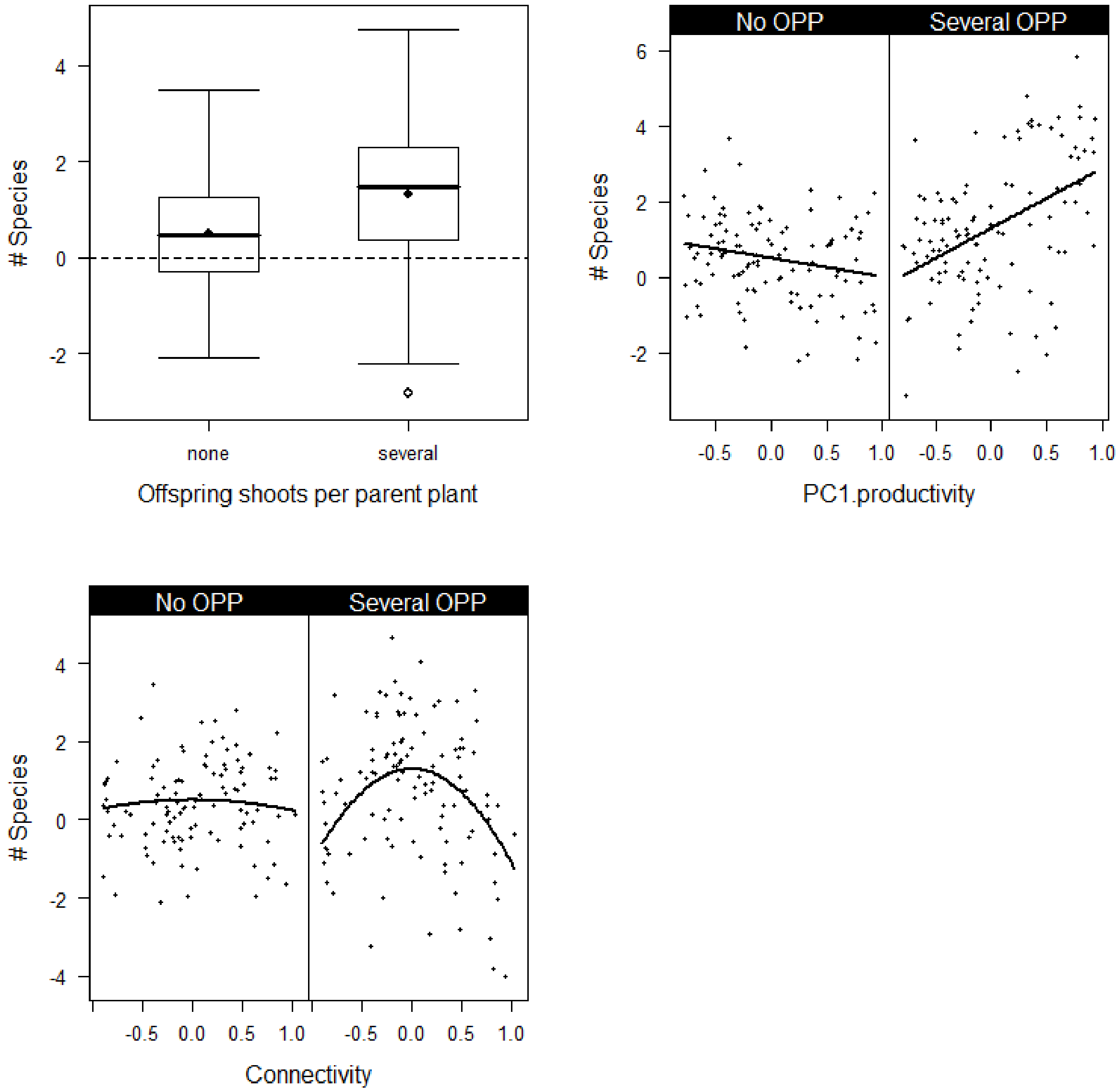
Appendix 3.1.2 Visualization of the effects of dispersal potential (DP), PC1.productivity, connectivity, edge length and patch age on the magnitude of the colonization credit as resulting from the linear mixed model accounting for species with low vs. high DP, presented in Table 3.2. Boxplots are standard boxplots.



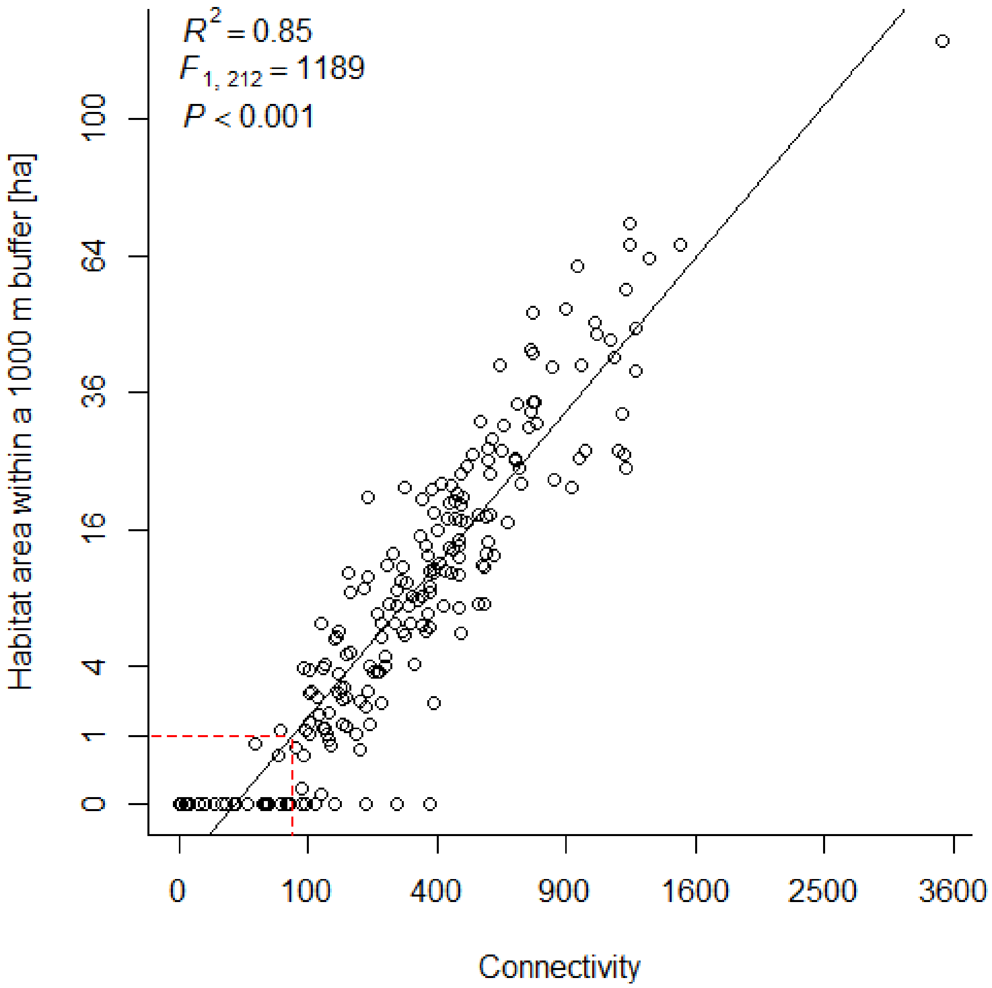
Appendix 3.1.3 Visualization of the effects of the number of seeds per ramet (SPR), PC2.pH, PC3.P, habitat area and connectivity on the magnitude of the colonization credit as resulting from the linear mixed model accounting for species with few vs. many SPR, presented in Table 3.2. Boxplots are standard boxplots.



Appendix 3.1.4 Visualization of the effects of PC3.P, connectivity and edge length on the magnitude of the colonization credit as resulting from the linear mixed model accounting for species with light vs. heavy seeds (seed mass not significant), presented in Table 3.2.



Appendix 3.1.5 Visualization of the effects of the number of offspring shoots per parent plant (OPP), PC1.productivity and connectivity on the magnitude of the colonization credit as resulting from the linear mixed model accounting for species with no vs. several OPP, presented in Table 3.2. Boxplots are standard boxplots.



Appendix 3.1.6 Linear regression of the habitat area within a 1000 m buffer around each patch against the connectivity measure used in the study (incidence function model derived from Hanski (1994); see Chapter 3.4. Both variables were sqrt-transformed. The approximate connectivity threshold referred to in the Discussion of the main text is marked in red.

Reference

Hanski, I., 1994. A practical model of metapopulation dynamics. J Anim Ecol 63:151–162.

Appendix 3.2 - Supplementary tables for Chapter 3

Appendix 3.2.1

Main deciduous forest community types in the Prignitz region.

Forest community type[a]	Dominant tree species	Site conditions	Share in deciduous forest area[b] (%)
Alder forest	*Alnus glutinosa*	Permanently wet, mostly nutrient-rich, organic soils (fenland)	18.7
Ash-alder forest	*Fraxinus excelsior*, *Alnus glutinosa*	Wet, nutrient-rich, mineral soils	2.2
Oak-hornbeam forest with *Stachys sylvatica*	*Quercus robur*, *Carpinus betulus*, *Fraxinus excelsior*	Moist, base-rich soils (loam with groundwater influence)	0.8
Oak-hornbeam forest with *Stellaria holostea*	*Quercus robur*, *Carpinus betulus*	Moist, moderately nutrient-rich soils (sandy-loamy with groundwater influence)	0.2
Birch-oak(-hornbeam) forest with *Molinia caerulea*	*Quercus robur*, *Betula pubescens*, *Carpinus betulus*	Moist, nutrient-poor soils (sand with groundwater influence)	6.2
Oak forest with *Agrostis capillaris*	*Quercus robur*, *Quercus petraea*, *Betula pendula*	Dry, sandy, nutrient-poor soils	50.0
Beech forest with *Galium odoratum*	*Fagus sylvatica*	Relatively nutrient-rich soils without groundwater influence (loamy moraines)	0.004
Beech forest with *Maianthemum bifolium*	*Fagus sylvatica*	Nutrient-poor soils without groundwater influence	22.0

Information on forest community types was available only for c. 44% of the deciduous forest area. Thus, the given figures represent only a very rough estimate of the real share of the forest communities. Particularly, the shares of oak-hornbeam forests and beech forest with *Galium odoratum* are probably higher in reality, judging from our field work experiences.

[a] According to Hofmann, G., Pommer, U., 2005. Potentielle Natürliche Vegetation von Brandenburg und Berlin mit Karte im Maßstab 1:200000. Eberswalder Forstliche Schriftenreihe XXIV, 1-315.

[b] According to Landesumweltamt Brandenburg (1995) Biotopkartierung Brandenburg. Kartieranleitung. Unze Verlagsgesellschaft, Potsdam, Germany

Appendix 3.2.2

Correlation among patch attributes, separately for ancient (a) and post-agricultural (b) forest patches.

a) Ancient forest patches

	Habitat area	Connec-tivity	Edge length	PC1	PC2	PC3	HH.geol	HH.stru	HH.topo
Habitat area		0.31	0.58	-0.11	0.13	-0.44	0.31	0.52	0.49
Connectivity	0.31		0.19	0.12	0.27	-0.24	0.04	0.07	-0.22
Edge length	0.58	0.19		0.05	0.17	-0.37	0.30	0.41	0.36
PC1.productivity	-0.11	0.12	0.05		0.19	0.26	0.00	-0.06	-0.09
PC2.pH	0.13	0.27	0.17	0.19		-0.27	0.15	0.25	0.01
PC3.P	-0.44	-0.24	-0.37	0.26	-0.27		-0.19	-0.35	-0.23
HH.geol	0.31	0.04	0.30	0.00	0.15	-0.19		0.23	0.11
HH.stru	0.52	0.07	0.41	-0.06	0.25	-0.35	0.23		0.43
HH.topo	0.49	-0.22	0.36	-0.09	0.01	-0.23	0.11	0.43	

b) Post-agricultural forest patches

	Habitat area	Connec-tivity	Edge length	PC1	PC2	PC3	HH.geol	HH.stru	HH.topo	Patch age
Habitat area		-0.04	0.67	0.22	0.27	-0.07	0.30	0.52	0.29	-0.05
Connectivity	-0.04		0.09	-0.09	-0.22	-0.08	-0.04	0.02	-0.04	-0.17
Edge length	0.67	0.09		0.27	0.29	-0.05	0.18	0.35	0.24	-0.07
PC1.productivity	0.22	-0.09	0.27		0.33	0.33	0.01	0.01	-0.17	-0.41
PC2.pH	0.27	-0.22	0.29	0.33		0.04	0.13	0.16	0.01	-0.11
PC3.P	-0.07	-0.08	-0.05	0.33	0.04		-0.20	-0.11	-0.18	0.06
HH.geol	0.30	-0.04	0.18	0.01	0.13	-0.20		0.36	0.23	-0.07
HH.stru	0.52	0.02	0.35	0.01	0.16	-0.11	0.36		0.24	0.04
HH.topo	0.29	-0.04	0.24	-0.17	0.01	-0.18	0.23	0.24		-0.01
Patch age	-0.05	-0.17	-0.07	-0.41	-0.11	0.06	-0.07	0.04	-0.01	

Appendix 3.2.3 Differences in patch attributes between ancient and post-agricultural forest patches.

	Ancient (n = 104)				Post-agricultural (n = 110)				Mann-Whitney test			Levene test		
	Min	Median	Max	SD	Min	Median	Max	SD	ΔMedian	*W*	*P*	ΔSD	*F*	*P*
PC1.productivity	-0.904	-0.161	1.098	0.396	-0.819	-0.056	1.158	0.571	-0.105	4919	0.077	-0.175	19.9	**<0.001**
PC2.pH	-1.219	0.043	0.984	0.504	-1.382	0.096	0.999	0.495	-0.053	5165	0.221	0.009	0.3	0.608
PC3.P	-1.156	-0.094	1.325	0.512	-1.258	0.034	1.434	0.490	-0.128	5321	0.379	0.022	0.5	0.492
HH.topo	-0.700	-0.083	1.559	0.517	-0.700	-0.113	1.235	0.485	0.030	5901	0.690	0.032	0.6	0.454
HH.geol	-0.539	0.068	1.014	0.504	-0.539	-0.073	1.239	0.498	0.141	5959	0.590	0.006	0.2	0.632
HH.stru	-0.511	-0.109	1.225	0.505	-0.511	-0.023	1.507	0.498	-0.086	5539	0.683	0.007	0.8	0.370
Habitat area	-0.881	0.018	1.077	0.521	-0.034	-0.081	0.890	0.478	0.099	6238	0.253	0.043	0.9	0.353
Connectivity	-0.805	0.140	2.250	0.489	-0.957	-0.245	0.695	0.431	0.385	8247	**<0.001**	0.058	0.1	0.739
Edge length	-0.710	-0.094	1.074	0.444	-1.222	-0.042	1.630	0.539	-0.052	4829	0.049	-0.095	3.1	0.078

Appendix 3.2.4

Differences in mean population size between ancient and post-agricultural forest patches.

	Ancient	Post-agricultural	Δ	*P*
Higher mean population size in ancient forest patches (*P* < 0.1)				
Betula pendula	1.567	1.173	0.395	0.013
Carpinus betulus	1.125	0.591	0.534	0.002
Fagus sylvatica	1.298	0.736	0.562	0.001
Pseudotsuga menziesii	0.154	0.055	0.099	0.058
Quercus robur	2.173	1.791	0.382	0.017
Higher mean population size in post-agricultural patches (*P* < 0.1)				
Alnus glutinosa	1.731	2.155	-0.424	0.045
Alnus incana	0.058	0.209	-0.151	0.022
Prunus padus	0.115	0.245	-0.130	0.054
Ulmus glabra	0.048	0.127	-0.079	0.069
No significant difference between ancient and post-agricultural patches				
Acer campestre	0.058	0.055	0.003	1.000
Acer platanoides	0.337	0.418	-0.082	0.421
Acer pseudoplatanus	0.346	0.327	0.019	0.822
Aesculus hippocastanum	0.115	0.109	0.006	1.000
Betula pubescens	0.317	0.455	-0.137	0.267
Crataegus monogyna s. l.	0.087	0.091	-0.004	1.000
Fraxinus excelsior	0.740	0.873	-0.132	0.339
Hedera helix	0.356	0.436	-0.081	0.476
Larix decidua	0.096	0.073	0.023	0.632
Picea abies	0.423	0.364	0.059	0.575
Pinus sylvestris	0.606	0.627	-0.022	0.844
Populus tremula	0.683	0.627	0.055	0.699
Populus x canadensis	0.212	0.327	-0.116	0.242
Prunus avium	0.096	0.136	-0.040	0.484
Quercus rubra	0.163	0.155	0.009	1.000
Robinia pseudoacacia	0.173	0.255	-0.081	0.379
Salix alba	0.038	0.091	-0.052	0.181
Salix caprea	0.029	0.082	-0.053	0.148
Salix fragilis	0.096	0.155	-0.058	0.253
Sorbus aucuparia	0.115	0.182	-0.066	0.230
Tilia cordata	0.067	0.136	-0.069	0.194
Tilia platyphyllos	0.125	0.182	-0.057	0.389
Ulmus laevis	0.298	0.200	0.098	0.250

Population size (individuals per patch) was estimated in the field on a five-degree scale: 1 (≤10), 2 (>10), 3 (>100), 4 (>1000), 5 (> 10.000). Tree species with a relative frequency of at least 5% were tested for a different mean population size between forest types with a randomization test, using the *T*-statistic as test statistic and 999 permutations. For randomization, forest patches were randomly assigned to either forest type while keeping the number of ancient and post-agricultural patches constant.

Appendix 3.2.5

Alternative models to those in Table 3.3 as referred to in the Discussion section 3.6.

	Colonization credit quantified as relative difference	**Only patches on former arable fields included (31 old and 30 recent patches)**	
	All forest specialists	All forest specialists	Low (L) vs. high (H) dispersal potential
Intercept	25.9 ***	see patch age	see patch age
PC1.productivity			L -0.6 $^{\text{n.s.}}$ a
			H 0.6 $^{\text{n.s.}}$ a
PC1.productivity^2			L -6.8 *** a
			H 1.9 $^{\text{n.s.}}$ b
PC2.pH^2	22.0 *		
Connectivity	-35.5 ***	-3.4 ***	L -1.3 ** a
			H -0.5 $^{\text{n.s.}}$ a
Connectivity^2	-48.2 ***	-3.8 *	-1.4 *
Edge length	-2.5 $^{\text{n.s.}}$	-0.1 $^{\text{n.s.}}$	0.8 *
Patch age old		3.9 *** a	L 2.8 *** a
			H 1.4 *** b
recent		2.6 ** a	L 2.6 *** a
			H 0.5 $^{\text{n.s.}}$ c

Given are the group means and standardized regression coefficients. Asterisks indicate significance against zero ($^{\text{n.s.}}$ $P > 0.05$, * $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$) based on *t*-tests. Significant differences between groups are indicated by lower-case letters.

Appendix 3.3 Details on the reconstruction of the land-use history in the Prignitz region

The land-use history of the Prignitz region can be traced back to the second half of the 18th century. We intersected topographical maps from three time periods: the so-called Schmettau map from 1767-1787 (hereafter 1780) at a 1:50,000 scale (Wulf and Groß, 2004); the map of the Prussian Government from 1879-1902 (hereafter 1880) at 1:25,000; and recent topographical maps from 2008 at 1:25,000. For 1780, no spatially explicit information on the distribution of deciduous and coniferous stands is available. However, the proportion of coniferous forest at that time was declared to be c. 22% (Bratring, 1804). We used toponyms in the Schmettau map indicating the presence of coniferous tree species (e.g., 'Kiehnheide', 'Fichten-', or 'Theerofen') to locate likely areas of coniferous forest. The map from 1880 indicates whether a forest stand was dominated by deciduous trees or coniferous trees. For the actual forest vegetation, this and even more detailed information on the forest community types could be drawn from a state-wide map of habitats (LUA, 1995) and verified by recent aerial photographs.

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Appendix 3.4 Details on the quantification of habitat quality, habitat heterogeneity and patch configuration

Habitat quality is often heterogeneous within patches. Therefore, we followed the approach of Kolb and Diekmann (2004) and assessed habitat quality by taking soil samples in the most base-rich part of a patch as indicated by Ellenberg indicator values (Ellenberg et al., 2001). Species richness in temperate forests is highest on base-rich sites, which are often also closer to the groundwater table (Härdtle et al., 2003b). Hence, the most base-rich part of a patch is best suited to predict species richness. Species richness may be underestimated when patches assumed to be base-rich contain also nutrient-poor soils. In such cases, variables of habitat heterogeneity (see below) will contribute to the prediction of species richness. We took five soil samples (0-10 cm) from below the litter layer in each forest patch within two weeks in September 2013. The soil samples for each patch were pooled, weighed, air-dried to constant mass and reweighed to determine water content. After sieving with a 2-mm mesh, the soil samples were analyzed in the central laboratory at our research institute (www.zalf.de). pH was determined from a solution of 5 ml of soil and 25 ml of 0.01M $CaCl_2$ using a standard pH-electrode (ISO 10390). The plant available amounts of K and P were extracted by mixing 4 g soil with 200 ml of a solution from calcium lactate and hydrochloric acid (0.04N calcium lactate and 0.02N HCl). The plant available amount of Ca was extracted by mixing 5 g soil with 50 ml of ammonium lactate solution (from lactic acid (1M), acetic acid and ammonium acetate). Concentrations of K, P and Ca were afterwards measured photometrically (VDLUFA, 1991). The plant available amount of Mg was extracted by mixing 5 g soil with 50 ml of $CaCl_2$ ($c(CaCl_2) = 0.0125$ mol/l) and afterwards measured via atomic absorption spectroscopy (VDLUFA, 1991). Total carbon (C) and nitrogen (N) contents were measured with an elemental analyzer (ISO 10694 and ISO 13878). C and N content were used to calculate the C/N-ratio. All soil variables were log-transformed to achieve approximately symmetric frequency distributions. We used principal components analysis (PCA) to reduce the number of soil variables for further analyses. The first three components together explained 85.6% of the variance (Fig. A). After varimax rotation, the first component was highly correlated with N (r = 0.97), C (0.96), soil moisture (0.94) and Mg (0.81). We will refer to it as PC1.productivity. The second component was highly correlated with pH (r = 0.93), Ca (0.82) and C/N-ratio (-0.78). We will refer to it as PC2.pH. The third component was highly correlated with P (r = 0.93) and thus will be referred to as PC3.P.

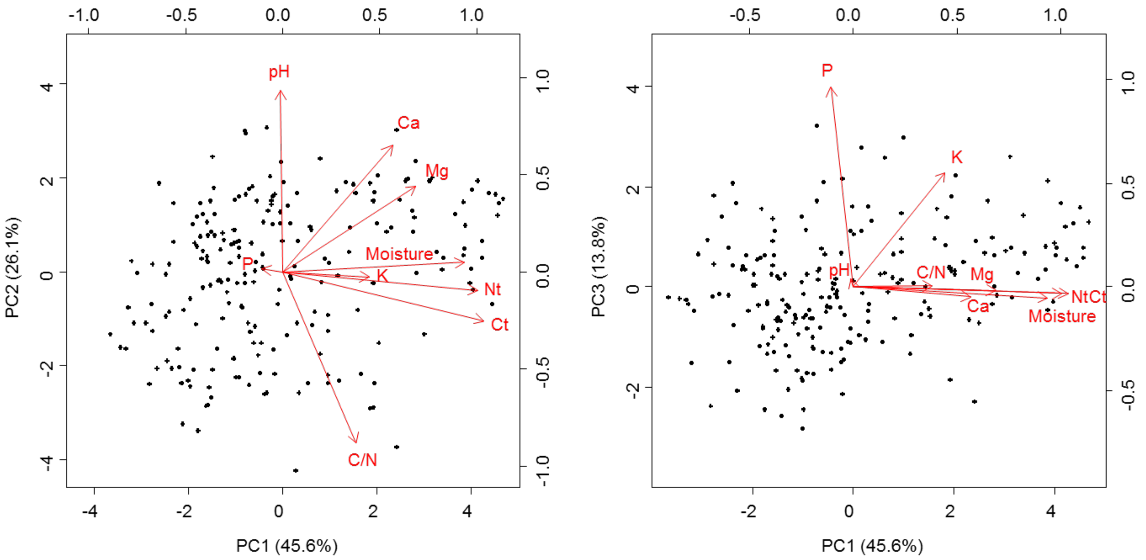

Fig. A. Principal components analysis of soil variables with varimax rotation. Eigenvalues of the principal components are given in parentheses. Arrow tips correspond to loadings, i.e. approximate correlations. Left and bottom axes are scaled in score units of observations; top and right axes are scaled in loading units of soil variables. Correlations between soil variables and principal components are as follows:

	PC1	PC2	PC3
C/N	0.14	-0.78	0.22
Ca	0.73	0.82	0.05
Ct	0.96	0.04	0.31
K	0.60	0.04	0.69
Mg	0.81	0.64	0.14
Moisture	0.94	0.32	0.23
Nt	0.97	0.19	0.28
P	0.19	-0.13	0.93
pH	0.26	0.93	-0.07

We quantified habitat heterogeneity with three complementary components: topographical heterogeneity (HH.topo), geological heterogeneity (HH.geol) and man-made structural heterogeneity (HH.stru). To measure topographical heterogeneity, we calculated the range in elevation based on a digital elevation model with a resolution of 25 m. The heterogeneity in geological substrates was quantified based on the Prussian Geological Land Survey 1:25,000 from 1895-1922. For c. 18% of the study region, this map was not available and we instead relied on official geological maps at scale 1:100,000 (LBGR, 2008, 2009). We distinguished 12 different substrate types (Table A), of which the area proportions were used to calculate a Shannon index of geological substrate heterogeneity. To quantify the man-made structural heterogeneity, we divided each patch into homogeneous subpatches, i.e., stands with a uniform overstory composition and structure. Then, we used the area proportions of the different subpatches to calculate a Shannon index of structural heterogeneity.

Table A
Geological substrate types used for quantifying geological heterogeneity.

Substrate type	Corresponding legend entries (in German) in the Prussian Geological Land Survey 1:25,000 from 1895-1922
(Minero-)Organic sediments above sand	Torf Torf über Sand Flachmoortorf über Sand Moorerde über nesterweisem Raseneisenstein über Sand Moorerde über Sand
(Minero-)Organic sediments above marly till or alluvial mud	Torf über Unterem Geschiebemergel Torf über Oberem Geschiebemergel Moorerde über nesterweisem Raseneisenstein über nesterweisem Schlick Moorerde über nesterweisem Raseneisenstein über Schlick über Sand Moorerde über nesterweisem Schlick über nesterweisem Wiesenkalk über Sand Moorerde über nesterweisem Schlick über Sand Moorerde über Unterem Geschiebemergel Moorerde über Schlick über Sand
(Minero-)organic sediments (unspecified)	Torf oder Moorerde
Marly-organic sediments	Moormergel über nesterweisem Schlick über nesterweisem Wiesenkalk über Sand Moormergel über nesterweisem Wiesenkalk über Sand Moormergel über Sand Moormergel über Schlick über Sand
Dry sand	Dünensand
Gravelly sand	Oberer Grand Kies und Geröll im Zuge der Endmoräne

Substrate type	Corresponding legend entries (in German) in the Prussian Geological Land Survey 1:25,000 from 1895-1922
Weakly humus-rich sand, close to the groundwater table	Talsand
	Talsand innerhalb der Hochfläche
	Talsand mit Geschieben innerhalb der Hochfläche
	Talsand (grandig)
	Talsand (grandig) über Unterem Sand
	Unterer Sand
Humus-rich sand, close to the groundwater table	Alluvialer Sand
	Sand über Schlick
	Sand mit Moorerdenestern
	Sand mit Raseneisensteinnestern
	Heidehumus über Talsand
Weakly loamy sand	Oberer Sand mit humoser Rinde
	Geschiebesand
	Grandiger Geschiebesand
	Geschiebesand über Geschiebemergel
	Oberer Geschiebesand über Rothem Unterem Geschiebemergel
	Geschiebesand über Unterem Sand
	Geschiebesand über Tonmergel
Loamy sand	Reste des Oberen Geschiebemergels über Sand
	Oberer Geschiebemergel
	Rother Unterer Geschiebemergel
	Reste des Oberen Geschiebemergels über Sand
Sandy clay and alluvial mud	Unterer Tonmergel
	Miozäner Ton/Tonsand
	Schlick über Sand
Unspecified	Aufgefüllter Boden
	Abrutsch- und Abschlemmmassen

As for habitat quality and habitat heterogeneity, we used three variables to quantify the patch configuration within the landscape: habitat area, connectivity and edge length. Habitat area refers to the part of the patch that was dominated by deciduous trees, where we recorded the plant species. We measured connectivity with the incidence function model derived from Hanski (1994): $C_j = \sum_{j \neq i} A_j^b \times \mathrm{e}^{-\alpha d_{ij}}$, where C_i is the connectivity of patch i, A_j is the habitat area of patch j, d_{ij} is the edge-to-edge distance between patches i and j and α and b are calibration parameters. Alpha was set to 0.002 m^{-1}, which corresponds to an average migration distance of 500 m from a source patch to a target patch (Verheyen et al., 2004; De Sanctis et al., 2010). As recommended by Moilanen and Nieminen (2002), we set $b = 0.5$. As potential source populations, we considered all deciduous forest fragments with at least 1000 m^2 of ancient forest. Habitat areas and edge-to-edge distances between patches were calculated using

ArcGIS 10.1 analysis tools (Esri, 2012). Edge length was included as a third patch configuration variable to account for patch shape. Patches with a long edge in relation to its area often contain more species than patches with a short edge and the same area because (a) the accessibility for migrating plants is greater and (b) forest fringes often provide more resources in terms of light and nutrients (Gonzalez et al., 2010). To measure edge length independent of area, we divided the length of all inner fringes (i.e., including the edge of the habitat area as well as trails, aisles etc.) by the potential minimum edge a patch can have, i.e., the perimeter of a corresponding circular patch.

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Appendix 3.5 Dispersal types used to quantify the dispersal potential of each forest specialist species

The dispersal types were assigned according to the following table, which was essentially adopted from Vittoz and Engler (2007):

Type	Dispersal distance [m][a]	Corresponding dispersal modes
1	1	Blastochory Boleochory for species < 30 cm Barochory Ombrochory
2	5	Ballochory Cystometeorochory Chamaechory Boleochory for species > 30 cm
3	15	Pterometeorochory for herbs Myrmecochory Trichometeorochory for species with little efficient plumes (terminal velocity > 0.3 m/s)
4	150	Pterometeorochory for trees Dyszoochory for seeds not stocked and dispersed by small animals
5	500	Trichometeorochory for species with efficient plumes (terminal velocity ≤ 0.3 m/s) Cystometeorochory for ferns, orchids and Pyrolaceae
6	1500	Dyszoochory for seeds stocked by large animals Endozoochory for seeds eaten by birds and large vertebrates Epizoochory by large mammals

[a] Dispersal distances were estimated as the upper limits of the distances within which 99% of the seeds of a plant population are dispersed. The actual dispersal distances will usually be lower than those given here.

Information on dispersal modes was mainly taken from Müller-Schneider (1986) and if necessary supplemented with information from Rothmaler (2005) and FloraWeb (www.floraweb.de). An exception is the information on zoochory, which was extracted from eight recent empirical studies (Mrotzek et al., 1999; Heinken et al., 2001; Heinken and Raudnitschka, 2002; Schaumann and Heinken, 2002; Schmidt et al., 2004; von Oheimb et al., 2005; Eycott et al., 2007; Panter and Dolman, 2012). Additionally, four species of the Liliaceae s.l. with fleshy, toxic fruits (namely *Convallaria majalis*, *Maianthemum bifolium*, *Paris quadrifolia and Polygonatum multiflorum*) were handled as 'not endozoochorous', although they look as if they were endozoochorous and are listed as such in trait databases. But these species are de facto not dispersed by animals (Schaumann and Heinken, 2002; Wulf and Heinken, 2008; personal communication with Thilo Heinken, 2013). Also *Adoxa moschatellina* was regarded as 'not endozoochorous' because it is dispersed only by snails and not by larger animals (Müller-Schneider, 1986; Wulf and Heinken, 2008). Some further corrections were made for species with fleshy fruits. These were treated as 'endozoochorous' (except those five species mentioned above) even though no evidence for their endozoochorous dispersal could be found in the empirical studies (cf. Wulf and Heinken, 2008).

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Appendix 4

Appendix 4.1 Details on methods for Chapter 4

1.1. Determination of light availability

To determine the proportion of visible sky in our plots, we took hemispherical photos under overcast conditions in the summer of 2014 using the HemiView camera system (DeltaT Devices). We divided the plot area into four quadrants and took three photos with different exposures within each quadrant. Subsequently, we selected one photo per quadrant with the best exposure, i.e., not under- or overexposed according to the histogram, and then applied the shadow/highlight function in Adobe Photoshop to maximize the light spectrum. We then extracted the blue channel to obtain the best separation of sky and non-sky (according to Frazer et al. 2001; Jelaska et al. 2006) and determined the threshold edge value, i.e., the brightness value that separates sky and non-sky, using the software SideLook (Version 1.1.01). Using this processed image file, we determined the proportion of visible sky in the skymap sectors above a zenith angle of 75° using the HemiView software and subsequently calculated the arithmetic mean of the visible sky values from the four photos.

1.2. Determination of soil conditions

We collected eight soil samples per plot (0-10 cm depth) in September 2014. The soil samples were mixed together plot-wise, air-dried and sieved (2 mm mesh).We analyzed the samples in the laboratory to determine the total carbon, total nitrogen, phosphorus, potassium, calcium, and magnesium contents and the pH value. The carbon and nitrogen contents were determined using a dry combustion method (ISO 10694 and ISO 13878). Phosphorus and potassium (per 100 g of soil) were determined photometrically using the double calcium lactate method at pH 3.6. The calcium content was measured using an extractant solution of ammonium acetate in combination with acetic acid and hydroxypropionic acid. To determine the magnesium content (per 100 g of soil) we used atom absorption spectrometry after extraction using a calcium chloride solution. Finally, the soil pH was determined in 0.01 M calcium chloride using a glass electrode following ISO 10390.

1.3. Adaptation of resurvey date to account for phenological shifts

We accounted for phenological shifts by first calculating the annual sums of hours (cumulative degree hours, CDH) with a temperature above 5 °C, i.e., the temperature at which plant metabolic processes start (Lindsey & Newman 1956), for each year from 1947 to 2013 using temperature data from two meteorological stations (Marnitz and Neuruppin, data available at dwd.de). Then, for every year and for a range of CDH between 20 °C h and 50 000 °C h, i.e., the CDH that may be reached from the beginning until the end of the vegetation period, we calculated the days where a specific cumulative degree hour (in 20 °C h steps) was reached. Using these data, we predicted the corresponding days of the year for which a specific CDH was reached in 1960 and 2014 using linear first-order autoregressive models. The CDH thresholds between April 1 and July 31 were reached between six and 17 (Marnitz station) or 14 and 30 (Neuruppin station) days earlier in 2014 compared with 1960. We averaged the values from the two stations and scheduled the resurvey dates based on the shifts that we found.

1.4. Determination of regional ancient forest indicator species

We determined the regional ancient forest species using the species distribution data from our previous studies in this area (Kolk & Naaf 2015; Naaf & Kolk 2015). We used the distribution data from 441 herb-layer species across 224 forest patches (104 ancient and 110 post-agricultural) and identified the regional ancient forest species by fitting generalized linear models (GLMM) with the glmer function in the lme4 R package (Bates et al. 2015), using a binomial link function and patch age (ancient vs. post-agricultural) as a predictor of species occurrence. Species with a significantly higher probability of occurrence in the ancient forests were classified as ancient forest species.

1.5. Selection of the optimization algorithm to identify winner/loser species

To identify winner and loser species, we used the glmer function in the lme4 package (Bates et al. 2015) using the Laplace approximation, Wald Z-test and Bobyqa algorithm. We used the Bobyqa optimization algorithm instead of the default Nelder Meat algorithm because this algorithm deals better with convergence issues (Mind the Brain Blog 2015). Convergence problems emerge when the optimization algorithm cannot reach the maximum improvement, i.e., the function does not converge to zero. This can be caused by omitting important random or fixed factors but may also result from other unknown reasons. This topic is currently debated among mathematicians and statisticians (stats.stackexchange 2015). Although we used the Bobyqa algorithm there were still convergence issues in some cases. Thus, we fitted all models using both algorithms (Nelder Meat and Bobyqa) and checked for differences in the fitted estimates, a method that is also proposed by the gmler help file lmerControl {lme4} (Bates et al. 2015). The differences in the coefficients were very small and the direction of the effects did not differ between the methods; thus, we can assume that our results are robust, although the coefficients can only be observed as an approximation of the real values.

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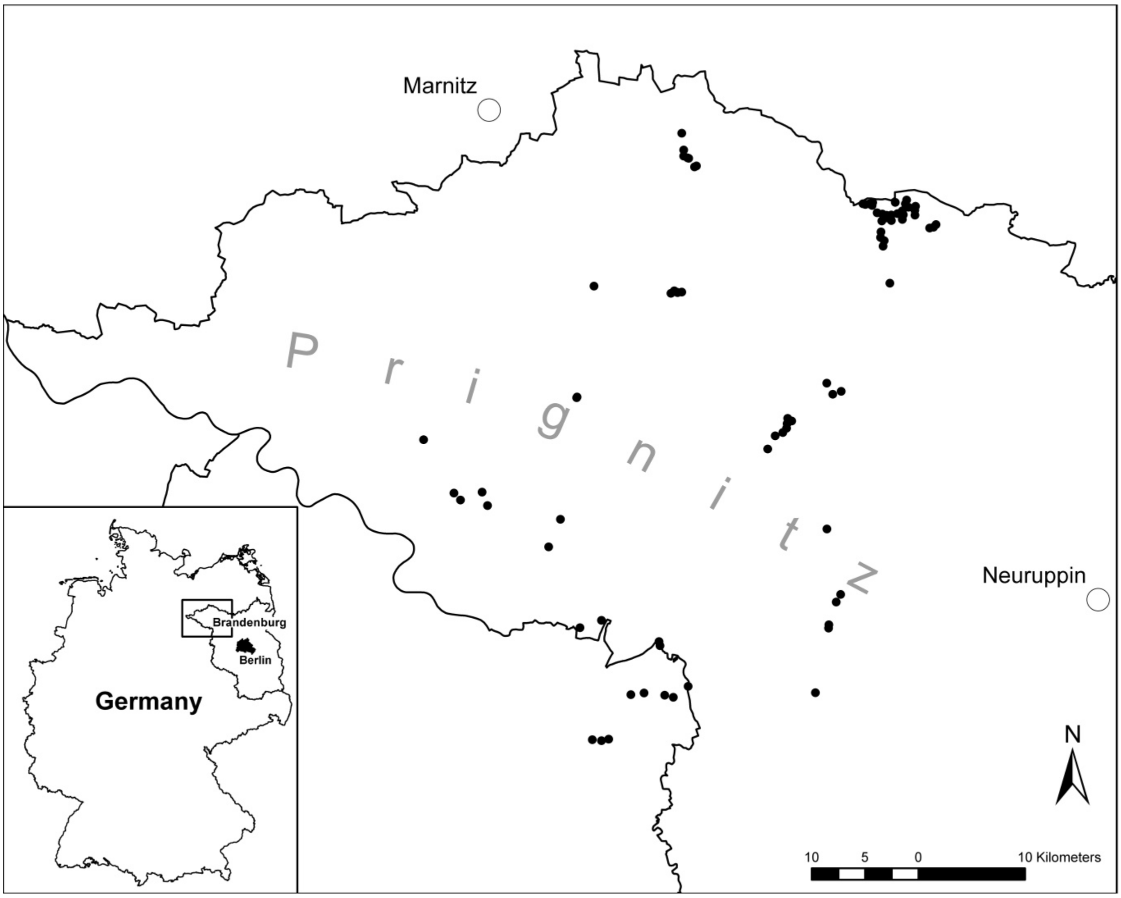
Appendix 4.2 - Table of model coefficients

Coefficients of species richness models with significance including year (1960 vs. 2014) and land use history (ancient ("ANC") vs. post-agricultural ("PA")) and interaction of year and land use history. Inclusion and standard deviation of random intercepts ("RE") of PlotID and PatchID are provided.

	1960 vs. 2014		ANC vs. PA		Interaction	RE PlotID	RE PatchID
	ANC	PA	1960	2014			
All species	3.64***	6.08***	-3.07$^{n.s.}$	-0.63$^{n.s.}$	2.44$^{n.s.}$	3.85	Not included
Forest specialists	0.25***	0.63***	-0.65***	-0.27*	0.38**	0.31	0.25
Ancient forest species	0.06$^{n.s.}$	0.28*	-0.55***	-0.33*	-0.22$^{n.s.}$	0.22	0.33

* Significance: $0.01 < P \leq 0.05$. ** Significance: $0.001 < P \leq 0.01$. *** Significance: $P \leq 0.001$. $^{n.s.}$Not significant

Appendix 5



Appendix 5.1 Map of the study area in the Prignitz region. Resurveyed plots are represented as dots.

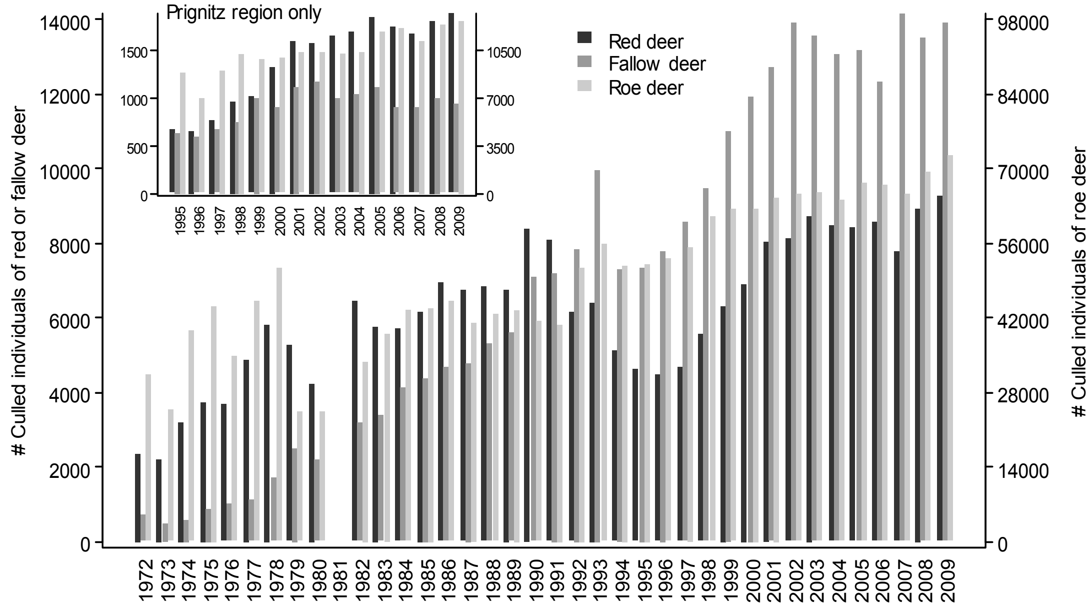
Appendix 5.2 - Regional environmental changes over the last five decades in the Prignitz region

5.2.1 Drainage

In many lowland parts of the Prignitz region, extensive drainage measures were taken after 1960 to improve site conditions for agri- and silviculture. In a master thesis project supervised by our working group and the centre for forestry expertise in Brandenburg (Landeskompetenzzentrum Forst Eberswalde, LFE), the soil profiles at seven site investigation pits in a large forest patch within the study area were resurveyed after four decades (Stengel 2002). The boundary between the permanently water-saturated soil horizon and the temporarily aerated soil horizon had generally shifted downwards, indicating a lowered groundwater table. Thus, we expected drainage to be an important driver for herb layer changes particularly on formerly moist or wet sites (e.g., Fischer 1993; Lameire et al. 2000).

5.2.2 Enhanced browsing pressure

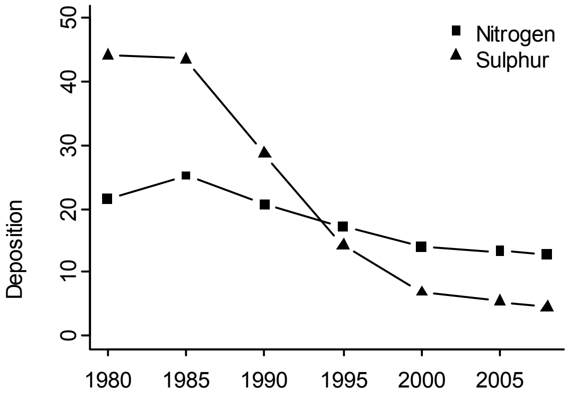
There are three deer species in the Prignitz region that are abundant enough to affect the herb layer through herbivory: Red deer (*Cervus elaphus* L.), fallow deer (*Dama dama* L.) and roe deer (*Capreolus capreolus* L.). As can be estimated from the number of culled individuals per year, deer abundances have substantially increased (even though not steadily) over the last four decades and are now significantly higher than in the 1960s (Figure in Appendix 5.1.2). One reason is inadequate hunting practices (MILB 2010). Population sizes have been called heavily inflated already in 1991 by the hunting authority of Brandenburg (Dittmar et al. 1991). We expected, therefore, that the browsing pressure on herb layer plant species would have increased, particularly for palatable herbs (Kirby 2001; Horsley et al. 2003; von Oheimb et al. 2003).



Development of the number of culled deer individuals per year in the federal state of Brandenburg since 1972 (data for 1981 are missing). For the Prignitz region (north-western Brandenburg), data were only available for the period since 1995 (small internal figure). Data were provided by the hunting authority of Brandenburg.

5.2.3 Atmospheric deposition

In the study area, total nitrogen deposition rates are moderate (c. 13 kg ha^{-1} yr^{-1}) compared to areas in western or southern Germany (>20 kg ha^{-1} yr^{-1}; figures from the EMEP database at www.emep.int). However, the throughfall deposition that reaches the forest floor must be considered about 1.5 times higher than these open field figures due to the high aerodynamic roughness of forest canopies (Fischer et al. 2010). The EMEP data shows also that nitrogen deposition rates were higher (>20 kg ha^{-1} yr^{-1}) in the 1980s and early 1990s (Figure in Appendix 5.1.3). Hence, nitrogen deposition rates in the study area have been exceeding the threshold for nitrogen deposition effects on herb layer biodiversity, which is estimated to be as low as 10-15 kg ha^{-1} yr^{-1} (Bobbink et al. 2010), for several decades. Sulphur deposition was high (>40 kg ha^{-1} yr^{-1}) in the 1980s and has since decreased below 10 kg ha^{-1} yr^{-1} (Figure in Appendix 5.1.3). However, soil acidification may still occur given the fact that the larger part of the nitrogen deposition is in the form of NH_4^+ (EMEP database). We expected, therefore, significant shifts in species composition since 1960 as a response to eutrophication and acidification (Gilliam 2006).

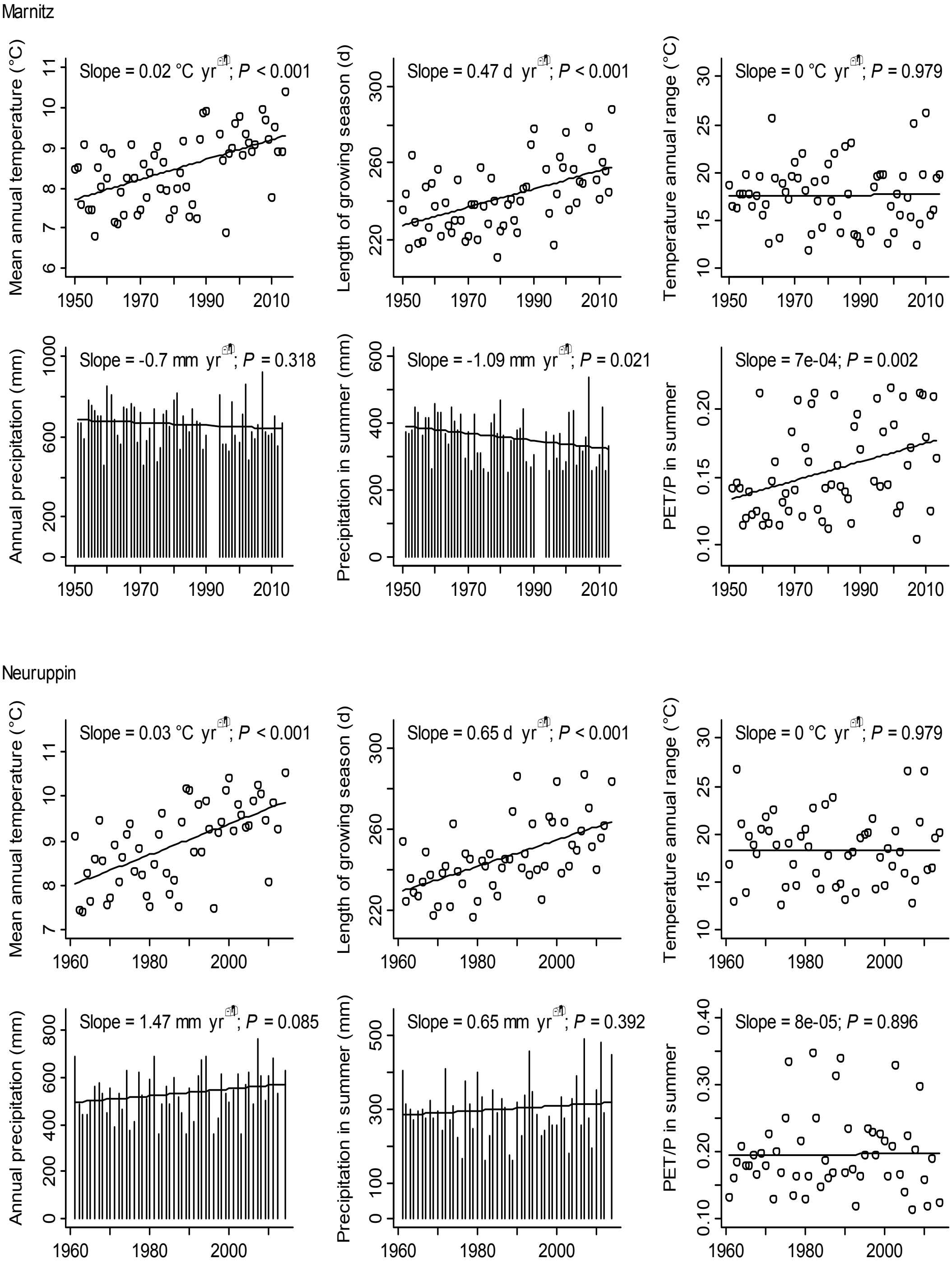


Estimated total deposition kg ha^{-1} yr^{-1} (wet and dry) of nitrogen (reduced and oxidized) and sulphur (oxidized) in the Prignitz region over the last three decades. Data from the EMEP database at http://www.emep.int.

5.2.4 Climate change

We analysed meteorological data from two measuring stations in the vicinity of the study area, Marnitz in the northwest and Neuruppin in the southeast (Figure in Appendix 5.1.4). These data show that the climate has become significantly warmer over the last six decades. The mean annual temperature has on average increased by 0.02 and 0.03 °C yr^{-1}, respectively. The length of the growing season has increased by an average rate of 0.47 and 0.65 d yr^{-1}, respectively. Temperature annual range has not changed. Changes in precipitation were less pronounced and less consistent across locations compared with temperature changes (Figure in Appendix 5.1.4). While annual precipitation generally did not change significantly, precipitation during the summer (April to September) decreased significantly in Marnitz. This resulted in a significant increase in aridity, i.e. the ratio of potential evapotranspiration over precipitation during summer.

We expected that the climate change since 1960 would have favoured species with a more southern distribution that have so far been limited by a too short growing season or species with a (sub-)continental distribution that are adapted to drier conditions during summer. In contrast, nordic species that tolerate low winter temperatures and (sub-)oceanic species that need a more humid climate may have lost competitive ability (Walther et al. 2002; Skov & Svenning 2004; van der Veken et al. 2004). This may be particularly true in the Prignitz region, where many species show(ed) a distribution boundary with (sub-)oceanic species in the northwest and (sub-)continental species in the southeast (Fischer 1959).



Climate change in the Prignitz region over the last five to six decades, observed at two meteorological stations close to the study region, Marnitz and Neuruppin (see Fig. S1). The data is available at http://www.dwd.de. Length of growing season refers to the number of days with an average temperature of ≥5 °C. Precipitation and PET/P in summer refer to the precipitation (P) and potential evapotranspiration (PET) during the months April to September. PET was calculated according to Thornthwaite (1948). The trends were calculated using first-order autoregressive models.

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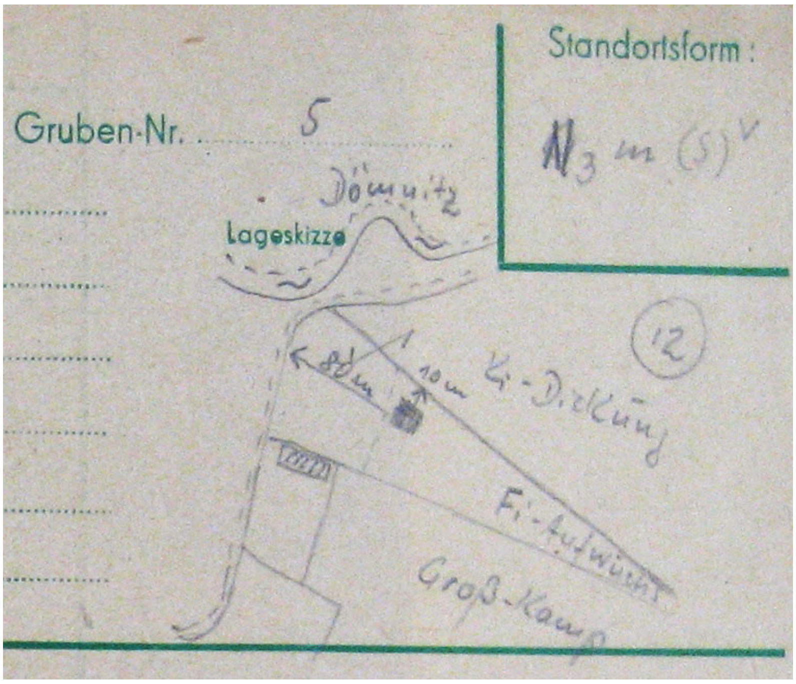
Appendix 5.3 - Relocation of historical vegetation plots

The site investigators from 1958-60 marked the exact location of each site investigation pit in a forestry map at scale 1:10,000 (Fig. a in Appendix 5.3) and in a hand-drawn sketch with exact distances in meters from forest roads, forest edges or draining ditches (Fig. b in Appendix 5.3). At most sites, the original site investigation pit is still recognizable by its characteristic shape (Fig. c in Appendix 5.3). Although the pits were refilled with the dug-out soil material by the original site investigators, small mounds of soil material remained to the left and right of the rectangular pit because the material was less densely packed than before. Over the years, the soil within the original pit sagged, leaving a more or less rectangular swale between two shallow mounds. Where the original pit is not visible anymore, the distances provided on the hand-drawn sketches together with the tree species composition allow to relocate the plots with an error of <30 m. The 400 m² plot for plant species recording was placed symmetrically around the pit unless otherwise noted.

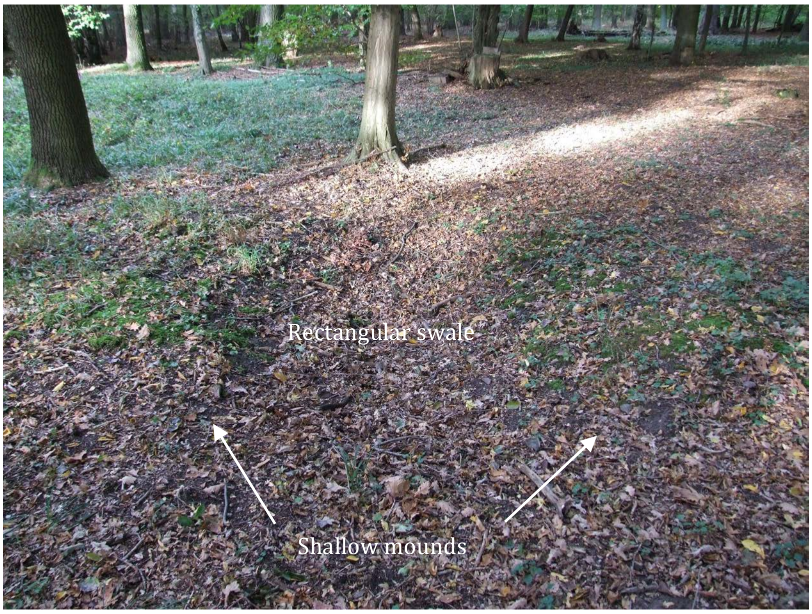
a) Section of a forestry map at scale 1:10,000, in which the positions of site investigation pits are marked with a small square and the corresponding pit number.



Gruben-Nr. 5

Standortsform: N3 m (5)v

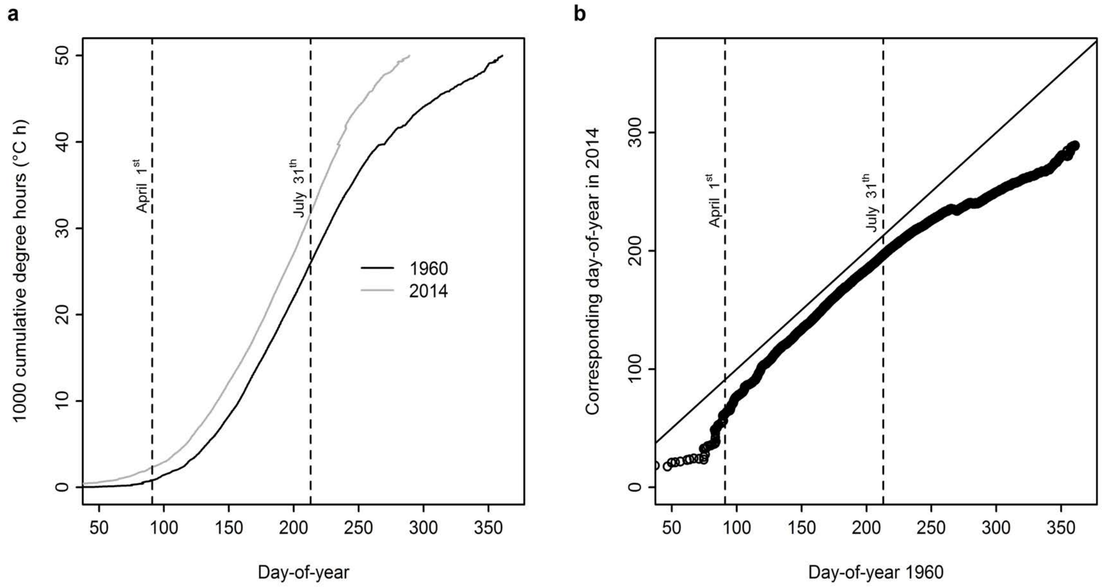
b) Example of a hand-drawn sketch on a site investigation record sheet, which shows the distances of the pit (black square) from a stand boundary (10 m) and a forest trail (80 m).



c) Photo of a site investigation pit today. We chose this example because here, the shallow mounds to the left and right of the original pit are clearly marked by certain plants growing on them.

Appendix 5.4 - Shifts in phenology between 1960 and 2014

To estimate the differences in the proceeding of the growing season between 1960 and 2014, we calculated degree hours for each day from 1958 and 2010, using daily minimum and maximum temperatures from two meteorological stations in the vicinity of the study area, Marnitz in the northwest and Neuruppin in the southeast (see Appendix 5.1; data available at www.dwd.de). Degree hours measure the amount of heat perceived by the plants in terms of both time per day and temperature above a defined threshold (Lindsey & Newman 1956). We chose a threshold temperature of 5 °C, above which plant metabolic processes could start. The degree hours accumulated over the days of a year, i.e. the cumulative degree hours (CDH), govern the phenology of many herbaceous species, particularly in spring (Lindsey & Newman 1956). In a first step, we calculated for every 20th integer CDH threshold between 20 °C h and 50,000 °C h, and for every year between 1947 (Marnitz) or 1961 (Neuruppin) and 2013 the day-of-year, when the threshold was reached. Then, for each CDH threshold, we modelled the day-of-year, when the threshold is reached, as a function of year, using linear, first-order autoregressive models. These models were then used to predict the day-of-year for the two years 1960 and 2014 (Fig. a in Appendix 5.4). The difference in the predicted phenology between the two years is not constant over the year (Fig. b in Appendix 5.4). Between April 1st and July 31th, phenology in 2014 runs between 6 and 17 (Marnitz) or 14 and 30 (Neuruppin) days ahead compared to 1960. The average phenological difference over the two meteorological stations was used to determine the dates for plant species recording for our survey in 2014. For convenience, we allocated the plots to one of four phenological stages according to their predicted survey date: spring (plots that had been surveyed before June 1st in 1960 and were surveyed before Mai 20th in 2014); early summer (plots that had been surveyed between June 2nd and June 26th in 1960 and were surveyed between Mai 21st and June 15th in 2014); summer (plots that had been surveyed after July 1st in 1960 and were surveyed in July in 2014) and autumn (plots that had been surveyed in October in 1960). In 2014, we surveyed the autumn plots in July and then, for those species that are likely to be not visible in autumn anymore, checked for any occurrence or abundance changes in October.



Phenological shift between 1960 and 2014 in Neuruppin. (a) Cumulative degree hours as a function of the day-of-year predicted for 1960 and 2014. (b) Comparison of the day-of-year when a specific threshold for cumulative degree hours (here between 20 and 50,000 °C h) is reached between 1960 and 2014. The straight line has a slope of 1, representing the line of no difference between the years.

Reference

Lindsey, A. A., Newman, J. E., 1956. Use of official weather data in spring time - temperature analysis of an Indiana phenological record. Ecology 37: 812-823.

Appendix 5.5 - Transformation and scaling of variables to improve the log response ratios

Preliminary analyses revealed two problems concerning the log response ratios: First, some log response ratios showed strong deviations from a normal distribution, which led to violations of the assumption of normally distributed residuals in linear models. Second, despite the log-transformation of the response ratios, the magnitudes of the RRs differed considerably. This caused not only problems for illustrating the overserved changes of different variables in one figure, but was also misleading because the magnitude of the log response ratio not only depends on the magnitude of change over time but also on the scaling of the original variables, i.e. the ratio of the maximum to the minimum value. To overcome the two problems we took two measures: First, we transformed the original variables using the power transformation of Tukey (1977): $x = \begin{cases} x^{\lambda} & \text{if } \lambda > 0 \\ \log x & \text{if } \lambda = 0 \\ -\left(x^{\lambda}\right) & \text{if } \lambda < 0 \end{cases}$

We tested a sequence of λ values and chose the value which resulted in the best approximation to a normal distribution of the resulting RR. Second, after power transformation, we scaled the variables between 1 and 10 (across sampling periods), so that all resulting log response ratios had a potential maximum of log(10/1) = 2.30 and a potential minimum of log(1/10) = -2.30. The true magnitude still depended on the true change over time, i.e. the distribution of small and large values across the sampling periods.

Reference

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Appendix 5.6 - Supplementary tables for Chapter 5

Appendix 5.6.1

Shade-casting ability (SCA) and litter quality (LQ) scores for the occurring tree and shrub species (n.a. = not available). Sources are Ellenberg & Leuschner 2010 (a), Verheyen et al. 2012 (b) and unpublished expert knowledge within our research group (c).

Species	SCA	Source	LQ	Source
Acer campestre	3	a	4	b
Acer platanoides	4	a	3	b
Acer pseudoplatanus	4	a	3	b
Aesculus hippocastanum	4	c	n.a.	
Alnus glutinosa	3	a	4	b
Alnus incana	3	a	3	b
Betula pendula	1	a	2	b
Betula pubescens	1	a	2	b
Carpinus betulus	5	a	3	b
Cornus mas	2	b	5	b
Cornus sanguinea	3	c	5	b
Corylus avellana	5	c	3	b
Crataegus laevigata	1	c	n.a.	
Crataegus monogyna	1	c	n.a.	
Cytisus scoparius	1	c	n.a.	
Euonymus europaea	2	c	n.a.	
Fagus sylvatica	5	a	1	b
Frangula alnus	2	c	n.a.	
Fraxinus americana	3	c	n.a.	
Fraxinus excelsior	3	a	5	b
Hedera helix	4	c	n.a.	
Humulus lupulus	1	c	n.a.	
Juniperus communis	3	c	n.a.	
Lonicera periclymenum	1	c	n.a.	
Picea abies	4	a	1	b
Picea sitchensis	4	c	1	c

Appendix 5.6.1 (continued)

Species	SCA	Source	LQ	Source
Pinus sylvestris	1	a	2	b
Populus tremula	2	a	3	b
Populus x canadensis	2	b	3	b
Prunus avium	3	a	4	b
Prunus padus	3	a	4	b
Prunus serotina	3	c	n.a.	
Pseudotsuga menziesii	4	c	n.a.	
Quercus petraea	3	a	2	b
Quercus robur	2	a	1	b
Quercus rubra	3	b	1	b
Rhamnus cathartica	2	c	n.a.	
Ribes nigrum	2	c	n.a.	
Ribes uva-crispa	1	c	n.a.	
Robinia pseudoacacia	3	b	4	b
Rubus fruticosus agg.	2	c	n.a.	
Rubus idaeus	2	c	n.a.	
Salix spp.	2	c	3	c
Sambucus nigra	3	c	5	b
Sambucus racemosa	3	c	n.a.	
Sorbus aucuparia	2	a	3	b
Symphoricarpos albus	1	c	n.a.	
Tilia cordata	4	a	4	b
Tilia platyphyllos	4	a	4	b
Ulmus glabra	4	a	5	b
Ulmus laevis	4	a	5	b
Ulmus minor	3	a	5	b

Appendix 5.6.2

Correlation among environmental change indicator variables.

	RR_F	RR_R	RR_N	RR_{BA}	RR_{FT}	RR_{FC}
RR_F		0.11	-0.02	-0.17	0.12	0.09
RR_R	0.11		0.74	0.05	0.52	0.16
RR_N	-0.02	0.74		0.16	0.23	0.29
RR_{BA}	-0.17	0.05	0.16		0.10	-0.23
RR_{FT}	0.12	0.52	0.23	0.10		0.08
RR_{FC}	0.09	0.16	0.29	-0.23	0.08	

Appendix 5.6.3

Change in mean cover (%) of the most important tree and shrub species between 1960 and 2014, separately for the three buffer range categories in 1960 (AlFe = aluminium and aluminium-iron buffer range; CatEx = cation-exchange buffer range; SiliCar = silicate and carbonate buffer range). Marked decreases are printed in red, marked increases in green. For convenience, shade-casting ability (SCA) and litter quality (LQ) scores according to Table S1 are provided (n.a. = not available).

	AlFe		CatEx		SiliCar		SCA	LQ
	1960	2014	1960	2014	1960	2014		
Tree layer								
Alnus glutinosa	5.9	3.5	5.6	5.1	37.8	21.2	3	4
Alnus incana	0.0	0.0	4.2	0.7	5.4	0.6	3	3
Betula pendula	5.3	1.3	2.6	0.4	3.1	0.7	1	2
Carpinus betulus	6.8	8.8	19.5	14.1	4.2	5.3	5	3
Fagus sylvatica	26.3	32.7	31.3	44.0	5.0	11.5	5	1
Fraxinus excelsior	0.0	0.1	4.9	0.1	6.8	3.8	3	5
Pinus sylvestris	4.9	0.6	1.9	0.1	0.0	0.0	1	2
Quercus robur	44.0	18.4	16.8	10.0	14.5	7.3	2	1
Ulmus laevis	0.0	1.1	0.1	2.5	0.1	4.0	4	5
Ulmus minor	0.0	0.0	0.0	0.0	0.6	3.5	3	5
Shrub layer								
Alnus incana	0.1	0.1	0.1	0.2	3.8	0.2	3	3
Corylus avellana	2.4	2.7	3.1	0.8	3.3	2.6	5	3
Fagus sylvatica	2.6	6.5	4.5	7.5	0.7	1.0	5	1
Frangula alnus	5.4	0.7	0.4	0.0	0.7	0.1	2	n.a.
Fraxinus excelsior	0.5	0.0	1.0	0.0	4.7	0.2	3	5
Prunus padus	0.4	0.4	1.4	4.4	2.7	1.1	3	4
Prunus serotina	0.0	2.5	0.0	1.8	0.0	0.1	3	n.a.
Ulmus glabra	0.0	0.0	0.0	0.0	2.5	0.0	4	5

Appendix 5.6.4

Species‘ frequencies in 1960 and 2014 for all sites, sites initially in the aluminium or aluminium-iron buffer range (AlFe), sites initially in the cation-exchange buffer range (CatEx) and sites initially in the silicate or carbonate buffer range (SiliCar). Winner species are species with an increase in absolute frequency by ≥ 4 occurrences AND with an increase in relative frequency by ≥ 20%. Loser species are species with a decrease in absolute frequency by ≥ 4 occurrences AND with a decrease in relative frequency by ≥ 20%. Indifferent species are species with ≥ 4 occurrences in at least one of the years but only a minor change in frequency. The following ecological traits are given to allow the interpretation of frequency changes (see main text for explanations): forest specialist (FS); Ellenberg values for light (L), soil moisture (F), soil reaction (R) and soil nutrient availability (N); browsing attractiveness (BA); geographical distribution: southern (S), nordic (N), (sub-)oceanic (O) and (sub-)continental (C).

Species	**All sites**		**AlFe**		**CatEx**		**SiliCar**		**FS**	**Ellenberg values**				**BA**	**Distribution**			
	1960	**2014**	**1960**	**2014**	**1960**	**2014**	**1960**	**2014**		**L**	**F**	**R**	**N**		**S**	**N**	**O**	**C**
Winner species																		
Agrostis capillaris	3	9	3	6	0	3	0	0	0	7	NA	4	4	1	0	1	1	0
Anemone nemorosa	27	41	17	20	6	13	4	8	1	NA	5	NA	NA	2	0	1	1	0
Athyrium filix-femina	30	41	6	10	12	15	12	16	1	3	7	NA	6	2	0	0	1	0
Atrichum undulatum	8	21	2	5	2	8	4	8	0	6	6	4	NA	NA	0	1	0	0
Calamagrostis epigejos	1	12	0	5	0	6	1	1	0	7	NA	NA	6	NA	0	0	0	1
Carex acutiformis	7	11	1	1	0	2	6	8	0	7	9	7	5	1	1	0	0	0
Carex pilulifera	12	18	11	13	1	5	0	0	0	5	5	3	3	1	0	0	1	0
Carex remota	1	11	0	2	1	3	0	6	1	3	8	NA	NA	2	1	0	1	0
Circaea lutetiana	13	23	0	2	5	3	8	18	1	4	6	7	7	3	0	0	1	0
Cirsium oleraceum	6	14	0	0	0	2	6	12	0	6	7	8	5	3	0	0	0	1
Dicranum scoparium	0	6	0	4	0	2	0	0	0	5	4	4	NA	NA	0	1	0	0
Dryopteris carthusiana	22	38	12	14	8	15	2	9	0	5	NA	4	3	3	0	0	0	0
Dryopteris dilatata	15	21	8	9	3	3	4	9	1	4	6	NA	7	3	0	0	0	0
Dryopteris filix-mas	10	18	2	8	5	6	3	4	1	3	5	5	6	3	0	0	0	0

Species	All sites		AlFe		CatEx		SiliCar		FS	Ellenberg values				BA	Distribution			
	1960	2014	1960	2014	1960	2014	1960	2014		L	F	R	N		S	N	O	C
Equisetum arvense	1	5	0	1	0	0	1	4	0	6	6	NA	3	1	0	0	0	0
Eurhynchium striatum	8	12	0	2	2	3	6	7	1	5	5	6	NA	NA	0	0	0	0
Fallopia dumetorum	0	5	0	4	0	0	0	1	0	6	5	NA	7	NA	0	0	0	1
Galium aparine	17	24	1	5	3	3	13	16	0	7	NA	6	8	2	0	0	0	0
Galium palustre	3	7	0	1	0	1	3	5	0	6	9	NA	4	1	0	0	1	0
Geum urbanum	15	21	1	1	1	5	13	15	0	4	5	NA	7	4	1	0	0	0
Winner species cont.																		
Glechoma hederacea	23	34	1	4	4	7	18	23	0	6	6	NA	7	NA	0	0	1	0
Glyceria fluitans	0	4	0	0	0	1	0	3	0	7	9	NA	7	2	0	1	0	0
Hedera helix	3	16	1	5	2	5	0	6	1	4	5	NA	NA	3	0	0	1	0
Humulus lupulus	5	9	0	0	0	2	5	7	0	7	8	6	8	1	1	0	0	1
Impatiens parviflora	6	52	0	13	1	17	5	22	1	4	5	NA	6	2	0	0	0	1
Juncus effusus	2	10	1	3	0	3	1	4	0	8	7	3	4	2	0	0	0	0
Lamium galeobdolon s. str.	14	19	0	1	4	5	10	13	1	3	5	7	5	2	1	0	1	0
Lapsana communis	0	4	0	1	0	1	0	2	0	5	5	NA	7	5	1	0	1	0
Lysimachia vulgaris	9	16	4	4	1	4	4	8	0	6	8	NA	NA	5	0	0	0	0
Maianthemum bifolium	28	34	14	14	13	15	1	5	1	3	5	3	3	1	0	1	0	1
Moehringia trinervia	13	29	4	13	3	7	6	9	1	4	5	6	7	1	1	0	1	0
Molinia caerulea	8	12	8	11	0	1	0	0	0	7	7	NA	1	2	0	0	1	0
Myosotis scorpioides agg.	0	4	0	0	0	0	0	4	0	7	8	NA	5	2	1	0	0	0
Poa trivialis	6	21	2	4	0	4	4	13	0	6	7	NA	7	NA	1	0	0	0
Pohlia nutans	0	4	0	4	0	0	0	0	0	5	4	2	NA	NA	0	1	0	0
Polygonatum multiflorum	12	21	4	5	6	9	2	7	1	2	5	6	5	5	1	0	0	0
Polytrichum formosum	11	21	10	13	1	6	0	2	0	4	6	2	NA	NA	0	1	0	0
Prunus serotina	0	18	0	12	0	3	0	3	0	6	5	NA	NA	NA	NA	NA	NA	NA

Species	All sites		AlFe		CatEx		SiliCar		FS	Ellenberg values				BA	Distribution			
	1960	2014	1960	2014	1960	2014	1960	2014		L	F	R	N		S	N	O	C
Ranunculus lanuginosus	4	8	0	0	1	1	3	7	1	3	6	7	7	5	0	0	0	1
Ranunculus repens	1	7	0	0	0	1	1	6	0	6	7	NA	NA	NA	0	0	0	0
Rubus fruticosus agg.	12	23	6	8	3	5	3	10	0	NA	NA	NA	NA	5	1	0	1	0
Rumex sanguinea	2	8	0	0	0	0	2	8	1	4	8	7	7	2	0	0	1	0
Scutellaria galericulata	0	5	0	1	0	2	0	2	0	7	9	7	6	1	0	0	1	0
Stachys sylvatica	17	23	0	2	2	3	15	18	1	4	7	7	7	4	0	0	1	0
Stellaria aquatica	0	4	0	1	0	0	0	3	0	7	8	7	8	NA	0	0	0	0
Veronica montana	0	4	0	0	0	1	0	3	1	4	7	5	6	2	0	0	1	0
Loser species																		
Agrostis stolonifera	10	5	4	1	4	1	2	3	0	8	NA	NA	5	NA	1	0	0	0
Ajuga reptans	14	7	2	1	7	3	5	3	0	6	6	6	6	NA	1	0	1	0
Deschampsia cespitosa	68	50	23	13	19	16	26	21	0	6	7	NA	3	3	0	0	0	0
Deschampsia flexuosa	36	19	31	16	5	2	0	1	0	6	NA	2	3	2	0	1	1	0
Festuca gigantea	40	22	6	1	15	4	19	17	1	4	7	6	6	3	1	0	0	0
Filipendula ulmaria	7	3	0	0	1	1	6	2	0	7	8	NA	4	5	0	0	0	0
Fragaria vesca	7	0	6	0	0	0	1	0	0	7	5	NA	6	3	0	0	1	0
Galium odoratum	24	12	9	2	11	4	4	6	1	2	5	6	5	2	0	0	1	0
Geranium robertianum	20	15	4	2	4	5	12	8	0	5	NA	NA	7	5	0	0	1	0
Gymnocarpium dryopteris	14	5	7	2	6	3	1	0	1	3	6	4	5	2	0	1	1	0
Hypericum perforatum	5	1	4	1	1	0	0	0	0	7	4	6	3	3	1	0	1	0
Mycelis muralis	14	5	3	2	9	2	2	1	0	4	5	NA	6	4	1	0	1	0
Poa nemoralis	23	3	14	1	7	2	2	0	1	5	5	5	4	2	1	0	0	0
Tanacetum vulgare	8	0	0	0	1	0	7	0	0	8	5	8	5	NA	0	0	1	0
Vaccinium myrtillus	12	7	12	7	0	0	0	0	0	5	NA	2	3	5	0	1	0	0

Species	All sites		AlFe		CatEx		SiliCar		FS	Ellenberg values				BA	Distribution			
	1960	2014	1960	2014	1960	2014	1960	2014		L	F	R	N		S	N	O	C
Veronica chamaedrys	17	2	9	2	6	0	2	0	0	6	5	NA	NA	NA	1	0	1	0
Vicia sepium	4	0	0	0	4	0	0	0	0	NA	5	6	5	3	0	0	1	0
Indifferent species																		
Aegopodium podagraria	19	16	0	1	6	2	13	13	0	5	6	7	8	4	0	0	0	1
Anthoxanthum odoratum	5	2	3	2	2	0	0	0	0	NA	NA	5	NA	NA	0	1	0	0
Brachypodium sylvaticum	13	15	1	3	2	1	10	11	1	3	5	6	6	2	1	0	0	0
Calamagrostis canescens	10	8	4	3	3	1	3	4	0	6	9	6	5	1	0	0	0	1
Carex elongata	4	7	1	2	0	1	3	4	1	4	9	7	6	1	0	0	1	0
Carex sylvatica	8	11	0	0	1	3	7	8	1	2	5	6	5	4	1	0	1	0
Dactylis glomerata	5	5	2	1	1	2	2	2	0	7	5	NA	6	NA	1	0	0	0
Indifferent species cont.																		
Equisetum sylvaticum	7	6	1	0	4	3	2	3	1	3	7	5	4	1	0	1	0	0
Galeopsis tetrahit	28	27	11	10	7	6	10	11	0	7	5	NA	6	4	0	0	0	0
Geum rivale	7	6	1	0	2	1	4	5	0	6	8	NA	4	3	0	1	0	0
Hepatica nobilis	4	2	1	0	3	2	0	0	1	4	4	7	5	NA	0	0	0	1
Holcus lanatus	4	6	3	3	0	3	1	0	0	7	6	NA	4	3	0	0	1	0
Holcus mollis	14	12	11	8	3	4	0	0	0	5	5	2	3	2	0	0	1	0
Impatiens noli-tangere	13	14	0	2	0	2	13	10	1	4	7	7	6	2	0	1	0	1
Iris pseudacorus	7	8	1	1	0	1	6	6	0	7	9	NA	7	NA	1	0	0	0
Lonicera periclymenum	13	12	11	7	1	2	1	3	0	6	NA	3	4	2	0	0	1	0
Luzula pilosa	26	23	18	17	8	6	0	0	1	2	5	5	4	2	0	0	1	0
Lycopus europaeus	5	5	0	1	0	0	5	4	0	7	9	7	7	2	1	0	0	0
Melampyrum pratense	7	6	6	5	1	1	0	0	1	NA	NA	3	2	3	0	0	1	0

Species	All sites		AlFe		CatEx		SiliCar		FS	Ellenberg values				BA	Distribution			
	1960	2014	1960	2014	1960	2014	1960	2014		L	F	R	N		S	N	O	C
Melica nutans	4	3	3	2	1	1	0	0	1	4	4	NA	3	1	0	0	0	1
Melica uniflora	13	13	5	3	8	8	0	2	1	3	5	6	6	1	0	0	0	1
Mercurialis perennis	5	5	0	0	1	1	4	4	1	2	NA	8	7	2	1	0	1	0
Milium effusum	46	53	19	16	15	18	12	19	1	4	5	5	5	3	0	1	1	0
Oxalis acetosella	47	54	22	22	18	16	7	16	1	1	5	4	6	2	0	1	1	0
Phalaris arundinacea	6	5	0	0	2	2	4	3	0	7	9	7	7	1	0	1	0	0
Plagiothecium affine	11	8	0	0	4	4	7	4	0	5	5	5	NA	NA	0	0	0	0
Plagiothecium undulatum	8	10	0	0	3	4	5	6	0	4	6	6	NA	NA	0	0	0	0
Pteridium aquilinum	4	5	3	3	1	2	0	0	1	6	5	3	3	1	0	0	1	0
Ranunculus auricomus agg.	4	5	1	0	0	0	3	5	0	5	NA	7	NA	3	0	0	0	1
Ranunculus ficaria	4	5	1	1	0	0	3	4	0	4	6	7	7	NA	1	0	1	0
Rubus caesius	4	4	0	1	0	1	4	2	0	6	NA	8	7	5	1	0	0	0
Rubus idaeus	47	50	17	17	15	14	15	19	0	7	NA	NA	6	5	0	1	0	0
Scrophularia nodosa	4	3	0	2	3	0	1	1	0	4	6	6	7	2	0	0	1	0
Stellaria holostea	43	46	17	15	15	17	11	14	1	5	5	6	5	3	0	0	1	0
Indifferent species cont.																		
Stellaria media	5	6	1	3	3	0	1	3	0	6	NA	7	8	NA	0	0	0	0
Stellaria nemorum	11	12	0	0	3	1	8	11	1	4	7	5	7	2	1	0	1	0
Thelypteris palustris	4	1	0	0	0	0	4	1	0	5	8	5	6	NA	0	1	0	0
Urtica dioica	44	46	5	9	16	13	23	24	0	NA	6	7	8	NA	0	0	0	0
Veronica officinalis	7	5	5	4	2	1	0	0	0	6	4	3	4	2	0	0	1	0
Viola reichenbachiana/riviniana	23	27	13	9	8	11	2	7	1	5	5	6	NA	NA	1	0	1	0

Appendix 5.6.5

Effects of the change in canopy shade-casting ability on the environmental change indicators. The results are based on either generalized least squares regression (mixed = 0) or linear mixed models with forest patch as random effect (mixed = 1). Given are the regression coefficients for the change in shade-casting ability (Est.), their standard errors (SE), the degrees of freedom (df) and the *t*- and *p*-value of the test against zero.

	Est.	**SE**	**df**	***t***	***p***	**mixed**
Change in mean Ellenberg value for soil moisture	-0.036	0.046	78	-0.78	0.440	0
Change in mean Ellenberg value for soil reaction	0.087	0.067	79	1.29	0.199	0
Change in mean Ellenberg value for nutrient availability	0.063	0.070	76	0.90	0.369	0
Change in browsing attractiveness	-0.024	0.079	79	-0.31	0.759	0
Change in floristic temperature	-0.060	0.077	80	-0.78	0.439	0
Change in floristic continentality	-0.246	0.139	57	-1.78	0.081	1

Appendix 5.6.6 (Table next page)

Effects of environmental change variables on changes in species diversity and composition as resulting from generalized least squares regression analyses. The estimates (Est.) are average standardized regression coefficients resulting from full averaging over all candidate models with a $\Delta AIC_C \leq 2$. Given are the unconditional standard errors (SE), the *z* and *p* value of the test against zero, the importance value (Imp.; see main text), the variance explained by the complete average model potentially including also initial buffer range as predictor (R^2_{TOT}), the variance that is uniquely explained by the environmental change variables (R^2_{ENV}), the number of candidate models (Cand.) and the sample size (*n*; varying due to missing values).

Response	**Predictors**	**Est.**	**SE**	*z*	***p***	**Imp.**	R^2_{TOT}	R^2_{ENV}	**Cand.**	***n***
RR_{SR}	Intercept (AlFe)	0.175	0.089	1.950	0.051		0.292	0.247	9	78
	CatEx	-0.009	0.145	0.061	0.951	0.54		(84.5%)		
	SiliCar	0.161	0.182	0.878	0.380	0.54				
	RR_{SCA}	-0.248	0.060	4.082	0.000	1.00				
	RR_F	0.133	0.055	2.361	0.018	1.00				
	RR_R	0.241	0.080	2.967	0.003	1.00				
	RR_N	-0.084	0.102	0.819	0.413	0.54				
	RR_{BA}	0.003	0.019	0.175	0.861	0.07				
	RR_{FC}	0.005	0.024	0.198	0.843	0.08				
	RR_{SCA}*RR_F	0.021	0.046	0.462	0.644	0.29				
RR_{SPEC}	Intercept (AlFe)	-0.002	0.071	0.033	0.974		0.391	0.242	4	79
	CatEx	0.065	0.161	0.397	0.692	1.00		(61.8%)		
	SiliCar	0.647	0.133	4.781	0.000	1.00				
	RR_{SCA}	-0.129	0.055	2.321	0.020	1.00				
	RR_F	0.064	0.062	1.036	0.300	0.66				
	RR_R	0.166	0.048	3.364	0.001	1.00				
	RR_{BA}	-0.009	0.031	0.280	0.780	0.38				
	RR_{FC}	0.180	0.055	3.192	0.001	1.00				
	RR_R*RR_{BA}	0.027	0.040	0.662	0.508	0.38				
RR_{BETA}	Intercept (AlFe)	-0.088	0.059	1.467	0.142		0.384	0.299	2	78
	CatEx	-0.473	0.112	4.146	0.000	1.00		(77.7%)		
	SiliCar	-0.323	0.083	3.851	0.000	1.00				
	RR_F	-0.021	0.031	0.680	0.496	0.58				
	RR_N	-0.165	0.050	3.221	0.001	1.00				
	CatEx*RR_N	-0.177	0.109	1.602	0.109	1.00				
	SiliCar*RR_N	0.152	0.092	1.613	0.107	1.00				
	RR_F*RR_N	0.039	0.040	0.969	0.332	0.58				
Temporal turnover	Intercept (AlFe)	0.227	0.040	5.691	0.000		0.300	0.299	12	78
	CatEx	0.022	0.047	0.453	0.651	0.22		(99.7%)		
	SiliCar	0.020	0.043	0.450	0.652	0.22				
	RR_{SCA}	0.003	0.010	0.286	0.775	0.26				
	RR_F	-0.015	0.017	0.871	0.384	0.68				
	RR_R	-0.075	0.028	2.668	0.008	1.00				
	RR_N	0.056	0.029	1.871	0.061	1.00				
	RR_{FC}	0.005	0.012	0.404	0.686	0.24				
	RR_{SCA}*RR_R	0.010	0.018	0.521	0.602	0.26				
	RR_F*RR_R	0.014	0.018	0.735	0.462	0.46				
	RR_R*RR_N	0.051	0.017	2.961	0.003	1.00				

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Individual contribution to Chapters 1 - 5

The Chapters 1 to 5 represent five individual research papers. For Chapter 1, I conducted the data compilation and data analysis and wrote the Methods and Results sections. The concept of Chapter 1 was developed to equal extent by myself and by apl. Prof. Dr. Monika Wulf, who provided the raw data and wrote the remaining sections.

All fieldwork for Chapters 2 to 5 and the reconstruction of the land use history was conducted by myself and by Dr. Tobias Naaf to equal extent.

The Chapters 2 and 4 were written by myself and were based on my own data analysis. I formed the concept of both chapters together with Dr. Tobias Naaf, who also assisted me in fieldwork and data analysis. In addition, for Chapter 4, apl. Prof. Dr. Monika Wulf helped with the relocation of plots in the field.

For the Chapters 3 and 5, I contributed 50% of the data, did half of the fieldwork and conducted parts of the statistical analysis. Dr. Tobias Naaf conducted the main data analysis and wrote the manuscripts. All Chapters were further reviewed by each of the three authors to improve the manuscripts.

Recklinghausen, Müncheberg, 25.01.2019

Jens Kolk	apl. Prof. Dr. Monika Wulf	Dr. Tobias Naaf

Declaration

Hiermit erkläre ich, Jens Kolk, geboren am 03.12.1982, dass mir die Promotionsordnung der Mathematisch-Naturwissenschaftlichen Fakultät der Universität Potsdam vom 18.09.2013 bekannt ist und ich diese anerkenne.

Insbesondere versichere ich, dass ich die vorliegende Arbeit selbst angefertigt habe, ohne unzulässige Hilfe und ohne Benutzung anderer als der angegebenen Hilfsmittel und dass die aus fremden Quellen direkt oder indirekt übernommenen Gedanken in der Arbeit als solche kenntlich gemacht worden sind.

Ich versichere, dass alle Personen, die mich bei der Durchführung der Analysen und Anfertigung der Manuskripte (Kapitel 1-5) unterstützt haben, als Co-Autoren genannt sind und dass Dritte weder unmittelbar noch mittelbar geldwerte Leistungen von mir für Arbeiten erhalten haben, die im Zusammenhang mit dem Inhalt der vorgelegten Dissertation stehen.

Ich versichere weiterhin, dass ich die vorgelegte Arbeit nicht bereits zuvor in gleicher oder in wesentlichen Teilen ähnlicher Form einer anderen staatlichen oder wissenschaftlichen Einrichtung zum Zwecke einer Promotion oder eines anderen Prüfungsverfahrens vorgelegt habe.

Recklinghausen, den 17.02.2019 **Jens Kolk**

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