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

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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

1 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 (Sutter et al., 2018; Van Vooren et al., 2017) 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; Van Den Berge et al., 2019; Wehling & Diekmann, 2009a) and dispersal corridors for several forest specialists (Closset-Kopp et al., 2016; Corbit et al., 1999; Lenoir et al., 2021; Wehling & Diekmann, 2009b). 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 (Smart et al., 2001; Tsiouris & Marshall, 1998).

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 (Closset-Kopp et al., 2016; Critchley et al., 2013; Deckers, Hermy, et al., 2004). Another fundamental factor influencing the number of forest specialists is the structure of the hedgerows, most notably the width and height (e.g. Closset-Kopp et al., 2016; Deckers, Hermy, et al., 2004; Litza & Diekmann, 2019, 2020), as wider hedgerows offer more forest-like conditions due to a more stable microclimate (Vanneste, Govaert, Spicher, et al., 2020). 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, Van Den Berge, et al., 2020). 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, Verheyen, et al., 2004). 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. Litza & Diekmann, 2019; Van Den Berge et al., 2019; Van Vooren et al., 2018), including research on a European scale (e.g. Vanneste, Govaert, De Kesel, et al., 2020). 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?

2 Methods

2.1 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 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 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 1000 m^2 were included to reduce inflated variance based on a large range of plot sizes.

2.1.1 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 1; Figure 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.1 in the appendix.

To correct the species number per plot for the wide range of plot sizes (Table 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 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 km^2 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).

2.1.2 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 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 1000 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 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.

2.1.3 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.

2.2 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/).

2.2.1 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 1000 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 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*).

2.2.2 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.2 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.

3 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 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 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 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*).

3.1 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 2, Table 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 2, Table 5).

Figure 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.

3.2 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 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 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.

4 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, Van Den Berge, et al., 2020). 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, Van Den Berge, et al., 2020).

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).

4.1 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, Govaert, Spicher, et al., 2020), 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, Govaert, Spicher, et al., 2020). 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).

4.2 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 (Closset-Kopp et al., 2016; de Blois et al., 2002; Deckers, Hermy, et al., 2004; Lenoir et al., 2021; Wehling & Diekmann, 2008). 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 (Litza & Diekmann, 2017; Staley et al., 2013). 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, Govaert, De Kesel, et al., 2020). 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.

4.3 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 (Carey et al., 2008; Garbutt & Sparks, 2002; 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, Hermy, et al., 2004) 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 (Alignier, 2018; Deckers, Hermy, et al., 2004; Graham et al., 2018). Numerous studies have shown that hedgerow width is a key factor in determining habitat quality for forest plants (e.g. Closset-Kopp et al., 2016; Deckers, Hermy, et al., 2004; 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, Govaert, Spicher, et al., 2020) 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.

4.4 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 (Herzon & Helenius, 2008; Le Cœur et al., 2002). 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, Van Den Berge, et al., 2020). 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.

4.5 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.

5 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.

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7 Tables

Table 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 (>1000 m^2); *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 m^2 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 (m^2)
1	Vanneste, Govaert, De Kesel, et al. (2020)	(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

ID	Dataset	Region	Survey year(s)	Survey months	No. of plots	Plot length range (m)	Plot size range (m²)
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

Table 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 3) and then summed up. The forest cover describes the cover within a radius of 1000 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 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

Table 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*	0.30
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*	0.60	*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*	0.30	*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*	0.20	*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

Rank	Germany – North-eastern lowlands		Germany – North-western lowlands		Belgium – lowlands		France – Atlantic region (Picardy)		UK – England		France – Atlantic region (Brittany)	
8	*Stachys sylvatica*	0.24	*Stachys sylvatica*	0.17	*Scrophularia nodosa*	0.02	*Adoxa moschatellina*	0.15	*Mercurialis perennis*	0.12	*Scrophularia nodosa*	0.10
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*	0.10	*Rumex sanguineus*	0.09	*Polygonatum multiflorum*	0.07
Woody species												
1	*Sambucus nigra*	0.61	*Carpinus betulus*	0.66	*Quercus robur*	0.66	*Rubus fruticosus* agg.	0.81	*Prunus spinosa*	0.47	*Rubus fruticosus* agg.	0.76
2	*Rubus fruticosus* agg.	0.60	*Rubus fruticosus* agg.	0.61	*Prunus serotina*	0.47	*Crataegus monogyna*	0.76	*Rubus fruticosus* agg.	0.38	*Quercus robur*	0.69
3	*Corylus avellana*	0.60	*Quercus robur*	0.60	*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	*Crategus monogyna*	0.23

Rank	Germany – North-eastern lowlands		Germany – North-western lowlands		Belgium – lowlands		France – Atlantic region (Picardy)		UK – England		France – Atlantic region (Brittany)	
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*	0.20
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	*Euonoymus europaea*	0.30	*Rubus caesius*	0.32	*Salix caprea*	0.16	*Rosa arvensis*	0.47	*Fraxinus excelsior*	0.02	*Ilex aquifolium*	0.17

Table 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, $R^2_{\text{conditional}}$ = 0.64), while the second included data of extreme climatic conditions (n = 1008, groups = 11, R^2_{marginal} = 0.09, $R^2_{\text{conditional}}$ = 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 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

8 Figures

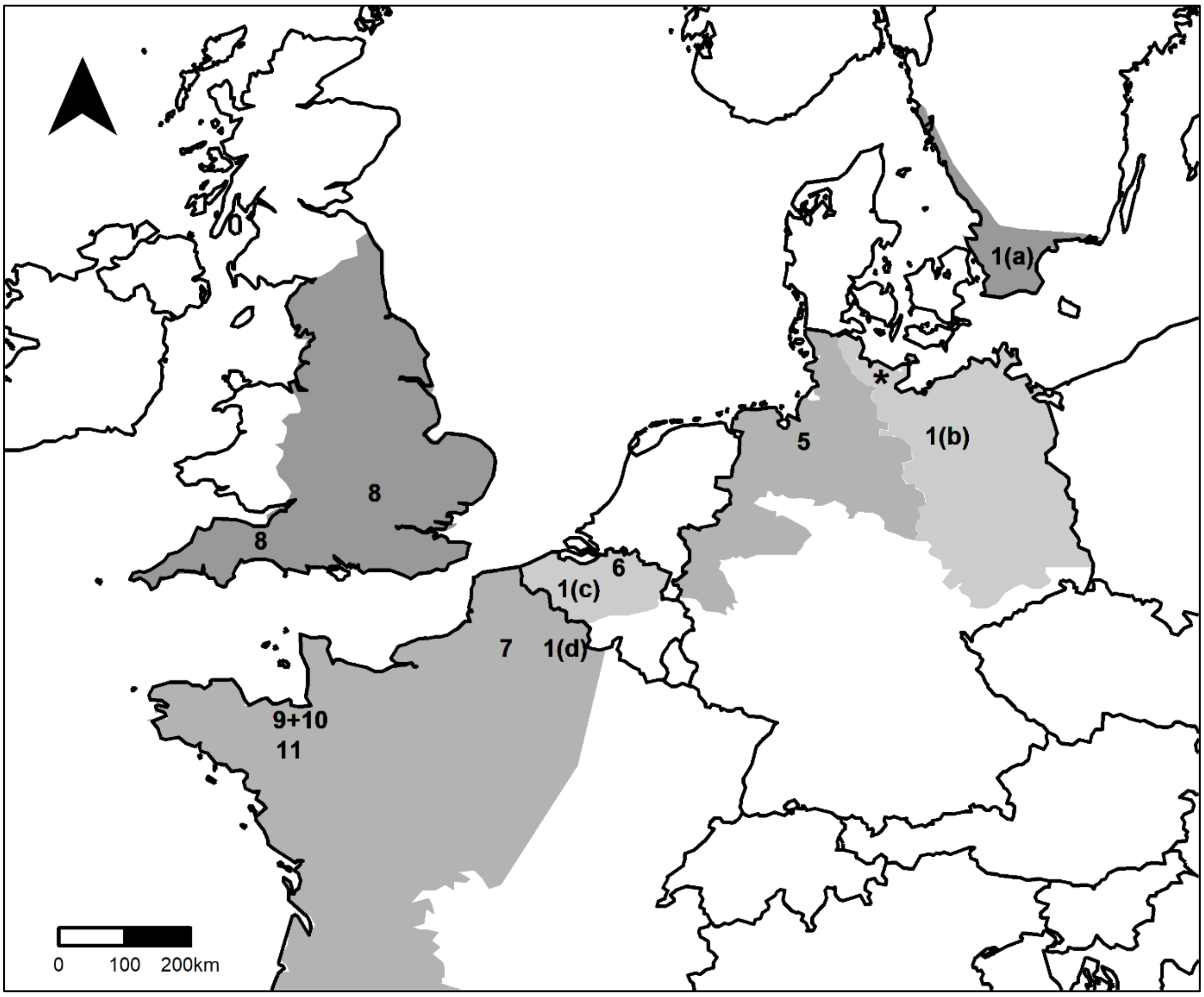

Figure 1 Map of the study area displaying the geographic locations of the datasets (numbered) as well as their respective geographic regions (shaded) from North-East to South-West: Sweden (nemoral zone), Germany (North-Eastern and North-Western lowlands), Belgium (lowlands), United Kingdom (England) 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 1. The asterisk (*) in Northern Germany represents the datasets 1(b) (in parts), 2, 3 and 4.

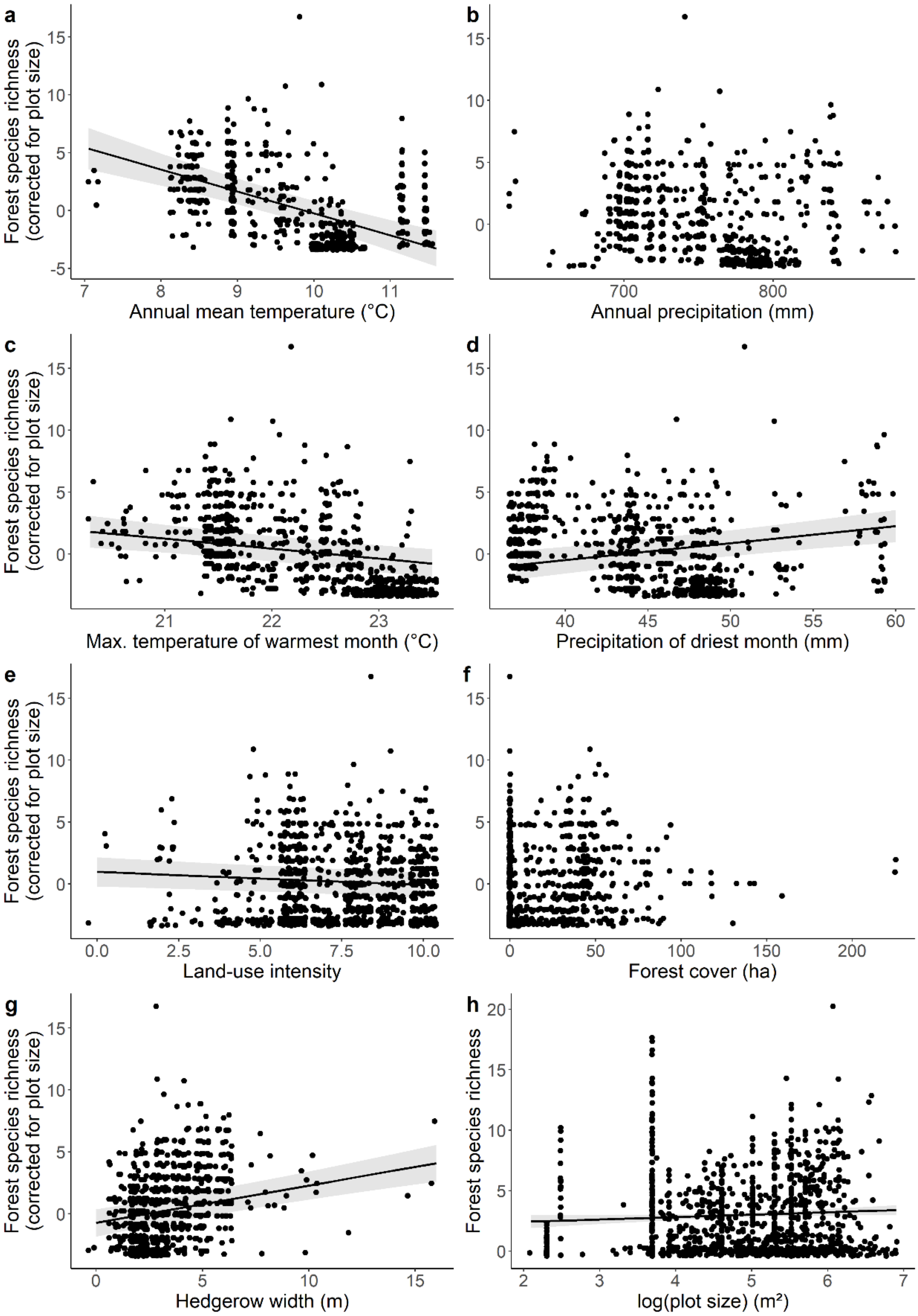

Figure 2 Forest species richness (corrected for plot size) plotted against a) annual mean temperature (°C), b) annual precipitation (mm) c) maximum temperature of the warmest month (°C), d) precipitation of the driest month (mm) e) adjacent land-use intensity, f) forest cover in the surrounding 1000 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.

9 Appendix

Table A.1 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 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

Species name	**Sweden nemoral zone**	**Germany North-eastern lowlands**	**Germany North-western lowlands**	**Belgium lowlands**	**UK, England**	**France Atlantic region**
Botrychium matricariifolium		1.2				
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
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			

Species name	**Sweden nemoral zone**	**Germany North-eastern lowlands**	**Germany North-western lowlands**	**Belgium lowlands**	**UK, England**	**France Atlantic region**
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			
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

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			
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

Species name	**Sweden nemoral zone**	**Germany North-eastern lowlands**	**Germany North-western lowlands**	**Belgium lowlands**	**UK, England**	**France Atlantic region**
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
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
Scrophularia nodosa				1.1	1, 3	1.1

Species name	**Sweden nemoral zone**	**Germany North-eastern lowlands**	**Germany North-western lowlands**	**Belgium lowlands**	**UK, England**	**France Atlantic region**
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			
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

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Table A.2 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 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