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# The vegetation of hedgerows in changing agricultural landscapes –

# Past and present patterns

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# SUMMARY

Hedgerows, a prominent landscape element across the oceanic regions of Western and Central Europe, separate agricultural fields and offer near-natural wooded habitat for a variety of plant and animal species. The majority of today's hedgerows were created in the 18th and 19th centuries during the Enclosure Acts, when a shortage of wood led to the planting of hedgerows as living fences. To keep them healthy and stock-proof, the hedgerow's shrub layer needed to be regularly managed, with the management technique employed depending on regional traditions. The intensification of agriculture taking place over the past several decades changed the European cultural landscape - with severe consequences for its biodiversity and ecosystem functioning. Hedgerow management was increasingly neglected and large parts of the European hedgerow network were removed during the land consolidation of the 1960s to 1980s. Since then few new hedgerows have been planted, leaving fragmented habitats and a cleared landscape. When managed properly, hedgerows provide important ecosystem services, such as linking otherwise isolated habitats, reducing erosion by wind and water, and protecting adjacent fields and cattle from strong weather conditions. Today, hedgerows are valued for their ecological and amenity functions and are protected in most European regions.

This thesis studies the vegetation of hedgerows and which factors influence their biodiversity. The patterns found were analysed on different temporal as well as spatial scales to include past and present effects, e.g. of management, agriculture, landscape structure and climate. The results of our resurvey studying historical vegetation plots in hedgerows (Schleswig-Holstein, Northern Germany) demonstrated that the influence of intensive agriculture led to a change in hedgerow vegetation over the past decades. The species composition shifted towards more nitrophilous species. This was due to eutrophication caused by the application of fertilisers on the adjacent agricultural fields. This led to the loss of several rare species and a general decline in species richness in hedgerows. Additionally, a neglect in management of the shrub layer has resulted in a reduction in the number of species.

Over the past centuries, the hedgerow networks varied in their extent, which caused different phases of colonisation and extinction in the hedgerows. When new habitats are created, e.g. by planting a new hedgerow, the colonisation by new plant species usually takes place with a time lag (called the colonisation credit). This particularly holds true for specialist species with low dispersal capacities, such as herbaceous forest plants. We compared pairs of recent and ancient hedgerows and were able to demonstrate that recent hedgerows contained fewer forest specialists, i.e. that there indeed is a colonisation credit. However, the recent hedgerows were colonised faster when the ancient hedgerow partners were in close proximity and could function as source populations. In general, hedgerows in the vicinity of ancient forests and with a wide shrub layer were particularly rich in forest species. Due to regular management hedgerows are preserved in an early stage of succession. Nevertheless, the species composition of recent hedgerows became more similar to that of ancient

hedgerows, suggesting the establishment of a stable vegetation in hedgerows. Hence, with appropriate management, recent hedgerows can develop into valuable habitats similar to the ancient hedgerows within several decades.

The loss or fragmentation of habitats can also lead to a time-lagged adaptation of the species richness (called the extinction debt). Long-living forest species can withstand suboptimal ecological conditions as adult plants. In the long run, however, due to a lack of population rejuvenation these species will go locally extinct if the ecological conditions do not improve. During the land consolidation of the 20th century almost half of the hedgerow network in the study area (Schleswig-Holstein, Northern Germany) was removed, reducing not only the area of the habitat but also its connectivity. We could not demonstrate an extinction debt for the overall group of forest specialists in hedgerows, however, the past landscape structure (hedgerow density and distance to the nearest forest) was found to influence the number of forest species belonging to the subgroup of ancient forest indicator species. These species have particularly low dispersal capacities and are therefore very slow to react to new conditions. This indicates that the habitat loss had been of such a large extent that the extinction debt for the forest specialists had been paid off relatively rapidly. However, analysis was made difficult by influential covariables, such as hedgerow width and distance to the nearest forest, which were negatively correlated to hedgerow density and therefore obscured the species-area-curve.

To also include spatial patterns of the distribution of forest specialists, another study included vegetation relevés of hedgerows with a gradient from Southern Sweden to Northern France. The available data enabled a comprehensive analysis, thus allowing a generalisation of previous results. We could demonstrate that forest species that are thermophilic, resilient to disturbances and can disperse efficiently are particularly frequent in hedgerows. Intensive land-use on adjacent fields reduced the number of forest species. The regional climate played an important role as well since hedgerows in warm regions or under stress of heat and drought events contained fewer forest species. This implies that the forest species richness in Europe is under threat of climate change. In accordance with previous studies, wider hedgerows were richer in forest specialists. The hedgerow width is essential for habitat quality as wide hedgerows provide a more stable microclimate. This will only gain importance in the future, in particular when extreme weather events increase in frequency.

Based on the findings of our research, best practice recommendations are given for future hedgerow management. Regular management is essential to keep hedgerows dense and healthy, and therefore conserving the quality of the habitat. A promotion of mechanical management which is economically profitable might lessen hedgerow neglect. Attention should be paid to maintaining a wide shrub layer which is crucial for the species diversity, particularly in times of climate change. Additionally, a reduction of fertiliser and pesticide input needs to be achieved, e.g. by buffer zones between agricultural fields and hedgerows. Forming hotspots of biodiversity, ancient hedgerows in particular need to be protected, however, the creation of new hedgerows is also vital for increasing the area and connectivity of the habitat in the long run. In conclusion, hedgerows provide a diverse habitat for various plant species, but are under considerable threat by agricultural intensification, habitat loss and climate change. Nature conservation efforts and appropriate management, however, can preserve hedgerows as key elements for the biodiversity in agricultural landscapes.

# ZUSAMMENFASSUNG

Wallhecken (oder „Knicks" wie sie in Schleswig-Holstein genannt werden), ein bedeutendes Landschaftselement in den Agrarlandschaften der von ozeanischem Klima geprägten Regionen West- und Zentraleuropas, grenzen landwirtschaftliche Flächen voneinander ab und bieten einen naturnahen waldähnlichen Lebensraum für zahlreichen Pflanzen- und Tierarten. Der Großteil der heutigen Wallhecken wurde im 18. und 19. Jahrhundert im Zuge der Verkoppelung angelegt, als Holzknappheit dafür sorgte, dass Wallhecken als lebende Zäune gepflanzt wurden. Um die Hecken vital und viehsicher zu halten, mussten die Sträucher regelmäßig gepflegt werden, wobei sich die Pflegemaßnahmen je nach regionaler Tradition unterschieden. Die Intensivierung der Landwirtschaft hat in den vergangenen Jahrzehnten für eine starke Veränderung der europäischen Kulturlandschaft gesorgt - mit dramatischen Auswirkungen für die Biodiversität und ökosystemaren Funktionen. Die Heckenpflege wurde zunehmend vernachlässigt und im Zuge der Flurbereinigungen in den 1960er bis 1980er Jahren wurden große Teile des europäischen Heckennetzwerkes entfernt. Seitdem wurden nur wenige neue Wallhecken angelegt, wodurch die Habitate fragmentiert und die Landschaft ausgeräumt hinterlassen wurden. Bei angemessener Pflege können Wallhecken wichtige Ökosystemdienstleistungen erfüllen, wie z.B. Vernetzung sonst isolierter Lebensräume, Verringerung von Erosion durch Wind und Wasser und Schutz angrenzender Felder und des Weideviehs vor starken Witterungseinflüssen. Heute werden Wallhecken vor allem wegen ihres ökologischen und ästhetischen Werts geschätzt und sind in den meisten europäischen Regionen geschützt.

Diese Doktorarbeit untersucht die Vegetation von Wallhecken und welche Faktoren maßgeblich ihre Artenvielfalt beeinflussen. Dabei wurden die gefundenen Muster sowohl auf verschiedenen zeitlichen als auch räumlichen Skalen analysiert, um frühere als auch heutige Einflüsse, z.B. der Pflege, Landwirtschaft, Landschaftsstruktur und des Klimas, mit einzubeziehen. Die Ergebnisse unserer Wiederaufnahme historischer Vegetationsplots in Wallhecken in Schleswig-Holstein zeigten, dass der Einfluss der Landwirtschaft über die vergangenen Jahrzehnte zu einer Veränderung der Wallhecken-Vegetation geführt hat. Die Artenzusammensetzung hat sich zugunsten von stickstoffliebenden Arten verschoben, was auf die Eutrophierung durch Düngereinsatz auf den angrenzenden landwirtschaftlichen Flächen zurückzuführen ist. Dies sorgte für den Verlust einiger seltener Arten und bedingte einen generellen Rückgang der Artenzahl in Wallhecken. Auch eine Vernachlässigung der Pflege der Strauchschicht sorgte für ein geringeres Artenreichtum.

Über die vergangenen Jahrhunderte gab es große Schwankungen in den Ausmaßen der Heckennetzwerke, was verschiedene Phasen von Besiedelung und Aussterben in den Wallhecken bedingte. Werden neue Habitate geschaffen, z.B. durch die Anlage neuer Hecken, findet die Einwanderung neuer Pflanzenarten meist erst zeitverzögert statt (colonisation credit bzw. „Besiedlungsguthaben" genannt). Dies gilt besonders für Spezialisten mit geringen

Ausbreitungskapazitäten, wie krautige Waldarten. Wir konnten durch den paarweisen Vergleich von jungen und historisch alten Wallhecken zeigen, dass junge Hecken weniger Waldarten beherbergten und somit ein colonisation credit vorliegt. Allerdings wurden die jungen Hecken schneller besiedelt, wenn die historisch alten Heckenpartner in unmittelbarer Nähe zu finden waren und als Quellpopulationen dienen konnten. Generell waren Hecken in der Nähe zu historisch alten Wäldern und mit einer breiten Strauchschicht besonders waldartenreich. Bedingt durch die regelmäßige Pflege werden Wallhecken stets in einem jungen Stadium der Sukzession gehalten. Doch näherte sich die Artenzusammensetzung der jungen Hecken mit der Zeit der der historisch alten Hecken an, was die Entwicklung einer stabilen Wallheckenvegetation nahelegt. Somit können sich neu angelegte Hecken bei geeigneter Pflege innerhalb weniger Jahrzehnte in wertvolle Lebensräume entwickeln, die den historisch alten ähnlich sind.

Auch bei Habitatverlust und -fragmentierung kann es zu einer zeitverzögerten Reaktion des Artenreichtums kommen (extinction debt bzw. „Aussterbeschuld" genannt). Langlebige Waldarten können suboptimale Bedingungen als adulte Pflanzen überdauern. Langfristig sind diese Arten allerdings durch fehlende Verjüngung der Populationen zum lokalen Aussterben bestimmt, wenn sich die Bedingungen nicht verbessern. Im Zuge der Flurbereinigung im 20. Jahrhundert wurde fast die Hälfte des Heckennetzwerkes im Untersuchungsgebiet in Schleswig-Holstein entfernt, was nicht nur die Fläche, sondern auch die Vernetzung des Habitats stark verringert hat. Unsere Untersuchungen konnten keine Aussterbeschuld für die gesamte Gruppe der Waldarten in Wallhecken feststellen, allerdings gab es einen Zusammenhang zwischen der früheren Landschaftsstruktur (Heckendichte und Entfernung zum nächsten Wald) und der Anzahl an Waldarten, die zu der Untergruppe der Zeigerpflanzen für historisch alte Wälder gehören. Diese haben besonders geringe Ausbreitungskapazitäten und passen somit ihre Verbreitung besonders langsam an neue Bedingungen an. Dies weist darauf hin, dass die Ausmaße des Habitatverlusts und der Fragmentierung so stark waren, dass die Aussterbeschuld für Waldarten bereits zeitnah nach dem Verlust beglichen wurde. Erschwert wurden die Analysen allerdings durch einflussreiche Kovariablen, wie Heckenbreite und die Entfernung zum nächsten Wald, die negativ mit der Heckendichte korreliert waren und somit die Arten-Areal-Kurve verzerrten.

Um auch räumliche Muster in der Verbreitung von Waldarten betrachten zu können, umfasste eine weitere Studie Vegetationsaufnahmen aus Wallhecken verteilt über einen Gradienten von Südschweden bis Nordfrankreich. Die Datenlage ermöglichte eine umfassende Auswertung und somit auch eine Verallgemeinerung bisheriger Ergebnisse. Wir konnten zeigen, dass besonders solche Waldarten, die thermophil sowie störungsresistent sind und sich effektiv ausbreiten können, zahlreich in Wallhecken zu finden waren. Eine intensive Landnutzung auf den angrenzenden landwirtschaftlichen Flächen verringerte die Waldartenzahl. Das regionale Klima war von besonderer Bedeutung, denn Wallhecken in warmen Gegenden oder welchen, die von Hitze- und Dürreereignissen beeinflusst wurden, beherbergten weniger Waldarten. Dies deutet auf eine Bedrohung der Waldartenvielfalt in europäischen Hecken unter Einfluss des Klimawandels hin. Wie bereits in früheren Untersuchungen festgestellt, sind breitere Hecken reicher an Waldarten. Die Heckenbreite ist essentiell für eine hohe Habitatqualität, da breitere Wallhecken ein stabileres Mikroklima bieten können. Dies wird besonders im Kontext von häufiger werdenden Extremwetterereignissen in Zukunft noch an Bedeutung gewinnen.

Basierend auf den Forschungsergebnissen wurden anschließend Empfehlungen für eine zukünftige Pflege von Wallhecken formuliert. Eine regelmäßige Pflege ist essentiell, damit die Wallhecken dicht und vital bleiben und so die Lebensraumqualität erhalten wird. Eine Förderung von mechanischer Heckenpflege, die wirtschaftlich rentabel ist, könnte die Vernachlässigung der Wallhecken verringern. Dabei ist zu beachten, dass eine breite Strauchschicht besonders in Zeiten des Klimawandels wesentlich für die Artenvielfalt ist. Auch eine Verringerung von Dünger- und Pestizideintrag muss erreicht werden, z.B. durch Pufferzonen zwischen den landwirtschaftlichen Flächen und den Hecken. Als Hotspots der Artenvielfalt müssen besonders historisch alte Hecken erhalten werden, aber auch die Anlage von neuen Hecken verbessert auf lange Sicht die Fläche und Vernetzung des Habitats. Zusammenfassend bieten Wallhecken einen vielfältigen Lebensraum für zahlreiche Pflanzenarten, der durch die Intensivierung der Landwirtschaft, Habitatverlust und Klimawandel gefährdet wird. Durch Naturschutzmaßnahmen und eine entsprechende Pflege können Wallhecken jedoch als ein Schlüsselelement für die Biodiversität in der Agrarlandschaft erhalten werden.

# CHAPTER 1

## Introduction



Hedgerow landscape in the Schleswig-Holstein Morainic Upland close to the Bungsberg, the highest elevation in Schleswig-Holstein.

## General introduction

The face of the earth has been shaped by humans for thousands of years. Since the adoption of agriculture in the Neolithic period (about 6,000 years ago in Northern Central Europe) the human influence on the landscape has steadily grown (Delcourt, 1987; Hooke, 2000; Kirleis et al., 2012). Forests were cleared for settlements, agricultural fields, pastures and gardens (Williams, 2008). To protect the crops from roaming livestock and deer, the cultivated land needed to be enclosed with fences. These were not only built from wood or brushwood but often also planted as "living fences", i.e. hedgerows (Burel, 1996). Instead of further depleting the often scarce timber resources, hedgerows were sustainable and even provided timber and firewood for the farmers. The first hedgerows were created probably already over 1,000 years ago and their importance steadily increased to later become a key element of the agricultural landscapes, fulfilling numerous ecosystem services (Pollard et al., 1974; Stamm & Welters, 1996; Van Vooren et al., 2017).

The recent cultural landscape is the product of a long time of human interaction with the environment (Phillips, 1998). Therefore, it is essential to consider the influence of past as well as present human activities on plant communities if we want to understand their patterns and processes. The peak in biodiversity of cultural landscapes was supposedly at the end of the 19th century, when many different land-use practices were applied in parallel on a small scale (Poschlod, 2015). Over the past century, the agricultural intensification, which included the introduction of artificial fertilisers, biocides, big machinery and organised clearing of small landscape elements, was identified as a major threat to species richness (Korneck et al., 1998; Stoate et al., 2001). The effect of changing landscapes on patterns of species richness needs to be investigated across different habitats as well as on different temporal and spatial scales to gain a comprehensive understanding of the underlying processes. This thesis strives to do so by focusing on hedgerows and their vegetation in the agricultural landscapes of Europe.

## Studying vegetation dynamics

### *On a temporal scale: Resurvey studies*

Cultural landscapes and their history are of growing interest to nature conservation (Phillips, 1998; Bridgewater & Rotherham, 2019). Human interaction with the surrounding environment has formed landscapes with a large biodiversity and high conservation value. The continuous traditional management is an essential part of these systems and any changes of this management regime can alter the ecological conditions and cause biodiversity loss (Rotherham, 2015). Historical ecology seeks to understand the long-term vegetation dynamics caused by the interaction of humans with their surrounding landscape (Szabó, 2015). The intensification of agriculture over the past decades has led to ongoing habitat change with a substantial, yet not fully understood, impact on biodiversity. Small natural features, such as hedgerows, field margins and forest fringes, were removed (Poschlod & Braun-Reichert, 2017), mineral fertilisers and biocides were introduced and increasingly big machinery was established to economically cultivate the land.

These changes can be investigated by comparing the earlier, less intensified landscape with the current, industrialised agricultural landscape. Thus, insights into past diversity patterns can increase the understanding of today's patterns and enable us to predict the effect of future changes. One

approach to understand vegetation dynamics over time are resurvey studies. Historical study plots are revisited by repeating the original methods as best as possible, and then the historical records of species composition are compared to the present species assemblages. The time span between the surveys ranges from several years to decades and exceptionally even centuries (Kapfer et al., 2017). By this, even slow vegetation changes can be detected and related to underlying environmental factors.

Resurvey studies have increased in popularity in recent years (Kapfer et al., 2017). They can be a very valuable tool when potential biases are minimised. When the original plot position was not well documented or information was lost over time, it can prove challenging to re-locate the original plots. However, also semi-permanent plots that are positioned carefully without knowing the exact location can provide valuable scientific results (Kopecký & Macek, 2015), especially in relatively homogenous landscapes. Other biases can be caused by differences in methodology, e.g. with respect to sampling time or plot size, or by deviating taxonomic specificity or expertise due to different observers.

Resurvey studies seek to relate the differences in species composition to changes in the environmental conditions (Hédl et al., 2017). However, the historical records often lack environmental measurements. Therefore, mean Ellenberg indicator values or functional traits have often been used as proxies for environmental change (Hédl et al., 2017). While many resurvey studies have been conducted on forests (e.g. Naaf & Wulf, 2011; Verheyen et al., 2012; Vanhellemont et al., 2014; Bernhardt-Römermann et al., 2015), other wooded habitats such as hedgerows have only rarely been studied (but see Huwer & Wittig, 2012; Staley et al., 2013; Van Den Berge et al., 2019).

### *On a spatial scale: Macroecological studies*

Most studies investigating species richness and its drivers are conducted on a local scale and therefore do not allow for generalisations of the findings. Studies on a broader, e.g. national or continental, scale can provide insight into large-scale ecological processes (Gaston & Blackburn, 1999). Macroecology deals with understanding species richness patterns at large spatial and temporal scales (Brown & Maurer, 1989), this thesis will focus on the spatial aspect of macroecology. Spatial studies often cover gradients of environmental, climate or land-use variables that are related to the vegetation patterns (Buckley & Puy, 2022). Studies including a sufficient amount of plot data can be used to differentiate large-scale general patterns from distinct local patterns (McGill, 2019). Another opportunity is to use the variation in ecological conditions along a spatial gradient as a proxy for variation in time, i.e. a climatic gradient can serve as a proxy for climate change. This approach, the space-for-time substitution, is often used to predict the effects of temporal change on biodiversity (Blois et al., 2013).

Many macroecological studies have been conducted on forest habitats across Europe with a focus on, e.g., the influence of environmental factors on forest understorey plant communities (Verheyen et al., 2012; Bernhardt-Römermann et al., 2015), colonisation processes (De Frenne et al., 2011), forest fragmentation (Naaf et al., 2021) or landscape characteristics (Naaf et al., 2022). In recent years, also hedgerows were studied along gradients across Europe in the context of dispersal along these corridors (Vanneste et al., 2020a), of being a habitat for forest understorey plants (Wehling &

Diekmann, 2010; Vanneste et al., 2020c) and of climate effects (Vanneste et al., 2020b). More macroecological studies on hedgerows including other variables or extending the spatial scale may improve the understanding of hedgerow vegetation across Europe.

## Ecological concepts describing dynamics of species richness

### *Extinction debt*

After habitat loss or degradation, species richness is likely to be reduced. While the destruction of habitats causes the immediate local extinction of species, the effects of habitat deterioration or fragmentation can occur with a time-lag (Figure 1.1) (Tilman et al., 1994). Many plant species are long-lived with extended generation times. Therefore, a plant population can over a long time withstand suboptimal conditions, even if individuals do not reproduce and population sizes are declining. This leads to a higher species richness than one might expect from the prevailing ecological conditions. However, because some of the species are predicted to go (locally) extinct in the long-run, this effect of delayed extinctions is called the extinction debt (Tilman et al., 1994).

The time it takes for a community to reach a new equilibrium after a habitat has changed is called the relaxation time (Diamond, 1972) and might be as long as several centuries (Vellend et al., 2006; Kolk & Naaf, 2015). An extinction debt is more likely to occur when the destruction event is less severe, however, the species are living just below their extinction threshold (Hylander & Ehrlén, 2013). If the habitat size is only slightly too small or if there are other habitat patches in the vicinity that are large or well connected, this might delay paying off the debt (Kuussaari et al., 2009). Likewise, low dispersal abilities, high habitat specificity and low generational turnover increase the relaxation time (Vellend et al., 2006).



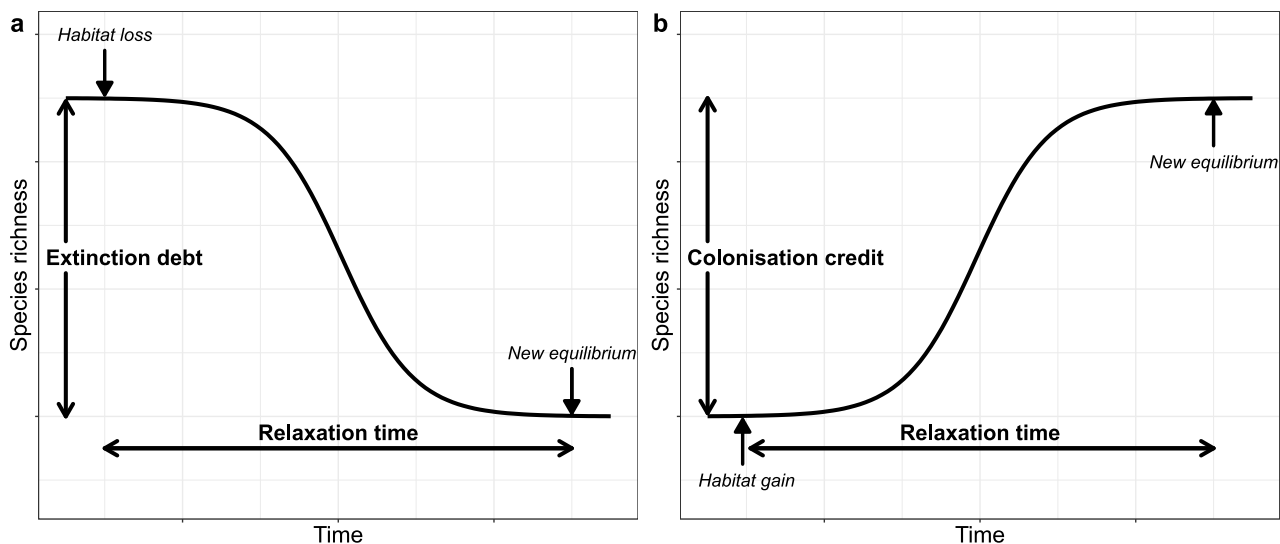Figure 1.1 The species richness adapts with a time-lag to habitat loss or gain (adapted from Kuussaari et al. (2009)). The time it takes from the impact on the habitat until a new equilibrium is reached is called the relaxation time. (a) The extinction debt describes species going extinct later than the time of habitat loss. (b) The colonisation credit is characterised by an immigration delay after new habitat is gained.

The study of extinction debts has increased in recent years (Tilman et al., 1994; Adriaens et al., 2006; Vellend et al., 2006; Jackson & Sax, 2010; Kolk & Naaf, 2015; Deák et al., 2021; Ridding et al., 2021). There are various ways of investigating this phenomenon, the choice of which mainly depends on the data available (Kuussaari et al., 2009; Ridding et al., 2021). When historical data of species richness is lacking, a very common approach includes linking present diversity patterns to past and present habitat characteristics (Figueiredo et al., 2019). If the past habitat quality, connectivity or size explains the present-day species occurrences better than today's habitat characteristics, an extinction debt is assumed (Lindborg & Eriksson, 2004; Adriaens et al., 2006; Deák et al., 2021). To estimate the number of species that are likely to go extinct, the species richness of present-day stable and unstable habitats can be compared, e.g. in intact vs. fragmented habitats. The predicted species richness of unstable habitats is modelled with a species-area-relationship using data from the stable habitats (Helm et al., 2006; Vellend et al., 2006). The difference between the model and the species richness found in the field describes the extinction debt. When historical species data as well as historical habitat data are available, this information can also be used to calculate the magnitude of the extinction debt. This approach has been shown to be the most reliable, but as it requires the most data is used only rarely (Ridding et al., 2021). First, the relationship between species and habitat data before the destruction event is modelled and used to predict the current situation. Then, the prediction is compared to the actual relationship and the extinction debt is estimated from the gap between the two approaches.

The extinction debt has been demonstrated for specialist plant species, e.g. in forests (Vellend et al., 2006) and calcareous grasslands (Helm et al., 2006), while in other studies of grasslands and forests no influence of past landscape characteristics on species richness were found anymore (Cousins et al., 2007; Kolk & Naaf, 2015). Kolk and Naaf (2015) studied highly fragmented forest patches and found the extinction debt to be paid off after 160 years. Even though studies have hinted at possible extinction debts in hedgerows before (Ernoult & Alard, 2011; Closset-Kopp et al., 2016), systematic studies are still lacking. The extinction debt poses a challenge for nature conservation because when the effect of prior habitat loss and fragmentation goes unrecognised, species loss might go on even in protected areas. If the threat is known and understood for varying habitats and land-use histories, there might still be time for habitat restoration and mitigating species loss before the extinction debt is paid off (Kuussaari et al., 2009).

*Colonisation credit*

A concept related to the extinction debt is the colonisation credit (also referred to as immigration credit; Jackson & Sax, 2010). When habitats are newly created or the connectivity, area or quality of suitable habitat patches is increased, the habitat is expected to gain species. However, the process of colonisation is complex and requires successful dispersal, establishment, survival and reproduction. If only one of these successive steps fails, the process must start anew. Therefore, there is often a temporary diversity deficit (namely the colonisation credit). The time until a new equilibrium is reached is called the relaxation time (congruent with the terminology of the extinction debt theory, Figure 1.1) (Jackson & Sax, 2010). The magnitude of the colonisation credit and the relaxation time depends on the efficiency of dispersal and establishment of the "missing" species and the proximity

of a source population (Kolk et al., 2017; Brunet et al., 2021). The timescales for the colonisation credit can range from years to centuries (Jackson & Sax, 2010; Naaf & Kolk, 2015).

The concept and definition of the colonisation credit were established later than that of the extinction debt (Jackson & Sax, 2010). To study or even quantify the colonisation credit, historical data from time periods before the environmental change can be used to compare it to data on the present species richness and composition. Another approach (in addition or by itself) can be to compare the species present in old and recently formed habitats. Several studies have examined the delayed immigration of forest specialists in post-agricultural forests by comparing the species richness of recent and ancient forests to quantify the colonisation credit (Naaf & Kolk, 2015; Kolk et al., 2017; Brunet et al., 2021). Other studies have focused on restoration ecology and demonstrated a colonisation credit for specialist species in restored wet heathlands (Cristofoli et al., 2010) and orchids in restored calcareous grasslands (Gijbels et al., 2012). Studies quantifying the colonisation credit in hedgerows have to the author's knowledge not been performed so far.

The delayed immigration of species poses challenges to nature conservationists and landscape managers, e.g. when restoring a habitat and creating a new nature reserve do not show immediate success. Colonisation credit and extinction debt can also cancel each other out or lead to a transient species surplus or deficit, respectively, when the relaxation times are offset. These processes need to be understood to enable the conservation of the habitats in question, promote species dispersal and predict future changes.

## Study habitat

### Hedgerows: Description and definitions

A hedgerow is a linear landscape element made up of shrubs, trees or both, which are planted in rows between agricultural fields, pastures or meadows. Hedgerows are man-made wooded habitats that are managed in various ways and act as border, barrier or boundary (Baudry et al., 2000). They form valuable biodiversity networks throughout the landscape, which is all the more important as they are often found in landscapes of intensive agriculture (Wehling & Diekmann, 2009b; Van Den Berge et al., 2019). The term bocage refers to a landscape that is characterised by a hedgerow network of many intersecting hedgerows (Forman & Baudry, 1984; Baudry et al., 2000). In German, the term "Wallhecke" is common (meaning hedgerow on a bank), while locally specific terms for hedgerows are used, such as "Knick" (referring to the former management practice of bending and intertwining the branches of shrubs) or "Redder" (describing two parallel hedgerows with each lining one side of a road) in the German province of Schleswig-Holstein.

Their features can be divided into the canopy layer made up of woody species, which are usually planted and managed, as opposed to the hedge bottom, which is usually colonised spontaneously by the herbaceous vegetation (Figure 1.2) (French & Cummins, 2001). The ground layer makes up most of the species diversity of a hedgerow (Deckers et al., 2004b; Critchley et al., 2013). Depending on the region and origin of the hedgerow the bottom might be raised to form an earthen bank and is sometimes accompanied by a ditch on one or both sides (Baudry et al., 2000). Field margins separate the hedgerow from the adjacent agricultural fields.
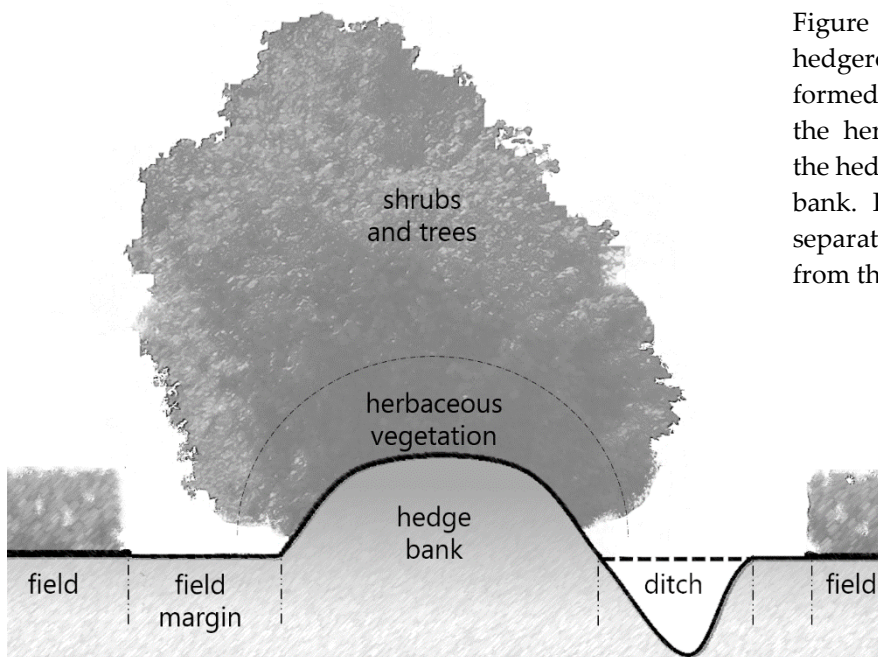
Figure 1.2 Cross section of a typical hedgerow. The canopy layer is formed by shrubs and/or trees while the herbaceous vegetation colonises the hedge bottom, which is raised to a bank. Field margins and/or ditches separate the hedgerow on both sides from the agricultural fields.

There is no uniform usage of the term "hedgerow" (Baudry et al., 2000) and in particular its distinction to a "hedge". Some authors use these terms interchangeably (Pollard et al., 1974). Others distinguish between the woody vegetation, termed the "hedge", and the herbaceous vegetation, termed the "hedge-bottom", while the combination of the two form the "hedgerow" (French & Cummins, 2001). Throughout this thesis, the individual layers are addressed as woody and herbaceous vegetation, while the term "hedgerow" is used for the entire habitat.

### History and origin of hedgerows

Hedgerows have a long tradition in the agricultural landscape of Europe, and their history is strongly intertwined with the development of agriculture in the different regions (Baudry et al., 2000; Poschlod, 2015). Already historical reports from Roman and medieval times mention hedgerows, sometimes in the context of military defence, but also in an agricultural context to protect the common land from roaming livestock and deer. That means that some hedgerows are likely more than 1,000 years old (Hooper, 1970; Pollard et al., 1974). However, the main time of hedgerow construction in Europe was in the 18th and 19th centuries during the time of the Enclosure Acts (Hooper, 1970; Weber, 2003). The open field system was abandoned and the formerly common land was divided and transformed into parcels owned by individuals (Poschlod, 2015). Because wood was sparse, it was decreed to create hedgerows as living fences instead of wooden fences, to enclose the land and mark property lines (Weber, 2003). This process was mainly concentrated on the oceanic areas of Central and Western Europe that were favourable for cattle farming.

The practice of planting hedgerows differed regionally, e.g. concerning size and species used, but they had the common purpose to be stock-proof. At first, two parallel drainage ditches were dug out and the soil mounted up in between to form a raised bank. The size of the bank depended on the region and were either determined by the local authorities or recommended in practical instructions (e.g. Oest, 1767; Graßmann, 1793). They were usually 1.5 to 4.0 metres wide and 0.5 to

2.0 metres high (Huwer & Wittig, 2012). The shrubs planted in two rows (sometimes only one) were fast-growing species with good sprouting abilities (e.g. *Carpinus betulus*, *Corylus avellana*) and often thorny (e.g. *Prunus spinosa*, *Crataegus* spp., *Ulex europaeus*). The density of the created networks depended on the property situation. In areas with large estates and manors, the lots remained large and the network density sparse, while many small farms resulted in a dense network (Weber, 2003). Because livestock could be left untended in the fenced pastures the literacy of peasant children was increased as they could go to school instead of herding the animals (Jensen-Gelting, 1844 as cited in Asmussen, 1912). The process of hedgerow planting was very labour intensive and, in some regions, took several decades to be finished. In Northern Germany and Southern Denmark, enclosing the fields started in 1766 and was mostly concluded in 1780 (Stamm & Welters, 1996), while Hooper (1970) states 1760 to 1845 to be the main period of hedgerow planting in England. Deckers et al. (2005b) report a similar period for Belgium.

Besides planting, which is the most common origin, hedgerows can also arise from assarting or spontaneous growth along a boundary (Forman & Baudry, 1984). Assarting describes the process of clearing a woodland up to the border for agriculture but leaving rows of trees and shrubs (Forman & Baudry, 1984). These forest remnant hedgerows are particularly species-rich (Pollard, 1973). Hedgerows can also grow spontaneously along uncultivated field margins or fences (Forman & Baudry, 1984). Those are also referred to as fencerows and are widespread in agricultural landscapes of the Americas, e.g. in Canada (Fritz & Merriam, 1996; Sykes & Hannon, 2001), Texas, USA (Riffell & Gutzwiller, 1996) or Argentina (Molina et al., 2016). The woody species are not planted but colonise the fencerow by natural dispersal via wind or animals, and there is no regular cutting (Fritz & Merriam, 1996).

For several generations, there was a discourse about the benefits of hedgerows and if they outweigh their costs, in any case, hedgerows were an integral part of the agricultural practices and cultural identity (Erichsen, 1898; Christiansen, 1907; Asmussen, 1912). With the introduction of wire fences, however, hedgerows lost their function as fences, which marked the beginning of their decline. In the 1960s to 1980s, there were profound land consolidation processes in Western and Central Europe to facilitate the intensification of agriculture and clear space for increasingly large machinery. Fields were enlarged by removing small natural features such as hedgerows, ditches, stone walls, single trees or woodlots (Poschlod & Braun-Reichert, 2017). Burel and Baudry (1990) report a loss of one third of the hedgerows in a bocage landscape in Brittany, France, during this period. Eastern Denmark lost about 40 % of the hedgerows (Agger & Brandt, 1988) and even 70 % were lost in networks in Belgium (Van Den Berge et al., 2021) and Northern Germany (Kellerhoff, 1984). This caused a tremendous decline of biodiversity in the cultural landscapes (Poschlod & Braun-Reichert, 2017). It is not known how large these losses were and if they are still on-going, i.e. if the mitigation of habitat loss is still possible or if the extinction debt has already been paid.

After their ecological and amenity functions had been recognised, hedgerow removals were halted in most European areas in the 1990s (Le Cœur et al., 2002; Deckers et al., 2005b). The plantation of new hedgerows was initiated even though these were assumed to be not as species-rich as the lost ancient hedgerows (Eigner, 1982). Knowledge is still lacking how new hedgerows can best be planted to fulfil a similar ecological role as ancient hedgerows. Agri-environment schemes (AES) by the European Union (EU) form a part of the Common Agricultural Policy and intend to protect the environment, use natural resources sustainably and maintain the cultural landscapes. Farmers can

receive subsidies when they choose to manage their farm according to good environmental practice (European Parliament and Council, 2020). Hedgerow establishment and management is part of the AES, however, the details about management, removals, relocations and restoration depend on the national or regional implementation by the EU member states. In Schleswig-Holstein, these are regulated in the "Knickschutzverordnung" that prohibits hedgerow relocations or removals (MLUR, 2013; MELUR, 2017). Exceptions can be made when appropriate compensation measures are included, but not for hedgerows that are ancient or of high ecological value.

*Past and present management*

Management is an integral part of the hedgerow habitat and also a key aspect to consider when studying hedgerows (Deckers et al., 2004a). Therefore, it is important to view hedgerows in the light of the regional agricultural system and traditions (Le Cœur et al., 2002). When they were still needed as stock-proof fences, management was done regularly and extensively, while the details depended on the regional traditions (systematic classification of management techniques is given in Höpfl et al. (2021)). The most widespread techniques included coppicing, pollarding and hedge-laying (Müller, 2013). Coppicing describes a rotational cut of the shrubs near ground level (Figure 1.3 a). This results in a stool from which new shoots emerge (Figure 1.3 b). The hedgerow rejuvenates and the canopy closes again within a few years. The cut off wood and branches were used as fuel, for handiwork and as fodder for the animals (Weber, 2003). Trees growing in the hedgerows were left standing to obtain timber, a practice similar to coppice with standards which was also common for forests. Coppicing was done periodically and in compliance with the crop rotation (Weber, 1967). To minimise shade on the arable fields, the hedgerows were coppiced before the crop period began (which lasted 6 years or more). The shrub layer would grow back over the coming years to be dense when the land was used as pasture again. This resulted in a coppicing cycle of roughly 10 years. As additional measures after coppicing, the ditches were cleared and the excavated soil used to maintain the banks (Weber, 2003). Pollarding is similar to coppicing but the rotational cut is performed at 1-2 m height, reducing browsing damage. Hedge-laying is a craft which was very



Figure 1.3 a) Hedgerow coppiced in the previous winter. A mature individual of *Quercus robur* is left as standard. *Anemone nemorosa* in bloom covers most of the bank. b) Old individual of *Carpinus betulus* that has been coppiced often and developed a wide stool.

common, especially in England, but is only rarely practised today (Müller, 2013; Staley et al., 2013). This involves cutting branches partially, bending and intertwining them in a way that they would form a stock-proof barrier. In addition to those management techniques that have a strong impact on the hedgerow habitat, trimming or pruning is performed more regularly to keep the hedgerows in form or remove only selective branches, respectively.

Today, hedgerow management is often done with large machinery like tractor-mounted flails for trimming (Croxton et al., 2004). When hedgerows are cut every year, the habitat quality for wildlife is reduced because shrubs carry less flowers and berries and the habitat misses structural heterogeneity (Deckers et al., 2004a; Graham et al., 2018). Mechanical flailing may leave branches shattered or smashed at the ends, which then need an additional cut by hand to prevent pathogen infestation. In addition, hedgerows may become very narrow after regular intensive lateral cuts. In Britain, agri-environment schemes are installed to motivate less intensive management and showed an impact on the species composition over relatively short timescales (Stanbury et al., 2020). For mechanical coppicing, tree shears have become popular (Eigner & Gerth, 2020; Smith et al., 2021). Those are mounted on a crawler excavator, can cut through stems of up to 20 cm and place the shrubbery in piles next to the hedgerows by tilting the gripper arm. This method saves time and effort and can be profitable when woodfuel is produced in the process (Eigner & Gerth, 2020; Smith et al., 2021). However, similar to the mechanical flail, the stems might be left injured when pinched off. Therefore, subsequent trimming with a chainsaw is important (Eigner & Gerth, 2020). Hedgerow management is traditionally done in winter when other farming activities are paused and the impact on wildlife is low.

The type of management influences the ecological conditions in the hedgerows. For the shrub species, the way and frequency of cuts influence their fitness in terms of survival and chance of reproduction. For animal species, the management impacts on the availability of shelter, nesting and foraging resources (Graham et al., 2018). Forest plant species are affected by the dimensions of the hedgerow, such as height and width (Deckers et al., 2004a), because wider hedgerows can provide a more stable microclimate, i.e., more forest-like conditions (Vanneste et al., 2020b). Without regular cutting hedgerows become gappy and eventually grow into a line of trees. AES intend to counteract this trend as described above by granting farmers subsidies that meet environmental standards on their farms, including proper hedgerow management. As the AES are implemented nationally or regionally, the form of hedgerow management spatially differs. The federal state of Schleswig-Holstein, Northern Germany, has very specific regulations (MELUR, 2017). Hedgerows need to be coppiced every 10 to 15 years, while trees are left standing at intervals of 40 to 60 m. Lateral cuts are allowed every 3 years but need to maintain a distance of 1 m from the bank. In addition, a protective margin of 50 cm from the bank needs to be maintained that is not tilled, sown or fertilised. These measures are based on the traditional hedgerow management of the region and are intended to ensure the maintenance of the hedgerow landscape and its quality as a habitat for plants and wildlife.

### Ecological properties and ecosystem services

Hedgerows are highly heterogeneous habitats. They resemble two forest edges which are moved very closely together and thus form an ecotone between open and forest-like conditions (Pollard et al., 1974). The main canopy is formed by shrubs and/or trees that provide a shaded interior, while

the hedgerows are bordered by open habitat, usually an agricultural field or grassland, sometimes a road. Because of their linear form, hedgerows have a very high edge-to-interior ratio. They experience strong edge effects and even though the living conditions in the interior are similar to forests, they might be viewed to be closer to forest edges than forest interiors (McCollin et al., 2000). Along a cross-section, a strong differentiation of conditions occurs. The insolation can be extreme on the sunny side but much reduced on the shady side and in the interior. This impacts the microclimate in terms of temperature, relative humidity and soil moisture (Vanneste et al., 2020b). The presence of a bank or even a ditch can further amplify the small-scale edaphic differentiation, e.g. soil moisture is usually highest at the field margins, decreases on the slopes of the bank and increases again on the bank ridge (K. Litza, unpublished). Additionally, the pH values can differ by as much as one unit when compared between the margins, the side and the ridge of the bank (K. Litza, unpublished).

Hedgerows are important semi-natural habitats that increase the woody cover and amount of semi-natural habitat in agricultural landscapes. They act as refuge habitats for forest specialists (Endels et al., 2004; Verheyen & Hermy, 2004; Wehling & Diekmann, 2009a; Van Den Berge et al., 2019; Vanneste et al., 2020c) and serve as migration corridors between otherwise fragmented and isolated forest habitats (Corbit et al., 1999; Wehling & Diekmann, 2009b; Closset-Kopp et al., 2016; Vanneste et al., 2020a), thus increasing the connectivity of a landscape (Almoussawi et al., 2020). A wide variety of mammals, birds and invertebrates uses hedgerows as shelter, nesting sites and foraging ground and forms complex food webs (Graham et al., 2018). Approximately 10,000 animal species can be found in Central European hedgerows, including one half of the native mammals and almost all reptile species (Weber, 2003). Many bird species show a preference for wide and tall hedgerows (Graham et al., 2018), intersections and double hedgerows (Redder) (Puchstein, 1980). The diversity of invertebrates within the agricultural landscape is highest in hedgerows (Graham et al., 2018), the most abundant taxa being Araneae (spiders), Coleoptera (beetles), Diptera (true flies), Hemiptera (true bugs) and Hymenoptera (bees, wasps, ants) (Pollard & Holland, 2006). Many of the organisms living in hedgerows provide crucial ecosystem services such as pest control and pollination (Nicholls & Altieri, 2013; Dainese et al., 2017).

From an agroeconomic point of view, planting hedgerows did not only save wood by creating sustainable "living fences", but they also provided wood which was used as timber, fuel or to make broomsticks, spoons or baskets (Struck, 1940). Hedgerows diversify food resources in the form of edible wildflowers, berries and nuts (Van Den Berge et al., 2018) and shelter the livestock from wind, rain and sun. By reducing the wind speed, they protect the soil from erosion and improve the microclimate as far as several times their height into the adjacent fields (Van Vooren et al., 2017). While in their direct reach crop growth is reduced and ripening delayed because the hedgerow plants shade the crops and compete with them for soil nutrients, the improved microclimate creates an even wider zone of increased yield (Mette, 1994; Van Vooren et al., 2017). The intensification of agriculture involved the increasing use of pesticides and fertilisers. Hedgerows can reduce the drift of those compounds to adjacent ecosystems (Lazzaro et al., 2008). They can also act as biofilters by reducing the amount of airborne nitrogen and thus act as nitrogen sinks (Kovář et al., 1996). Groundwater contamination by nitrate or other non-point source pollution from agricultural fertilisers can also be reduced by the presence of hedgerows around fields (Thomas & Abbott, 2018;

Zheng et al., 2020). Agroforestry systems, such as hedgerows, increase the standing crop and act as a carbon sink mitigating the effects of climate change (Follain et al., 2007; Kay et al., 2019; Biffi et al., 2022), while the removal of hedgerows releases the soil carbon stock back into the atmosphere (Van Den Berge et al., 2021).

*Vegetation of hedgerows*

The woody layer is mainly shaped by the hedgerow management. The shrub layer consists of species that can tolerate the management regime of rotational trimming, coppicing or pollarding such as *Carpinus betulus* and *Corylus avellana*. Because of their origin as fences and boundaries, many shrub species are also well equipped against browsing, e.g. *Prunus spinosa* and *Crataegus* spp. Lianas such as *Lonicera periclymenum* and *Clematis vitalba*, which are typical for forest edges, are also common in hedgerows. Hedgerows are well known as a habitat for a large diversity of *Rosa* spp. and *Rubus* spp. (Weber, 1967). Resulting from the traditional coppice-with-standards management, the most common tree species in many regions is *Quercus robur* because it was valued for providing high-quality timber and fuel. The species richness and composition of the shrub layer depend in a large part on the selection of species that were originally planted. Especially in the beginning of the enclosure movement, saplings were taken from nearby forests or fallow land (Weber, 2003). Thus, the species composition showed a high variability and represented the local climatic and edaphic conditions. Later plants from nurseries were used, resulting in species-poor assemblages that often contained non-natives such as *Syringa vulgaris* (Weber, 2003). British hedgerows are dominated by *Crataegus* spp. until today (French & Cummins, 2001). Over the years, hedgerows can become more species-rich by the input of seeds, in particular of bird-dispersed species. Fertilisation of adjacent fields facilitates the spread of nitrophilous species such as *Sambucus nigra* (Forman & Baudry, 1984).

The herbaceous vegetation can be very diverse on a small spatial scale due to the hedgerow's role as an ecotone between open land and forest and the environmental heterogeneity of the habitat. In the margins, grassland and agricultural weed species, such as *Achillea millefolium*, *Anthoxanthum odoratum*, *Bromus sterilis*, *Calystegia sepium*, *Hypericum perforatum* and *Ranunculus repens*, are frequent (Weber, 1967; Smart et al., 2002; Alignier & Baudry, 2015; Alignier, 2018). Nitrophilous species, such as *Aegopodium podagraria*, *Anthriscus sylvestris*, *Elymus repens*, *Galium aparine* and *Urtica dioica*, can be abundant when the adjacent land is managed with fertilisers (Roßkamp, 1999). Heliophilous climbers, like *Humulus lupulus*, *Polygonum dumetorum*, *Solanum dulcamara* and *Vicia cracca*, use the shrubs as growth support on the sunny side of the hedgerows (Weber, 1967; Roßkamp, 1999). In spring, the interior of many hedgerows is characterised by geophytes, such as *Adoxa moschatellina*, *Anemone nemorosa* and *Ficaria verna*, while in summer, *Moehringia trinervia* and *Galeobdolon luteum* tolerate the shade from the shrub layer. Under a dense canopy, *Hedera helix* and *Poa nemoralis* dominate the interior (Weber, 1967; Roßkamp, 1999; Wehling & Diekmann, 2009a). The shaded parts of the flanks and margins contain species mainly found in closed forests, forest openings and forest edges (Weber, 1967). These areas can be colonised by *Alliaria petiolata*, *Arum maculatum*, *Chaerophyllum temulum*, *Glechoma hederacea*, *Polygonatum multiflorum*, *Scrophularia nodosa*, *Stachys sylvatica* and *Stellaria holostea* (Roßkamp, 1999; Closset-Kopp et al., 2016; Alignier, 2018). Fern species, such as *Dryopteris filix-mas* or *Athyrium filix-femina*, are frequent as well. As they depend on a high relative humidity, fern patches are most pronounced alongside roads which are lined with hedgerows on both sides (Eigner & Gerth, 2020). These double hedgerows (Redder) are particularly

rich in forest specialists because they provide stable microclimatic conditions similar to forests (Deckers et al., 2005a).

Of special interest to this thesis are the forest specialists that are found in the interior and on the shady side of the hedgerow. These species are adapted to shaded and relatively stable microclimatic conditions as usually observed in forests. However, they are threatened by forest loss and fragmentation that is prevailing in the cultural landscapes of Europe. Hence, hedgerows are valued as refuge habitats for forest specialists (McCollin et al., 2000; Van Den Berge et al., 2019). It is still under debate for which forest plants they may provide a habitat and if a certain set of traits is beneficial for the dispersal, establishment and survival in hedgerows (Deckers et al., 2004b; Roy & de Blois, 2006; Vanneste et al., 2020c). These traits may also vary across regions that differ in climate, traditional management and landscape composition (Vanneste et al., 2020a; Vanneste et al., 2021). Another point of discussion is the corridor function of hedgerows and if they can facilitate the dispersal of forest specialists between isolated forest patches (Davies & Pullin, 2007; Wehling & Diekmann, 2009b; Closset-Kopp et al., 2016; Lenoir et al., 2021).

Even though there are no species that are restricted to hedgerows (Baudry, 1988), they can profoundly increase the biodiversity in cultural landscapes and contribute to the conservation of a range of endangered species.

## Study area

Data sampling took place in the hedgerow-rich landscapes of Europe. While CHAPTER 2 to CHAPTER 4 focus on Northern Germany, CHAPTER 5 comprises data from Southern Sweden, Northern Germany, Belgium, England and Northern France. All studied regions have a tradition in hedgerow management that dates back at least several centuries.

The study region in Northern Germany is situated in the eastern part of the federal state of Schleswig-Holstein, which is characterised by a Young Drift morainic landscape. The soils are in large parts calcareous and rather fertile, while the climate is sub-oceanic. The mean annual temperature is 8.9°C and the yearly precipitation amounts to about 770 mm (DWD, 2015). The area for the European study covers a temperature gradient of 7.1°C to 11.8°C and the annual precipitation ranges from 623 mm to 938 mm (Fick & Hijmans, 2017; WorldClim, 2020).

In Europe, the distribution of hedgerows is mainly concentrated to the oceanic regions along the Atlantic including the North and Baltic Sea. This includes Southern Sweden (Sarlöv Herlin & Fry, 2000), Denmark (Aude et al., 2003), Northern and Western Germany (Weber, 1967; Wehling & Diekmann, 2008; Huwer & Wittig, 2012), the Netherlands and Belgium (Van Den Berge et al., 2019), the British Isles (Pollard et al., 1974) as well as Northern and Western France (Closset-Kopp et al., 2016), Northern Spain (Hernández & Zaldívar, 2013) and Portugal (Pita et al., 2020). These areas have some similarities that favour the establishment and the maintenance of hedgerows: The oceanic and therefore moist climate made livestock farming profitable in these regions, forests are generally sparse, and fields often small and fragmented (Jessen, 1937). Knowledge is lacking to what extent these regional similarities cause common patterns in hedgerow communities across Europe and how edaphic, climatic and cultural differences further diversify the hedgerow vegetation.

The hedgerow networks in Great Britain and France are well known and studied. Most work in these countries was carried out since the 1950s when ecologists became particularly interested in the properties of hedgerows, to counteract widespread removals (Baudry et al., 2000). This was also the motivation for increasing studies in other parts of Europe, such as Germany (Eigner, 1982). Early studies were usually published in German (e.g. Jessen, 1937; Marquardt, 1950; Weber, 1967), and thus not easily accessible for an international readership. This changed over the last decades with more hedgerow research in Germany published in English (e.g. Tenbergen, 2001; Wehling & Diekmann, 2008; Huwer & Wittig, 2012). This thesis draws on earlier research from the study area, enhances the knowledge about hedgerow networks and their vegetation, and puts the results into an international context.

## Outline of this thesis

In many European regions, hedgerows are an important element of agricultural landscapes. They can form networks of biodiversity hotspots across the landscape and link otherwise fragmented habitats. The dynamics of their establishment and removal, the ecological conditions of an ecotone as well as their widespread distribution including different forms of management and climatic conditions make hedgerows a fascinating study habitat. Consequently, the interest in hedgerow studies steadily increased over recent years (García de León et al., 2021). This thesis operates on different temporal and spatial scales to understand the patterns of hedgerow vegetation in the changing agricultural landscapes of Europe. It incorporates today's influences such as hedgerow management, land-use, distance to source populations and climate as well as past influences such as hedgerow age, historical plot data, former network density and landscape configuration.

The main research questions of this thesis are:

I.   How did the vegetation of hedgerows in agricultural landscapes change over the past five decades and can this change be linked to a change in environmental variables or management?

II.  Are recent hedgerows less rich in forest specialists than ancient hedgerows (i.e. is there a colonisation credit) and which factors can facilitate the colonisation of recent hedgerows?

III. Can we detect the effect of past hedgerow loss until today (i.e. an extinction debt) or is the present habitat quality the main driver of forest species richness in hedgerows?

IV.  How does the vegetation of hedgerows differ across European regions and which variables influence the number and frequencies of forest specialists in hedgerows?

The ecological concepts and methods used in this thesis (Table 1.1) to tackle the above research questions are outlined in this **CHAPTER 1**. It also gives a general characterisation of hedgerows, including their history, management, ecology and ecosystem services. It also includes a description of the study area. As most of the research was conducted in Schleswig-Holstein, Northern Germany, this chapter focusses not only on European hedgerows in general, but includes additional details about hedgerows in this particular region.

**CHAPTER 2** studies the impact of habitat change on the vegetation of hedgerows. A resurvey based on mapping data from 50 years ago was conducted on hedgerows in Northern Germany. We link changes in environmental and management variables to shifts in the species composition.

When new hedgerows are planted, e.g. for ecological and aesthetical reasons or to compensate hedgerow loss, these recent hedgerows are often assumed to contain fewer forest specialists and therefore be less valuable for conservation purposes than the ancient hedgerows. **CHAPTER 3** investigates whether there is a colonisation credit in recent hedgerows and examines which factors influence the relaxation time. This is done by a pairwise design that compares the species richness and composition of recent and ancient hedgerows.

Over the last century, the hedgerow density decreased considerably. In **CHAPTER 4**, we link past and present landscape characteristics as well as habitat variables to the current species richness of forest specialists in hedgerows to examine a possible extinction debt. We explore how the habitat density is correlated to the quality of the habitat and why this complicates extinction debt analyses.

While the first three studies focus on hedgerows in Northern Germany, **CHAPTER 5** widens the spatial scope and includes data on a gradient across Europe. The regional climate, landscape characteristics and management are correlated to the forest plant richness and their functional traits in hedgerows. We seek to find out which characteristics are beneficial for plants living in hedgerows.

**CHAPTER 6** provides a synthesis of the results and insights of the previous chapters, gives implications for the management of hedgerows and future research perspectives. The thesis is completed by an **APPENDIX** that contains the appendices to CHAPTERS 2, 3 and 5 as well as additional administrative information regarding this dissertation.

Table 1.1 Overview of the thesis CHAPTERS 2 to 5 and the underlying ecological concepts and methods used. The presented studies act on different temporal and spatial scales. The focal species group is given as well.

| Chapter | Ecological concept | Method | Scale | Focal species group |
|---|---|---|---|---|
| 2 | Habitat change and vegetation dynamics | Resurveying hedgerows to link changes in environmental variables to changes in species richness and composition | Time: 50 years | Vascular plants |
| 3 | Colonisation credit | Comparing the species richness of ancient and recent hedgerows | Time: 80 years | Forest specialists |
| 4 | Extinction debt | Linking past and present landscape configuration and habitat variables to present species richness in hedgerows | Time: 120 years | Forest specialists |
| 5 | Vegetation patterns on a macro-gradient | Comparing the species richness and functional traits across hedgerow-rich regions in Europe | Space: Continental | Forest specialists |

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# Resurveying hedgerows in Northern Germany: Plant community shifts over the past 50 years

Kathrin Litza & Martin Diekmann (2017)

Hedgerow landscape in the Schleswig-Holstein Morainic Upland close to Plön, in autumn after the harvest.

## Abstract

Resurveying is a powerful approach to investigate responses of plant species communities to a changing environment. We present a resurvey of hedgerows from the "Knick" landscape of eastern Schleswig-Holstein, Germany. The original survey was done by H. E. Weber in 1967 and new data from totally 51 semi-permanent plots was sampled in 2015. Hedgerows are a key near-natural habitat that can harbour a great biodiversity in otherwise agriculturally intensified landscapes.

Our study reveals a distinct shift in the herbaceous species composition of the hedgerows over the past five decades. To understand the reasons for these changes, we compared the mean Ellenberg indicator values (EIVs) and measured pH values, as well as hedge shape parameters of the hedgerows between the recent and the original study. The main driver behind the change in species composition appeared to be the increase in nutrient supply. The hedge shape changed as well, indicating an altered hedgerow management. Interestingly, we found a contradictory relationship between measured pH values and mean EIVs for reaction: while the former showed a decrease over time, the latter suggested an increase.

Species richness decreased in some groups (shrubs and herbaceous forest species) but increased in others (grass species and arable weed species), with an overall decline in species richness. An analysis of the species' changes in frequency in relation to their EIVs showed that species with higher nitrogen and temperature scores were more likely to have increased.

**Keywords**: acidification · Ellenberg indicator values · eutrophication · nitrogen input · resurvey

## Introduction

In an agriculturally intensified landscape, hedgerows often remain the last near-natural wooded habitat. Especially in sparsely wooded areas they perform an important function as possible refuge habitats for vascular plants that are otherwise restricted to forests (McCollin et al., 2000; Wehling & Diekmann, 2009a). Additionally, they can form linear corridors or even networks of woody habitat strips, and are thus able to connect fragmented forests (Roy & de Blois, 2008; Wehling & Diekmann, 2009b) and enable genepool linkage of forest species (Van Rossum & Triest, 2012). In the context of habitat fragmentation and climate change this can be essential because species are expected to shift their distribution ranges polewards and need migration corridors. In recent time, hedgerows have received an increasing attention from conservation biologists because of their high biodiversity (Roy & de Blois, 2008).

In many European countries, hedgerows were laid out after the 17th century and maintained as living fences between fields and pastures, and to shelter agricultural land from erosion until today (Knauer, 1993; Weber, 2003). They typically consist of a bank on which shrubs were planted in one or two rows. Management such as coppicing is needed to keep the hedgerows thick and vital. Adjacent to the hedge banks, field margins are often established to protect the banks from accidental destruction by ploughing and herbicides or fertilisers. Those strips can be rich in endangered ruderal and arable weeds (Albrecht et al., 2009) as well as grassland species (Smart et al., 2002). Next to

traditionally preserved hedgerows there are ditches on each side adjoining the banks. Hedgerows are thus structurally very heterogeneous, including shaded parts in the interior as well as forest edge conditions and open habitat in the adjacent field margins. There is also variation in exposure to solar radiation and wind. As a consequence, hedgerows offer a habitat to many different plant species (French & Cummins, 2001; Critchley et al., 2013), such as the functional groups of forest specialists and arable weeds, occurring closely together.

Over the past five decades, agricultural and hedgerow management practices have changed dramatically. Hedgerows are prone to an increasing load of agricultural fertilisers and other chemicals because they are adjacent to agricultural fields (Tsiouris & Marshall, 1998). The chemicals tend to accumulate in the hedgerow because they act as windbreaks and because crops grow less well in the shade in the direct proximity of the hedgerow and utilise less of the applied fertilisers (Mette, 1994). The deposition of atmospheric nitrogen is also amplified by the hedgerows' biofiltering function (Kovář et al., 1996). This all leads to eutrophication which herbaceous forest plants have been found to be susceptible to (Strengbom et al., 2003), especially species flowering in early spring (Diekmann & Falkengren-Grerup, 2002). Additionally, the hedgerow management practices have changed in a way that shrubs are coppiced less often compared to previous times (Carey et al., 2008) but with increasingly heavy machinery, and the banks are no longer maintained and degrade slowly (Höper et al., 1987; Schrautzer et al., 1996). Land-use changes and especially the increasing use of fertilisers and herbicides can cause a general loss of arable weed species but an increase in nitrophilous and herbicide-tolerant species (Hilbig & Bachthaler, 1992a, 1992b; Baessler & Klotz, 2006; Storkey et al., 2012).

To be able to detect changes in species richness and composition, historical vegetation plots need to be visited again and the collected vegetation data be compared. Such resurveys offer an opportunity to find out more about temporal shifts in species composition and to evaluate underlying causes (Kapfer et al., 2017). This in turn enables us to develop conservation practises to protect the remaining diversity in the agricultural landscape.

Up to now, there have been only few resurvey studies of hedgerow habitats. Huwer and Wittig (2012) presented a study from the Westphalian Basin, Western Germany, which focused on changes in the frequencies of plant species of different phytosociological groups, and Staley et al. (2013) in a study from England emphasised the influence of management practises on woody species and typical herbs of the hedgerow interior. So far, no resurvey has been conducted in the very hedgerow-rich area of Schleswig-Holstein, Northern Germany, for which a large historical data set is available. The original study was done by H. E. Weber (1967a, 1967b) about 50 years ago in the summers of 1962 and 1963, including an extensive vegetation sampling of hedgerows distributed all over Schleswig-Holstein. The resurvey provides a unique insight to the floristic changes of hedgerows in Northern Germany. Whereas hedgerow research most often has focused exclusively on forest specialists (McCollin et al., 2000; Wehling & Diekmann, 2009a; Staley et al., 2013), we also include the functional group of arable weed species being a natural part of the hedgerows (MLUR, 2013). Additionally, unlike other resurvey studies of hedgerows, there were old pH measurements available that offer a rare opportunity to directly assess the influence of a changing soil environment.

Our main research questions were:

(1) Was there a shift in the herbaceous plant species richness and composition of hedgerows over the past five decades?

(2) Can this shift be linked to a change in environmental factors or in the hedge shape and if so, which are the most influential variables?

(3) Does the direction of change differ between functional plant groups such as herbaceous and woody species or forest and arable weed species and what does this mean for hedgerow management and conservation?

## Methods

### Study Area

The study was conducted in the hedgerow-rich east of Schleswig-Holstein, the northern-most federal state of Germany (Figure 2.1). This area is characterized by a young morainic, hilly landscape formed during the last glaciation. The soils are predominantly calcareous and relatively nutrient-rich. The climate in the study area is suboceanic and characterised by moderately warm summers and mild winters. The mean annual temperature is 8.9 °C, the yearly precipitation amounts to about 770 mm (DWD, 2012).

In the federal state of Schleswig-Holstein, only 166,800 ha (10.6 %) are covered by forests, while 1,102,400 ha (69.8 %) are used for agriculture (DESTATIS, 2014a). This enhances the importance of hedgerows for the area because they offer additional wooded habitat within the agricultural land. In the study area, the construction and management of hedgerows, which are locally called "Knicks", has a long tradition. They originally served as living fences but they soon also proved to be a highly valued source for timber and firewood and protected the fields as well as the cattle from wind and rain.

In Schleswig-Holstein and many other regions in North-western Europe, hedgerows were usually planted on a raised bank, the material for which was gained by digging ditches on each side. While these ditches have mostly been filled up by now, the hedge banks are still an important part of the hedgerows. Traditional management includes coppicing of the shrub layer every 9 to 11 years as well as frequent mending of the banks and planting of saplings in gaps of the shrub layer (Jessen, 1937). Even though the land consolidation processes taking place during the second half of the last century reduced the hedgerow network in Schleswig-Holstein from roughly 75,000 (Marquardt, 1950) to 46,000 km (Eigner, 1982), it is still very dense compared to other parts of the country.

### Vegetation sampling & environmental variables

A list of locations of the original plots from Weber (1967a, 1967b) was obtained from the Botanical Institute at the University of Kiel. The information provided was used to transfer the position data into the geographic coordinate system. Hedgerows were included in the resurvey if they could be identified on a recent map according to their geographic location and their direction. In consequence of the imprecise position data (± 25 m), a plot was accepted for a resurvey if the possible deviation between the original plot location and the next appropriate hedgerow was smaller than 30 m. The

plot centre of the resurvey was placed as close to the original plot position as possible. However, vegetation resurveys are robust to plot location uncertainties (Kopecký & Macek, 2015). Due to the land consolidation processes many hedgerows included in the original study no longer exist. Newly coppiced hedgerows were included, while partly degraded hedgerows were only considered if a bank was still visible and if at least 50 % of the bank was covered with shrubs. Of 286 hedgerows that were reported from the area in the original study, 220 could not be recovered on a recent map, 15 had to be excluded due to strong degradation and finally, 51 could be resurveyed.

Because the original study was carried out in summer, the sampling was done in June and July 2015 even though this might miss spring flowering plants. The plot length in the original study was given as usually varying between 60 and 80 m of a hedgerow. For the resurvey, we applied a fixed length of 70 m. The plot width was defined by the borders of the adjacent fields in accordance with the original study, meaning that the field margins were also included in the sampling. The vegetation survey included all vascular plants and was based on percentage cover estimation of each species. Brambles, although distinguished on a lower taxonomic level in the original survey by Weber (1967a, 1967b), were recorded as *Rubus fruticosus* agg. and *Rubus corylifolius* agg.
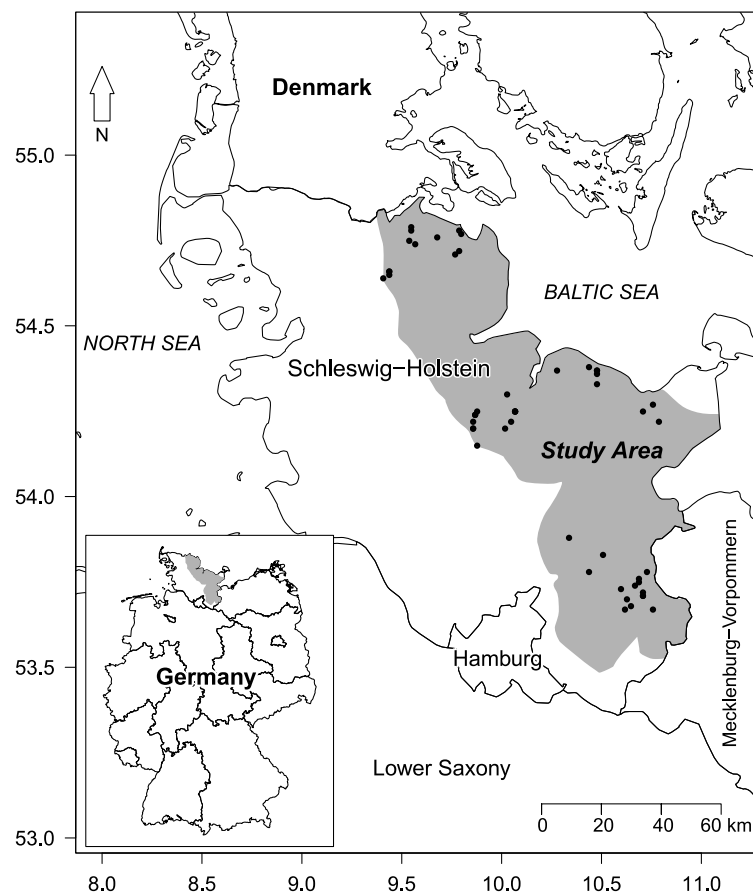


Figure 2.1 Map showing the location of the study area (grey) in the province of Schleswig-Holstein in the north of Germany. The study area covers the whole of the Schleswig-Holstein Morainic Upland, except for the easternmost parts. Dots indicate the plot locations.

We determined the width of the bank foundation, the height of the hedge bank relative to the field (excluding ditches) and the height of the shrub layer (Figure 2.2). In accordance with the original study, soil samples from the upper 30 cm were taken in the middle of the plot and the hedge bank in April 2016 at all plots for which the old pH values were available (27 of 51 plots). Because Weber (1967a) reported a sample depth variability of $30 - 40$ cm, 15 samples were additionally taken from down to a depth of 40 cm to test if this influences the results. The soil samples were analysed with the same methods as used in the original study. In the laboratory, 10 g of air-dried and sieved soil were mixed with 25 ml of 0.1 M KCl and shaken for 1.5 hours. The pH value was measured using a pH meter with glass electrode. There was no significant difference in the subsample between the pH values measured for the upper 30 cm and the upper 40 cm of soil in a pairwise Wilcoxon test (median$_{30cm}$ = 3.78, median$_{40cm}$ = 3.77; $V$ = 4.5, $p$ = 0.59, $n$ = 15) which is why we uniformly used the values for the upper 30 cm for further analyses.
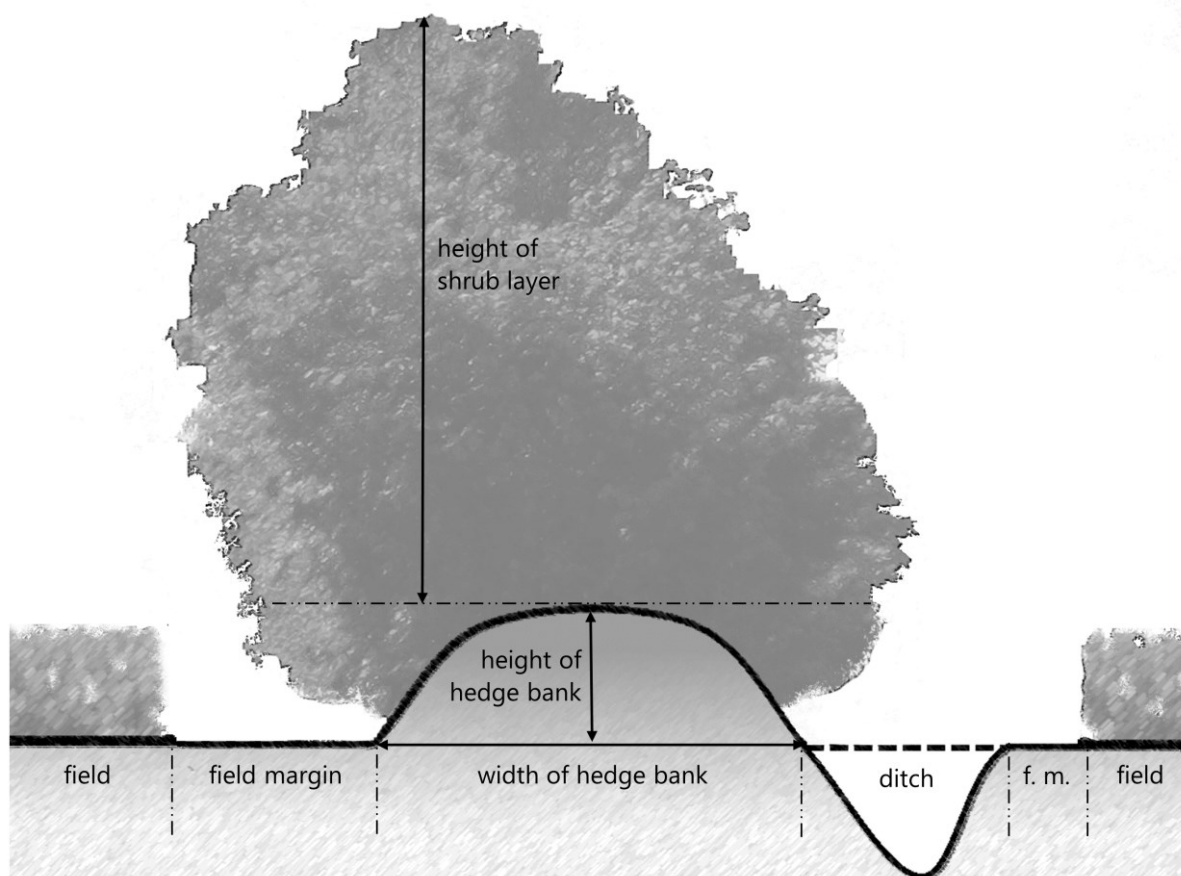


Figure 2.2 Cross-section of a representative hedgerow. The height of the shrub layer was measured from the top of the hedge bank to the top of the shrubs. The height of the hedge bank was measured from the field to the top of the bank, excluding ditches if present. Hedge bank width was defined as the width of the bank foundation. Field margins (f. m.) were defined as the strips between the hedge bank and the edge of the field. Ditches can only rarely be found today but were exemplarily included in the graphic.

## Data Analysis

Because in the original study only pH was measured, the comparison of environmental conditions between old and new plots had to rely on the mean Ellenberg indicator values (EIVs) for soil nutrient availability (mean N), soil reaction (mean R), soil moisture (mean F), light availability (mean L), temperature (mean T) and continentality (mean K) (Ellenberg et al., 2001), based on presence-absence. Only herbaceous plant species were included in the calculation of mean Ellenberg values, assuming that the woody species are likely to be planted and thus do not necessarily reflect the natural environmental conditions (French & Cummins, 2001).

For the pairwise comparison of environmental variables (mean Ellenberg values and soil pH) and hedge shape variables (height and width of the hedge bank, height of the hedgerow's shrub layer) between the original and the resurveyed plots, multiple Wilcoxon signed-rank tests were applied (most variables were not normally distributed) and corrected for multiple comparisons using the Benjamini-Hochberg (BH) procedure. The difference in pH between the two surveys was tested to assess if they were influenced by the pH value of the original study in Spearman correlation. We also used the Wilcoxon test (including BH correction) to compare the overall species richness between the original survey and the resurvey, as well as the species richness within the functional groups of woody species, herbaceous species, forest species, weed species, grasses, forbs, red-listed species and neophytes. The classification of forest species follows Schmidt et al. (2011) and includes the categories 1.1 (largely restricted to closed forests) and 1.2 (preferring forest edges and clearings). Weed species were distinguished according to Hofmeister and Garve (2006) and neophytes according to Wisskirchen and Haeupler (1998). Red List status was assigned according to the regional Red List by Mierwald and Romahn (2006).

To test if the timing of our resurvey fitted the one of the original study, we excluded the three species that are only visible in early spring (*Adoxa moschatellina*, *Anemone nemorosa*, *Ficaria verna*) from the comparison of total species richness and forest species and compared the results to the ones using the complete species set. This changed the results only slightly, indicating an analogous timing of the original study and the resurvey.

Detrended Correspondence Analyses (DCA) were performed to analyse the effects of environmental variables on the hedgerow vegetation and the change in floristic composition in the studied hedgerows over the past five decades. This was done separately for the herbaceous and the woody species as well as for herbaceous forest plants and arable weed species. The environmental and hedge shape variables, the geographic coordinates and the year of sampling were post-hoc fitted to the ordination.

For each pair of original and resurveyed plots we calculated the Sørensen similarity index (*S*) (only including herbaceous species) and related the values to the differences in the environmental and hedge shape variables (value of resurvey *minus* value of original survey) in a linear model, including the variables not only as linear but also as quadratic terms to enable the regression curves to have minima or maxima. By performing a stepwise backward selection, we wanted to find out which of the variables are driving the change in species composition and whether there is a linear or curved relationship for the given variables. To analyse the change in the beta diversity of plots over time, we calculated the *S* for each plot with each other plot separately for the old and new data sets (Keith

et al., 2009). The means of these values across plots were compared pairwise between the data sets applying the Wilcoxon signed-rank test. A high Sørensen similarity equals a low beta diversity and vice versa.

To examine the underlying factors for the species richness of the herb layer, the environmental and hedge shape variables were entered into a Generalized Linear Mixed Effect Model (GLMM) with Poisson distribution. The plot identity was used as a random term to account for the paired design. In both analyses mean R was replaced by the measured pH values ($n = 27$) because mean R was considered not to reliably reflect the soil pH (see results).

We determined the frequency of occurrence for all herbaceous species in the old and in the resurveyed data sets and correlated the changes in frequency with the corresponding species' EIVs. We then performed a stepwise backward selection to find out which ecological requirements determine how well the species can cope with a changing environment. To also measure the combined overall frequency (*CF*) of species we multiplied their frequency by their mean abundance per plot.

All data analyses were carried out using the free statistical software R, version 3.2.2 (R Core Team, 2015). Analyses of variance were always conducted as type II analyses using the package "car" (Fox & Weisberg, 2011). The multivariate analyses were performed using the "vegan" package (Oksanen et al., 2015) and the GLMMs using the "lme4" package (Bates et al., 2015).

## Results

### Environmental conditions and hedge shape

The shape of the hedgerows and of their banks showed a significant change since the time of the original study (Table 2.1). The bank foundations got wider and the banks became less high over the past 50 years. The shrub layer of the hedgerows increased in height. It was noted in the field that the last coppicing often was long ago so that the shrubs had almost turned into a line of trees and no longer formed a canopy close to the hedge bank.

The pairwise comparison of mean Ellenberg indicator values of the plots showed a significant increase in mean N and mean T. We found no significant changes over time for the values of mean L, mean F and mean K. Mean R significantly increased whereas there was a significant decrease in the measured pH (Figure 2.3). Neither mean R and the pH (Spearman's rho = -0.15, $p = 0.29$, $n = 54$, Figure 2.3) nor the difference in mean R and in pH were correlated to each other (Spearman's rho = 0.27, $p = 0.17$, $n = 27$), whereas mean N and mean R were highly positively correlated (Spearman's rho = 0.74, $p < 0.001$, $n = 54$; Figure 2.3). Also, the N and R scores were positively correlated across species (Spearman's rho = 0.45, $p < 0.001$, $n = 119$). The higher the original pH was, the stronger was also the decline in pH over time (Spearman's rho = -0.74, $p < 0.001$, $n = 27$; Figure A 1).
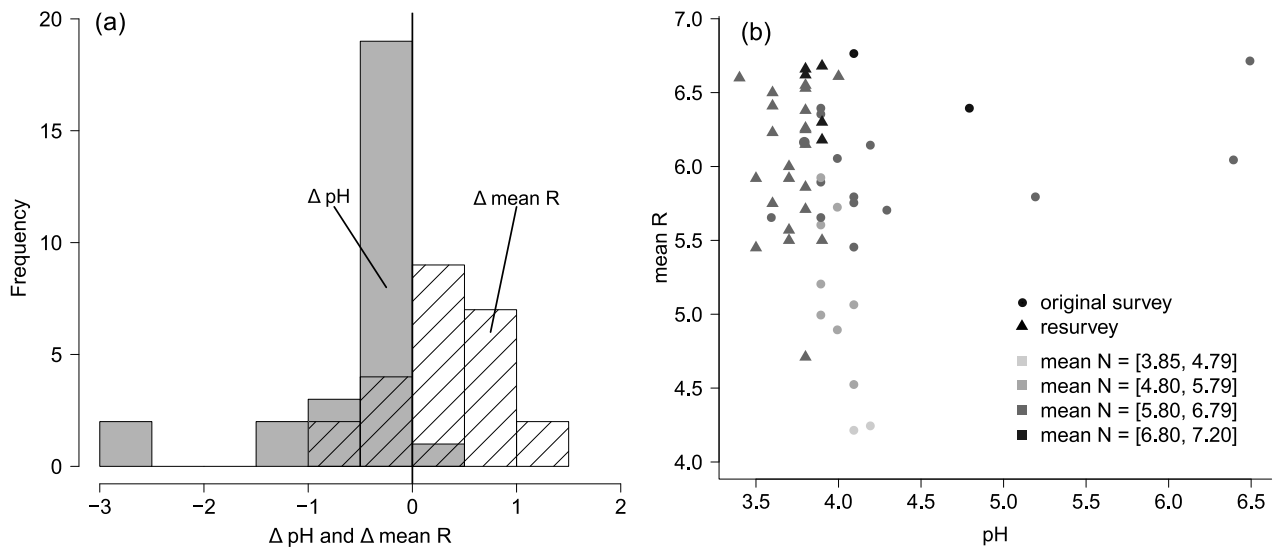
Figure 2.3 (a) The histogram shows the contradictory shifts in the measured pH value and mean Ellenberg indicator value for reaction, mean R ($n = 27$, value in the resurvey *minus* value in the original survey). (b) The plot shows the measured pH value versus mean R. Dots represent plots from the original survey, triangles plots from the resurvey (both $n = 27$). The mean indicator value for nutrient availability (mean N) of the plots is symbolised by different shades of grey.

### Species richness

The total species richness of the hedgerows decreased, particularly the number of woody species, forb species and herbaceous forest species (Table 2.1). In contrast, there was a significant increase in the richness of grass species and a marginally significant increase in the number of arable weeds. Species that are red-listed today declined over the years. Near-threatened species which were formerly common in hedgerows but could no longer be found included *Campanula rotundifolia* and *Knautia arvensis*. Also *C. rapunculoides* which is critically endangered was moderately common in the original survey but absent from the resurvey. We did not find a significant difference in beta diversity between the years.

The overall herbaceous species richness was negatively influenced by the height of the shrub layer ($R^2 = 0.19$, $p = 0.011$, $n_{old} = 51$, $n_{new} = 48$). The other environmental and hedge shape variables did not significantly contribute to the model and were therefore removed.

The cumulative number of species in all plots decreased from 182 to 164 species. Fewer woody species (46 instead of 51) and also fewer herbaceous species (118 instead of 131) were found in the resurvey. The number of forest species decreased from 26 to 21 while the number of weed species increased from 52 to 62. We also found an overall increase in neophyte species from 2 to 5 species.

Table 2.1 Results of Wilcoxon signed-rank tests comparing the total species richness and the richness of functional species groups as well as the hedge shape variables and environmental variables between the original and the resurveyed plots. Medians of the old (m-old) and the new plots (m-new) are given. *V* is the test statistic. *p*-values are corrected for multiple-testing by the Benjamini-Hochberg (BH) procedure. *p*-values of significant differences between years are given in bold. The direction of change is indicated by arrows. Beta diversity is expressed as Sørensen similarity across plots with a higher similarity reflecting less diversity. *n* = 51 in all cases except shrub layer height (*n* = 48) and measured soil pH (*n* = 27). Mean Ellenberg indicator values: soil nutrient availability (mean N), temperature (mean T), light availability (mean L), soil moisture (mean F), continentality (mean K), and soil reaction (mean R).

| | m-old | m-new | *V* | *p*-value (BH) | Direction of change |
|---|---|---|---|---|---|
| *Diversity* | | | | | |
| Overall species richness | 39 | 36 | 977.5 | 0.002 | ↓ |
| Woody species | 12 | 10 | 885 | < 0.001 | ↓ |
| Herbaceous species | 26 | 26 | 765.5 | 0.092 | (↓) |
| Herbaceous forest species | 6 | 5 | 669.5 | 0.063 | (↓) |
| Arable weed species | 14 | 15 | 331 | 0.080 | (↑) |
| Forb species | 21 | 17 | 885 | 0.012 | ↓ |
| Grass species | 7 | 7 | 263 | 0.048 | ↑ |
| Red List species | 1 | 0 | 553.5 | < 0.001 | ↓ |
| Neophyte species | 0 | 0 | 12 | 0.423 | - |
| Beta diversity | 0.504 | 0.501 | 483 | 0.116 | - |
| | | | | | |
| *Hedge shape variables* | | | | | |
| Bank width | 2.5 | 3 | 188.5 | < 0.001 | ↑ |
| Bank height | 1 | 0.7 | 932.5 | < 0.001 | ↓ |
| Shrub layer height | 3 | 4.5 | 110.5 | < 0.001 | ↑ |
| | | | | | |
| *Environmental variables* | | | | | |
| Mean N | 6.1 | 6.6 | 145 | < 0.001 | ↑ |
| Mean T | 5.5 | 5.7 | 113 | < 0.001 | ↑ |
| Mean L | 6.1 | 6.2 | 511.5 | 0.185 | - |
| Mean F | 5.3 | 5.3 | 601.5 | 0.567 | - |
| Mean K | 3.6 | 3.6 | 731 | 0.267 | - |
| Mean R | 5.7 | 6.1 | 183.5 | < 0.001 | ↑ |
| pH | 4.1 | 3.8 | 348 | < 0.001 | ↓ |

Table 2.2 Result of the linear model analysing the change in species composition between the original survey and the resurvey, represented by the Sørensen similarity index. Negative coefficients of quadratic terms indicate that the corresponding curve opens downward and thus has a maximum, vice versa for positive coefficients

|  | coefficient | p-value |
|---|---|---|
| *Intercept* | 0.641181 | < 0.001 |
| Δ pH | 0.180683 | 0.031 |
| (Δ pH)2 | 0.022343 | 0.034 |
| (Δ mean N)² | -0.087278 | < 0.001 |
| Δ mean T | -0.563918 | 0.028 |
| (Δ mean T)² | 1.131699 | 0.032 |
| Δ mean F | 0.135958 | 0.026 |
| (Δ mean F)² | 0.362658 | 0.010 |
| (Δ mean K)² | -0.885993 | 0.010 |
| Δ width hedge bank | 0.142459 | 0.019 |
| (Δ width hedge bank)² | -0.092723 | 0.022 |
| Δ height hedgerow | -0.033185 | 0.002 |

## *Species composition*

The composition of herbaceous plants (including the two subgroup analyses) showed significant temporal changes, while the DCA for the woody plants showed only minor differences in species composition between the years (Figure 2.4). The first axes were correlated to the geographic location of the plots, except for the one including forest herbs which was correlated to the sampling year. Many of the environmental variables had a significant influence on the herbaceous species composition, but the ones likely to have caused the shift in composition over time are pH and the height of the hedge bank, which have both decreased over the past decades, and the height of the shrub layer, which has increased. In the DCA for the woody plants, the most influential variables for the species composition were mean N and mean L, both being closely correlated to the second axis and opposite to each other.

The effect of the year of sampling was significant for both forest herbs and arable weeds, but the separation of old and new plots was more distinct for the latter (Figure 2.4). An important environmental variable for the arable weeds was mean N, while the species composition of forest herbs was significantly influenced by both mean N and mean L.

When modelling the change in species composition, reflected by the Sørensen similarity index ($S$), many variables contributed to the final model ($R^2 = 0.66$, $p < 0.01$, $df = 13$; Table 2.2). Among the environmental variables, differences in pH, mean N, mean T, mean F and mean K were significantly related to $S$. For most variables the linear as well as the quadratic term contributed to the model,

while for mean N and mean K only the quadratic terms were significant, meaning that there was the least change in species composition if those variables did not vary over the years. Of the hedge shape variables, the differences in the width of the hedge bank (linear and quadratic term) and differences in the height of the hedgerow (only linear term) were significant. The height of the hedgerow was negatively related to $S$.

Changes in frequency of the herbaceous plant species were best explained by the species' individual Ellenberg N and T values (final model: $R^2 = 0.131$, $p < 0.01$, $df = 89$; Figure 2.5). Species with a high N score increased in frequency, whereas those with a low N score decreased, and the same holds true for the T values.

In both surveys, *Elymus repens* was the most common species if the composite measure of frequency and abundance, *CF*, was considered (Table A 1). In the original survey, *Urtica dioica* had a high frequency, but its abundance was relatively low. *U. dioica* and also *Galium aparine*, both being indicator plants for nutrient-rich soils, increased noticeably and were among the four most common species in the survey of 2015. Also *Hedera helix* showed both a higher frequency and higher mean abundance. The three most abundant woody species (*Corylus avellana*, *Carpinus betulus*, *Prunus spinosa*) did not show striking changes. *Sambucus nigra* largely increased in both frequency and abundance.

## Discussion

There was a distinct shift in the herbaceous species composition, and even though species richness has increased in some of the functional groups, the total number of species in the hedgerows has declined over the past 50 years.

Among the different groups, grasses profited most from the agricultural intensification during the past decades. Some grasses such as *Elymus repens*, *Poa trivialis* and *Apera spica-venti* benefit from their tolerance towards herbicides (Hilbig & Bachthaler, 1992b), while the new appearance of *Bromus sterilis* and the extreme increase in frequency of *Arrhenatherum elatius* are likely caused by a positive response to an increase in deposited nitrogen at the field margins (Tsiouris & Marshall, 1998). The increase in grasses and decrease in forbs is a pattern also found by Carey et al. (2008) for hedgerows in the UK and has been linked to nitrogen input for other habitat types such as grasslands (Duprè et al., 2010).

There was also a slight increase in the number of arable weed species, for example *Stellaria media*, *Sisymbrium officinale* and *Tripleurospermum perforatum*. Species common in the old inventory like *Knautia arvensis* and *Rumex acetosella* were absent in 2015. *Viola tricolor* subsp. *tricolor* also vanished from the field margins, whereas *Viola arvensis* has become common. An overall increase in richness of arable weeds might be explained by the recently revised hedgerow management regulations in the study area which direct farmers since 2013 to have field margins of at least 0.50 m (MLUR, 2013). Field margins increase the habitat for arable weeds, but overall the once typical arable weed species were largely lost and replaced by nitrophilous generalists (see also Šilc and Čarni (2005) for weed vegetation in Slovenia).

The group of forest herbs decreased in number which is in accordance with findings by Huwer and Wittig (2012) for resurveyed hedgerows in Westphalia, a province in North-western Germany. The

observed drop in pH (see below) may play a role in this as forest specialists often have a narrow ecological pH range and cannot deal with a decreasing pH (Michaelis et al., 2016).

We do not think that the widening of the banks and thereby an increase in plot size biased our results concerning species richness. On the one hand we found no significant correlation between a wider hedge bank and species richness, on the other hand the hedge banks remained comparable in surface area because the banks got wider but also decreased in height.



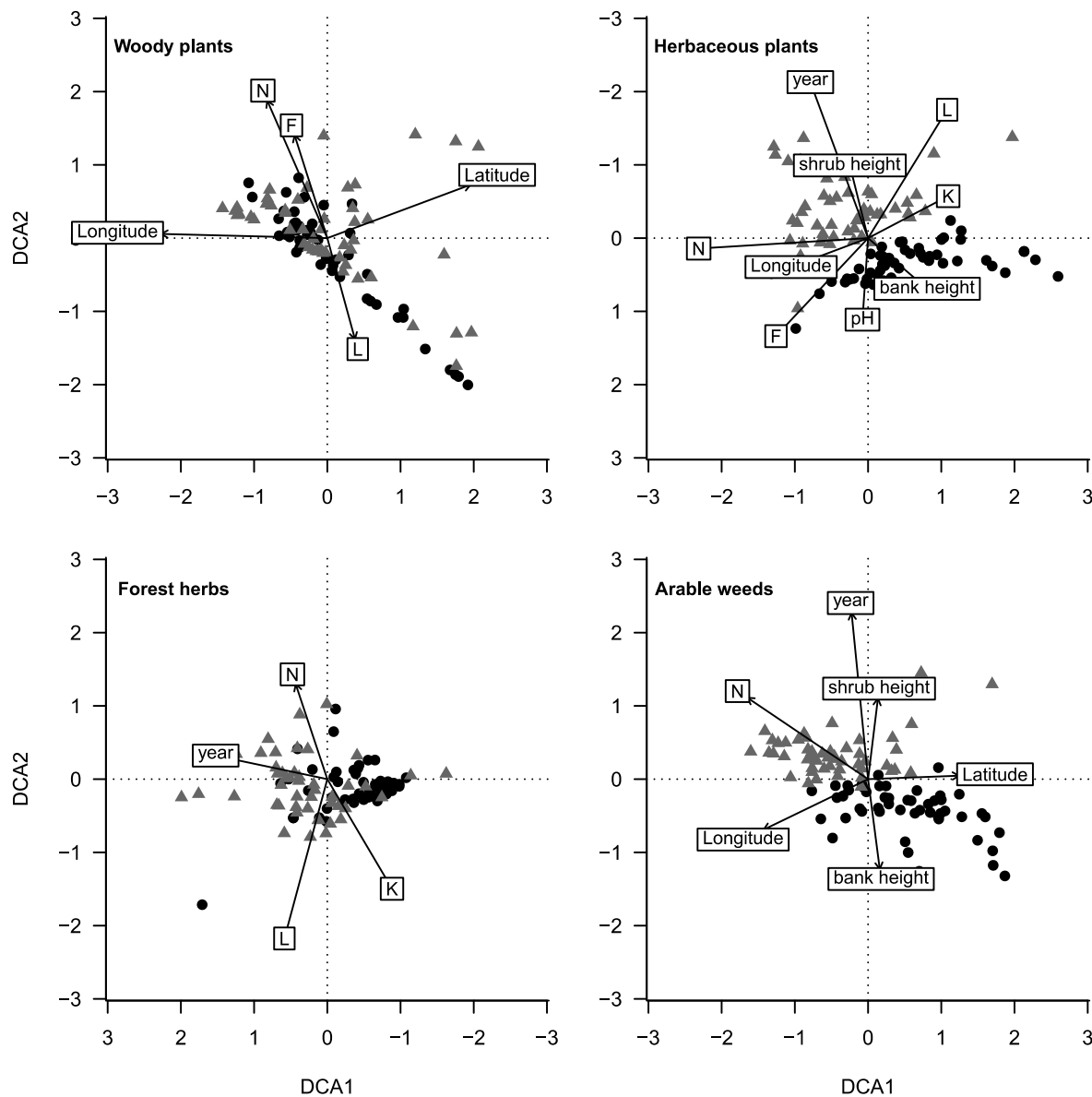Figure 2.4 DCA ordination diagrams including the original plots (black dots, $n$ = 51) and the resurveyed plots (grey triangles, $n$ = 51). Geographic, environmental and hedge shape variables were post-hoc fitted if significant at $p < 0.05$ (N – mean Ellenberg indicator value (EIV) for nutrient availability, F – mean EIV for soil moisture, L – mean EIV for light, K – mean EIV for continentality, year – the sampling year).
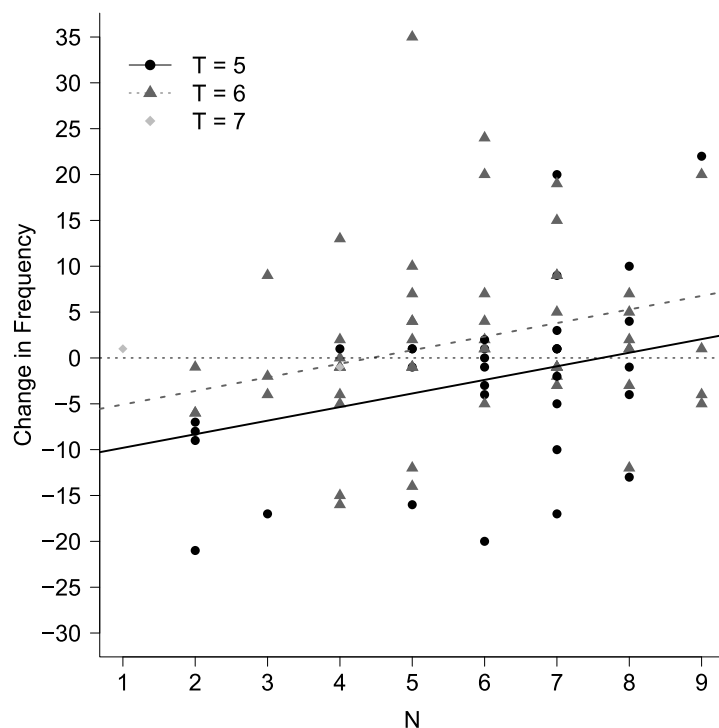
Figure 2.5 Relationship between the Ellenberg indicator value for nutrient availability (N) and the change in frequency over time from the original survey to the resurvey across herbaceous species. The species symbols are plotted with different shapes according to their EIV for temperature (T). The regression line of T = 7 could not be drawn due to a lack of data points.

The plots of the original survey and of the resurvey for the herbaceous species clustered separately in the ordination space which means that plots surveyed in the same year were more similar to each other than the respective pairs of plots, indicating a dramatic compositional change in the herb layer. In contrast, the composition of woody species did not change much over the years. Because shrubs are more long-lived species than herbs, their composition is less rapidly affected by environmental change. In addition, they are likely to have been planted by farmers and thus do not necessarily reflect the edaphic conditions. French and Cummins (2001) proposed that the woody and the herbaceous part of the hedgerows should be treated as separate units because they were found to differ in their responses to environmental factors. Staley et al. (2013) found similar trends of woody and herbaceous plants for alpha and beta diversity of resurveyed hedgerows but an increase in gamma diversity for woody species, while the overall richness of herbaceous species decreased.

The species composition was also influenced by the geographic position of the plots which might indicate that the data is spatially autocorrelated. However, as most of our analyses are based on pairwise comparisons, this is not expected to have biased our results. Care should also be taken when interpreting Ellenberg indicator values that were fitted to a DCA ordination because both are calculated from the same species-plot matrix (Zelený & Schaffers, 2012). However, the most distinctive pattern is the separate grouping of the old and the new plots which is independent of EIVs.

Arable weeds showed a more pronounced community shift than forest herbs over the past 50 years. This can be explained by the differing lifespan of the two groups, with arable weeds being mainly annual species and forest herbs being almost exclusively perennials, and also by the higher extent of disturbance in the field margins compared to the hedgerow interior. The composition of the shrub layer, which strongly influences the conditions for the herb layer in the interior in terms of shading (Baeten et al., 2009) and litter quality (Reich et al., 2005), showed only minor temporal changes.

We could not find a significant difference in beta diversity between the years and thus no evidence of homogenisation while most studies report an increasing homogenisation (thus a decrease in beta diversity) of the landscape. In England, Staley et al. (2013) showed a homogenisation of herbaceous forest plants in a resurvey of hedgerows and Keith et al. (2009) in a resurvey of forests. Our results are unexpected especially because we found a homogenisation of soil pH. However, the structural differences between hedgerows caused by different management regimes, ranging from traditional management to almost an abandonment of coppicing, might maintain beta diversity.

### Increase in nutrient-demanding species

The frequency of nutrient demanding species and therefore also the mean Ellenberg indicator value for nutrient availability have increased significantly over time. Species being regarded as problematic for agriculture, such as *Elymus repens*, *Urtica dioica*, *Galium aparine* and *Bromus sterilis*, have increased greatly in frequency and abundance. Similarly, Staley et al. (2013) found eutrophication to be a driving factor underlying the changes of plant communities in a hedgerow resurvey in England. Also the UK Countryside Survey reported an increase in species associated with high soil fertility for hedgerows (Carey et al., 2008).

The increase in the nutrient availability of hedgerows is for a large part caused by the increased usage of artificial fertilisers in Schleswig-Holstein: for nitrogen, the input doubled from 50.8 kg N/ha in 1962/63 to 100.3 kg N/ha in 2013/14 (DESTATIS, 2014b). Hedgerows bordering agricultural land are particularly exposed to agricultural fertilisers. Those parts of the fields adjacent to hedgerows were found to be extremely prone to an accumulation of nutrients. The crop plants in the shade of hedgerows grow usually less high and thus use less of the applied fertilisers which therefore accumulate in the soil over time (Mette, 1994). Additionally, hedgerows can act as biofilters for the run-off as well as for air-borne chemicals and are therefore exposed to particularly high atmospheric nitrogen deposition (Kovář et al., 1996).

Differences in mean N between the old and the new plots influenced the similarity of the herbaceous species composition between years. The optimum curve obtained in the model indicates that the greatest similarity is found in those plots where the mean N of the plot had not changed over time. Thus, even though the presence or absence of nitrogen was not found to influence the species richness in general, it has a strong impact on the composition of the species. This can also be seen in the DCA ordination diagrams with mean N being the only variable having a significant influence on the species composition of all functional groups. Nutrient input usually leads to a pronounced growth of some dominant herbs by which specialist groups such as forest plants get easily outcompeted.

### Decrease in pH and relation to mean R

The pairwise comparison of old and new pH values clearly showed a decrease in pH over the past five decades, which is a widespread pattern in agricultural land mainly caused by the input of organic fertilisers (Barak et al., 1997). These contain ammonium which is oxidised to nitrate by which protons are released. Deposition of atmospheric nitrogen and other acidifying pollutants can also lead to acidification, as shown for e.g. forest soils (Heisner et al., 2003; Van Calster et al., 2007; Baeten et al., 2009).

The decrease in pH was very pronounced in some plots, especially in those that had relatively high values in the original study. Heisner et al. (2003) in a study of forests over the course of 70 years also found a strong decrease in pH especially for formerly rather basic soils. The pH values in our resurvey were all below 4.2 and thus in the aluminium buffer range which is characterised by a high bio-availability of aluminium (Ulrich, 1983) and heavy metals such as lead. This is of particular interest because hedgerows were shown to be efficient biofilters and to accumulate lead in the soil underneath the hedgerows (Krinitz et al., 1996).

Interestingly, while measured soil pH decreased, the mean R values increased, and pH and mean R were found to be uncorrelated. It has been argued before that mean R does not reflect the pH well at values > 5, because at higher values mean R no longer increases (Schaffers & Sýkora, 2000). But even though most pH values in our study were lower than 5 we still do not see a correlation with mean R. This and the fact that Δ pH and Δ mean R are negatively related might be caused by the positive correlation between R and N scores across the species encountered in the hedgerows. Such correlations between indicator values can create problems in the interpretation of ecological resurvey studies (Diekmann, 2003). Here, the acidification found in most hedgerow sites has most likely not resulted in pH values below the lower limit of many or any of the species, and we therefore believe that the increasing nutrient availability reflected in increasing mean N overrules the responses of species to pH.

### Increase in temperature

The mean Ellenberg indicator value for temperature has significantly increased over time, reflecting a change of the species composition in response to the warming environment. Also the strong increase in *Hedera helix* indicates a changing climate because this evergreen broad-leaved plant is sensitive to low winter temperatures (Dierschke, 2005). Accordingly, the mean long-term annual temperature in the study area has increased by 0.6 °C over the last decades (comparing long-term data of 1961-1990 to 1981-2010; DWD (2012)). Even though the resolution of the scores for T is very low, we could show that species with a high T score were more likely to have increased in frequency than those with a lower score, an effect described as thermophilisation (De Frenne et al., 2013). This also confirms results from a study by Huwer and Wittig (2012) in which increasing temperature was the best explanatory variable for changes in species composition in resurveyed hedgerows. Diekmann (2010) found similar results for resurveyed forests in Germany and Sweden.

### Changes in management

We found that the shape of the hedge bank as well as the hedgerow height have changed over the past 50 years, indicating a change in management. The hedge banks which are a vital part of the hedgerows slowly erode and dissolve to both sides which causes them to decrease in height and get wider at the same time. Whereas, in former times, the hedge banks and the shrub layer were maintained well, today regular management is often neglected (Schrautzer et al., 1996).

A higher shrub layer was found to negatively influence species richness. When farmers still depended on the hedgerows as living fences the coppicing cycle used to be 9 to 11 years long (Weber, 1967a), while today it is recommended to coppice the hedgerows every 10 to 15 years (MLUR, 2013), and as hedgerows no longer serve the original function the cycle often is even longer. The farmers are by law obliged to manage the hedgerows (MLUR, 2013), but often do not have a practical interest

in doing so. This leads to gaps in the bank as well as the shrub layer, a process that probably has already started before the study from Weber (1967a) but worsened since. Many hedgerows had to be excluded from the resurvey because the shrub layer was too gappy or not present at all. If coppicing is delayed and shrubs grow too old, light levels on the ground floor increase which also allows less specialised species, particularly grasses such as *Elymus repens*, to invade the inner part of the hedgerows (Huwer & Wittig, 2012). The same holds true if gaps in the shrub layer are not refilled with new shrubs or if deer are not fenced out to allow natural regeneration of the shrub layer. Another factor that might negatively influence the diversity of herbaceous forest species is the decreasing shrub species richness which is associated with a decrease in structural heterogeneity.

Coppicing used to be a common management practice in deciduous forests in Central Europe but was mostly abandoned during the 20th century (Ellenberg & Leuschner, 2010). Shrub layers grew into tree layers which caused the canopy to become denser and led to an increase in shade tolerant herbaceous species (Baeten et al., 2009). In hedgerows, an abandonment of the traditional management usually leads to an increasing light availability, because shrubs grow into lines of trees which shade the banks less (Huwer & Wittig, 2012). It was obvious in the field that banks which were not stocked with a continuous shrub layer were overgrown by grasses.

## Consequences for conservation practises

We have shown that forest herb species richness has declined while arable weeds and grasses have increased in species richness. These different trajectories challenge nature conservation (Critchley et al., 2013). The field margins are considered as a natural part of the hedgerow flora (MLUR, 2013) and support most of the arable weed community. To increase their diversity it would be necessary to further promote field margins on which no fertilisers or herbicides are applied.

Hedgerows are an anthropogenic habitat and therefore need regular management to be maintained. The abandonment of coppicing has often been shown to be detrimental to the diversity of understorey species, and it is therefore an important management tool to maintain biodiversity (Moonen & Marshall, 2001). As mentioned before, many of the visited hedgerows were gappy or overgrown which increases the light availability. A change in management towards creating denser hedgerows would favour shade-tolerant forest herbs that also often have a low colonisation capacity (Verheyen & Hermy, 2001). Additionally, intact hedgerows can protect agricultural fields from erosion by wind (Knauer, 1993) and by water (Schernewski et al., 1996). The banks need to be maintained and broad gaps in the shrub layer need to be closed so that the hedgerows provide a connected habitat. A few small gaps could also be left open to promote structural heterogeneity of the shrub layer which favours herbaceous species richness (Deckers et al., 2004).

## Conclusions

Hedgerows are influenced by a large variety of factors. The variable most strongly affecting changes in species composition was the increase in nutrient availability, while changing management practises led to a loss of species richness. In landscapes of intensive agriculture, hedgerows often remain the last near-natural and potentially very heterogeneous habitat and therefore deserve special protection. This study has demonstrated dramatic changes of hedgerows over the past 50 years, including the loss of many formerly common red-listed species.

## List of appendices

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# Hedgerow age affects the species richness of herbaceous forest plants

Kathrin Litza & Martin Diekmann (2019)

Hedgerows in spring in between fields of corn and rape. The trees have different ages and sizes. The species-rich shrub layer is in bloom.

## Abstract

**Questions**: Are recent hedgerows less rich in forest vascular plants than ancient hedgerows? Does the proximity to potential source populations influence the forest species richness in recent hedgerows? Is there a difference in the dispersal potential of forest specialists found in recent and ancient hedgerows? How similar is the species composition between hedgerows of different ages?

**Location:** South-eastern Schleswig-Holstein, Northern Germany.

**Methods**: We investigated 30 hedgerows in a pairwise design to compare the species composition of ancient and recent hedgerows.

**Results**: While recent hedgerows already function as habitats for herbaceous forest specialists, they contained significantly fewer forest species than ancient hedgerows. Besides hedgerow age also proximity to ancient forests, a wide shrub layer, high pH values and a low phosphorus content were positively associated with the number of forest specialists. The similarity in species composition between recent and ancient hedgerows increased with the age of the recent hedgerow. Epizoochorous dispersal and reproduction by seed favoured the colonisation of recent hedgerows by forest species. Most environmental and hedgerow structural parameters did not differ between the age categories except for pH being significantly higher in recent hedgerows.

**Conclusions**: Ancient hedgerows are important for the regional biodiversity, especially as source populations for recent hedgerows, and therefore need to be protected. If the recent hedgerows are managed traditionally, they can over time transform into valuable habitats similar to ancient hedgerows.

**Keywords:** ancient hedgerows · ancient woodland indicator · colonisation credit · dispersal · forest species diversity · historical ecology · plant migration · recent hedgerows

## Introduction

The colonisation of new habitats is essential to a species' long-term survival in a changing environment. This challenges specialist species such as forest vascular plants because suitable habitats, such as deciduous forests, are often fragmented or degenerated (Jacquemyn et al., 2002; Vellend et al., 2006; Kolb, 2008). In addition, forest herbs are overall rather slow colonisers which means that new patches need time to increase in herb diversity after reforestation (Verheyen & Hermy, 2001, 2004). The payment of this colonisation credit, i.e. the deficit in species richness due to a delay in colonisation (Jackson & Sax, 2010), can take up to several centuries after the establishment of recent forests (Naaf & Kolk, 2015), but the process might be strongly accelerated when the patch connectivity is high (Kolk et al., 2017). Hedgerows have often been described as dispersal corridors for forest species (Corbit et al., 1999; Wehling & Diekmann, 2009b) and are thus able to increase the connectivity between otherwise isolated wooded habitats and to facilitate colonisation. They are also known to be refuge habitats for forest species (Baudry et al., 2000; Wehling & Diekmann, 2009a). Especially in areas depleted of forests they may represent the last near-natural wooded habitat and form woody networks within the agricultural land contributing to an increase in biodiversity

(French & Cummins, 2001; Freemark et al., 2002). Forming an ecotone between forest conditions and open agricultural land, hedgerows offer diverse environmental conditions and thus can provide suitable habitats for many taxa (Graham et al., 2018). How well they can function as a habitat for forest species depends e.g. on the width of their shrub layer (Roy & de Blois, 2008; Closset-Kopp et al., 2016), the prevailing soil conditions (Critchley et al., 2013; Litza & Diekmann, 2017) and the management regime (Staley et al., 2013).

Ancient forests with a continuous existence for several centuries are often regarded as biodiversity hotspots because of their high number of species with low dispersal potential (Wulf, 2003; Kelemen et al., 2014). These ancient woodland indicator species can therefore be used to define the continuity and nature conservation value of a forest (Hermy et al., 1999; Wulf, 2003; Schmidt et al., 2014). In addition, these diverse forests can function as source populations for nearby wooded habitats, such as other forests or hedgerows (Roy & de Blois, 2008; Paal et al., 2017). Likewise, the continuity of hedgerow habitats has been recognised as an important factor for forest species richness (Roy & de Blois, 2008; Closset-Kopp et al., 2016). It is therefore reasonable to assume that the presence of species-rich ancient hedgerows nearby acting as source populations increases the number of species in surrounding, possibly more recent, hedgerows as well. However, it remains unknown how fast recently established hedgerows can function as a suitable habitat for and be colonised by forest species.

The species composition also is likely to change with hedgerow age, but until now little is known about the dynamics of the plant community of newly established hedgerows. In an early phase, the shrub layer consists of young individuals of planted species (which are nowadays usually taken from tree nurseries instead of the surrounding land) and the herbaceous layer is dominated by ruderal, nitrophilous species (Starkmann, 1993). Over the years, the shade casting ability of the shrubs increases, and the ruderal species shift to the field margins and get replaced by shade-tolerant species in the interior. The colonisation of hedgerows by forest species is a rather slow process (Starkmann, 1993) but dispersal traits such as efficient dispersal vectors (Roy & de Blois, 2006) and light dispersule weight (Liira & Paal, 2013) were shown to positively influence their colonisation rate. In this way, species with certain functional traits become dominant during the process of hedgerow development while others decline.

One approach to gain insight into the development of recently established habitats that has proven very useful for forests is to compare pairs of ancient and recent forests regarding their species richness and composition (e.g. Bossuyt et al., 1999; Brunet et al., 2000; Dzwonko, 2001; Orczewska, 2009). This approach reduces the influence of confounding factors such as variations in climate, landscape properties and regional species pools which might otherwise distort the investigated patterns. To our knowledge such a pairwise study has never been used for examining the importance of historical age for the forest species richness, species composition or dominating functional traits of hedgerows.

By careful plot selection we were able to sample 15 pairs of recent and ancient hedgerows to test the following hypotheses:

1. Ancient hedgerows are more diverse than recent hedgerows and contain in particular more herbaceous forest species and ancient woodland indicator species.

2. Recent hedgerows that are located close to ancient hedgerows or ancient forests are richer in forest species than more isolated recent hedgerows.

3. Forest-like environmental conditions such as e.g. a wide shrub layer favour the establishment of forest species.

4. Recent hedgerows contain more ruderal species and a higher proportion of species with a better dispersal potential than ancient hedgerows.

5. Over time the species composition of recent hedgerows becomes more similar to that of ancient hedgerows.

## Methods

### Study Area

The study was conducted in the south-eastern part of the federal state of Schleswig-Holstein, Northern Germany (Figure A 2). The area is characterized by a young morainic, hilly landscape formed during the last glaciation. The soils are predominantly calcareous and relatively nutrient-rich. The climate in the study area is sub-oceanic and characterised by moderately warm summers and mild winters with a mean annual temperature of 8.9°C (DWD, 2015).

The landscape of Schleswig-Holstein is mainly used for agriculture (1,088,390 ha, 68.9 %) while only 10.3 % (162,014 ha) are covered by forests (Statistikamt Nord, 2018) of which about half are ancient, i.e. older than 200 years (Glaser & Hauke, 2004). This enhances the importance of (ancient) hedgerows for the area because they can form networks of wooded habitats within the agricultural land. Many hedgerows in north-western Europe were planted centuries ago and therefore offer a long habitat continuity (Pollard et al., 1974; Weber, 2003). In the study area, the construction and management of hedgerows, which are locally called "Knicks", started mainly in the 18th century (Weber, 1967). The original purpose of hedgerows was to confine livestock and to mark property boundaries, later also to offer resources such as firewood, timber, and fruits as well as effective protection against erosion. They were created by first raising a bank and then planting two rows of shrubs on top. Since the 1930s, hedgerows are legally protected and the land-owners are accountable for the appropriate management. This includes the coppicing of the shrub layer while trees are left standing every 60 to 80 m. This is traditionally done roughly every 10 years to keep the hedgerows in a healthy and dense state. Coppicing was shown to promote colonisation of recent forests by forest specialists (De Keersmaeker et al., 2011) and generally favours a high species diversity of endangered forest herbs (Roleček et al., 2017).

### Sampling design

The hedgerows were sampled in a pairwise design, each pair comprising one ancient and one recent hedgerow. The 15 sites were found by comparing recent satellite images with historical maps. All ancient hedgerows were already present on maps from 1877 ('Preußische Landesaufnahme') but it is likely that they are considerably older. Most of the hedgerow network was created in the late 18th and early 19th century, reaching its peak density in the 1880s (Müller, 2013), while the recent hedgerows were established between 1938 and 2004 (compare Table A 2) and thus were much younger. Their age was determined by consulting the land owners and aerial photographs as well

as time series of maps and satellite images. The used distinction of ancient and recent hedgerows based on the maps from 1877 was a compromise resulting from the insufficient quality of the oldest historical maps of the area (Varendorffsche Karten, 1789 – 1796) and the definition usually used for forests (stands should be continuously stocked for at least 200 years to be considered ancient). As hedgerow structures can be confused more easily than forests on maps of different ages, we decided not to use the 18th century maps because these proved to be nearly impossible to georeference with the needed quality.

To be included in the study, both hedgerow partners of a pair had to have the same direction and a maximum distance of 300 m ($min_{distance}$ = 37 m, $median_{distance}$ = 110 m, $max_{distance}$ = 296 m) (compare Table A 2 and Figure A 3). Because of their close proximity we assumed similar soil and climatic conditions. In addition, the hedgerows were likely to be owned and managed by the same farmers. This included also the adjacent land whose use was similar or even identical (when the compared hedgerows flanked two sides of one field). QGIS (QGIS Development Team, 2016) was used to determine the distance to the nearest ancient forest (according to Glaser and Hauke (2004)) which was similar for the ancient and recent hedgerows.

During sampling it was assured that both hedgerows had the typical structure of hedgerows in the study area, i.e. construction on a bank and/or a plantation in two rows. Additionally, they had to be at least 2 m high to exclude recently coppiced hedgerows from the sampling.

*Vegetation sampling*

The sampling of the hedgerow vegetation was done in spring 2017 and repeated in the summer of the same year to capture both vernal and late seasonal species. The plot length was set to 70 m and the plot width was confined by the borders of the adjacent fields, meaning that the field margins were included in the sampling (plot width ranged from 3.5 m to 6.8 m for ancient hedgerows and from 2.9 m to 7 m for the recent hedgerows). One plot per hedgerow was sampled and positioned in such a way that the paired plots were situated close to each other, yet never at the very end of a hedgerow to exclude possible edge effects. The vegetation survey included all vascular plant species, the cover of which was estimated on a percentage scale, but only presence/absence data was used in later analysis. The nomenclature follows Wisskirchen and Haeupler (1998). The tree layer was defined as including those woody individuals that had one main trunk likely not to be coppiced (typically *Quercus robur*), while shrubs were defined as being multi-branched. The herb layer comprised all herbaceous species plus *Hedera helix* because it was highly dominant on the ground and therefore not considered as a liana.

Herbaceous species need to be studied separately from shrub species because herbs are likely to represent a naturally formed community, whereas shrubs are usually planted and their presence thus is not exclusively explained by environmental conditions or management regime (French & Cummins, 2001). For detailed analyses, the herbaceous species can be further categorised into forest species (categories 1.1 "largely restricted to closed forests" and 1.2 "preferring forest edges and clearings" according to Schmidt et al., 2011) and ancient woodland indicator species (AWI) (Schmidt et al., 2014).

*Hedgerow structural and environmental variables*

In spring, we determined several structural variables that are known to influence the growth conditions of forest specialists: the width and height of the shrub layer, the width and height of the bank foundation, and the cover of the herb, shrub and tree layers. In the centre of each plot we measured the soil moisture using a portable soil moisture sensor and took soil samples of the upper 10 cm. The soil was air-dried and sieved in the laboratory. 10 g of soil were mixed with 25 ml of 0.1 M $CaCl_2$ and after 1.5 h of shaking the pH was measured using a pH meter with a glass electrode. Acetate-lactate soil extracts were prepared to measure magnesium, calcium and potassium content by means of atomic absorption spectroscopy (Philips AAS) and to measure the phosphorus content photometrically using UV/Vis spectroscopy. To determine the carbon-to-nitrogen ratio the soil was ground and then analysed chromatographically for carbon and nitrogen content in an Element Analyzer (HEKAtech Euro EA, Milano, Italy).

*Data Analysis*

All statistical analyses were carried out in R (version 3.4.3, R Foundation for Statistical Computing, Vienna, AT).

*Testing prerequisites*

To test whether the environmental conditions (structural and soil variables) in ancient and recent hedgerows are similar to each other we ran multiple pairwise Wilcoxon tests. The plot width was tested as well because due to our site-dependent definition it may differ between the hedgerows. We did not correct the results of these tests for multiple testing because, while reducing the false discovery rate, adjusting the *p*-values would at the same time increase the risk of false negatives. As we assumed similar conditions this would unacceptably bias the results.

*Comparing species richness*

The species numbers per plot were compared between the two age categories (ancient vs. recent) for all species present as well as separately for shrubs, herbs, forest specialists and ancient woodland indicator species (AWI) using multiple Wilcoxon signed-rank tests. To correct for multiple testing the Benjamini-Hochberg procedure was applied to reduce the number of falsely rejected null hypotheses and thereby controlling the false discovery rate (Benjamini & Hochberg, 1995).

The number of forest species in the recent hedgerows was related to the number of forest species in the corresponding ancient hedgerows with Spearman correlation. The frequencies were compared between AWI species and other forest specialists in a Wilcoxon signed-rank test to see whether the species classified as AWI were less frequent in hedgerows than other forest specialists. We also examined the influence of the age of the recent hedgerows on the richness of shrubs, herbs and forest specialists using Generalized Linear Models (GLMs) with quasipoisson distribution.

*GLMM to analyse forest species richness patterns*

A Generalized Linear Mixed Model (GLMM) with Poisson distribution (glmer function in the lme4 package (Bates et al., 2015) in R) was run to examine the influence of the age category (ancient vs. recent), structural variables (the width and height of the hedgerow shrub layer, the width and height of the bank foundation, and the cover of the herb and shrub layers), soil variables (pH, Mg, Ca, K,

P, C/N and soil moisture) and distance to the nearest ancient forest on the number of forest species present in the hedgerows. The hedgerow pair ID was included as a random term to account for the pairwise design. We inspected the variance inflation factors (VIF) of the included variables to avoid multicollinearity (Zuur et al., 2010) and excluded all variables with VIF > 3. Based on this, three of the soil variables (Ca, Mg and K) had to be taken out of the model. Model simplification was done as a step-wise backwards selection based on Akaike's information criterion (AIC).

*Comparing the dispersal, reproduction and ecological traits*

For each species, the dispersal mode (autochory, myrmecochory, anemochory, epizoochory, endozoochory) was derived from FloraWeb (www.floraweb.de, last accessed: 1. Dec 2017), while the classification into reproductive types (only by seed, mostly by seed, by seed and vegetatively, mostly vegetatively) was obtained from Klotz et al. (2002). A list of all found forest specialists and their properties can be found in Table A 3. One species can utilise more than one dispersal mode while the classification of reproductive type is distinct. We determined the proportion per plot for each dispersal mode. Then these were compared between the age categories in multiple pairwise Wilcoxon tests to examine whether the proportion of efficient dispersal modes (i.e. anemochory, epizoochory and endozoochory) - and thus the species' dispersal potential - is higher in recent hedgerows. Afterwards the Benjamini-Hochberg procedure was applied. The same analyses were run for the proportion of reproductive types per plot to see whether the proportion of species reproducing by seed was higher in recent hedgerows.

With respect to the ecological strategy (CSR) types, we calculated the mean coordinates for competitors, stress-tolerators and ruderals according to Pierce et al. (2017) for the herbaceous species. The values for those species not included in their published list were calculated following the instructions given in the supplementary data provided by the authors. We then compared the mean values between the age categories using Wilcoxon signed-rank tests with Benjamini-Hochberg correction. Additionally, we ran a Linear Model (LM) to explain the mean values of the CSR in recent hedgerows with the age gradient of the recent hedgerows.

*Analysing the species composition*

The Sørensen similarity index (*S*) for the herbaceous community was calculated for each of the hedgerow pairs: S = 2a/(2a + b + c)

where *a* is the number of shared species in the two compared hedgerows, *b* is the number of species that can only be found in the ancient hedgerow and *c* is the number only found in the recent one.

We ran a LM to explain the similarity in species composition by different variables including the spatial distance between the hedgerow partners, the specific age of the recent hedgerows, the difference in structural variables between the partners (bank height, width and cover of the shrub layer) as well as in soil pH. The structural variables and pH were also entered as quadratic terms to allow for non-linear relationships, i.e. for maxima and minima. This is useful when expecting that no difference in the variables leads to the highest similarity in species composition (Litza & Diekmann, 2017). Model simplification was done as a step-wise backwards selection based on the AIC.
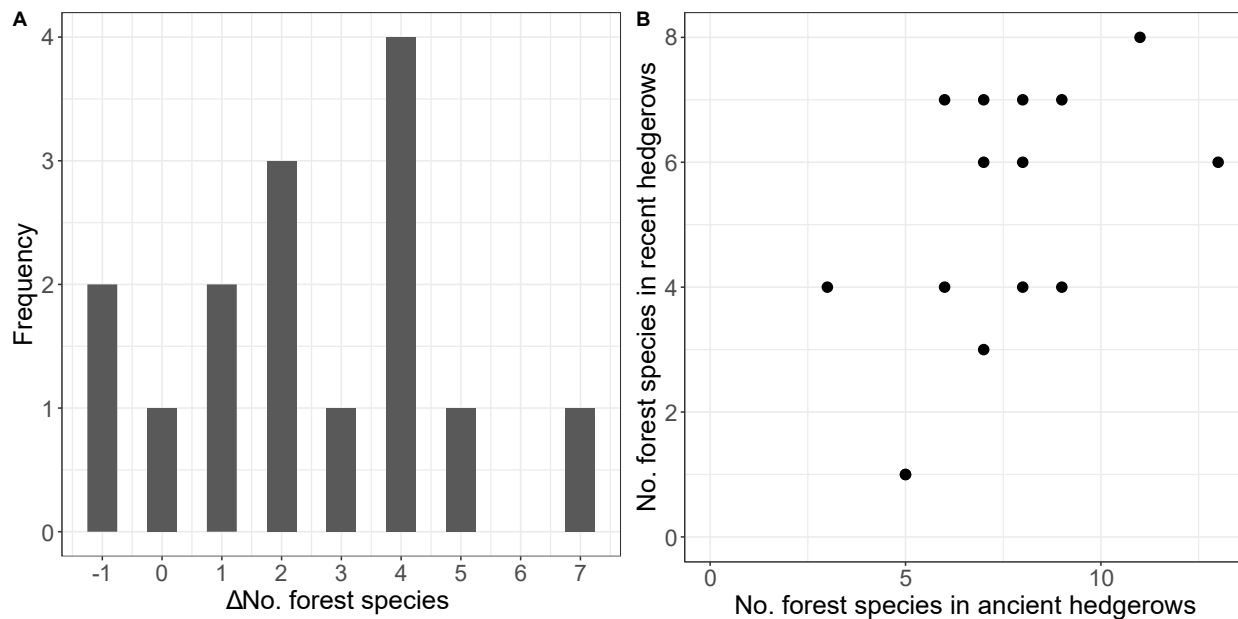
Figure 3.1 A Histogram of the difference in the number of forest specialists between recent and adjacent ancient hedgerows. Positive values indicate higher numbers in ancient hedgerows. B Correlation between the number of forest specialists in recent and the adjacent ancient hedgerows.

## Results

### Hedgerow structural and environmental variables

There were no significant differences in plot width or in hedgerow structure (the width and height of the shrub layer, the width and height of the bank foundation, and the cover of the herb, shrub and tree layers) between recent and ancient hedgerows. Only tree cover tended to be higher in the older hedgerows ($V = 24$, $n = 15$, $median_{ancient} = 10$ %, $median_{recent} = 8$ %, $p = 0.078$).

The soil variables partly differed between the age categories. The pH-value was significantly higher in recent hedgerows ($V = 107$, $n = 15$, $median_{ancient} = 3.8$, $median_{recent} = 4.68$, $p < 0.01$), which also contained marginally more calcium ($V = 93$, $n = 15$, $median_{ancient} = 62.48$, $median_{recent} = 101.78$, $p = 0.064$). No significant differences were found for magnesium, potassium, phosphorus, C/N ratio or soil moisture.

### Species richness of ancient and recent hedgerows

The cumulative number of species was higher in recent hedgerows than in ancient ones (166 vs. 153). In total we found 36 woody species and 117 herbaceous species in ancient hedgerows, in contrast to 38 woody species and 128 herbaceous species in recent hedgerows. The mean number of species per plot did not significantly differ between ancient and recent hedgerows though, and neither did the number of herbaceous or woody species.

There were significantly more herbaceous forest species in ancient hedgerows than in recent hedgerows ($V = 5$, $n = 15$, $median_{ancient} = 7$, $median_{recent} = 6$, $p = 0.015$, Figure 3.1 A, Table A 2). Recent hedgerows rich in forest specialists were associated with ancient hedgerows also rich in forest specialists ($rho = 0.54$, $n = 15$, $p = 0.039$, Figure 3.1 B), while the number of forest specialists was not

influenced by the age gradient of the (recent) hedgerows. The latter was also true for the herb richness but not for woody species which decreased in richness with increasing age of the hedgerows ($X^2 = 11.4$, $n = 15$, $p < 0.001$).

Interestingly, the number of ancient forest indicator species did not differ between the hedgerow age categories ($V = 28.5$, $n = 15$, $median_{ancient} = 1$, $median_{recent} = 1$, $p = 0.459$). However, when the total plot frequency was investigated independently of age categories and compared between ancient forest indicator species and the other forest specialists, AWI species were found to be significantly less frequent in hedgerows ($X^2 = 29$, $n = 21$, $median_{AWI} = 1$, $median_{others} = 13$, $p < 0.001$).

### GLMM modelling forest species diversity

In the GLMM relating the number of forest specialists to the hedgerow structural, environmental and spatial variables as explanatory variables, six of the included variables contributed to the final model (Table 3.1). The ancient hedgerows contained more forest species than recent hedgerows (as was already shown in the Wilcoxon test). Ancient as well as recent hedgerows which were situated close to an ancient forest were richer in forest species (Figure 3.2 A). Regarding the hedgerow structure, a large shrub width and a high cover of the herb layer and, additionally, a more base-rich pH and low phosphorus content led to a higher forest species richness.
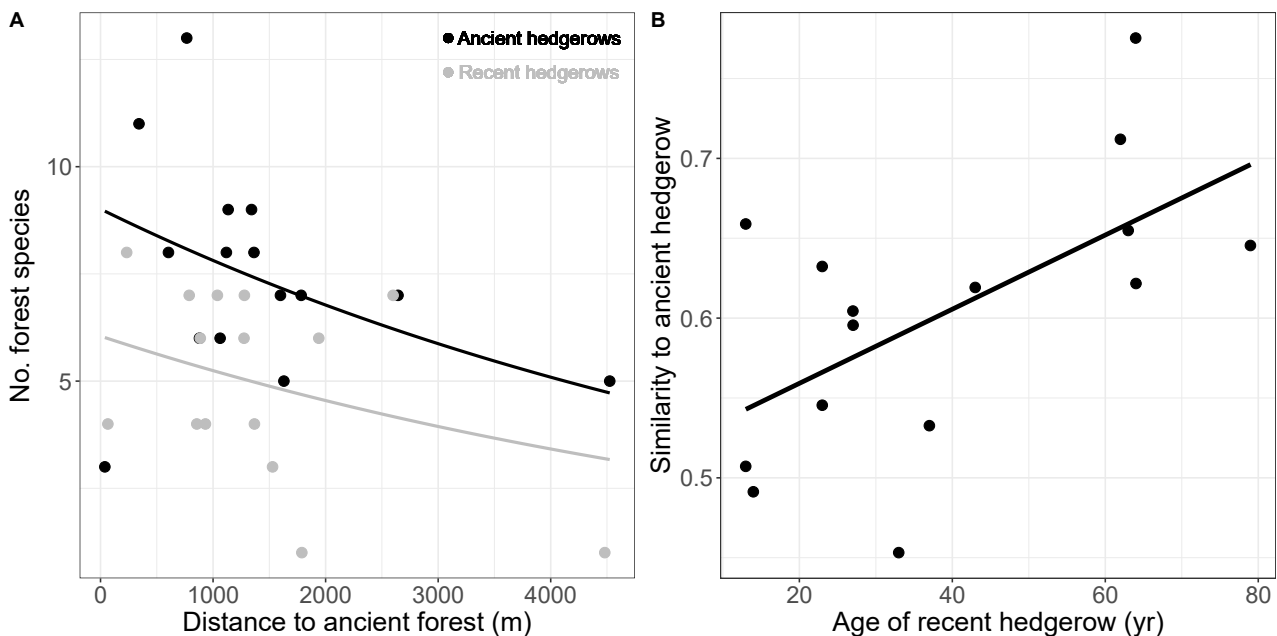


Figure 3.2 A Number of forest species per hedgerow in relation to the distance to the nearest ancient forest. The curves are fitted by Poisson distribution. B The Sørensen similarity of the herbaceous community between paired recent and ancient hedgerows against the age of the recent hedgerows (in years).

Table 3.1 Results of the GLMM modelling forest species diversity. Given are the model estimates, the standard error (SE), the test statistic (*z*-value) and the *p*-value of the variables included in the final model. Model simplification was based on the AIC which is why not all of the remaining variables have significant *p*-values. The variables bank width and bank height, shrub cover and shrub height, soil moisture and C/N ratio did not significantly contribute to the final model.

| Variable | Estimate | SE | *z*-value | *p*-value |
|---|---|---|---|---|
| *Intercept* | 1.467 | 0.147 | 9.988 | < 0.001 |
| Ancient/recent hedgerow | 0.625 | 0.218 | 2.866 | 0.004 |
| Distance to ancient forest | -0.254 | 0.107 | -2.377 | 0.017 |
| Width of the shrub layer | 0.132 | 0.078 | 1.695 | 0.090 |
| Herb cover | 0.162 | 0.095 | 1.710 | 0.087 |
| pH | 0.194 | 0.134 | 1.451 | 0.147 |
| Phosphorus content | -0.121 | 0.087 | -1.398 | 0.162 |

### Reproduction and dispersal traits

When examining the proportion per plot of forest species with specific dispersal modes, recent hedgerows contained a significantly higher proportion of species that can be dispersed by epizoochory than ancient hedgerows (Table 3.2), which is a comparatively efficient dispersal mode. Surprisingly, anemochory and endozoochory showed no such patterns. The proportion of species dispersing autochorously tended to be higher in ancient hedgerows as one would expect but the pattern was not significant.

Of the different reproductive types only reproduction by seed showed significant differences between the ancient and recent hedgerows with the proportion of species reproducing by seed being significantly higher in recent hedgerows (Table 3.2). Only one species was classified as reproducing "mostly by seed" (compare Table A 3) which is why the results for this reproductive type are not meaningful.

### Ecological traits

The mean CSR coordinates for herbaceous plants did not differ between ancient and recent hedgerows for any of the three investigated categories, while the mean values for herbaceous stress-tolerators significantly decreased with increasing age of the recent hedgerows ($F = 5.55$, $n = 15$, $p = 0.035$).

### Species composition

The hedgerow partners were most similar in herbaceous species composition when the bank height, width of the shrub layer and pH differed the least (i.e. they had maxima close to x = 0). In addition, the similarity increased along the age gradient of the recent hedgerows (Figure 3.2 B) and with proximity of the hedgerow partners (Table 3.3, final model: $R^2_{adj} = 0.74$, $df = 7$, $p = 0.012$).

Table 3.2 Results of pairwise Wilcoxon tests. The proportion of each dispersal mode and reproductive type present per plot between recent and ancient hedgerows were compared. *V* is the test statistic. Significant *p*-values are in bold. The *p*-values were adjusted for multiple testing using the Benjamini-Hochberg procedure.

| | *V* | **Median**$_{ancient}$ | **Median**$_{recent}$ | *p*-value |
|---|---|---|---|---|
| *Dispersal modes* | | | | |
| Autochory | 9 | 0.12 | 0 | 0.115 |
| Myrmecochory | 29.5 | 0.14 | 0.14 | 0.755 |
| Anemochory | 21 | 0.5 | 0.43 | 0.212 |
| Epizoochory | 103 | 0.27 | 0.43 | **0.010** |
| Endozoochory | 19.5 | 0.29 | 0.14 | 0.115 |
| *Reproductive type* | | | | |
| By seed | 93 | 0.14 | 0.29 | **0.048** |
| Mostly by seed | 0 | 0 | 0 | 1 |
| By seed and vegetatively | 18.5 | 0.67 | 0.5 | 0.070 |
| Mostly vegetatively | 23.5 | 0.15 | 0.14 | 0.177 |

Table 3.3 Result of the LM analysing the difference in environmental, structural and spatial conditions on the similarity of the species composition (Sørensen index). Given are the model estimates, the standard error (SE), the test statistic (*t*-value) and the *p*-value of the variables included in the final model. Model simplification was based on the AIC which is why not all of the remaining variables have significant *p*-values. The main effect of the bank height and the main as well as the quadratic term of the cover of the shrub layer did not significantly contribute to the final model.

| Variable | Estimate | SE | *t*-value | *p*-value |
|---|---|---|---|---|
| *Intercept* | 5.883 | 1.288 | 4.569 | 0.003 |
| Bank height$^2$ | -0.043 | 0.038 | -1.130 | 0.296 |
| Width of the shrub layer | 0.057 | 0.013 | 4.511 | 0.003 |
| Width of the shrub layer$^2$ | 0.017 | 0.009 | 1.913 | 0.097 |
| pH | 0.108 | 0.032 | 3.387 | 0.012 |
| pH$^2$ | -0.036 | 0.018 | -1.988 | 0.087 |
| Distance between hedgerows | -0.0003 | 0.0002 | -1.430 | 0.195 |
| Age of the recent hedgerows | -0.003 | 0.0007 | -4.086 | 0.005 |

## Discussion

### Forest species richness in ancient and recent hedgerows

Recent hedgerows were shown to function as a habitat for herbaceous forest specialists even though they contained a significantly lower number of forest species than ancient hedgerows. However, the forest species richness of recent hedgerows was higher than expected. Their development into valuable habitats appears to take only a few decades, provided that they are traditionally laid out and managed. Because the environmental conditions were shown to be mostly similar within the studied hedgerow pairs, the pairwise design allows us to link the difference in the number of forest specialists to the age difference and the slow colonisation rates of forest herbs. This confirmed the results found in similar studies conducted in forests (e.g. Bossuyt et al., 1999; Brunet et al., 2000; Dzwonko, 2001; Orczewska, 2009) and shows that there is a colonisation credit of forest species in hedgerows. This credit was paid off more efficiently when there was a potential source population – such as a species-rich ancient hedgerow – situated nearby. This emphasises the conservation value of ancient hedgerows for the plant diversity in agriculturally intensified landscapes. Also a short distance to the nearest ancient forest was beneficial for the richness of forest specialists in hedgerows of all ages. This function of ancient forests as source population was shown before, both for the colonisation of hedgerows (Paal et al., 2017) and for recent forest patches (Dzwonko, 2001; Graae et al., 2003).

Contrary to our expectations, the number of ancient woodland indicator species did not differ between the age categories. AWI species were overall rare, independent of hedgerow age most plots contained only one species. In general, the concept of ancient woodland indicator species does not seem to apply to hedgerows, suggesting that dispersal efficiency and thus time needed to reach a new habitat are not the main factors limiting the distribution of AWI species but their adaptation to stable habitats.

### Forest species richness and environmental conditions

One variable contributing to a high species richness of forest specialists was a wide shrub layer which shades the ground and thus creates the habitat for the specialists. A wide shrub layer can be linked to more stable and more forest-like conditions not only with respect to light availability but also to the microclimate (e.g. Roy & de Blois, 2008; Closset-Kopp et al., 2016). Unfortunately, farmers often have the motivation to keep hedgerows between agricultural fields as narrow as possible to reduce their loss in tilled area. To lessen this harmful effect the lateral cutting is strictly defined in the hedgerow management regulations for the study area (MELUR, 2017). Not only the ground vegetation depends on a wide shrub layer for hedgerows to form suitable habitats but also mammals, birds and invertebrates benefit from it (Graham et al., 2018).

Among the soil factors, we found a low pH value and a high phosphorus content to negatively influence the species richness of forest vascular plants in hedgerows. Low pH values are known to decrease species richness in forests (e.g. Peet et al., 2003; Peppler-Lisbach & Kleyer, 2009), and in the light of ongoing soil acidification, the sensitivity of forest specialists to low soil pH needs to be in the focus of conservation efforts. The pH value was also the only variable that differed between the age categories. However, as the recent hedgerows were even more base-rich than ancient hedgerows this difference is unlikely to have biased our conclusion about the colonisation credit in recent

hedgerows. It can further be explained by the ongoing pedogenesis in the raised banks which is characterised by accumulation of humus, leaching of nutrients and acidification (Schleuß, 1996). The acidification might be accelerated by the input of organic fertilisers on the adjacent land reaching the hedgerows (Barak et al., 1997). A resurvey study analysing the change of the pH values in hedgerows over the last 50 years found a decrease in pH of on average about 0.5 units (Litza & Diekmann, 2017).

The second soil variable found to be detrimental to forest species richness was a high phosphorus content, facilitating the growth of competitive species and likely to be caused by the adjacent agricultural land-use adding high amounts of fertilisers. The increase in the number of competitive species was identified as a major threat to the diversity in hedgerows by Litza and Diekmann (2017). In forests, Honnay et al. (1999) also found a negative correlation between phosphorus content and the number of ancient forest species due to increased competition. De Keersmaeker et al. (2004) demonstrated that soils with increased phosphorus content favoured the dominance of *Urtica dioica* when light availability was sufficiently high, resulting in a lower colonisation rate by woodland plants. However, we did not see this negative impact of *U. dioica* in our hedgerows.

### Species richness

The mean species richness per plot did not differ between ancient and recent hedgerows, while the cumulative number was even higher in recent hedgerows. Pellissier et al. (2004) who compared the seed banks of ancient and recent hedgerows also found a decrease in total species richness during succession but an increase in the number of forest specialists, coinciding with our findings.

We found no difference in the number of woody species between the age categories which contradicts the results of Pollard et al. (1974) who showed a clear increase in shrub species over time. On the contrary, we found a negative relationship between the number of shrub species and the age gradient of recent hedgerows. This was surprising but may be explained by the increasing effort that is put into constructing diverse new hedgerows which means that this is most likely a management effect and not caused by natural colonisation. In addition, the regular coppicing reduces the species pool in later years to those able to cope with this disturbance. A woody species particularly frequent in recent hedgerows was *Prunus padus*, probably caused by its good ability to take root after planting and its fast growth (Starkmann, 1993).

### Reproduction and dispersal traits

Recent hedgerows contained comparably many species not relying on vegetative propagation but reproducing by seed. This is in coincidence with results found for forests by Dzwonko (2001) and Brunet and von Oheimb (1998) who demonstrated the importance of efficient seed dispersal for the colonisation of recent forest patches, while species relying on vegetative reproduction or dispersal by ants had far lower migration rates. In our study, only the proportion of forest species that are dispersed by epizoochory was higher in recent hedgerows than in ancient hedgerows. As hedgerows form linear landscape elements that are widely used as migration corridors by mammals (Burel, 1996), the potential of epizoochory is high (Hernández & Zaldívar, 2013). Wehling and Diekmann (2009b) found epizoochory and anemochory to be the most prominent dispersal types in hedgerows and Graae (2002) concluded that tall species with epizoochorous seeds are well adapted for the

colonisation of new forest habitats. One example for this strategy in our study is the tall-growing *Chaerophyllum temulum* that was not only present in most of the ancient hedgerows but more interestingly represented the most common forest species in recent hedgerows. Surprisingly, we found no difference between ancient and recent hedgerows for the distribution of anemochorous or endozoochorous species. Anemochory, however, might be not very effective in hedgerow habitats because these act as windbreaks (Burel, 1996). Therefore, wind dispersal is unlikely to cross long distances with diaspores being filtered out by and accumulated in neighbouring hedgerows.

In general, the recent hedgerows are all imbedded in a network of ancient hedgerows and forests which might obliterate dispersal patterns because it is not always easy to determine the source population (compare Figure A 3). One of the studied recent hedgerows, being only about 25 years old but directly adjacent to an ancient forest, contained the impressive number of eight forest species of which three were found only in this hedgerow (*Circaea lutetiana*, *Epipactis helleborine*, *Galium odoratum*) and probably originated from the ancient forest. When only short dispersal distances need to be bridged forest specialists might cross these rapidly, independent of their dispersal mode (Dzwonko & Gawroński, 1994).

### Ecological traits

One very important stress factor on hedge banks for the herbaceous community is drought stress as the banks are elevated above the surrounding terrain which increases the distance to the ground water level. In addition, the banks are exposed to increased solar radiation, especially when south facing, and wind. Over time the influence of solar radiation and wind is mitigated by the establishing shrub layer which profoundly reduces the drought stress. This might explain why the mean stress-tolerance of the herbaceous species community decreased the older the recent hedgerows were. Surprisingly, this pattern was not confirmed by the pairwise comparisons and also the expectation that recent hedgerows contained more ruderal species was not substantiated.

### Species composition

The similarity in species composition between the partners of a pair increased with an increasing age of the recent hedgerow. Because coppicing causes a regular disturbance, hedgerows do not reach the climax stage - being a forest - but are kept in an intermediate state of succession. However, this result shows that there is a transition from a young to an established hedgerow community which takes place within a few decades. This transition is facilitated when the hedgerow structure, especially the shrub layer width and the bank height, and important environmental conditions such as the pH are similar to those found in the ancient hedgerows. Hedgerows are man-made habitats, but given time and proper management they represent a plant community that can be very diverse and considered semi-natural.

## Conclusions

von Oheimb et al. (2007) stressed the importance of ancient forests to maintain the regional biodiversity and our study underlined that ancient hedgerows can largely contribute to this. In contrast to forests, they do not form islands but even networks of biodiversity across the agricultural landscape. It is important that these species-rich semi-natural habitats are sustainably managed to

protect the remaining biodiversity in the region. Our study showed that the immigration of forest herbs into recent hedgerows was facilitated when ancient forests or hedgerows, and thus potential source populations, could (still) be found nearby. If the recent hedgerows are managed traditionally they can over time develop into ecosystems that are similar to today's ancient hedgerows and thus contribute to the conservation of forest specialist species.

## Acknowledgements

## Data accessibility

The data are available from vegetweb https://www.vegetweb.de/home#!quellendetails//1375 (Jansen et al., 2015).

## List of appendices

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# The effect of hedgerow density on habitat quality distorts species-area relationships and the analysis of extinction debts in hedgerows

Kathrin Litza & Martin Diekmann (2020)

Land consolidation in Wangels, Northern Germany, between 2004 and 2015 (coordinates: 54.276494, 10.769722, Google Earth, 9th Feb. 2018).

## Abstract

**Context:** Hedgerows are highly important for maintaining the biodiversity in deforested landscapes. Especially for habitat specialists such as several forest plants they can provide important refuge habitats.

**Objectives:** This study aims to examine whether there is an extinction debt for forest plants in hedgerows.

**Methods:** In a study area in Northern Germany that had lost 47 % of the hedgerow network over the past 120 years, hedgerows were mapped for the presence of forest vascular plants. In a multi-model approach, we compared the explanatory power of present and historical landscape variables and habitat quality on diversity patterns.

**Results:** The change in landscape configuration had no effect on the species richness of forest plants in hedgerows, i.e. there was no sign of an extinction debt. The best explanatory variable was the hedgerow width with more species found in wider hedgerows. This demonstrates the importance of including local habitat variables in the study of extinction debt. For ancient woodland indicator species models including both the landscape configuration and habitat variables were superior to simple models. The best models included the historical distance to the nearest forest, suggesting an extinction debt.

Counterintuitively, a high density of hedgerows had a negative influence on species richness, most likely because hedgerows are narrower in areas with higher densities due to land-saving measures by farmers. There was also a negative correlation between hedgerow density and the hedgerow proximity to forests.

**Conclusions:** The effects of important covariates may obscure species-area relationships and undermine extinction debt analyses.

**Keywords**: Extinction debt · habitat loss · hedgerow density · historical vegetation ecology · multi-model approach · species-area relationship

## Introduction

Habitat loss is one of the main threats to biodiversity (Sala et al., 2000; Dirzo & Raven, 2003). When habitats are destructed this has a negative influence on species diversity, mainly due to a reduced carrying capacity of the habitat, stronger edge effects and an increased probability of extinction by stochastic processes. However, a decline in species numbers will not always occur immediately after habitat reduction but might occur with a time-lag (Tilman et al., 1994). When species have long generation times, a population can persist for decades or longer even though regeneration is lacking. In this way species are expected to go locally extinct even if no further habitat change occurs. This time-delayed loss of species is called the extinction debt, a concept which has received increasing attention in recent years (e.g. Tilman et al., 1994; Vellend et al., 2006; Kuussaari et al., 2009; Jackson & Sax, 2010; Kolk & Naaf, 2015). When species have long relaxation times, i.e. the time delay for predicted extinction to take place after a habitat has been altered or reduced, the extent of species

loss may be underestimated. This poses a challenge for conservation efforts because the effect of habitat reduction often goes unrecognised (Jackson & Sax, 2010). It is therefore important to study the extinction debt across different habitats and species groups in order to counteract habitat loss as long as species have not gone extinct.

Theory suggests that the likelihood of a time-lagged extinction is stronger for species with a high persistence, long generation times, and dispersal limitations (Kuussaari et al., 2009). A precondition is that species depend on a specific habitat type and are affected by the spatial configuration of this habitat. Forest plants are therefore prone to show an extinction debt, as they are dependent on woody habitats, which are strongly fragmented in large parts of Europe, and are known to have slow metapopulation dynamics (Kolb, 2008; Brunet et al., 2011). Among forest specialists, the subgroup of ancient woodland indicator species (AWI, Schmidt et al. (2014)) is especially interesting to study in this context. These species indicate woodlands of a high conservation value and are likely to exhibit an extinction debt because of their low dispersal capacities (Kolk & Naaf, 2015).

Until now, the presence of an extinction debt for forest specialists was examined for true forests (e.g. Vellend et al., 2006; Kolk & Naaf, 2015) but not for other wooded habitats such as hedgerows, which are semi-natural linear habitats that form wooded networks across the landscapes in Central and Western Europe. They were originally set up in the 18th and 19th centuries as living fences but have been severely reduced in size during the agricultural intensification of the 20th century (Deckers et al., 2005). We studied an area in which 47 % of the network was lost within 120 years (see Methods section and Table 4.1 of this article for more details on the hedgerow loss). When intact, hedgerows can provide ecosystem services such as water purification, erosion reduction and pest regulation (Van Vooren et al., 2017), and may have an ecological effect disproportionately larger than their size (Poschlod & Braun-Reichert, 2017). For specialised species that are dependent on wooded habitats, such as forest vascular plants, they can form migration corridors (Corbit et al., 1999; Roy & de Blois, 2008; Wehling & Diekmann, 2009b; Closset-Kopp et al., 2016) as well as refuge habitats (Endels et al., 2004; Wehling & Diekmann, 2009a). This is especially important in areas that have been largely deforested with only fragmented forest patches left.

Landscape properties such as the connectivity of the surrounding network (Roy & de Blois, 2008; Ernoult & Alard, 2011; Paal et al., 2017) and the proximity to forests (Corbit et al., 1999; Litza & Diekmann, 2019) have been shown to influence the number of forest specialists in hedgerows. Consequently, an area reduction of the hedgerow network as well as further destruction of the remaining forest fragments is expected to lead to a decrease in forest species richness. Besides habitat area and connectedness, the habitat quality also affects the diversity of forest plants in hedgerows (Adriaens et al., 2006; Paal et al., 2017). Previous studies have found several habitat conditions to be of importance, e.g. the prevailing soil conditions, particularly nutrient availability and pH (Critchley et al., 2013; Litza & Diekmann, 2017, 2019). Additionally, the hedgerow structure has been repeatedly shown to be one of the key factors influencing the species assemblage, with wider hedgerows leading to more forest specialists due to a more favourable and stable microclimate (in terms of solar radiation, wind and temperature) (e.g. Sitzia, 2007; Roy & de Blois, 2008; Closset-Kopp et al., 2016; Litza & Diekmann, 2019).

There are different ways of studying extinction debts and the choice of method depends on the study habitat and the available information. Historical data of species distributions is scarce which is why the most commonly used approach is to compare the influence of the past vs. present habitat configuration on today's species distributions (Kuussaari et al., 2009). If the current species occurrences are better explained by the past than by the present habitat configuration, an extinction debt is invoked. This configuration is often expressed as the area (when the influence of habitat loss is studied) or the connectivity of the habitat patches (when habitat fragmentation is assessed). Fahrig (2003) underlined the importance of separating the effects of habitat loss and fragmentation, but as hedgerows are linear landscape elements these two variables are strongly correlated and the assessment of one also expresses the other. The fundamental assumption behind the concept of extinction debt is a positive species-area relationship, meaning that habitat destruction has a negative impact on species number. Challenges for studying the extinction debt may arise when habitat destruction is difficult to quantify or if other variables distort the positive species-area relation. This has not been covered by research until now. Many studies of extinction debts only include landscape variables (e.g. Vellend et al., 2006; Cousins et al., 2007), but Kolk and Naaf (2015) demonstrated for forests that it is very important to also consider measures of habitat quality to not over- or underestimate the effect. Our study aims to demonstrate that covariates can impede disentangling the effects of habitat loss from effects of changing habitat quality and, consequently, studying the extinction debt.

We hypothesise that (1) the species number of forest specialists in hedgerows can better be explained by past than by present landscape configuration, i.e. that there is an extinction debt, (2) ancient woodland indicator species show a larger extinction debt than other forest species, and (3) habitat quality distorts the analysis of the effects of landscape variables on species richness.

## Methods

### Study area and data sampling

The study area comprises the Schleswig-Holstein Uplands which are located in the east of the federal state of Schleswig-Holstein, Northern Germany (Figure 4.1), and is characterised by a Young Drift morainic landscape. The climate is suboceanic with an annual precipitation of 770 mm and a mean annual temperature of 8.9 °C (DWD, 2015).

The main land use in the study region is agriculture (1,088,390 ha = 68.9 %) while only 10.3 % (162,014 ha) are covered by forests (Statistikamt Nord, 2018). About half of the forests can be characterised as being ancient i.e. older than 200 years (Glaser & Hauke, 2004). The estimates for today's hedgerow length vary between 44,915 km (Müller, 2013), 68,281 km (MLUR, 2005) and 73,400 km (Jungelt, 2016). Based on this, the land cover by hedgerows can roughly be estimated. If the most widely used estimate of total hedgerow length of 68,281.2 km is multiplied by the mean hedgerow width in the study area of 4.5 m (Table 4.1), this sums up to an area covered by hedgerows of as much as 30,726.5 ha (1.9 %).

Figure 4.1 Map displaying the study area in the east of the federal state of Schleswig-Holstein, Germany.

The establishment of hedgerows has a century-long tradition in Europe. Some hedges can be dated back more than 1,000 years (Pollard et al., 1974; Stamm & Welters, 1996) while most of the hedgerows in Central and Western Europe were established in the 18th and 19th centuries (Weber, 1967; Pollard et al., 1974). As part of the Enclosing Acts, they were created as living fences that surrounded fields, marked boundaries and restrained the livestock. They also supplied fruits and were important sources of firewood and timber through periodical coppicing. Even though farmers do not depend on these features of hedgerows anymore, regular management is required until today to maintain the habitat. Poorly managed hedgerows are threatened to lose their important ecological functions and show a decrease in species diversity (Staley et al., 2013). In the study area, the land-owners are until today obliged by law to manage the hedgerows in an appropriate manner (regulations in MELUR, 2017). During the 1950s to 1980s the land consolidation process in Central and Western Europe had the purpose of generating larger agricultural fields that could be managed more efficiently. In the course of this process, large parts of the hedgerow network were removed, locally more than 70 %, while only few hedgerows were newly planted to compensate for those measures (Kellerhoff, 1984). The most frequent shrub species found in hedgerows are *Corylus avellana*, *Prunus spinosa*, *Sambucus nigra* and *Rubus fruticosus* agg., while the tree layer is most often formed by *Quercus robur*.

### Data sampling

We investigated 89 hedgerow plots in total. Of those, 42 were sampled in summer (June and July) 2015 and again in April 2016. Another 32 were investigated in May 2016 and the remaining 15 in spring (April and May) 2017 and summer (July) 2017. The plots had a length of 70 m and were confined by the borders of the adjacent fields, i.e. included the field margins in the analysis. The surveys recorded presence/absence data of all forest specialists (classified by Schmidt et al. (2011) as 1.1 'largely restricted to closed forests' and 1.2 'preferring forest edges and clearings'). We distinguished the ancient woodland indicator (AWI) species as a subgroup (Schmidt et al., 2014). These are forest specialists that have particularly low dispersal capacities, are thus mainly confined to habitats with a long stability in the landscape and indicate habitats of a high conservation value. All investigated hedgerows were already present on maps from 1877-1879 and can thus be considered as ancient (Litza & Diekmann, 2019). Recent hedgerows were shown to have not yet

attained equilibrium diversity (Litza & Diekmann, 2019) and were therefore excluded from the sampling.

We measured the width of the shrub layer once per plot at a representative point close to the plot centre. Only hedgerows with a minimum height of 2 m were included in the sampling to exclude newly coppiced hedgerows. Hedgerow width is known to be an important proxy for local habitat quality (Closset-Kopp et al., 2016; Litza & Diekmann, 2019), but it cannot be measured directly after coppicing, i.e. the removal of the shrub layer. One soil sample per plot was taken in the centre of the plot to determine the pH values. For the analysis, the soil was air-dried and sieved in the laboratory, and 10 g of soil were mixed with 25 ml of 0.1 M $CaCl_2$. After 1.5 h of shaking the pH was measured using a pH meter with glass electrode.

### Present and historical landscape properties

Spatial analyses were carried out in QGIS (QGIS Development Team, 2016) and *R* (version 3.6.1, R Foundation for Statistical Computing, Vienna, AT) using the package 'rgeos' (Bivand & Rundel, 2018).

We used the maps of the 'Preußische Landesaufnahme' (1:25,000) by the Prussian government (1877-1879, hereafter referred to as from 1877), which are likely to reflect the historical peak in hedgerow density, to gather information about the former landscape composition. The newest maps covering the complete study area were published in 2003-2008 (Topographische Karte 1:25,000) with most of the map sheets dated from 2004 (and hereafter referred to accordingly). The hedgerow network was digitised in a radius of 500 m around the plots on both sets of maps to calculate the density in meters per hectare (m/ha). For linear landscape elements the length (or density) is a good representative for habitat area and connectivity (Zuur et al., 2010). There was a considerable loss in the density of hedgerows in the study area (Table 4.1). While the historical density amounts to 116 m/ha on average, there was a mean loss of almost half of the density until today (47 %). Occasionally, the loss even exceeded 77 % of the network. One single plot gained more hedgerows than it lost but the net gain was only 8 m/ha. An exemplary change can be seen in Figure 4.2.

Table 4.1 Landscape and habitat variables included in the models. The landscape composition was digitised as found on historical maps (1877) and present maps (2004). The hedgerow density was measured in a radius of 500 m around the investigated hedgerows (n = 89).
Variable groups: PL = Present landscape, PLAF = Present landscape with distance to nearest ancient forest, HL = Historical landscape, HQ = habitat quality.

|  | Mean | Range | Variable Group |
|---|---|---|---|
| Present hedgerow density (m/ha) | 62 | 21 - 122 | PL, PLAF |
| Present distance to nearest forest (m) | 500 | 27 - 1450 | PL |
| Present distance to nearest ancient forest (m) | 720 | 32 - 1989 | PLAF |
| Historical hedgerow density (m/ha) | 116 | 32 - 184 | HL |
| Historical distance to nearest forest (m) | 664 | 15 - 1987 | HL |
| Hedgerow width (m) | 4.5 | 2.3 – 7.5 | HQ |
| pH | 4 | 3.2 – 7.0 | HQ |
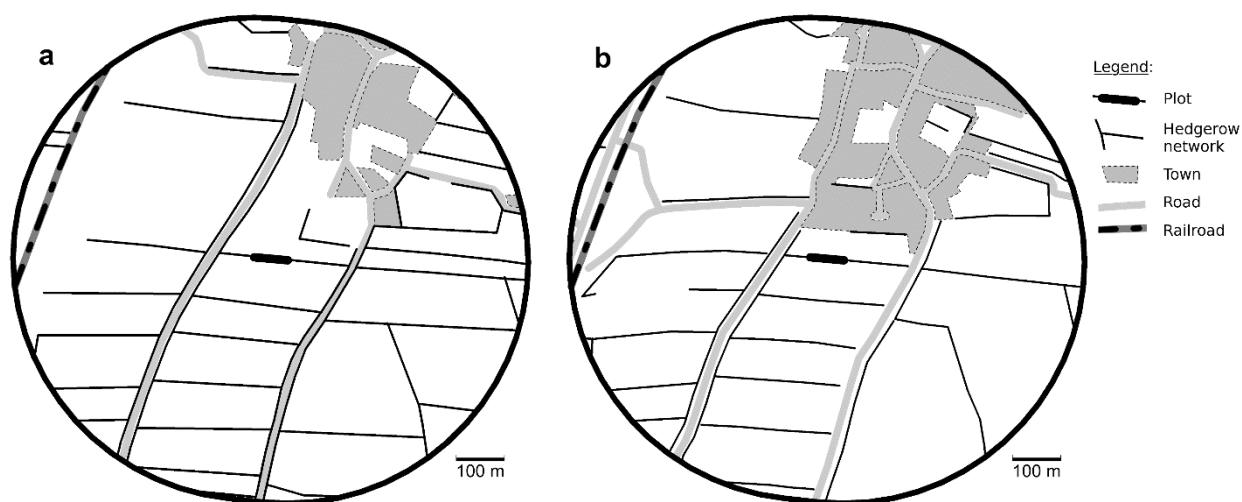
Figure 4.2 One exemplary hedgerow network in a 500 m radius around the plot is shown for (a) the historical landscape (1877) and (b) the present landscape (2004). While there were only few hedgerows created recently, large parts were cleared at the expense of the town and to gain larger agricultural fields. The density decreased from 114 m/ha to 83 m/ha.

Additionally, the distance of the hedgerow plots to the closest forests (as a potential source of forest species populations) was measured in the historical and present landscapes. Only deciduous or mixed forests with a minimum size of 0.5 ha were considered. For the present landscape, we also measured the distance to the nearest ancient forest which was defined as already being present on the historical maps. Recent forest patches are known to be less species rich than ancient ones (Naaf & Kolk, 2015) and therefore we also calculated the distance to the nearest ancient forest to control for the difference in source population quality. The distance to the nearest forest decreased over time from on average 664 m to 500 m (Table 4.1) which means that the study area in parts gained recent forest. At the same time, ancient forests were lost and the mean distance to the nearest ancient forest increased by 56 m.

*Forest species richness*

All statistical analyses were carried out using *R*. To analyse which of the compiled habitat and landscape variables had an influence on the forest species richness in hedgerows we ran several Generalized Linear Models (GLMs) with Poisson distribution in a multi-model approach. The models were tested for collinearity based on the variance inflation factor (VIF) and all included variables had VIF < 2 (Zuur et al., 2010). The dispersion parameters of the Poisson distribution ranged from 0.84 to 1.28, meaning that there was neither over- nor underdispersion in the data and a simple Poisson distribution could be used. Additionally, a correlation matrix of all explanatory variables was created and the Pearson-correlation coefficients were tested for significance.

Similar to Kolk and Naaf (2015), we started with simple models that contained only one variable group (compare Table 4.1: PL = Present landscape, PLAF = Present landscape with distance to nearest ancient forest, HL = Historical landscape, HQ = habitat quality) and determined the Minimal
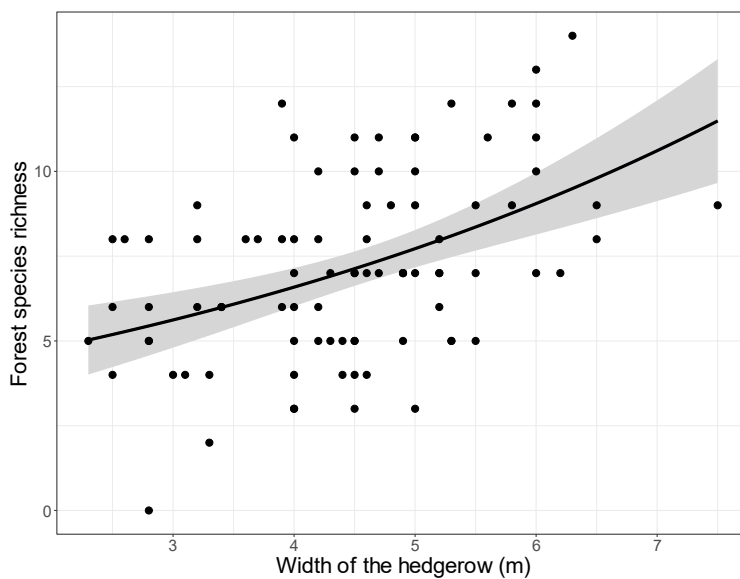
Figure 4.3 Relationship between forest species richness and hedgerow width in hedgerow plots of 70 m length (n = 89). The curve is based on a Poisson distribution. The shaded area indicates the 95 % confidence interval.

Adequate Models (MAM) that contained only significant variables. We repeated this for the three complex models that each contained one of the landscape variable groups together with the habitat quality variables. This resulted in a list of seven models (four simple models and three complex models). The final AICs of each MAM were then compared to determine which set of variables best explained the found diversity patterns. A difference in the AIC was considered significant if it was larger than 2. The same procedure was applied to model the richness of AWI species.

The best models were analysed further for both forest specialists and AWI species by assessing the remaining variables for their relative explanatory power by means of variance partitioning (varpart function in the 'vegan' package (Oksanen et al., 2019)).

## Results

We found no difference between the present and the historical landscape in explaining today's forest species richness in hedgerows, i.e. no extinction debt (Table 4.2). Further, the complex models did not perform better than the simple models. In the simple models, the present and the historical density as well as the hedgerow width were all found significant. In all the complex models only the hedgerow width remained in the final models rendering it congruent with the habitat quality model. Even though hedgerow density was significant when entered on its own, in combination with the hedgerow width it provided no additional explanatory power and was thus excluded. Overall, the simple habitat quality model was the one with the lowest AIC ($\Delta$AIC = 10.35 to the next best model) which means that the hedgerow width is the most important variable in explaining current species richness patterns. The wider the hedgerows were, the more forest specialists could be found in the hedgerows (Figure 4.3).

In all the simple landscape models, the distance to the nearest forest was removed while the hedgerow density remained in the model. Therefore, the two models of the present landscape including either the shortest distance to any forest or the distance to the nearest ancient forest resulted in the same final model. As thus all final models contained only one variable, no variance partitioning was applied.

For the AWI species the results differed. Both for the simple and the complex approaches, the two superior models were those including the present landscape with the distance to the nearest ancient forest and the historical landscape, while overall the complex models performed best (Table 4.3). The habitat quality model had the highest AIC. More AWI species were found in hedgerows that were close to a forest in historical times, or close to one that was continuously present until today (and thus being ancient). The species richness of AWI species was, like overall forest species richness, positively influenced by the width of the hedgerow. Overall, most of the variables remained in the final models.

Interestingly, a denser hedgerow network was negatively correlated to the number of forest species in the hedgerow, which may find its explanation in the correlation matrix of explanatory variables (Table 4.4). The hedgerow density is negatively correlated to the hedgerow width in both present and historical times. In addition, in historical times the hedgerow networks were denser when being further away from a forest. Today, this relationship can still be seen in the distance to the nearest ancient forest. That means that there are two covariates that result into the counter-intuitive negative correlation of network density and species richness.

Congruent results were seen in the variance partitioning for the AWI species. Most of the variation in AWI species richness was explained by the distance to the nearest forest for both of the best final models, i.e. the complex present landscape model with distance to the nearest ancient forest and the complex historical landscape model. The distance accounted for 38 % and 24.3 %, respectively, of the explained variation. The hedgerow width explained 22.5 % and 21.5 % and the hedgerow density another 13.4 % and 13.2 %, respectively. The strong overlap of the hedgerow density with other variables is expressed in the high proportion of shared variation: 16.5 % and 31 % in combination with the respective forest distance and 18.4 % and 19.3 %, respectively, with the shrub width. The variation shared between all three variables was less than 1 % for both models.

Table 4.2 Overview of the GLMs to analyse the effects of landscape and habitat variables on the forest specialist richness in hedgerows (n = 89). The AIC values are listed for each model. "Hedgerow density" and "Forest distance" refer to the respective variables of the specific model. For variables that remained in the minimal adequate model the estimates (log-transformed) and the significance levels are given (***: $p \leq 0.001$, **: $0.001 < p \leq 0.01$, *: $0.01 < p \leq 0.05$). Variables that were removed from the models during model optimisation are crossed out. The final complex models were equivalent to the habitat quality model because the landscape variables were not significant. Also the present landscape models including the shortest distance to any forest or only the nearest ancient forest did not differ from another because forest distance was not significant in either of the models.

| | AIC | Intercept | Hedgerow density | Forest distance | Hedgerow width | pH value |
|---|---|---|---|---|---|---|
| Present landscape | 426.41 | 2.274 | -0.005 ** | - | | |
| Historical landscape | 427.39 | 2.294 | -0.003 ** | - | | |
| Habitat quality | 416.06 | 1.249 | | | 0.159 *** | - |
| Landscape + habitat quality | 416.06 | 1.249 | - | - | 0.159 *** | - |

Table 4.3 Overview of the GLMs to analyse the effects of landscape and habitat variables on the species richness of ancient woodland indicators in hedgerows ($n$ = 89). The AIC values are listed for each model. "Hedgerow density" and "Forest distance" refer to the respective variables of the specific model. For variables that were included in the minimal adequate model the estimates (log-transformed) and the significance levels are given (***: $p \leq 0.001$, **: $0.001 < p \leq 0.01$, *: $0.01 < p \leq 0.05$). Variables that were removed from the models during model optimisation are crossed out.

| | AIC | Intercept | Hedgerow density | Forest distance | Hedgerow width | pH value |
|---|---|---|---|---|---|---|
| Present landscape (distance to any forest) | 256.05 | 1.713 | -0.017 *** | -0.0011 *** | | |
| Present landscape (distance to ancient forests) | 252.87 | 1.745 | -0.016 *** | -0.0009 *** | | |
| Historical landscape | 253.99 | 1.631 | -0.009 *** | -0.0003 ** | | |
| Habitat quality | 266.25 | -2.424 | | | 0.307 *** | 0.297 ** |
| Present landscape (distance to any forest) + Habitat quality | 253.64 | 0.643 | -0.014 ** | -0.0011 ** | 0.191 * | - |
| Present landscape (distance to ancient forests) + Habitat quality | 246.94 | 0.330 | -0.012 ** | -0.0010 *** | 0.262 ** | - |
| Historical landscape + Habitat quality | 247.92 | 0.126 | -0.006 ** | -0.0010 *** | 0.272 ** | - |

Table 4.4 Correlation matrix of variables included in the models. The values given are Pearson correlation coefficients with their significance levels (***: $p \leq 0.001$, **: $0.001 < p \leq 0.01$, *: $0.01 < p \leq 0.05$). n = 89. The greyed coefficients of the landscape variables are included for informative reasons but are not used together in one model.

| | Present hedgerow density | Historical hedgerow density | Hedgerow width | pH |
|---|---|---|---|---|
| **Historical distance to nearest forest** | 0.24 * | 0.39 *** | -0.09 | -0.22 * |
| **Present distance to nearest forest** | 0.18 | 0.26 * | -0.11 | -0.19 |
| **Present distance to nearest ancient forest** | 0.21 * | 0.34 ** | 0.08 | -0.19 |
| **Hedgerow width** | -0.29 ** | -0.27 * | - | -0.01 |
| **pH** | 0.03 | -0.02 | -0.01 | - |

## Discussion

### *Covariates obscure the species-area relationship*

We found no indication for an extinction debt of forest specialists in hedgerows. The models including the historical landscape configuration did not outcompete the models for the present landscape. Instead, the habitat quality, represented by the width of the shrub layer, was the best model in explaining the patterns of forest species richness found today. This underlines the importance of integrating local effects into landscape models. Forest plant species can display an extinction debt as evidenced in other studies from forest fragments (Paltto et al., 2006; Vellend et al., 2006). But even though hedgerows are wooded habitats, they differ from forests in some important aspects. Because of their linear structure, hedgerows have a high edge-to-area ratio, are prone to strong fluctuations in temperature and humidity and face frequent disturbances caused by the adjacent land use. With increasing width this effect is mitigated which causes the microclimate to be more stable and increasingly similar to forests (Vanneste et al., 2020). This is in accordance with many studies which found hedgerow width to be essential for forest plants (e.g. Forman & Baudry, 1984; Le Cœur et al., 1997; Roy & de Blois, 2008; Closset-Kopp et al., 2016; Litza & Diekmann, 2019). Deckers et al. (2004) found structural variables such as hedgerow width, length and height to be more important for the species richness than spatial variables such as distance to the nearest forest and the density of the hedgerow network. Roy and de Blois (2008) described hedgerow width to be the most important local variable for forest specialists but also found a positive effect of the nearby forest cover and hedgerow age. Ernoult and Alard (2011) studied the influence of landscape configuration at different spatial and temporal scales on hedgerow species richness and report an effect of past adjacent land-use and network connectivity.

The strong influence of hedgerow width might also explain why we found more forest specialists in sparser networks. There was a negative correlation between the density of the hedgerow network and the width of the hedgerows, and it is thus possible to link the density of a network to differences in habitat quality. Because of this strong correlation, we believe that the hedgerow width is not only a local variable but can also function as a proxy for habitat quality on a landscape scale. This relationship has already been described early on in hedgerow research by Marquardt (1950) who explained this phenomenon with the land loss that resulted from the construction of hedgerows. Areas that were dominated by manorialism and thus divided into large manors had always had larger fields and thus a lower hedgerow density. Peasantry-dominated areas on the other hand were divided into many small fields that all had to be enclosed with hedgerows. When farmers owned less land they tried to keep the hedgerow banks as narrow as possible to save farmable land (Marquardt, 1950). Large landowners in contrast could afford to keep wider hedgerows. In this way, the construction of less dense networks often resulted in a higher habitat quality.

The hedgerow density also depends on the soil quality as soils with lower quality are often associated with larger fields (Marquardt, 1950). At the same time areas with low soil quality were not clear cut for agriculture (Behre, 2008). Thus networks around (ancient) forests are likely to be less dense. Another aspect is related to differences in the age of networks of different densities. Hedgerows on the land of manors were often created before the enclosure movement (i.e. before the

18th century) and are therefore likely older than hedgerows in the dense, well-structured networks of later times (Weber, 2003). Litza and Diekmann (2019) indeed found more forest specialists in ancient hedgerows (created before 1877) but it can be assumed that the colonisation credit of the hedgerows from the times of the enclosure was already paid off and that there is no difference between these hedgerows and older ones. Depending on the proximity of source populations Litza and Diekmann (2019) found that the colonisation credit in recent hedgerows could be paid off within several decades.

Overall, the hedgerow density integrates several covariates and thus represents a complex set of variables and not mainly, as expected, habitat area and connectivity. This obscures the species-area relationship which in turn hampers the analysis of an extinction debt. This problem was not caused by the sampling method or the statistical analysis but instead is an inherent problem of the specific data set and thus cannot be overcome with the usual statistical approaches.

### Extinction debt for ancient woodland indicator species

Despite the overall difficulties, we found historical patterns to be more important for ancient woodland indicator (AWI) species richness than present patterns suggesting an extinction debt. This emphasises the importance of investigating relevant subgroups of species as these may respond differently to landscape compositional changes (Adriaens et al., 2006; Van Den Berge et al., 2018). Also for AWI species the species-area relationship was inversely proportional, however, the variable most influential for AWI species richness was the proximity to forests. Here it is important to note that the distance to the nearest forest actually decreased over time because new forests were planted on former agricultural land. The improvement of habitat conditions is again an uncommon phenomenon in extinction debt studies. However, recent forests are in general less species rich than ancient forests (Kolk et al., 2017) and thus represent less potent source populations. The average distance to ancient forests actually increased because some of those particularly species rich forests were destructed. AWI species have very low dispersal capacities and therefore depend on the close proximity to potent source populations (Wulf, 2003). Our results reflect this because even though the forest distance was significant in both models of the present landscape, the model including the distance to the nearest ancient forest performed considerably better. This confirms that species with different dispersal capacities are differently affected by a change in landscape composition and patch configuration.

### Implications for management

We found no evidence for a general extinction debt for forest plants in hedgerows but owing to the strong influence of several covariates on hedgerow density we cannot exclude its presence. Therefore, we do not know how the loss of surrounding habitat affected the forest plant community. Hedgerows are a very dynamic habitat with a high edge-to-area ratio. It is therefore conceivable that the fragmentation per se has a negligible effect. But the loss of habitat area is likely to have reduced the carrying capacity of the habitat and to have resulted in declining species numbers. Whether this happened immediately or over time cannot be concluded from our data. The extinction debt found for ancient woodland indicator species was mainly caused by the different distances to ancient forests in the surrounding when comparing the historic and present landscapes. This highlights the

importance of conserving ancient woodlands as biodiversity hotspots and potential source populations on a landscape level.

We conclude that the quality of the habitat is more important for forest plants in hedgerows than the decline in the hedgerow network. For management and conservation this does not imply that the remaining hedgerows do not need to be protected but instead that an even stronger focus needs to be put on the habitat quality and the width of the hedgerows in particular. The decline in the hedgerow network was severe over the last century but was halted in recent years when stricter management regulations were introduced. Potential land loss is used as an argument against maintaining hedgerows and there is still a tendency of land-owners of keeping the hedgerows as narrow as possible when less agricultural land is available. This is very unfortunate because the hedgerow width was confirmed to be a key element for the habitat quality.

## Acknowledgements

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# Hedgerows as a habitat for forest plant species in the agricultural landscape of Europe

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Upper left to lower right: *Gagea spathacea*; *Stellaria holostea*; *Anemone nemorosa*; *Ficaria verna* and *Lathraea squamaria* being pollinated.

## Abstract

Hedgerows are semi-natural wooded habitats and an important element in agricultural landscapes across Western and North-Western Europe. They reduce erosion, function as carbon sinks and thus provide essential ecosystem services. Moreover, they form a structurally diverse ecosystem for numerous taxa and connect otherwise fragmented forest habitats. This study compiled data from the hedgerow-rich oceanic regions of Europe, covering a gradient from Southern Sweden to Northern France, to analyse the influence of management, landscape context and climate variables on the number of herbaceous forest specialists in hedgerows. The species frequencies in hedgerows were related to their functional traits to identify plant characteristics that are beneficial for species dispersal and persistence in hedgerows. Our results show that numerous forest plant species, but not all, can thrive in hedgerows. Those are likely thermophilic, tolerant against regular disturbance and able to disperse efficiently. Hedgerows in regions that are warm or that are impacted by heat and drought events contain fewer forest species. Intensive adjacent land-use had a negative impact on forest species richness, while the surrounding forest cover was not significantly important. In congruence with previous regional studies, wider hedgerows contain more forest species, which is most likely caused by a more effective buffering of the microclimate. Thus, hedgerow width gains in importance in times of climate change and increasing extreme weather events. It is a key factor for habitat quality also on a European scale that needs to be considered for future management strategies.

**Keywords:** Climate change · Forest herbs · Functional traits · Hedgerow width · Linear landscape elements · Microclimate

## Introduction

Over the past millennia and centuries, the forest cover in Central and Western Europe was severely reduced and fragmented in favour of farmable land (Kaplan et al., 2009). Agricultural intensification and associated land-use changes have led to a dramatic decrease in biodiversity, which was accelerated over the last decades (Stoate et al., 2001; Storkey et al., 2012). In Europe, small natural features deriving from traditional agriculture such as stone walls, field margins or hedgerows were also largely eliminated from the landscape in the process of land consolidation (Poschlod & Braun-Reichert, 2017), even though these semi-natural habitats provide valuable ecosystem services (Van Vooren et al., 2017; Sutter et al., 2018) and offer diverse living conditions for many species (Van Den Berge et al., 2018).

Hedgerows and hedged landscapes, often referred to as "bocage", have a long tradition in the cultural landscapes of Europe (Baudry et al., 2000). While hedgerows were originally created as fences or marked property lines and also served as local source for fire wood, timber and fruits (Baudry et al., 2000), they are now mainly valued for their aesthetic and ecological properties (Burel & Baudry, 1995; Marshall & Moonen, 2002). Acting as wind-breaks, they reduce erosion by wind and protect adjacent fields and pastures from extreme weather events. They provide a barrier for

surface runoff and thus reduce erosion by water. Increasing the standing carbon stock within agricultural landscapes, they also function as carbon sinks (Kay et al., 2019).

Hedgerows form a diverse habitat for a wide range of plant species (Van Den Berge et al., 2019). As semi-woodland habitats they may function as refuge habitats (Baudry et al., 2000; Endels et al., 2004; Wehling & Diekmann, 2009a; Van Den Berge et al., 2019) and dispersal corridors for several forest specialists (Corbit et al., 1999; Wehling & Diekmann, 2009b; Closset-Kopp et al., 2016; Lenoir et al., 2021). This is of particular importance in regions that are largely deforested but still offer a comparatively dense hedgerow network. However, even though hedgerows form forest-like habitats, they differ from forests in several ways, owing to their linear structure and high edge-to-interior ratio. The light availability in hedgerows is higher because of lateral radiation, while the soil water content tends to be lower than in forests (Schmucki & de Blois, 2009; Wehling & Diekmann, 2009a). In addition, the disturbance from adjacent agricultural land by tillage as well as by the use of fertilisers and pesticides can be profound (Tsiouris & Marshall, 1998; Smart et al., 2001).

Several factors were shown to be positively related to the species richness of forest specialists in hedgerows. On a local scale, a high pH, less intensive adjacent land-use and appropriate periodic management have a positive impact (Deckers et al., 2004a; Critchley et al., 2013; Closset-Kopp et al., 2016). Another fundamental factor influencing the number of forest specialists is the structure of the hedgerows, most notably the width and height (e.g. Deckers et al., 2004a; Closset-Kopp et al., 2016; Litza & Diekmann, 2019, 2020), as wider hedgerows offer more forest-like conditions due to a more stable microclimate (Vanneste et al., 2020b). On a landscape scale, the nearby forest cover (Roy & de Blois, 2008) and the proximity to source populations in forests or ancient hedgerows increases forest species richness (Corbit et al., 1999; Litza & Diekmann, 2019).

Hedgerows may provide migration routes by which forest plants can increase their range or shift it to a more suitable regional climate (Roy & de Blois, 2008). While several studies have found hedgerows to function as refuge habitat and dispersal corridors, others have argued that these functions apply only to a subset of forest species capable of colonising hedgerows (McCollin et al., 2000; Roy & de Blois, 2006; Vanneste et al., 2020c). In general, forest specialists are adapted to a relatively stable environment in terms of temperature, moisture, wind and disturbance. Due to the linear structure of hedgerows and the pronounced edge effects it is reasonable to assume that hedgerow habitats are not suitable for forest specialists sensitive to disturbances or climatic and edaphic conditions more extreme than those of nearby forests. This pattern is likely to be influenced by the regional climate with less species inhabiting hedgerows when the climate is warm and dry, causing a hedgerow microclimate too extreme to support forest specialists.

Determining limiting or beneficial functional traits can help to understand the distribution patterns of forest specialist species and thus to create and manage hedgerows in a way that is beneficial for those species (Roy & de Blois, 2006). Therefore, it is crucial to recognise the abiotic and biotic filters selecting those species from the regional species pool that can cope with the specific environmental conditions in hedgerows (Deckers et al., 2004b). This may reveal general patterns as well as different responses across landscapes and regions. In addition, trait analyses have the potential to detect shifts in response to environmental or climatic changes (Naaf & Wulf, 2011).

The scientific interest in hedgerows has increased in recent years (e.g. Van Vooren et al., 2018; Litza & Diekmann, 2019; Van Den Berge et al., 2019), including research on a European scale (e.g. Vanneste et al., 2020a). Though their origin, management and species composition might differ between regions in Europe, their overall habitat characteristics are similar. This study combines data from six European regions into a comprehensive analysis to gain insight into regional and general patterns. Our main research questions were: (1) How does the regional climate (annual mean temperature, maximum temperature of the warmest month, annual precipitation and precipitation of the driest month), the surrounding landscape (adjacent land-use intensity and nearby forest cover) and the management (hedgerow width) influence the number of forest specialists in hedgerows across Europe? (2) Can the frequencies of forest specialists in hedgerows be related to specific functional traits?
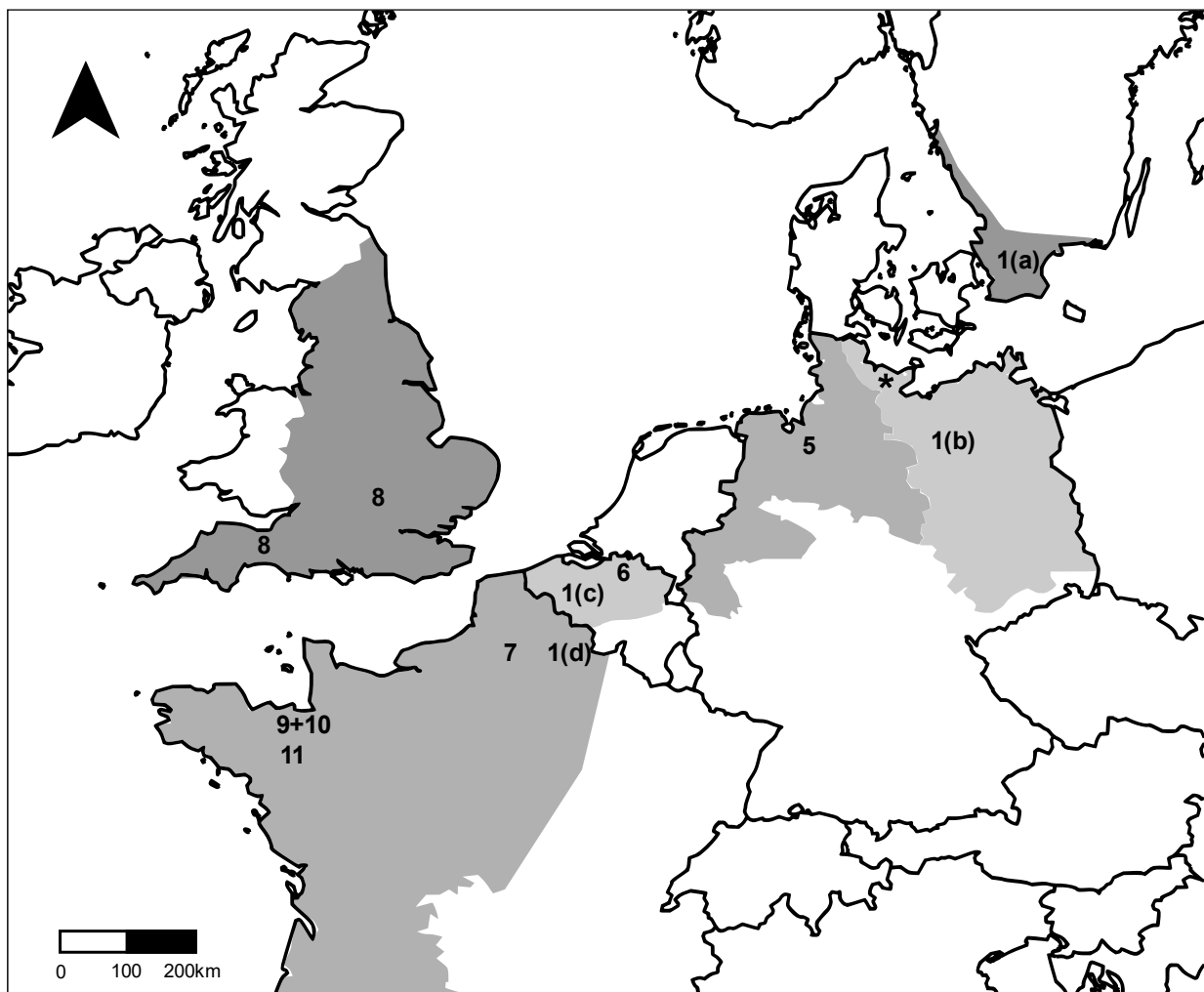


Figure 5.1 Map of the study area displaying the geographic locations of the datasets (numbered) as well as their respective geographic regions (shaded) from North-East to South-West: Sweden (nemoral zone), Germany (North-Eastern and North-Western lowlands), Belgium (lowlands), United Kingdom (England) and France (Atlantic region). Regions as defined by the forest species list by Heinken et al. (2019), plus England, UK (not included in the list by Heinken et al. (2019)). The numbers refer to the dataset IDs in Table 5.1. The asterisk (*) in Northern Germany represents the datasets 1(b) (in parts), 2, 3 and 4.

Methods

*Study area and data sampling*

The study area comprises the hedgerow-rich regions of Europe and stretches along a large geographical and climatic gradient from Southern Sweden in the North-East, across Northern Germany, Belgium and England to the Atlantic region in France in the South-West of Europe (Figure 5.1). The mean annual temperature ranges from 7.1°C (Hörby, Sweden) to 11.8°C (Val d'Anast, France) and the annual precipitation from 623 mm (Prignitz, Germany) to 938 mm (Yarcombe, England, UK) (long-term average values for 1970-2000 from https://www.worldclim.org/data/worldclim21.html; last accessed 11.05.2020; Fick & Hijmans, 2017).

Data from 1109 hedgerow plots originating from 11 studies from six European geographic regions were included in the analysis (Table 5.1). To be included the plots had to represent complete vegetation surveys, complemented by geographic location data, plot size and a description of the adjacent land-use on both sides of the hedgerow. Only plots with a length less than 500 m and a plot size less than 1,000 m² were included to reduce inflated variance based on a large range of plot sizes.

*Floristic surveys*

Only herbaceous species classified as forest specialists were included in the analyses. However, we later discuss the woody species to give a more coherent overview of the species composition and conditions in the hedgerows. For the European mainland we referred to the list of forest specialists by Heinken et al. (2019) and included species belonging to the groups 1.1 (taxa found mainly in the closed forest) and 1.2 (taxa predominantly growing along forest edges and in forest openings). This list distinguishes several regions on the European mainland and takes regional differences in the habitat preferences of species into account, i.e. a species may be considered a forest specialist in one region but not in another region. Five regions from Heinken et al. (2019) were relevant to our analysis (Table 5.1; Figure 5.1), and the species were classified with respect to each regional list. Additionally, the species data from England, UK, was classified using PLANTATT by Hill et al. (2004), which lists plant attributes of the British Isles. This publication, however, does not use the same categories as the list for mainland Europe. In particular, it does not distinguish distinct habitat preference groups but classifies species into several "broad habitats". To comply with the list for mainland Europe, species were classified as forest species if they were listed as solely preferring the broad habitats 1 (broadleaved, mixed and yew woodland) and/or 2 (coniferous woodland), i.e. taxa which are found mainly in the closed forest. To also consider those species that are typical along forest edges and in forest openings, we included taxa that were listed for one or several of three other broad habitats in addition to 1 and/or 2, namely 3 (boundary and linear features, e.g. hedges, roadsides, walls), 15 (montane habitats such as acid grassland and heath with montane species) or 16 (inland rock such as quarries, cliffs, screes). Species that were classified solely for broad habitat 3, comprising hedges but also roadsides and walls, were classified as forest species in England if they were considered true forest species in most of the regions in mainland Europe (Heinken et al., 2019). The complete list of forest species included in the analysis and their respective classification is given in Table A 4 in the appendix.

Table 5.1 Datasets included in the analyses, ordered along a gradient from North-East to South-West. The datasets 1 (a) to (d) were treated as four separate datasets in the analyses because they were sampled in different regions. The datasets 2 to 4 were sampled in one region by the same investigator and therefore treated as one dataset in the analyses.

In several datasets, plots were removed or pooled to improve the comparability of plot sizes. The following adjustments were done as compared to the original data sets: *1* – Three plots of 2 m length were pooled to form one plot per hedgerow.; *6* – 25 plots were removed because they were too long (> 500 m) or too large (>1,000 m²); *8* – Each plot was aggregated from four plots of 1 m width placed along the hedgerow profile, the plots were removed if only one side was surveyed; *9 & 10* – Hedgerows were surveyed separately on both sides and pooled to form an aggregated plot, plots were removed if only one side was surveyed; *11* – 10 Plots of 1 m² distributed along a 50 m hedgerow were aggregated.

| ID | Dataset | Region | Survey year(s) | Survey months | No. of plots | Plot length range (m) | Plot size range (m²) |
|---|---|---|---|---|---|---|---|
| 1 | Vanneste et al. (2020a) | (a) Sweden, nemoral zone | 2017 - 2018 | April-August | 4 | 6 | 12 |
|  |  | (b) Germany, North-Eastern lowlands |  |  | 8 | 6 | 12 |
|  |  | (c) Belgium, lowlands |  |  | 4 | 6 | 12 |
|  |  | (d) France, Atlantic region |  |  | 4 | 6 | 12 |
| 2-4 | Litza and Diekmann (2017, 2019, unpublished) | Germany, North-Eastern lowlands | 2015 - 2017 | April-July | 104 | 70 | 189 - 728 |
| 5 | Osthaus et al. (unpublished) | Germany, North-Western lowlands | 2017 | May-July | 235 | 50 | 50 - 500 |
| 6 | Van Den Berge et al. (2018) | Belgium, lowlands | 2010 - 2012 | April-May | 342 | 4 - 494 | 8 - 999 |
| 7 | Closset-Kopp et al. (2016) | France, Atlantic region | 2014 - 2015 | May-August | 99 | 51 - 473 | 34 - 940 |
| 8 | Stanbury et al. (2020) | UK, England | 2016 | May-August | 104 | 10 | 40 |
| 9 | Alignier (2018) | France, Atlantic region | 2015 | May-July | 120 | 25 | 28 - 167 |
| 10 | Alignier et al. (unpublished) | France, Atlantic region | 2017 | June-July | 25 | 25 | 50 - 250 |
| 11 | Alignier (unpublished) | France, Atlantic region | 2019 | June-July | 60 | 10 | 10 |

To correct the species number per plot for the wide range of plot sizes (Table 5.1), we first modelled the species-area relationship in a Linear Model (LM) of the log-transformed plot size against the number of forest species per plot ($R^2$ = 0.003, $p < 0.05$, $n$ = 1109; Figure 5.2 h). We used a semi-logarithmic approach because there were many plots with no forest species and the logarithm is not defined for zero. For later analyses, we used the residuals of this model (henceforth, corrected species richness) instead of the original species richness values.

Furthermore, we did not use the raw frequencies (i.e. the number of plots with species present per total number of plots in that region) but weighted them by summing up the log-transformed sizes of plots with the particular species present and divided this by the total log-transformed plot size per region (henceforth, the corrected species frequencies), again to control for the differences in plot size.

European occurrence data of the forest species was retrieved from GBIF.org (30 January 2020) to quantify the species' frequencies in each region and exclude regionally uncommon species from the analyses. This database provides occurrence data as point data differing in resolution depending on the country (usually caused by varying national grids used for data sampling). To standardise and then quantify the frequencies of each forest species, the data was first set out as a grid with a grid size of 100 km² to correct for differences in accuracy. The regional frequency was then expressed as the number of grid cells with the species present divided by the total number of grid cells in the region (as defined by the forest species list by Heinken et al. (2019), plus England, UK, not included in the list).

*Environmental data*

Seven environmental variables were sampled for each plot including the regional climate (annual mean temperature, maximum temperature of the warmest month, annual precipitation and precipitation of the driest month), landscape patterns (adjacent land-use intensity and nearby forest cover) and management variables (hedgerow width). An overview of the data, respectively for each region, is given in Table 5.2.

Climate data, in particular the bioclimatic variables "annual mean temperature (°C)", "maximum temperature of the warmest month (°C)", "annual precipitation (mm)" and "precipitation of the driest month (mm)", was extracted from GeoTiff files (respectively BIO 1, BIO5, BIO12 and BIO14 at a spatial resolution of 30 seconds) provided by WorldClim version 2 (Fick & Hijmans, 2017). The surrounding cover of deciduous forest was measured in a buffer of 1,000 m radius around the plot centre using the CORINE land cover data (resolution 100 m; EEA, 2018). Land-use was ranked on an intensity scale introduced by Closset-Kopp et al. (2016) which was slightly modified for the purpose of this study to cover all recorded land-use types (Table 5.3). The ranks from both sides of the hedgerows were summed up to result in one value for land-use intensity per plot. Hedgerow width was measured on-site in most plots (in 1047 out of 1109 cases) and rounded to the next integer to account for differences in accuracy.

Table 5.2 Explanatory variables and their values (mean, range in parentheses) in the six study regions. For the land-use intensity both sides of the hedgerows were classified (Table 5.3) and then summed up. The forest cover describes the cover within a radius of 1,000 m around the plots.

| | Sweden – nemoral zone | Germany – North-eastern lowlands | Germany – North-western lowlands | Belgium – lowlands | UK – England | France – Atlantic region |
|---|---|---|---|---|---|---|
| Annual mean temperature (°C) | 7.1 (7.1 – 7.2) | 8.4 (8.1 – 9) | 8.9 (8.9 – 9) | 10.4 (10 – 10.7) | 9.9 (9.6 – 10.2) | 10.6 (9.1 – 11.8) |
| Maximum temperature of the warmest month (°C) | 19.3 (19.3 – 19.4) | 19.5 (18.5 – 21.2) | 19.8 (19.7 – 19.8) | 21.1 (20.2 – 21.3) | 19.7 (19.4 – 20.1) | 22.7 (21.6 – 24.1) |
| Annual precipitation (mm) | 771.3 (759 – 781) | 765 (623 – 882) | 703 (697 – 716) | 785.3 (766 – 817) | 781.6 (682 – 938) | 752.3 (650 – 845) |
| Precipitation of the driest month (mm) | 44 (44 – 44) | 44.3 (37 – 49) | 38 (37 – 38) | 48.4 (45 – 51) | 50 (43 – 60) | 46.6 (40 – 60) |
| Land-use intensity | 9.5 (8 – 10) | 9 (4 – 10) | 6.5 (2 – 10) | 7 (0 – 10) | 8.4 (6 – 10) | 8.3 (0 – 10) |
| Forest cover (ha) | 4.8 (0 – 19) | 19.1 (0 – 130) | 51.4 (10 – 99) | 39.2 (0 – 205) | 11 (0 – 45) | 13.4 (0 – 231) |
| Hedgerow width (m) | 5 (3.7 – 6.3) | 4.9 (2.3 – 16.3) | 3.7 (1 – 10) | 2.4 (1 – 12) | 2.9 (1 – 7) | 2.9 (0.5 – 14.7) |

Table 5.3 Land-use intensity scale describing the land-use adjacent to the hedgerows. The scale was modified from Closset-Kopp et al. (2016) by newly introducing level 0 and level 3 to cover all land-use types found in the datasets.

| Land-use intensity scale | Type of land-use |
|---|---|
| 0 | Forest |
| 1 | Unpaved road Water body |
| 2 | Paved road |
| 3 | Fallow land Garden |
| 4 | Grassland |
| 5 | Arable field |

*Species trait data*

To relate the frequency of species to their attributes, trait data was downloaded from the TRY trait database (Kattge et al., 2020). We included the leaf dry matter content (LDMC, mg/g) defined as the oven-dry mass of a young but fully expanded leaf (mg) per fresh mass (g). This trait is positively related to leaf toughness and lifespan (Pérez-Harguindeguy et al., 2013). Ellenberg indicator values (EIV) for temperature, light, soil moisture, soil nutrients and soil reaction represent a species' preferred environmental conditions and are expressed on an ordinal scale of 1 to 9 (1 to 12 for soil moisture) (Ellenberg et al., 2001). Due to the microclimatic conditions in hedgerows, it is expected that species frequently occurring in hedgerows display high values for temperature and light as well as low values for moisture. Further, we expect a correlation of the corrected species frequencies and high nutrient values because hedgerows are exposed to fertiliser input from adjacent land-use. The EIV for continentality was not included because all data was sampled in the oceanic climate regions rendering a low variation of this variable. Plant height (cm) is expected to have a positive influence on the corrected species frequencies because it is related to the competitiveness of species (Westoby, 1998). We also included the specific dispersal syndromes, which are related to a species' potential for efficient dispersal. We transformed the information provided by TRY (Kattge et al., 2020) into a coarser classification of five different syndromes: anemochory, anthropochory, autochory, hydrochory, and zoochory. Because one species can display several of those syndromes they were each included as a separate binary variable into the analysis. We expect species with efficient long-distance dispersal such as zoochory or anthropochory to be more frequent in hedgerows than species with other dispersal modes.

In addition to the aforementioned trait data downloaded from TRY, we used the degree of ruderality (Pierce et al., 2017) being part of the competitor, stress tolerator and ruderal (CSR) theory (Grime, 1974). Due to high intercorrelation of the three variables, only ruderality was used for the analysis as disturbance is an integral part of the hedgerow habitat. CSR values for species missing in the list of Pierce et al. (2017) were calculated following the authors' instructions.

*Data analysis*

All analyses were carried out in *R* (version 3.6.2, R Core Team (2020). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/).

*Species richness analyses*

We ran two Linear Mixed Models (LMMs) using the package "lme4" (Bates et al., 2015) to explain the corrected species richness. In both models, we included the total forest cover in a 1,000 m radius (ha), the land-use intensity and the hedgerow width (m) as fixed effects. In addition, we included one set of climatic variables in each of the models, in the first model the annual mean temperature (°C) and the annual precipitation (mm) and in the second model two variables representing extreme climate conditions, namely the maximum temperature of the warmest month (°C) and the precipitation of the driest month (mm). Including variable sets of mean as well as extreme climatic conditions enables us to analyse the influence of the regional climate more comprehensively. Due to

strong intercorrelation of the temperature and precipitation variables, respectively, this was analysed in separate models. In both models, the dataset ID (not the region) was used as a random term to account for possible methodological differences between the datasets (also within regions) as well as spatial autocorrelation (see also Table 5.1 for the allocation of dataset IDs). One dataset from France (dataset ID 11, 60 plots) did not contain information about the hedgerow width and was therefore excluded from this analysis. To avoid multicollinearity, the variance inflation factors (VIF) of the variables were checked to be VIF < 3 (Zuur et al., 2010). Model optimisation was done by step-wise backwards selection based on the $p$-values. Marginal and conditional $R^2$ values were calculated using the package "MuMIn" (Barton, 2019).

The resolution of the climate variables was lower than that of the other variables. This resulted in plots situated close to each other having similar values and the potential to have a disproportionally strong impact on the model outcome. The models were therefore also tested for the influence of grouped outliers using the package "influence.ME" (Nieuwenhuis et al., 2012). This helped to identify a group of 39 plots with particularly high values for annual precipitation as well as precipitation in the driest month that were removed from both LMMs.

Several vernal species needed to be excluded prior to the analyses because some datasets were sampled too late to catch the period in which they were visible (*Adoxa moschatellina, Anemone nemorosa, A. ranunculoides, Galanthus nivalis, Lathraea clandestina, L. squamaria, Ranunculus ficaria* and *Scilla bifolia*).

*Trait analyses*

To test which traits are beneficial for forest species in hedgerows, i.e. correlated to high corrected frequencies of those species, we fitted a Generalized Linear Mixed Model (GLMM) using Penalized Quasi-Likelihood from the "MASS" package (Venables & Ripley, 2002). This allowed for a quasibinomial distribution and thereby took care of overdispersion. We used the corrected species frequencies as success variable and the plots without the species as failure variable (also log-transformed to correct for differences in plot size as described above). The dataset ID was used as a random factor to control for autocorrelation and the traits as fixed effects. Traits included the leaf dry matter content (LDMC, mg/g), Ellenberg indicator values (EIV) for temperature, light, soil moisture, soil nutrients and soil reaction, the plant height (cm), the degree of ruderality and the dispersal syndromes anemochory, anthropochory, autochory, hydrochory, and zoochory. To avoid multicollinearity the variables were inspected to have VIF < 3 (Zuur et al., 2010). In addition to the model including all data, we also ran separate GLMMs with the same set of variables for each single region to detect regional patterns. Because of the low number of plots from Sweden, the four plots from this region were only included in the overall analysis but not in the separate analyses per region.

As we considered the forest specialist status per dataset (based on the specific region), we did not exclude all of the vernal species as mentioned previously, but were able to adapt the list individually for each dataset (additional information about specific species removals are detailed in Table A 5 in the appendix). All species with a regional frequency of at least 10 % (based on the data received from GBIF.org) were included in the analyses, i.e. also species not found in any of the studied hedgerows.
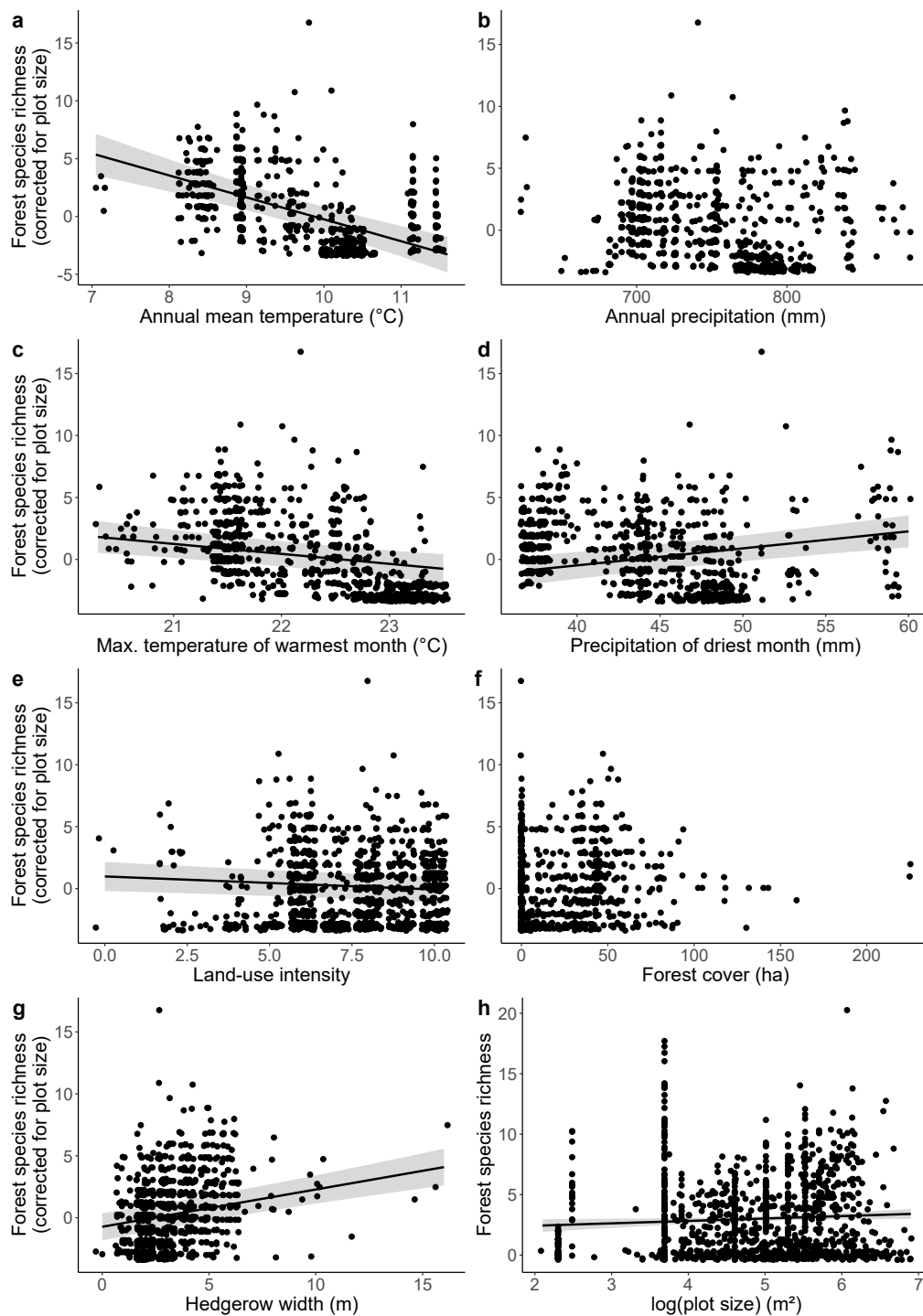
Figure 5.2 Forest species richness (corrected for plot size) plotted against a) annual mean temperature (°C), b) annual precipitation (mm), c) maximum temperature of the warmest month (°C), d) precipitation of the driest month (mm), e) adjacent land-use intensity, f) forest cover in the surrounding 1,000 m (ha) and g) hedgerow width (m). The forest species richness was corrected for plot size by using the residuals of the linear model (forest species richness against the log-transformed plot size) shown in h). The points are jittered to avoid overplotting. Shaded areas denote 95 % confidence intervals. Plots e) and g) represent the results of the second LMM (including extreme climate variables). However, there was no obvious difference between the outcomes of the two LMMs for those two fixed effects.

Table 5.4 The 10 most frequent forest species and woody species in hedgerows in each of the investigated regions with their respective corrected frequencies. The datasets from France were here subdivided into the provinces Picardy and Brittany because of the strong variation between the two regions. Results for the nemoral zone in Sweden are not shown because of the low number of plots in that region.

| Rank | Germany – North-eastern lowlands | | Germany – North-western lowlands | | Belgium – lowlands | | France – Atlantic region (Picardy) | | UK – England | | France – Atlantic region (Brittany) | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Forest species** | | | | | | | | | | | | |
| 1 | *Stellaria holostea* | 0.65 | *Stellaria holostea* | 0.65 | *Dryopteris dilatata* | 0.11 | *Arum maculatum* | 0.56 | *Arum maculatum* | 0.37 | *Digitalis purpurea* | 0.3 |
| 2 | *Poa nemoralis* | 0.64 | *Poa nemoralis* | 0.62 | *Dryopteris filix-max* | 0.06 | *Stachys sylvatica* | 0.42 | *Silene dioica* | 0.34 | *Potentilla sterilis* | 0.26 |
| 3 | *Chaerophyllum temulum* | 0.62 | *Anemone nemorosa* | 0.6 | *Dryopteris carthusiana* | 0.04 | *Chaerophyllum temulum* | 0.27 | *Stachys sylvatica* | 0.31 | *Viola riviniana* | 0.26 |
| 4 | *Adoxa moschatellina* | 0.35 | *Milium effusum* | 0.32 | *Polygonatum multiflorum* | 0.04 | *Viola reichenbachiana* | 0.23 | *Geranium robertianum* | 0.26 | *Euphorbia amygdaloides* | 0.19 |
| 5 | *Anemone nemorosa* | 0.3 | *Lamium galeobdolon* | 0.25 | *Stachys sylvatica* | 0.04 | *Polygonatum multiflorum* | 0.22 | *Brachypodium sylvaticum* | 0.25 | *Moehringia trinervia* | 0.16 |
| 6 | *Polygonatum multiflorum* | 0.28 | *Rumex sanguineus* | 0.18 | *Epilobium angustifolium* | 0.03 | *Moehringia trinervia* | 0.21 | *Glechoma hederacea* | 0.2 | *Stachys sylvatica* | 0.12 |
| 7 | *Moehringia trinervia* | 0.25 | *Circaea lutetiana* | 0.17 | *Athyrium filix-femina* | 0.03 | *Scrophularia nodosa* | 0.16 | *Asplenium scolopendrium* | 0.13 | *Rumex sanguineus* | 0.1 |
| 8 | *Stachys sylvatica* | 0.24 | *Stachys sylvatica* | 0.17 | *Scrophularia nodosa* | 0.02 | *Adoxa moschatellina* | 0.15 | *Mercurialis perennis* | 0.12 | *Scrophularia nodosa* | 0.1 |
| 9 | *Dryopteris filix-mas* | 0.22 | *Dryopteris filix-mas* | 0.08 | *Anemone nemorosa* | 0.01 | *Poa nemoralis* | 0.12 | *Geum urbanum* | 0.09 | *Dryopteris filix-mas* | 0.08 |
| 10 | *Arum maculatum* | 0.18 | *Carex remota* | 0.08 | *Chaerophyllum temulum* | 0.01 | *Vinca minor* | 0.1 | *Rumex sanguineus* | 0.09 | *Polygonatum multiflorum* | 0.07 |

**Woody species**

| Rank | Germany – North-eastern lowlands | | Germany – North-western lowlands | | Belgium – lowlands | | France – Atlantic region (Picardy) | | UK – England | | France – Atlantic region (Brittany) | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | *Sambucus nigra* | 0.61 | *Carpinus betulus* | 0.66 | *Quercus robur* | 0.66 | *Rubus fruticosus* agg. | 0.81 | *Prunus spinosa* | 0.47 | *Rubus fruticosus* | 0.76 |
| 2 | *Rubus fruticosus* | 0.6 | *Rubus fruticosus* | 0.61 | *Prunus serotina* | 0.47 | *Crataegus monogyna* | 0.76 | *Rubus fruticosus* | 0.38 | *Quercus robur* | 0.69 |
| 3 | *Corylus avellana* | 0.6 | *Quercus robur* | 0.6 | *Alnus glutinosa* | 0.41 | *Sambucus nigra* | 0.69 | *Crataegus monogyna* | 0.29 | *Castanea sativa* | 0.47 |
| 4 | *Prunus spinosa* | 0.58 | *Prunus spinosa* | 0.59 | *Betula pendula* | 0.38 | *Prunus spinosa* | 0.69 | *Acer campestre* | 0.27 | *Corylus avellana* | 0.35 |
| 5 | *Rosa canina* | 0.54 | *Corylus avellana* | 0.56 | *Sambucus nigra* | 0.37 | *Fraxinus excelsior* | 0.65 | *Corylus avellana* | 0.24 | *Euonymus europaea* | 0.28 |
| 6 | *Quercus robur* | 0.46 | *Rosa canina* | 0.46 | *Sorbus aucuparia* | 0.36 | *Carpinus betulus* | 0.58 | *Rosa canina* | 0.14 | *Crataegus monogyna* | 0.23 |
| 7 | *Crataegus monogyna* | 0.46 | *Crataegus monogyna* | 0.44 | *Frangula alnus* | 0.25 | *Rosa canina* | 0.57 | *Cornus sanguinea* | 0.07 | *Prunus avium* | 0.21 |
| 8 | *Carpinus betulus* | 0.43 | *Alnus glutinosa* | 0.37 | *Corylus avellana* | 0.21 | *Crataegus laevigata* | 0.55 | *Quercus robur* | 0.05 | *Prunus spinosa* | 0.2 |
| 9 | *Rubus idaeus* | 0.35 | *Crataegus laevigata* | 0.34 | *Salix x multinervis* | 0.21 | *Corylus avellana* | 0.49 | *Ulmus procera* | 0.04 | *Ulex europaeus* | 0.19 |
| 10 | *Euonymus europaea* | 0.3 | *Rubus caesius* | 0.32 | *Salix caprea* | 0.16 | *Rosa arvensis* | 0.47 | *Fraxinus excelsior* | 0.02 | *Ilex aquifolium* | 0.17 |

Table 5.4 continued.

## Results

Across the study area, we generally found a high richness of forest species in the hedgerows, with some similarities for the most frequent species among regions (Table 5.4). *Stachys sylvatica* was frequent in hedgerows in almost all investigated regions. Five other species, such as *Polygonatum multiflorum*, *Dryopteris filix-mas*, *Anemone nemorosa*, *Poa nemoralis* and *Arum maculatum*, were frequent in several of the regions. Other species were never or only rarely found in hedgerows even though they are regionally very common in forests, e.g. *Torilis japonica*, *Oxalis acetosella*, *Senecio sylvaticus*, *Convallaria majalis*, *Luzula pilosa* or *Sanicula europaea*. The Belgium hedgerows showed overall low frequencies of forest specialists, but a comparatively high frequency of fern species. The two German regions had similar species pools while the French Atlantic region showed a remarkable variety between the datasets from the provinces of Picardy in the north and Brittany in the north-west (see Table 5.4). Of the 289 species classified as forest specialists (in at least one region of the study area), 86 were excluded because of their low regional frequencies (< 10 %). Of the 203 remaining species, 87 were recorded in hedgerows, of which nearly half (*n* = 41) were found in only one of the regions.

Woody species composition was also similar between the regions (Table 5.4). Several species, such as *Quercus robur*, *Corylus avellana*, *Crataegus* spp. and *Rubus fruticosus* agg., were frequently found in hedgerows across the whole study area. In Brittany, two evergreen species were among the most frequent species *(Ulex europaeus* and *Ilex aquifolium*).

### Species richness analyses

The first LMM showed a positive relationship of the corrected species richness with the hedgerow width, while the annual mean temperature and the adjacent land-use intensity had a negative impact (Figure 5.2, Table 5.5). The annual precipitation and the surrounding forest cover were not significant and therefore removed from the final model.

In the second LMM including the variable set representing extreme climate conditions, four of the five explanatory variables remained in the final model. Only the surrounding forest cover was excluded. The maximum temperature of the warmest month and the adjacent land-use intensity were negatively related to the corrected forest species richness, while a higher precipitation within the driest month and an increasing hedgerow width improved the corrected species richness (Figure 5.2, Table 5.5). Figure 5.2 g) suggested the assumption that the four most extreme plots (hedgerow width > 10 m) severely influenced the slope of the regression line. However, besides the outlier test not indicating any problems, the strong positive relationship between the hedgerow width and the corrected species richness was also robust against the removal of these plots.

### Trait analyses

Only six of the trait variables remained in the final GLMM analysing the influence of species' attributes on their frequencies in hedgerows (Table 5.6). Species with high EIV moisture and EIV temperature as well as high values for ruderality were more likely to occur in hedgerows. Additionally, the dispersal by anemochory, anthropochory or zoochory was linked to higher species frequencies.

The regional results partly differed from the overall patterns (Table 5.6). While the positive effects for species occurrence of high values for ruderality, EIV moisture and the dispersal by anthropochory were stable across regions (albeit not significant in all of them), the patterns for Ellenberg values for nutrients and temperature varied among regions. Surprisingly, the leaf dry matter content and EIV light did not remain in any of the final regional models.

Table 5.5 Results from the LLMs explaining the corrected forest species richness. The first LMM included annual climate data ($n$ = 1008, groups = 11, $R^2_{marginal}$ = 0.37, $R^2_{conditional}$ = 0.64), while the second included data of extreme climatic conditions ($n$ = 1008, groups = 11, $R^2_{marginal}$ = 0.09, $R^2_{conditional}$ = 0.46). Non-significant variables were removed from the models.

| Fixed effects | Estimates | Standard Error | $t$-value | $p$-value |
|---|---|---|---|---|
| **LMM1: Including annual climate data** | | | | |
| (Intercept) | 18.665 | 2.857 | 6.532 | < 0.001 |
| Annual mean temperature | -1.896 | 0.289 | -6.551 | < 0.001 |
| Adjacent land-use intensity | -0.112 | 0.035 | -3.172 | 0.002 |
| Hedgerow width | 0.284 | 0.048 | 5.898 | < 0.001 |
| **LMM2: Including extreme climate data** | | | | |
| (Intercept) | 11.809 | 5.062 | 2.333 | < 0.001 |
| Maximum temperature of the warmest month | -0.804 | 0.214 | -3.764 | < 0.001 |
| Precipitation of the driest month | 0.137 | 0.029 | 4.670 | < 0.001 |
| Adjacent land-use intensity | -0.105 | 0.035 | -2.978 | 0.003 |
| Hedgerow width | 0.301 | 0.048 | 6.247 | < 0.001 |

| Random effects | Variance | Standard Deviation |
|---|---|---|
| Dataset ID (LMM1) | 2.840 | 1.685 |
| Dataset ID (LMM2) | 2.620 | 1.619 |

Table 5.6 Result of the GLMMs modelling the influence of traits on the species frequencies in hedgerows. We ran one model including all regions as well as separate models for each region. Sweden was excluded from the regional analyses due to the low number of plots from this region. The table entries give the logit-transformed estimates. Only significant variables are included in the final models. The leaf dry matter content, EIV light and autochory were not significant in any of the models and therefore not displayed.
EIV = Ellenberg indicator value.

| | All regions | Germany - North eastern lowlands | Germany - North western lowlands | Belgium - lowlands | UK - England | France - Atlantic region |
|---|---|---|---|---|---|---|
| Intercept | -14.482 | -23.575 | -12.398 | -9.19 | -12.875 | -4.113 |
| EIV temperature | 0.541 | 2.202 | | | 1.107 | -1.341 |
| EIV moisture | 0.5 | | 1.1 | 0.425 | | 0.522 |
| EIV nutrients | | 0.584 | -0.781 | | | 0.816 |
| EIV reaction | | | | | | -0.376 |
| Plant height (cm) | | | 0.028 | | | |
| Ruderality | 0.042 | 0.049 | 0.09 | | | 0.033 |
| Dispersal syndrome | | | | | | |
| Anemochory | 1.093 | 2.665 | | | | |
| Anthropochory | 1.586 | | 2.379 | 1.632 | | 1.033 |
| Hydrochory | | | | | | -1.664 |
| Zoochory | 1.725 | | | | | 1.878 |

## Discussion

Our study shows that hedgerows across Europe harbour a remarkably high richness of forest plant specialists, supporting the hypothesis that hedgerows can form a suitable habitat for many forest taxa. These species, however, represent only a subset of the total forest species pool included, corroborating the conclusion of previous studies (Roy & de Blois, 2006; Vanneste et al., 2020c). There is no typical species composition for hedgerows across the study region, even though several species of all layers can frequently be found throughout the study area. *Anemone nemorosa* and *Poa nemoralis* were already earlier recognised as being frequent hedgerow companions on a long climate gradient across Europe (Vanneste et al., 2020c).

The woody species frequently found in hedgerows are able to withstand regular cuts (e.g. *Corylus avellana*), and/or are well protected against herbivory (e.g. *Crataegus* spp. and *Prunus spinosa*) (French & Cummins, 2001). The more regular presence of evergreen shrubs such as *Ulex europaeus* and *Ilex aquifolium* in the southern parts of Europe can be linked to the warmer winter climate. The high frequency of *Quercus robur* dates back to the history of the hedgerows when these were often

managed as coppice-with-standards in which the species was commonly used as standard due to its highly valued timber (Weber, 2003). In Brittany, France, hedgerows of *Q. robur* are common and were pollarded for firewood (Burel, 1996).

## Climate

The regional climate plays a major role for the richness of forest specialists in hedgerows. A high annual mean temperature negatively affected the forest plant richness. In accordance with this, high temperatures in the warmest month (and thus extreme heat events) impede forest plant richness, while more rainfall in the driest months (and thus less extreme drought conditions) was shown to promote forest species richness. We conclude that in a warm macroclimate, the environmental conditions in hedgerows are challenging for forest species, especially when extreme heat or drought events occur. Hedgerows are less able to buffer extreme weather events than forests because of their high edge-to-interior ratio (De Frenne et al., 2013; Vanneste et al., 2020b), while forest species are adapted to shaded habitats and therefore require more stable microclimatic conditions. Our expectation that the traits of frequent species reflect the less well-buffered microclimate in hedgerows was, however, only partly met. As expected, thermophilic forest species were more frequent in hedgerows than cold-adapted species. This is most likely because hedgerows generally have a warmer understorey microclimate than forests, owing to lateral light penetration and wind attenuation leading to reduced air mixing (Schmucki & de Blois, 2009; Vanneste et al., 2020b). Even still, EIV light did not significantly contribute to any of the final models as it did in previous studies (Wehling & Diekmann, 2010).

With climate change the frequency of extreme weather events such as heat and drought is expected to increase substantially (IPCC, 2019). Hence, our study covering a continental-scale climatic gradient may help to gain insight into the effects of such events on plant communities in hedgerows. In addition, our study suggests that warmer conditions in hedgerows might lead to an overall loss of species richness. Resurvey studies of hedgerows have already found an increase in thermophilic species over the last decades, which have the potential to outcompete shade-adapted specialist species such as forest plants (Huwer & Wittig, 2012; Litza & Diekmann, 2017). Hedgerows have the potential to mitigate climate change effects. Through carbon sequestration in their biomass and soil, they increase the standing stock within agricultural landscapes, and thus function as carbon sinks (Kay et al., 2019; Van Den Berge et al., 2021). They also enhance water use, storage and efficiency, improve the microclimate of adjacent fields, and diversify income and food sources in agroforestry systems (Lasco et al., 2014).

## Adjacent land-use and surrounding forest cover

The negative influence of intensive land-use on forest species richness in adjoining hedgerows found in our study is in agreement with previous research (de Blois et al., 2002; Deckers et al., 2004a; Wehling & Diekmann, 2008; Closset-Kopp et al., 2016; Lenoir et al., 2021). The influence of adjacent land-use can be profound and involves disturbance caused by tillage, mowing and grazing that stretches into the hedgerows, but also the drift of herbicides (Jobin et al., 1997) and fertilisers (Tsiouris & Marshall, 1998). The high input of nutrients over the last decades caused a shift in species composition in hedgerows towards more nutrient-demanding species and a decline in forest species

richness in hedgerows (Staley et al., 2013; Litza & Diekmann, 2017). Indeed, a high nutrient availability favours fast-growing and competitive species such as *Urtica dioica* with the potential to outcompete (often stress-tolerant) forest herbs (De Keersmaeker et al., 2004). Hedgerows next to organic fields, on the other hand, were shown to harbour a higher diversity (Aude et al., 2003).

We did not find a beneficial effect of a high forest cover in the surrounding landscape that was demonstrated by previous research (Roy & de Blois, 2008; Vanneste et al., 2020a). This might be because the resolution of the CORINE land cover data was not sufficient. At a resolution of 100 m small wooded patches are not captured even though these can function as biodiversity hot spots and stepping stones for migration (Decocq et al., 2016). As most forest plants are short-distance dispersers the distance to the nearest potential source population might be of greater importance than the forest cover. Lenoir et al. (2021) also found that habitat connectivity was more important than forest cover with hedgerows attached to forests containing more forest herb species. Unfortunately, our data did not comprise the connectivity of hedgerows.

*Management*

The trait analyses showed a strong positive signal of high values for ruderality, and thus the ability to cope with regular disturbance, in three of the five regions as well as in the overall model. Hedgerows are exposed to regular levels of disturbance, not only by adjacent land-use activities, but also by dedicated management. To prevent them from growing into the adjacent agricultural lands or roads and to keep them in a young, healthy and dense state, hedgerows need to be regularly cut (Baudry et al., 2000). While some management is always necessary for maintaining the habitat, the management techniques differ between regions depending on the hedgerow's origin, usage, traditions and legal regulations (Baudry et al., 2000). A lack of or inappropriate management leads to a loss in hedgerow quality and an associated decline in diversity (Garbutt & Sparks, 2002; Carey et al., 2008; Staley et al., 2013). Traditional management forms include coppicing (cut of the shrub layer at ground level), pollarding (cut of the shrub layer at 1–2 m height) and hedge-laying (shrub layer is partially cut, laid horizontally and intertwined), but are today often reduced to trimming with a mechanical flail or even completely neglected (Staley et al., 2013). In Brittany and Picardy, France, the traditional management also includes the pruning of trees (selective removal of branches) for firewood (Le Cœur et al., 2002). In Northern Germany, regular coppicing (every 10 years) with standards and more frequent lateral cuts are still the most common form of management while this practice has largely been abandoned in Belgium (Deckers et al., 2004a) and England (Staley et al., 2013; Stanbury et al., 2020). Those are also the two regions where, according to the models, the ruderality of the species was not a beneficial trait. This indicates that a shift to other management practices implies also a shift in forest species composition that favours species with different sets of traits. Even if the former techniques are in part no longer practised, the legacy of historical management is still visible today, e.g. in the form of wide stools of formerly coppiced shrubs or multi-branched pollarded trees.

The practices of hedgerow management are included in the cross-compliance system of the Common Agricultural Policy of the European Union (EU), which means that appropriate hedgerow management is the pre-requisite for EU subsidies, even though this depends on the national implementation of management rules (European Parliament and Council, 2020). In many cases, agri-

environment schemes were shown to influence the species richness in hedgerows over relatively short time periods (Stanbury et al., 2020). The form of management defines the structure of the woody layer, e.g. its height and width as well as being one- or multi-layered, which in turn impacts the herbaceous vegetation at the hedge-bottom (Deckers et al., 2004a; Alignier, 2018; Graham et al., 2018). Numerous studies have shown that hedgerow width is a key factor in determining habitat quality for forest plants (e.g. Deckers et al., 2004a; Closset-Kopp et al., 2016; Litza & Diekmann, 2020), but also for other taxa such as mammals, birds and invertebrates (Graham et al., 2018). This is mainly linked to a more stable microclimate in wider hedgerows (Vanneste et al., 2020b) which in turn also reduces competition with thermophilic species and generalists. Likewise, this study emphasises the positive effect of hedgerow width, but now on a European scale, which also needs to be implemented into future agri-environment schemes and national hedgerow management plans.

*Soil conditions*

Unexpectedly, high Ellenberg indicator values for moisture were beneficial for the forest species richness even though the soils of hedgerows are usually not moist but, on the contrary, relatively dry due to their exposure to solar radiation and winds (Murcia, 1995). In addition, hedgerows were often planted on a raised bank and are therefore more distant from the ground water level than the surrounding land. Correspondingly, McCollin et al. (2000) and Schmucki and de Blois (2009) found the soil in hedgerows to be significantly drier than in forests. On the other hand, in hedgerows with a roughly west-east orientation the bank provides shade on the northern side where more moisture-demanding species such as ferns can grow. Originally, most hedgerows were lined by drainage ditches (Baudry et al., 2000), which strongly increased the variability in soil moisture along the cross-section of the hedgerows and facilitated the colonisation by moisture-demanding species. The majority of the ditches, however, has been removed to increase the area of arable land when drainage pipes became common (Le Cœur et al., 2002; Herzon & Helenius, 2008). Unfortunately, we did not have sufficient data to analyse whether ditches increased the species richness or were linked to signals in the species composition for higher moisture. In Belgium, the investigated hedgerows were often accompanied by a ditch or located at the edge of rivers or lakes, which might also explain the high frequency of fern species in those hedgerows. Overall, *Stachys sylvatica*, *Anemone nemorosa*, *Arum maculatum*, *Poa nemoralis* and *Polygonatum multiflorum*, which are among the most frequent forest plant specialists in hedgerows across Europe, have EIV for moisture ranging from 5 to 7 (indicating moist soils), while, at the same time, being largely indifferent to temperature. They are also able to use several dispersal modes, including zoochory and anthropochory (Kattge et al., 2020).

Overall, there is no consistent pattern for the EIV for nutrients over the regions. As explained above, hedgerows often face a strong, and over recent decades increasing, input of nutrient drift from adjacent fields. Nutrient input also comes from water run-off, especially when the hedgerows are perpendicular to the slope of the field (Van Vooren et al., 2017), and through the filtering of pollutants such as nitrogen from the air (Kovář et al., 1996). An increasing nutrient availability has the potential to change the species composition (Litza & Diekmann, 2017; Van Den Berge et al., 2019) by favouring fast-growing, competitive species such as *Urtica dioica* (De Keersmaeker et al., 2004). The positive influence of plant height on species frequency in the NW German lowlands also hints at an increased competition among plant species in the hedgerows. On the other hand, higher

resource and light availability were indeed linked to a higher vegetative performance of forest species in hedgerows when compared to forests (Baeten et al., 2010; Vanneste et al., 2020c). Hence, the effect of EIV for nutrients depends on the amount of nutrients available, which is likely to differ regionally. The contradictive signals across regions might explain a lacking overall pattern.

*Dispersal*

The influence of dispersal modes on the forest species composition in European hedgerows is difficult to assess based on our results. On a European scale, species dispersed by wind, animals or humans were found more frequently in hedgerows than those which are self- or water dispersed. The former dispersal types can all be considered as favourable for long-distance dispersal (Vittoz & Engler, 2007). Within hedgerow landscapes, however, anemochory is not likely to be effective over long distances because hedgerows act as wind-breaks and can filter propagules from the air which therefore accumulate in close-by hedgerows (Sarlöv Herlin & Fry, 2000). Anthropochory can range on very different scales from accidental dispersal when propagules attach to shoes, other clothing or the tyres of vehicles to intentional sowing and planting of species (Vittoz & Engler, 2007). It can therefore take place over very long distances but also in the close proximity, such as along roads next to hedgerows. Across the different regions, a positive effect of anthropochory is the most consistent pattern. Zoochory acts on similar scales as anthropochory, depending on the species and the specific form of dispersal. While ants cross only relatively short distances (Roy & de Blois, 2006), large mammals and birds transport seeds frequently over distances of several kilometres (Graae, 2002). Hedgerows are a regular migration route as well as habitat for many species (Burel, 1996; Davies & Pullin, 2007) and a positive influence of zoochory is therefore not surprising. Sarlöv Herlin and Fry (2000) found that species dispersed by zoochory are more often found in wide hedgerows, suggesting that these are preferred by the dispersing animals due to increased food resources and better protection from predators.

## Conclusions

Our study demonstrates that a high number of forest species can thrive in European hedgerows. However, as many other forest species were never found in hedgerows we agree with previous studies that hedgerows offer a forest-like environment that is, due to more extreme environmental conditions compared to true forests, only suitable for a subset of species. These species are likely tolerant against high temperatures and regular disturbance. The regional patterns partly resemble the overall patterns, but also show some variability across regions reflecting differences in climate and management. Hedgerows in regions that are warm or that are impacted by heat and drought events have fewer forest species. Hence, ongoing climate change is likely to further alter the species composition in hedgerows, and to threaten their forest species richness. Management strategies should therefore focus on reducing the impacts of climate change, e.g. by letting hedgerows grow wider. While hedgerows can themselves help mitigating the global as well as local effects, wider hedgerows that offer a more stable microclimate and can buffer extreme weather events might help in maintaining the habitat's diversity on a European scale.

## List of appendices

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Synthesis



*Ray field with Centaurea cyanus. A gap in the opposite hedgerow allows the view on the Baltic Sea.*

## General discussion

The agricultural landscape has changed dramatically over the past decades, with profound effects on hedgerows. As border habitats, hedgerows are strongly impacted by the adjoining agricultural practices. We saw how the fertiliser induced eutrophication of the habitat caused a shift in hedgerow vegetation towards nutrient-demanding species, associated with an overall species loss (CHAPTER 2). Hedgerows can form important refuge habitats and migration corridors for forest specialists and CHAPTER 5 confirmed the detrimental effects of intense adjacent land-use on their species richness. Another influencing factor for the hedgerows and their vegetation was demonstrated by the dynamics of the size of hedgerow networks. After the majority of hedgerows was created in the 18th and 19th centuries, roughly half of the network was removed in the course of only a few decades of the 20th century (CHAPTER 4). Since this period, only few hedgerows were newly created, leaving the network fragmented. New hedgerows are less species rich, however, given time and the appropriate management, they can develop into habitats similar to the ancient hedgerows and increase the connectivity (CHAPTER 3). Furthermore, this thesis repeatedly linked a wide shrub layer to a high richness of forest specialists, and thereby stressed the importance of the canopy structure as a proxy for the habitat quality for forest specialists (CHAPTER 3, CHAPTER 4, CHAPTER 5). In addition to the local factors, the regional climate was identified to be important as well, with climate change as a potential future threat to forest specialist richness in European hedgerows (CHAPTER 5).

This CHAPTER 6 will present a synthesis of our findings and answer the research questions posed in CHAPTER 1. Based on this, management recommendations are given on how to maintain and improve the conservation value of hedgerows. The chapter is concluded with future perspectives on hedgerow research.

### *Influences on hedgerows in changing agricultural landscapes*

The resurvey study in CHAPTER 2 revealed many changes of the hedgerow habitats regarding their structure, edaphic conditions and vegetation that can be linked to agricultural intensification and neglected management taking place over the past decades. As a result, we saw a strong shift towards more nutrient-demanding species in the composition of the herbaceous species, combined with a general decline in species richness. CHAPTER 5 affirmed the negative influence of intense adjacent land-use on the forest species richness.

The influences by agricultural practices on hedgerows can be of both chemical and physical form. CHAPTER 2 demonstrated that a change in management can cause a change in the species richness and composition. The shrub layer was found to grow higher in the resurvey, indicating less frequent coppicing with negative results for the richness of herbaceous species. Contrary to this, other studies have shown that a higher shrub layer can lead to an increase in forest specialists (Closset-Kopp et al., 2016; Lenoir et al., 2021). However, when the cutting is neglected for too long, the shrub layer becomes gappy close to the ground and ultimately transforms into a line of trees. Due to increased lateral solar radiation, this results in a less shaded interior, reduces the habitat quality for forest specialists and facilitates the invasion of light-demanding species (Huwer & Wittig, 2012). The increased heat stress is indicated by the detected increase of thermophilic species over the years

(CHAPTER 2). In addition, the change of the banks' shape revealed slow erosion due to a lack of management as they decreased in height while becoming wider.

One major issue for agro-ecosystems is the drift of agricultural substances like pesticides and fertilisers into the habitat (Jobin et al., 1997; Tsiouris & Marshall, 1998). The use of these substances has increased profoundly in European countries over the course of the 20th century, and only slightly decreased for nitrogen and phosphorus in recent years (Stoate et al., 2001; DESTATIS, 2014; Eurostat, 2022). Hedgerows act as a barrier to the adjacent habitat and thus agricultural chemicals tend to accumulate in the soil (Tsiouris & Marshall, 1998). The eutrophication has strong effects on the richness and composition of the habitat (Baessler & Klotz, 2006; Carey et al., 2008; Staley et al., 2013) as demonstrated in CHAPTER 2. Although the composition changes were seen in both the shaded and the open parts of the hedgerows, arable weed species underwent the most drastic changes. The field margin community is mostly made up of annual species and therefore has a high species turnover and. Additionally, the agricultural impact is higher in the margins than the inner parts of the hedgerows. Overall, the weed species richness increased over the years. The number of grass species also increased, especially competitive species such as *Bromus sterilis* and *Arrhenatherum elatius* profited from the increase in nutrients. Furthermore, species tolerant of herbicide use, such as *Elymus repens*, *Poa trivialis* and *Apera spica-venti*, thrived in the field margins (Hilbig & Bachthaler, 1992). There was also an overall increase in neophytes, even though in small numbers. However, other species groups decreased in richness, such as forest plant species. CHAPTER 3 confirmed the negative impact of eutrophication on specialist groups as hedgerows with high phosphorus content displayed a lower forest specialist richness. The number of endangered species decreased as well, indicating an ongoing floral impoverishment and homogenisation of the landscape (Staley et al., 2013).

Another problem associated with eutrophication is the acidification of habitats. Agro-ecosystems are often characterised by a high fertiliser input of organic fertilisers containing ammonium, which is oxidised to nitrate in the soil (Barak et al., 1997). This process releases protons, lowering the pH value of the soil. The deposition of atmospheric nitrogen is likely to add to this effect and was shown to cause a decline of forest herbs and to alter their composition in forests (Baeten et al., 2009). CHAPTER 3 found recent hedgerows to have a more base-rich pH compared to ancient hedgerows, and CHAPTER 2 showed a decrease in pH values of about 0.5 units over the past five decades in hedgerows. This means that hedgerow soils acidify over time, partly caused by natural soil forming processes (Schleuß, 1996) but likely accelerated by anthropogenic factors. In our resurvey study, the drop in pH was linked to a change in species composition and a decrease of forest specialists. In accordance, CHAPTER 3 demonstrated that a high forest species richness could be linked to hedgerows displaying more base-rich pH values. Forest specialists often have a narrow ecological pH range and are sensitive to low pH values (Michaelis et al., 2016). Especially values within the aluminium buffer range, i.e. values below 4.2 (Ulrich, 1983), as we found them in the majority of hedgerows, are expected to hinder the successful establishment and growth of forest herbs (Falkengren-Grerup & Tyler, 1991).

Detrimental physical influences can be caused by the adjacent land-use when ploughing, grazing or trampling by livestock expand to the banks of the hedgerows (or the respective area for hedgerows planted on ground floor) (Müller, 2013). Ploughing removes the vegetation cover, potentially harms

the roots of the woody vegetation and destabilises the banks. In the field, this can be recognised by an abrupt drop of the bank's edge to the agricultural field (personal observation). While in earlier times grazing was frequent when hedgerows served as fences, trampling was stopped by the hedgerows being stock-proof. As today most hedgerows have gaps, they need to be protected by a fence from the livestock to prevent destruction by trampling (Weber, 2003; MELUR, 2017). However, intense browsing, especially by horses, needs to be prevented as well, because it can completely remove the herbaceous and the shrub layer (Weber, 2003; Müller, 2013) or at the very least favours species with spikes or thorns. This leads to many other species being outcompeted and thus a gradual reduction in species richness. Additionally, hedgerows next to roads can be damaged by passing agricultural machines or other vehicles.

**In short**, we saw a neglect in management and a significant eutrophication and acidification of the hedgerows, which caused the establishment of competitive nutrient-demanding species and a subsequent floral impoverishment of the hedgerows over the past five decades (cf. **Research Question I**).

### *Species richness dynamics in hedgerow networks: Ups and downs*

The application of extinction debt and colonisation credit theory revealed new insights for hedgerow research. The hedgerow network was a suitable study habitat as it was subjected to strong dynamics of habitat increase and decrease since their wide-spread establishment roughly 250 years ago. Then, large parts of the network were created in a rather short time period and extensive colonisation processes were enabled (Stamm & Welters, 1996). The results from CHAPTER 3 suggest that the colonisation credit of forest specialists was paid off fast, assuming that ancient forest patches or hedgerows were found in the proximity. Also, the practice of collecting saplings from the surrounding woods to plant them into the hedgerows facilitated the colonisation by forest plants because diaspores, bulbs or rhizomes were imported with the root balls (Weber, 2003). We therefore presume that the hedgerow habitats were at species equilibrium before the next decisive turning point about 200 years after their establishment, when roughly half of the network was removed in the cause of land consolidation (CHAPTER 4). This major habitat loss entailed immediate local species extinctions where hedgerows were destroyed. Additionally, it likely caused a general but delayed decline of species richness in the remaining hedgerows due to a decrease of habitat connectivity (Burel & Baudry, 1990; Deckers et al., 2005). However, in CHAPTER 4, we could not demonstrate an extinction debt for forest plant species in hedgerows. For one part, our analyses were hindered by very influential covariates that obscured the species-area-relationship for hedgerows. On the other hand, it is plausible that the magnitude of habitat destruction caused the extinction debt to be paid off rather rapidly. This is supported by the subgroup of ancient woodland indicator (AWI) species, whose distribution patterns suggested an extinction debt was still present. AWI species have particularly low dispersal capacities within the group of forest species, which makes them slow to adapt to new conditions and might cause longer relaxation times. These results are similar to findings by Kolk and Naaf (2015) who investigated highly fragmented forests and found the extinction debt to be largely paid off except for species with low dispersal capacities.

Overall, the most important explanatory variable in our study for the distribution patterns of forest specialists was the hedgerow width. This can be used as proxy for the habitat quality, with wide hedgerows harbouring a high number of forest plants. Hedgerows with wide shrub layers have an

increased shaded interior, shield direct solar radiation and reduce wind speeds, which results in a more stable and forest-like microclimate (Vanneste et al., 2020b). This has repeatedly been linked to a high forest specialist richness in other studies (e.g. Roy & de Blois, 2008; Closset-Kopp et al., 2016).

Following the tremendous hedgerow losses during the land consolidation processes, few hedgerows were created as compensation measures (Kellerhoff, 1984; Deckers et al., 2005; Müller, 2013). Ancient hedgerows have been described to be very species-rich both in the shrub layer and in the herbaceous layer (Eigner, 1982) and in CHAPTER 3, we studied the allegedly lower conservation value of recent hedgerows. Indeed, we saw that in pairs of recent and ancient hedgerows the number of forest specialists was lower in recent hedgerows, which suggests a persisting colonisation credit. However, one to several decades after their establishment, the recent hedgerows were already richer in herbaceous forest plants than expected and also the shrub layer of recent hedgerows was very species rich. The proximity to source populations in ancient hedgerows and ancient forest patches was demonstrated to facilitate the colonisation, which stresses the importance of ancient habitats for the conservation of forest specialists in agricultural landscapes (von Oheimb et al., 2007; Roy & de Blois, 2008; Closset-Kopp et al., 2016; Paal et al., 2017). As was also shown in CHAPTER 4, a wide shrub layer was essential for the successful colonisation by forest specialists. The overall species number was higher in the recent hedgerows indicating ongoing succession and suggesting that the recent hedgerows were still in a transitioning state of open habitats to forest-like conditions (Starkmann, 1993; Pellissier et al., 2004; Van Den Berge et al., 2019). This was confirmed by the species composition of the recent hedgerows, which became more similar to the composition of the ancient hedgerow partner with increasing age. Managed hedgerows will never reach a climax state of succession. Nevertheless, we can find well-adapted, stable species compositions in older hedgerows.

**In short**, we could not detect an extinction debt for forest specialist in hedgerows, likely because it was already paid off (cf. **Research Question III**). However, the analysis was hindered by covariates such as the hedgerow width, which proved to be the most important variable shaping the distribution patterns of forest specialists in hedgerows. The colonisation credit of forest specialists in hedgerows can be paid off after several decades when nearby source populations and a wide shrub layer reduce the relaxation time (cf. **Research Question II**).

*European forest specialists: Species richness under threat of climate change*

While the studies in CHAPTER 2, CHAPTER 3 and CHAPTER 4 acted on different temporal scales by comparing plot data representing different points in time, CHAPTER 5 compared a large number of plots across the hedgerow-rich agricultural regions of Europe, thus focussing on a spatial gradient. This enabled us to put the previous knowledge about the vegetation of hedgerows into a broader context and to generalise the patterns we found. One important result is that across our study area we found a high richness of forest specialists in hedgerows. Even though these represent only subsets of the regional species pools, these findings demonstrate that hedgerows all over Europe can form suitable habitats for forest specialists (Van Den Berge et al., 2019; Vanneste et al., 2020a; Lenoir et al., 2021). Those species able to colonise hedgerows tend to be tolerant against high temperatures in comparison to all forest species. Thermophilic species are common in hedgerows because the higher levels of solar radiation, air mixing and lower humidity cause less effective thermal buffer

capacity of hedgerow canopies when compared to forests (Honnay et al., 2005; Vanneste et al., 2020b). Frequent species are also tolerant against high levels of disturbance, which is caused by the management as well as the adjacent land-use (Baudry et al., 2000; Smart et al., 2001). The shrub layer composition reflects the origin as living fences as well as the typical management, as it consists of many species protected against herbivory by thorns or spikes (e.g. *Crataegus* spp., *Prunus* spinosa, *Rosa* spp. and *Rubus* spp.) as well as species well enduring regular cuts (e.g. *Corylus avellana* and *Sambucus nigra*).

We could demonstrate the influence of the regional climate on the number of forest specialists in hedgerows and found that hedgerows in regions with a high mean annual temperature had fewer forest species. In compliance with space-for-time substitution, this implies a potential threat for the species richness in hedgerows, as hedgerows situated in less warm regions today might lose species when the temperature rises under ongoing climate change (Blois et al., 2013). Such insights into large scale patterns are made possible by the macroecological basis of studies such as the one presented in CHAPTER 5. Vanneste et al. (2021) demonstrated that the effects of higher temperatures in hedgerows depend on the species and can even be beneficial when plants grow taller and produce heavier seeds. However, they stress that the response to climate change of non-forest, competitive plants is just as important because those might be able to outcompete forest plants under changing conditions. Species not able to adapt to the changing conditions need to shift their range, which hedgerows can facilitate as migration corridors (Vanneste et al., 2020a; Vanneste et al., 2021). Climate change is a global threat to biodiversity that is predicted to lead not only to higher mean temperatures but also an increase in extreme weather events, including heat waves and droughts (Seneviratne et al., 2012). Our study showed that regional heat and drought events led to a reduction in the number of forest specialists, which is another indication for a future threat by a changing climate.

The effects of macroclimatic warming could be mitigated by local processes, referred to as microclimatic buffering, thus delaying the shift of communities towards more thermophilic species (De Frenne et al., 2013; De Frenne et al., 2021). In CHAPTER 2 we found a thermophilisation of hedgerows within the last five decades. Microclimates are able to buffer extreme weather events, such as heat and drought, and thus provide suitable conditions despite macroclimatic warming (De Frenne et al., 2021). In forests, the canopy is essential for providing a cooler microclimate and buffering extreme temperatures (De Frenne et al., 2019). Accordingly, the canopy of hedgerows determines their buffer capacities, where a high canopy cover and a wide shrub layer increase the microclimatic buffering (Vanneste et al., 2020b). Hedgerows with wide shrub layers have repeatedly been shown to have a high richness of forest specialists (cf. CHAPTER 3, CHAPTER 4, CHAPTER 5 of this thesis; Roy & de Blois, 2008; Closset-Kopp et al., 2016; Lenoir et al., 2021) and more effective microclimatic buffering is likely a major factor for this occurrence.

**In short**, the macroecological context helped identify that a changing climate, i.e. increased mean annual temperatures and more extreme heat and drought events, poses a threat to forest species richness in hedgerows (cf. **Research Question IV**). Wider hedgerows are better able to buffer the microclimate, against extreme weather events in particular, and thus have a higher forest species richness.

## Implications for management

The previous chapters have demonstrated four major challenges for hedgerows in the past, present and future: the abandonment of traditional management practices, the input of agricultural chemicals such as pesticides and fertilisers, the habitat loss through hedgerow removal, and a changing climate. The following section will give recommendations on how to meet those challenges with appropriate management and hopefully mitigate the effects to preserve the biodiversity of hedgerows.

In the beginning of the 20th century, hedgerows have lost their economic value for the farmers because wire fences became readily available, timber no longer needed to be logged by the farmers themselves, and property lines were documented in land registers. As a consequence, the traditional techniques that require large amounts of time and labour have lost their importance and hedgerow management was increasingly neglected, despite a subsequent reduction in biodiversity and ecological functions (Critchley et al., 2013; Staley et al., 2013). Agri-environment schemes can help to put a focus on the value of the habitat and motivate farmers to apply appropriate hedgerow management (Batáry et al., 2015). Additionally, along with increasingly big machinery for tilling, sewing and harvesting, the management of hedgerows was mechanised as well. The use of mechanical flails and tree shears has increased in recent years and holds the potential to stop hedgerow degradation (Eigner & Gerth, 2020). This form of hedgerow management is cost- and time-efficient and therefore complies with the requirements of farmers. They do not need to buy the machinery themselves but can hire local hedge management contractors. To increase financial profit from the management, the harvested wood can be used as wood fuel either on the own farm or sold as bioenergy (Smith et al., 2021). However, it is important to also keep in mind the needs of the habitat and its inhabitants. When the machines leave the stools or branches injured, subsequent cuts are needed to maintain the health of the hedgerow shrubs. Also, trimming should only occur every two or better even three years to enable flowering and fruit-set of the shrubs. The banks, which increase the heterogeneity of edaphic and microclimatic conditions and protect the plant roots, need to be maintained and repaired as well after coppicing to avoid gradual erosion (CHAPTER 2; Weber, 2003).

Intense adjacent land-use was demonstrated to have a negative impact on the forest species richness (CHAPTER 5). The proximity to agricultural fields makes hedgerows vulnerable to the input of many agricultural substances such as pesticides as well as artificial fertilisers that drift from the fields into the hedgerows with ecotoxicological consequences (Jobin et al., 1997; Tsiouris & Marshall, 1998; Lazzaro et al., 2008). Accordingly, the eutrophication and acidification of hedgerows was identified to endanger species richness of herbaceous plants in hedgerows (CHAPTER 2). A possible solution is the wide-spread introduction of buffer zones next to hedgerows that are uncropped, not sprayed with any agrochemicals and only extensively managed to prevent woody plant encroachment (Burn, 2003). Buffer zones can receive subsidies under various agri-environment schemes and are a mandatory practice in e.g. Schleswig-Holstein, Northern Germany, where strips of 50 cm width next to the hedgerows have to be spared (MELUR, 2017). This reduces the physical damage by agricultural machines. However, even wider field margins would be needed to largely reduce the accumulation of agricultural chemicals (Burn, 2003). The optimisation of substance application in

amounts as well as techniques can also help to reduce the drift into adjacent habitats (Matthews & Thomas, 2000). Yet, the most effective way of limiting the accumulation of agrochemicals in hedgerows (or any other adjacent habitat) is the abandonment of said substances as it is done in organic farming. Compared to hedgerows next to fields under conventional farming, organic farming leads to a higher species richness of herbaceous plants and a composition more similar to semi-natural habitats (Aude et al., 2003; Aude et al., 2004).

The large-scale hedgerow removals of the land consolidation processes in Western and Central Europe were halted after several decades, however, large parts of the hedgerow network had already been lost (CHAPTER 4). This resulted in a strong decline of habitat connectivity within the remaining networks (Deckers et al., 2005). Hence, it is all the more important to protect those hedgerows that are left, especially species rich, ancient hedgerows (CHAPTER 3). The construction of new hedgerows is a promising measure, as CHAPTER 3 demonstrated, although it is only implementable to a limited extent. The hedgerows need to be planted at sites where they are well integrated into the agricultural matrix and thus can be preserved in the long run. Land owners
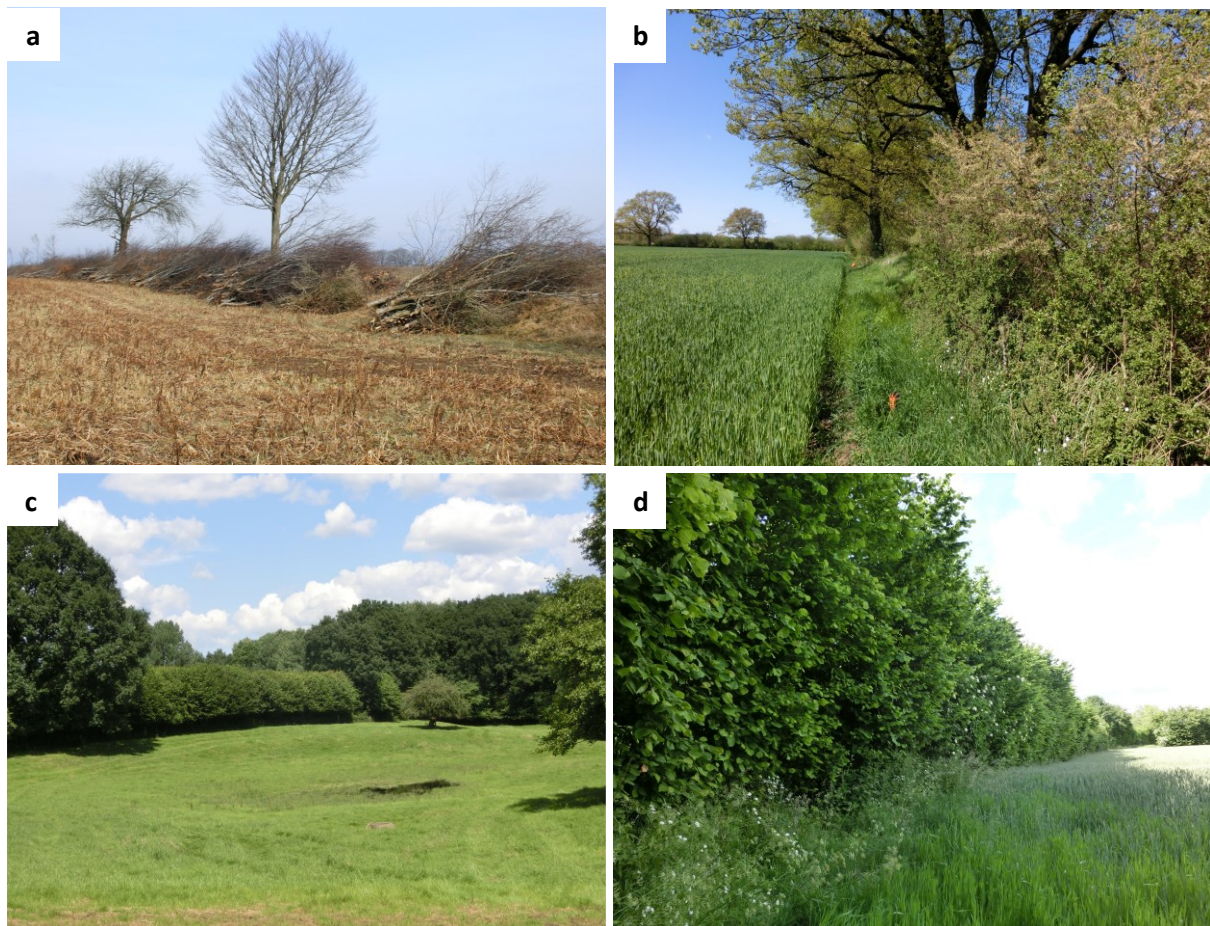


Figure 6.1 Examples of best practice recommendations for hedgerow management. a) Hedgerow after coppicing with a tree shear. The cut off branches are placed in neat piles next to the hedgerow to be fetched later. b) Buffer zones in the form of field margins next to the hedge banks separate the hedgerow from the agricultural field and thereby reduce the impact of the adjacent land-use. c) Ancient hedgerows have a high forest species richness, especially when attached to a forest, and need to be protected. d) A wide shrub layer, which here not only shades the banks but also the field margins, is essential for the habitat quality of hedgerows.

should be motivated by providing compensation for the costs and labour invested into the construction and maintenance of hedgerows and the area they take out of production, as well as by demonstrating the benefits of the ecosystem services provided by hedgerows (Batáry et al., 2015). When newly created hedgerows are adding to a hedgerow network, they can increase its connectivity and facilitate species movement, even though the development of a closed canopy and the succession of a stable species composition typical for hedgerows take time (Starkmann, 1993). CHAPTER 3 and CHAPTER 4 demonstrated that the presence of ancient hedgerows and ancient forests in the surrounding landscape leads to a higher number of forest specialists in hedgerows, which underlines the importance of ancient habitats as source populations and their value for nature conservation.

A consistent pattern throughout this thesis is the strong positive effect of wider hedgerows for the species richness of forest plant specialists (CHAPTER 3, CHAPTER 4, CHAPTER 5). A wider canopy increases not only the area of the habitat but, more importantly, also its quality. Wider hedgerows offer a more stable microclimate regarding temperatures and humidity by effectively shielding solar radiation and reducing wind speeds (Vanneste et al., 2020b). Consequently, they are also better capable of buffering extreme weather events, such as heat and drought. This is not only beneficial for the herbaceous vegetation, but also mammals, birds and invertebrates were shown to profit from wide hedgerows (Graham et al., 2018). This in turn might increase the dispersal potential for zoochorous plant species. Climate change is predicted to be a major threat in the upcoming future. An increase in mean temperatures as well as an increased frequency of heat and drought events will challenge the species richness in hedgerows (CHAPTER 5). Already today the hedgerow width is a key factor for the habitat quality of European hedgerows and its importance will further increase in the future. Therefore, European measures such as agri-environment schemes need to incorporate this and promote management towards wider hedgerows.

To sum this up, four measures are emphasized by this thesis to maintain or increase the ecological value of hedgerows:

❖ To conserve hedgerows, regular management needs to be ensured. To reach this goal, not only the needs of the habitat but also of the land-owners have to be considered. Agri-environment schemes and the promotion of mechanical management (Figure 6.1 a) can help to end mismanagement and neglect of hedgerows.

❖ To reduce the drift of pesticides and fertilisers into the hedgerows, the wide-spread adaptation of buffer zones can help if they are wide enough (Figure 6.1 b). In the long term, expanding organic farming holds the most potential for reducing the pollution of the environment with toxic substances.

❖ Ancient hedgerows as well as ancient forests need to be protected as biodiversity hotspots and potential source populations (Figure 6.1 c). The construction of new hedgerows can increase the connectivity of the network, given time and appropriate management.

❖ To ensure the habitat quality and the resilience of the herbaceous community against a warming climate and extreme weather events, a wide shrub layer is essential (Figure 6.1 d).

## Future perspectives and conclusion

This thesis has demonstrated that research on large temporal as well as large spatial scales can offer new insights into the vegetation dynamics of hedgerow habitats. In the future, this should be extended to combine both temporal and spatial scales in one study by e.g. performing a meta-analysis of European resurvey studies on hedgerows. This might show different trajectories of change for separate regions and indicate how different management and conservation strategies in combination with the regional climate impact the species richness. At the moment the basis for this is lacking as only few resurvey studies have been performed in European hedgerows. One focus for upcoming years could therefore be the detection of historical data sets of hedgerow vegetation suitable for resampling. This would broaden the knowledge about changes in different regions, and furthermore provide the opportunity of a comprehensive meta-analysis, generating insights to see the bigger picture.

Further potential for future hedgerow research lays in the complex topic of climate change. This thesis demonstrated a potential threat for forest specialists in hedgerows that can be met by supplying a more stable microclimate within wider hedgerows. More detailed research into this might present further insights into management strategies under climate change. This can best be done by conducting research across disciplines including e.g. agricultural science, agricultural economics, forestry, soil science, climatology and meteorology. The interest in agroforestry, i.e. a land-use strategy that combines agriculture and forestry by cultivating crop plants in combination with shrubs or trees, has increased strongly over the last three decades (Castle et al., 2022). The benefits lay in increased carbon sequestration, reduction of soil erosion, improved nutrient and water cycling, increased biodiversity and increased agricultural productivity. Linear plantings between agricultural fields such as hedgerows represent one form of agroforestry practice, however, it can have many forms and also be more complex with several strata. Agroforestry in general and carbon sequestration in particular hold the potential to mitigate global climate change. On a local scale, microclimate buffering of the hedgerow habitat itself as well as the adjacent fields attenuates the effects of a warming climate and extreme weather for vegetation and wild-life. However, more research is needed to better understand the impact of hedgerows on microclimatic processes and which management technique can improve the microclimate, increasing both the agricultural yield and the biodiversity of agro-ecosystems.

Hedgerows are heterogeneous and dynamic semi-natural habitats with great potential for biodiversity, offering habitats and dispersal corridors for a large variety of plant species, including forest specialists. They provide many ecosystem services, such as carbon sequestration, the reduction of erosion by wind or water as well as shielding adjacent habitats from weather conditions and the drift of agrochemicals. Hedgerow habitats face many challenges, though, and to maintain their functionality in the future, appropriate management and protection from further habitat loss will be essential.

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# APPENDIX

## Appendices to Chapter 2

Table A 1 Herbaceous and woody species with the highest frequency (F) and mean plot abundance (A) in the original survey and the resurvey. The lists are sorted by the combined overall frequency (CF = frequency · mean abundance). Total plot number was 51.

| Original survey | F | A | CF | Resurvey | F | A | CF |
|---|---|---|---|---|---|---|---|
| **Herbaceous species** | | | | **Herbaceous species** | | | |
| *Elymus repens* | 51 | 13.8 | 704 | *Elymus repens* | 48 | 13.3 | 639 |
| *Poa nemoralis* | 41 | 15.1 | 619 | *Urtica dioica* | 47 | 10.9 | 512 |
| *Stellaria holostea* | 45 | 7.1 | 321 | *Hedera helix* | 25 | 14.9 | 373 |
| *Urtica dioica* | 48 | 5.1 | 245 | *Galium aparine* | 49 | 7.6 | 371 |
| *Holcus mollis* | 43 | 5.6 | 243 | *Chaerophyllum temulum* | 40 | 8.0 | 321 |
| *Dactylis glomerata* | 50 | 4.7 | 236 | *Poa trivialis* | 46 | 6.6 | 305 |
| *Arrhenatherum elatius* | 16 | 11.3 | 180 | *Bromus sterilis* | 35 | 8.5 | 297 |
| *Agrostis capillaris* | 24 | 6.1 | 147 | *Stellaria holostea* | 44 | 6.3 | 279 |
| *Moehringia trinervia* | 28 | 5.0 | 139 | *Dactylis glomerata* | 50 | 5.5 | 276 |
| *Anthriscus sylvestris* | 43 | 3.1 | 134 | *Arrhenatherum elatius* | 36 | 5.6 | 202 |
| *Galium aparine* | 44 | 2.8 | 123 | *Alliaria petiolata* | 27 | 7.2 | 195 |
| *Chaerophyllum temulum* | 33 | 3.6 | 118 | *Poa nemoralis* | 43 | 4.0 | 173 |
| *Festuca rubra* agg. | 36 | 3.2 | 114 | *Anthriscus sylvestris* | 32 | 4.0 | 127 |
| *Ranunculus repens* | 40 | 2.2 | 90 | *Holcus mollis* | 26 | 4.0 | 104 |
| *Hedera helix* | 15 | 5.8 | 88 | *Galeopsis tetrahit* agg. | 45 | 2.0 | 92 |
| **Woody species** | | | | **Woody species** | | | |
| *Corylus avellana* | 45 | 27.3 | 1228 | *Prunus spinosa* | 38 | 33.9 | 1288 |
| *Carpinus betulus* | 41 | 22.6 | 926 | *Corylus avellana* | 41 | 22.6 | 927 |
| *Prunus spinosa* | 39 | 19.8 | 771 | *Carpinus betulus* | 29 | 22.1 | 642 |
| *Rubus fruticosus* agg. | 43 | 11.3 | 486 | *Sambucus nigra* | 46 | 9.9 | 457 |
| *Fagus sylvatica* | 24 | 19.1 | 460 | *Rubus fruticosus* agg. | 44 | 8.4 | 369 |
| *Crataegus laevigata* | 39 | 6.2 | 242 | *Crataegus monogyna* | 35 | 8.1 | 285 |
| *Rubus idaeus* | 40 | 5.4 | 218 | *Quercus robur* | 32 | 7.9 | 251 |
| *Quercus robur* | 34 | 4.8 | 162 | *Acer campestre* | 14 | 17.1 | 239 |
| *Rosa canina* | 32 | 5.0 | 161 | *Rubus idaeus* | 28 | 7.9 | 220 |
| *Acer campestre* | 19 | 7.6 | 145 | *Acer pseudoplatanus* | 15 | 13.0 | 196 |
| *Lonicera periclymenum* | 31 | 4.5 | 140 | *Fagus sylvatica* | 11 | 17.8 | 196 |
| *Sambucus nigra* | 30 | 4.1 | 124 | *Rosa canina* | 36 | 4.9 | 177 |
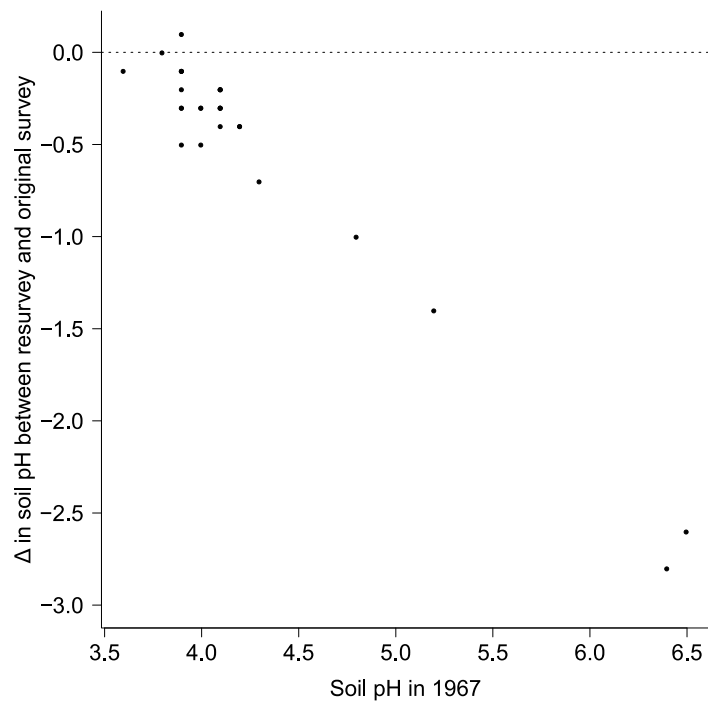
Figure A 1 The relationship between the soil pH value of plots in the original study and the difference in pH between the two surveys ($n$ = 27, value of resurvey *minus* value of original survey).

## Appendices to Chapter 3
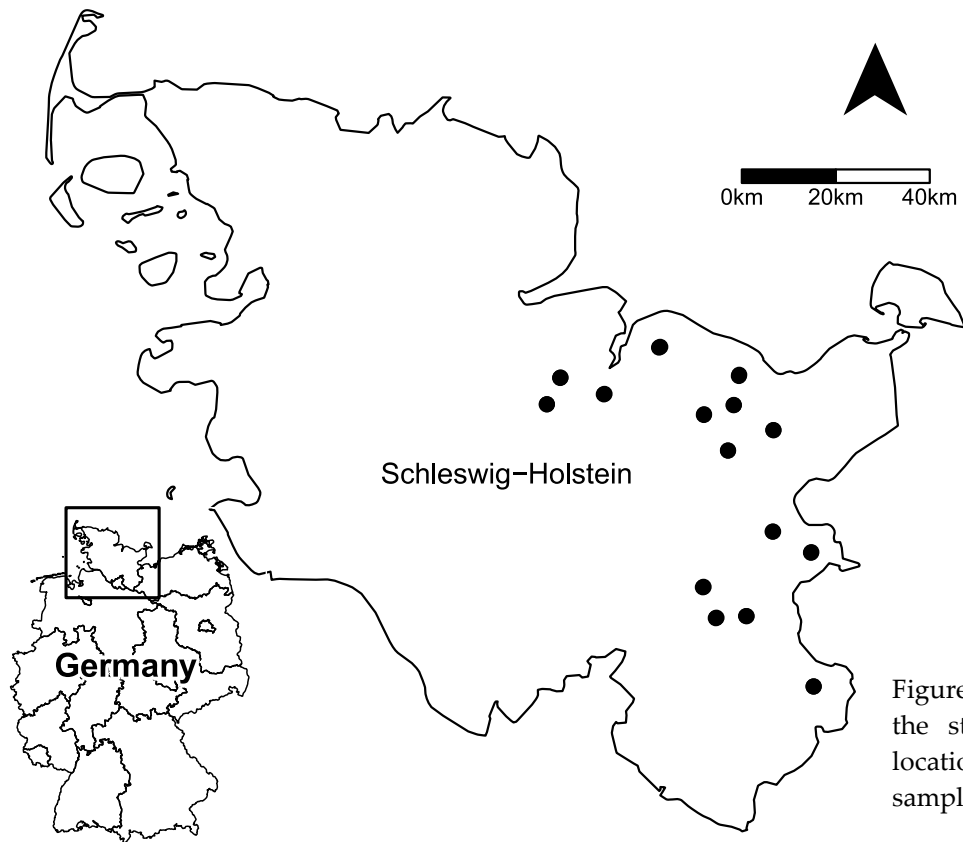


Figure A 2 Map showing the study area and the locations of the 15 sampled hedgerow pairs.
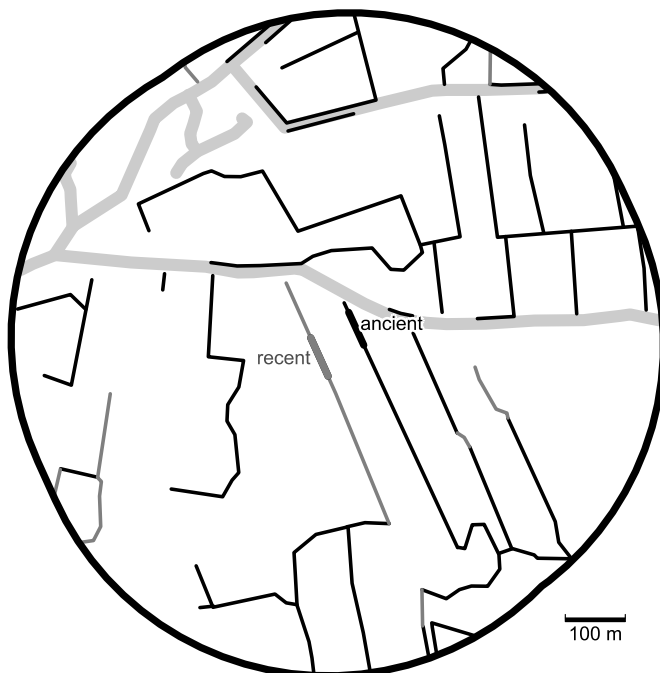


Figure A 3 Example of a hedgerow network in a 500 m radius around a hedgerow pair comprising a historically recent and ancient hedgerow section. Bold lines mark the plot positions. Black = ancient hedgerows, grey = recent hedgerows, light grey = streets.

Table A 2 List of the 15 investigated hedgerow pairs with their numbers of shrub species, herb species, forest species and ancient woodland indicator species (AWI). The first number always refers to the ancient hedgerow and the second number to the recent hedgerow partner (ancient|recent). Additionally, the distance between the paired hedgerows (in m) and the date when the recent hedgerow partner was established are shown.

| ID | No. shrub species | No. herb species | No. forest species | No. AWI species | Distance between the hedgerows (m) | Date of establishment of recent hedgerow |
|----|----|----|----|----|----|----|
| 1  | 5 \| 8   | 42 \| 45 | 3 \| 4  | 1 \| 1 | 74  | 1955 |
| 2  | 9 \| 12  | 32 \| 26 | 8 \| 4  | 1 \| 0 | 164 | 1953 |
| 3  | 11 \| 8  | 27 \| 22 | 6 \| 4  | 2 \| 0 | 182 | 1953 |
| 4  | 18 \| 23 | 45 \| 31 | 7 \| 6  | 1 \| 1 | 110 | 1990 |
| 5  | 14 \| 16 | 37 \| 23 | 13 \| 6 | 4 \| 2 | 63  | 1994 |
| 6  | 15 \| 19 | 25 \| 30 | 11 \| 8 | 3 \| 4 | 59  | 1994 |
| 7  | 14 \| 17 | 36 \| 37 | 7 \| 3  | 0 \| 1 | 101 | 2004 |
| 8  | 15 \| 16 | 33 \| 28 | 5 \| 1  | 1 \| 1 | 148 | 2003 |
| 9  | 17 \| 8  | 22 \| 33 | 8 \| 6  | 4 \| 1 | 56  | 1954 |
| 10 | 14 \| 16 | 48 \| 36 | 9 \| 4  | 3 \| 1 | 75  | 1990 |
| 11 | 12 \| 16 | 28 \| 32 | 5 \| 1  | 2 \| 1 | 296 | 1980 |
| 12 | 9 \| 10  | 30 \| 23 | 9 \| 7  | 1 \| 3 | 170 | 1984 |
| 13 | 9 \| 10  | 31 \| 24 | 8 \| 7  | 1 \| 3 | 270 | 1974 |
| 14 | 11 \| 12 | 34 \| 31 | 6 \| 7  | 1 \| 2 | 37  | 1938 |
| 15 | 16 \| 14 | 36 \| 47 | 7 \| 7  | 2 \| 1 | 148 | 2004 |

Table A 3 List of forest specialists found in the 15 hedgerow pairs. The dispersal mode is according to FloraWeb (www.floraweb.de, last accessed: 1. Dec 2017) and only the most efficient dispersal mode is given, while the reproduction mode is based on information provided by Klotz et al. (2002). The classification of ancient woodland indicator species (AWI) follows Schmidt et al. (2014). Also shown are their total frequencies as well as their frequencies separately for ancient and recent hedgerows.

| Species | Dispersal mode | Reproduction mode | AWI | total | ancient | recent |
|---|---|---|---|---|---|---|
| *Adoxa moschatellina* | endozoochory | mostly vegetatively | - | 17 | 11 | 6 |
| *Anemone nemorosa* | myrmecochory | mostly vegetatively | - | 9 | 6 | 3 |
| *Arum maculatum* | endozoochory | by seed and vegetatively | AWI | 5 | 3 | 2 |
| *Chaerophyllum temulum* | epizoochory | by seed | - | 26 | 12 | 14 |
| *Circaea lutetiana* | epizoochory | by seed and vegetatively | AWI | 1 | 0 | 1 |
| *Dryopteris filix-mas* | anemochory | by seed and vegetatively | - | 8 | 5 | 3 |
| *Epipactis helleborine* | anemochory | by seed and vegetatively | AWI | 1 | 0 | 1 |
| *Gagea lutea* | anemochory | by seed and vegetatively | - | 3 | 3 | 0 |
| *Galium odoratum* | endozoochory | by seed and vegetatively | AWI | 1 | 0 | 1 |
| *Hedera helix* | endozoochory | by seed and vegetatively | - | 15 | 10 | 5 |
| *Humulus lupulus* | anemochory | by seed and vegetatively | - | 5 | 4 | 1 |
| *Lamium galeobdolon agg.* | autochory | by seed and vegetatively | AWI | 5 | 4 | 1 |
| *Melica uniflora* | epizoochory | by seed and vegetatively | AWI | 1 | 0 | 1 |
| *Mercurialis perennis* | myrmecochory | by seed and vegetatively | AWI | 2 | 1 | 1 |
| *Milium effusum* | epizoochory | by seed and vegetatively | AWI | 3 | 2 | 1 |
| *Moehringia trinervia* | myrmecochory | by seed | - | 13 | 6 | 7 |
| *Poa nemoralis* | epizoochory | by seed and vegetatively | - | 27 | 15 | 12 |
| *Polygonatum multiflorum* | endozoochory | by seed and vegetatively | - | 10 | 8 | 2 |
| *Rumex sanguineus* | epizoochory | mostly by seed | AWI | 1 | 1 | 0 |
| *Stachys sylvatica* | autochory | by seed and vegetatively | AWI | 7 | 5 | 2 |
| *Stellaria holostea* | anemochory | by seed and vegetatively | - | 26 | 15 | 11 |
| *Viola x bavarica* | myrmecochory | by seed and vegetatively | AWI | 1 | 1 | 0 |

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## Appendices to Chapter 5

Table A 4 List of 203 forest species included in the analysis. Forest species status is derived either from Hill et al. (2004) (UK, England) or Heinken et al. (2019) (all else). We only considered herbaceous forest specialists classified as 1.1 (Taxa found mainly in the closed forest) and 1.2 (Taxa predominantly growing along forest edges and in forest openings) by Heinken et al. (2019). For England we intended a classification similar to that of Heinken et al. (2019) and therefore included species occurring solely in broad habitats 1 (broadleaved, mixed and yew woodland) and/or 2 (coniferous woodland), and those that additionally occurred in the broad habitats 3 (boundary and linear features, e.g. hedges, roadsides, walls), 15 (montane habitats such as acid grassland and heath with montane species) or 16 (inland rock such as quarries, cliffs, screes). See the description of the floristic surveys in the methods section for further details.
nk = Habitat preference not known

| Species name | Sweden nemoral zone | Germany North-eastern lowlands | Germany North-western lowlands | Belgium lowlands | UK, England | France Atlantic region |
|---|---|---|---|---|---|---|
| *Aconitum variegatum* | | 1.1 | | | | |
| *Actaea spicata* | 1.1 | 1.1 | 1.1 | | | 1.1 |
| *Adoxa moschatellina* | 1.1 | 1.1 | 1.1 | 1.1 | 1 | 1.1 |
| *Aethusa cynapium* subsp. *elata* | | 1.2 | 1.2 | | | 1.2 |
| *Ajuga reptans* | | | | | 1 | |
| *Allium ursinum* | 1.1 | 1.1 | 1.1 | 1.1 | 1 | 1.1 |
| *Anemone nemorosa* | | 1.1 | 1.1 | 1.1 | 1, 16 | 1.1 |
| *Anemone ranunculoides* | 1.1 | 1.1 | 1.1 | 1.1 | | 1.1 |
| *Aquilegia vulgaris* | | 1.2 | 1.2 | | | 1.2 |
| *Arctium nemorosum* | 1.2 | 1.2 | 1.2 | 1.2 | | 1.2 |
| *Aristolochia clematitis* | | | 1.2 | | | |
| *Arum italicum* | | | | 1.2 | 1, 3 | 1.2 |
| *Arum maculatum* | 1.1 | 1.1 | 1.1 | 1.1 | 1 | 1.1 |
| *Asarum europaeum* | 1.1 | 1.1 | 1.1 | | | 1.1 |
| *Asplenium scolopendrium* | | | | | 1, 16 | 1.1 |
| *Athyrium filix-femina* | 1.1 | 1.1 | 1.1 | 1.1 | 1, 16 | 1.1 |
| *Atropa bella-donna* | | 1.2 | 1.2 | 1.2 | 1, 3 | 1.2 |
| *Blechnum spicant* | 1.1 | 1.1 | 1.1 | 1.1 | | 1.1 |
| *Botrychium matricariifolium* | | 1.2 | | | | |

| Species name | Sweden nemoral zone | Germany North-eastern lowlands | Germany North-western lowlands | Belgium lowlands | UK, England | France Atlantic region |
|---|---|---|---|---|---|---|
| *Brachypodium sylvaticum* | 1.1 | 1.1 | 1.1 | 1.1 | 1 | 1.1 |
| *Bromus ramosus* | 1.1 | 1.1 | 1.1 | 1.2 | 1 | 1.2 |
| *Calamagrostis arundinacea* | 1.1 | 1.1 | 1.1 | | | |
| *Calamagrostis villosa* | | 1.1 | | | | |
| *Campanula latifolia* | 1.1 | 1.1 | 1.1 | 1.1 | 1 | |
| *Campanula persicifolia* | 1.2 | 1.2 | 1.2 | | 1, 3 | 1.2 |
| *Campanula trachelium* | 1.2 | 1.1 | 1.1 | 1.1 | 1 | 1.1 |
| *Cardamine bulbifera* | 1.1 | 1.1 | 1.1 | | 1 | 1.1 |
| *Cardamine flexuosa* | 1.2 | 1.2 | 1.2 | 1.2 | 1 | 1.2 |
| *Cardamine impatiens* | 1.2 | 1.2 | 1.2 | | 1, 3 | 1.2 |
| *Carex digitata* | 1.1 | 1.1 | 1.1 | 1.1 | 1, 16 | 1.1 |
| *Carex elongata* | 1.1 | 1.1 | 1.1 | 1.1 | 1 | 1.1 |
| *Carex montana* | | 1.1 | | | | 1.2 |
| *Carex pallescens* | | | | | 1 | |
| *Carex pendula* | | 1.1 | 1.1 | 1.1 | | 1.1 |
| *Carex pilosa* | | | | | | 1.1 |
| *Carex remota* | 1.1 | 1.1 | 1.1 | 1.1 | | 1.1 |
| *Carex spicata* | | 1.2 | 1.2 | | | |
| *Carex strigosa* | | 1.1 | 1.1 | 1.1 | | 1.1 |
| *Carex sylvatica* | 1.1 | 1.1 | 1.1 | 1.1 | 1 | 1.1 |
| *Cephalanthera damasonium* | | 1.1 | 1.1 | 1.2 | 1 | 1.1 |
| *Cephalanthera rubra* | | 1.1 | 1.1 | | 1 | 1.1 |
| *Ceratocapnos claviculata* | 1.2 | 1.2 | 1.2 | 1.2 | | |
| *Chaerophyllum temulum* | 1.2 | 1.2 | 1.2 | 1.2 | 3 | 1.2 |
| *Chimaphila umbellata* | 1.1 | 1.1 | | | | 1.1 |
| *Chrysosplenium alternifolium* | 1.1 | 1.1 | 1.1 | 1.1 | | 1.1 |
| *Chrysosplenium oppositifolium* | 1.1 | 1.1 | 1.1 | 1.1 | | 1.1 |

Table A 4 continued.

| Species name | Sweden nemoral zone | Germany North-eastern lowlands | Germany North-western lowlands | Belgium lowlands | UK, England | France Atlantic region |
|---|---|---|---|---|---|---|
| *Circaea alpina* | 1.1 | 1.1 | 1.1 | | 1 | |
| *Circaea lutetiana* | 1.1 | 1.1 | 1.1 | 1.1 | 1 | 1.1 |
| *Circaea x intermedia* | 1.1 | 1.1 | 1.1 | | 1 | 1.1 |
| *Cirsium tuberosum* | | | | | | 1.2 |
| *Claytonia sibirica* | | | | | 1, 3 | |
| *Clematis recta* | | 1.2 | | | | 1.2 |
| *Clinopodium vulgare* | | 1.2 | | 1.2 | | |
| *Convallaria majalis* | 1.1 | 1.1 | 1.1 | 1.1 | | 1.1 |
| *Corydalis cava* | 1.1 | 1.1 | 1.1 | | | 1.1 |
| *Corydalis intermedia* | 1.1 | 1.1 | 1.1 | | | |
| *Corydalis pumila* | 1.1 | 1.1 | 1.1 | | | |
| *Corydalis solida* | | 1.1 | 1.1 | 1.1 | | 1.1 |
| *Digitalis grandiflora* | | 1.2 | 1.2 | | | |
| *Digitalis purpurea* | 1.2 | 1.2 | 1.2 | 1.2 | | 1.2 |
| *Dipsacus pilosus* | | 1.2 | 1.2 | | | 1.2 |
| *Doronicum pardalianches* | | 1.2 | 1.1 | 1.1 | 1, 3 | |
| *Dryopteris affinis* | | | | 1.1 | 1, 16 | 1.1 |
| *Dryopteris carthusiana* | 1.1 | | | 1.1 | 1 | 1.1 |
| *Dryopteris dilatata* | 1.1 | 1.1 | 1.1 | | 1, 2 | 1.1 |
| *Dryopteris expansa* | 1.1 | 1.1 | 1.1 | | 1, 15, 16 | |
| *Dryopteris filix-mas* | | 1.1 | 1.1 | | 1, 2 | 1.1 |
| *Elymus caninus* | 1.1 | 1.1 | 1.1 | 1.1 | 1, 3 | 1.1 |
| *Epilobium angustifolium* | 1.2 | 1.2 | 1.2 | 1.2 | | 1.2 |
| *Epipactis helleborine* | 1.1 | 1.1 | 1.1 | | | 1.1 |
| *Epipactis muelleri* | | | | 1.2 | | 1.2 |
| *Equisetum hyemale* | 1.1 | | 1.1 | 1.1 | | 1.1 |
| *Equisetum pratense* | 1.1 | 1.1 | 1.1 | | | |

Table A 4 continued.

| Species name | Sweden nemoral zone | Germany North-eastern lowlands | Germany North-western lowlands | Belgium lowlands | UK, England | France Atlantic region |
|---|---|---|---|---|---|---|
| *Equisetum sylvaticum* | 1.1 | 1.1 | 1.1 | | 1, 16 | 1.1 |
| *Equisetum telmateia* | | | 1.1 | | | |
| *Eranthis hyemalis* | | 1.1 | 1.1 | 1.1 | | |
| *Euphorbia amygdaloides* | | 1.1 | 1.1 | 1.1 | 1 | 1.1 |
| *Euphorbia dulcis* | | 1.1 | | 1.1 | | 1.1 |
| *Festuca gigantea* | 1.1 | 1.1 | 1.1 | 1.2 | 1 | 1.1 |
| *Festuca heterophylla* | | 1.1 | | | | 1.1 |
| *Fragaria vesca* | | | | 1.2 | | |
| *Gagea spathacea* | 1.1 | 1.1 | 1.1 | 1.1 | | 1.1 |
| *Galanthus nivalis* | | 1.1 | 1.1 | | | |
| *Galium odoratum* | 1.1 | 1.1 | 1.1 | 1.1 | 1 | 1.1 |
| *Galium sylvaticum* | | 1.1 | 1.1 | | | |
| *Geranium lucidum* | | 1.2 | | | | 1.2 |
| *Geranium phaeum* | | 1.2 | 1.2 | 1.1 | | |
| *Geranium robertianum* | | | | | 1, 16 | |
| *Geranium sanguineum* | | 1.2 | 1.2 | | | |
| *Geum rivale* | | | | | 1, 16 | |
| *Geum urbanum* | | | | | 1 | |
| *Glechoma hederacea* | | | | | 1, 3 | |
| *Goodyera repens* | 1.1 | 1.1 | 1.1 | 1.1 | 2 | 1.1 |
| *Gymnocarpium dryopteris* | 1.1 | 1.1 | 1.1 | 1.1 | 1, 16 | 1.1 |
| *Helleborus foetidus* | | 1.1 | 1.1 | | 1, 3 | 1.2 |
| *Helleborus viridis* | | 1.1 | 1.1 | 1.1 | 1, 3 | 1.1 |
| *Hepatica nobilis* | 1.1 | 1.1 | 1.1 | | | 1.1 |
| *Hesperis matronalis* | | 1.2 | 1.2 | 1.2 | | |
| *Hieracium murorum* | 1.1 | | | | | |
| *Hordelymus europaeus* | 1.1 | 1.1 | 1.1 | | 1 | 1.1 |

Table A 4 continued.

| Species name | Sweden nemoral zone | Germany North-eastern lowlands | Germany North-western lowlands | Belgium lowlands | UK, England | France Atlantic region |
|---|---|---|---|---|---|---|
| *Hyacinthoides non-scripta* | | | 1.1 | 1.1 | | 1.1 |
| *Hypericum androsaemum* | | | | | 1, 3 | 1.1 |
| *Hypericum hirsutum* | 1.2 | 1.2 | 1.2 | 1.2 | | |
| *Hypericum montanum* | | 1.2 | 1.2 | 1.2 | 1, 3 | 1.2 |
| *Hypopitys monotropa* | 1.1 | 1.1 | 1.1 | | | 1.1 |
| *Impatiens edgeworthii* | | 1.2 | | | | |
| *Impatiens noli-tangere* | 1.1 | 1.1 | 1.1 | 1.1 | 1 | 1.1 |
| *Impatiens parviflora* | 1.1 | 1.1 | 1.1 | 1.1 | 1 | 1.1 |
| *Iris foetidissima* | | | | | 1 | |
| *Lamium galeobdolon* | 1.1 | 1.1 | 1.1 | | 1 | |
| *Lathraea clandestina* | | | | | | 1.1 |
| *Lathraea squamaria* | 1.1 | 1.1 | 1.1 | | 1, 3 | 1.1 |
| *Lathyrus latifolius* | | | | | | 1.2 |
| *Lathyrus niger* | 1.2 | 1.2 | 1.2 | | | 1.2 |
| *Lathyrus vernus* | 1.1 | 1.1 | 1.1 | | | |
| *Leucojum vernum* | | | | 1.1 | 1 | |
| *Lilium martagon* | 1.2 | 1.1 | 1.1 | | | 1.1 |
| *Limodorum abortivum* | | | | | | 1.2 |
| *Linnaea borealis* | 1.1 | 1.1 | | | 2 | |
| *Lithospermum officinale* | | 1.2 | | | | |
| *Lunaria rediviva* | 1.1 | 1.1 | | | | |
| *Luzula forsteri* | | | | 1.1 | 1 | 1.1 |
| *Luzula luzuloides* | | 1.1 | 1.1 | | | 1.1 |
| *Luzula Pilosa* | 1.1 | 1.1 | 1.1 | 1.1 | 1, 2 | 1.1 |
| *Luzula sylvatica* | | | | | 1, 16 | |
| *Luzula sylvatica* subsp. *sylvatica* | | 1.1 | 1.1 | 1.1 | | 1.1 |
| *Lycopodium annotinum* | 1.1 | 1.1 | 1.1 | | | |

Table A 4 continued.

| Species name | Sweden nemoral zone | Germany North-eastern lowlands | Germany North-western lowlands | Belgium lowlands | UK, England | France Atlantic region |
|---|---|---|---|---|---|---|
| *Lysimachia nemorum* | 1.1 | 1.1 | 1.1 | 1.1 | 1 | 1.1 |
| *Maianthemum bifolium* | 1.1 | 1.1 | 1.1 | 1.1 | 1, 2 | 1.1 |
| *Matteuccia struthiopteris* | 1.1 | 1.1 | 1.1 | | 1 | 1.1 |
| *Meconopsis cambrica* | | | | | 1 | |
| *Melampyrum cristatum* | | 1.2 | | | | |
| *Melampyrum nemorosum* | | 1.2 | 1.2 | | | |
| *Melampyrum pratense* | | 1.1 | 1.1 | 1.2 | 1, 2 | 1.2 |
| *Melampyrum sylvaticum* | 1.1 | 1.1 | 1.1 | | 1, 16 | |
| *Melica nutans* | 1.1 | 1.1 | 1.1 | | | 1.1 |
| *Melica uniflora* | 1.1 | 1.1 | 1.1 | 1.1 | 1 | 1.1 |
| *Melittis melissophyllum* | | 1.1 | 1.1 | | 1, 3 | 1.2 |
| *Mercurialis perennis* | 1.1 | 1.1 | 1.1 | 1.1 | 1 | 1.1 |
| *Milium effusum* | 1.1 | 1.1 | 1.1 | 1.1 | 1 | 1.1 |
| *Moehringia trinervia* | 1.1 | 1.1 | 1.1 | 1.1 | 1 | 1.1 |
| *Moneses uniflora* | 1.1 | 1.1 | 1.1 | | 2 | |
| *Mycelis muralis* | | | | | 1, 16 | |
| *Myosotis sylvatica* | | 1.2 | 1.2 | 1.2 | 1 | 1.2 |
| *Neottia nidus-avis* | 1.1 | 1.1 | 1.1 | 1.1 | 1 | 1.1 |
| *Oreopteris limbosperma* | 1.1 | 1.1 | 1.1 | | 1, 16 | |
| *Orobanche hederae* | | 1.2 | 1.2 | 1.2 | | 1.1 |
| *Orthilia secunda* | 1.1 | 1.1 | 1.1 | | | |
| *Osmunda regalis* | | 1.2 | 1.2 | | | 1.1 |
| *Oxalis acetosella* | 1.1 | 1.1 | 1.1 | 1.1 | 1, 2, 16 | 1.1 |
| *Paris quadrifolia* | 1.1 | 1.1 | 1.1 | 1.1 | 1 | 1.1 |
| *Petasites albus* | 1.1 | | | | 1, 3 | |
| *Phegopteris connectilis* | 1.1 | 1.1 | 1.1 | | 1, 16 | 1.1 |
| *Phyteuma nigrum* | | 1.1 | 1.1 | 1.1 | | 1.1 |

Table A 4 continued.

| Species name | Sweden nemoral zone | Germany North-eastern lowlands | Germany North-western lowlands | Belgium lowlands | UK, England | France Atlantic region |
|---|---|---|---|---|---|---|
| *Phyteuma spicatum* | | 1.1 | 1.1 | 1.2 | 1, 3 | 1.1 |
| *Platanthera chlorantha* | | 1.1 | 1.1 | | | |
| *Poa chaixii* | 1.1 | 1.1 | 1.1 | | 1 | 1.1 |
| *Poa nemoralis* | 1.1 | 1.1 | 1.1 | 1.1 | 1 | 1.1 |
| *Polygonatum multiflorum* | 1.1 | 1.1 | 1.1 | 1.1 | 1 | 1.1 |
| *Polygonatum odoratum* | | 1.2 | 1.2 | | 1, 16 | |
| *Polygonatum verticillatum* | 1.1 | 1.1 | 1.1 | | 1 | 1.1 |
| *Polystichum aculeatum* | 1.1 | 1.1 | | 1.1 | 1, 16 | 1.1 |
| *Polystichum braunii* | 1.1 | | | | | |
| *Polystichum setiferum* | | | | 1.1 | 1 | 1.1 |
| *Potentilla sterilis* | | 1.2 | 1.2 | 1.2 | 1 | 1.2 |
| *Primula elatior* | 1.1 | 1.1 | 1.1 | 1.1 | 1 | 1.1 |
| *Primula vulgaris* | | 1.1 | 1.1 | | 1, 16 | |
| *Pulmonaria angustifolia* | | 1.1 | 1.1 | | | 1.1 |
| *Pulmonaria obscura* | 1.1 | 1.1 | 1.1 | | 1 | |
| *Pulmonaria officinalis* | 1.1 | 1.1 | 1.1 | 1.1 | | 1.1 |
| *Pyrola chlorantha* | 1.1 | 1.1 | | | | |
| *Pyrola media* | 1.1 | 1.1 | | | | |
| *Pyrola minor* | 1.1 | 1.1 | 1.1 | 1.1 | 1, 16 | 1.1 |
| *Pyrola rotundifolia* | 1.1 | 1.1 | 1.1 | | | 1.1 |
| *Ranunculus ficaria* | | | | | 1, 3 | |
| *Ranunculus lanuginosus* | | 1.1 | 1.1 | | | |
| *Rubus saxatilis* | 1.1 | 1.1 | 1.1 | | | 1.2 |
| *Rumex sanguineus* | 1.1 | 1.1 | 1.1 | 1.1 | 1 | 1.1 |
| *Sambucus ebulus* | | 1.2 | 1.2 | | 3 | |
| *Sanicula europaea* | 1.1 | 1.1 | 1.1 | 1.1 | 1 | 1.1 |
| *Scilla bifolia* | | | nk | | | 1.1 |

Table A 4 continued.

| Species name | Sweden nemoral zone | Germany North-eastern lowlands | Germany North-western lowlands | Belgium lowlands | UK, England | France Atlantic region |
|---|---|---|---|---|---|---|
| *Scrophularia nodosa* | | | | 1.1 | 1, 3 | 1.1 |
| *Scrophularia vernalis* | | | | | 1, 3 | 1.2 |
| *Sedum cepaea* | | | | | | 1.2 |
| *Senecio ovatus* | | 1.2 | 1.2 | 1.2 | | 1.2 |
| *Senecio sylvaticus* | 1.2 | 1.2 | 1.2 | 1.2 | | 1.2 |
| *Silene dioica* | | | | | 1 | |
| *Solidago virgaurea* | | | | 1.1 | | |
| *Stachys alpina* | | | | | 1, 3 | 1.2 |
| *Stachys sylvatica* | 1.1 | 1.1 | 1.1 | 1.2 | 3 | 1.2 |
| *Stellaria holostea* | 1.1 | 1.1 | 1.1 | | 1 | |
| *Stellaria longifolia* | 1.1 | 1.1 | 1.1 | | | |
| *Stellaria neglecta* | 1.2 | 1.2 | 1.2 | | 1, 3 | 1.2 |
| *Stellaria nemorum* subsp. *montana* | 1.1 | 1.1 | 1.1 | 1.1 | | 1.1 |
| *Stellaria nemorum* subsp. *nemorum* | 1.1 | 1.1 | 1.1 | 1.1 | | 1.1 |
| *Teucrium scorodonia* | | 1.2 | 1.2 | | | |
| *Thalictrum aquilegiifolium* | 1.1 | | | | | |
| *Tolmiea menziesii* | | | | | 1 | |
| *Torilis japonica* | | 1.2 | 1.2 | 1.2 | 3 | 1.2 |
| *Trientalis europaea* | 1.1 | 1.1 | 1.1 | | | |
| *Trifolium rubens* | | 1.2 | 1.2 | | | 1.2 |
| *Veronica montana* | 1.1 | 1.1 | 1.1 | 1.1 | 1 | 1.1 |
| *Veronica officinalis* | | | | 1.2 | | |
| *Vicia cassubica* | | 1.2 | 1.2 | | | 1.2 |
| *Vicia dumetorum* | 1.2 | 1.2 | 1.2 | | | |
| *Vicia sylvatica* | 1.2 | 1.2 | 1.2 | | | |
| *Vinca minor* | | 1.1 | 1.1 | 1.1 | | 1.1 |
| *Viola mirabilis* | 1.1 | 1.1 | 1.1 | | | |

Table A 4 continued.

| Species name | Sweden nemoral zone | Germany North-eastern lowlands | Germany North-western lowlands | Belgium lowlands | UK, England | France Atlantic region |
|---|---|---|---|---|---|---|
| *Viola odorata* | | 1.2 | 1.2 | | | |
| *Viola reichenbachiana* | 1.1 | 1.1 | 1.1 | 1.1 | 1 | 1.1 |
| *Viola riviniana* | 1.1 | 1.1 | 1.1 | 1.1 | | 1.1 |

Table A 4 continued.

Heinken, T., Diekmann, M., Liira, J., Orczewska, A., Brunet, J., Chytrý, M., . . . Wulf, M. (2019). *European forest vascular plant species list. figshare. Dataset*. https://doi.org/10.6084/m9.figshare.8095217.v1

Hill, M. O., Preston, C. D., & Roy, D. B. (2004). *PLANTATT - Attributes of British and Irish Plants: Status, Size, Life History, Geography and Habitats*. Cambridgeshire: NERC Centre for Ecology and Hydrology.

Table A 5 List of vernal species and the respective IDs of the dataset they had to be removed from for the trait analyses. IDs refer to Table 5.1 in the manuscript.

| Vernal species | Dataset IDs species was removed from |
|---|---|
| *Adoxa moschatellina* | 8, 10, 11 |
| *Anemone nemorosa* | 8, 10, 11 |
| *Anemone ranunculoides* | 10, 11 |
| *Corydalis solida* | 10, 11 |
| *Lathraea clandestina* | 10, 11 |
| *Lathraea squamaria* | 8, 10, 11 |
| *Ranunculus ficaria* | 8 |
| *Scilla bifolia* | 10, 11 |
| *Galanthus nivalis* | 1(b), 2, 3, 4, 5 |

## List of publications

Diekmann, M., Härdtle, W. & **Stoltenberg, K.** (2014). Verbreitung und Ökologie des Scheiden-Gelbsterns (*Gagea spathacea*). Abhandlungen des Naturwissenschaftlichen Vereins zu Bremen, 47/2: 355-365.

**Litza, K.** & Diekmann, M. (2017). Resurveying hedgerows in Northern Germany: Plant community shifts over the past 50 years. *Biological Conservation.* 206, 226-235. https://doi.org/10.1016/j.biocon.2016.12.003

**Litza, K**. & Diekmann, M. (2019). Hedgerow age affects the species richness of herbaceous forest plants. *Journal of Vegetation Science.* 30, 553-563. https://doi.org/10.1111/jvs.12744

**Litza, K**. & Diekmann, M. (2020). The effect of hedgerow density on habitat quality distorts species-area relationships and the analysis of extinction debts in hedgerows. *Landscape Ecology.* 35, 1187-1198. https://doi.org/10.1007/s10980-020-01009-5

Vanneste, T., Govaert, S., De Kesel, W., Van Den Berge, S., Vangansbeke, P., Meeussen, C., Brunet, J., Cousins, S.A.O., Decocq, G., Diekmann, M., Graae, B. J., Hedwall, P.-O., Heinken, T., Helsen, K., Kapás, R., Lenoir, J., Liira, J., Lindmo, S., **Litza, K.**, Naaf, T., Orczewska, A., Plue, J., Wulf, M., Verheyen, K. & de Frenne, P. (2020). Plant diversity in hedgerows and road verges across Europe. *Journal of Applied Ecology.* 57, 1244-1257. https://doi.org/10.1111/1365-2664.13620

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Vanneste, T., Van Den Berge, S., Riské, E., Brunet, J., Decocq, G., Diekmann, M., Graae, B. J., Hedwall, P.-O., Lenoir, J., Liira, J., Lindmo, S., **Litza, K.**, Naaf, T., Orczewska, A., Wulf, M., Verheyen, K. & De Frenne, P. (2020). Hedging against biodiversity loss: forest herbs' performance in hedgerows across temperate Europe. *Journal of Vegetation Science.* 31, 817-829. https://doi.org/10.1111/jvs.12917

**Litza, K**., Alignier, A., Closset-Kopp, D., Ernoult, A., Mony, C., Osthaus, M., Staley, J., Van Den Berge, S., Vanneste, T. & Diekmann, M. (2022). Hedgerows as a habitat for forest plant species in the agricultural landscape of Europe. *Agriculture, Ecosystems & Environment.* 326, 107809. https://doi.org/https://doi.org/10.1016/j.agee.2021.107809