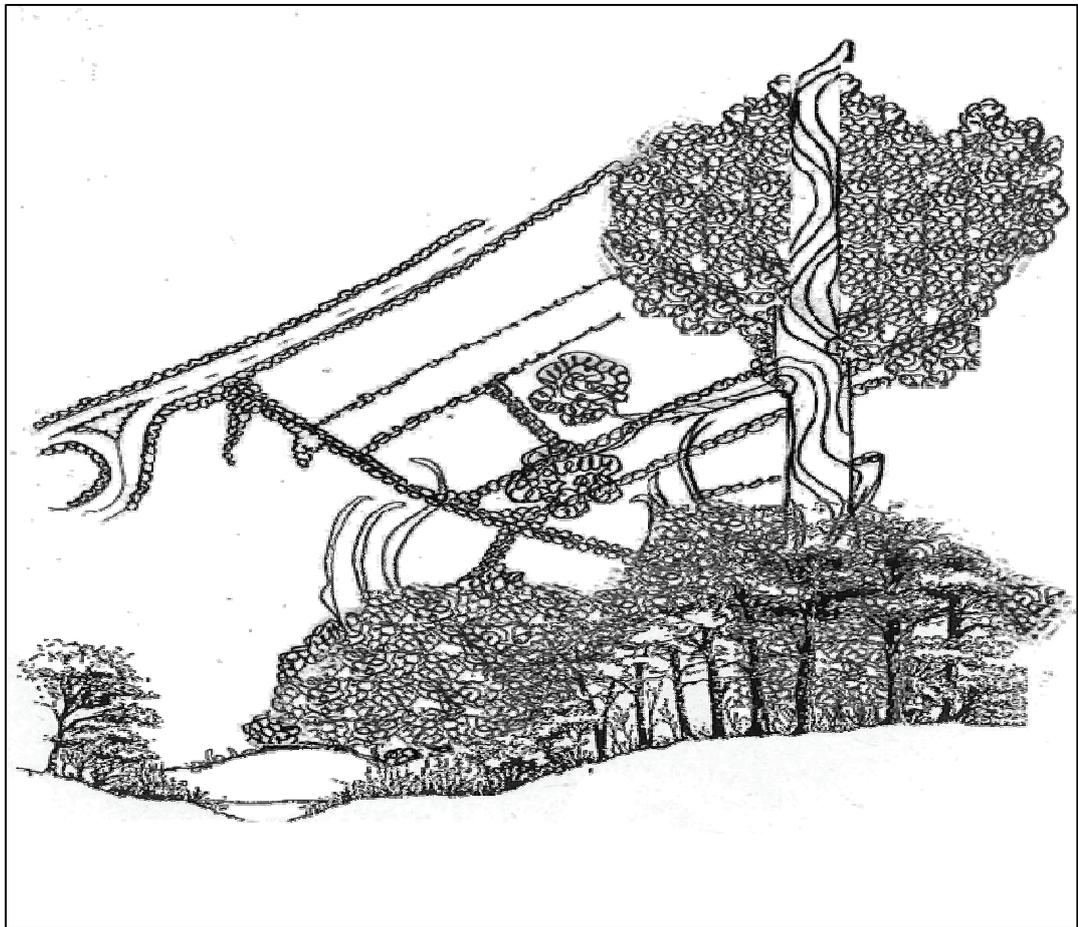


Stephan Wehling

*Hedgerows in agricultural landscapes as
a habitat for forest plant species*



University Bremen

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*Hedgerows in agricultural landscapes as
a habitat for forest plant species*

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In all four papers integrated in this thesis, Martin Diekmann contributed to ideas and discussion, while I carried out the field work and was responsible for data analyses and writing of the manuscripts.

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Zusammenfassung

Ein Großteil der Landschaften dieser Welt wird von land- und forstwirtschaftlicher Nutzung dominiert. Die früher vorhandenen natürlichen Lebensräume, wie z.B. Wälder, wurden im großen Ausmaß zerstört oder in ihrer Größe und Qualität stark reduziert. In Folge dieser Prozesse sind viele krautige Waldpflanzen in ihrem Vorkommen gefährdet. Dies gilt insbesondere für die ackerbaulich genutzten Regionen Mitteleuropas. Ein häufiges Element dieser ländlichen Regionen, die Hecke, bietet in Teilen eine waldähnliche Umgebung, die für Waldarten ein Ersatzlebensraum und Ausbreitungskorridor darstellen könnte. Beweise für diese Funktionen konnten jedoch noch nicht in ausreichender Zahl erbracht werden. Daher wurde im Rahmen dieser Arbeit der Einfluss der Hecken auf den Erhalt von Waldpflanzen unter besonderer Berücksichtigung der dafür ursächlichen Faktoren untersucht. Durchgeführt wurde diese Studie in einem Gebiet im Umland von Bremen, einer Stadt in Nordwestdeutschland, welches sich durch stark fragmentierte Wälder und ein relativ dichtes Heckennetzwerk auszeichnet.

Am Anfang dieser Arbeit stand die Untersuchung der Vorkommen von Waldarten in Hecken und die Bestimmung der Faktoren, die diese Vorkommen beeinflussten. In dem Untersuchungsgebiet gehörte ca. ein Viertel aller gefundenen Arten zu den typischen Waldpflanzen. Gefährdete Arten wurden dagegen öfter in den die Hecken umgebenden Wäldern als in den Hecken selbst gefunden. Ursächlich für die Vorkommen waren hauptsächlich Umweltfaktoren; wobei Waldarten vor allem von niedriger Licht- und Nährstoffverfügbarkeit gefördert wurden.

Ein weiteres Ziel war es, die Eignung des Habitats Hecke für das längerfristige Überleben von fünf ausgewählten Waldarten (*Adoxa moschatellina*, *Anemone nemorosa*, *Circaea lutetiana*, *Polygonatum multiflorum* und *Stellaria holostea*), die häufig in Hecken gefunden wurden, zu testen. Der Vergleich von verschiedenen individuellen und reproduktiven Parametern pflanzlicher Fitness zwischen den Lebensräumen Wald und Hecke erbrachte nur wenige Unterschiede, die zwischen den Arten nicht einheitlich ausfielen. Gleiche Leistungsstärke, verglichen zwischen den Habitaten, wurde für *Adoxa*, *Anemone* und *Polygonatum* gefunden. *Stellaria* zeigte bessere Werte in Hecken, während *Circaea* sich besser in Wäldern fortpflanzte. Generell hing die pflanzliche Fitness vor allem von der Licht- und Bodenwasserverfügbarkeit ab.

Die Untersuchung der Veränderung von Anzahl und Häufigkeit von Waldarten in Wald-Hecke-Transekten zeigte eine stark negative Beziehung zwischen wachsender Entfernung zum Waldrand und der Anzahl von Waldarten, was als Anzeichen für eine bestehende

Ausbreitungskorridorfunktion von Hecken gedeutet wurde. Es ist aber zu bedenken, dass beinahe ein Viertel der in den benachbarten Wäldern gefundenen Arten sich nicht entlang von Hecken ausbreiten konnten. Das Alter der Hecken beeinflusste in diesem Zusammenhang nicht die Anzahl beherbergter Waldarten sondern es zeigte sich, dass mit steigendem Alter die Varianz innerhalb der Artzusammensetzung geringer wurde. Weiterhin wiesen vor allem solche Arten hohe Frequenzen in Hecken auf, denen vergleichsweise hohe Ellenbergwerte für Licht sowie Samenausbreitung mittels Wind oder Tieren nachgewiesen wurden.

Zum Abschluss dieser Arbeit wurde versucht eine Gruppe von Faktoren zu finden, die die gesicherte Vorhersage von Waldartenvorkommen in Hecken verschiedener europäischer Heckennetzwerke ermöglicht. Entgegen der Erwartungen hatte der einzelne Faktor Lichtverfügbarkeit eine stärkere Beziehung zu der Waldartenfrequenz eines getesteten Heckennetzwerkes als die ausgewählte Faktorengruppe, die aber aus Variablen bestand, deren Einfluss auf das Vorkommen von Waldarten in Hecken nachgewiesen werden konnte. Daher ist es wahrscheinlich, dass die in den lokalen Wäldern vorhandene Artengemeinschaft entscheidender für die Artzusammensetzung in den Hecken war als andere Faktoren. Gefundene Veränderungen innerhalb der Umweltbedingungen und Artzusammensetzung verschiedener Hecken entlang eines Klimagradienten, wie z.B. Anzeichen für trockenere und basischere Böden sowie geringere Anteile an Chamaephyten und wintergrünen Arten in kontinentaleren Gebieten, ließen sich größtenteils durch die Veränderung im Klima erklären. Sowohl klimatische Veränderungen als auch die Variation in der lokal verfügbaren Artengemeinschaft sind wichtige Einflussgrößen, die die Frequenz von Waldarten in Hecken bestimmen.

Zusammenfassend lässt sich davon ausgehen, dass die Hecken in Nordwestdeutschland der Mehrheit der lokalen Waldarten ein geeignetes Habitat bieten und dass sie diesen Arten, wahrscheinlich aufgrund von erhöhter Konnektivität zwischen Lebensraumfragmenten, helfen zu überleben. Viele bedrohte Waldarten dagegen scheinen ausschließlich an (alte) Wälder gebunden zu sein und können keine Vorteile aus den vorhandenen Heckennetzwerken ziehen. Zukünftige Untersuchungen in diesem Bereich müssen die lokale Artengemeinschaft der Wälder berücksichtigen, da sie entscheidend für die Artzusammensetzung von Hecken sind.

Summary

In many countries of the world the landscape today is dominated by agri- and silvicultural land, whereas the former natural habitats, such as forests, have largely been destroyed or reduced in size and quality. As a consequence, many herbaceous forest plant species are endangered, especially in the intensively used farming landscapes of Central Europe. Hedgerows, common elements of rural landscapes, partly offer a similar environment as forests. They have been proposed as habitat and conservation corridor for woodland herbs, but their importance for the survival of these species is still not clear. In this study the value of hedgerows for the conservation of forest plant species was examined with special attention paid to the influencing factors mainly responsible for the occurrence of these herbs. Selected for study was an agricultural used region with a highly fragmented forest cover and a relatively dense hedgerow network in the hinterland of Bremen, a city in north-western Germany.

The first objective of this study was to survey the hedgerows for the occurrence of forest specialists and to determine which factors are influencing their distribution. In the study region almost a quarter of all found herbaceous species (43 of 173) could be classified as typical woodland plants. Endangered species were found more often in forests than in the adjacent hedgerows. Averaged across species there was a predominant effect of environmental factors on the occurrence of forest species in hedges. Forest herbs were favoured by low nutrient and light availability and a close distance to nearby woodland.

A further objective was to test the suitability of the habitat hedgerow for the survival of five selected forest species (*Adoxa moschatellina*, *Anemone nemorosa*, *Circaea lutetiana*, *Polygonatum multiflorum* and *Stellaria holostea*) with common occurrence in hedges. The comparison of several life-history attributes (as a measurement of plant fitness) between the habitat types forest and hedgerow resulted only in few differences, which show no consistent patterns across species. *Adoxa*, *Anemone* and *Polygonatum* performed equally well in hedgerows and forests, whereas *Stellaria* appeared to have a higher fitness in hedgerows. In contrast, *Circaea* showed a higher reproduction under forest conditions. However, performance of these species was mainly influenced by light and soil water availability.

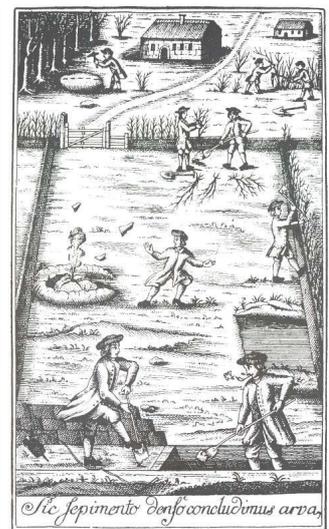
The survey of forest-hedgerow transects for changes in forest species richness and frequency revealed a strong negative relationship with species number and distance from the forest edge. This was assumed to be an indication for the conservation corridor function of hedgerows for these species. However, almost a quarter of the forest species of the surrounding forests were not able to spread within hedgerows. Hedgerow age was not influencing the number of

species, but older hedgerows showed a smaller variation in species composition. Furthermore, woodland species with high frequencies in forest-hedgerow transects had comparatively high Ellenberg values for light, and were mostly associated with seed dispersal by wind or animals. The last objective was to examine the suitability of a set of ecological and life-history variables, reported to have some effect on the occurrence of woodland species, predicting the occurrence of forest herbs in hedgerow networks throughout Europe. The single factor light availability had a stronger relationship to the frequency of forest herbs of a tested hedgerow network than the chosen set of variables. It is likely that the regional pool of woodland species is more influential for the species composition of the tested hedgerow network than other variables. The investigation of changes in environmental conditions and species composition along a climate gradient across Europe resulted in some differences, which are mainly explained by changes in climate. Hedgerows in more continental areas showed species compositions indicating drier and less acid soils and had lower proportions of chamaephytes and wintergreen species. In sum, climatic differences together with variations in the regional forest species pool have an important effect on the woodland species composition of hedgerows.

In conclusion, hedgerows of north-western Germany provide for the majority of woodland herbs a suitable habitat and they help them to survive in an otherwise hostile environment most probably by increased connectivity between habitat patches. Endangered forest species seemed, in contrast, to be restricted to (ancient) forests and not to thrive in hedgerows. Further analyses have to consider the regional pool of forest species, which was found to be most decisive for the species composition of hedgerow networks.

CHAPTER 1

INTRODUCTION



Sic fepimento denfo concludimus arva,

Top left: *Hedgerows on both sides of a rural road.* **Top right:** *Anemone nemorosa at a hedge bottom.* **Bottom left:** *Hedgerow adjacent to forest fragment within grassland. (Photographs taken by Stephan Wehling).* **Bottom right:** *Plantation of hedgerows in the 18th century (Weber, 2003).*

GENERAL INTRODUCTION

Today's world is mainly the result of anthropogenic influences over the last millennia. More than 60% of the earth's habitable surface has been changed by human activities with still ongoing alterations, particularly in regions with a strong increase in human population (Vitousek *et al.*, 1997). Large forested areas have been cleared mostly in favour of reclamation for farming purposes, *e.g.* crop production and livestock breeding (Donald & Evans, 2006). Due to this loss of natural habitats conventional farming is one of the major threats for biodiversity, particularly for plant species restricted to formerly widespread woodlands (Foley *et al.*, 2005; Green *et al.*, 2005). This is also true for Europe, where nowadays more than half of the landscapes can be classified as agricultural, whereas natural habitats (mainly deciduous forests) are dramatically reduced in size and quality (Rounsevell *et al.*, 2003). Here, the loss of plant species was and still is high (van Calster *et al.*, 2008), especially within herbaceous forest plant species, due to their dispersal limitations and the severe reduction, fragmentation and degradation of forests (Bailey, 2007).

Apart from the reduction of habitable sites, many plant species suffer from the intensification of agriculture due to a higher usage of mineral fertilizer and herbicides during the last 60 years (Foley *et al.*, 2005). Connected to the intensification process is an increase in field size due to the removal of large amount of non-productive but species-rich landscape elements (*e.g.*, hedgerows, shrubberies or ponds) (Macdonald & Johnson, 2000). The cover with cultivated area has increased, even in the last two decades, to the expense of non-productive habitats (Stoate *et al.*, 2001). A similar development has also taken place in north-western Germany, whose landscape is dominated by agricultural land-use - forest remnants cover only about 10% of the region and are highly fragmented (Kelm, 1994). Here, almost 40% of all plants species are endangered, and among these are many forest species (Garve, 2004).

FOREST PLANT SPECIES IN AGRICULTURAL LANDSCAPES

As mentioned above, the major challenges for forest herbs are, especially in regions dominated by agriculture, habitat size reduction and fragmentation together with their low dispersal capacity (Haila, 1999). In such landscapes hedgerows, as the most forest-like habitat, may represent a possible refuge for woodland species. However, to which extent hedgerows are beneficial for the survival of these species in farming areas is still questioned.

Forest plant species – characteristics, habitat fragmentation and problems of spread

Forest species are by definition those plants that grow in deeply shaded habitats (Peterken, 1974) and are restricted to the forest interior or edges and clearings (Schmidt *et al.*, 2002). The classification is partially region dependent, *i.e.* a plant classified as a forest species in Germany might be typical for open landscapes in the UK (*cf.*, McCollin *et al.*, 2000; Schmidt *et al.*, 2002). Nevertheless, the classification of the majority of these species is identical for most European countries.

Most forest herbs are long-living perennials, which are stress-tolerant and able to tolerate low light availabilities (Grime *et al.* 1988). They mainly produce few but heavy seeds (Bierzychudek, 1982), have low germination rates (*e.g.*, Slade & Causton, 1979) and form no persistent seed bank (*e.g.*, Taylor, 1997). Many forest plants lack a dispersal vector or rely on ‘slow’ vectors such as ants (Cain *et al.*, 1998). Together with the low seed production (seed limitation *sensu* Turnbull *et al.*, 2000) these species are dispersal limited (Verheyen & Hermy, 2001). In dynamic agricultural landscapes, *e.g.* north-western Germany, these limitations are obstructive for long-time persistence of forest species (Takahashi & Kamitani, 2004; Matlack, 2005).

Important abiotic factors influencing the occurrence of forest herbs are light soil nutrient availability (Kolb & Diekmann, 2004; Whigham, 2004). With higher light availability plants are larger and the reproductive output (number of seeds and seed mass) increases (Elemans, 2004). However, the competitive pressure by light-demanding competitors increases, as well (De Keersmaeker *et al.*, 2004). Furthermore, most forest species are found in habitats with low concentrations of soil nutrients, especially phosphate, due to competition with nutrient-demanding species and not as a result of high nutrient concentration avoidance (Hippes *et al.*, 2005). The effects of high light and nutrient availability occur often in combination with forest fragmentation, due to a rising edge-to-interior ratio, leading to increased lateral radiation and nutrient input from adjacent fields into the forest patches.

Most European forests are highly fragmented and degraded in habitat quality, resulting in reduced habitable sites for almost all forest species. This leads to increased isolation and a disruption of habitat continuity (Bennett, 1999). The habitat fragmentation resulted in reduced connectivity and formerly large populations are divided in several small meta-populations, which are more or less isolated from each other (Primack & Miao, 1992). High isolation brings fourth numerous problems for the remaining populations – loss of genetic diversity, inbreeding, genetic drift and in consequence increased extinction rates. Extinction rates are additionally enhanced due to the higher susceptibility to stochastic events in small populations

(Oostermeijer, 1996). Therefore, in most cases fragmented and isolated forest remnants harbour fewer forest species than a non-fragmented forest of the same area (Dzwonko & Loster, 1988; Honnay & Jacquemyn, 2007). Furthermore, the present occurrence of forest herbs reflects the diversity found in these landscapes in former times (de Blois *et al.*, 2001). Due to their longevity, many species react to changes in the landscape matrix only after several decades or even centuries (Honnay *et al.*, 2005). It is feasible that many forest plants will go extinct in the future as a reaction of fragmentation in the past, a phenomenon called “extinction debt” (Lindborg & Eriksson, 2004; Vellend *et al.*, 2006).

The difficulties of forest herbs in fragmented forests, which are embedded in a more or less hostile landscape are intensified by their low dispersal speed and seed limitation (Verheyen & Hermy, 2004). To counteract the effects of reduced connectivity and isolation, the reconnection of forest fragments by corridors has been recommended by several ecologists (*e.g.*, Verkaar, 1990; Poschlod *et al.*, 1996). Corridors may facilitate an increase in the movement rates of individuals and genes between formerly connected habitat patches to offset local extinction events. They can also help to increase genetic diversity to reduce harmful effects of inbreeding and genetical drift (Haddad & Tewksbury, 2006). For a plant species a corridor could be a habitat and in consequence a source for colonising adjacent habitats (*e.g.* recently planted woodlands). Moreover, if the establishment is not followed by subsequent reproduction the corridor could function as a sink, as well (Laurance, 2004). However, the effects of corridors for plants are argued controversially and benefits have rarely been demonstrated (Simberloff & Cox, 1987; Simberloff *et al.*, 1992; Beier & Noss, 1998; Kirchner *et al.*, 2003). Accordingly, advantages for the persistence and survival of forest herbs have not been shown. Hedgerows may well be an agreeable type of corridor for woodland plants. In many agricultural landscapes throughout the world hedgerows are the most forest-like landscape elements, incorporating many characteristics of formerly widespread forests, and may help to prevent further forest species losses by providing an increased connectivity between forest fragments (Baudry *et al.*, 2003).

Hedgerows – elements of traditional agricultural landscapes

In most cases a hedgerow (or hedge) is defined as “a row of shrubs and/or trees managed in various ways” (Baudry *et al.*, 2000). Hedgerows are a common feature of production landscapes and are found all over the planet, such as Asia (Tang Ya *et al.*, 2003), North America (Sullivan & Sullivan, 2006), Central and South America (Harvey *et al.*, 2004) and Australia (Bird *et al.*, 1992), but most hedgerow networks were located in Europe. From

Portugal and Spain (Schmitz *et al.*, 2007), over the British Isles (Garbutt & Sparks, 2002), France (Le Cœur *et al.*, 1997) and northern Germany (Weber, 2003) up to the north of Denmark (Tybirk *et al.*, 2001) – many coastal regions of Europe show high densities of hedgerows (Fig. 2a in Chapter 2). In the continental areas, such as South Germany (Reif *et al.*, 1982) and Eastern Europe (Molnárová, 2008), linear wooded features are also part of many production landscapes.

Most hedgerows have a linear character with widths from three to twelve metres and show a high edge to area ratio. The microclimate within hedgerows shows similarities to both the forest interior (Tischler, 1951) and the forest edge (Andrews *et al.*, 1999). Therefore, many forest interior and forest edge species may thrive in hedges (Forman & Baudry, 1984). Due to different types of management (*e.g.*, coppicing, pruning) hedgerows are highly disturbed habitats (Mieth *et al.*, 1996), and rank among those landscape elements that are richest in animal and plant species (Weber, 2003). For many species, they provide an adequate shelter, refuge and especially for plants suitable habitat conditions in areas which are subject to intense management pressure (Bunce & Hallam, 1993).

The species composition of hedgerows in agricultural used areas is influenced by numerous factors, whose importance differs depending on the study region and species group. Several studies could demonstrate the effects of light availability (Bates, 1937; Miller & Gorchov, 2004), hedgerow width (Andrews *et al.*, 1999), management and landscape history (Deckers *et al.*, 2004) and land use types (Le Cœur *et al.*, 2002). In addition, the misplacement and run-off of fertilizers and herbicides are also decisive for the plant biodiversity in hedgerows (Boutin & Jobin, 1998; Marshall & Moonen, 2002). However, the largest influence is visible when the factors mentioned above arise in combination. To which extent a factor contributes to this combination is depends foremost on the history of the region in which the study was conducted.

Hedgerows were for at least two millennia an important part of European farming landscapes. The first historical records of hedgerows were found in ‘*De Bello Gallico*’ by Julius Caesar. He mentioned a Germanic tribe, which erected thorny hedges for its defence (Muir & Muir, 1987). Hedgerows were planted to delimit ownership of fields or feudal properties from the Neolithic period on (Barnes & Williamson, 2006) over the antiquity (Groppali, 1993) until the mediaeval times throughout Europe and particularly in the UK (Hooper, 1970). This is reflected in the nowadays common term ‘hedge’, which developed from the old Saxon vocable ‘hecg’, which may be translated as ‘territorial boundary’ (Dowdeswell, 1987). In the 17th century the destructive exploitation of forests led to a severe paucity of wood products.

The establishment of new sources of firewood and timber and an innovation in agricultural policy resulted in further hedgerow plantations. Farmers of several European countries were forced by law to enclose newly established fields and private livestock with hedgerows, especially at the end of the 18th century (Weber, 2003; Barnes & Williamson, 2006)). In the 19th century, the European hedgerow networks reached their largest dimensions (Muir & Muir, 1987). With the beginning of the 20th century, many hedgerows were removed by farmers due to production intensification and mechanisation, *e.g.* in France (Merot, 1999), in the UK (Petit *et al.*, 2003), in Germany (Weber, 2003), in the Czech Republic (Sklenicka *et al.*, 2009) and in Denmark (Agger & Brandt, 1988). By the end of the 20th century, many European governments recognised the conservation value of hedgerows and enforced the protection of a large amount of remnant networks by law (*e.g.*, Weber, 2003). Beyond their intended function as a simple boundary and source of wood hedgerows are very advantageous in agricultural landscapes and their values has been revealed in the last decades. In fields enclosed by hedges the crop production is generally increased, due to reduced wind speed, higher soil moisture and mean temperature (Davis & Norman, 2009). Hedgerows are also a hatchery for beneficial organisms controlling pests (Jobin *et al.*, 2001) and finally inhibit soil erosion by water fluxes (Burel *et al.*, 1993) and/or wind (Bird *et al.*, 1992; Röser, 1995). Besides these agricultural benefits, hedgerows may be of interest to nature conservation. Even though they are located within intensively used areas, they are among the species-richest landscape elements, implying that hedgerows may be able to maintain a distinct level of biodiversity under hostile conditions. Moreover, they show many similarities to the microclimate within forests. Therefore, hedgerows might additionally be of interest for the conservation of forest species, too.

Forest plant species in hedgerows?

Over the last decades ecologists have controversially discussed the potential of hedgerows to sustain viable populations of forest species (habitat function) and to connect forest fragments (conservation corridor function). Consequently, three main theories were postulated.

The first encompasses the assumption that almost all hedgerows are suitable habitats and conservation corridors for forest species. This is supported by findings from the UK, which show an increase in the number of forest species in woodland fragments, if hedgerows connected them (Petit *et al.*, 2004). Hedgerow networks were able to increase the number of woodland species in farming landscapes and helped to conserve endangered species (Freemark *et al.*, 2002). It could also be demonstrated that up to 70% of all forests species

typical for the studied region were also found in an adjacent hedgerow network (Corbit *et al.*, 1999). Furthermore, individuals of forest plant species were larger and produced more flowers and seeds in hedgerows compared to those in forests (Endels *et al.*, 2004). In an additional comparison of an endangered forest species with occurrence in both forest fragments connected by hedges and unconnected forest patches Belgian ecologists observed an increased survival in connected patches (Endels *et al.*, 2002).

Contrary to this, the second theory states that hedgerows differ strongly from forests and are too heavily disturbed by human activities to be beneficial for the conservation of forest species. Studies from the UK and France found only very few forest species of the forest interior in hedgerows of intensively used agricultural regions (Burel *et al.*, 1998; French & Cummins, 2001). Comparative studies of forest plants populations showed a decrease in the reproductive output for one species in hedgerows (Cunningham, 2000) and a reduced survival of seedlings and juveniles for another species (Schmucki & de Blois, 2009). Furthermore, transplantation experiments demonstrated a low suitability of hedgerows for the tested forest herbs (Fritz & Merriam, 1993). Recent reviews showed either no direct evidence for the corridor function of hedgerows (Bailey, 2007) or the results were unconvincing due to shortcomings in the experimental design (Davies & Pullin, 2006). This is supported by studies from France, which found no indication for enhanced survival of an endangered forest species, when the habitat patches were connected by hedgerows (Campagne *et al.*, 2009).

A third theory has an intermediated view on the presence of forest species in hedgerows: Hedges provide a suitable habitat and a conservation corridor for only a subset of woodland species. Merely such plants were found in hedges, which are able to withstand the disturbances within hedgerows (Sage *et al.*, 2009) and tolerate the differing habitat conditions compared to forests (de Blois *et al.*, 2002; Bailey, 2007). Investigations of the corridor function of hedgerows revealed a colonisation of forest herbs only in those parts of a hedge, which were in direct contact to the forest. Therefore, it was concluded that the corridor function is given only on very short distances (Forman, 1991). In addition, many species may benefit from hedgerows only after many decades or centuries, due to the low dispersal capacity characteristic for forest plant species (Burel & Baudry, 1990).

AIMS AND OUTLINE OF THIS THESIS

Thus, there is no general agreement about the potential of hedgerows to serve as a suitable habitat and conservation corridor for forest herbs. Furthermore, the majority of recent studies concerning this topic were conducted in North America (*e.g.*, Corbit *et al.*, 1999; Roy & de

Blois, 2008) or in Western Europe (*e.g.*, Burel & Baudry, 1990; McCollin *et al.*, 2000). The extensive hedgerow networks in Central Europe and especially in north-western Germany have been widely neglected in international nature conservation research. Along with the equivocal importance of hedgerows for woodland herbs it is still under controversial discussion which set of factors from the multitude of revealed variables is most crucial for determining the species composition of hedgerow networks. The availability of such a set of factors, which allows the assured prediction of forest plants in hedgerows throughout Europe, would support future landscape planning and decisions on conservation policy.

In the intensively used and sparsely wooded farming regions of north-western Germany, hedgerows may be of particular interest for the conservation of forest herbs, because a large amount of hedgerows has persisted in this landscape despite of agricultural intensification and mechanisation. However, the importance of the local hedges for the survival of forest plant species has yet to be revealed and detailed knowledge of the factors influencing these plants is required.

Therefore, the major objectives of this thesis are

- I. to demonstrate whether herbaceous plant species typically found in forests are also part of the floral composition of hedgerows and furthermore to explore the relative importance of different variable groups related to environmental conditions, management, spatial configuration and structure for the occurrence of these species;
- II. to determine the suitability of hedgerows for the long-term survival of woodland herbs by investigating the differences between values of important life-history attributes of five selected forest species with occurrence both in forest and in hedgerows;
- III. to investigate the importance of hedgerows to act as a conservation corridor for forest plants and which environmental and/or structural factors are influential for this function;
- IV. to find a set of explanatory variables, which allow the prediction of forest herb occurrence in different European hedgerow networks.

To achieve these objectives, an area with relatively dense hedgerow networks and a notable amount of species-rich deciduous forest fragments in north-western Germany was chosen for study (for details see Chapter 2). The Chapters 3 – 6 are in accordance with the four main objectives and are subsequently summarized.

Chapter 3

To date, only little information is available on the presence of woodland herbs in the hedgerows of Central Europe. Forest species occurrence in hedgerows is depends on a multitude of factors, which can be classified into four different variable groups related to environmental conditions, management of the adjacent field, spatial configuration and hedgerow structure. The relative importance of these groups is still equivocal (Le Cœur *et al.*, 1997; Deckers *et al.*, 2004). In this chapter, the distribution and abundance of forest species were surveyed and related to environmental factors. The relative importance of the variable groups mentioned above was determined. Differences in life history traits and ecological responses between forest specialists occurring in hedgerows and those missing in hedgerows were investigated.

Chapter 4

The presence of forest herbs in hedgerows as such is not proof enough for the suitability of this habitat type. In hedges, many forest plant species are able to withstand unsuitable conditions due to their longevity and their stress-tolerating capacity. However, they suffer from reduced offspring recruitment and enhanced extinction rates after colonisation (Schmucki & de Blois, 2009). Based on the results obtained from Chapter 3, in this chapter forest and hedgerow populations of five forest species were selected and compared in terms of live-history attributes. The second aim was to reveal the differences in the abiotic conditions between the two habitats, by focusing on the comparison of soil samples.

Chapter 5

The increase in connectivity of woodland fragments by reconnection with hedges may be crucial for the conservation of forest herbs. However, knowledge on the factors, which are decisive for the spread of forest species along hedges is scarce and needs further experimental studies. Recent studies emphasized the impact of hedgerow age on the patterns of species occurrence and richness (*e.g.*, Roy & de Blois, 2008). Therefore, the major aim of this chapter was to examine the changes in frequency of forest herbs along forest-hedgerow transects and to relate these findings to environmental variables (in terms of soil and climatic factors). Furthermore, the influence of hedgerow age on forest species richness and frequency changes was determined.

Chapter 6

As mentioned above the results and conclusions of previous studies concerning forest species in hedgerow networks are controversial and therefore equivocal. To support landscape planning and nature conservation decisions on a European scale, the prediction of forest herb occurrences in hedgerows is needed. In this chapter, a set of ecological and life-history variables, reported for their effects on forest herb occurrence, was tested for its suitability to predict the occurrence of woodland herbs in hedgerow networks throughout Europe. A further aim was to reveal differences in environmental conditions and species composition along a climate gradient across Europe.

Chapter 7

In this chapter, the results of the previous chapters are summarized and discussed. The obtained results are used to suggest future research approaches. In addition, guidelines for management strategies for the regional conservation of forest plant species in the agricultural landscape of north-western Germany are presented.

REFERENCES

- Agger, P., Brandt, J., 1988. Dynamics of small biotopes in Danish agricultural landscapes. *Landscape Ecology* 1, 227-240.
- Andrews, M., Mercer, C., Griffin, P., Andrews, M. E., Cherrill, A., 1999. Autecology of common herbaceous hedgerow species in Britain. *Aspects of Applied Biology* 54, 353-360.
- Bailey, S.-A., 2007. Increasing connectivity in fragmented landscapes: An investigation of evidence for biodiversity gain in woodlands. *Forest Ecology and Management* 238, 7-23.
- Barnes, G., Williamson, T., 2006. *Hedgerow history: Ecology, history and landscape character*. Windgather Press, Bollington, UK.
- Bates, G. H., 1937. The vegetation of wayside and hedgerow. *Journal of Ecology* 25, 469-481.
- Baudry, J., Bunce, R. G. H., Burel, F., 2000. Hedgerows: An international perspective on their origin, function and management. *Journal of Environmental Management* 60, 7-22.
- Baudry, J., Burel, F., Aviron, S., Martin, M., Ouin, A., Pain, G., Thenail, C., 2003. Temporal variability of connectivity in agricultural landscapes: do farming activities help? *Landscape Ecology* 18, 303-314.
- Beier, P., Noss, R. F., 1998. Do habitat corridors provide connectivity? *Conservation Biology* 12, 1241-1252.

- Bennett, A. F., 1999. *Linkages in the Landscape - The Role of Corridors and Connectivity in Wildlife Conservation*, IUCN, Cambridge, UK.
- Bierzzychudek, P., 1982. Life history and demography of shade-tolerant temperate forest herbs: a review. *New Phytologist* 90, 757-776.
- Bird, P. R., Bicknell, D., Bulman, P. A., Burke, S. J. A., Leys, J. F., Parker, J. N., Van der Sommen, F. J., Voller, P., 1992. The role of shelter in Australia for protecting soils, plants and livestock. *Agroforestry Systems* 20, 59-86.
- Boutin, C., Jobin, B., 1998. Intensity of agricultural practices and effects on adjacent habitats. *Ecological Applications* 8, 544-557.
- Bunce, R. G. H., Hallam, C. J., 1993. The ecological significance of linear features in agricultural landscapes in Britain. In: Bunce, R. G. H., Ryszkowski, L., Paoletti, M. G. (eds). *Landscape Ecology and Agroecosystems*. Lewis Publishers, Boca Raton, USA, 11-19.
- Burel, F., Baudry, J., 1990. Hedgerow networks as habitats for forest species: implications for colonising abandoned agricultural land. In: Bunce, R. G. H., Howard, D. C. (eds). *Species dispersal in agricultural habitats*. Belhaven Press, London, UK, 238-255.
- Burel, F., Baudry, J., Butet, A., Clergeau, P., Delettre, Y., Le Cœur, D., Dubs, F., Morvan, N., Paillat, G., Petit, S., Thenail, C., Brunel, E., Lefeuvre, J.-C., 1998. Comparative biodiversity along a gradient of agricultural landscapes. *Acta Oecologica* 19, 47-60.
- Burel, F., Baudry, J., Lefeuvre, J.-C., 1993. Landscape structure and the control of water runoff. In: Bunce, R. G. H., Ryszkowski, L., Paoletti, M. G. (eds). *Landscape Ecology and Agroecosystems*. Lewis Publishers, Boca Raton, USA, 41-47.
- Cain, M. L., Damman, H., Muir, A., 1998. Seed dispersal and the holocene migration of woodland herbs. *Ecological Monographs* 68, 325-347.
- Campagne, P., Affre, L., Baumel, A., Roche, P., Tatoni, T., 2009. Fine-scale response to landscape structure in *Primula vulgaris* Huds.: does hedgerow network connectedness ensure connectivity through gene flow? *Population Ecology* 51, 209-219.
- Corbit, M., Marks, P. L., Gardescu, S., 1999. Hedgerows as habitat corridors for forest herbs in central New York, USA. *Journal of Ecology* 87, 220-232.
- Cunningham, S. A., 2000. Effects of habitat fragmentation on the reproductive ecology of four plant species in mallee woodland. *Conservation Biology* 14, 758-768.
- Davies, Z. G., Pullin, A. S., 2006. *Do hedgerow corridors increase the population viability of woodland species? Systematic Review No. 8 Part A*, University of Birmingham, Birmingham, UK.
- Davis, J. E., Norman, J. M., 2009. Effects of shelter on plant water use. *Agriculture, Ecosystems and Environment* 22/23, 393-402.
- de Blois, S., Domon, G., Bouchard, A., 2001. Environmental, historical, and contextual determinants of vegetation cover: a landscape perspective. *Landscape Ecology* 16, 421-436.

- de Blois, S., Domon, G., Bouchard, A., 2002. Factors affecting plant distribution in hedgerows of southern Quebec. *Biological Conservation* 105, 355-367.
- De Keersmaecker, L., Martens, L., Verheyen, K., Hermy, M., De Schrijver, A., Lust, N., 2004. Impact of soil fertility and insolation on diversity of herbaceous woodland species colonizing afforestations in Muizen forest (Belgium). *Forest Ecology and Management* 188, 291-304.
- Deckers, B., Hermy, M., Muys, B., 2004. Factors affecting plant species composition of hedgerows: relative importance and hierarchy. *Acta Oecologica* 26, 23-37.
- Donald, P. F., Evans, A. D., 2006. Habitat connectivity and matrix restoration: the wider implications of agri-environment schemes. *Journal of Applied Ecology* 43, 209-218.
- Dowdeswell, W. H., 1987. *Hedgerows and verges*. Allen & Unwin, London, UK.
- Dzwonko, Z., Loster, S., 1988. The number and distribution of vascular plant species in island forest communities in the northern part of the West Carpathian foothills. *Folia geobotanica et phytotaxonomica* 23, 1-16.
- Elemans, M., 2004. Light, nutrients and the growth of herbaceous forest species. *Acta Oecologica* 26, 197-202.
- Endels, P., Adriaens, D., Verheyen, K., Hermy, M., 2004. Population structure and adult plant performance of forest herbs in three contrasting habitats. *Ecography* 27, 225-241.
- Endels, P., Jacquemyn, H., Brys, R., Hermy, M., De Blust, G., 2002. Temporal changes (1986-1999) in populations of primrose (*Primula vulgaris* Huds.) in an agricultural landscape and implications for conservation. *Biological Conservation* 105, 11-25.
- Foley, J. A., DeFries, R., Asner, G. P., Barford, C., Bonan, G., Carpenter, S. R., Chapin, F. S., Coe, M. T., Daily, G. C., Gibbs, H. K., Helkowski, J. H., Holloway, T., Howard, E. A., Kucharik, C. J., Monfreda, C., Patz, J. A., Prentice, I. C., Ramankutty, N., Snyder, P. K., 2005. Global consequences of land use. *Science* 309, 570-574.
- Forman, R. T. T., 1991. Landscape corridors: from theoretical foundations to public policy. In: Saunders, D. A., Hobbs, R. J. (eds). *Nature Conservation 2: The Role of Corridors*. Surrey Beatty & Sons, Chipping Norton, UK, 71-84.
- Forman, R. T. T., Baudry, J., 1984. Hedgerows and hedgerow networks in landscape ecology. *Environmental Management* 8, 495-510.
- Freemark, K. E., Boutin, C., Keddy, C. J., 2002. Importance of farmland habitats for conservation of plant species. *Conservation Biology* 16, 399-412.
- French, D. D., Cummins, R. P., 2001. Classification, composition, richness and diversity of British hedgerows. *Applied Vegetation Science* 4, 213-228.
- Fritz, R., Merriam, G., 1993. Fencerow habitats for plants moving between farmland forests. *Biological Conservation* 64, 141-148.
- Garbutt, R. A., Sparks, T. H., 2002. Changes in the botanical diversity of a species rich ancient hedgerow between two surveys (1971-1998). *Biological Conservation* 106, 273-278.

- Garve, E., 2004. Rote Liste und Florenliste der Farn- und Blütenpflanzen in Niedersachsen und Bremen. *Informationsdienst Naturschutz Niedersachsen* 24, 1-76.
- Green, R. E., Cornell, S. J., Scharlemann, J. P. W., Balmford, A., 2005. Farming and the fate of nature. *Science* 307, 550-555.
- Grime, J. P., Hodgson, J. P., Hunt, R., 1988. *Comparative plant ecology: a functional approach to common British species*. Unwin Hyman, London, UK.
- Groppali, R., 1993. Breeding birds in traditional tree rows and hedges in the central Po Valley (Province of Cremona, Northern Italy). In: Bunce, R. G. H., Ryszkowski, L., Paoletti, M. G. (eds). *Landscape Ecology and Agroecosystems*. Lewis Publishers, Boca Raton, USA, 153-158.
- Haddad, N. M., Tewksbury, J. J., 2006. Impacts of corridors on populations and communities. In: Crooks, K. R., Sanjayan, M. (eds). *Connectivity Conservation*. Cambridge University Press, Cambridge, UK, 390-415.
- Haila, Y., 1999. Islands and fragments. In: Hunter, M. L. (ed). *Maintaining biodiversity in forest ecosystems*. Cambridge University Press, Cambridge, UK, 234-264.
- Harvey, C. A., Tucker, N. I. J., Estrada, A., 2004. Live fences, isolated trees, and windbreaks: tools for conserving biodiversity in fragmented tropical landscapes. In: G. Schroth, G., da Fonseca, G. A. B., Harvey, C. A., Gascon, C., Vasconcelos, H. L., Izac, A.-M. N. (eds). *Agroforestry and biodiversity conservation in tropical landscapes*. Island Press, Washington, USA, 261-289.
- Hipps, N. A., Davies, M. J., Dodds, P., Buckley, G. P., 2005. The effects of phosphorus nutrition and soil pH on the growth of some ancient woodland indicator plants and their interaction with competitor species. *Plant and Soil* 271, 131-141.
- Honnay, O., Jacquemyn, H., 2007. Susceptibility of common and rare plant species to the genetic consequences of habitat fragmentation. *Conservation Biology* 21, 823-831.
- Honnay, O., Jacquemyn, H., Bossuyt, B., Hermy, M., 2005. Forest fragmentation effects on patch occupancy and population viability of herbaceous plant species. *New Phytologist* 166, 723-736.
- Hooper, M. D., 1970. Hedges and history. *New Scientist* 31, 598-600.
- Jobin, B., Boutin, C., Bélanger, L., 2001. Hedgerows as refuges for pest birds and plants: could Quebec's farmers be wrong? In: Barr, C. J., Petit, S. (eds). *Hedgerows of the world: their ecological functions in different landscapes*, IALE, Birmingham, UK, 207-212.
- Kelm, H.-J., 1994. Zur Waldgeschichte des Elbe-Weser-Dreiecks. *Norddeutsche Naturschutzakademie Berichte* 7, 50-59.
- Kirchner, F., Ferdy, J.-B., Andalo, C., Colas, B., Moret, J., 2003. Role of corridors in plant dispersal: an example with the endangered *Ranunculus nodiflorus*. *Conservation Biology* 17, 401-410.
- Kolb, A., Diekmann, M., 2004. Effects of environment, habitat configuration and forest continuity on the distribution of forest plant species. *Journal of Vegetation Science* 15, 199-208.
- Laurance, S. G. W., 2004. Landscape connectivity and biological corridors. In: G. Schroth, G., da Fonseca, G. A. B., Harvey, C. A., Gascon, C., Vasconcelos, H. L., Izac, A.-M. N. (eds).

- Agroforestry and biodiversity conservation in tropical landscapes*. Island Press, Washington, USA, 50-63.
- Le Cœur, D., Baudry, J., Burel, F., 1997. Field margins plant assemblages: variation partitioning between local and landscape factors. *Landscape and Urban Planning* 37, 57-71.
- Le Cœur, D., Baudry, J., Burel, F., Thenail, C., 2002. Why and how we should study field boundary biodiversity in an agrarian landscape context. *Agriculture, Ecosystems and Environment* 89, 23-40.
- Lindborg, R., Eriksson, O., 2004. Historical landscape connectivity affects present plant species diversity. *Ecology* 85, 1840-1845.
- Macdonald, D. W., Johnson, P., 2000. Farmers and the custody of the countryside: trends in loss and conservation of non-productive habitats. *Biological Conservation* 94, 221-234.
- Marshall, E. J. P., Moonen, A. C., 2002. Field margins in northern Europe: their functions and interactions with agriculture. *Agriculture, Ecosystems and Environment* 89, 5-21.
- Matlack, G. R., 2005. Slow plants in a fast forest: local dispersal as a predictor of species frequencies in a dynamic landscape. *Journal of Ecology* 93, 50-59.
- McCollin, D., Jackson, J. I., Bunce, R. G. H., Barr, C. J., Stuart, R., 2000. Hedgerows as habitat for woodland plants. *Journal of Environmental Management* 60, 77-90.
- Merot, P., 1999. The influence of hedgerow systems on the hydrology of agricultural catchments in a temperate climate. *Agronomie* 19, 655-669.
- Mieth, B., Kutsch, W. L., Kappen, L., 1996. *Lamium galeobdolon* und *Galium aparine* als erfolgreiche Knickbodenpflanzen. *EcoSys: Beiträge zur Ökosystemforschung* 5, 163-174.
- Miller, K. E., Gorchov, D. L., 2004. The invasive shrub, *Lonicera maackii*, reduces growth and fecundity of perennial forest herbs. *Oecologia* 139, 359-375.
- Molnárová, K., 2008. Hedgerow-defined medieval field patterns in the Czech Republic and their conservation - a literature review. *Journal of Landscape Studies* 1, 27-47.
- Muir, R., Muir, N., 1987. *Hedgerows: their history and wildlife*, Michael Joseph Ltd, London, UK.
- Oostermeijer, J. G. B., 1996. Population size, genetic variation, and related parameters in small, isolated plant populations: a case study. In: Settele, J., Margules, C., Poschlod, P., Henle, K. (eds). *Species survival in fragmented landscapes*. Kluwer Academic Publishers, Dordrecht, The Netherlands, 61-68.
- Peterken, G. F., 1974. A method for assessing woodland flora for conservation using indicator species. *Biological Conservation* 6, 239-245.
- Petit, S., Griffiths, L., Smart, S. S., Smith, G. M., Stuart, R. C., Wright, S. M., 2004. Effects of area and isolation of woodland patches on herbaceous plant species richness across Great Britain. *Landscape Ecology* 19, 463-471.
- Petit, S., Stuart, R., Gillespie, M. K., Barr, C. J., 2003. Field boundaries in Great Britain: stock and change between 1984, 1990 and 1998. *Journal of Environmental Management* 67, 229-238.

- Poschlod, P., Bakker, J., Bonn, S., Fischer, S., 1996. Dispersal of plants in fragmented landscapes. In: Settele, J., Margules, C., Poschlod, P., Henle, K. (eds), *Species survival in fragmented landscapes*, Kluwer Academic Publishers, Dordrecht, The Netherlands, 123-127.
- Primack, R. B., Miao, S. L., 1992. Dispersal can limit local plant distribution. *Conservation Biology* 6, 513-519.
- Reif, A., Schulze, E.-D., Zahner, K., 1982. Der Einfluß des geologischen Untergrundes, der Hangneigung, der Feldgröße und der Flurbereinigung auf die Heckendichte in Oberfranken. *Akademie für Naturschutz und Landschaftspflege* 6, 231-253.
- Rounsevell, M. D. A., Annetts, J. E., Audsley, E., Mayr, T., Reginster, I., 2003. Modelling the spatial distribution of agricultural land use at the regional scale. *Agriculture, Ecosystems and Environment* 95, 465-479.
- Roy, V., de Blois, S., 2008. Evaluating hedgerow corridors for the conservation of native forest herb diversity. *Biological Conservation* 141, 298-307.
- Röser, B., 1995. *Saum- und Kleinbiotope: ökologische Funktion, wissenschaftliche Bedeutung und Schutzwürdigkeit in Agrarlandschaften*. ecomed, Landsberg/Lech, Germany.
- Sage, R. B., Woodburn, M. I. A., Draycott, R. A. H., Hoodless, A. H., Clarke, S., 2009. The flora and structure of farmland hedges and hedgebanks near to pheasant release pens compared with other hedges. *Biological Conservation* 142, 1362-1369.
- Schmidt, M., von Oheimb, G., Kriebitzsch, W.-U., Ellenberg, H., 2002. Liste der im norddeutschen Tiefland typischen Waldgefäßpflanzen. *Mitteilungen der Bundesforschungsanstalt für Forst- und Holzwirtschaft* 206, 1-37.
- Schmitz, M. F., Sánchez, I. A., de Aranzabal, I., 2007. Influence of management regimes of adjacent land uses on the woody plant richness of hedgerows in Spanish cultural landscapes. *Biological Conservation* 135, 542-554.
- Schmucki, R., de Blois, S., 2009. Population structures and individual performances of *Trillium grandiflorum* in hedgerow and forest habitats. *Plant Ecology* 202, 67-78.
- Simberloff, D., Cox, J., 1987. Consequences and costs of conservation corridors. *Conservation Biology* 1, 63-71.
- Simberloff, D., Farr, J. A., Cox, J., Mehlman, D. W., 1992. Movement corridors: conservation bargains or poor investments? *Conservation Biology* 6, 493-504.
- Sklenicka, P., Molnarova, K., Brabec, E., Kumble, P., Pittnerova, B., Pixova, K., Salek, M., 2009. Remnants of medieval field patterns in the Czech Republic: Analysis of driving forces behind their disappearance with special attention to the role of hedgerows. *Agriculture, Ecosystems and Environment* 129, 465-473.
- Slade, E. A., Causton, D. R., 1979. The germination of some woodland herbaceous species under laboratory conditions: a multifactorial study. *New Phytologist* 83, 549-557.

- Stoate, C., Boatman, N., Borralho, R. J., Carvalho, C. R., De Snoo, G. R., Eden, P., 2001. Ecological impacts of arable intensification in Europe. *Journal of Environmental Management* 63, 337-365.
- Sullivan, T. P., Sullivan, D. S., 2006. Plant and small mammal diversity in orchard versus non-crop habitats. *Agriculture, Ecosystems and Environment* 116, 235-243.
- Takahashi, K., Kamitani, T., 2004. Effect of dispersal capacity on forest plant migration at a landscape level. *Journal of Ecology* 92, 778-785.
- Tang Ya, Zhang Yan-zhou, Xie Jia-sui, Sun Hui, 2003. Incorporation of mulberry in contour hedgerows to increase overall benefits: a case study from Ningnan County, Sichuan Province, China. *Agricultural Systems* 76, 775-785.
- Taylor, K., 1997. *Geum urbanum* L. *Journal of Ecology* 85, 705-720.
- Tischler, W., 1951. Die Hecke als Lebensraum für Pflanzen und Tiere, unter besonderer Berücksichtigung ihrer Schädlinge. *Erdkunde* 5, 125-132.
- Turnbull, L. A., Crawley, M. J., Rees, M., 2000. Are plant populations seed-limited? A review of seed sowing experiments. *Oikos* 88, 225-238.
- Tyrbirk, K., Aude, E., Ejrnæs, R., Reddersen, J., Hald, A. B., Riberholdt, L., Jönsson, C., Jørgensen, J. E., Gramstrup, M., Andreasen, P. R., Vind, L. R., Dalsgaard, A., Jensen, N. V., Odderskær, P., Sell, H., 2001. Botanical conservation values in Danish hedgerows. In: Barr, C. J., Petit, S. (eds). *Hedgerows of the world: their ecological functions in different landscapes*. IALE, Birmingham, UK, 299-308.
- van Calster, H., Vandenberghe, R., Ruysen, M., Verheyen, K., Hermy, M., Decocq, G., 2008. Unexpectedly high 20th century floristic losses in a rural landscape in northern France. *Journal of Ecology* 96, 927-936.
- Vellend, M., Verheyen, K., Jacquemyn, H., Kolb, A., van Calster, H., Peterken, G., Hermy, M., 2006. Extinction debt of forest plants persists for more than a century following habitat fragmentation. *Ecology* 87, 542-548.
- Verheyen, K., Hermy, M., 2001. The relative importance of dispersal limitation of vascular plants in secondary forest succession in Muizen Forest, Belgium. *Journal of Ecology* 89, 829-840.
- Verheyen, K., Hermy, M., 2004. Recruitment and growth of herb-layer species with different colonizing capacities in ancient and recent forests. *Journal of Vegetation Science* 15, 125-134.
- Verkaar, H. J., 1990. Corridors as a tool for plant species conservation? In: Bunce, R. G. H., Howard, D. C. (eds). *Species dispersal in agricultural habitats*. Belhaven Press, London, UK, 82-97.
- Vitousek, P. M., Mooney, H. A., Lubchenco, J., Melillo, J. M., 1997. Human domination of earth's ecosystems. *Science* 277, 494-499.
- Weber, H. E., 2003. *Gebüsche, Hecken, Krautsäume*. Verlag Eugen Ulmer, Stuttgart, Germany.
- Whigham, D. F., 2004. Ecology of woodland herbs in temperate deciduous forests. *Annual Review of Ecology, Evolution and Systematics* 35, 583-621.

CHAPTER 2

STUDY AREA



Top left: Hedgerow network 'Hasbruch'. **Top right:** Hedgerow network 'Eggestedt'. **Bottom left:** Hedgerow network 'Stendorf'. **Bottom right:** Hedgerow network 'Wollingst'.
(Satellite photographs obtained from: <http://earth.google.de/>, [23.05.2009]).

NATURAL CONDITIONS

The study area is situated in the lowlands of north-western Germany on both sides of the river Weser, in the far vicinity of the city of Bremen (53° 07-30' N, 8° 31-48' E; Fig. 1). The landscape is characterised by a mosaic of fields, meadows, forests and hedgerow networks. The latter show their highest densities in four subsections of this area. The first section 'Hasbruch' is located in the west of Bremen in the natural geographical region of the *Oldenburger Geest*. The other sections 'Eggestedt', 'Stendorf' and 'Wollingst' are located in the north and are assigned to the natural area of the *Stader Geest* (Meynen *et al.*, 1962). The study area covers parts of the rural districts of Oldenburg, Osterholz-Scharmbeck and Cuxhaven, which are part of the federal state Lower Saxony.

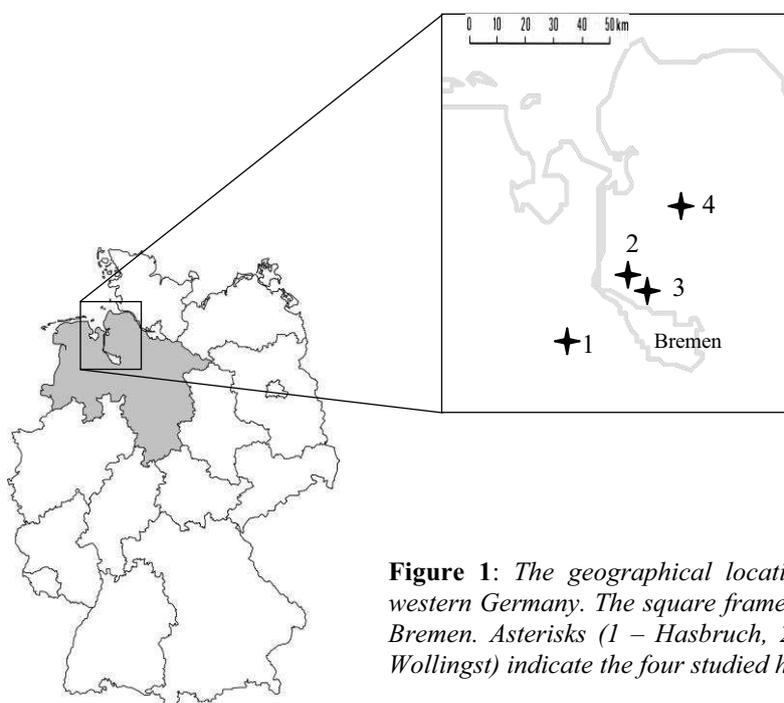


Figure 1: The geographical location of the study area in north-western Germany. The square frames the study area in the vicinity of Bremen. Asterisks (1 – Hasbruch, 2 – Eggestedt, 3 – Stendorf, 4 – Wollingst) indicate the four studied hedgerow networks.

The four studied hedgerow networks are embedded in a flat to weakly undulating landscape. Their elevations vary between 10 and 25 m above sea level. The geological conditions of the region are based in main parts on till and glacial depositions of the Saale glaciation 200.000 – 100.000 years ago (Seedorf & Meyer, 1992; Niedersächsisches Ministerium für Ernährung, Landwirtschaft und Forsten, 1999b). In most cases, a layer of silt partly mixed with sands and gravel is found above till, the so-called Lauenburg clay. Due to complex glacial processes, the soils of the section 'Wollingst' show marginal higher contents of limestone, clay and silt as the other sections, but they are still composed of more than 50% gravel and sand (Höfle,

1980; Wulf, 1992). Characteristic soil types of the selected sections are pseudogley, podsol, para-brown earth and brown earth, which are in sum not very nutrient-rich (Wulf & Kelm, 1994).

The study area shows a more or less (sub-)atlantic climate with relatively high amounts of rainfall over the year and mild winters. All study sections are located in the climate region of the interior lowlands of Lower Saxony, which is characterised by a mean temperature of 0°C in January and 16.5°C in July and a mean annual precipitation of 700 mm. The section 'Hasbruch' is close to the border of the so-called Emsland climate region, with a higher mean temperature in January (1.5°C). Moreover, the section 'Wollingst' is at the border to the coastal North Sea climate region, with a slightly higher mean temperature in January (0.5°C), but with a mean annual precipitation of more than 800mm (Liedke & Marcinek, 2002; Jeschke, 2007).

LANDSCAPE CHARACTERISTICS

The landscape of the study area is in majority used for agricultural purposes. Dairy cattle farming dominates with large areas of grassland (in terms of meadows, pastures or a combination of both) and arable land, which is mainly used for the cultivation of fodder corn. A lesser proportion of fields is dedicated to the cultivation of cereals or other field crops (<http://www.lwk-niedersachsen.de>, [10.05.2009]). In spite of agricultural intensification and mechanisation the field sizes remained relatively small compared to other regions and a large amount of non-productive habitats, especially hedgerows, have overcome the land consolidation processes in the last decades. The soils of many parts of the study region are classified as relatively unsuitable for agricultural production (Seedorf & Meyer, 1992) and this may be an explanation for the preservation of large amounts of hedgerow networks.

As mentioned earlier, the density of hedgerow networks is not the same for all regions in Lower Saxony. The general distribution of hedgerows is almost identical to the distribution of hedges with banks, a hedgerow type that is predominant in the study region and in Lower Saxony (Roßkamp, 1999). There are some 'hotspots' with highly dense networks, especially in East Frisia, but also near the city of Bremen (Schupp & Dahl, 1992). The four study sections are located in such areas, which show relatively high densities of hedgerows (Fig. 2b). On a regional scale, the hedgerow densities for the four sections are as followed: Hasbruch 0.7 km/km², Eggestedt 1.5 km/km², Stendorf 0.8 km/km², Wollingst 0.7 km/km². The forest cover of the three regarding rural districts is 7.3% in Cuxhaven and 10.6% in Osterholz-Scharmbeck (Kelm, 1994) and about 10.0% in Oldenburg (Müller, 1989). The

proportion of relatively species-rich deciduous forest is for all districts between 35 and 40%, whereas the remaining wooded areas are used for timber production from conifers.

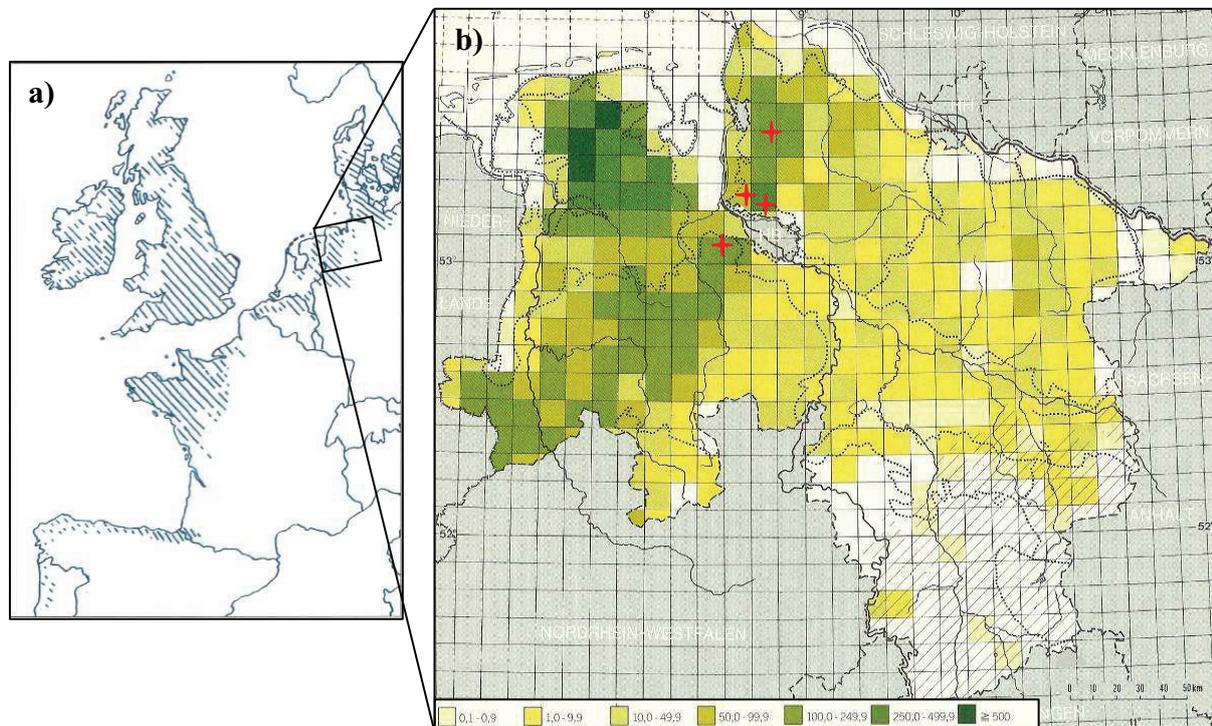


Figure 2: a) The distribution of hedgerows (with banks) in the coastal regions of Western and Central Europe (Weber, 2003). b) Density of hedgerows (with banks) in Lower Saxony in km/map square; map square = 121 km² (Schupp & Dahl, 1992), modified. The density increases from the pale yellow regions (0.1-0.9 km/map square) up to the dark green regions (>500 km/ map square); white regions – no hedgerows present. Red asterisks indicate the location of the studied hedgerow networks.

The forest stands in the vicinity of the studied hedgerow networks belong to the phytosociological order *Fagetalia sylvaticae*. The present alliances are *Alno-Ulmion*, *Carpinion betuli*, and *Fagion sylvaticae* (Wilmanns, 1993). The phytosociological classification of the hedgerows is not as clear as for the woodland communities (Weber, 2003).

Hedgerows mainly containing shrubs and almost no trees may be assigned to the class *Rhamno-Prunetea* and in more detail to the association *Carpino-Prunetum*, which is a surrogate community for a typical oak-hornbeam forest (Wilmanns, 1993). For such hedgerows *Carpinus betulus*, *Corylus avellana*, *Crataegus laevigata*, *Crataegus monogyna*, *Prunus spinosa*, *Quercus robur*, and *Sambucus nigra* are typical woody species, whereas *Aegopodium podagraria*, *Alliaria petiolata*, *Anthriscus sylvestris*, *Chaerophyllum temulum*, *Geum urbanum*, *Humulus lupulus*, *Moehriniga trinervia*, *Poa nemoralis*, *Stachys sylvatica*, and *Urtica dioica* are typical herbaceous species. However, this thesis followed the wider

international definition of a hedgerow as ‘a row of trees and shrubs managed in various ways’ by Baudry *et al.* (2000) and not the narrow national definition, which declares only hedgerows without a mature tree-layer as real hedgerows (Weber, 2003). As mature trees from the species *Quercus robur*, *Carpinus betulus* or *Fagus sylvatica*, dominate most of the local hedges and a transition from pure shrub- to woodland-communities is observed, the studied hedgerow networks cannot be categorized with the existing phytosociological system.

LANDSCAPE HISTORY

In the past large parts of the study area and also of north-western Germany were covered by deciduous forests, composed of pure *Fagus sylvatica* stands or mixtures with other deciduous tree species, especially *Quercus robur* (Kelm, 1994). With the beginning of the Common Era, anthropogenic influences formed the landscape to much higher extent than before. Many forests in Central Europe were cleared for land reclamation and/or the construction of new settlements (Müller, 1989). This destructive landscape exploitation was intensified with an increase in the human population over the following centuries. Forest clearance reached its maximum at the end of the 18th century (Niedersächsisches Ministerium für Ernährung, Landwirtschaft und Forsten, 1999a). At this time, only about 5% of the study area were covered by highly fragmented deciduous forests (Kelm, 1994). Since 1850, the local authorities have undertaken large afforestation efforts mainly by planting conifers on former heathlands or fields. Coniferous forests still represent the majority of forest types in the study area and in Lower Saxony (Niedersächsisches Ministerium für den ländlichen Raum, Ernährung, Landwirtschaft und Verbraucherschutz, 2004). The proportion of continuously forested areas since the end of the 18th century is only at about 25% (Kolb, 2005), but these forests are of great conservation interest, due to their richness in endangered species (Niedersächsisches Ministerium für Ernährung, Landwirtschaft und Forsten, 1999b).

The history of the hedgerow networks in the study region also reflects the human activities in the last millennia. Since the 10th century it was common in North Germany to enclose collectively used farmland of settlements (*‘Esch’*) by thorny hedges in order to exclude pasturing livestock (Tüxen, 1952). In medieval times, hedges in this region were established to delimit feudal properties or for defensive purposes (Pott, 1989). By the end of the 16th and the beginning of the 17th century further hedgerows were planted. Farmers were forced to do so, because the paucity of firewood and timber due to the overexploitation of forests increased and all land not enclosed by hedges devolved into baronial ownership (Müller, 1989). At this time, hedgerows were firstly recorded in maps of the study region (*‘Kurhannoversche*

Landesaufnahme’ dating from 1764-1786) and from this date on the development of the hedgerow networks can be followed with reliable data (Fig. 3). In the beginning of the 19th century, a land reform was ordered by the local authorities (*‘Gemeinheitsteilung’*), which caused an exponential increase in the amount of newly erected hedgerows. Formerly collectively used land and livestock were replaced by fields and herds under private ownership. Hedgerows were planted to delimit this ownership and to separate the private livestock herds. Furthermore, the hedges provided firewood, timber, fodder and fruits for the farmers (Weber, 1967; Müller, 1989). The local hedgerows were coppiced every eight to ten

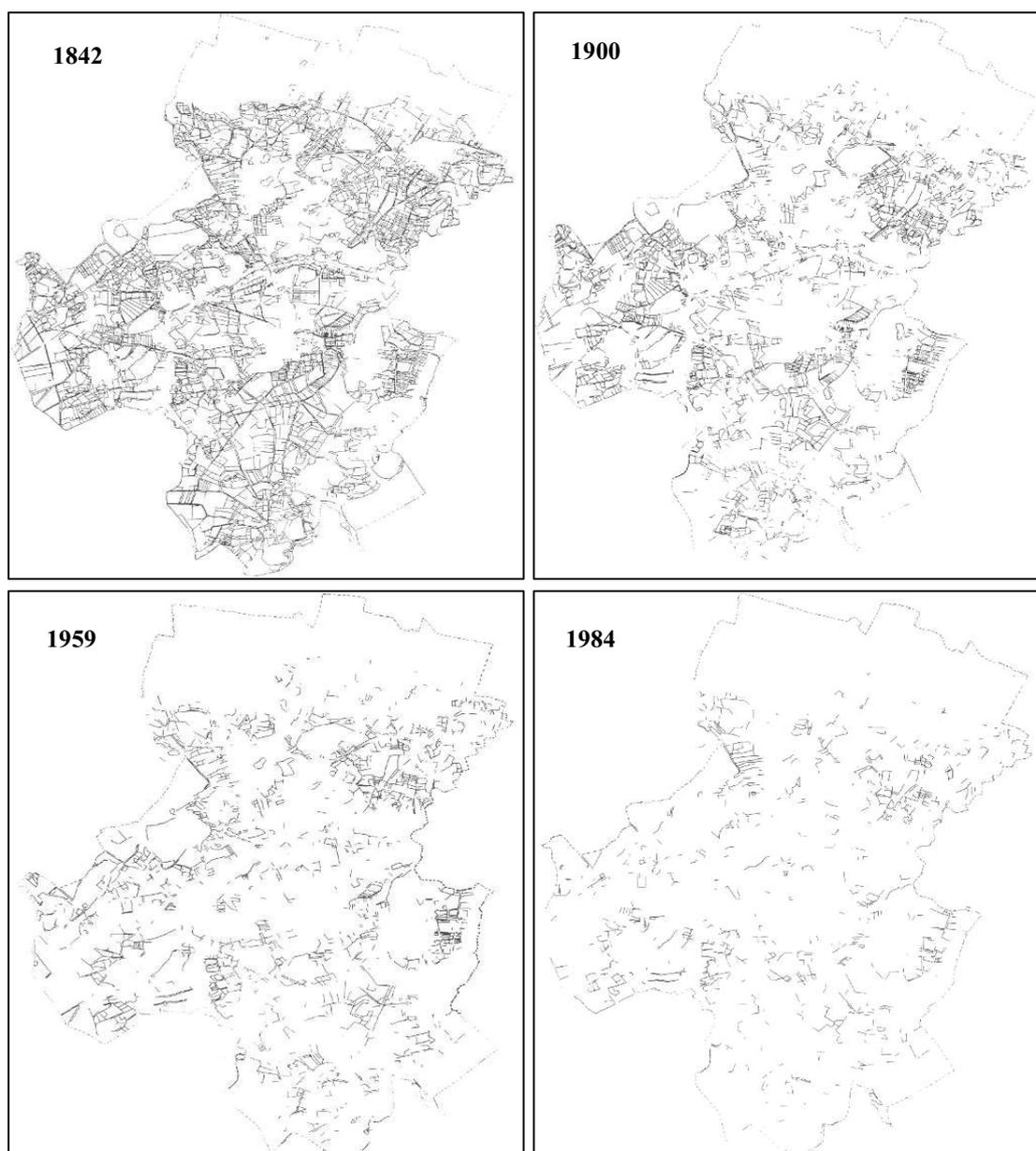


Figure 3: Historical development of the hedgerow network in the municipality of Ganderkesee in the rural district of Oldenburg from 1842 to 1984 (Müller, 1989). The north-west of the municipality is part of the studied hedgerow network Hasbruch. The shown reduction in hedgerow length and network density over time is comparable to the three other studied hedgerow networks.

years to conserve their linear characteristic; only some mature trees (mainly oaks) remained. The work- and time-consuming management requirements caused the removal of many hedges by the farmers in the following century. In addition, with the development of wire fences, particularly after 1950, hedgerows lost their former function. The occupation of valuable field space and hampering of the use of heavy tractors and other machines were given as further reasons for extended hedge clearance (Müller, 1989; Pott, 1989). The hedgerow removal reached its maximum in the 1960s and 70s due to land consolidation efforts. From 1980 onwards the local authorities recognised the ecological and nature conservation value of hedgerows and the first laws for the protection of these landscape elements were enacted (Weber, 2003).

REFERENCES

- Baudry, J., Bunce, R. G. H., Burel, F., 2000. Hedgerows: An international perspective on their origin, function and management. *Journal of Environmental Management* 60, 7-22.
- Höfle, H. C., 1980. Klassifikation von Grundmoränen in Niedersachsen. *Verhandlungen des Naturwissenschaftlichen Vereins in Hamburg* 23, 81-91.
- Jeschke, L., 2007. Bundesweit bedeutsame Waldgebiete mineralischer Standorte im norddeutschen Tiefland aus geobotanischer Sicht. In: Scherfose, V. (ed). *Bundesweit bedeutsame Gebiete für den Naturschutz*. Bundesamt für Naturschutz, Bonn, Germany, 67-106.
- Kelm, H.-J., 1994. Zur Waldgeschichte des Elbe-Weser-Dreiecks. *Norddeutsche Naturschutzakademie Berichte* 7, 50-59.
- Kolb, A., 2005. *The distribution of forest plant species in a fragmented landscape: patterns and processes*. University of Bremen, Bremen, Germany.
- Liedke, H., Marcinek, J., 2002. *Physische Geographie von Deutschland*. Klett-Perthes Verlag, Gotha, Germany.
- Meynen, E., Schmithüsen, J., Gellert, J., Neef, E., Müller-Miny, H., Schultze, J. H. (eds), 1962. *Handbuch der naturräumlichen Gliederung Deutschlands*. Selbstverlag der Bundesanstalt für Landeskunde und Raumforschung, Bad Godesberg, Germany.
- Müller, G., 1989. Wallhecken: *Entstehung, Pflege, Neuanlage am Beispiel der Gemeinde Ganderkesee und allgemeine Hinweise zu Wallhecken im nordwestdeutschen Raum*. BSH-Verlag, Wardenburg, Germany.
- Niedersächsisches Ministerium für den ländlichen Raum, Ernährung, Landwirtschaft und Verbraucherschutz (ed), 2004. Der Wald in Niedersachsen: Ergebnisse der Bundeswaldinventur II. *Schriftenreihe Aus dem Walde - Waldentwicklung in Niedersachsen* 55, 1-43.

- Niedersächsisches Ministerium für Ernährung, Landwirtschaft und Forsten (ed), 1999a. Waldprogramm Niedersachsen: Fachgutachten. *Schriftenreihe Waldentwicklung in Niedersachsen* 3, 1-98.
- Niedersächsisches Ministerium für Ernährung, Landwirtschaft und Forsten (ed), 1999b. Der Hasbruch - Naturkundliche Beschreibung eines norddeutschen Waldes. *Schriftenreihe Waldentwicklung in Niedersachsen* 8, 1-136.
- Pott, R., 1989. Entwicklung von Hecken in der Kulturlandschaft Nordwestdeutschlands. *Verhandlungen der Gesellschaft für Ökologie* 17, 663-670.
- Roßkamp, T., 1999. *Die Vegetation der Feld- und Wallhecken in Niedersachsen*. Martina Galunder-Verlag, Wiehl, Germany.
- Schupp, D., Dahl, H.-J., 1992. Wallhecken in Niedersachsen. *Informationsdienst Naturschutz Niedersachsen* 12, 109-176.
- Seedorf, H. H., Meyer, H.-H., 1992. *Landeskunde Niedersachsen – Natur- und Kulturgeschichte eines Bundeslandes*. Wachholtz Verlag, Neumünster, Germany.
- Tüxen, R., 1952. Hecken und Gebüsch. *Mitteilungen der Geographischen Gesellschaft Hamburg* 50, 85-117.
- Weber, H. E., 1967. *Über die Vegetation der Knicks in Schleswig-Holstein Teil 1*. Raabe, E.-W., Kiel, Germany.
- Weber, H. E., 2003. *Gebüsch, Hecken, Krautsäume*. Verlag Eugen Ulmer, Stuttgart, Germany.
- Willmanns, O., 1993. *Ökologische Pflanzensoziologie: eine Einführung in die Vegetation Mitteleuropas*. Quelle & Meyer, Heidelberg, Germany.
- Wulf, M., 1992. Vegetationskundliche und ökologische Untersuchungen zum Vorkommen gefährdeter Pflanzenarten in Feuchtwäldern Nordwestdeutschlands. *Dissertationes Botanicae* 185, 1-246.
- Wulf, M., Kelm, H.-J., 1994. Zur Bedeutung "historisch alter Wälder" für den Naturschutz - Untersuchungen naturnaher Wälder im Elbe-Weser-Dreieck. *Norddeutsche Naturschutzakademie Berichte* 3, 15-50.

Chapter 3

Factors influencing the spatial distribution of forest plant species in hedgerows of North-western Germany

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Left: Hedgerows on both sides of a meadow with mature oak-trees. **Right:** *Mercurialis perennis* at a hedge bottom. (Photographs taken by Stephan Wehling).

ABSTRACT

In North-western Germany woodland fragmentation has caused a decline in many forest plant species. Hedgerows partly offer a similar environment as forests and have been identified as potential habitats for forest plants in various studies from North America and Western Europe. The objective of this study was to examine whether this applies also to Central Europe and which variables affect the spatial distribution and abundance of forest plant species in hedgerows on a local scale.

Three hedgerow networks north of the city of Bremen, Germany, were selected as study areas and divided into totally 515 hedgerow segments. In each segment we recorded all vascular plants and a large number of explanatory variables relating to structure, spatial configuration, environment and management.

Averaged across species there was a predominant effect of environmental factors on the occurrence of forest species in the hedgerows, followed by spatial configuration and management. Hedgerow structure was found to be less important. In general, forest species were favoured by low nutrient and light availability as well as high connectivity with other hedgerows or forest; they avoided hedgerows with a west-easterly orientation and an adjacent land use in the form of fields or grasslands. Forest species found and not found in hedgerows did not differ in their environmental preferences or life history traits. The number of threatened forest species in the hedgerows, however, was lower than expected with respect to their overall proportion to the total number of forest species in the region.

KEY WORDS:

environmental variables; forest fragmentation; hedgerow structure; land use; life history traits; partial regression analysis; spatial configuration.

ABBREVIATIONS:

hF_{int} - Herbaceous species preferring the forest interior; hF_{edge} - Herbaceous species preferring forest edges and gaps; ENV - Variable group environment; MAN - Variable group management; SPA - Variable group spatial configuration; STR - Variable group structure.

INTRODUCTION

Forest fragmentation has caused a decline in many forest plant species in many parts of the world (Grashof-Bokdam, 1997; Petit *et al.*, 2004). This is especially true for regions such as Northern Germany where agricultural land has strongly increased at the expense of forested land. Here, forest plant species are largely restricted to small woodlots and the few larger forest remnants (Kolb, 2005). It has been shown that many of these species in such deforested landscapes may suffer from habitat degradation, but also a lack of habitat continuity and an unfavourable habitat configuration in terms of decreasing forest size and increasing forest isolation (Dupré & Ehrlén, 2002). The fact that many forest species have become rare and endangered raises an important question: Are there other vegetation types than true forest that may serve as suitable habitats for forest species? In this context, forest ecologists and conservation biologists have started to study other habitats of the rural landscape, especially hedgerows (*e.g.*, Helliwell, 1975; Burel & Baudry, 1990a; Corbit *et al.*, 1999; Deckers *et al.*, 2005; Roy & de Blois, 2006).

Hedgerows, defined as linear stripes of woody vegetation dominated by shrubs and/or trees (Baudry *et al.*, 2000), are today recognized as important habitats and refuges for plants and animals (de Blois *et al.*, 2002). However, whether hedgerows provide a surrogate habitat for forest species remains equivocal (Fritz & Merriam, 1993; French & Cummins, 2001; Smart *et al.*, 2001), although this function is seen as one of the main incentives for the conservation of hedgerows in agricultural landscapes that have lost forest species. The presence of woodland plants in relatively exposed edge habitats suggests that hedgerows may link populations occurring in remnant woodland patches of fragmented landscapes (Burel & Baudry, 1990a; Corbit *et al.*, 1999; McCollin *et al.*, 2000; de Blois *et al.*, 2002).

The species composition of hedgerows is strongly affected by neighbouring agricultural activities (Mercer *et al.*, 1999). Adjacent land use, especially ploughing near the basement of a hedgerow, misplacement of herbicides (Jobin *et al.*, 1997) and fertilizers (Tsiouris & Marshall, 1998), leads to a high level of disturbance, with notable effects on the distribution of herbaceous plants (Kleijn & Verbeek, 2000). In addition, the structural and spatial configuration of a hedgerow is known to affect its species composition (Hegarty *et al.*, 1994).

The general species composition and environment of hedgerows has recently been studied in North America (Boutin *et al.*, 2001; Jobin *et al.*, 2001; de Blois *et al.*, 2002; Roy & de Blois, 2006) and Western Europe (Burel & Baudry, 1990b; Burel *et al.*, 1998; McCollin *et al.*, 2000; Deckers *et al.*, 2004). The relative importance of different explanatory variables for the occurrence of hedgerow species has been examined by de Blois *et al.* (2002) and Deckers *et*

al. (2004), but, to our knowledge, there has been no specific study of the group of forest specialists and the underlying factors for their occurrence in hedgerows. In this study, we address the following questions:

- Do hedgerows in the study area regularly contain typical forest plant species?
- Which environmental variables determine the distribution and abundance of forest species in hedgerows, and what is the relative importance of different variable groups, relating to management, spatial configuration, environmental conditions, and hedgerow structure?
- Do forest specialists occurring in hedgerows and those being absent from hedgerows differ in their life history traits and ecological responses?

METHODS

Study areas

The study area was located in the lowlands of North-western Germany north of the city of Bremen. The landscape is flat to weakly undulating, with elevations varying between 5 and 30 m a.s.l. The soils, mainly deriving from the Pleistocene Saale glaciation, are fine-textured (loam and clay), relatively base- and nutrient-poor, and often moist to wet because of poor drainage. The study area is characterized by the presence of dense and intact networks of hedgerows and by a relatively large areal extension of species-rich deciduous forests. Three hedgerow networks were selected: 1) Eggestedt, 180 ha, 12 hedgerows of totally 5.95 km length, 2) Stendorf, 220 ha, 13 hedgerows of 6.9 km length, and 3) Wollingst, 750 ha, 22 hedgerows of 12.9 km length. Apart from a minor fraction of non-managed hedgerows, the trees and shrubs are regularly pruned by periodical mechanical cutting, where the cut branches are left on the ground, or coppiced by rotational cut at ground level every 8 to 10 years. Pollarding is not applied in the study area.

The most common woody species found in the hedgerows are *Quercus robur*, *Carpinus betulus*, *Corylus avellana*, *Sorbus aucuparia* and *Sambucus nigra*. The neighbouring forests (except those planted with conifers) are usually dominated by *Quercus robur*, *Fraxinus excelsior* and *Alnus glutinosa*.

Data collection

Each hedgerow was divided into 50 m long segments that were located by means of a GPS device. The segments were kept short to ascertain relative uniformity concerning environmental conditions, adjacent land use, orientation, etc. We studied in total 47 hedgerows with 515 discrete segments.

During summer 2005, the hedgerow segments were surveyed for the occurrence of all vascular plants (nomenclature followed Wisskirchen & Haeupler, 1998). For this we systematically walked both sides of the hedgerow over the entire length of the segment. First, simple presence-absence data were recorded, later the relative frequency of each species was estimated on an ordinal scale (woody species: 1-3, herbaceous species: 1-5). All species were classified into groups of different life form and habitat preference, applying a list of forest vascular plants in the North German lowlands (Schmidt *et al.*, 2002; Table 1).

Table 1: Classification into life forms and habitat preference types of vascular plant species in the North German lowlands (Schmidt *et al.*, 2002).

Layer	Habitat preference of species	Symbol
Woody		w
	growing into the tree layer of forests, partly forming the upper canopy	wF _{tree}
	predominantly growing in the shrub layer, at forest edges or in gaps	wF _{shrub}
Herbaceous		h
	mainly growing in forests	hF
	predominantly growing in the forest interior	hF _{int}
	predominantly growing at forest edges and in gaps	hF _{edge}
	growing both in forests and in the open landscape	hFO
	growing equally well in both habitat types	hFO _{equal}
	growing mainly in the open landscape, less often in forests	hFO _{open}
growing only in the open landscape	hO	

The regional pool of species that prefer the forest interior (hF_{int}) or forest edges and gaps (hF_{edge}), in the following summarized as “forest species”, was defined as the number of forest species occurring in a 5 km radius around the hedgerows according to a local flora (Cordes *et al.*, 2006). For information on threatened species we used a regional list for North-western Germany (Garve, 2004).

In each segment, we recorded data on several variables assumed to affect the distribution of species. These were divided into four groups (Table 2):

- 1) Structural variables: Hedgerow width (measured with a tape) and canopy cover (estimated on an ordinal scale).
- 2) Management variables: The adjacent land use on both sides of the hedgerow segment was classified as a management variable. Information on the current cutting regime of the hedgerow was not available.
- 3) Spatial variables: The spatial configuration of hedgerow segments is characterized by their orientation (determined with a compass), the number of adjacent hedgerows with contact to the segment, and the presence of a direct or loose (forest within 50 m distance) connection to woodland.
- 4) Environmental variables: We collected soil samples in the hedgerow segments 1 m from the mid line, thus within the presumed centre of plant species diversity (Forman & Baudry, 1984). The soil was taken from the top 5 cm after litter removal and composed of 5 sub-samples from different parts of the segment. All samples were air-dried and passed through a 2 mm sieve. Carbon and nitrogen were determined in % using an elemental analyser (Hecatech). The nutrients were extracted with ammonium lactate and determined photometrically by flow injection analysis for P and Atomic Absorption Spectroscopy (AAS) for cations (Ca, K, Mg). In addition, we determined soil pH in a solution of 10 g of soil and 25 ml of 0.01 M CaCl₂ with a standard glass electrode. Light was measured as photosynthetic photon flux density (PPFD) of photosynthetically active radiation ($\mu\text{mol s}^{-1} \text{m}^{-2}$; LI-COR) inside and simultaneously outside the hedgerow in the open under overcast sky conditions; the relative light intensity was then expressed as $\text{PPFD}_{\text{hedgerow}}/\text{PPFD}_{\text{open}}$ in %.

Data analysis

We aimed to relate the distribution patterns of all forest species in the hedgerows (groups hF_{int} and hF_{edge} , Table 1) to their ecological demands and life history traits. For this, the Ellenberg indicator values were used, expressing the species' ecological optima for light, temperature, continentality, soil moisture, soil pH and soil nitrogen (Ellenberg *et al.*, 1992). Furthermore, we extracted data from the literature and databases (BIOLFLOR, Klotz *et al.*, 2002; Kolb, 2005) with respect to the following variables: general life form according to Raunkiær, life span/dispersal strategy (perennial and strongly clonal; perennial and weakly clonal; perennial and non-clonal; annual), leaf persistence (evergreen, wintergreen, summergreen, vernal), pollination mode (main type: wind, insect, self), mean plant height, mean number of diaspores, and mean diaspore mass.

Table 2: Explanatory variables recorded in the hedgerows. The variables are classified into four groups relating to: STR - structure; MAN - management; SPA - spatial configuration; ENV - environmental conditions.

Variable	Symbol	Specification of variable	Group	
Width of hedgerow	width	in m; 0.5 m steps	STR	
Canopy cover	CC	ordinal; 0 – 3 (no cover – high cover)	STR	
Use of neighbouring land	L/F	road (lane) / forest	0/1 (no/yes)	MAN
	L/G	road / grassland	0/1 (no/yes)	MAN
	L/C	road / field (crop)	0/1 (no/yes)	MAN
	G/F	grassland / forest	0/1 (no/yes)	MAN
	G/G	grassland / grassland	0/1 (no/yes)	MAN
	G/C	grassland / field	0/1 (no/yes)	MAN
	Orientation	N	north	0/1 (no/yes)
NNE		north-north-east	0/1 (no/yes)	SPA
NE		north-east	0/1 (no/yes)	SPA
ENE		east-north-east	0/1 (no/yes)	SPA
E		east	0/1 (no/yes)	SPA
ESE		east-south-east	0/1 (no/yes)	SPA
SE		south-east	0/1 (no/yes)	SPA
SSE		south-south-east	0/1 (no/yes)	SPA
Contact with other hedgerows	H con	0/1 (no contact/contact)	SPA	
Contact with forest	F con	ordinal; 0/1/2 (no contact/loose contact/close contact)	SPA	
Relative light intensity	light	in % (0-100)	ENV	
Soil water content	W%	in % (after air drying) (0-100)	ENV	
Water factor	WF	after drying at 105 °C	ENV	
pH	pH	measured in KCl	ENV	
Content of calcium	Ca	in mg/100 g soil	ENV	
Content of magnesium	Mg	in mg/100 g soil	ENV	
Content of potassium	K	in mg/100 g soil	ENV	
Content of phosphate	P	in mg/100 g soil	ENV	
Content of carbon	C%	%	ENV	
Content of nitrogen	N%	%	ENV	
C/N ratio	C/N	ratio	ENV	

To assess which explanatory variables or variables groups influence the distribution of species, we applied multiple linear regression analysis including the species of groups hF_{int} and hF_{edge} with a relative frequency of occurrence of > 2% in the 515 segments. First, stepwise backward regression ($\alpha = 0.05$) was performed separately for all species with the full set of explanatory variables (some of which were log-transformed prior to the analysis); by this we obtained a list of variables with a significant impact on the species' distribution in the hedgerows. To determine the relative importance of the four distinct groups of variables for the single species and as a whole, partial regression analysis was used (Legendre & Legendre, 1998; Deckers *et al.*, 2004). For this, all significant variables remaining in the single species models, except for those for the variable group in question, were again entered into a second multiple linear regression. The relative importance of the variable group in question for a particular species is given by its partial R^2 , computed as the difference between the R^2 of the full model including all significant variables and the corresponding reduced model; the resulting relative value can then be compared with the corresponding partial R^2 values for the other factor groups. Finally, the average partial R^2 value for all screened species together gives an overall assessment of the relative importance of a certain factor group for the occurrence of typical forest plant species in the hedgerows.

To examine differences in the ecological responses and life history traits between herbaceous forest species (groups hF_{int} and hF_{edge}) that were observed in the hedgerows and those found in the study region, but absent from hedgerows, different tests were applied: Kruskal-Wallis test for variables on ordinal scales, Chi-square test for nominal data, and One-way analysis of variance (ANOVA) for variables measured on an interval scale. All statistical analyses were carried out with SPSS 11.5 for Windows.

RESULTS

General

Totally 173 vascular plant species were recorded in the 515 discrete hedgerow segments studied. Of these about 25% (43 species) were woody taxa, while 75% (130 taxa) had a herbaceous life form. A single hedgerow contained on average 48 plant species, a single segment on average 18 species. About 6% (10 taxa) were included in the list of threatened species. Among the herbaceous species preferring the forest interior (hF_{int}) or forest edges and gaps (hF_{edge}), 34 and 9 species, respectively, were recorded (Table 3).

Table 3: Numbers of recorded species with different life forms and habitat preferences, given separately for the three surveyed areas and summarized for all areas.

	Symbol	Eggestedt	Stendorf	Wollingst	All areas
Woody species					
tree layer	wF _{tree}	17	16	17	21
shrub layer	wF _{shrub}	13	20	19	23
Herbaceous species					
forest	hF _{int}	21	21	24	34
forest edge, gaps	hF _{edge}	7	6	7	9
forest = open landscape	hFO _{equal}	20	27	36	43
forest < open landscape	hFO _{open}	7	12	16	18
open landscape	hO	9	16	22	25
Total		94	118	141	173

A complete list of forest species found in the hedgerows can be obtained from S.W. The ratio of hF_{int} to hF_{edge} species was the same in the hedgerows (4.3) as in the regional pool of forest species as a whole (4.2). The total number of species per segment was highly significantly positively correlated with the number of forest species ($r = 0.536, p < 0.001$). The relationship remained weakly significant ($r = 0.114, p = 0.010$) also when, to avoid autocorrelation, the number of forest species was correlated with the total number of species minus the number of forest species. We observed five threatened forest plant species in the hedgerows, *Blechnum spicant*, *Equisetum hyemale*, *E. sylvaticum*, *Mercurialis perennis* and *Phyteuma nigrum*. The proportion of threatened forest species to all forest species was lower for the hedgerows studied (15%) than for the regional pool of species (35%).

Effects of single explanatory variables

On average, a variable affected 20% of the surveyed species (groups hF_{int} and hF_{edge}) with a relative frequency of occurrence > 2%. Only two and four variables, respectively, did not remain significant in any of the models (Fig. 1).

For species of group hF_{int}, management variables affected between 11 and 45% (mean 28%) of the species. If one or both sides of the hedgerow were bordered by a road or forest, positive effects predominated. Larger proportions of negative effects were observed only in hedgerows with neighbouring grasslands and/or fields. For the species of group hF_{edge}, about 80% of the species were affected by a management adjacent to the hedgerow in the form of road/forest or

road/grassland. Other combinations of neighbouring land use had no or much lower effects on the distribution of species.

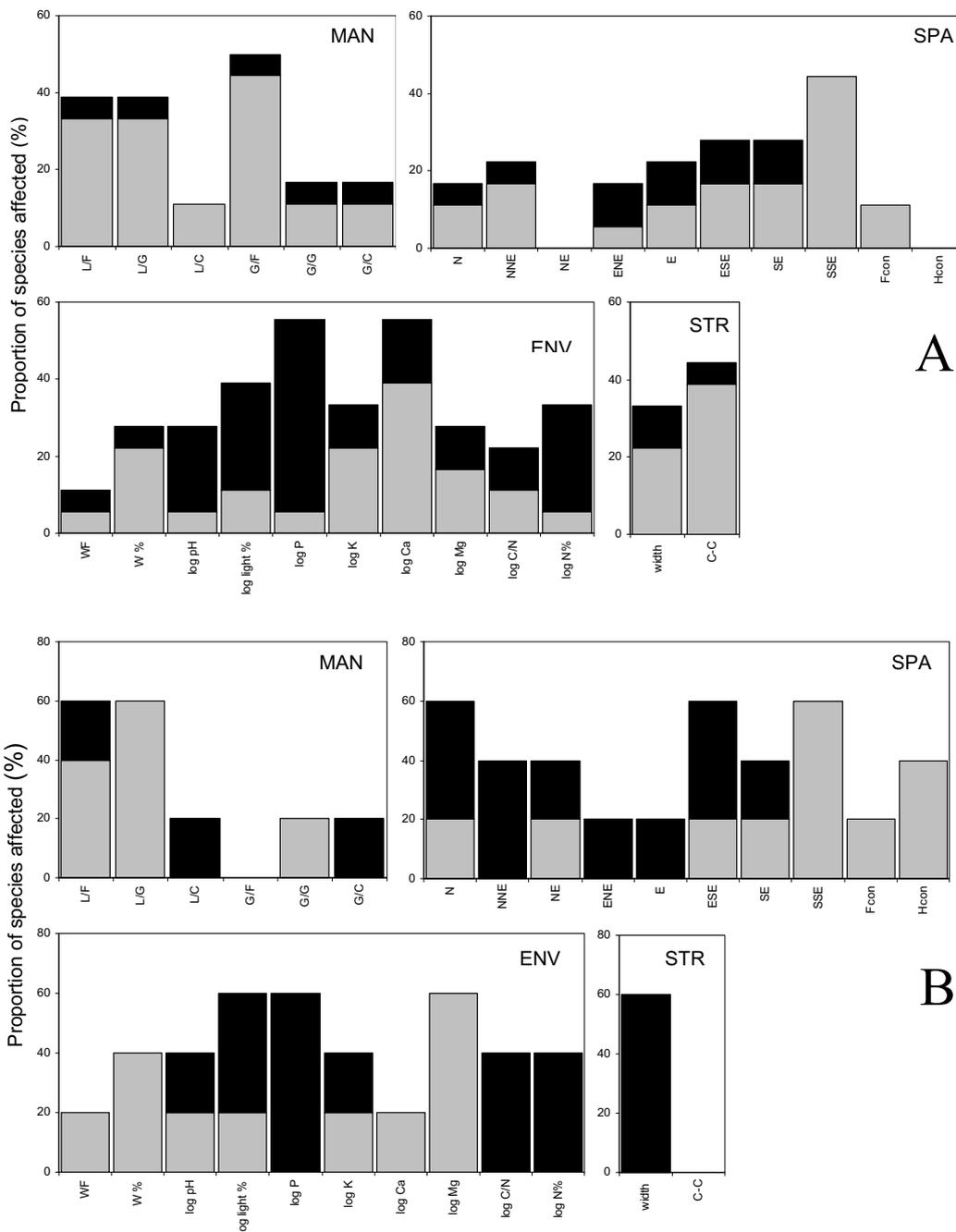


Figure 1: Proportion of species that were significantly affected in their distribution by single explanatory variables, as resulting from multiple regression analyses including all species with a relative frequency of occurrence in the hedgerow segments > 2%. Black bars denote negative relationships, grey bars positive relationships. (A) herbaceous species preferring the forest interior (group hF_{in}), and (B) herbaceous species of forest edges and gaps (group hF_{edge}). MAN, management variables; SPA, variables relating to spatial configuration; ENV, environmental variables; STR, structural variables. For abbreviations of explanatory variables, see Table 2.

The variables relating to spatial characteristics affected between 0 and 44% (mean 19%) of species in group hF_{int}. The orientation south-south-east showed the highest proportion of significant, exclusively positive relationships. The species of the forest interior were not or only weakly influenced by the contact to other hedgerows or forest, respectively. Spatial variables affected between 0 and 80% (mean 40%) of the species of group hF_{edge}. Most of the orientation types showed predominantly negative effects on these species. Again, a south-south-east orientation was associated with positive relationships. The proportion of species favoured by a hedgerow's contact to forest or other hedgerows was higher for hF_{edge} than hF_{int}.

The environmental variables affected on average 36% of hF_{int} species (range 22-56%). High values of pH, relative irradiance, phosphate and nitrogen had predominantly negative effects, whereas high values of calcium, potassium and magnesium showed mostly positive effects. The results were similar for the species of group hF_{edge} (range 20-80%, mean 44%), with pronounced negative influences of high values of P and N.

The structural variables hedgerow width and canopy cover affected 33 and 45%, respectively, of the hF_{int} species, mainly in a positive way. For the group of hF_{edge}, only hedgerow width was found to be relevant, being negatively related to the occurrence of 60% of the species.

Relative importance of variable groups

The overall performance of the regression models (total R^2 values) and the relative importance of single variable groups (partial R^2 values) differed widely among the studied species (Fig. 2).

The multiple regressions of the occurrences of hF_{int} species on all explanatory variables resulted in total R^2 values between 0.031 and 0.347, with an average value of 0.192 (Table 4). The corresponding values for the hF_{edge} species ranged from 0.115 to 0.290 (mean: 0.211).

High partial R^2 values were often observed for the environmental and spatial variable groups. Herbaceous species of the forest interior with particularly high values for environmental factors were *Dryopteris carthusiana* (0.177), *Milium effusum* (0.148) and *Impatiens noli-tangere* (0.100). Species such as *Dryopteris filix-mas*, *Pteridium aquilinum* and *Anemone nemorosa* were strongly affected by the spatial configuration (partial R^2 values: 0.129, 0.121 and 0.109, respectively). *Oxalis acetosella* and *Circaea lutetiana* were mainly governed by management / adjacent land use (partial R^2 values: 0.157 and 0.107). In none of the species structure had the highest value for explained variation. Species of group hF_{edge} with high partial R^2 values for environmental conditions included *Epilobium angustifolium* (0.152) and

Geum urbanum (0.117), while *Humulus lupulus* was relatively strongly affected by variables related to spatial configuration (value: 0.136). The variable groups management and especially structure had only weak effects on the distribution of species of forest edges and gaps.

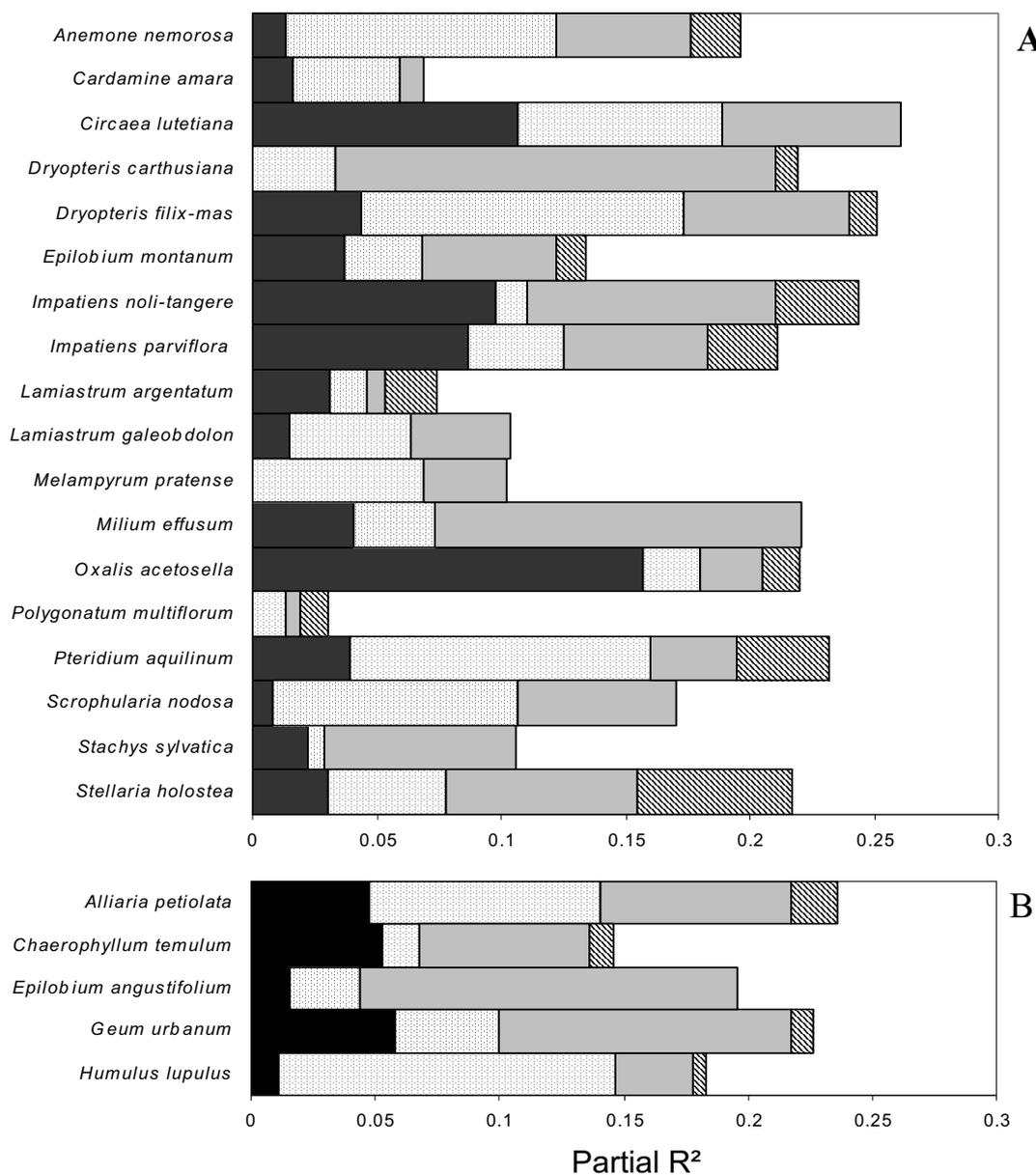


Figure 2: Partial R^2 values of the four variable groups obtained from (partial) multiple regression analysis. Values are given for all herbaceous forest species with a relative frequency of occurrence in the hedgerow segments $> 2\%$. (A) species preferring the forest interior (group hF_{int}), and (B) species of forest edges and clearings (group hF_{edge}). Symbols for the variable groups: ENV, environmental conditions - grey; MAN, management - black; SPA, spatial configuration - dotted; STR, structure - striped.

The overall importance of the four variable groups can be assessed by the average partial R^2 values for all species (Table 4). Environmental conditions were most relevant with means of 0.061 (species group hF_{int}) and 0.089 (hF_{edge}). Somewhat lower values were observed for spatial configuration (0.053 and 0.063, respectively) and management (0.041 and 0.037). The variable group hedgerow structure was of minor importance, as reflected by the mean values 0.014 (hF_{int}) and 0.009 (hF_{edge}).

Table 4: Summary of results of the partial regression analyses of herbaceous forest species preferring the forest interior (A) or forest edges and clearings (B). All species with a relative frequency of occurrence in the hedgerow segments > 2% were considered. Variable groups: ENV, environmental conditions; SPA, spatial configuration; MAN, management; STR, structure. The total R^2 for the complete models are also given.

	Variable group	Minimum	Partial R^2	
			Maximum	Mean
A	ENV	0.006	0.177	0.061
	SPA	0.007	0.129	0.053
	MAN	0.000	0.157	0.041
	STR	0.000	0.062	0.014
	Total R^2	0.031	0.347	0.192
B	ENV	0.031	0.152	0.089
	SPA	0.028	0.136	0.063
	MAN	0.011	0.058	0.037
	STR	0.000	0.019	0.009
	Total R^2	0.115	0.290	0.211

Ecological responses and life histories of forest species in hedgerows

The comparison of forest species found in the hedgerows and those absent from the hedgerows (but occurring in the surrounding) revealed, with one exception, no differences (Table 5), both with respect to the Ellenberg indicator values and to the life history attributes. Only among the hF_{edge} species, life form was found to be significantly different between groups: While all edge and gap species found in hedgerows were hemicryptophytes, species of the neighbouring woodlands absent in the hedgerows were more diverse in terms of their life form (hemicryptophytes, therophytes and geophytes).

Table 5: Comparison of ecological responses and life history traits between forest species observed in the studied hedgerows, and those occurring in the region, but absent from the hedgerows. Species preferring the interior and forest edges, respectively, were treated separately. Data type - N: numerical data; O: ordinal data; C: categorical data. Numerical data were analyzed with One-way ANOVA, ordinal data with the Kruskal-Wallis test, and categorical data with the χ^2 test.

Parameter	Data type	hF _{int} species		hF _{edge} species	
		χ^2 / F	<i>p</i>	χ^2 / F	<i>P</i>
L	O	0.915	0.339	0.453	0.501
T	O	0.507	0.476	0.402	0.526
K	O	0.083	0.774	0.707	0.400
F	O	1.612	0.204	0.082	0.775
R	O	0.653	0.419	0.506	0.477
N	O	2.687	0.101	1.218	0.270
Life form	C	0.509	0.476	5.947	0.015
Leaf persistence	C	0.958	0.328	0.495	0.482
Life span / dispersal strategy	C	1.768	0.184	0.584	0.445
Pollination mode	C	0.000	1.000	0.001	0.973
Plant height (cm)	N	1.805	0.183	2.163	0.156
Number of seeds	N	1.533	0.224	1.597	0.262
Seed mass (mg)	N	0.002	0.967	0.038	0.848

DISCUSSION

General

The results showed that hedgerows in northern Germany generate a suitable habitat for many herbaceous forest species. As much as 25% of the species found in the hedgerows are assigned to the groups hF_{int} or hF_{edge}, and thus regarded as forest specialists. Older studies from Great Britain revealed much lower fractions of forest species in hedgerow networks, 5% (Pollard, 1973), 3% (Helliwell, 1975), and 15% (Cummins & French, 1994). In a recent work from Belgium, the proportion of forest species was 12% (Deckers *et al.*, 2004). The importance of hedgerows as habitat for forest species is also reflected in the observation that nearly 40% of forest species occurring in the study region were found in the surveyed hedgerow networks.

It has been claimed that forest species in hedgerows are mostly forest edge and gap species (Andrews *et al.*, 1999; Smart *et al.*, 2001), due to the similarity in environmental conditions between forest edges and hedgerows (Forman & Baudry, 1984). Our results, however, disagree with this assumption: in total 34 hF_{int} species, but only 9 hF_{edge} species were observed in the hedgerows. This predominance of specialist species of the forest interior is not due to the generally low proportion of forest edge species in the regional species pool (2.2%; data from Cordes *et al.*, 2006), because the ratios between hF_{int} and hF_{edge} were the same among the forest species found in the hedgerows and the total number of forest species in the region.

Effects of single explanatory variables

Among the management variables, the strongest positive effects were found for the land use forms forest and lane, both with regard to hF_{int} and hF_{edge} species. It appears plausible that an adjacent forest allows forest species to colonize the hedgerows more easily and also contributes to a favourable microclimate. This effect was observed also in studies from France (Burel & Baudry, 1994; Burel, 1996) and from the USA (Corbit *et al.*, 1999). The positive effect on many forest species of an adjacent hedgerow may also be explained by reduced disturbance from agricultural activities (*e.g.*, ploughing, fertilizer misplacement; see also below; Boatman *et al.*, 1994), and the presence of lanes is in most cases associated with the occurrence of hedgerows on both sides, again resulting in a forest-like microclimate. In agreement, species-rich hedgerows in the UK were bordered by lanes or roads, while species-poor hedgerows were adjacent to cornfields (Mercer *et al.*, 1999; Dover & Sparks, 2001). In contrast, another study from Great Britain did not provide evidence for such favourable effects of nearby woodlands or lanes (Helliwell, 1975). Previous observations that hedgerows with adjacent arable fields are relatively poor in forest species (Burel, 1996; Boutin *et al.*, 2001) was supported in our study. Agricultural activities cause a high level of disturbance, and the application of fertilizers may increase the nutrient contents of the soil, resulting in a competitive dominance of nitrophilous non-forest species (Jobin *et al.*, 1997). The deposition of pesticides may also reduce species diversity (Tsiouris & Marshall, 1998).

Most species were affected by the factor spatial orientation, which may be explained by microclimatic differences between differently exposed hedgerows. With a west-east orientation, hedgerows have both a sun and a shade side and thus face a relatively extreme microclimate. The southern side is drier and warmer, and has a higher evapotranspiration (Fritz & Merriam, 1993), a situation avoided by most forest species because of their

hygrophilous character (Martin *et al.*, 2001). Hedgerows with other orientations have a more balanced microclimate, a situation favourable to most hF_{int} and hF_{edge} species. In contrast to our results, a French study (Le Coeur *et al.*, 1997) did not support the importance of hedgerow orientation for the occurrence of forest plant species.

Connectivity to forests or other hedgerows had only weak effects. Some species of the forest interior were positively influenced by a close contact to a forest, a result that was found also in a study of a hedgerow network in Brittany, France (Burel & Baudry, 1994). Contact to other hedgerows has also been shown to enhance plant species richness in hedgerows (Burel & Baudry, 1990a; Boutin *et al.*, 2001), but in our study, only a few forest edge species were promoted by hedgerow connectivity.

Among the environmental variables, high contents of soil nutrients, especially phosphorus and nitrogen, were negatively correlated with the occurrences of several hF_{int} and hF_{edge} species. A likely explanation is that many forest species have a stress tolerance strategy (mainly with respect to the low light levels in woodlands) and are not capable of competing with nitrophilous species of more open vegetation that are favoured by nutrient addition (*cf.*, Tsiouris & Marshall, 1998). This is supported by other studies showing that hedgerows with low nutrient status had a more similar environment and flora to forests than more nutrient-rich sites (Hegarty *et al.*, 1994; Mercer *et al.*, 1999). In accordance, high light levels were shown to have a negative effect on several forest (primarily hF_{int}) species (Andrews *et al.*, 1999).

Many species of the forest interior were positively affected by increasing canopy cover and hedgerow width, which was observed also in several other studies (Burel and Baudry, 1990a; Hegarty *et al.*, 1994; Burel, 1996). The authors assume that, the broader and darker a hedgerow is, the more similar to a forest the environment becomes. However, no positive effects of hedgerow width on forest species were found in other studies from the USA (Corbit *et al.*, 1999) and from Great Britain (Cherrill *et al.*, 2001). The declining abundance of several forest edge species with increasing hedgerow width may have to do with the decreasing edge-like conditions of broader hedgerows.

Relative importance of variable groups

It is difficult to compare the results concerning the relative importance of the variable groups found in our study with results obtained in other studies, because of differences in grouping single explanatory variables into factor groups and in the selection of studied variables. Some general patterns may still be pointed out. Our finding of the primary importance of environmental factors for the occurrence of forest species is supported by a Belgian study

using a similar approach (Deckers *et al.*, 2004), as well as by a Canadian study (de Blois *et al.*, 2002).

Surprisingly, structural variables had the lowest relative importance of all studied groups, which is contrary to results from France where hedgerow structure was found to be the factor with the strongest influence on plant species distribution (Le Coeur *et al.*, 1997). In the latter study, however, not only forest specialists, but all hedgerow species, were considered. In contrast to similar studies, the factor group spatial configuration (hedgerow orientation) was of second largest importance.

Comparison of ecological parameters

It has been hypothesized (Fritz & Merriam, 1993; French & Cummins, 2001) that the absence of forest specialists from hedgerows is caused by their special demands on habitat conditions that are not fulfilled in the hedgerow environment, and by their particular life history attributes, e.g. dispersal strategy. There were, however, hardly any differences in the analyzed parameters between the forest species found in the hedgerows and those not found there. We cannot dismiss the possibility that factors of large significance to the forest species were not analyzed in our study. Especially the history of the hedgerow (network) may affect the occurrence of many species (Roy & de Blois, 2006). In this context, a crucial question would be whether the populations of forest species in hedgerows represent relics after clear-cutting of the forest in the past, or have colonized the hedgerows from neighbouring source populations at a later period. Considering the proportion of endangered forest species in the region to all forest species in the region, only few threatened taxa were present in the hedgerows. This may indicate that there are some life history attributes not shared by most rare species that facilitate the establishment of forest plants in hedgerows.

Implications for preserving forest plant species in hedgerows

Hedgerows appear to offer a suitable habitat for a large number of forest specialist species. There was no evidence that the forest species occurring in hedgerows represent a special subset of forest species with specific habitat requirements or life history traits. The effects of variables belonging to different factors groups on single species varied considerably, *i.e.*, most variables may be of importance for at least some species. However, when considering how a hedgerow favourable for the occurrence of forest species should look like, some general points may be stressed:

- Nutrient enrichment appears to have a negative effect on many forest specialists in hedgerows. Thus, a less intensive use of the agricultural land nearby favours many of the species in question, alongside with wide buffer zones between hedgerow and field or grassland to minimize disturbance and eutrophication.
- The occurrence of many forest plant species is associated with a well-developed canopy cover in terms of dense tree and shrub layers.
- The orientation of hedgerows also is of some importance; especially species of the forest interior tend to prefer hedgerows with a more or less N-S orientation, probably because of their relatively forest-like microclimate.
- Finally, a high connectivity of the hedgerows and their proximity to forest favour species both of the forest interior and of forest edges.

As hedgerows with a high number of forest species also have a high total number of species, a result similarly reported in an Irish hedgerow survey (Hegarty *et al.*, 1994), the above features may apply also to the general plant species diversity of hedgerows.

Some questions of high relevance to the preservation of forest plant species in hedgerows remain to be answered, and will be dealt with in a follow-up of this study. This includes the study of the function of hedgerows as corridors for the dispersal of forest plant species, and of the viability and fitness of hedgerow populations of forest species compared to forest populations.

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REFERENCES

- Andrews, M., Mercer, C., Griffin, P., Andrews, M. E., Cherrill, A., 1999. Autecology of common herbaceous hedgerow species in Britain. *Aspects of Applied Biology* 54, 353-360.
- Baudry, J., Bunce, R. G. H., Burel, F., 2000. Hedgerows: An international perspective on their origin, function and management. *Journal of Environmental Management* 60, 7-22.

- Boatman, N., Blake, K. A., Aebischer, N. J., Sotherton, N. W., 1994. Factors affecting the herbaceous flora of hedgerows on arable farms and its value as wildlife habitat. In: Watt, T.A., Buckley, P. (eds). *Hedgerow management and nature conservation*. Wye College Press, Ashford, UK, 33-46.
- Boutin, C., Jobin, B., Bélanger, L., Baril, A., Freemark, K. E., 2001. Hedgerows in the farming landscapes of Canada. In: Barr, C. J., Petit, S. (eds). *Hedgerows of the world: their ecological functions in different landscapes*. IALE, Birmingham, UK, 33-42.
- Burel, F., 1996. Hedgerows and their role in agricultural landscapes. *Critical Reviews in Plant Science* 15, 169-190.
- Burel, F., Baudry, J., 1990a. Hedgerow networks as habitats for forest species: implications for colonising abandoned agricultural land. In: Bunce, R. G. H., Howard, D. C. (eds). *Species dispersal in agricultural habitats*. Belhaven Press, London, UK, 238-255.
- Burel, F., Baudry, J., 1990b. Structural dynamic of a hedgerow network landscape in Brittany France. *Landscape Ecology* 4, 197-210.
- Burel, F., Baudry, J., 1994. Control of biodiversity in hedgerow network landscapes in Western France. In: Watt, T. A., Buckley, P. (eds). *Hedgerow management and nature conservation*. Wye College Press, Ashford, UK, 47-57.
- Burel, F., Baudry, J., Butet, A., Clergeau, P., Delettre, Y., Le Coeur, D., Dubs, F., Morvan, N., Paillat, G., Petit, S., Thenail, C., Brunel, E., Lefeuvre, J. C., 1998. Comparative biodiversity along a gradient of agricultural landscapes. *Acta Oecologica* 19, 47-60.
- Cherrill, A., Mercer, C., McClean, C., Tudor, G., 2001. Assessing the floristic diversity of hedge networks: a landscape perspective. *Landscape Research* 26, 55-64.
- Corbit, M., Marks, P. L., Gardescu, S., 1999. Hedgerows as habitat corridors for forest herbs in central New York, USA. *Journal of Ecology* 87, 220-232.
- Cordes, H., Feder, J., Hellberg, F., Metzging, D., Wittig, B. (eds), 2006. *Atlas der Farn- und Blütenpflanzen des Weser-Elbe-Gebietes*. H.M. Hausschild, Bremen, Germany.
- Cummins, R. P., French, D. D., 1994. Floristic diversity, management and associated land use in British hedgerows. In: Watt, T. A., Buckley, P. (eds). *Hedgerow management and nature conservation*. Wye College Press, Ashford, UK, 95-106.
- de Blois, S., Domon, G., Bouchard, A., 2002. Factors affecting plant distribution in hedgerows of southern Quebec. *Biological Conservation* 105, 355-367.
- Deckers, B., De Becker, P., Honnay, O., Hermy, M., Muys, B., 2005. Sunken roads as habitats for forest plant species in a dynamic agricultural landscape: effects of age and isolation. *Journal of Biogeography* 32, 99-109.
- Deckers, B., Hermy, M., Muys, B., 2004. Factors affecting plant species composition of hedgerows: relative importance and hierarchy. *Acta Oecologica* 26, 23-37.

- Dover, J. W., Sparks, T. H., 2001. Green lanes: biodiversity reservoirs in farmland? In: Barr, C. J., Petit, S. (eds). *Hedgerows of the world: their ecological functions in different landscapes*. IALE, Birmingham, UK, 241-250.
- Dupré, C., Ehrlén, J., 2002. Habitat configuration, species traits and plant distributions. *Journal of Ecology* 90, 796-805.
- Ellenberg, H., Weber, H. E., Düll, R., Wirth, V., Werner, W., Paulißen, D., 1992. Zeigerwerte von Pflanzen in Mitteleuropa. *Scripta Geobotanica* 18, 1-258.
- Forman, R. T. T., Baudry, J., 1984. Hedgerows and hedgerow networks in landscape ecology. *Environmental Management* 8, 495-510.
- French, D. D., Cummins, R. P., 2001. Classification, composition, richness and diversity of British hedgerows. *Applied Vegetation Science* 4, 213-228.
- Fritz, R., Merriam, G., 1993. Fencerow habitats for plants moving between farmland forests. *Biological Conservation* 64, 141-148.
- Garve, E., 2004. Rote Liste und Florenliste der Farn- und Blütenpflanzen in Niedersachsen und Bremen. *Informationsdienst Naturschutz Niedersachsen* 24, 1-76.
- Grashof-Bokdam, C., 1997. Forest species in an agricultural landscape in the Netherlands: Effects of habitat fragmentation. *Journal of Vegetation Science* 8, 21-28.
- Hegarty, C. A., McAdam, J. H., Cooper, A., 1994. Factors influencing the plant species composition of hedges - implications for management in environmentally sensitive areas. *British Crop Protection Council Monographs* 58, 227-234.
- Helliwell, D. R., 1975. The distribution of woodland plant species in some Shropshire hedgerows. *Biological Conservation* 7, 61-72.
- Jobin, B., Boutin, C., Bélanger, L., 2001. Hedgerows as refuges for pest birds and plants: could Québec's farmers be wrong? In: Barr, C. J., Petit, S. (eds). *Hedgerows of the world: their ecological functions in different landscapes*. IALE, Birmingham, UK, 207-212.
- Jobin, B., Boutin, C., DesGranges, J., 1997. Effects of agricultural practices on the flora of hedgerows and woodland edges in southern Quebec. *Canadian Journal of Plant Science* 77, 293-299.
- Kleijn, D., Verbeek, M., 2000. Factors affecting the species composition of arable field boundary vegetation. *Journal of Applied Ecology* 37, 256-266.
- Klotz, S., Kühn, I., Durka, W., 2002. Eine Datenbank mit biologisch-ökologischen Merkmalen zur Flora von Deutschland. *Schriftenreihe für Vegetationskunde* 38, 1-334.
- Kolb, A., 2005. *The distribution of forest plant species in a fragmented landscape: patterns and processes*. Dissertation, University of Bremen, Bremen, Germany.
- Le Coeur, D., Baudry, J., Burel, F., 1997. Field margins plant assemblages: variation partitioning between local and landscape factors. *Landscape and Urban Planning* 37, 57-71.
- Legendre, P., Legendre, L., 1998. *Numerical Ecology*. Elsevier Science, Amsterdam, The Netherlands.

- Martin, B., Vanpeene-Bruhier, S., Brun, J. J., 2001. Spatial and ecological knowledge of the mountain bocage of Champsaur (French Alps). In: Barr, C. J., Petit, S. (eds). *Hedgerows of the world: their ecological functions in different landscapes*. IALE, Birmingham, UK, 273-278.
- McCollin, D., Jackson, J. I., Bunce, R. G. H., Barr, C. J., Stuart, R., 2000. Hedgerows as habitat for woodland plants. *Journal of Environmental Management* 60, 77-90.
- Mercer, C., Cherrill, A., Tudor, G., Andrews, M., 1999. Hedgerow plant communities: relationship with adjacent land use and aspect. *Aspects of Applied Biology* 54, 345-52.
- Petit, S., Griffiths, L., Smart, S. S., Smith, G. M., Stuart, R. C., Wright, S. W., 2004. Effects of area and isolation of woodland patches on herbaceous plant species richness across Great Britain. *Landscape Ecology* 19, 463-471.
- Pollard, E., 1973. Hedges: VII. Woodland relic hedges in Huntington and Peterborough. *Journal of Ecology* 61, 343-352.
- Roy, V., de Blois, S., 2006. Using functional traits to assess the role of hedgerow corridors as environmental filters for forest herbs. *Biological Conservation* 130, 592-603.
- Schmidt, M., von Oheimb, G., Kriebitzsch, W. U., Ellenberg, H., 2002. Liste der im norddeutschen Tiefland typischen Waldgefäßpflanzen. *Mitteilungen der Bundesforschungsanstalt für Forst- und Holzwirtschaft* 206, 1-37.
- Smart, S. M., Bunce, R. G. H., Stuart, R. C., 2001. An assessment of the potential of British hedges to act as corridors and refuges for ancient woodland indicator plants. In: Barr, C. J., Petit, S. (eds). *Hedgerows of the world: their ecological functions in different landscapes*. IALE, Birmingham, UK, 137-146.
- Tsiouris, S., Marshall, E. J. P., 1998. Observations on patterns of granular fertiliser deposition beside hedges and its likely effects on the botanical composition of field margins. *Annals of Applied Biology* 132, 115-127.
- Wisskirchen, R., Haeupler, H., 1998. *Standardliste der Farn- und Blütenpflanzen Deutschlands*. Ulmer, Stuttgart, Germany.

Chapter 4

Hedgerows as an environment for forest plants: a comparative case study of five species

Wehling, S. & Diekmann, M., 2009.

Plant Ecology 204, 11-20.



Top left: Anemone nemorosa. **Top right:** Polygonatum multiflorum. **Bottom left:** Adoxa moschatellina.
Bottom middle: Stellaria holostea. **Bottom right:** Circaea lutetiana. (*Photographs of A. moschatellina and C. lutetiana obtained from <http://www.floraweb.de/>, [23.03.2009]; all other photographs taken by Stephan Wehling*).

ABSTRACT

Many areas in Europe are dominated by agricultural land use, and as a consequence many typical forest plant species suffer from habitat loss and fragmentation. Hedgerows as common elements of rural landscapes have been considered as potential refuges for these species. The main objective of this study was to examine whether forests and hedgerows differ in environmental conditions, and whether important life-history attributes of the populations differ between the two habitat types. We selected five species commonly found in the region in both forests and hedgerows (*Adoxa moschatellina*, *Anemone nemorosa*, *Circaea lutetiana*, *Polygonatum multiflorum* and *Stellaria holostea*), and sampled data on 10 populations of each species in each habitat type, including measurements of light and various soil factors.

Hedgerows had higher relative light availability and tended to have higher soil nutrient contents and lower soil water values than forests. The comparison of plant performance values between habitat types did not show consistent patterns across species. *Anemone* and *Polygonatum* performed equally well in hedgerows and forests, while *Stellaria* appeared to have a higher fitness in hedgerows. In contrast, *Circaea* showed a higher reproduction under forest conditions. For *Adoxa* the results were somewhat contradictory: whereas the reproductive output of this species was higher in forests, population density was higher in hedgerows. The abiotic factors most closely related to the performance values were relative light and soil water availability.

The majority of plant performance values did not differ between hedgerows and forests. We therefore conclude that the tested forest species are capable of growing also in hedgerows and will survive equally well in forest and its “surrogate” habitat.

KEYWORDS:

agricultural land use; light availability; plant performance; reproductive output; soil nutrients.

INTRODUCTION

In many countries of the world the landscape today is dominated by agri- and silvicultural land, while the former natural habitats, such as forests or mires, have largely been destroyed or reduced in size and quality (Forman, 1995; Green *et al.*, 2005). In some low-elevated regions of Central Europe such as the Netherlands or northern Germany, forests - although representing the natural vegetation of most of the area - nowadays cover only a tiny fraction

of their original size (Grashof-Bokdam, 1997). As a consequence, many forest species have become rare in these regions, and conservation actions need to be taken (Ellenberg, 1996).

Hedgerows, defined as linear landscape elements containing shrubs and trees, were advocated as potential surrogate habitat for forest species, especially in North America (Corbit *et al.*, 1999) and Western Europe (Baudry *et al.*, 2000). In general, hedgerows in agricultural areas are assumed to increase plant species diversity (French & Cummins, 2001; Freemark *et al.*, 2002). It was shown that hedgerow networks and a system of forest fragments contained up to 90% of the plant species pool of a single contiguous forest of the same area (Middleton & Merriam, 1983). Hedgerows may also serve as a source for the colonization of forest plant species into newly established woodlands (Grashof-Bokdam, 1997). The question remains whether the environment of hedgerows is similar enough to that of forests to serve as a suitable habitat for a majority of forest plant species and to sustain viable populations of these species.

The existing evidence from comparative studies of hedgerows and forests is partly contradictory. A transplant experiment of forest plant species into hedgerows in Canada resulted in low survival rates and reproduction, supporting the view that hedgerows hardly represent a suitable habitat for the tested forest species (Fritz & Merriam, 1993). The same conclusions were drawn from a study in Great Britain (French & Cummins, 2001). In contrast, a majority of woodland plants were shown to form viable populations also in hedgerows both on the British Isles (Hegarty *et al.*, 1994; Peterken, 2000), in Belgium (Deckers *et al.*, 2005) and in Eastern USA (Corbit *et al.*, 1999). These results, however, were based mainly on presence / absence or abundance data and not on comparative population studies. An intermediate view was expressed by Helliwell (1975) who hypothesized that hedgerows serve as a refuge only for a sub-set of forest species (with most species unable to inhabit them), which was supported in more recent studies from Great Britain (McCollin *et al.*, 2000) and Canada (de Blois *et al.*, 2002; Roy & de Blois, 2006). Yet, there is only little evidence about the long-term suitability of the “hedgerow” habitat for forest plants, or about the habitat conditions in hedgerows (compared to forests) in terms of structure and environment.

Despite the above observational studies it is unclear to what extent forest species need a minimum area of woodland in order to survive. On the one hand, it has been stated that there is no evidence for forest plant species requiring some kind of threshold area for establishment and survival (Peterken, 2000); on the other hand, it has been shown that very small forest fragments contained almost no forest herbs (Usher *et al.*, 1992). Hedgerows may be very long

and narrow, but still offer a limited area with forest-like environmental conditions. Apart from recording and monitoring the population sizes of forest plants in hedgerows, an interesting approach consists in the comparison of population characteristics in terms of life history attributes and fitness parameters between forests and hedgerows. The only studies known to us are from Belgium, reporting on better plant performance in hedgerows compared to ancient forests (Endels *et al.*, 2004) and from Canada, showing that, while a forest species may thrive in hedgerows, reduced recruitment can limit long-term survival and expansion (Schmucki & de Blois, in press).

Here we present a comparative study between hedgerows and forests from northern Central Europe, a region for which little is known about the occurrence and performance of forest plant species in hedgerows. We focus on some selected species of the forest interior, so-called ‘true forest species’ sensu Schmidt *et al.* (2002), addressing the following research questions:

- Does the abiotic environment of the sites with populations of the selected forest species differ between forests and hedgerows?
- Are the values of important life-history attributes of these species in forests different from those in hedgerows?
- What are the relationships between plant performance and the measured environmental variables?

METHODS

Study area

The study area was located in the lowlands of North-western Germany north of the city of Bremen (53° 13' N, 8° 39' E). The landscape is flat to weakly undulating, varying in elevation between 5 and 30 m a.s.l. The soils, mainly deriving from the Pleistocene Saale glaciation, are fine-textured (loam and clay), relatively base- and nutrient-poor, and often moist to wet because of poor drainage. While most of the forests in the regions have been cleared or transformed to coniferous plantations, the study area has still a relatively large proportion of semi-natural deciduous forest, and is characterized by the presence of dense and intact networks of hedgerows. The hedgerows are often connected to forest stands, but otherwise surrounded by intensively used agricultural land, managed as fields, pastures or meadows. The hedgerows had an average breadth of about 4 m, and their mean age was approximately 150 years. Most hedges, characterised by a mixture of trees and shrubs, were used as field

boundaries or planted alongside farm tracks. None of the hedgerows studied were forest remnants. Within the study area all forest patches and hedgerows were surveyed in 2005 for the occurrence of typical forest species (Wehling & Diekmann, 2008).

The most common woody species found in the hedgerows were *Quercus robur*, *Carpinus betulus*, *Corylus avellana*, *Sorbus aucuparia* and *Sambucus nigra*. The neighbouring forests (except those planted with conifers) were usually dominated by *Quercus robur*, *Fraxinus excelsior* and *Alnus glutinosa*.

Study species

Five forest species were selected based on their frequent occurrence in the study region both in forests and hedgerows: *Adoxa moschatellina* L. (Adoxaceae), *Anemone nemorosa* L. (Ranunculaceae), *Circaea lutetiana* L. (Onagraceae), *Polygonatum multiflorum* (L.) All. (Convallariaceae) and *Stellaria holostea* L. (Caryophyllaceae) (Table 1). All five taxa were described as ancient forest indicators in Europe (Hermy *et al.*, 1999), whereas for north-western Germany only *A. moschatellina* and *C. lutetiana* are considered as belonging to this group of species (Wulf, 1997).

Table 1: Life history traits and ecological behaviour of the five study species. Strategy type is according to Grime *et al.* (1988). CSR - competitive and stress-tolerant ruderal, CS - stress-tolerant competitor, the indicator values for light (L), soil moisture (M) and soil pH (R) were obtained from Ellenberg *et al.* (1992). All other information was compiled from the BIOLFLOR database (Klotz *et al.*, 2002).

	<i>Adoxa moschatellina</i>	<i>Anemone nemorosa</i>	<i>Circaea lutetiana</i>	<i>Polygonatum multiflorum</i>	<i>Stellaria holostea</i>
Life form	perennial geophyte	perennial geophyte	perennial geophyte	perennial geophytes	perennial chamaephyte
Strategy	CSR	CSR	CS	CSR	CSR
Height (cm)	8-16	10-25	20-60(-75)	30-60(-100)	20-60
Flowering time	March-May	March-May	June-August	May-June	April-May
Pollination type	insect	insect, self	insect, self	insect, self	insect, self
Dispersal type	endozoochory	myrmecochory	epizoochory	endozoochory	barochory
Mean seed mass (mg)	0.6	2.0-4.0	2.0	16.2-26.1	2.4-3.7
L	5	indifferent	4	2	5
M	6	5	6	5	5
R	7	indifferent	7	6	6

Data collection

We randomly selected 10 populations of each species in forests and the same number of populations in hedgerows. Populations were defined as groups of individuals with the highest distance between these individuals being less than 50 meters. Populations were only considered if they had at least 25 individuals. To avoid spatial autocorrelation we studied only one population per hedgerow or forest, with a minimum distance of 75 m. All study sites in which populations were located had an age of more than 100 years of uninterrupted use as forest or hedgerow.

During spring and summer 2006 we determined a number of parameters: population size (number of individuals [ramets]), population density (number of individuals m^{-2}) and the proportion of reproductive individuals (PRI in %). In each population 20 reproductive individuals were chosen randomly to measure plant height and, after seed maturation, to collect the seeds (for *Anemone* in May, *Adoxa* and *Stellaria* in June, *Polygonatum* in August, and *Circaea* in September). After air drying for three weeks the seeds were counted and their mass determined by weighing. As a measure of the cumulative investment in sexual reproduction, the total reproductive output was calculated as the product of the number of seeds and seed mass.

In addition, we measured the values of some environmental factors considered to affect plant performance, separately for each species and population (total n thus = 100). Soil samples were taken from the top 5 cm after litter removal and were composed of 5 sub-samples from different parts of the plot. Each sample was weighed, air dried to constant mass and re-weighed to determine its water content. Afterwards the soil was passed through a 2 mm sieve. Carbon and nitrogen were determined in % with an elemental analyser (Hecatech). Nutrients were extracted with ammonium lactate and determined photometrically by flow injection analysis for P and Atomic Absorption Spectroscopy (AAS) for cations (Ca, K, Mg). Soil pH was measured in a solution of 10 g of soil and 25 ml of 0.01 M CaCl_2 with a standard glass electrode. Finally, light was measured as photosynthetic photon flux density (PPFD) of photosynthetically active radiation ($\mu\text{mol s}^{-1} \text{m}^{-2}$; LI-COR), simultaneously inside and in the open outside the forest or hedgerow under overcast sky conditions. As measure of radiation for the statistical analysis we calculated the relative light intensity as the ratio of $\text{PPFD}_{\text{hedgerow/forest}}$ and $\text{PPFD}_{\text{open}}$ in %.

Data analysis

To check for differences in abiotic conditions between the two habitat types we performed unpaired t-tests separately for the different species and variables. Except in one case all data were normally distributed (Kolmogorov-Smirnov test). Normality tests were also conducted for the population characteristics and plant performance values.

To assess the relationship between the plant performance values (plant height, number of seeds, seed mass, reproductive output and PRI) and environmental factors we conducted stepwise multiple linear regressions (backward method; $\alpha = 0.05$). All abiotic factors (soil nutrients, pH, relative water content and relative irradiance, see Table 2) were first considered as independent variables. To avoid multicollinearity Pearson correlations were carried out between all variables separately for the five species, followed by the exclusion of highly inter-correlated variables. We kept relative irradiance, soil water content and phosphate in the initial regression models, because these variables were known to have a major influence on the occurrence of forest species in hedgerows (Wehling & Diekmann, 2008). Also potassium was used in all species models, while Calcium was entered only in the cases of *Circaea* and *Polygonatum*, N% only for *Adoxa* and *Stellaria*, and the C/N-ratio for all species except *Anemone*. Accordingly, the following variables were excluded from the analysis: for *Adoxa* pH, Ca, Mg and C, for *Anemone* pH, Ca, Mg, and C/N ratio, for *Circaea* pH, Mg, N and C, for *Polygonatum* pH, Mg N and C, and for *Stellaria* pH, Ca, Mg and C. All analyses were performed with SPSS 12.0 (SPSS, Chicago, USA).

RESULTS

Environmental differences between forests and hedgerows

The comparison of environmental characteristics between habitat types revealed clear differences for some factors and species (Table 2). The most consistent pattern found across all species was, as expected, the much higher relative irradiance in hedgerows compared to forests. Hedgerows had significantly (*Anemone*, *Polygonatum*, *Stellaria*) or marginally significantly (*Circaea*) higher soil pH than forests, and they also had or tended to have higher values for P, Ca, Mg and K. In contrast, the soil water content was higher (*Adoxa*, *Circaea*) or marginally higher (*Polygonatum*) in forests. Weak differences between habitat types were found for C and N as well as for the C/N ratio.

Table 2: Comparison of mean values for different environmental variables between forests (F) and hedgerows (H), analyzed by unpaired T-test. Significant differences between habitat types are indicated with asterisks (+ = $p < 0.10$, * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$). In all cases $dF = 18$.

Factor	<i>Adoxa moschatellina</i>		<i>Anemone nemorosa</i>		<i>Circaea lutetiana</i>		<i>Polygonatum multiflorum</i>		<i>Stellaria holostea</i>	
	F	H	F	H	F	H	F	H	F	H
Relative irradiance [%]	1.49	11.89 ***	2.81	10.37 ***	2.66	8.74 ***	2.22	21.04 ***	4.48	14.31 ***
Soil water content [%]	23.08	16.94 **	22.00	21.24	31.98	23.94 *	26.04	21.78 +	22.19	20.94
Soil pH	4.11	4.74	3.65	4.80 *	5.03	6.01 +	3.25	4.55 *	3.68	4.58 **
P [mg/100g dry soil]	2.05	4.75 *	2.50	4.08	2.65	5.25 +	1.90	2.55	1.96	4.11
K [mg/100g dry soil]	12.28	16.62	12.72	16.58	14.29	12.12	9.74	18.56 **	9.17	16.57 *
Ca [mg/100g dry soil]	115.64	119.19	80.46	167.70 +	177.88	250.97	58.57	156.98	55.72	134.25 *
Mg [mg/100g dry soil]	10.85	13.58	10.67	16.61 +	17.87	17.18	11.05	18.81	8.72	16.37 *
N%	0.38	0.27	0.39	0.34	0.28	0.22	0.43	0.40	0.22	0.34
C%	5.04	3.38 +	5.67	4.76	4.54	3.61	7.21	5.98	3.58	4.87
C/N	13.26	12.57	14.27	13.75	16.58	16.45	16.59	14.99 +	15.61	14.17

Differences in plant performance between habitat type

The comparison of values of plant performance between the populations in hedgerows and those in forests resulted in six significant differences out of 35 possible ones (Fig. 1). In *Circaea*, population size was higher, and in *Adoxa*, population density was lower in forests than in hedgerows. There were no differences in plant height between habitat types in any of the species.

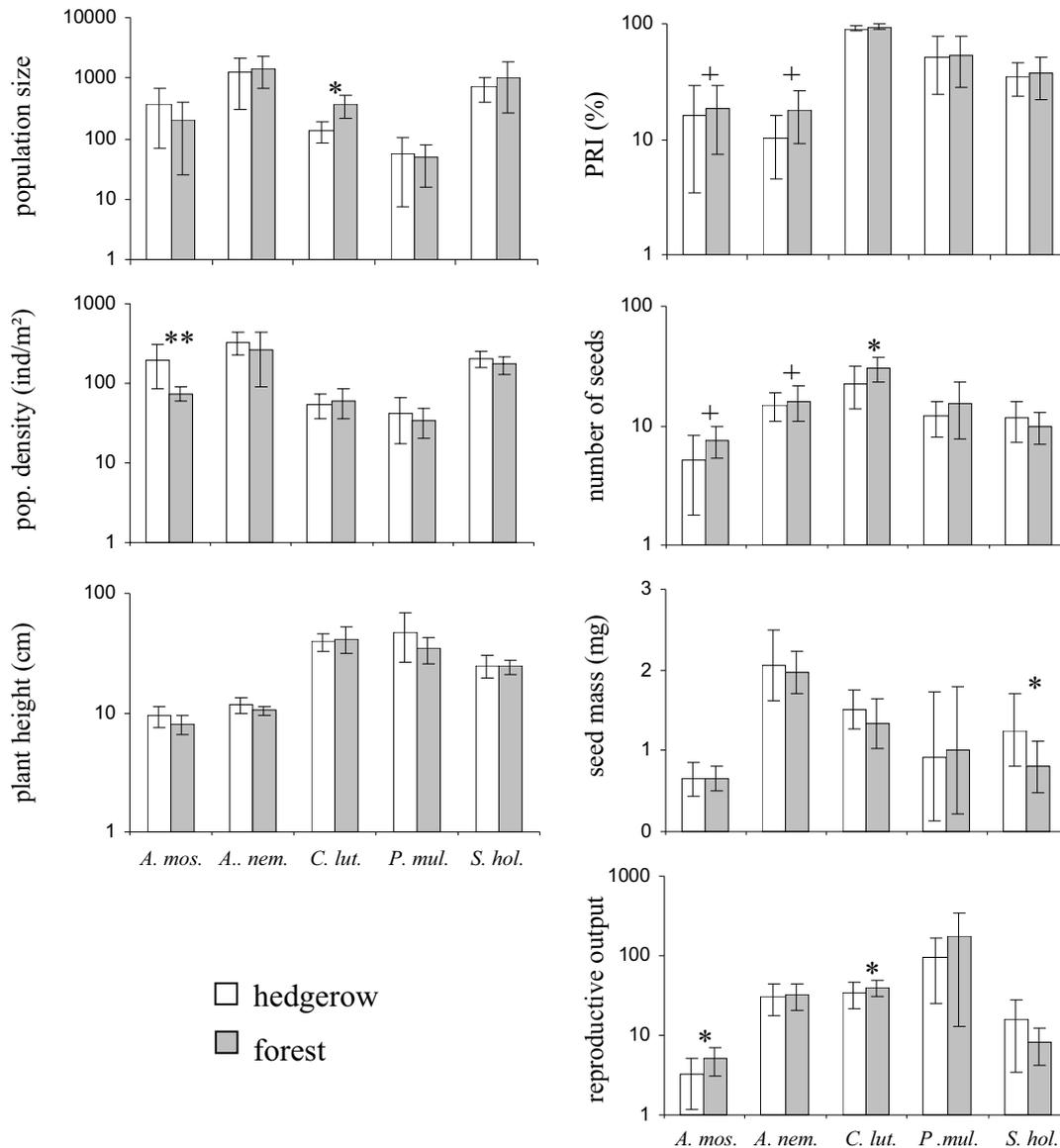


Figure 1: Plant performance values in *Adoxa moschatellina* (*A. mos.*), *Anemone nemorosa* (*A. nem.*), *Circaea lutetiana* (*C. lut.*), *Polygonatum multiflorum* (*P. mul.*) and *Stellaria holostea* (*S. hol.*) in comparison of the two habitat types, hedgerow and forest. Mean values \pm standard deviation are given, with the y axis log-scaled (except for seed mass, for which only the values for *Polygonatum* are log-transformed). Asterisks indicate significant and + marginally significant differences between habitat types. PRI = proportion of reproductive individuals.

Both *Adoxa* and *Anemone* showed marginally significant trends towards higher proportions of reproductive individuals in forests (Fig. 1). Forests also had or tended to have higher numbers of seeds in *Circaea* and *Adoxa* & *Anemone*, respectively. The seed mass of species did not differ between habitat types except in *Stellaria* having heavier seeds in hedgerows. For *Polygonatum* no significant differences between habitat types were found for any of the parameters.

Relationship between plant performance and environment

The multiple linear regression of plant performance on environmental variables showed few significant and, across species, not always consistent results (Table 3). Water content, when remaining in the final model, in all cases had positive effects on reproduction. Relative irradiance, in contrast, showed a positive impact on plant height in *Adoxa* and *Polygonatum*, and on seed mass and total reproductive output in *Anemone*, but a negative impact on the number of seeds in *Circaea*. Phosphate content only affected the proportion of reproductive individuals in two of the species (positively in *Adoxa*, negatively in *Circaea*). For potassium and nitrogen we found negative relationships with some of the performance variables in *Adoxa*, in which the C/N ratio also had significant effects (positive for most variables, but negative for seed mass).

Table 3: Effects of soil variables and light on plant performance values of the five study species, assessed by multiple linear regression analyses (backward with $\alpha = 0.05$). For each species R^2 -values of the full models are given. Only significant results are shown (* = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$). PRI = Proportion of reproductive individuals.

Species	Envir. variable	Plant height	PRI	No. of seeds	Seed mass	Reproductive Output
<i>A. moschatellina</i>	Water content			0.793***		0.891***
	Rel. irradiance	0.753***				
	P		0.575**			
	K		-0.597**			
	N	-0.386*			-0.616**	-0.653***
	C/N ratio	0.597**	0.452*	0.415*	-0.549*	
	R² full model	0.564***	0.451**	0.518**	0.262*	0.602***
<i>A. nemorosa</i>	Water content		0.436*			
	Rel. irradiance		-0.469*			
	R² full model		0.318*			
<i>C. lutetiana</i>	Rel. irradiance			-0.465*		
	P		-0.497*			
	R² full model		0.205*	0.173*		
<i>P. multiflorum</i>	Rel. irradiance	0.512*				
	R² full model	0.210*				
<i>S. holostea</i>	Water content				0.397*	
	Rel. irradiance				0.652**	0.495*
	C/N ratio	-0.626**				
	R² full model	0.358**			0.455**	0.201*

DISCUSSION

In intensively used agricultural areas hedgerows are assumed to be the most forest-like landscape element. In this study we show, however, that there are distinct environmental differences between the two habitat types. Light availability was much higher in hedgerows than in forests, caused by the narrow linear form of most surveyed hedgerows (width <4 m) allowing lateral radiation to reach the interior (Forman & Baudry, 1984). The higher soil pH values found in hedgerows confirm the results observed in other studies from the United Kingdom (Hegarty *et al.*, 1994; McCollin *et al.*, 2000) and in a previous study from the study region (Wehling & Diekmann, 2008). The tendency towards lower soil water contents in the studied hedgerows is supported by results of a recent Canadian study, which found significantly lower soil moisture in hedges compared to forests (Schmucki & de Blois, in press). The lower acidity and also the generally higher nutrient contents in hedgerow soils are most likely explained by agricultural activities such as fertilizer misplacement or runoff from adjacent fields, leading to nutrient enrichment (Jobin *et al.*, 1997; Kleijn & Snoeiijing, 1997; Tsiouris & Marshall, 1998). Again, these results are similar to those obtained in another study from Belgium (Endels *et al.*, 2004). In summary, the environments of hedgerows and forests differ in terms of irradiance and nutrient contents, rendering it likely that also the general and reproductive performance of forest species differs between the two habitat types.

When comparing the performance values of the studied species between forests and hedgerows, however, we found only few differences. This general pattern may partly be explained by the wide amplitudes of some of the species with respect to their realized habitat conditions. For example, *Anemone* and *Stellaria* are known to grow on soils with a broad range of pH without differing in their performance (Schlenker, 1968; Shirreffs, 1985). There are few other studies available that examine differences in plant performance values between forest and hedgerow populations of herbaceous forest species. In Australia, fruit production in linear scrub elements was significantly lower than that in forests (Cunningham, 2000). In contrast, a higher reproductive output of plants was observed in hedgerow populations in Belgium (Endels *et al.*, 2004). A recent Canadian study on *Trillium grandiflorum* showed contrasting effects on the performance of the species in hedgerows and forests depending on its growth stage (Schmucki & de Blois, in press). Here, mature plants grew faster and produced more flowers and ovules per flower in hedgerows, seed production and germination rate did not differ among habitat types, while recruitment in terms of establishment of seedlings and juveniles was significantly higher in forests. The authors concluded that

reduced recruitment may hamper the establishment of new populations and migration processes in hedgerows.

It thus appears that the suitability of hedgerows for the survival and reproduction of forest plants depends on the specific requirements of species. Plant performance may be better in the forest interior due to the lower nutrient availability in the soil (McCollin *et al.*, 2000) and the lower light availability, simply by hampering nutrient- and light-demanding, highly competitive species such as *Urtica dioica* from attaining dominance (Honnay *et al.*, 1998, 1999; De Keersmaecker *et al.*, 2004; Endels *et al.*, 2004). In contrast, other studies providing evidence for a better plant performance of forest species in hedgerows compared to forests (Valverde & Silvertown, 1995, 1998) emphasized a direct positive effect of a higher light availability, stressing that most forest plants are not shade-demanding, but shade-tolerant (Hughes & Fahey, 1991). Another possible reason for the advantage of linear structures is enhanced germination as a result of the better nutrient supply of the hedgerow soils (Pigott & Taylor, 1964).

Looking at the response patterns of single species, the results for *Adoxa* were somewhat contradictory. Whereas some performance values were higher for the forest populations, others were higher for the hedgerows. Accordingly, reproductive output increased with increasing soil water content (shown to be higher in forests), reflecting the hygromorph character of the species, while plant height was positively affected by light availability shown to be higher in hedgerows. There was no relationship between plant height and reproductive output. However, the results correspond to the species' relatively high indicator values for light (Bossuyt *et al.*, 1999).

The results for *Anemone* reveal that the species can be considered a true forest species in the sense that the proportion of reproductive individuals (PRI) and the number of seeds were higher in forests, and that PRI increased with increasing soil water content and decreasing light values. These observations are also supported by a study from Great Britain (Shirreffs, 1985). However, as the species is highly clonal, reproduction by seed is not necessarily crucial for the species (Holderegger *et al.*, 1998), and hedgerows appear to offer it a suitable habitat in which it maintains viable populations.

The comparison between habitat types shows that also *Circaea* is favoured by a forest environment with its relatively low light and nutrient availability. This conforms to the notion of Wulf (1997) describing the species as an ancient woodland indicator for northern Germany. As it has been reported as being mainly seed dispersed (Verburg *et al.*, 2000), and that less than 40% of the seeds of the species are able to germinate (Slade & Causton, 1979), a

reduction in seed production may be more severe for *Circaea* than for *Adoxa* or *Anemone*. Least affected by habitat type and the differences in environmental conditions was *Polygonatum*, an endozoochorous species (Bossuyt *et al.*, 1999) that appears to be able to form viable populations also in the hedgerow habitat.

Among the five species, *Stellaria* appears to be the one with the highest affinity to hedgerows, also considering its generally high frequency in the hedgerows of the area (Wehling, unpubl.). High frequencies of *Stellaria* in hedgerows were also reported for Great Britain (Andrews *et al.*, 1999; Sparks *et al.*, 2000; Cherrill *et al.*, 2001). Especially the higher light availability, but partly also the lower C/N ratio of the hedgerows have a positive impact on reproduction, notably seed mass. The preference for light environments is reflected in the relatively high light indicator value and has also been reported by Verheyen & Hermy (2001).

Only a minor part of all measured plant performance values showed significant differences between habitat types. However, 8 of 10 differences found suggested a better plant performance in forests, which may be a sign for a lower long-term suitability of hedgerows in providing habitats for the tested forest plant species. Most of these, however, concerned variables of sexual reproduction, and it has to be kept in mind that all five species are more or less clonal (Klotz *et al.*, 2002). Such species may counteract unfavourable conditions for sexual reproduction with a higher investment in vegetative propagation; accordingly, they were found more often in hedgerows than non-clonal species by Roy & de Blois (2006). Thus, differences in sexual reproductive values do not necessarily reflect differences in short-time survival, at most they are an indication for differences in long-term population viability.

CONCLUSIONS

Based on the results we hypothesize that three types of forest plant species occurring in hedgerows may be distinguished. The first type, represented by *Circaea*, comprises species that may be more or less abundant in hedgerows, but perform better in closed forests. Members of the second group, such as *Stellaria*, show a higher reproductive fitness in hedgerows. The last and perhaps most frequent type is represented by *Adoxa*, *Anemone* and *Polygonatum*, comprising species for which it makes almost no difference whether they grow in forests or hedgerows. These groupings are supported by findings of McCollin *et al.* (2000), who developed a habitat preference index for British woodland plants, which classified the tested species accurately in the same way: *Circaea* preferred forests, *Adoxa*, *Anemone* and *Polygonatum* were associated with both habitat types (with a tendency towards forests), and *Stellaria* clearly favoured hedgerows.

By attempting this generalisation it has to be kept in mind that only forest species able to survive in hedgerows were considered. An important subset of forest species may never be found in hedgerows and deserves closer attention.

Whether such classifications make sense and how many forest species can be assigned to one of the above types based on differences in their growth and reproductive performance between habitats, can only be answered by a more extensive study of a larger number of species, and particularly by a long-term monitoring of populations over several growing seasons to examine the demography of the populations.

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REFERENCES

- Andrews, M., Mercer, C., Griffin, P., Andrews, M.E., Cherrill, A., 1999. Autecology of common herbaceous hedgerow species in Britain. *Aspects of Applied Biology* 54, 353-360.
- Baudry, J., Bunce, R. G. H., Burel, F., 2000. Hedgerows: An international perspective on their origin, function and management. *Journal of Environmental Management* 60, 7-22.
- Bossuyt, B., Hermy, M., Deckers, B., 1999. Migration of herbaceous plant species across ancient-recent forest ecotones in Central Belgium. *Journal of Ecology* 87, 628-638.
- Cherrill, A., Mercer, C., McClean, C., Tudor, G., 2001. Assessing the floristic diversity of hedge networks: a landscape perspective. *Landscape Research* 26, 55-64.
- Corbit, M., Marks, P. L., Gardescu, S., 1999. Hedgerows as habitat corridors for forest herbs in central New York, USA. *Journal of Ecology* 87, 220-232.
- Cunningham, S. A., 2000. Effects of habitat fragmentation on the reproductive ecology of four plant species in mallee woodland. *Conservation Biology* 14, 758-768.
- de Blois, S., Domon, G., Bouchard, A., 2002. Factors affecting plant distribution in hedgerows of southern Quebec. *Biological Conservation* 105, 355-367.
- De Keersmaeker, L., Martens, L., Verheyen, K., Hermy, M., De Schrijver, A., Lust, N., 2004. Impact of soil fertility and insolation on diversity of herbaceous woodland species

- colonizing afforestations in Muizen forest (Belgium). *Forest Ecology and Management* 188, 291-304.
- Deckers, B., De Becker, P., Honnay, O., Hermy, M., Muys, B., 2005. Sunken roads as habitats for forest plant species in a dynamic agricultural landscape: effects of age and isolation. *Journal of Biogeography* 32, 99-109.
- Ellenberg, H., 1996. *Vegetation Mitteleuropas mit den Alpen*. Eugen Ulmer, Stuttgart, Germany.
- Ellenberg, H., Weber, H. E., Düll, R., Wirth, V., Werner, W., Paulißen, D., 1992. Zeigerwerte von Pflanzen in Mitteleuropa. *Scripta Geobotanica* 18, 1-258.
- Endels, P., Adriaens, D., Verheyen, K., Hermy, M., 2004. Population structure and adult plant performance of forest herbs in three contrasting habitats. *Ecography* 27, 225-241.
- Forman, R. T. T., 1995. *Land mosaics: the ecology of landscapes and regions*. University Press, Cambridge, USA.
- Forman, R. T. T., Baudry, J., 1984. Hedgerows and hedgerow networks in landscape ecology. *Environmental Management* 8, 495-510.
- Freemark, K. E., Boutin, C., Keddy, C. J., 2002. Importance of farmland habitats for conservation of plant species. *Conservation Biology* 16, 399-412.
- French, D. D., Cummins, R. P., 2001. Classification, composition, richness and diversity of British hedgerows. *Applied Vegetation Science* 4, 213-228.
- Fritz, R., Merriam, G., 1993. Fencerow habitats for plants moving between farmland forests. *Biological Conservation* 64, 141-148.
- Grashof-Bokdam, C., 1997. Forest species in an agricultural landscape in the Netherlands: Effects of habitat fragmentation. *Journal of Vegetation Science* 8, 21-28.
- Green, R. E., Cornell, S. J., Scharlemann, J. P. W., Balmford, A., 2005. Farming and the fate of wild nature. *Science* 307, 550-555.
- Grime, J. P., Hodgson, J. P., Hunt, R., 1988. *Comparative plant ecology: a functional approach to common British species*. Unwin Hyman, London, UK.
- Hegarty, C. A., McAdam, J. H., Cooper, A., 1994. Factors influencing the plant species composition of hedges - implications for management in environmentally sensitive areas. *British Crop Protection Council Monographs* 58, 227-234.
- Helliwell, D. R., 1975. The distribution of woodland plant species in some Shropshire hedgerows. *Biological Conservation* 7, 61-72.

- Hermý, M., Honnay, O., Firbank, L., Grashof-Bokdam, C., Lawesson, J. E., 1999. An ecological comparison between ancient and other forest plant species of Europe, and the implications for forest conservation. *Biological Conservation* 91, 9-22.
- Holderegger, R., Stehlik, I., Schneller, J. J., 1998. Estimation of the relative importance of sexual and vegetative reproduction in the clonal woodland herb *Anemone nemorosa*. *Oecologia* 117, 105-107.
- Honnay, O., Degroote, B., Hermý, M., 1998. Ancient-forest plant species in Western Belgium: A species list and possible ecological mechanisms. *Belgian Journal of Botany* 130, 139-154.
- Honnay, O., Hermý, M., Coppin, P., 1999. Impact of habitat quality on forest plant species colonization. *Forest Ecology and Management* 115, 157-170.
- Hughes, J. W., Fahey, T. J., 1991. Colonization dynamics of herbs and shrubs in a disturbed northern hardwood forest. *Journal of Ecology* 79, 605-616.
- Jobin, B., Boutin, C., DesGranges, J., 1997. Effects of agricultural practices on the flora of hedgerows and woodland edges in southern Quebec. *Canadian Journal of Plant Science* 77, 293-299.
- Kleijn, D., Snoeiijing, G. I. J., 1997. Field boundary vegetation and the effects of agrochemical drift: botanical change caused by low levels of herbicide and fertilizer. *Journal of Applied Ecology* 34, 1413-1425.
- Klotz, S., Kühn, I., Durka, W., 2002. Eine Datenbank mit biologisch-ökologischen Merkmalen zur Flora von Deutschland. *Schriftenreihe für Vegetationskunde* 38, 1-334.
- McCollin, D., Jackson, J. I., Bunce, R. G. H., Barr, C. J., Stuart, R., 2000. Hedgerows as habitat for woodland plants. *Journal of Environmental Management* 60, 77-90.
- Middleton, J., Merriam, G., 1983. Distribution of woodland species in farmland woods. *Journal of Applied Ecology* 20, 625-644.
- Peterken, G. F., 2000. Rebuilding Networks of Forest Habitats in Lowland England. *Landscape Research* 25, 291-303.
- Pigott, C. D., Taylor, K., 1964. The distribution of some woodland herbs in relation to the supply of nitrogen and phosphorus in the soil. *Journal of Animal Ecology* 33, 175-185.
- Roy, V., de Blois, S., 2006. Using functional traits to assess the role of hedgerow corridors as environmental filters for forest herbs. *Biological Conservation* 130, 592-603.
- Schlenker, G., 1968. Kulturversuche mit Waldbodenpflanzen bei abgestufter Azidität und variierter Stickstoff-Form. *Oecologia Plantarum* 3, 7-27.

- Schmidt, M., von Oheimb, G., Kriebitzsch, W.-U., Ellenberg, H., 2002. Liste der im norddeutschen Tiefland typischen Waldgefäßpflanzen. *Mitteilungen der Bundesforschungsanstalt für Forst- und Holzwirtschaft* 206, 1-37.
- Schmucki, R., de Blois, S., in press. Population structures and individual performances of *Trillium grandiflorum* in hedgerow and forest habitats. *Plant Ecology*, doi: 10.1007/s11258-008-9460-8.
- Shirreffs, D. A., 1985. *Anemone nemorosa* L. *Journal of Ecology* 73, 1005-1020.
- Slade, E. A., Causton, D. R., 1979. The germination of some woodland herbaceous species under laboratory conditions: a multifactorial study. *New Phytologist* 83, 549-557.
- Sparks, T. H., Meek, W. R., Mountford, J. O., Pywell, R. F., 2000. The spatial distribution of herbs and woody species in the hedgerows of an arable farm. *Aspects of Applied Biology* 58, 401-406.
- Tsiouris, S., Marshall, E. J. P., 1998. Observations on patterns of granular fertiliser deposition beside hedges and its likely effects on the botanical composition of field margins. *Annals of Applied Biology* 132, 115-127.
- Usher, M. B., Brown, A. C., Bedford, S. E., 1992. Plant species richness in farm woodlands. *Forestry* 65, 1-13.
- Valverde, T., Silvertown, J., 1995. Spatial variation in the seed ecology of a woodland herb (*Primula vulgaris*) in relation to light environment. *Functional Ecology* 9, 942-950.
- Valverde, T., Silvertown, J., 1998. Variation in the demography of a woodland understorey herb (*Primula vulgaris*) along the forest regeneration cycle: projection matrix analysis. *Journal of Ecology* 86, 545-562.
- Verburg, R., Maas, J., During, H. J., 2000. Clonal diversity in differently-aged populations of the pseudo-annual clonal plant *Circaea lutetiana* L. *Plant Biology* 2, 646-652.
- Verheyen, K., Hermy, M., 2001. The relative importance of dispersal limitation of vascular plants in secondary forest succession in Muizen Forest, Belgium. *Journal of Ecology* 89, 829-840.
- Wehling, S., Diekmann, M., 2008. Factors influencing the spatial distribution of forest plant species in hedgerows of North-western Germany. *Biodiversity and Conservation* 17, 2799-2813.
- Wulf, M., 1997. Plant species as indicators of ancient woodland in northwestern Germany. *Journal of Vegetation Science* 8, 635-642.

Chapter 5

Importance of hedgerows as habitat corridors for forest species in agricultural landscapes

Wehling, S. & Diekmann, M., in press.

Biological Conservation.



Top left: Hedgerow with well developed tree- and shrub-layer. **Top right:** Hedgerow adjacent to forest without tree layer. **Bottom left:** Hedgerow adjacent to forest without shrub-layer. **Bottom right:** Forest edge. (Photographs taken by Stephan Wehling).

ABSTRACT

Hedgerows have been proposed as habitat and conservation corridor for forest plant species, but their importance for the survival of these species is still not clear. The objective of our study was to examine the frequency of occurrence of forest species and total forest species richness in different parts of the hedgerows, and to relate these patterns of occurrence to the species' habitat requirements and life history traits. We surveyed in total 130 forest-hedgerow transects in North-western Germany, including three age classes.

About 77% of all forest plant species (including some endangered taxa) occurring in the neighbouring forests were also found in the adjacent hedgerows. In all age classes, there was a negative relationship between distance from the forest-hedgerow ecotone and the number of species. Ancient hedgerows were not significantly more species-rich than more recent ones. Within 100 m distance from the forest edge, forest species richness increased with an increasing number of species in the nearby forest and with an increasing cover of the tree canopy as well as a decreasing cover of the shrub layer. Species with high frequency had comparatively high Ellenberg indicator values for light, and were mostly associated with anemochorous and epizoochorous seed dispersal.

The frequency of occurrence in hedgerows of species with common attributes was partly in agreement, partly in disagreement with the results obtained in previous studies. We conclude that patterns are difficult to generalize, probably due to a strong regional variation in the pool of forest species and in the specific environments of both forests and hedgerows.

Keywords:

Connectivity; conservation; forest fragmentation; hedgerow transect; seed dispersal.

INTRODUCTION

Nature has been and still is strongly altered by human activities. Especially the intensive agricultural land use has resulted in dramatically high losses of biodiversity (Van Calster *et al.*, 2008), first of all in forests (Bailey, 2007). Herbaceous forest plant species, usually being long-lived, producing few seeds, lacking long-distance dispersal and a persistent seed bank, are not able to respond quickly to habitat loss and fragmentation (Bierzychudek, 1982; Herny *et al.*, 1999), which makes them susceptible for extinction events (Peterken & Game, 1984; Dzwonko & Loster, 1989). Forest species are also prone to an 'extinction debt', which means extinction delayed for years or even decades after habitat fragmentation (Vellend *et al.*, 2006).

In this context corridors have been proposed as an important conservation tool (Verkaar, 1990), assuming that the connectivity of forest fragments is crucial for the survival of many forest species (Honnay *et al.*, 1999; Jacquemyn *et al.*, 2003). In agricultural landscapes hedgerows as linear forest-like elements often increase the number of herbaceous forest plant species (Pollard *et al.*, 1974; Freemark *et al.*, 2002) and may serve as a potential corridor. The efficiency of conservation corridors, however, has mostly been studied in animals (Noss, 1987; Simberloff & Cox, 1987; Beier & Noss, 1998), and recently also potential negative effects of corridors were discussed, such as increased spread of contagious diseases, parasites and invasive neobiota (Simberloff *et al.*, 1992; Hess, 1994). For plants, especially animal-dispersed species, it could be shown that corridors may help to maintain viable populations (Grashof-Bokdam, 1997). On the other hand, many species appear not to be able to use such corridors (Dawson, 1994). With respect to plant species many aspects remain unclear.

Whether hedgerows may act as conservation corridors is still disputed. In two studies from Western Europe (Burel, 1996) and Italy (Sitzia, 2007), forest plants were shown to find suitable habitats in farmland hedgerows. On the other hand, transplantation experiments with forest plant species in Canada gave evidence for an insufficient habitat function of hedgerows, because, two years after the start of the experiment, nearly all plants had died in their new environment (Fritz & Merriam, 1993). In a later study the authors also found considerable differences in habitat conditions between hedgerows and forests or forest edges (Fritz & Merriam, 1996). In contrast to findings from Pollard *et al.* (1974), herbaceous plant species typical for forests or ancient forests were only rarely found in some British hedgerow-networks (French & Cummins, 2001; Smart *et al.*, 2001). A recent review referring mainly to rare and specialized forest species did not lend support for a corridor function of hedgerows in Europe or elsewhere (Bailey, 2007).

An intermediate view regards hedgerows as suitable habitat for forest plants, but only for a sub-set of species with particular life history traits (Helliwell, 1975). This is supported by recent results from a study in Germany showing the suitability of hedgerows for some selected forest species (Wehling & Diekmann, 2009). In the province Quebec in Canada, several forest plants with relatively broad ecological ranges were able to disperse along hedgerows (de Blois *et al.*, 2002), and similar results were obtained in a study from the UK (McCollin *et al.*, 2000).

The impact of stand age on the occurrence and survival of forest species in hedgerows has rarely been studied, and the results are contradictory. In Great Britain shrub species richness was considerably higher in older hedgerows than in younger ones (Hooper, 1970), and

herbaceous forest species were almost exclusively found in older hedgerows or hedges assumed to be woodland relics (Pollard *et al.*, 1974). A more recent study from the USA could not support an impact of hedgerow age on forest species richness and abundance (Corbit *et al.*, 1999).

The starting point of our study was the assumption that, at least for some forest plants with a relatively high competitive ability and broad tolerance with respect to environmental conditions, hedgerows may function as a suitable habitat for long-term survival and as dispersal corridor. The definition of the term 'forest species' follows Schmidt *et al.* (2002) who classified herbaceous plant species in the North German lowlands as forest species if they had their main occurrence inside forests or in forest edges and gaps (see also below).

Our main objectives were to examine (1) which species out of the regional pool of forest plants can be found in hedgerows, and whether their frequency changes along forest-hedgerow transects, (2) whether hedgerow age has an impact on the patterns of forest species occurrence and richness, and (3) whether the frequencies of forest species along the hedgerows can be related to their responses to environmental variables (in terms of soil and climatic factors) and to their life histories.

METHODS

Study area

The study was conducted in 2007 in a region north and west of the city of Bremen in North-western Germany. The landscape is flat to weakly undulating, varying in elevation between 5 and 30 m a.s.l. The soils, mainly deriving from the Pleistocene Saale glaciation, are relatively base- and nutrient-poor, and often moist to wet because of poor drainage. Mean annual precipitation in the area amounts to about 700 mm, while mean annual temperature is ca. 8.8°C (data available at <http://dwd.de/>, [26 October 2008]).

The landscape in the region is dominated by intensive agricultural land use, and most of the forests have been cleared or transformed to coniferous plantations. The study area, however, still contains relatively large proportions of ancient deciduous forest as well as dense and intact networks of hedgerows (almost all fields are enclosed by hedgerows). These are usually connected to forest stands, but otherwise surrounded by fields, pastures and meadows. In the study area all forest patches and hedgerows were surveyed in 2005 for the occurrence of typical forest species (Wehling & Diekmann, 2008). For the current study we selected only those forests that were already found on the oldest reliable historical maps from the region

from 1764-1786 (“Kurhannoversche Landesaufnahme”) and were also depicted on maps from 1898 and 1970, and thus are considered historically ancient. To be selected the forest also had to have direct contact (distance between forest and hedgerow < 5 m) to at least one hedgerow. The 48 forests fulfilling these pre-conditions varied considerably in size between 2 and 580 ha (mean: 85 ha). We then selected hedgerows with a more or less perpendicular orientation to the forest edge, and only a minor fraction of all hedgerows in the study area ($n = 130$) conformed to these conditions. These were composed of shrubs and often also full-grown trees, ranged in width from 3.5 to 5 m and were often bordered by ditches. Both the age of the hedgerows and the age of forests were determined with the help of historical maps. All hedgerows already found on the map “Kurhannoversche Landesaufnahme” from 1764-1786 were classified as older than 200 years (referred to as age class 200, $n = 14$). Those first shown on the map “Königlich Preußische Landesaufnahme” from 1898 were categorized as 100-199 years old (age class 100, $n = 97$; the maximum age of this class was based on the assumption that some of the hedges were planted only a few years after data recording for the map from 1764-1786). Finally, hedgerows lacking on the two above-mentioned maps but found on more recent maps (dating back to 1970-1980) were considered as 40-99 years old (age class 50, $n = 19$). All hedgerows of the age classes 50 and 100 were planted on former agricultural land. Only in the age class 200 hedgerows may represent ancient woodland relics, but no data of their origin was available.

The most common woody species found in the hedgerows were *Quercus robur*, *Carpinus betulus*, *Corylus avellana*, *Sorbus aucuparia* and *Prunus spinosa*. The neighbouring forests (except those planted with conifers) were usually dominated by *Quercus robur*, *Fraxinus excelsior*, *Fagus sylvatica* and *Alnus glutinosa*.

Data collection

Hedgerows and the adjacent parts of the connected forest were surveyed from May to July 2007 for the presence / absence of forest plant species. As previously mentioned this term encompasses those herbaceous plants that have their main occurrences in the interior of forests or in forest edges and gaps (Schmidt *et al.*, 2002). This classification is an expert system based on more than 6.000 sample plots from the North German lowlands, as well as on the field experience of a large number of vegetation ecologists, and separates forest species from those species that are more frequent and vital in open habitat types and that are only accidentally found in woodlands. Some forest species, like *Anemone nemorosa* or *Pteridium aquilinum*, may, however, with lower frequency also be found in the open landscape. The

nomenclature of species follows Wisskirchen & Haeupler (1998), and the classification of species rarity is based on the Red List of the study region (Garve, 2004).

The sampling design was largely adopted from Corbit *et al.* (1999), only the length of the transects differed because of the higher mean hedgerow length in the study area (200-250 m). Each forest-hedgerow site was surveyed as a transect of 230 m length and 4 m width, subdivided into 10 m long segments, i.e., each transect was made up of 23 contiguous 10 m segments. Three of these reached into the forest, 20 extended at the other side of the ecotone into the hedgerow. All segments were situated closer to the forest at the transect origin than to any other woodland. We studied a total of 130 transects with 2.990 segments. Furthermore, the forest in the vicinity of each hedgerow transect was searched for the occurrence of forest species in a 700 m² circular plot centred at the end of the transect. We assumed the adjacent forest to be the most probable colonisation source for the hedgerows, because the vast majority of hedgerows were shown to be younger than the adjacent forests. Apart from recording the forest species the percent cover of tree and shrub layers was estimated in each segment.

To examine changes in environmental conditions along the forest-hedgerow transects, we used measurements in a sub-set of the forests ($n = 20$) and the adjacent transects at 30 m ($n = 38$), 60 m ($n = 28$) and 90 m ($n = 11$) distance from the forest edge. The values were derived from a previous study designed for a different purpose that was carried out in 2005. Soil samples were collected and analyzed with respect to pH, water content and the concentrations of P, K, Ca, Mg, C and N (C/N), applying standard techniques (in more detail described in Wehling & Diekmann, 2008). Light was measured as photosynthetically active radiation simultaneously inside the hedgerow and outside in the open under overcast sky conditions, and expressed as relative light intensity.

Data analysis

Differences in frequency of occurrence between forests and hedgerows and between hedgerow age classes were tested for all observed forest species with Chi-square tests. Two main measures of species richness of forest plants were calculated: the cumulative number of species in each transect, and the number of species in each segment. All species richness values showed a normal distribution (Kolmogorov-Smirnov test). We assumed that hedgerow age had a strong effect on the number of forest plant species and the change in species richness along the transect. Therefore, we compared both the cumulative number of species per transect and the mean numbers of species in each segment along the transect between age

classes by One-way ANOVA, followed by Tukey tests to check for pair-wise differences between age classes.

To examine the relationships between the number of species and the distance from the forest-hedgerow ecotone, regression analysis was used. We compared four different regression models that we assumed to allow a meaningful ecological interpretation: linear, sigmoidal, polynomial, and exponential. The general assumption was that most species would, across all transects, display some type of decrease in frequency away from the ecotone, resulting in a decline in species richness along the transect. For each regression the best fitting model in terms of variation explained (R^2_{adj}) was determined. The dependent variable was the mean number of species per segment calculated separately for the three age classes (50, 100, 200).

We furthermore assumed that the species' overall frequencies as well as their changes in frequency along the transect are related to some ecological and life history traits. Therefore the following variables were compiled for the 20 most common species (except *Stellaria holostea* that was present in almost all segments): the Ellenberg indicator values for light and temperature (as surrogates of the species' shade tolerance and temperature requirements) as well as for soil moisture, pH and nitrogen (Ellenberg *et al.*, 1992), plant height, and dispersal type (<http://floraweb.de/>, [20 June 2008]). Seed dispersal types were defined as autochory (self-dispersal), anemochory (dispersal by wind), epizoochory (dispersal by animals, diaspores attached to their surface), endozoochory (dispersal by animals, diaspores ingested) and myrmecochory (dispersal by ants). To examine at which distances the traits had a significant impact on the frequencies of forest species, the relationship between trait values and the observed frequencies of occurrence for different distances from the forest-hedgerow ecotone was then analyzed with Spearman rank correlation or One-way ANOVA (in the case of dispersal type). To examine whether the mean cover of the tree and shrub layers and the number of forest plant species occurring in nearby woodlands affected the number of species in different transect segments, Pearson correlation was used. For each distance the observed number of species / transect segment was correlated with the corresponding cover values ($n = 130$). To consider possible interactions between explanatory variables in their effects on species richness, we applied multiple linear regression, including the factors distance of transect segment, hedgerow age and covers of tree and shrub layer, as well as interaction terms. For each possible combination of two variables, a separate variable was included. We conducted a stepwise backward method ($\alpha = 0.05$), but a forward method revealed the same results. In addition, we examined the changes in environmental conditions along the forest-hedgerow transect with paired t-tests. The regression analyses were carried out with

SigmaPlot 10.0 (Systat Software, San Jose, USA), all other analyses with SPSS 15.0 (SPSS, Chicago, USA).

RESULTS

In the surveyed forest-hedgerow transects we found in total 48 taxa classified as typical herbaceous forest plant species (Appendix). The majority of these ($n = 37$ or 77%) were recorded both in the forest and hedgerow parts of the transects (Fig. 1a).

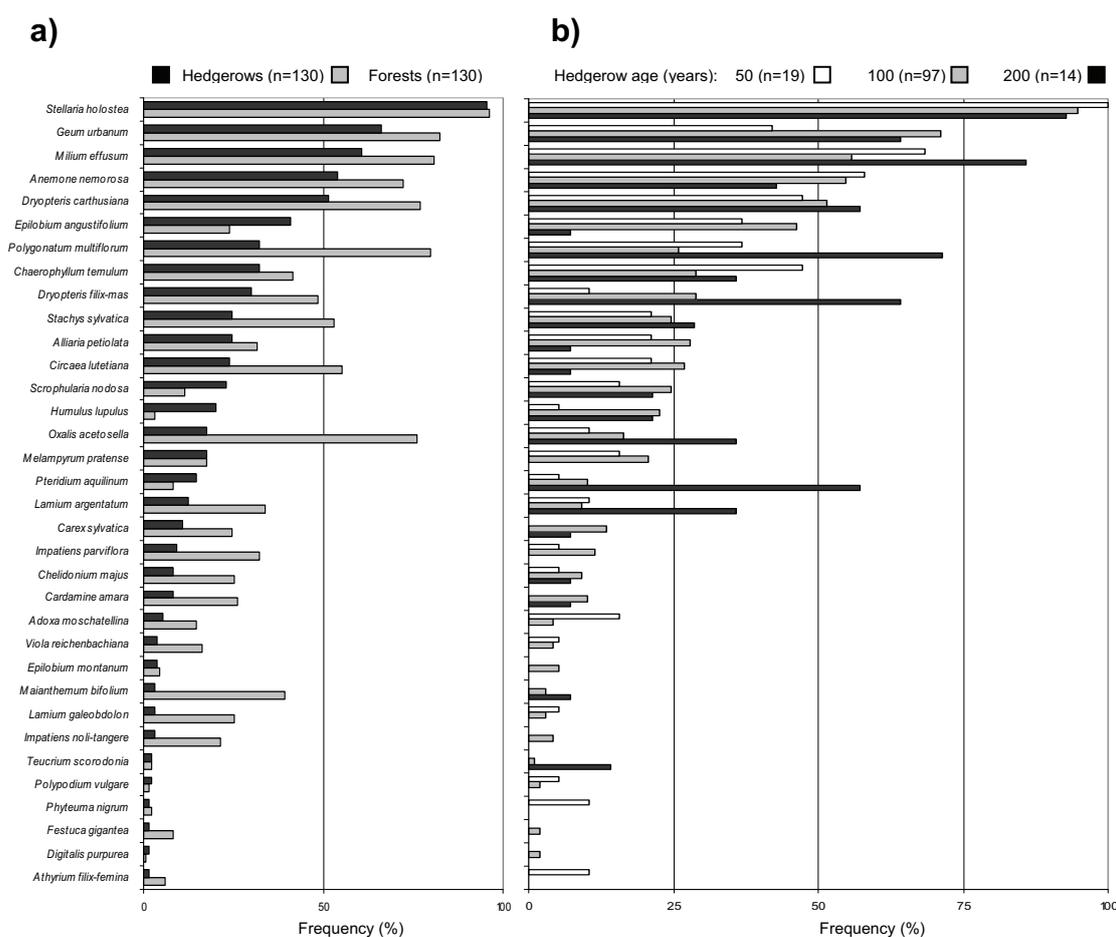


Figure 1: Frequency of occurrence of herbaceous forest plant species found in forest-hedgerow transects, being present in at least one transect. a) Comparison of habitat types (forests = grey bars, hedgerows = black bars), and b) Comparison of hedgerow age classes (50 = 50-99 years = white bars, 100 = 100-199 years = grey bars, 200 = > 200 years = black bars). The species are ordered by decreasing frequency of occurrence in the hedgerow part of the transects.

Some of the species found (*Equisetum hyemale*, *Phyteuma nigrum*, *Primula elatior* and *Sanicula europaea*) are considered as endangered in the region. Only few forest edge and gap species were recorded ($n = 9$ or 19%). The most common herbaceous plants were *Stellaria*

holostea, *Geum urbanum* and *Milium effusum*. Some species like *Oxalis acetosella* ($\chi^2 = 89.199$), *Polygonatum multiflorum* ($\chi^2 = 60.048$) and *Maianthemum bifolium* ($\chi^2 = 50.939$, all $p < 0.001$) were clearly more frequent in forest segments than in hedgerow segments, whereas only few, relatively uncommon, species were detected almost exclusively in hedgerows, for example *Humulus lupulus* ($\chi^2 = 18.238$, $p < 0.001$). Many species differed in their frequency of occurrence between hedgerow age classes (Fig. 1b). *Polygonatum multiflorum* ($\chi^2 = 11.870$, $p = 0.003$), *Pteridium aquilinum* ($\chi^2 = 23.063$, $p < 0.001$) and *Lamium argentatum* ($\chi^2 = 7.987$, $p = 0.018$) showed their highest values in the oldest hedgerows. The most frequent species, *Stellaria holostea*, occurred in all hedgerows of age class 50 and in nearly all hedgerows of the two other classes.

Species richness was highest in the forest segments of the transect, averaging to about 6. At the ecotone, species number dropped to about 3 (Fig. 2a). In general, species richness then slightly decreased with increasing distance from the ecotone to a mean value of 1.5, meaning, however, that also at 200 m distance to the neighbouring forest at least some forest plants were found. There was, however, a considerable variation along the transect, and, when examining the different age classes, there were pronounced differences in species richness between age classes 50 and 200 especially at the beginning and the end of the transect (Fig. 2b).

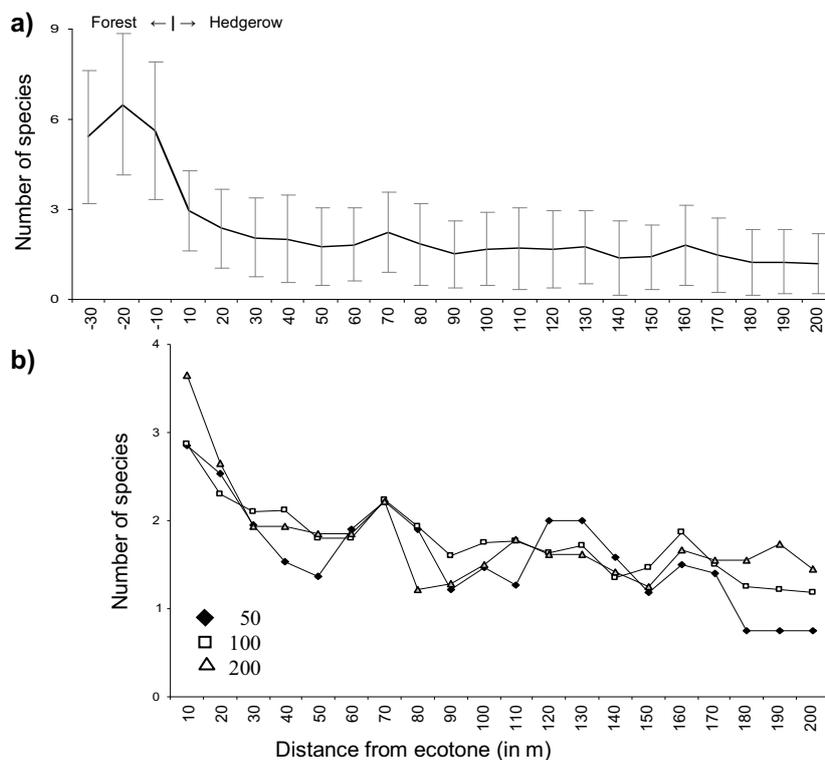


Figure 2: Mean number of herbaceous forest plant species per 10 m segment in forest-hedgerow transects, shown for a) the whole transect, with standard deviations, and b) for the hedgerow segments subdivided into hedgerow age classes (black diamonds = 50-99 years, white squares = 100-199 years, white triangles = > 200 years).

The cumulative number of species per transect increased with increasing hedgerow age (means: 50: 6.2, 100: 7.0, 200: 7.5; Table 1), but the differences between age classes were not significant. The mean number of species per segment also showed no clear differences between age classes. In contrast, the variation in segment species richness among transects decreased with increasing hedgerow age (Table 1). Hedgerows of age class 200 had significantly lower values than those of age classes 50 and 100 (Tukey tests).

Table 1: Mean cumulative number of species per transect and mean number of species per segment (with their standard deviations, SD) given separately for the three age classes of hedgerows. Species richness measures were tested for differences between age classes by One-way ANOVA; F-values are presented in the last row (in all cases total $dF = 129 [2, 127]$; n.s. - non-significant, *** - $p < 0.001$).

Age class	Mean cumulative number of species / transect \pm SD	Mean number of species / segment	SD mean number of species / segment
	<i>F-value</i>	<i>F-value</i>	<i>F-value</i>
50	6.2 \pm 2.40	1.6	1.34
100	7.0 \pm 2.15	1.8	1.25
200	7.5 \pm 0.94	1.8	0.91
<i>ANOVA</i>	1.45 n.s.	0.76 n.s.	23.08 ***

When further comparing the three hedgerow types, the change in the mean number of forest species per segment along the hedgerow followed different models (Fig. 3). While the age classes 50 and 100 were best fitted with a simple linear regression showing lines almost identical in slope and elevation, an exponential decay model gave the best fit for age class 200 (exponential decay - $R^2_{adj} = 0.851$, $p < 0.001$, compared to a linear model - $R^2_{adj} = 0.354$, $p = 0.039$). In the latter species number dropped fast within the first 50 m and then levelled off.

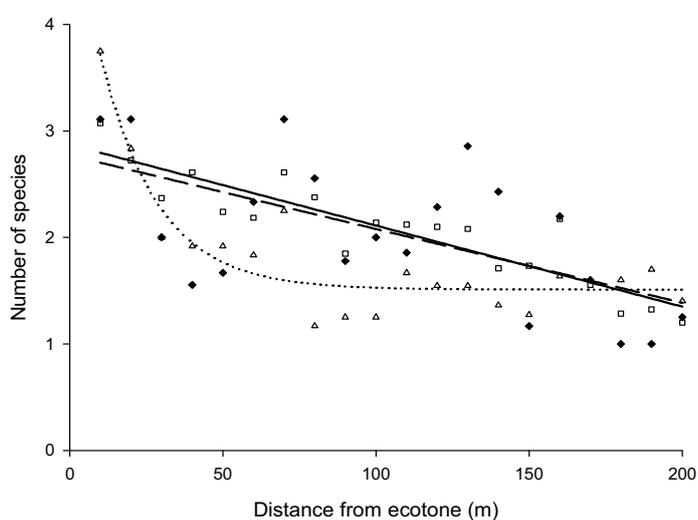


Figure 3: Relationship between the mean number of herbaceous forest species in hedgerow transects and distance from the forest-hedgerow ecotone, calculated separately for the three hedgerow age classes (50 [50-99 years] - black diamonds, solid line, $R^2_{adj} = 0.323$, $p = 0.005$; 100 [100-199 years] - white squares, dashed line, $R^2_{adj} = 0.801$, $p < 0.001$; 200 [older than 200 years] - white triangles, dotted line, $R^2_{adj} = 0.851$, $p < 0.001$; for all regressions $n = 20$).

The general decline in species richness away from the ecotone found for all transects and for the different age classes did not always reflect the behaviour of single species (Fig. 4). Most species showed a strong decline along the hedgerow transect (for example, *Milium effusum*, *Anemone nemorosa* and *Dryopteris carthusiana*), others only a moderate decline but with a high overall frequency (*Stellaria holostea* and *Geum urbanum*). Species such as *Epilobium montanum*, *Chaerophyllum temulum* and *Oxalis acetosella* did not systematically change in frequency along the transect, and another group included species with a highly irregular occurrence (*Polygonatum multiflorum*, *Stachys sylvatica* and *Alliaria petiolata*). Among the few forest species that increased in frequency with increasing distance from the ecotone were *Humulus lupulus* and *Pteridium aquilinum*.

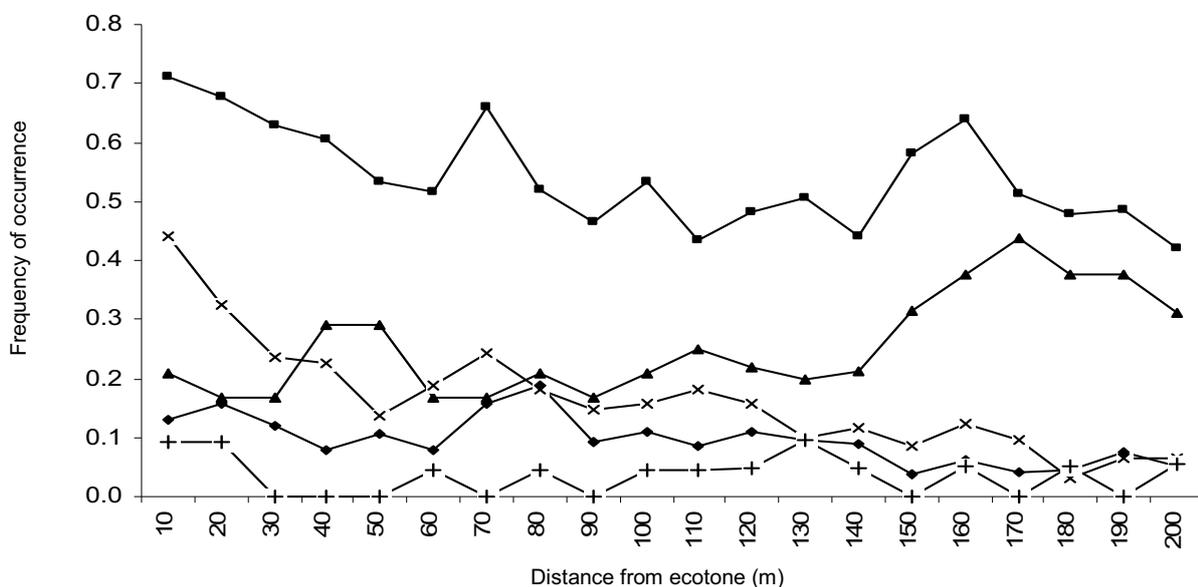


Figure 4: Patterns of change in the mean frequency of occurrence of some representative forest plant species along the hedgerow transects in which the species in question were found. *Stellaria holostea* (black squares, $n = 124$) highly frequent, showing a moderate decline with increasing distance from the forest edge; *Milium effusum* (crosses, $n = 111$) with a strong decline; *Pteridium aquilinum* (black triangles, $n = 24$) with a moderate increase; *Circaea lutetiana* (black diamonds, $n = 76$) with no systematic change in frequency; and *Adoxa moschatellina* (plus symbols, $n = 22$) with irregular occurrence.

The environmental conditions partly differed between forests and hedgerows and changed along the hedgerows (Fig. 5). Soil water content decreased significantly from the forest into the hedgerow (forest vs 30 m: $t = 2.96$, $p = 0.008$; 30 m vs 60 m segments: $t = 3.55$, $p = 0.001$), whereas P and K concentrations increased with increasing distance to the ecotone (30 m vs 90 m: $t = -2.64$, $p = 0.025$ and $t = -2.49$, $p = 0.032$, respectively). Relative light intensity

was higher in hedgerow segments (forest vs 30 m: $t = -4.30$, $p < 0.001$). Soil pH tended to be lower and the C/N ratio higher in forests compared to the hedgerow. For other soil variables, no systematic differences between forests and hedgerows were found.

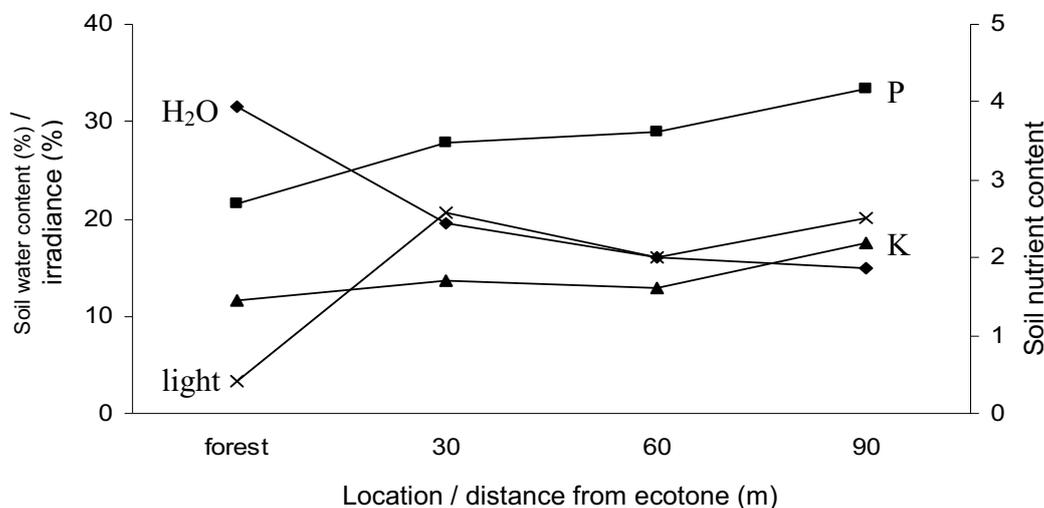


Figure 5: Changes in environmental conditions across forest-hedgerow transects, measured in the forest ($n = 20$) and along the adjacent hedgerow at 30 m ($n = 38$), 60 m ($n = 28$) and 90 m ($n = 11$) distance from the forest edge. Variables shown are soil water content in % (diamonds), phosphate (squares) and potassium (triangles) contents both expressed in mg / 100 g dry soil, and relative light availability in % (crosses).

The modelled frequencies of occurrence of the most common species were also affected by the species' habitat requirements (Table 2). In all segments except those close to the ecotone, species frequency was positively related to the indicator value for light, i.e., species with higher shade requirements or tolerance were less common in the hedgerows. The importance of light is also reflected in Table 3 showing that the number of forest species was significantly positively related to canopy cover (but negatively to the cover of the shrub layer). In the hedgerow segments 10-30 m away from the ecotone, species frequency decreased with an increasing indicator value for temperature. There was no relationship between the frequencies of species and their corresponding indicator values for soil moisture, pH and nitrogen. Plant height was found to be important only at larger distances from the ecotone, being positively related to species frequency. Multiple regressions revealed significant negative influences of distance from the ecotone and cover of shrub layer ($R^2_{adj} = 0.564$, $p < 0.001$) on the number of forest species, whereas cover of tree layer and hedgerow age did not remain as significant in the final model. Multiple stepwise regressions confirmed these relations - only cover of shrub layer and distance remained as significant in the model ($R^2_{adj} = 0.574$, $p < 0.001$). No interaction term was found to be significantly important for the number of forest species.

Table 2: Relationship between the observed frequencies of occurrence of the 20 most common forest species found in the hedgerow transects and their ecological / life-history traits (*Stellaria holostea* excluded from the analysis, see methods). All tests were carried out separately for each transect segment. Traits included Ellenberg indicator values for light (L), temperature (T), soil moisture (M), pH (R) and nitrogen (N), mean plant height (all analyzed with Spearman rank correlation) and dispersal type (anemochory, epizoochory, endozoochory, myrmecochory and autochory, analyzed with One-way ANOVA). Spearman rank correlation coefficients and F-Values (dispersal type) are given. Indicator values were derived from Ellenberg et al. (1992), all other data obtained at <http://floraweb.de/> (last access on 20 June 2008). n.s. – non-significant, + - $p < 0.100$, * - $p < 0.05$, ** - $p < 0.01$.

Distance from ecotone (m)	L	T	M	R	N	Plant height	Dispersal type
10	0.093 n.s.	-0.669 *	-0.400 n.s.	0.080 n.s.	0.015 n.s.	0.073 n.s.	1.100 n.s.
20	0.545 *	-0.660 *	-0.349 n.s.	0.082 n.s.	0.149 n.s.	0.070 n.s.	1.451 n.s.
30	0.499 *	-0.423 n.s.	-0.357 n.s.	-0.216 n.s.	0.063 n.s.	0.363 n.s.	3.262 *
40	0.524 *	-0.351 n.s.	-0.366 n.s.	-0.229 n.s.	0.148 n.s.	0.400 n.s.	4.116 *
50	0.569 *	-0.320 n.s.	-0.250 n.s.	-0.272 n.s.	0.073 n.s.	0.337 n.s.	3.645 *
100	0.533 *	-0.265 n.s.	-0.075 n.s.	-0.115 n.s.	0.155 n.s.	0.595 **	2.452 +
150	0.501 *	-0.274 n.s.	-0.126 n.s.	0.244 n.s.	0.411 n.s.	0.561 *	3.030 *
200	0.492 *	-0.260 n.s.	-0.010 n.s.	0.018 n.s.	0.249 n.s.	0.588 **	0.882 n.s.

Species with an epizoochorous and anemochorous dispersal were more common than species showing myrmecochory and especially autochory and endozoochory (Table 2, Fig. 6).

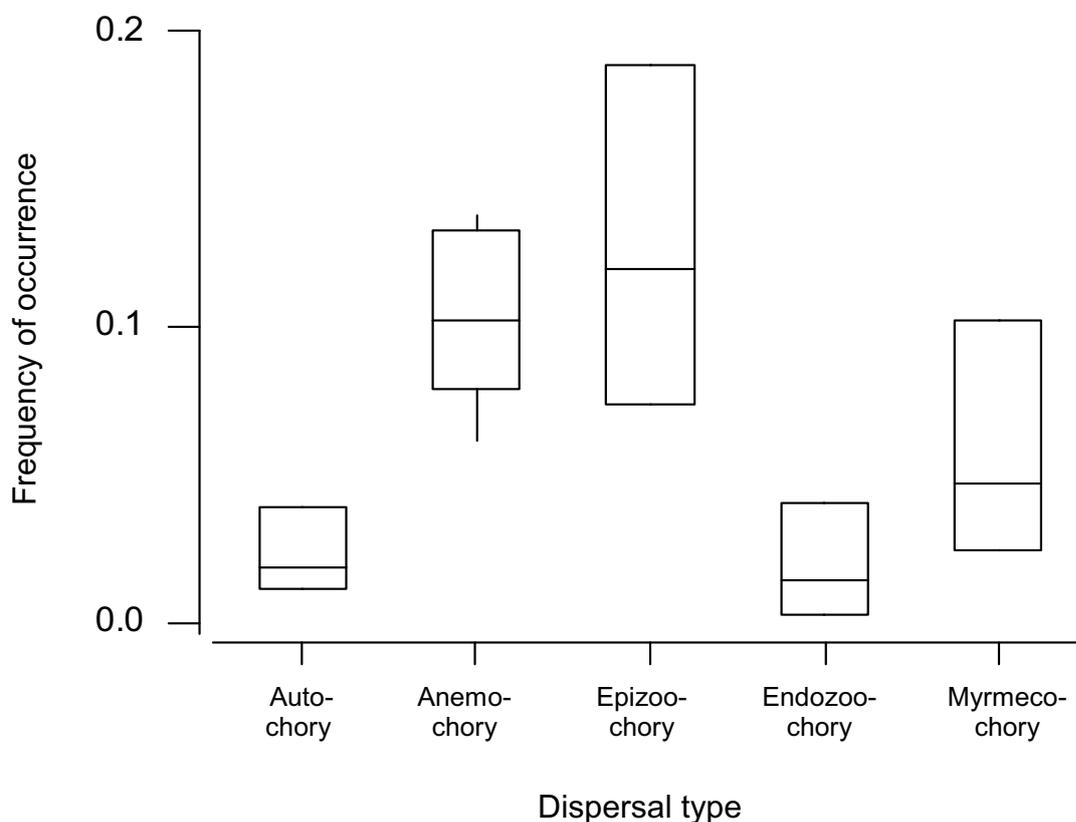


Figure 6: Boxplots of the frequency of occurrence of the twenty most frequent forest species found in the transects (*Stellaria holostea* and *Humulus lupulus* were excluded from the analysis, because the former was present in almost all transect segments, whereas populations of the latter may often originate from plantations. To increase the number of endozoochorous species *Adoxa moschatellina* and *Maianthemum bifolium* were added to the analysis), sub-divided into dispersal types. Autochory ($n = 4$, self-dispersal), anemochory ($n = 6$, dispersal by wind), epizoochory ($n = 3$, dispersal by animals, diaspores attached to their surface), endozoochory ($n = 3$, dispersal by animals, diaspores ingested), myrmecochory ($n = 4$, dispersal by ants).

The number of forest species in the hedgerow segments (except those most distant from the ecotone) was positively related to the species richness in the nearby forest (Table 3).

Table 3: Correlation between the number of herbaceous forest species in different hedgerow transect segments and the mean cover of tree and shrub layer, the number of herbaceous forest species in the neighbouring forest, and hedgerow age (Pearson correlation). *n.s.* – non-significant, + - $p < 0.100$, * - $p < 0.05$, ** - $p < 0.01$, *** - $p < 0.001$.

Distance from ecotone (m)	Mean cover of tree layer (%)	Mean cover of shrub layer (%)	No. of species in nearby forest	Age of hedgerow
10	0.209 *	-0.348 ***	0.236 **	0.163 +
20	0.275 **	-0.281 **	0.228 **	0.036 <i>n.s.</i>
30	0.256 **	-0.233 **	0.187 *	-0.012 <i>n.s.</i>
40	0.298 ***	-0.239 **	0.182 *	0.048 <i>n.s.</i>
50	0.263 **	-0.187 *	0.253 **	0.081 <i>n.s.</i>
100	0.188 *	-0.224 *	0.232 **	-0.009 <i>n.s.</i>
150	0.141 <i>n.s.</i>	-0.043 <i>n.s.</i>	0.160 <i>n.s.</i>	-0.013 <i>n.s.</i>
200	0.185 <i>n.s.</i>	-0.199 <i>n.s.</i>	-0.062 <i>n.s.</i>	0.085 <i>n.s.</i>

DISCUSSION

The hedgerows contained 77% of all forest species observed in the matrix of neighbouring woodlands. This proportion is comparable to findings from the USA, where about 70% of all forest species were able to colonise hedgerows of the same region (Corbit *et al.*, 1999). In contrast to previous results from Western Europe (Baudry, 1988), the hedgerows in our study region were not dominated by forest edge species but by plants of the interior (ca. 75%). Furthermore, whereas in a Belgian study hedgerows were colonised almost exclusively by common, highly competitive species (Endels *et al.*, 2004), we also found some species considered as endangered in the region.

There is a wide agreement about the corridor function of hedgerows, supported by the continuous decline in the number of forest species in hedgerows (sink) with increasing distance to the forest (source) as found in our study and in studies from other regions, including USA (Corbit *et al.*, 1999), Canada (Roy & de Blois, 2008), Italy (Sitzia, 2007), France (Burel & Baudry, 1990) and Belgium (Verheyen *et al.*, 2003a). The correlation between species richness and distance to the forest ecotone was observed in all hedgerow age

classes. However, this must not necessarily indicate a true corridor function in terms of a continuous immigration of forest plants from the forest. The measurements showed that, compared to hedgerows, forests had wetter soils, lower light availability and lower concentrations of soil nutrients. Hedgerow segments close to the ecotone were more forest-like in their environment than segments farther away from the ecotone. In the latter, relatively nutrient-rich soils may favour the growth of highly competitive non-forest species at the expense of forest species. Thus, even in the absence of colonization events starting from the woodland, forest species richness is expected to be higher closer to the ecotone. On the other hand, the positive effect of species richness in the nearby forest on the number of species in segments along the first 100 m of the transects supports the notion that woodlands act as a source for forest plants in hedgerows.

Across all hedgerows, cumulative and average species numbers tended to be higher in older (100 and 200 years) than younger hedgerows (50 years), but the results of the ANOVAs were not significant. This pattern was found to be more pronounced in studies from Ireland (Hegarty *et al.*, 1994) and Belgium (Deckers *et al.*, 2005) where the highest number of forest plants was observed in hedgerows older than about 200 years. In a study from Great Britain forest plants were restricted either to very old hedgerows (> 250 yrs) or to hedges that were relics of ancient woodland (Pollard *et al.*, 1974). In contrast, no relationship between the number of forest species and hedgerow age was found in an American study (Corbit *et al.*, 1999). These differences in the importance of hedgerow age may indicate that colonisation processes differ in their speed between regions with different climate, hedgerow management and species pools.

A closer look at the change in frequency along the hedgerow of single species allows to distinguish different response patterns (Fig. 4), in line with other recent studies of herbaceous forest plants (Brunet & von Oheimb, 1998b; Verheyen *et al.*, 2003a). Species showing a *strong* or *moderately strong decline* away from the forest edge are assumed to depend more or less on true forest habitat conditions. *No systematic change* applies to species lacking clear preference for either forests or hedgerows. An *irregular occurrence* may indicate irregular colonization and extinction events of single individuals (Brunet & von Oheimb, 1998b), and *moderate increase* away from the forest edge points at species that prefer hedgerows for forests. These contrasting distribution patterns may reflect different functional groups within the cluster of forest plant species (see also Deckers *et al.*, 2004).

Despite the idiosyncratic behaviour of species there are some response patterns with regard to environmental variables and life history traits that increase the likelihood of occurrence in hedgerows. Soil water content was significantly lower in hedgerows than in forests, and decreased with increasing distance from the forest edge. Lower water availability is known to reduce reproduction in at least some forest species (Wehling & Diekmann, 2009). In the actual study, however, no relationship between Ellenberg values for soil moisture and the frequency of occurrence of forest species was found, whereas soil water content differed significantly between segments. It is possible that the differences in measured values were too small to affect the occurrence of forest species in the hedgerows. Light availability is known to influence the colonisation capacity of woodland plants (Dzwonko & Gawronski, 1994). Our results clearly showed that hedgerows with a dense tree canopy and a sparse shrub layer contain more forest species than hedgerows with a more open tree but denser shrub layer. This is in agreement with findings from hedgerows in Canada (Boutin *et al.*, 2002) and forests in Sweden (Brunet & von Oheimb, 1998a). It was hypothesized that a dense shrub layer suppresses herbaceous species by strongly competing for root space and light (Gould & Gorchoy, 2000). On the other hand, hedgerows are still lighter than forests (Fig. 5, see also Wehling & Diekmann, 2008) and therefore favour the occurrence of more light-demanding (or less shade-tolerant) forest species (Table 2).

Herbaceous forest plants are known to have a low fecundity, often possessing heavy seeds and lacking dispersal vectors (Verheyen *et al.*, 2003b). Therefore colonisation by these species is affected by seed limitation (Verheyen & Hermy, 2004) and seed dispersal mode (Dzwonko & Gawronski, 1994; Matlack, 1994; Brunet & von Oheimb, 1998b; Matlack, 2005), and often depends on stochastic events (Cain *et al.*, 1998). Evidence for the importance of dispersal strategy in forest plants was given in a study of Canadian hedgerows (Roy & de Blois, 2006). Our own results showed a predominance of species with epizoochory and anemochory, consistent with observations made by Matlack (1994), Grashof-Bokdam & Geertsema (1998), Whitney & Foster (1998) and Takahashi & Kamitani (2004). Ant-dispersed species also reached relatively high frequencies, in contrast to several other studies (Corbit *et al.*, 1999; Roy & de Blois, 2006) that have reported on a low dispersal ability of myrmecorous species. Surprisingly, species with endozoochory showed a low frequency in hedgerows, which is difficult to explain, but may be caused by a lack of vector animals in this highly managed agricultural landscape. The positive effect of animals on plants in conservation corridors in terms of higher reproductive output and better dispersal was shown by Tewksbury *et al.* (2002).

CONCLUSIONS

More than three quarter of all forest plant species present in the survey area were found in hedgerows, among these several endangered taxa. This shows that hedgerows generally may serve as a habitat for forest plants, especially in vicinity to the forest edge where colonization from the forest is more likely and environmental conditions are more favourable for forest specialists. However, not all species are obviously capable of growing in hedgerows. The comparison of our own results with those from the literature reveals few general patterns and does not allow far-reaching predictions about incidence probabilities, probably due to a strong regional variation in the pool of forest species and in the environment of both forests and hedgerows. We may, however, conclude that species with certain habitat requirements and life history attributes have a somewhat higher probability of occurrence in hedgerows than others: these 'favourable' characteristics include the ability to successfully compete outside the forest shade, and the adaptation to wind and partly animal dispersal. At the same time, some hedgerows, or parts of hedgerows, are more likely to be colonized by forest plants than others. To conclude, in an agricultural landscape with low forest cover, hedgerows add to the available habitat of many forest plant species and may even contribute to their survival and dispersal.

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REFERENCES

- Bailey, S.-A., 2007. Increasing connectivity in fragmented landscapes: An investigation of evidence for biodiversity gain in woodlands. *Forest Ecology and Management* 238, 7-23.
- Baudry, J., 1988. Hedgerows and hedgerow networks as wildlife habitats in agricultural landscapes. In: Park, J. R. (ed). *Environmental management in agriculture - European perspectives*. Belhaven Press, London, UK, 111-124.
- Beier, P., Noss, R. F., 1998. Do habitat corridors provide connectivity? *Conservation Biology* 12, 1241-1252.

- Bierzychudek, P., 1982. Life history and demography of shade-tolerant temperate forest herbs: a review. *New Phytologist* 90, 757-776.
- Boutin, C., Jobin, B., Bélanger, L., Choinière, L., 2002. Plant diversity in three types of hedgerows adjacent to cropfields. *Biodiversity and Conservation* 11, 1-25.
- Brunet, J., von Oheimb, G., 1998a. Colonization of secondary woodlands by *Anemone nemorosa*. *Nordic Journal of Botany* 18, 369-377.
- Brunet, J., von Oheimb, G., 1998b. Migration of vascular plants to secondary woodlands in southern Sweden. *Journal of Ecology* 86, 429-438.
- Burel, F., 1996. Hedgerows and their role in agricultural landscapes. *Critical Reviews in Plant Sciences* 15, 169-190.
- Burel, F., Baudry, J., 1990. Hedgerow networks as habitats for forest species: implications for colonising abandoned agricultural land. In: Bunce, R. G. H., Howard, D. C. (eds). *Species dispersal in agricultural habitats*. Belhaven Press, London, UK, 238-255.
- Cain, M. L., Damman, H., Muir, A., 1998. Seed dispersal and the holocene migration of woodland herbs. *Ecological Monographs* 68, 325-347.
- Corbit, M., Marks, P. L., Gardescu, S., 1999. Hedgerows as habitat corridors for forest herbs in central New York, USA. *Journal of Ecology* 87, 220-232.
- Dawson, D., 1994. Are habitat corridors conduits for animals and plants in a fragmented landscape? A review of the scientific evidence. *English Nature Research Report* 94, 1-89.
- de Blois, S., Domon, G., Bouchard, A., 2002. Factors affecting plant distribution in hedgerows of southern Quebec. *Biological Conservation* 105, 355-367.
- Deckers, B., De Becker, P., Honnay, O., Hermy, M., Muys, B., 2005. Sunken roads as habitats for forest plant species in a dynamic agricultural landscape: effects of age and isolation. *Journal of Biogeography* 32, 99-109.
- Deckers, B., Verheyen, K., Hermy, M., Muys, B., 2004. Differential environmental response of plant functional types in hedgerow habitats. *Basic and Applied Ecology* 5, 551-566.
- Dzwonko, Z., Gawronski, S., 1994. The role of woodland fragments, soil types, and dominant species in secondary succession on the western Carpathian foothills. *Vegetatio* 111, 149-160.
- Dzwonko, Z., Loster, S., 1989. Distribution of vascular plant species in small woodlands on the western Carpathian foothills. *Oikos* 56, 77-86.
- Ellenberg, H., Weber, H. E., Düll, R., Wirth, V., Werner, W., Paulißen, D., 1992. Zeigerwerte von Pflanzen in Mitteleuropa. *Scripta Geobotanica* 18, 1-258.

- Endels, P., Adriaens, D., Verheyen, K., Hermy, M., 2004. Population structure and adult plant performance of forest herbs in three contrasting habitats. *Ecography* 27, 225-241.
- Freemark, K. E., Boutin, C., Keddy, C. J., 2002. Importance of farmland habitats for conservation of plant species. *Conservation Biology* 16, 399-412.
- French, D. D., Cummins, R. P., 2001. Classification, composition, richness and diversity of British hedgerows. *Applied Vegetation Science* 4, 213-228.
- Fritz, R., Merriam, G., 1993. Fencerow habitats for plants moving between farmland forests. *Biological Conservation* 64, 141-148.
- Fritz, R., Merriam, G., 1996. Fencerow and forest edge architecture in eastern Ontario farmland. *Agriculture, Ecosystems and Environment* 59, 159-170.
- Garve, E., 2004. Rote Liste und Florenliste der Farn- und Blütenpflanzen in Niedersachsen und Bremen. *Informationsdienst Naturschutz Niedersachsen* 24, 1-76.
- Gould, A. M. A., Gorchov, D. L., 2000. Effects of the exotic invasive shrub *Lonicera maackii* on the survival and fecundity of three species of native annuals. *American Midland Naturalist* 144, 36-50.
- Grashof-Bokdam, A., 1997. Forest species in an agricultural landscape in the Netherlands: Effects of habitat fragmentation. *Journal of Vegetation Science* 8, 21-28.
- Grashof-Bokdam, A., Geertsema, W., 1998. The effect of isolation and history on colonization patterns of plant species in secondary woodland. *Journal of Biogeography* 25, 837-846.
- Hegarty, C. A., McAdam, J. H., Cooper, A., 1994. Factors influencing the plant species composition of hedges - implications for management in environmentally sensitive areas. *British Crop Protection Council Monographs* 58, 227-234.
- Helliwell, D. R., 1975. The distribution of woodland plant species in some Shropshire hedgerows. *Biological Conservation* 7, 61-72.
- Hermy, M., Honnay, O., Firbank, L., Grashof-Bokdam, C., Lawesson, J. E., 1999. An ecological comparison between ancient and other forest plant species of Europe, and the implications for forest conservation. *Biological Conservation* 91, 9-22.
- Hess, G. R., 1994. Conservation corridors and contagious disease: a cautionary note. *Conservation Biology* 8, 256-262.
- Honnay, O., Hermy, M., Coppin, P., 1999. Effects of area, age and diversity of forest patches in Belgium on plant species richness, and implications for conservation and reforestation. *Biological Conservation* 87, 73-84.
- Hooper, M. D., 1970. Hedges and history. *New Scientist* 31, 598-600.

- Jacquemyn, H., Butaye, J., Hermy, M., 2003. Influence of environmental and spatial variables on regional distribution of forest plant species in a fragmented and changing landscape. *Ecography* 26, 768-776.
- Matlack, G. R., 1994. Plant species migration in a mixed-history forest landscape in Eastern North America. *Ecology* 75, 1491-1502.
- Matlack, G. R., 2005. Slow plants in a fast forest: local dispersal as a predictor of species frequencies in a dynamic landscape. *Journal of Ecology* 93, 50-59.
- McCollin, D., Jackson, J. I., Bunce, R. G. H., Barr, C. J., Stuart, R., 2000. Hedgerows as habitat for woodland plants. *Journal of Environmental Management* 60, 77-90.
- Noss, R. F., 1987. Corridors in real landscapes: A reply to Simberloff and Cox. *Conservation Biology* 1, 159-164.
- Peterken, G. F., Game, M., 1984. Historical factors affecting the number and distribution of vascular plant species in the woodlands of central Lincolnshire. *Journal of Ecology* 72, 155-182.
- Pollard, E., Hooper, M. D., Moore, N. W., 1974. *Hedges*. William Collins Sons & Co Ltd, London, UK.
- Roy, V., de Blois, S., 2006. Using functional traits to assess the role of hedgerow corridors as environmental filters for forest herbs. *Biological Conservation* 130, 592-603.
- Roy, V., de Blois, S., 2008. Evaluating hedgerow corridors for the conservation of native forest herb diversity. *Biological Conservation* 141, 298-307.
- Schmidt, M., von Oheimb, G., Kriebitzsch, W.-U., Ellenberg, H., 2002. Liste der im norddeutschen Tiefland typischen Waldgefäßpflanzen. *Mitteilungen der Bundesforschungsanstalt für Forst- und Holzwirtschaft* 206, 1-37.
- Simberloff, D., Cox, J., 1987. Consequences and costs of conservation corridors. *Conservation Biology* 1, 63-71.
- Simberloff, D., Farr, J. A., Cox, J., Mehlman, D. W., 1992. Movement corridors: conservation bargains or poor investments? *Conservation Biology* 6, 493-504.
- Sitzia, T., 2007. Hedgerows as corridors for woodland plants: a test on the Po Plain, northern Italy. *Plant Ecology* 188, 235-252.
- Smart, S. M., Bunce, R. G. H., Stuart, R. C., 2001. An assessment of the potential of British hedges to act as corridors and refuges for Ancient Woodland Indicator plants. In: Barr, C. J., Petit, S. (eds). *Hedgerows of the world: their ecological functions in different landscapes*. IALE, Birmingham, UK, 137-146.

- Takahashi, K., Kamitani, T., 2004. Effect of dispersal capacity on forest plant migration at a landscape level. *Journal of Ecology* 92, 778-785.
- Tewksbury, J. J., Levey, D. J., Haddad, N. M., Sargent, S., Orrock, J. L., Weldon, A., Danielson, B. J., Brinkerhoff, J., Damschen, E. I., Townsend, P., 2002. Corridors affect plants, animals, and their interactions in fragmented landscapes. *PNAS* 99, 12923-12926.
- Van Calster, H., Vandenberghe, R., Ruysen, M., Verheyen, K., Hermy, M., Decocq, G., 2008. Unexpectedly high 20th century floristic losses in a rural landscape in northern France. *Journal of Ecology* 96, 927-936.
- Vellend, M., Verheyen, K., Jacquemyn, H., Kolb, A., van Calster, H., Peterken, G., Hermy, M., 2006. Extinction debt of forest plants persists for more than a century following habitat fragmentation. *Ecology* 87, 542-548.
- Verheyen, K., Guntenspergen, G. R., Biesbrouck, B., Hermy, M., 2003a. An integrated analysis of the effects of past land use on forest herb colonization at the landscape level. *Journal of Ecology* 91, 731-742.
- Verheyen, K., Hermy, M., 2004. Recruitment and growth of herb-layer species with different colonizing capacities in ancient and recent forests. *Journal of Vegetation Science* 15, 125-134.
- Verheyen, K., Honnay, O., Motzkin, G., Hermy, M., Foster, D. R., 2003b. Response of forest plant species to land-use change: a life-history trait-based approach. *Journal of Ecology* 91, 563-577.
- Verkaar, H. J., 1990. Corridors as a tool for plant species conservation? In: Bunce, R. G. H., Howard, D. C. (eds). *Species dispersal in agricultural habitats*. Belhaven Press, London, UK, 82-97.
- Wehling, S., Diekmann, M., 2008. Factors influencing the spatial distribution of forest plant species in hedgerows of North-western Germany. *Biodiversity and Conservation* 17, 2799-2813.
- Wehling, S., Diekmann, M., 2009. Hedgerows as an environment for forest plants: a comparative case study of five species. *Plant Ecology* 204, 11-20.
- Whitney, G. G., Foster, D. R., 1998. Overstorey composition and age as determinants of the understorey flora of woods of central New England. *Journal of Ecology* 76, 867-876.
- Wisskirchen, R., Haeupler, H., 1998. *Standardliste der Farn- und Blütenpflanzen Deutschlands*. Ulmer, Stuttgart, Germany.

Chapter 6

Forest herbs in European hedgerows: prediction of changes in the species composition of different hedgerow networks along a climate gradient

Wehling, S. & Diekmann, M., submitted.



Left: Two hedgerows on both sides of a lane with closed tree layer, indicating forest-like microclimate. **Right:** Hedgerow under intense grazing without herb- and shrub-layer (front part) and without grazing with well developed shrub-layer (back part). (Photographs taken by Stephan Wehling).

ABSTRACT

Many herbaceous forest plant species are endangered and suffer from habitat loss and fragmentation, especially in agricultural landscapes. Here, hedgerow networks represent a forested habitat that may serve as a refuge for woodland species, even though also hedges have recently been strongly reduced in number and size. It is, however, still disputed to which extent hedgerows are suitable for forest herbs and which environmental factors are affecting the frequency of the plants in the hedgerows.

To prevent the loss of further hedgerows, the development of an instrument for the assessment of forest herb occurrence in hedgerows across Europe would be helpful. Therefore a set of ecological and life history variables, reported to have some effect on the occurrence of woodland species, was tested for its combined impact on the frequency of forest plants in hedgerows. In addition, we examined the regional differences in environmental conditions of hedgerows by studying the species composition along a climate gradient throughout Europe.

Contrary to our expectation the chosen set of variables had a weaker multiple relationship to the frequency of forest herbs than the single variable light availability. It is likely that the regional differences in the pool of forest species have an overriding effect on the species composition of the tested hedgerows. Also climatic factors may explain parts of the regional differences, as areas with higher continentality had species compositions, which showed a lower proportion of chamaephytes and wintergreen plants and were indicating drier and less acid soils. Finally, also landscape history, management and agricultural practices contribute to explaining the region-specific set-up of forest herbs in hedgerows.

KEYWORDS: conservation; forest fragmentation; hedgerow history; agricultural landscapes; regional forest species pool.

INTRODUCTION

The loss of biodiversity in intensively managed agricultural landscapes is one of the major challenges in nature conservation (Vitousek *et al.*, 1997; van Calster *et al.*, 2008). During the last centuries the increasing human population required large areas of natural habitats for cultivation, especially in Western Europe where today more than 50% of the land surface can be classified as agricultural (Rounsevell *et al.*, 2003). One of the natural habitats affected most by human activities is woodland (Ellenberg, 1996), which has been drastically reduced in extension. In many regions, remnants are few and highly fragmented, and as a consequence

several forest species have become threatened or even gone extinct (Bailey, 2007). Herbaceous forest plant species, mostly lacking long-distance dispersal, are not able to respond quickly to habitat loss and fragmentation (Hermy *et al.*, 1999), which makes them particularly susceptible to these processes (Dzwonko & Loster, 1989), the more so under the ongoing climate change (Honnay *et al.*, 2002).

In various agricultural landscapes throughout the world hedgerows significantly contribute to the area of wooded land (Pollard *et al.*, 1974; Forman, 1995; Cunningham, 2000; Tang Ya *et al.*, 2003; Zuria & Gates, 2006). They serve as a refuge for numerous forest species that have once been widespread in the near-natural forest landscape, but have now largely vanished from agricultural areas (French & Cummins, 2001; Stoate *et al.*, 2001; Freemark *et al.*, 2002). In general, hedgerows are defined as linear semi-natural habitats containing narrow strips of woody vegetation and its associated organisms, and they are usually subject to human management (Baudry *et al.*, 2000). There are three types of hedgerow origin: planted, spontaneous, and remnant. Planted hedgerows are usually dominated by a single or few species and can mainly be found in European countries. Hedgerows of spontaneous origin grow along uncultivated field margins or fences (therefore often referred to as fencerows), with the trees and shrubs deriving from seeds dispersed by wind and animals, and are often found in North America. Remnant hedgerows result from forest clearings due to land reclamation and are often characterised by high species diversity (Forman, 1995).

In Europe, hedgerows are an important part of the landscape history. It is known from Great Britain and Germany that, during pre-Roman and medieval times, hedges with their thorny shrubs were used for the purpose of defence (Weber, 2003; Barnes & Williamson, 2006). With the beginning of the 17th century, a change in agricultural policy took place, resulting in the transformation of commonly used fields to parcels with private ownership, and leading to the plantation of hedgerows all over Europe to delimit ownership or to enclose livestock. The climax in hedgerow planting was reached at different times in different regions: in Germany and Denmark at about 1770 (Weber, 2003), in Britain at 1800 (Burel, 1996) and in Belgium at 1850 (Deckers *et al.*, 2005b). Also hedgerow structure and species composition differed between regions. British hedges, for example, were mainly planted with *Crataegus* sp. and those in Ireland and Brittany predominantly with *Ulex europaeus* (Baudry *et al.*, 2000), whereas, in German hedgerows, a mixture of *Corylus avellana* and *Crataegus* sp. was preferred (Weber, 2003). Apart from these differences in selected seed stock (due to regional differences in habitat requirements and species pools), the hedgerow networks were influenced by cultural (management, agricultural practices), edaphic (soil nutrient content),

and climatic factors (wind, rainfall) (Burel, 1996; Baudry *et al.*, 2000; Weber, 2003; Barnes & Williamson, 2006). From World War II up to now, however, there has been an enormous decline in the number of hedgerows as a result of agricultural intensification and mechanisation (Macdonald & Johnson, 2000; Le Cœur *et al.*, 2002), and the loss of hedgerow habitat was documented in many countries, for example in Britain (Barr & Gillespie, 2000; Petit *et al.*, 2003), France (Burel & Baudry, 1995), Germany (Reif *et al.*, 1982), Denmark (Agger & Brandt, 1988), and Belgium (Deckers *et al.*, 2005b).

The regional differences in hedgerow history and structure form the background for the ongoing debate about the potential of hedgerows to act as a habitat and conservation corridor for forest species. Some studies deny the habitat function of hedgerows because of the recorded low numbers of forest species (Helliwell, 1975; French & Cummins, 2001; Smart *et al.*, 2001), whereas others give support for the suitability of hedgerows for these species (Pollard *et al.*, 1974; Sitzia, 2007). In an intermediate view it is stressed that hedgerows may serve as a suitable habitat only for a sub-set of forest herbs (McCollin *et al.*, 2000; Deckers *et al.*, 2005a; Wehling & Diekmann, 2008). Also the corridor function of hedgerows for forest plants is perceived differently (Helliwell, 1975; Corbit *et al.*, 1999; Bailey, 2007). It seems that the multitude of factors influencing the structure and ecological conditions of hedgerows render generalizations difficult (*e.g.*, Le Cœur *et al.*, 1997; Deckers *et al.*, 2004a).

Up to present, models explaining the occurrence of forest plants in hedgerows have worked well only on a limited regional scale (Chincarini & Padoa-Schioppa, 2001). The potential of different hedgerow network landscapes for woodland species conservation on a European scale has still to be evaluated, especially to prevent further habitat loss. In this framework the aims of this study were: 1) to examine the suitability of a set of ecological and life-history variables to predict the occurrence of forest herbs in hedgerow networks throughout Europe, and 2) to reveal the differences in environmental conditions and species composition in hedgerows along a climate gradient across Europe to enable a better and region-specific prediction of forest plant occurrence.

METHODS

Data collection

A list of forest species was derived from several vegetation surveys in hedgerow networks in the vicinity of Bremen, northern Germany (S. Wehling, unpublished data). For each species we calculated its frequency as the proportion of the surveyed hedges in which the species was

To reveal the changes in species composition in different hedgerow networks along a climate gradient we searched literature databases, e.g., the ISI Web of Knowledge and BIOSIS, for papers relating to plants in hedgerows or linear wooded habitats. The extracted studies were then screened for detailed information on plant species occurrence and frequency. For our analysis we only considered European studies of hedgerows including at least ten forest species characteristic for the specific region. The processed 13 studies were from Belgium, France, Germany, Italy and the United Kingdom (Table 2).

Each species list was filtered separately for species fulfilling the definition of forest species of the specific region. In general, the term forest species was defined as: ‘*a species that is predominantly or only found in forests capable of tolerating the typical habitat conditions in these forests*’. This definition largely follows the classifications of forest species from Germany (Schmidt *et al.*, 2002), Belgium (Tack *et al.*, 1993) and Great Britain (Peterken, 1974). For the final assignment lists of forest species were compiled for the lowlands of northern Germany (Schmidt *et al.*, 2002), for Great Britain (McCollin *et al.*, 2000) and for Belgium (Honnay *et al.*, 1999). The species list from Italy contained only forest species of the region (Sitzia, 2007). For the classification of French species data we used general knowledge of species behaviour in relation to shade, supplemented by a list of European ancient woodland indicator species (Hermy *et al.*, 1999).

To detect region-specific differences in ecological and life history trait combinations we compiled a set of variables for each forest species, containing Ellenberg values for light intensity (L), temperature (T), continentality (C), soil moisture (M), pH (R) and soil nitrogen (N), data on life form (classified as geophyte, hemicryptophyte, chamaephyte, therophyte and other types [nanophanerophyte and woody chamaephyte]) and leaf persistence (classified as vernal, summergreen, wintergreen, evergreen) derived from literature (Ellenberg *et al.*, 1992). Information on the dispersal type (classified as anemochory, epizoochory, endozoochory, myrmecochory and other types [autochory, barochory and hydrochory]) and on life span / clonality (perennial, annual/biennial; clonal, intermediate clonal, non clonal) was obtained from the database FLORAWEB (<http://www.floraweb.de/>, [24 March 2009]).

Table 2: Summary of studies satisfying the pre-conditions for being included in the analysis of the relationship between climatic continentality and species composition. In addition, Conrad's continentality index for each study included in the analysis is presented.

Country	Code	Region	Conrad's index	Studied plant species group	No. of forest species	Mean hedgerow width (in m)	Matrix	Reference
United Kingdom	1	across Britain	8.98	forest	88	-	mixed	McCollin <i>et al.</i> , 2000
Belgium	2	Flanders	15.10	forest	84	-	arable/meadow	Deckers <i>et al.</i> , 2005a
Germany	3	Lower Saxony	16.49	forest	43	4.0	pasture	unpublished
United Kingdom	4	across Britain	8.98	all	38	-	mixed	Smart <i>et al.</i> , 2001
France	5	Brittany	12.24	all	36	~3.0	arable/meadow	Le Cœur <i>et al.</i> , 1997
Belgium	6	Flanders	15.91	all	27	7.5	arable/meadow	Deckers <i>et al.</i> , 2004a
United Kingdom	7	Shropshire	9.89	all	27	3.2	road	Helliwell, 1975
Belgium	8	Flanders	15.91	all	26	7.5	arable/meadow	Deckers <i>et al.</i> , 2004b
United Kingdom	9	across Britain	8.98	all	23	-	mixed	Andrews <i>et al.</i> , 1999
Italy	10	Po Plain	28.14	forest	19	9.5	arable	Sitzia, 2007
United Kingdom	11	Durham	9.25	all	16	1.8	grassland	Cherrill <i>et al.</i> , 2001
United Kingdom	12	Yorkshire	6.91	all	13	-	arable	Sparks <i>et al.</i> , 2000
United Kingdom	13	across Britain	8.98	all	12	-	mixed	Cummins & French, 1994

Data analysis

To verify the relevance of our selected set of variables for explaining the occurrence of forest species in hedgerows we conducted a Principal Component Analysis (PCA) with the matrix of ranked species traits and Ellenberg indicator values. Then the relationship between the resulting PCA scores and the frequency or relative frequency of occurrence of forest species in the studied hedgerow networks was tested, using Spearman's rank correlation. We also correlated the frequency of occurrence with single variables to examine whether the model composed of a set of variables was better in explaining the occurrence of forest species in hedgerows than a single variable could do.

We decided to use Conrad's continentality index to describe the climate gradient in oceanicity within the selected studies. This index, or coefficient of continentality, k , is calculated as follows:

$$k = 1.7 \times A / \sin(\varphi + 10^\circ) - 14,$$

where A is the difference between the mean temperature ($^\circ\text{C}$) of the warmest and coldest months and φ is the latitude of the specific study area (Conrad, 1946). The higher the value of k is, the more continental are the climatic conditions. We calculated k for each selected study with its mean regional latitude. In the case of nationwide studies we used mean latitude for the whole country (Table 2).

We furthermore assumed that changes in the species' ecological and life history traits are related to changes in climate. For each set of species we calculated at first the mean Ellenberg values and in addition the relative proportions of different categories of Ellenberg values (ranging from 1 to 9) and the percentages of each included category of dispersal type, life form and leaf persistence. Linear regression analyses were conducted between the mean and percentage values of the ecological traits and the corresponding continentality index across the studies.

The PCA was carried out with PC-ORD 4.17 (MjM Software, Gleneden Beach, USA). All other calculations were done with SPSS 15.0 (SPSS, Chicago, USA).

RESULTS

For the correlation analysis we used the first three axes of a PCA conducted with the set of explanatory variables (Table 1). The fraction of variation explained by all three axes was about 76% (axis 1 – 43.13%, axis 2 – 19.57%, axis 3 – 13.27%). The correlations between the

PCA scores of species and their frequency or relative frequency in hedgerows revealed only one significant relationship between axis 3 and relative frequency; Table 3). Contrary to our expectations the correlation between a single variable (Ellenberg indicator value for light) and the relative frequency of forest species resulted in a slightly higher correlation coefficient than the multivariate analysis. In addition, the correlation between the relative frequency of forest species and mean plant height was found to be significant.

Table 3: Spearman rank correlations (r_s) between the relative frequency of forest plant species in hedgerows and the values of predicting variables: Ellenberg values for light (L), soil moisture (M) and nitrogen/nutrients (N), and the ranked scores of some life history traits (see Table 1). The PCA scores summarize the responses of species to this set of explanatory variables. *n.s.* – not significant, * - $p < 0.05$, ** - $p < 0.01$, *** - $p < 0.005$.

Attribute	Relative frequency	
	r_s	p
L value	- 0.461	***
M value	0.088	<i>n.s.</i>
N value	- 0.196	<i>n.s.</i>
Plant height	- 0.358	*
Clonality / life span	0.255	<i>n.s.</i>
Seed mass	0.023	<i>n.s.</i>
Dispersal mode	- 0.228	<i>n.s.</i>
PCA axis 1	0.254	<i>n.s.</i>
PCA axis 2	- 0.047	<i>n.s.</i>
PCA axis 3	+ 0.421	**

The survey of the literature resulted in 26 studies, which presented lists of surveyed herbaceous plant species in hedgerows. 19 of these studies were located in Europe. Not more than 13 of these studies provided lists of species including more than ten regionally typical forest species (Table 2). These studies were located in the United Kingdom, France, Belgium, Germany and Italy and encompassed in total 139 species that were typically found in forests of the study regions (Appendix 2). The number of species per study ranged from 12 to 88. Conrad's continentality index for the study sites (Table 2) ranged from 6.91 (no. 11; UK) to 28.14 (no. 10; Italy).

Regression analyses of life history traits and ecological indicators on the continentality gradient (based on Conrad's index) revealed several significant relationships (Table 4). Higher Conrad's indices were only associated with higher mean Ellenberg values for continentality (C). Other mean Ellenberg values showed no such relation. Further associations were found between Conrad's indices and the proportions of single categories of Ellenberg

values. With increasing continentality the proportion of species with low indicator values for light (L) increased significantly, and the proportion of plants with L values tended to decrease. Further interrelations were found for Ellenberg continentality values (C): the proportion of species with low values decreased (as a trend) and the proportion of species with higher values increased significantly with increasing continentality. Higher continentality was significantly related to a decrease in the proportion of species with lower indicator values for soil reaction (R), and to an increase in the proportion of species with higher R values. Higher proportions of chamaephytes were observed in study areas with lower Conrad indices. Leaf persistence was also significantly influenced by continentality: the proportion of vernal species increased and the proportion of wintergreen species decreased with increasing index values.

Table 4: Relationship between Conrad's continentality index and ecological / life-history traits, calculated for species composition of each study, based on linear regression analyses. Traits included Ellenberg indicator values for light (L) and continentality (C), soil moisture (M), pH (R), and the life-history attributes dispersal type, life form, leaf persistence and life span / clonality (*p* – perennial, *a* – annual/biennial). With exception of the mean values for L, C, M and R (\emptyset) all other values were calculated as the relative proportion of all species named in the specific study and were included in the analysis. Together with the adjusted R^2 -values the type of relation (positive or negative) is given. Only significant (* - $p < 0.05$, ** - $p < 0.01$, *** - $p < 0.005$) results and trends (\circ - $p < 0.10$) are shown. Variables in italics had a proportion of zero and were not included in the analysis. The results for all nine value classes of T and N showed no significant relationship and were not presented.

Variable Ellenberg value	R^2_{adj}	Variable Ellenberg value	R^2_{adj}	Variable Life-history attribute	R^2_{adj}
L \emptyset		M \emptyset		Geophyte	
L 1 %		<i>M 1 %</i>		Hemicryptophyte	
L 2 %		<i>M 2 %</i>		Chamaephyte	0.216 (-) \circ
L 3 %		M 3 %	0.670 (+) ***	Therophyte	
L 4 %	0.553 (+) ***	M 4 %		Other	
L 5 %		M 5 %			
L 6 %	0.233 (-) \circ	M 6 %	0.423 (+) **	Vernal	0.591 (+) ***
L 7 %		M 7 %		Summergreen	
L 8 %		M 8 %		Wintergreen	0.394 (-) *
L 9 %		M 9 %		Evergreen	
C \emptyset	0.532 (+) ***	R \emptyset		P, highly clonal	
C 1 %		<i>R 1 %</i>		P, intermediate clonal	
C 2 %		R 2 %		P, non clonal	
C 3 %	0.133 (-) \circ	R 3 %		A, non clonal	
C 4 %	0.670 (+) ***	R 4 %	0.178 (-) \circ		
C 5 %	0.200 (+) \circ	R 5 %	0.247 (-) *	Anemochory	
C 6 %	0.352 (+) *	R 6 %		Epizoochory	
C 7 %		R 7 %	0.347 (+) *	Endozoochory	
C 8 %		R 8 %		Myrmecochory	
C 9 %		R 9 %		Other	

DISCUSSION

The applicability of the chosen set of ecological and life history variables – expected to, in combination, explain the frequency of forest plant species in hedgerows well - could not be validated in our analysis. Although the variables are known to influence the occurrence of forest herbs, there was no clear multiple effect on the (relative) frequency of the species. This result may be due to an inappropriate selection of variables, but according to the literature, the most important factors were considered in our study. Another reason may be the difference in the pools of forest species between the regions. The species composition of hedgerows is always a sub-set of the species pool of the woodlands in the vicinity of the studied networks (assuming the woodlands to be the primary source for colonization events), and these pools most determine the species composition of adjacent hedgerows far more than any ecological or life history variable.

This explanation is probably not only applicable to the results of our study. Differences in species pools may also be the cause for a series of contrasting findings in several studies from the last decades relating to the species composition of hedgerows. For example, hedgerows in Germany were dominated by forest plants known to prefer the forest interior (Wehling & Diekmann, 2008), whereas in France (Baudry, 1988) and in the UK (Andrews *et al.*, 1999; Smart *et al.*, 2001) most forest herbs found in hedgerows were associated more with the forest edge. This is also reflected in the controversy about the question whether hedgerows are more similar to forest edges (Forman, 1995) or not (Fritz & Merriam, 1996). Also the proportions of forest species in hedgerows differed considerably between studies – in Britain the values differed between 5 and 15% (Pollard, 1973; Cummins & French, 1994), whereas in Germany up to 25% of all hedgerow species were categorized as forest herbs (Wehling & Diekmann, 2008). A further indication of the strong influence of the regional forest herb pool on the species composition of hedgerows is the difference in the shares of the dispersal types of hedgerow species between studies / regions. Some hedgerow networks were dominated mainly by anemochorous species (Wehling & Diekmann, in press), while this dispersal type was found to be rare in other hedgerow landscapes (Roy & de Blois, 2006). Some studies reported forest species in hedgerows to mainly have myrmecochorous seed dispersal (Sitzia, 2007); these species are usually assumed to be rarely or even never found in such habitats, because of their very low dispersal capacity (Corbit *et al.*, 1999). Furthermore, species like *Anemone nemorosa* and *Adoxa moschatellina* that are often found in hedgerows of North-western Germany (Wehling & Diekmann, 2009) were only rarely encountered in hedgerows of north-eastern Belgium (Verheyen *et al.*, 2003).

All these contrasting results give a strong indication of the influence of different regional species pools on the current species composition of hedgerows. A plenty of factors may be responsible for this. Several studies have shown the importance of land use and land use history (Le Cœur *et al.*, 2002; Deckers *et al.*, 2005b), others have emphasized the relevance of local topography and geology (Reif *et al.*, 1982; Burel & Baudry, 1990), while landscape history and hedgerow management were also assumed to play a significant role (Burel, 1996; Baudry *et al.*, 2000). This makes it difficult to find a set of variables explaining the occurrence of forest herbs in hedgerow networks that would be valid on the European scale, without taking regional characteristics into account. This is especially important for regions where the species pool is restricted to relic-woodland hedges and where forests or forest fragments are absent, which is true for some parts of Brittany (Baudry *et al.*, 2000) and Britain (Pollard *et al.*, 1974). The major difference between relic and planted hedgerows could be shown in a previous study (Boutin *et al.*, 2002).

The single variable *light availability* had a stronger relationship to the relative frequency of forest herbs in hedgerows than our selected set of factors. This coincides with earlier findings from British hedgerows, which reported low levels of light as one of the most important factors influencing species composition (Bates, 1937). Several other studies underlined the importance of light or its proxies, *e.g.*, the cover of the tree or shrub layer, for the occurrence of forest herbs (Pollard, 1973; Boutin *et al.*, 2002). In our analysis the positive effect of lower light availability is accompanied by the effects of a larger mean plant height in forest species. Compared to forests hedgerows are somewhat less dark (Forman & Baudry, 1984) and are therefore preferred by relatively light-demanding non-forest species (*e.g.*, *Urtica dioica*), which are often highly competitive (De Keersmaeker *et al.*, 2004). Therefore, if plant height is considered as a measure of competitive strength, only rather tall woodland herbs are able to persist.

The analysis of the changes in species composition of European hedgerow networks along a climate gradient resulted in some expected and a few unexpected results. First of all, the chosen Conrad's continentality index worked well, which is reflected by the strong positive correlation between the mean Ellenberg values for continentality and the index values. The climatic conditions within the gradient covered by our studies changed from oceanic to sub-continental. Other mean Ellenberg values showed no such relationships, which may reflect that there were no major differences in the general environment of the tested hedgerow networks.

It is known that, with increasing continentality, there is a greater difference between maximum and minimum temperature during the course of a year with a higher probability of severe frost and a decrease in annual precipitation (Lauer & Bendix, 2004). The soils of regions closer to the sea are often nutrient-poorer and have lower pH values, due to a leaching effect caused by the higher precipitation compared to more continental areas (Sumner, 2000). These patterns are reflected by the changes in species composition along our studied climate gradient. With increasing continentality, the proportion of species with low Ellenberg values for soil moisture (indicating drier soils) and high Ellenberg values for soil reaction (indicating more basic soils) increased. In addition, chamaephytes and wintergreen species were significantly more often present in hedgerow networks of oceanic regions, which is probably caused by the low risk of severe frost events that would damage the leaves and other above-ground organs of such species (Woodward, 1987).

However, some of the findings of our analysis were unexpected, especially the increase in the proportion of vernal species and plants with high Ellenberg values for soil moisture with increasing continentality. It is possible that, in more continental regions, species with higher water requirements depend on habitats like hedgerows, which provide a wetter environment than the surrounding landscape. In oceanic regions such species are probably not bound to forested habitats. The sensitivity of forest herbs to changes in soil moisture has widely been shown (Brunet *et al.*, 2000; McLachlan & Bazely, 2001), also with reference to hedgerows (Schmucki & de Blois, 2009). Furthermore, our results showed a higher proportion of species with low Ellenberg values for light with increasing continentality. Most likely, hedgerows in more continental regions are not darker than oceanic ones, but they probably offer a refuge to many forest herbs in an otherwise unsuitable landscape. This may be caused by the competitive pressure from light- and nutrient-demanding species outside the hedges, which prefer the richer soils, more frequent in continental regions. Forest plants are known as being far more shade-tolerant than shade-demanding (Hermy *et al.*, 1999; De Keersmaecker *et al.*, 2004) and avoid this pressure only in habitats with low light availability, namely in hedgerows or forests. In oceanic regions the competitive pressure in the open landscape is probably not lower than in continental regions.

CONCLUSIONS

The development of an instrument for the prediction of forest herb occurrence in hedgerows on a European scale was not entirely successful, as multiple factors did not explain the frequencies of forest herbs better than single factors, notably light availability. We believe

that the regional forest species pool is a primary factor determining the species composition of the tested hedgerow networks. Many differences in hedgerow species composition between regions are also explained by the strong climatic differences between regions, especially with respect to continentality and moisture conditions.

In summary, a prediction of the occurrence of forest herbs in hedgerow networks is only possible when taking the regional pool of forest species and the climatic characteristics of the regions into account.

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REFERENCES

- Agger, P., Brandt, J., 1988. Dynamics of small biotopes in Danish agricultural landscapes. *Landscape Ecology* 1, 227-240.
- Andrews, M., Mercer, C., Griffin, P., Andrews, M. E., Cherrill, A., 1999. Autecology of common herbaceous hedgerow species in Britain. *Aspects of Applied Biology* 54, 353-360.
- Bailey, S.-A., 2007. Increasing connectivity in fragmented landscapes: An investigation of evidence for biodiversity gain in woodlands. *Forest Ecology and Management* 238, 7-23.
- Barnes, G., Williamson, T., 2006. *Hedgerow history: Ecology, history and landscape character*. Windgather Press, Bollington, UK.
- Barr, C. J., Gillespie, M. K., 2000. Estimating hedgerow length and pattern characteristics in Great Britain using Countryside Survey data. *Journal of Environmental Management* 60, 23-32.
- Bates, G. H., 1937. The vegetation of wayside and hedgerow. *Journal of Ecology* 25, 469-481.
- Baudry, J., 1988. Hedgerows and hedgerow networks as wildlife habitats in agricultural landscapes. In: Park, J. R. (ed). *Environmental management in agriculture - European perspectives*. Belhaven Press, London, UK, 111-124.
- Baudry, J., Bunce, R. G. H., Burel, F., 2000. Hedgerows: An international perspective on their origin, function and management. *Journal of Environmental Management* 60, 7-22.
- Boutin, C., Jobin, B., Bélanger, L., Choinière, L., 2002. Plant diversity in three types of hedgerows adjacent to cropfields. *Biodiversity and Conservation* 11, 1-25.

- Brunet, J., von Oheimb, G., Diekmann, M., 2000. Factors influencing vegetation gradients across ancient-recent woodland borderlines in southern Sweden. *Journal of Vegetation Science* 11, 515-524.
- Burel, F., 1996. Hedgerows and their role in agricultural landscapes. *Critical Reviews in Plant Sciences* 15, 169-190.
- Burel, F., Baudry, J., 1990. Structural dynamic of a hedgerow network landscape in Brittany France. *Landscape Ecology* 4, 197-210.
- Burel, F., Baudry, J., 1995. Species biodiversity in changing agricultural landscapes: A case study in Pays d'Auge, France. *Agriculture, Ecosystems and Environment* 55, 193-200.
- Cherrill, A., Mercer, C., McClean, C., Tudor, G., 2001. Assessing the floristic diversity of hedge networks: a landscape perspective. *Landscape Research* 26, 55-64.
- Chincarini, M., Padoa-Schioppa, E., 2001. The ecological evaluation of hedgerows: a first attempt at a practical approach. In: Barr, C. J., Petit, S. (eds). *Hedgerows of the world: their ecological functions in different landscapes*. IALE, Birmingham, UK, 81-92.
- Conrad, V., 1946. *Methods in Climatology*. Harvard University Press, Cambridge, USA.
- Corbit, M., Marks, P. L., Gardescu, S., 1999. Hedgerows as habitat corridors for forest herbs in central New York, USA. *Journal of Ecology* 87, 220-232.
- Cummins, R. P., French, D. D., 1994. Floristic diversity, management and associated land use in British hedgerows. In: Watt, T. A., Buckley, P. (eds). *Hedgerow management and nature conservation*. Wye College Press, Ashford, UK, 95-106.
- Cunningham, S. A., 2000. Effects of habitat fragmentation on the reproductive ecology of four plant species in mallee woodland. *Conservation Biology* 14, 758-768.
- De Keersmaecker, L., Martens, L., Verheyen, K., Hermy, M., De Schrijver, A., Lust, N., 2004. Impact of soil fertility and insolation on diversity of herbaceous woodland species colonizing afforestations in Muizen forest (Belgium). *Forest Ecology and Management* 188, 291-304.
- Deckers, B., De Becker, P., Honnay, O., Hermy, M., Muys, B., 2005a. Sunken roads as habitats for forest plant species in a dynamic agricultural landscape: effects of age and isolation. *Journal of Biogeography* 32, 99-109.
- Deckers, B., Hermy, M., Muys, B., 2004a. Factors affecting plant species composition of hedgerows: relative importance and hierarchy. *Acta Oecologica* 26, 23-37.
- Deckers, B., Kerselaers, E., Gulinck, H., Muys, B., Hermy, M., 2005b. Long-term spatio-temporal dynamics of a hedgerow network landscape in Flanders, Belgium. *Environmental Conservation* 32, 20-29.
- Deckers, B., Verheyen, K., Hermy, M., Muys, B., 2004b. Differential environmental response of plant functional types in hedgerow habitats. *Basic and Applied Ecology* 5, 551-566.
- Dzwonko, Z., Loster, S., 1989. Distribution of vascular plant species in small woodlands on the western Carpathian foothills. *Oikos* 56, 77-86.

- Ellenberg, H., 1996. *Vegetation Mitteleuropas mit den Alpen*. Ulmer, Stuttgart, Germany.
- Ellenberg, H., Weber, H. E., Düll, R., Wirth, V., Werner, W., Paulißen, D., 1992. Zeigerwerte von Pflanzen in Mitteleuropa. *Scripta Geobotanica* 18, 1-258.
- Forman, R. T. T., 1995. *Land mosaics: the ecology of landscapes and regions*. University Press, Cambridge, USA.
- Forman, R. T. T., Baudry, J., 1984. Hedgerows and hedgerow networks in landscape ecology. *Environmental Management* 8, 495-510.
- Freemark, K. E., Boutin, C., Keddy, C. J., 2002. Importance of farmland habitats for conservation of plant species. *Conservation Biology* 16, 399-412.
- French, D. D., Cummins, R. P., 2001. Classification, composition, richness and diversity of British hedgerows. *Applied Vegetation Science* 4, 213-228.
- Fritz, R., Merriam, G., 1996. Fencerow and forest edge architecture in eastern Ontario farmland. *Agriculture, Ecosystems and Environment* 59, 159-170.
- Helliwell, D. R., 1975. The distribution of woodland plant species in some Shropshire hedgerows. *Biological Conservation* 7, 61-72.
- Hermý, M., Honnay, O., Firbank, L., Grashof-Bokdam, C., Lawesson, J. E., 1999. An ecological comparison between ancient and other forest plant species of Europe, and the implications for forest conservation. *Biological Conservation* 91, 9-22.
- Honnay, O., Hermý, M., Coppin, P., 1999. Effects of area, age and diversity of forest patches in Belgium on plant species richness, and implications for conservation and reforestation. *Biological Conservation* 87, 73-84.
- Honnay, O., Verheyen, K., Butaye, J., Jacquemyn, H., Bossuyt, B., Hermý, M., 2002. Possible effects of habitat fragmentation and climate change on the range of forest plant species. *Ecology Letters* 5, 525-530.
- Klotz, S., Kühn, I., Durka, W., 2002. Eine Datenbank mit biologisch-ökologischen Merkmalen zur Flora von Deutschland. *Schriftenreihe für Vegetationskunde* 38, 1-334.
- Lauer, W., Bendix, J., 2004. *Klimatologie*. Westermann, Braunschweig, Germany.
- Le Cœur, D., Baudry, J., Burel, F., 1997. Field margins plant assemblages: variation partitioning between local and landscape factors. *Landscape and Urban Planning* 37, 57-71.
- Le Cœur, D., Baudry, J., Burel, F., Thenail, C., 2002. Why and how we should study field boundary biodiversity in an agrarian landscape context. *Agriculture, Ecosystems and Environment* 89, 23-40.
- Macdonald, D. W., Johnson, P., 2000. Farmers and the custody of the countryside: trends in loss and conservation of non-productive habitats. *Biological Conservation* 94, 221-234.
- McCollin, D., Jackson, J. I., Bunce, R. G. H., Barr, C. J., Stuart, R., 2000. Hedgerows as habitat for woodland plants. *Journal of Environmental Management* 60, 77-90.
- McLachlan, S. M., Bazely, D. R., 2001. Recovery patterns of understorey herbs and their use as indicators of deciduous forest regeneration. *Conservation Biology* 15, 98-110.

- Peterken, G. F., 1974. A method for assessing woodland flora for conservation using indicator species. *Biological Conservation* 6, 239-245.
- Petit, S., Stuart, R., Gillespie, M. K., Barr, C. J., 2003. Field boundaries in Great Britain: stock and change between 1984, 1990 and 1998. *Journal of Environmental Management* 67, 229-238.
- Pollard, E., 1973. Hedges: VII. Woodland Relic Hedges in Huntington and Peterborough. *Journal of Ecology* 61, 343-352.
- Pollard, E., Hooper, M. D., Moore, N. W., 1974. *Hedges*. William Collins Sons & Co Ltd, London, UK.
- Reif, A., Schulze, E.-D., Zahner, K., 1982. Der Einfluß des geologischen Untergrundes, der Hangneigung, der Feldgröße und der Flurbereinigung auf die Heckendichte in Oberfranken. *Berichte der Akademie für Naturschutz und Landschaftspflege* 6, 231-253.
- Rounsevell, M. D. A., Annetts, J. E., Audsley, E., Mayr, T., Reginster, I., 2003. Modelling the spatial distribution of agricultural land use at the regional scale. *Agriculture, Ecosystems and Environment* 95, 465-479.
- Roy, V., de Blois, S., 2006. Using functional traits to assess the role of hedgerow corridors as environmental filters for forest herbs. *Biological Conservation* 130, 592-603.
- Schmidt, M., von Oheimb, G., Kriebitzsch, W.-U., Ellenberg, H., 2002. Liste der im norddeutschen Tiefland typischen Waldgefäßpflanzen. *Mitteilungen der Bundesforschungsanstalt für Forst- und Holzwirtschaft* 206, 1-37.
- Schmucki, R., de Blois, S., 2009. Population structure and individual performances of *Trillium grandiflorum* in hedgerows and forest habitats. *Plant Ecology* 202, 67-78.
- Sitzia, T., 2007. Hedgerows as corridors for woodland plants: a test on the Po Plain, northern Italy. *Plant Ecology* 188, 235-252.
- Smart, S. M., Bunce, R. G. H., Stuart, R. C., 2001. An assessment of the potential of British hedges to act as corridors and refuges for Ancient Woodland Indicator plants. In: Barr, C. J., Petit, S. (eds). *Hedgerows of the world: their ecological functions in different landscapes*. IALE, Birmingham, UK, 137-146.
- Sparks, T. H., Meek, W. R., Mountford, J. O., Pywell, R. F., 2000. The spatial distribution of herbs and woody species in the hedgerows of an arable farm. *Aspects of Applied Biology* 58, 401-406.
- Stoate, C., Boatman, N., Borralho, R. J., Carvalho, C. R., De Snoo, G. R., Eden, P., 2001. Ecological impacts of arable intensification in Europe. *Journal of Environmental Management* 63, 337-365.
- Sumner, M. E. (ed), 2000. *Handbook of Soil Science*. CRC Press, Boca Raton, USA.
- Tack, G., van der Bremt, P., Hermy, M., 1993. *Flanders forests: a historical ecology*. Davidsfonds, Leuven, Belgium.
- Tang Ya, Zhang Yan-zhou, Xie Jia-sui, Sun Hui, 2003. Incorporation of mulberry in contour hedgerows to increase overall benefits: a case study from Ningnan County, Sichuan Province, China. *Agricultural Systems* 76, 775-785.

- van Calster, H., Vandenberghe, R., Ruysen, M., Verheyen, K., Hermy, M., Decocq, G., 2008. Unexpectedly high 20th century floristic losses in a rural landscape in northern France. *Journal of Ecology* 96, 927-936.
- Verheyen, K., Guntenspergen, G. R., Biesbrouck, B., Hermy, M., 2003. An integrated analysis of the effects of past land use on forest herb colonization at the landscape level. *Journal of Ecology* 91, 731-742.
- Vitousek, P. M., Mooney, H. A., Lubchenco, J., Melillo, J. M., 1997. Human domination of earth's ecosystems. *Science* 277, 494-499.
- Weber, H. E., 2003. *Gebüsche, Hecken, Krautsäume*. Ulmer, Stuttgart, Germany.
- Wehling, S., Diekmann, M., 2008. Factors influencing the spatial distribution of forest plant species in hedgerows of North-western Germany. *Biodiversity and Conservation* 17, 2799-2813.
- Wehling, S., Diekmann, M., 2009. Hedgerows as an environment for forest plants: a comparative case study of five species. *Plant Ecology* 204, 11-20.
- Wehling, S., Diekmann, M., in press. Importance of hedgerows as habitat corridors for forest plants in agricultural landscapes. *Biological Conservation*, doi:10.1016/j.biocon.2009.05.023.
- Wisskirchen, R., Haeupler, H., 1998. *Standardliste der Farn- und Blütenpflanzen Deutschlands*. Ulmer, Stuttgart.
- Woodward, F. I., 1987. *Climate and plant distribution*. Cambridge University Press, Cambridge, UK.
- Zuria, I., Gates, J. E., 2006. Vegetated field margins in Mexico: Their history, structure and function, and management. *Human Ecology* 34, 53-77.

Chapter 7

Summary and perspectives



Top left: *Species-rich hedgerow along paved road.* **Top right:** *Dumping within hedgerows.* **Bottom left:** *Stellaria holostea at a hedge bottom.* **Bottom right:** *Hedgerow with gaps and few remaining trees; degradation probably due to worse management. (Photographs taken by Stephan Wehling).*

SUMMARY OF RESULTS

The main scope of this study was to determine the value of hedgerows for the conservation of herbaceous forest plant species in an intensely used agricultural landscape in north-western Germany. Special interest was given to the possible habitat and conservation corridor function of hedgerows for woodland herbs.

Hedgerows as habitats for forest herbs

In the past and contrary to some findings from other European countries, the hedgerows of Central Europe were thought to contain almost no herbaceous species typically found in the forest interior due to differences in the microclimate compared to forests and the high degree of disturbance (Weber, 1967; Schrautzer *et al.*, 1996). In contrast to this assumption, we found a total of 43 woodland plant species (ca. 25% of all species found; Chapter 3) in the studied hedgerow networks. This is an extraordinary high number, especially when compared to other European studies, which revealed proportions of forest herbs in hedgerows, as low as 5% (Pollard, 1973) and 15% (Cummins & French, 1994) in different regions of Great Britain, and 12% in Belgium (Deckers *et al.*, 2004). Thus, our finding emphasizes the importance of the studied hedgerows as a habitat for forest plants. Furthermore, about 77% of the species found in the neighbouring forests were also present in the adjacent hedgerows surveyed in this study (Chapter 5). Similar results were obtained in a study conducted in a North American hedgerow network; here 70% of the forest plants of the surrounding forests were detected in hedges (Corbit *et al.*, 1999).

Of the 43 woodland herbs found, five species are classified as regionally endangered (Garve, 2004). However, the proportion of threatened forest plants was lower in hedgerows than in the surrounding forests (Chapter 3), which may indicate a low relevance of hedgerows for the conservation of endangered species compared to forest stands. This might be explained by differences in habitat requirements between rare and common woodland herbs, although our results could not demonstrate such differences in environmental preferences (Chapter 3). Contrary to our findings, Canadian researchers found such forest species to be absent from hedges that require a similar combination of ecological factors characteristic for forests and that are able only to tolerate very small deviations from their optima of these factors (de Blois *et al.*, 2002). Similar results were described in a more recent study (Roy & de Blois, 2006).

The mere presence of forest species is only an indication for the habitat function of hedgerows and no evidence for their long-term suitability. The latter is only given, if forest

species show the same individual and reproductive performance in hedgerows as in forests. Therefore we conducted a comparison of different life-history values (as a measurement for plant fitness) between populations of five selected common forest species occurring in both hedgerows and forests. This comparison revealed within the same species only marginal differences, and between the species inconsistent patterns (Chapter 4). Three groups of forest species could be determined: a) plants which show higher fitness in hedgerows (*e.g.*, *Stellaria holostea*), b) plants which show higher fitness in forests (*e.g.*, *Circaea lutetiana*), and c) plants which grow equally well in both habitats (*e.g.*, *Anemone nemorosa*, *Polygonatum multiflorum*). Again, the suitability of hedgerows for enhanced survival and reproduction of forest plants is only given for a subset of species. These variations may be due to differences in the habitat requirements, found to be important by other studies (McCollin *et al.*, 2000; Endels *et al.*, 2004).

The most important group of factors influencing the distribution of the found forest species in hedges consisted of environmental variables, mainly soil nutrients and light availability (Chapter 3). The hedgerows of the study regions showed significantly higher relative irradiance at the ground and slightly higher contents of nutrients in the soil compared to the local forests (Chapter 4). The importance of light availability is consistent through all parts of the study. Within hedgerows, relative irradiance was important for the presence of forest herbs (Chapter 3; Chapter 6) and it led to an increased plant height and reduced investment in generative reproduction of some of the studied forest plants (Chapter 4). Light (and its proxies shrub and tree cover) also affected the frequency of occurrence of forest species and their abundance along a forest-hedgerow transect (Chapter 5). Moreover, hedgerows with a very dense shrub layer are too much shaded to harbour notable amounts of woodland species, whereas only hedgerows with a dense tree and a sparse shrub layer provide suitable light conditions for forest plants (Chapter 5). This is supported by findings from other hedgerow networks in Europe (Pollard, 1973; Boutin *et al.*, 2002). The general relevance of irradiance for forest herbs is well documented in literature – forest species are typical for habitats with a very low light availability, since they are capable of tolerating deep shading (Bierzychudek, 1982; Hughes & Fahey, 1991; Whigham, 2004). Furthermore, in habitats with a higher light availability woodland herbs are replaced by more competitive and light-demanding plants (Honnay *et al.*, 2002a; De Keersmaecker *et al.*, 2004). In the past, several studies have stated that light may also affect forest species in hedgerows (Bates, 1937; Tischler, 1951; Eschenbach *et al.*, 1996).

Another important factor influencing the distribution of forest species in hedgerows is the nutrient content of the soil. Hedgerows with relatively high nutrient contents, particularly phosphate and nitrogen, harbour fewer forest herbs than others (Chapter 3). This is reflected also by an increased investment in generative reproduction by some forest species on sites with relatively low contents of soil nutrients (Chapter 4). High soil nutrient concentrations favour the growth of highly competitive species, such as *Urtica dioica* (Jobin *et al.*, 1997). Forest herbs are generally not capable of competing with such species due to their stress tolerance strategy and low competitive ability (Verheyen & Hermy, 2001). Other studies also show a reduced number of woodland species in nutrient-rich hedgerows (Hegarty *et al.*, 1994; Mercer *et al.*, 1999). The higher soil nutrient contents within hedgerows compared to forests are mainly caused by agricultural fertilizer misplacement (Tsiouris & Marshall, 1998; Kleijn & Verbeek, 2000) and the natural accumulation of organic materials at the hedge bottom (Follain *et al.*, 2009).

The spatial configuration of a hedgerow was less important than the environmental conditions, but still explained a relatively large amount of the variation in species composition. Hedgerows with a more or less north-south orientation showed high numbers of forest species (Chapter 3). This might be due to a more balanced microclimate within the hedgerows compared to east-west orientated hedges with a sun- and a shade-side (Fritz & Merriam, 1993). The strong variations in the microclimate of hedgerows, *e.g.* the low soil moisture at the sun-side, are avoided by forest specialists (Mieth *et al.*, 1996; Martin *et al.*, 2001). Only hedges with forest-like conditions, *i.e.* the absence of major extremes in temperature or humidity, are tolerable for forest plants (Tischler, 1951; Roy & de Blois, 2006).

In contrast to the results of other studies (*cf.*, Le Cœur *et al.*, 1997; Deckers *et al.*, 2004), the variable groups of management/land use (mainly a combination of road, forest, conventional used crop field, and grassland) and structure (mainly hedge width) were less important for the distribution of forest species in hedges. The land use type 'forest' showed the strongest influence on the occurrence of forest species (Chapter 3). This is supported by the significant relation between the forest species richness of a forest and the species richness in parts of an adjacent hedgerow, which are closest to the forest (Chapter 5). Comparable results are known from French hedgerows, where the distance to the neighbouring forest is highly influential for the occurrence of woodland plants, because it is the most important source for the colonisation of hedgerows (Burel & Baudry, 1994). Furthermore, British hedgerow networks

surrounded by forests showed higher numbers of forest species than isolated hedgerows (Marshall & Arnold, 1995). However, other ecologists assumed high numbers of woodland herbs to be caused by low distance to the forest and not by direct contact (Matlack, 1994; Roy & de Blois, 2008).

In conclusion, the habitat function of hedgerows in intensively used agricultural areas is given only for a subset of forest species, which show a broad tolerance against variations in environmental conditions. Species endangered in the region, were only rarely found in the studied hedgerow networks. Therefore, the preservation of the remaining populations of these species in the local ancient forests is of major importance. However, the presence of hedgerows increases for the majority of woodland herbs the amount of habitable sites and allows further spread in an otherwise more or less hostile environment. Furthermore, hedgerows may help to enhance the plant species richness in species-poor landscapes.

Light availability, soil nutrient content and the presence of nearby forests are the most influential factors to the occurrence of woodland plants in hedgerows. Low light availabilities together with a full developed tree and a sparse shrub layer, low nutrient concentrations – especially of phosphate and nitrogen – and short distances to species-rich forests as a source for colonisation are beneficial for the occurrence and viability of forest herbs.

Hedgerows as conservation corridors for forest herbs

The long-term survival of forest herbs in intensively used landscapes with highly fragmented forests is not only dependant on the presence of additional ‘surrogate’ habitats, as hedgerows, but also on an increase in the connectivity between the forest remnants. This corridor function can hardly be revealed for forest plant species, mainly due to their relative immobility and low dispersal speed (mostly few metres/year) when compared to other plant species or animals (Cain *et al.*, 1998; Dzwonko, 2001; Matlack & Monde, 2004).

The analysis of forest-hedgerow transects in the study area revealed a highly significant negative relationship between the number of forest species and the distance from the forest edge (Chapter 5). In other studies, this interrelation is assumed to be evidence for the corridor function of hedgerows (Corbit *et al.*, 1999; Sitzia, 2007). However, considering the changes in environmental conditions along the transects (Chapter 5), which could be a further cause for the changes in species numbers, this relationship can only be interpreted as indicative for the corridor function. In spite of these limitations in the experimental design, forest species were even found in 200 m distance to the nearest forest edge (Chapter 5). Compared to other

studies – *e.g.* 50 m as the furthest distance to the source in a North American hedgerow network (Forman, 1991) – this is a relatively large distance. Thus, the presence of forest species in large distances from a possible source population can be regarded as a further indication for the corridor function. In sum, hedgerows may reconnect two forest patches only at close distances (≤ 200 m), because the impact of the forest species richness in the woodlands on the forest species richness in the adjacent hedgerows is given only in the first 100 m of the transects (Chapter 5). In intensively used farming areas with very large field sizes such distances are much too short for effective increase in connectivity, due to distances between forest fragments of at least 500 m or even several kilometres.

Only a subset of woodland herbs was able to spread within hedgerows, as reflected by the result that 23% of the forest species of the neighbouring forests were not found in the hedgerow networks of the study area (Chapter 5). This might be explained by the limited dispersal capacity of many forest species. Comparable findings from France show that species with a low dispersal speed are absent from hedgerows (Burel & Baudry, 1994). Bossuyt *et al.* (1999) demonstrated in addition that only a fraction of all forest species is able to colonise new habitats (*e.g.*, recently planted woodlands or hedgerows).

Most forest herbs may need a long time to be able to benefit from hedgerows. Therefore, effects and functionality of such corridors can only be demonstrated decades or even centuries after their establishment in the landscape. Hedgerow age was, in consequence, included in our analysis. Although forest species richness was not significantly increasing with hedgerow age, there was a smaller variation in the number of species in hedgerows older than 200 years compared to younger hedges (Chapter 5). Apparently, hedgerows planted more than two centuries ago provided the longest habitat continuity in time within the studied hedges. Apart from habitat quality, continuity has been shown as one of the major factors explaining forest herb survival in woodlands (Kolb & Diekmann, 2004) and therefore we assumed also for hedgerow age to be at least an influencing factor for the spread of forest species.

In conclusion, only such woodland species able to tolerate hedgerow conditions may benefit from hedgerows as a conservation corridor. Almost a quarter of the observed forest species of the region is not able to spread within these corridors. Furthermore, the reconnection of forest patches seemed to be effective only on short distances and woodland herbs may need at least several decades to benefit from these features, if they are newly established in the landscape. Nevertheless, hedgerows may help to enhance the survival of the majority of woodland plants, by increasing the connectivity between closely neighboured forest fragments.

Hedgerow networks on a European scale

The comparison of the results of this study with the findings from other countries revealed several discrepancies (Chapter 3-6). Therefore, we tried to find a set of variables, which allows the prediction of the distribution of forest species throughout European hedgerow networks. We furthermore tried to determine differences in environmental conditions and species compositions of hedgerows along a climate gradient across Europe.

The chosen set of variables consisting of factors highly influential to the distribution of forest herbs had a slightly weaker relationship to the frequency of forest species than the single variable light availability (Chapter 6). Although the relevance of the factors for the occurrence of woodland herbs was proven in several studies before, the combination of these variables did not work satisfyingly. A comparable attempt for Italian hedgerows worked only on a limited local scale with a set of factors, selected especially for the region (Chincarini & Padoa-Schioppa, 2001). Therefore, we assumed the regional pool of forest species to be more decisive for the distribution of these species in hedgerows than other factors (*e.g.*, species life-history attributes).

Several differences could be revealed comparing environmental conditions and species composition of 13 different hedgerow networks along a climatic gradient throughout Europe. The species composition of hedgerows in continental regions showed a lower proportion of chamaephytes and wintergreen species and a higher proportion of species indicating drier and less acid soils (Chapter 6). These alterations in species composition and environmental conditions are mainly due to the climatic changes in terms of a lessened precipitation and a higher risk of extremes in temperature with an increasing distance to the ocean (Woodward, 1987; Lauer & Bendix, 2004). Others stated a higher proportion of vernal species and species with low Ellenberg values for light (Chapter 6). These discrepancies could not be explained by climatic changes. For these cases, we assumed again the local forest species pool to be important in determining the species composition. This assumption is supported by the findings in other European hedgerow networks (Baudry *et al.*, 2000; Burel, 1996).

In conclusion, in further investigations of the forest species inventory of hedgerow networks on a European scale the regional pool composition of forest species should be taken into consideration. Furthermore, climatic variations resulting in different environmental conditions and species compositions cannot be neglected for meaningful comparisons of different hedgerow networks in Europe.

IMPLICATIONS FOR FUTURE RESEARCH

The value of hedgerows for the survival of the majority of forest plant species in agricultural landscapes has been demonstrated in this thesis, however, several questions are still in need of accurate answers. Firstly, extended knowledge on the factors influencing the distribution of endangered forest herbs in hedgerow networks is required to improve the conservation management of these species. Due to their low frequencies both in the studied hedgerow networks and in the surrounding forests the survey of further networks in North Germany and probably in Denmark and/or in The Netherlands as well is needed. Thereby the differences in the regional forest species pools and possible changes in climatic conditions have to be taken into account. An increased number of replications may help to reveal why most hedgerows are unsuitable habitats for this subset of woodland species.

In addition, we merely obtained indications, albeit strong ones, for the corridor function of hedgerows. Significant and replicable evidence for this feature may strengthen the conclusions of this study. Such evidence could be adduced by long-time monitoring of forest species populations in hedgerows, especially if they are newly established in the vicinity of species rich forests. Repeated collection of population structure and size data and the determination of the distance of the individual most distant to the forest edge may help to explore how and in which phase forest plants spread within hedgerows. However, this type of examination is very time-consuming and may require at least decades of research, due to the long time forest species need to spread into new habitats and also for the subsequent establishment and further reproduction (Francis *et al.*, 1992; McLachlan & Bazely, 2001; Vellend *et al.*, 2006). The lack of knowledge about the corridor function is even more severe considering the upcoming changes in the world climate. Without increased connectivity many forest species will not be able to either adapt to or even avoid new conditions, caused by habitat isolation and their low dispersal capacity (Honnay *et al.*, 2002b).

In the course of this study, several continuative questions concerning forest herbs in hedgerows emerged. There is a need to increase the knowledge about the mechanisms of genetical adaptation of forest species to hedgerow conditions. In studies hitherto the formation of different genotypes within a forest species with occurrences in hedgerows and forests was assumed, but only different phenotypes could be accounted for (Packham & Willis, 1982; Bain & Attridge, 1988; Mieth *et al.*, 1996). The existence of different genotypes could be an explanation for the absence of several forest plants in hedgerows (*cf.*, Chapter 3 and 5), because they are probably not able to adapt quickly enough to hedgerow conditions. Variations in genotype could also explain the lacking differences between life-history

attributes of the five selected forest species occurring both in hedgerows and forests (*cf.*, Chapter 4). Therefore, further analyses with comparisons of the genetical composition of forest plants found in hedges and in forests are required. Another approach may be the transplantation of individuals of forest herbs selected from populations in forests into hedgerows. With the help of measured survival rates or differences in individual or reproductive fitness and plant size, predictions about the capability to adapt to hedgerow conditions can be made. The question to what extent the genetic variability of a forest herb increases in fragmented forests connected by hedgerows compared to unconnected woodland patches is a further application for genetic experimental trials. Two recent studies dealt with this topic, however, opposing results were attained and the conclusions seemed to be equivocal or at least species-specific (Campagne *et al.*, 2009; Schmidt *et al.*, in press).

A further objective that needs to be explored are plant-animal interactions of forest plant species. Plant-animal interactions are multifaceted – the most important ones are between a plant and its pollinators and seed dispersal vectors, but herbivores, seed predators and parasites have also to be considered (Haddad & Tewksbury, 2006). Several studies have emphasized the strong influence of animals on the distribution and survival of forest plants in fragmented habitats (*e.g.*, Noss, 1993; Tewksbury *et al.*, 2002). For other corridor types as hedgerows, the beneficial effects on the plant species distribution, due to a further seed transport by animals, could be demonstrated in the last years (Haddad *et al.*, 2003; Levey *et al.*, 2005; Sullivan & Sullivan, 2009). However, for hedgerows the interactions between animals and forest herbs have only rarely been studied (*e.g.*, Kolb, 2008) and need further exploration.

PERSPECTIVES FOR NATURE CONSERVATION

Based on the results obtained from this study, several recommendations for the conservation of existent hedgerows and the plantation of new hedgerow networks in agricultural landscapes can be made.

The primary aim of the conservation schemes in north-western Germany must be the preservation of forest plant species in the remnant forest patches, as the present hedgerows are not able to provide a suitable habitat for all observed forest species of the region. Many endangered species are restricted to the interior of (ancient) forests and are not able to thrive in hedgerows. The importance of ancient forests for the conservation of these species could be demonstrated for large parts of the study region by the findings of Wulf (1992) and Kolb (2005). The creation of new hedgerow networks will probably not be as effective as

afforestations for an increase in available habitats for endangered woodland species. Therefore, further plantations of deciduous forest are recommended where possible.

Nevertheless, the preservation of the present hedgerow networks in the study region is highly recommended, as well. Hedges add to the habitable sites of the majority of woodland herbs and may even contribute to their survival and dispersal in an otherwise unsuitable environment. Hedgerows furthermore substantially increase the biodiversity in intensively used agricultural regions (Weber, 2003; Aavik & Liira, 2009), even for the group of forest species (Freemark *et al.*, 2002).

Considering the requirements of forest herbs on environmental conditions in hedgerows, local conservationists should pay attention to four main issues:

- The density of the tree layer of a hedgerow is important for the distribution of forest herbs – the denser the tree cover the higher the number of woodland species, probably due to a similar light regime as in the forest.
- The density of the shrub layer is also important. Hedgerows with high densities of shrubs are avoided by woodland herbs, most likely due to severe competition for root space, light and water (Gould & Gorchov, 2000).
- There is a strong negative relationship between the number of woodland herbs in hedgerows and the distance to the nearest forest. This emphasises again the importance of the preservation of the remaining forest patches, because hedges are only able to contribute to the survival of forest plants in combination with forest fragments (as colonisation sources). This coherence is additionally supported by findings from other countries (Corbit *et al.*, 1999; Sitzia, 2007).
- Further nutrient enrichment of the hedge soils has to be prevented, in order to prevent the strong abundance of highly competitive and nutrient-demanding non-forest species (Garbutt & Sparks, 2002; Marshall & Moonen, 2002). For maintaining the present populations of woodland plants, the dumping of organic material within the hedgerow must be inhibited and the use of fertilizers and herbicides in the adjacent fields should be reduced. Therefore, the creation of buffering stripes along hedgerows is recommended. The efficiency of these stripes could be demonstrated clearly for other habitat types (De Snoo & van der Poll, 1999; Moonen & Marshall, 2001; Willi *et al.*, 2005). In addition, buffer stripes may increase the abundance of several pollinator species, which may be crucial for long-time survival of forest herbs (Hopwood, 2008).

Organic agriculture is advantageous to the preservation of hedgerow networks and consequently to the conservation of forest species. Several studies conducted in Europe and North America could show that hedgerows within organic cultivated fields were longer, broader (Bates & Harris, 2009), higher, less disturbed and richer in species (Hole *et al.*, 2005; Norton *et al.*, 2009) – especially endangered and forest plants (Boutin *et al.*, 2008) – compared to hedgerows adjacent to conventional fields. These beneficial effects were assumed to be mainly caused by a weaker input of mineral fertilizers and herbicides (Aude *et al.*, 2004; Fuller *et al.*, 2005).

Contrary to the positive impact of organic farming the production of corn is of major disadvantage for the preservation of forest herbs in hedgerows. Compared to grasslands or other cereals, corn production (mainly as fodder or biomass energy generation) is only efficient with a very high input of mineral fertilizers and herbicides. In most cases these inputs are overdosed and lead to an undesirable accumulation of these substances in the field margins (and hedgerows if present) (Rode, 2005). In addition, the presence of hedgerows diminishes the crop of corn by increased competition for light and nutrients at the field margins and for this reason many farmers tend to reduce remaining hedges in size and refuse to plant new ones (Mette, 1996). These problems for hedgerow and forest species conservation become even worse with the knowledge that in Lower Saxony from 2002 up to 2007 the area cultivated with corn increased by almost 60% at the expense of grassland (Niedersächsisches Landesamt für Statistik, 2007). This development is also true for the study area (personal observation). In consequence, the intensive cultivation of corn and the preservation of hedgerow networks or the creation of new hedgerows in the study area are diametrically opposed.

A supporting conservation activity could be systematically planting of forest species in hedgerows, which have been tested for their suitability. This may support the natural dispersal strategies, which are crucial and very time-consuming for most woodland herbs. Such an approach may help these species to colonise habitable sites, which they are unable to reach or which they will reach only after decades (Verheyen *et al.*, 2003).

Apart from the preservation aspect, enlargement of existing and planting of new hedgerows is highly recommended, as well. The beneficial influences of hedgerows on the survival of forest species and the increase in biodiversity of agriculturally used landscapes could be enhanced and extended by the establishment of new hedges. For the creation of new hedges the use of autochthonous seed stock is preferable where possible, due to its good adaptation to local climatic conditions (Jones *et al.*, 2001). Furthermore, additional hedgerows may

contribute to the reduction of the CO₂-concentration in the atmosphere due to their function as the most effective carbon-sink in farming regions (Follain *et al.*, 2007). The plantation of new hedgerow networks in more or less cleared agricultural areas may furthermore enhance crop production of most cereals (except corn). By improving the microclimate of the fields surrounded by hedgerows growth of arable crops is supported (Bird *et al.*, 1992; Kort, 1988; Mette, 1996). To increase the financial advantages of hedgerows, organic materials (braches, *etc.*) obtained from hedge management (pollarding or coppicing) may be used for biomass energy production (Mette, 2005).

As discussed in the former paragraph, the development of schemes for effective and long-time conservation of hedgerows and forest species in arable landscapes can only be successful, when incorporating the local people in these trials (Baudry, 1993; Saunders, 2007). Without the farmers, which are mainly the owners, users and managers of hedges, almost all approaches would fail. Therefore, the pursuit to intensify the awareness and knowledge of ecological and economical values of hedgerows is recommended (Burel & Baudry, 1995).

The combination of ecological knowledge and political influence enables the effective conservation of hedgerows and herbaceous forest plant species in agricultural used landscapes. For future hedgerow conservation two issues are important:

- The understanding of ecological processes determining the present distribution of forest herbs and their habitat requirements.
- An advanced agricultural policy, which offers detailed information and financial support for the preservation and creation of hedgerows to the local farmers.

REFERENCES

- Aavik, T., Liira, J., 2009. Agrotolerant and high nature-value species - Plant biodiversity indicator groups in agroecosystems. *Ecological Indicators* 9, 892-901.
- Aude, E., Tybirk, K., Michelsen, A., Ejrnæs, R., Hald, A. B., Mark, S., 2004. Conservation value of the herbaceous vegetation in hedgerows - does organic farming make a difference? *Biological Conservation* 118, 467-478.
- Bain, A. B., Attridge, T. H., 1988. Shade-light mediated responses in field and hedgerow populations of *Galium aparine* L. *Journal of Experimental Botany* 39, 1759-1764.
- Bates, F. S., Harris, S., 2009. Does hedgerow management on organic farms benefit small mammal populations? *Agriculture, Ecosystems and Environment* 129, 124-130.

- Bates, G. H., 1937. The vegetation of wayside and hedgerow. *Journal of Ecology* 25, 469-481.
- Baudry, J., 1993. Landscape dynamics and farming systems: problems relating patterns and predicting ecological changes. In: Bunce, R. G. H., Ryszkowski, L., Paoletti, M. G. (eds). *Landscape Ecology and Agroecosystems*. Lewis Publishers, Boca Raton, USA, 21-40.
- Baudry, J., Bunce, R. G. H., Burel, F., 2000. Hedgerows: An international perspective on their origin, function and management. *Journal of Environmental Management* 60, 7-22.
- Bierzuchudek, P., 1982. Life history and demography of shade-tolerant temperate forest herbs: a review. *New Phytologist* 90, 757-776.
- Bird, P. R., Bicknell, D., Bulman, P. A., Burke, S. J. A., Leys, J. F., Parker, J. N., Van der Sommen, F. J., Voller, P., 1992. The role of shelter in Australia for protecting soils, plants and livestock. *Agroforestry Systems* 20, 59-86.
- Bossuyt, B., Hermy, M., Deckers, B., 1999. Migration of herbaceous plant species across ancient-recent forest ecotones in central Belgium. *Journal of Ecology* 87, 628-638.
- Boutin, C., Baril, A., Martin, P. A., 2008. Plant diversity in crop fields and woody hedgerows of organic and conventional farms in contrasting landscapes. *Agriculture, Ecosystems and Environment* 123, 185-193.
- Boutin, C., Jobin, B., Bélanger, L., Choinière, L., 2002. Plant diversity in three types of hedgerows adjacent to cropfields. *Biodiversity and Conservation* 11, 1-25.
- Burel, F., 1996. Hedgerows and their role in agricultural landscapes. *Critical Reviews in Plant Sciences* 15, 169-190.
- Burel, F., Baudry, J., 1994. Control of biodiversity in hedgerow network landscapes in Western France. In: Watt, T. A., Buckley, P. (eds). *Hedgerow management and nature conservation*. Wye College Press, Ashford, UK, 47-57.
- Burel, F., Baudry, J., 1995. Social, aesthetic and ecological aspects of hedgerows in rural landscapes as a framework for greenways. *Landscape and Urban Planning* 33, 327-340.
- Cain, M. L., Damman, H., Muir, A., 1998. Seed dispersal and the holocene migration of woodland herbs. *Ecological Monographs* 68, 325-347.
- Campagne, P., Affre, L., Baumel, A., Roche, P., Taton, T., 2009. Fine-scale response to landscape structure in *Primula vulgaris* Huds.: does hedgerow network connectedness ensure connectivity through gene flow? *Population Ecology* 51, 209-219.
- Chincarini, M., Padoa-Schioppa, E., 2001. The ecological evaluation of hedgerows: a first attempt at a practical approach. In: Barr, C. J., Petit, S. (eds). *Hedgerows of the world: their functions in different landscapes*. IALE, Birmingham, UK, 81-86.
- Corbit, M., Marks, P. L., Gardescu, S., 1999. Hedgerows as habitat corridors for forest herbs in central New York, USA. *Journal of Ecology* 87, 220-232.

- Cummins, R. P., French, D. D., 1994. Floristic diversity, management and associated land use in British hedgerows. In: Watt, T. A., Buckley, P. (eds). *Hedgerow management and nature conservation*. Wye College Press, Ashford, UK, 95-106.
- de Blois, S., Domon, G., Bouchard, A., 2002. Factors affecting plant distribution in hedgerows of southern Quebec. *Biological Conservation* 105, 355-367.
- De Keersmaecker, L., Martens, L., Verheyen, K., Hermy, M., De Schrijver, A., Lust, N., 2004. Impact of soil fertility and insolation on diversity of herbaceous woodland species colonizing afforestations in Muizen forest (Belgium). *Forest Ecology and Management* 188, 291-304.
- De Snoo, G. R., van der Poll, R. J., 1999. Effect of herbicide drift on adjacent boundary vegetation. *Agriculture, Ecosystems and Environment* 73, 1-6.
- Deckers, B., Hermy, M., Muys, B., 2004. Factors affecting plant species composition of hedgerows: relative importance and hierarchy. *Acta Oecologica* 26, 23-37.
- Dzwonko, Z., 2001. Effect of proximity to ancient deciduous woodland on restoration of the field layer vegetation in a pine plantation. *Ecography* 24, 198-204.
- Endels, P., Adriaens, D., Verheyen, K., Hermy, M., 2004. Population structure and adult plant performance of forest herbs in three contrasting habitats. *Ecography* 27, 225-241.
- Eschenbach, C., Lilienfein, U., von Stamm, S., 1996. Bestandesklima im Knick. *EcoSys: Beiträge zur Ökosystemforschung* 5, 77-89.
- Follain, S., Walter, C., Bonté, P., Marguerie, D., Lefevre, I., 2009. A-horizon dynamics in a historical hedged landscape. *Geoderma* 150, 334-343.
- Follain, S., Walter, C., Legout, A., Lemercier, B., Dutin, G., 2007. Induced effects of hedgerow networks on soil organic carbon storage within an agricultural landscape. *Geoderma* 142, 80-95.
- Forman, R. T. T., 1991. Landscape corridors: from theoretical foundations to public policy. In: Saunders, D. A., Hobbs, R. J. (eds). *Nature Conservation 2: The Role of Corridors*. Surrey Beaty & Sons, Chipping Norton, UK, 71-84.
- Francis, J. L., Morton, A. J., Boorman, L. A., 1992. The establishment of ground flora species in recently planted woodland. *Aspects of Applied Biology* 29, 171-178.
- Freemark, K. E., Boutin, C., Keddy, C. J., 2002. Importance of farmland habitats for conservation of plant species. *Conservation Biology* 16, 399-412.
- Fritz, R., Merriam, G., 1993. Fencerow habitats for plants moving between farmland forests. *Biological Conservation* 64, 141-148.
- Fuller, R. J., Norton, L., Feber, R., Johnson, P., Chamberlain, D., Joys, A., Mathews, F., Stuart, R., Townsend, M. C., Manley, W., Wolfe, M., Macdonald, D. W., Firbank, L., 2005. Benefits of organic farming to biodiversity vary among taxa. *Biology Letters* 1, 431-434.
- Garbutt, R. A., Sparks, T. H., 2002. Changes in the botanical diversity of a species rich ancient hedgerow between two surveys (1971-1998). *Biological Conservation* 106, 273-278.

- Garve, E., 2004. Rote Liste und Florenliste der Farn- und Blütenpflanzen in Niedersachsen und Bremen. *Informationsdienst Naturschutz Niedersachsen* 24, 1-76.
- Gould, A. M. A., Gorchov, D. L., 2000. Effects of the exotic invasive shrub *Lonicera maackii* on the survival and fecundity of three species of native annuals. *American Midland Naturalist* 144, 36-50.
- Haddad, N. M., Bowne, D. R., Cunningham, A., Danielson, B. J., Levey, D. J., Sargent, S., Spira, T., 2003. Corridor use by diverse taxa. *Ecology* 84, 609-615.
- Haddad, N. M., Tewksbury, J. J., 2006. Impacts of corridors on populations and communities. In: Crooks, K. R., Sanjayan, M. (eds). *Connectivity Conservation*. Cambridge University Press, Cambridge, UK, 390-415.
- Hegarty, C. A., McAdam, J. H., Cooper, A., 1994. Factors influencing the plant species composition of hedges - implications for management in environmentally sensitive areas. *British Crop Protection Council Monographs* 58, 227-234.
- Hole, D. G., Perkins, A. J., Wilson, J. D., Alexander, I. H., Grice, P. V., Evans, A. D., 2005. Does organic farming benefit biodiversity? *Biological Conservation* 122, 113-130.
- Honnay, O., Bossuyt, B., Verheyen, K., Butaye, J., Jacquemyn, H., Hermy, M., 2002a. Ecological perspectives for the restoration of plant communities in European temperate forests. *Biodiversity and Conservation* 11, 213-242.
- Honnay, O., Verheyen, K., Butaye, J., Jacquemyn, H., Bossuyt, B., Hermy, M., 2002b. Possible effects of habitat fragmentation and climate change on the range of forest plant species. *Ecology Letters* 5, 525-530.
- Hopwood, J. L., 2008. The contribution of roadside grassland restorations to native bee conservation. *Biological Conservation* 141, 2632-2640.
- Hughes, J. W., Fahey, T. J., 1991. Colonization dynamics of herbs and shrubs in a disturbed northern hardwood forest. *Journal of Ecology* 79, 605-616.
- Jobin, B., Boutin, C., DesGranges, J., 1997. Effects of agricultural practices on the flora of hedgerows and woodland edges in southern Quebec. *Canadian Journal of Plant Science* 77, 293-299.
- Jones, A. T., Hayes, M. J., Sackville Hamilton, N. R., 2001. The effect of provenance on the performance of *Crataegus monogyna* in hedges. *Journal of Applied Ecology* 38, 952-962.
- Kleijn, D., Verbeek, M., 2000. Factors affecting the species composition of arable field boundary vegetation. *Journal of Applied Ecology* 37, 256-266.
- Kolb, A., 2005. *The distribution of forest plant species in a fragmented landscape: patterns and processes*. University of Bremen, Bremen, Germany.
- Kolb, A., 2008. Habitat fragmentation reduces plant fitness by disturbing pollination and modifying response to herbivory. *Biological Conservation* 141, 2540-2549.
- Kolb, A., Diekmann, M., 2004. Effects of environment, habitat configuration and forest continuity on the distribution of forest plant species. *Journal of Vegetation Science* 15, 199-208.

- Kort, J., 1988. Benefits of windbreaks to field and forage crops. *Agriculture, Ecosystems and Environment* 22/23, 165-190.
- Lauer, W., Bendix, J., 2004. *Klimatologie*. Westermann, Braunschweig, Germany.
- Le Cœur, D., Baudry, J., Burel, F., 1997. Field margins plant assemblages: variation partitioning between local and landscape factors. *Landscape and Urban Planning* 37, 57-71.
- Levey, D. J., Bolker, B. M., Tewksbury, J. J., Sargent, S., Haddad, N. M., 2005. Effects of landscape corridors on seed dispersal by birds. *Science* 309, 146-148.
- Marshall, E. J. P., Arnold, G. M., 1995. Factors affecting field weed and field margin flora on a farm in Essex, UK. *Landscape and Urban Planning* 31, 205-216.
- Marshall, E. J. P., Moonen, A. C., 2002. Field margins in northern Europe: their functions and interactions with agriculture. *Agriculture, Ecosystems and Environment* 89, 5-21.
- Martin, B., Vanpeene-Bruhier, S., Brun, J. J., 2001. Spatial and ecological knowledge of the mountain bocage of Champsaur (French Alps). In: Barr, C. J., Petit, S. (eds). *Hedgerows of the world: their functions in different landscapes*. IALE, Birmingham, UK, 273-278.
- Matlack, G. R., 1994. Plant species migration in a mixed-history forest landscape in Eastern North America. *Ecology* 75, 1491-1502.
- Matlack, G. R., Monde, J., 2004. Consequences of low mobility in spatially and temporally heterogeneous ecosystems. *Journal of Ecology* 92, 1025-1035.
- McCollin, D., Jackson, J. I., Bunce, R. G. H., Barr, C. J., Stuart, R., 2000. Hedgerows as habitat for woodland plants. *Journal of Environmental Management* 60, 77-90.
- McLachlan, S. M., Bazely, D. R., 2001. Recovery patterns of understorey herbs and their use as indicators of deciduous forest regeneration. *Conservation Biology* 15, 98-110.
- Mercer, C., Cherrill, A., Tudor, G., Andrews, M., 1999. Hedgerow plant communities: relationship with adjacent land use and aspect. *Aspects of Applied Biology* 54, 345-352.
- Mette, R., 1996. Funktion und Wirkung von Knicks in der Agrarlandschaft. *EcoSys: Beiträge zur Ökosystemforschung* 5, 175-191.
- Mette, R., 2005. Energetische Verwertung von Landschaftspflegeholz am Beispiel der schleswig-holsteinischen Knicklandschaft. *Natur und Landschaft* 80, 416-420.
- Mieth, B., Kutsch, W. L., Kappen, L., 1996. *Lamiaeum galeobdolon* und *Galium aparine* als erfolgreiche Knickbodenpflanzen. *EcoSys: Beiträge zur Ökosystemforschung* 5, 163-174.
- Moonen, A. C., Marshall, E. J. P., 2001. The influence of sown margin strips, management and boundary structure on herbaceous field margin vegetation in two neighbouring farms in southern England. *Agriculture, Ecosystems and Environment* 86, 187-202.
- Niedersächsisches Landesamt für Statistik (ed), 2007. Bodennutzung und Ernte 2007. *Statistische Berichte Niedersachsen* 2007, 1-54.

- Norton, L., Johnson, P., Joys, A., Stuart, R., Chamberlain, D., Feber, R., Firbank, L., Manley, W., Wolfe, M., Fuller, R. J., 2009. Consequences of organic and non-organic farming practices for field, farm and landscape complexity. *Agriculture, Ecosystems and Environment* 129, 221-227.
- Noss, R. F., 1993. Wildlife Corridors. In: Smith, D. S., Hellmund, P. C. (eds). *Ecology of greenways: design and function of linear conservation areas*. University of Minnesota Press, Minneapolis, USA, 43-68.
- Packham, J. R., Willis, A. J., 1982. The influence of shading and of soil type on the growth of *Galeobdolon luteum*. *Journal of Ecology* 70, 491-512.
- Pollard, E., 1973. Hedges: VII. Woodland Relic Hedges in Huntington and Peterborough. *Journal of Ecology* 61, 343-352.
- Rode, M., 2005. Energetische Nutzung von Biomasse und der Naturschutz. *Natur und Landschaft* 80, 403-412.
- Roy, V., de Blois, S., 2006. Using functional traits to assess the role of hedgerow corridors as environmental filters for forest herbs. *Biological Conservation* 130, 592-603.
- Roy, V., de Blois, S., 2008. Evaluating hedgerow corridors for the conservation of native forest herb diversity. *Biological Conservation* 141, 298-307.
- Saunders, D. A., 2007. Connectivity, corridors and stepping stones. In: Lindenmayer, D. B., Hobbs, R. J. (eds). *Landscapes for conservation: moving from perspectives to principles*. Blackwell Publishing, Oxford, UK, 280-289.
- Schmidt, T., Arens, P., Smulders, M. J. M., Billeter, R., Liira, J., Augenstein, I., Durka, W., in press. Effects of landscape structure on genetic diversity of *Geum urbanum* L. populations in agricultural landscapes. *Flora*, doi:10.1016/j.flora.2008.07.005.
- Schrautzer, J., von Stamm, S., Tidow, S., 1996. Vegetation der Knicks. *EcoSys: Beiträge zur Ökosystemforschung* 5, 29-37.
- Sitzia, T., 2007. Hedgerows as corridors for woodland plants: a test on the Po Plain, northern Italy. *Plant Ecology* 188, 235-252.
- Sullivan, T. P., Sullivan, D. S., 2009. Are linear habitats in agrarian landscapes source areas of beneficial or pest rodents? *Agriculture, Ecosystems and Environment* 129, 52-56.
- Tewksbury, J. J., Levey, D. J., Haddad, N. M., Sargent, S., Orrock, J. L., Weldon, A., Danielson, B. J., Brinkerhoff, J., Damschen, E. I., Townsend, P., 2002. Corridors affect plants, animals, and their interactions in fragmented landscapes. *PNAS* 99, 12923-12926.
- Tischler, W., 1951. Die Hecke als Lebensraum für Pflanzen und Tiere, unter besonderer Berücksichtigung ihrer Schädlinge. *Erdkunde* 5, 125-132.
- Tsiouris, S., Marshall, E. J. P., 1998. Observations on patterns of granular fertiliser deposition beside hedges and its likely effects on the botanical composition of field margins. *Annals of Applied Biology* 132, 115-127.

- Vellend, M., Verheyen, K., Jacquemyn, H., Kolb, A., van Calster, H., Peterken, G., Hermy, M., 2006. Extinction debt of forest plants persists for more than a century following habitat fragmentation. *Ecology* 87, 542-548.
- Verheyen, K., Hermy, M., 2001. Spatio-temporal colonization patterns of forest plant species in a mixed deciduous forest. *Journal of Vegetation Science* 12, 567-578.
- Verheyen, K., Honnay, O., Motzkin, G., Hermy, M., Foster, D. R., 2003. Response of forest plant species to land-use change: a life-history trait-based approach. *Journal of Ecology* 91, 563-577.
- Weber, H. E., 1967. *Über die Vegetation der Knicks in Schleswig-Holstein Teil 1*. Raabe, E.-W.; Kiel, Germany.
- Weber, H. E., 2003. *Gebüsche, Hecken, Krautsäume*. Verlag Eugen Ulmer, Stuttgart, Germany.
- Whigham, D. F., 2004. Ecology of woodland herbs in temperate deciduous forests. *Annual Review of Ecology, Evolution and Systematics* 35, 583-621.
- Willi, J. C., Mountford, J. O., Sparks, T. H., 2005. The modification of ancient woodland ground flora at arable edges. *Biodiversity and Conservation* 14, 3215-3233.
- Woodward, F. I., 1987. *Climate and plant distribution*. Cambridge University Press, Cambridge, UK.
- Wulf, M., 1992. Vegetationskundliche und ökologische Untersuchungen zum Vorkommen gefährdeter Pflanzenarten in Feuchtwäldern Nordwestdeutschlands. *Dissertationes Botanicae* 185, 1-246.

APPENDICES

- Appendix 1** Supplement to Chapter 3: Wehling, S. & Diekmann, M., 2008. Factors influencing the spatial distribution of forest plant species in hedgerows of North-western Germany. *Biodiversity and Conservation* 17, 2799-2813.
- Appendix 2** Supplement to Chapter 6: Wehling, S., Diekmann, M. Forest herbs in European hedgerows: prediction of changes in the species composition of different hedgerow networks along a climate gradient. submitted.

Appendix 1: List of forest species (definition according to Schmidt et al., 2002) found in the forests neighbouring the studied hedgerow transects. In addition, information about the presence of these species in the hedgerow transects is given (presence - 1, absence - 0). Forest edge and gap species are indicated by an asterisk, others are true forest specialists.

	Hedgerow
<i>Adoxa moschatellina</i>	1
<i>Alliaria petiolata</i> *	1
<i>Anemone nemorosa</i>	1
<i>Athyrium filix-femina</i>	1
<i>Blechnum spicant</i>	1
<i>Cardamine impatiens</i> *	0
<i>Cardamine amara</i>	1
<i>Carex sylvatica</i>	1
<i>Chaerophyllum temulum</i> *	1
<i>Chelidonium majus</i> *	1
<i>Chrysosplenium alternifolium</i>	0
<i>Circaea lutetiana</i>	1
<i>Convallaria majalis</i>	0
<i>Digitalis purpurea</i> *	1
<i>Dryopteris carthusiana</i>	1
<i>Dryopteris filix-mas</i>	1
<i>Epilobium angustifolium</i> *	1
<i>Epilobium montanum</i>	1
<i>Equisetum hyemale</i>	0
<i>Equisetum sylvaticum</i>	1
<i>Festuca gigantea</i>	1
<i>Galium odoratum</i>	0
<i>Geum urbanum</i> *	1
<i>Humulus lupulus</i> *	1
<i>Hyacinthoides non-scripta</i>	0
<i>Impatiens noli-tangere</i>	1
<i>Impatiens parviflora</i>	1
<i>Lamium argentatum</i>	1
<i>Lamium galeobdolon</i>	1
<i>Lysimachia nemorum</i>	1
<i>Maianthemum bifolium</i>	1
<i>Melampyrum pratense</i>	1
<i>Mercurialis perennis</i>	0
<i>Milium effusum</i>	1
<i>Oxalis acetosella</i>	1
<i>Phyteuma nigrum</i>	1
<i>Polygonatum multiflorum</i>	1
<i>Polypodium vulgare</i>	1
<i>Primula elatior</i>	0
<i>Pteridium aquilinum</i>	1
<i>Rumex sanguineus</i>	0
<i>Sanicula europaea</i>	0
<i>Scrophularia nodosa</i>	1
<i>Stachys sylvatica</i>	1
<i>Stellaria holostea</i>	1
<i>Teucrium scorodonia</i> *	1
<i>Vinca minor</i>	0
<i>Viola reichenbachiana</i>	1

Appendix 2: List of taxa considered as forest species and their presence / absence (+ / -) in the selected studies. Botanical nomenclature follows Wisskirchen & Haeupler (1998). The numbers refer to the studies listed in Table 1: 1 – UK (McCollin et al., 2000), 2 – Belgium (Deckers et al., 2005a), 3 – Germany (unpublished), 4 – UK (Smart et al., 2001), 5 – France (Le Cœur et al., 1997), 6 – Belgium (Deckers et al., 2004a), 7 – UK (Helliwell, 1975), 8 – Belgium (Deckers et al., 2004b), 9 – UK (Andrews et al., 1999), 10 – Italy (Sitzia, 2007), 11 – UK (Cherrill et al., 2001), 12 – UK (Sparks et al., 2000), 13 – UK (Cummins & French, 1994).

	1	2	3	4	5	6	7	8	9	10	11	12	13
<i>Adoxa moschatellina</i>	+	+	+	-	-	-	-	-	-	-	-	-	-
<i>Aegopodium podagraria</i>	+	-	-	-	-	-	-	-	-	+	+	-	-
<i>Agrimonia eupatoria</i>	-	+	-	-	-	-	-	-	-	-	-	-	-
<i>Ajuga reptans</i>	+	+	-	-	-	+	+	+	-	-	-	-	-
<i>Alliaria petiolata</i>	+	+	+	-	-	+	-	+	+	-	-	+	-
<i>Allium ursinum</i>	+	+	-	-	-	-	-	-	-	-	-	-	-
<i>Anemone nemorosa</i>	+	+	+	+	-	-	-	-	-	+	-	-	-
<i>Arum maculatum</i>	+	+	-	-	-	-	+	-	+	+	+	-	+
<i>Asarum europaeum</i>	-	-	-	-	-	-	-	-	-	+	-	-	-
<i>Asparagus tenuifolius</i>	-	-	-	-	-	-	-	-	-	+	-	-	-
<i>Asplenium adiantum-nigrum</i>	+	-	-	-	-	-	-	-	-	-	-	-	-
<i>Asplenium scolopendrium</i>	-	-	-	+	-	-	-	-	-	-	-	-	-
<i>Athyrium filix-femina</i>	+	+	+	+	-	+	-	+	-	-	-	-	-
<i>Atropa bella-donna</i>	+	-	-	-	-	-	-	-	-	-	-	-	-
<i>Betonica officinalis</i>	-	+	-	+	+	-	+	-	-	-	-	-	-
<i>Blechnum spicant</i>	+	-	+	+	-	-	-	-	-	-	-	-	-
<i>Brachypodium sylvaticum</i>	+	+	-	-	+	-	+	-	+	+	-	-	+
<i>Bromus ramosus</i>	+	-	-	+	-	-	+	-	+	-	+	-	-
<i>Calamagrostis epigejos</i>	-	+	-	+	-	-	-	-	-	-	-	-	-
<i>Campanula trachelium</i>	-	+	-	-	-	-	-	-	-	-	-	-	-
<i>Cardamine amara</i>	-	-	+	-	-	-	-	-	-	-	-	-	-
<i>Cardamine flexuosa</i>	+	+	-	-	-	+	-	+	-	-	-	-	-
<i>Cardamine impatiens</i>	+	-	-	-	-	-	-	-	-	-	-	-	-
<i>Carex laevigata</i>	+	-	-	-	-	-	-	-	-	-	-	-	-
<i>Carex pendula</i>	+	-	-	-	-	-	-	-	-	+	-	-	-
<i>Carex remota</i>	+	-	-	-	+	-	-	-	-	-	-	-	-
<i>Carex sylvatica</i>	+	+	+	-	-	-	-	-	-	-	+	-	-
<i>Cephalanthera damasonium</i>	-	-	-	-	-	-	-	-	-	+	-	-	-
<i>Chaerophyllum temulum</i>	-	+	+	-	+	+	-	+	+	-	-	-	-
<i>Chelidonium majus</i>	+	-	+	-	-	-	-	-	-	-	-	-	-
<i>Chrysosplenium oppositifolium</i>	+	-	-	+	-	-	-	-	-	-	-	-	-
<i>Circaea lutetiana</i>	+	+	+	-	+	-	-	-	-	-	-	-	-
<i>Cirsium oleraceum</i>	-	+	-	-	-	-	-	-	-	-	-	-	-
<i>Clinopodium vulgare</i>	-	-	-	-	+	-	+	-	-	-	-	-	-
<i>Conopodium majus</i>	+	-	-	+	+	-	-	-	-	-	-	-	-
<i>Convallaria majalis</i>	+	+	+	-	-	-	-	-	-	-	-	-	-
<i>Corydalis solida</i>	-	+	-	-	-	-	-	-	-	-	-	-	-
<i>Cruciata laevipes</i>	+	+	-	+	-	-	-	-	-	-	+	+	-
<i>Deschampsia cespitosa</i>	+	+	-	+	-	+	-	+	-	-	-	-	-
<i>Deschampsia flexuosa</i>	+	+	-	-	-	+	+	+	-	-	-	-	-
<i>Digitalis purpurea</i>	+	+	+	-	+	+	-	+	+	-	-	-	+
<i>Dyopteris carthusiana</i>	+	+	+	+	-	+	-	-	-	-	-	-	-
<i>Dyopteris dilatata</i>	+	+	-	+	-	+	-	+	+	-	-	-	-

	1	2	3	4	5	6	7	8	9	10	11	12	13
<i>Dryopteris filix-mas</i>	+	+	+	-	+	+	+	+	+	-	+	-	-
<i>Elymus caninus</i>	-	-	-	+	-	-	-	-	-	-	-	-	-
<i>Epilobium angustifolium</i>	-	+	+	-	-	+	-	+	-	-	+	+	+
<i>Epilobium montanum</i>	+	+	+	-	+	-	+	-	-	-	-	-	+
<i>Epilobium obscurum</i>	+	-	-	-	-	-	-	-	-	-	-	-	-
<i>Epipactis helleborine</i>	+	+	-	-	+	-	-	-	-	-	-	-	-
<i>Equisetum hyemale</i>	-	-	+	-	-	-	-	-	-	-	-	-	-
<i>Equisetum sylvaticum</i>	+	-	+	-	-	-	-	-	-	-	-	-	-
<i>Equisetum telmateia</i>	+	-	-	-	-	-	-	-	-	-	-	-	-
<i>Euphorbia amygdaloides</i>	+	-	-	-	+	-	-	-	-	-	-	-	-
<i>Euphorbia dulcis</i>	-	-	-	-	-	-	-	-	-	+	-	-	-
<i>Festuca gigantea</i>	+	+	+	+	-	-	-	-	-	-	-	-	-
<i>Fragaria vesca</i>	+	+	-	+	+	-	+	-	-	-	+	-	-
<i>Galium odoratum</i>	+	+	-	-	-	-	+	-	-	-	-	-	-
<i>Geranium robertianum</i>	+	-	-	+	+	-	+	-	+	-	+	+	-
<i>Geum rivale</i>	+	-	-	+	-	-	-	-	-	-	-	-	-
<i>Geum urbanum</i>	+	+	+	-	+	-	+	-	+	+	+	-	-
<i>Glechoma hederacea</i>	+	-	-	-	+	-	-	-	+	-	+	+	+
<i>Goodyera repens</i>	+	-	-	-	-	-	-	-	-	-	-	-	-
<i>Helleborus viridis</i>	-	+	-	-	-	-	-	-	-	-	-	-	-
<i>Hesperis matronalis</i>	-	-	+	-	-	-	-	-	-	-	-	-	-
<i>Hieracium lachenalii</i>	-	+	-	-	-	-	-	-	-	-	-	-	-
<i>Hieracium laevigatum</i>	-	+	-	-	-	+	-	+	-	-	-	-	-
<i>Hieracium murorum</i>	-	+	-	-	-	-	-	-	-	-	-	-	-
<i>Hieracium sabaudum</i>	-	+	-	-	-	-	-	-	-	-	-	-	-
<i>Holcus mollis</i>	+	+	-	+	-	-	-	-	+	-	-	+	+
<i>Humulus lupulus</i>	+	+	+	-	-	+	-	+	-	-	-	-	-
<i>Hyacinthoides non-scripta</i>	+	+	+	+	+	-	+	-	-	-	-	+	-
<i>Hypericum hirsutum</i>	+	-	-	-	-	-	-	-	-	-	-	-	-
<i>Hypericum maculatum</i>	-	+	-	-	-	-	-	-	-	-	-	-	-
<i>Hypericum pulchrum</i>	+	+	-	-	+	-	+	-	-	-	-	-	-
<i>Impatiens noli-tangere</i>	-	-	+	-	-	-	-	-	-	-	-	-	-
<i>Impatiens parviflora</i>	+	+	+	-	-	-	-	-	-	-	-	-	-
<i>Iris foetidissima</i>	+	-	-	-	-	-	-	-	-	+	-	-	-
<i>Knautia arvensis</i>	-	+	-	-	-	-	-	-	-	-	-	-	-
<i>Lamium galeobdolon</i>	+	+	+	+	-	-	-	-	-	-	-	-	-
<i>Lapsana communis</i>	+	+	-	-	+	+	-	+	+	-	-	+	-
<i>Lilium martagon</i>	+	-	-	-	-	-	-	-	-	-	-	-	-
<i>Listera ovata</i>	+	-	-	-	-	-	-	-	-	-	-	-	-
<i>Luzula pilosa</i>	+	+	-	-	-	-	-	-	-	-	-	-	-
<i>Luzula sylvatica</i>	+	-	-	-	-	-	-	-	-	-	-	-	-
<i>Lysimachia nemorum</i>	+	+	+	+	-	-	-	-	-	-	-	-	-
<i>Lysimachia nummularia</i>	-	-	-	-	-	-	+	-	-	-	-	-	-
<i>Maianthemum bifolium</i>	-	+	+	-	-	-	-	-	-	-	-	-	-
<i>Melampyrum pratense</i>	+	-	+	-	+	-	-	-	-	-	-	-	-
<i>Melica uniflora</i>	+	+	-	+	-	-	+	-	-	-	-	-	-
<i>Mercurialis perennis</i>	+	+	+	-	-	-	+	-	+	-	+	+	-
<i>Milium effusum</i>	+	+	+	-	-	-	-	-	-	-	-	-	-
<i>Moehringia trinervia</i>	+	+	-	+	+	-	-	-	-	-	-	-	-
<i>Mycelis muralis</i>	-	+	-	-	-	-	-	-	-	-	-	-	-
<i>Origanum vulgare</i>	-	+	-	-	-	-	-	-	-	-	-	-	-
<i>Ornithogalum umbellatum</i>	-	+	-	-	-	+	-	+	-	-	-	-	-

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