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Taxonomic, phylogenetic and functional diversity of understorey plants respond differently to environmental conditions in European forest edges

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Abstract

1. Forest biodiversity worldwide is affected by climate change, habitat loss and fragmentation, and today 20 % of the forest area is located within 100 m of a forest edge. Still, forest edges harbour a substantial amount of terrestrial biodiversity, especially in the understorey. The functional and phylogenetic diversity of forest edges have never been studied simultaneously at a continental scale, in spite of their importance for the forests' functioning and for communities' resilience to future change.

2. We assessed nine metrics of taxonomic, phylogenetic and functional diversity of understorey plant communities in 225 plots spread along edge-to-interior gradients in deciduous forests across Europe. We then derived the relative effects and importance of edaphic, stand and landscape conditions on the diversity metrics.

3. Here, we show that taxonomic, phylogenetic and functional diversity metrics respond differently to environmental conditions. We report an increase in functional diversity in plots with stronger microclimatic buffering, in spite of their lower taxonomic species richness. Additionally, we found increased taxonomic species richness at the forest edge, but in forests with intermediate and high openness, these communities had decreased phylogenetic diversity.

4. Functional and phylogenetic diversity revealed complementary and important insights in community assembly mechanisms. Several environmental filters were identified as potential drivers of the patterns, such as a colder macroclimate and less buffered microclimate for functional diversity. For phylogenetic diversity, edaphic conditions were more important. Interestingly, plots with lower soil pH had decreased taxonomic species richness, but led to increased phylogenetic diversity, challenging the phylogenetic niche conservatism concept.

5. *Synthesis.* Taxonomic, phylogenetic and functional diversity of understorey communities in forest edges respond differently to environmental conditions, providing insight in different community assembly mechanisms and their interactions. Therefore, it is important to look beyond species richness with phylogenetic and functional diversity approaches when focusing on forest understorey biodiversity.

Keywords: Biodiversity, forest edge, forest understorey, functional diversity, microclimate, phylogenetic diversity, species richness

Introduction

Forest biodiversity worldwide is affected by climate change, land-use change and habitat loss (Foley et al. 2005, Lenoir et al. 2008, Pereira et al. 2012, Vellend et al. 2013, Zellweger et al. 2020). Future climate change is predicted to cause further biodiversity losses (Thomas et al. 2004, Malcolm et al. 2006, Thuiller et al. 2011, Trisos et al. 2020) as biodiversity redistribution is hampered by habitat fragmentation in terrestrial systems (Lenoir et al. 2020). In forests, the largest part of plant species richness, up to more than 80%, is located in the understorey (Gilliam 2007). Furthermore, understorey communities play an important role in forest ecosystem dynamics by mediating nutrient cycling, tree regeneration and other crucial ecosystem functions (Gilliam 2007, Landuyt et al. 2019).

Resurvey studies showed no general decline in species richness of understorey communities over the past decades due to balanced local colonisations and extinctions (Keith et al. 2009, Vellend et al. 2013). However, if a limited set of taxa replaces many different species across the forest biome, homogenization can lead to losses of total biodiversity on the scale of the forest biome, even though locally no decline in species richness is registered (Staude et al. 2020). During the past century, herbaceous understorey plant communities homogenized by an increasing presence of nutrient-demanding and shade-tolerant species (Keith et al. 2009, Naaf and Wulf 2010, Prach and Kopecky 2018, Van den Berge et al. 2019, Staude et al. 2020). Simultaneously, climate change causes an increasing dominance of warm-adapted species in understorey communities, a process referred to as thermophilization (Bertrand et al. 2011, De Frenne et al. 2013, Zellweger et al. 2020). Such changes in community composition might affect the functional or phylogenetic diversity of understorey communities, as well as the role of the understorey in forest ecosystem dynamics (Wardle et al. 2011). Therefore, it is important to expand our understanding from species richness to functional and phylogenetic diversity and to investigate which environmental factors are driving different diversity patterns in understorey plant communities.

Human pressure on forests leads to forest fragmentation, and consequently to increasing forest edge to interior ratios with important consequences for forest biodiversity (Haddad et al. 2015) and its redistribution as climate warms (Lenoir et al. 2020). Currently, 70% of forested area is located closer than one km to a forest edge and 20% is even closer than 100 m (Haddad et al. 2015). Therefore, it is important to understand the ecological processes occurring in forest edges, in addition to those of forest interiors. Many environmental factors change drastically from the forest's edge to its interior (Matlack 1993, Gehlhausen et al. 2000). Forest edges receive more atmospheric acidifying and eutrophying deposition (Devlaeminck et al. 2005, Wuyts et al. 2008) and have higher nitrogen and carbon stocks, compared to the interior (Remy et al. 2016, Meeussen et al. 2021). Therefore, the increasing proportion of forest edges might accelerate the current homogenization of understorey plant communities, which is characterised by an increasing presence of nutrient-demanding species (Verheyen et al. 2012, Van den Berge et al. 2019,

Staude et al. 2020). Furthermore, forest edges are characterised by increased wind speeds and incoming solar radiation, resulting in more variable microclimates and drier soil conditions than forest interiors (Matlack 1993, Chen et al. 1999, Gehlhausen et al. 2000). Such conditions typically harbour communities with a high proportion of generalist species, as forest generalists avoid the shady, humid and strongly buffered microclimate of forest interiors (Normann et al. 2016, Govaert et al. 2020). Such edge conditions and a dominance of forest generalists might locally reduce the functional or phylogenetic diversity of these forest edge communities. However, it is not yet clear which environmental factors affect functional and phylogenetic diversity of understories in forest edges.

The macroclimate and surrounding landscape matrix have an additional effect on understorey diversity next to edaphic and stand conditions. Macroclimate is a well-known driver of biodiversity (Francis and Currie 2003, Kreft and Jetz 2007). Mean annual temperature and potential evapotranspiration, for example, are important predictors of plant species richness (Francis and Currie 2003, Kreft and Jetz 2007, Qian and Ricklefs 2007). In Europe, many forests are situated in fragmented landscapes and many forest specialists have low colonization capacities (Verheyen et al. 2003, Hermy and Verheyen 2007); the amount of habitat and fragmentation can thus have a considerable effect on understorey diversity (Valdes et al. 2015, Govaert et al. 2020). The habitat amount hypothesis states that not necessarily patch isolation or size, but the amount of habitat present in the 'local landscape' affects species density (Fahrig 2013, Watling et al. 2020). Lower species richness of forest generalists and especially specialists were found in forest patches surrounded by less forested area (within a radius of 100-500 m) (Valdes et al. 2015, Takkis et al. 2018, Govaert et al. 2020).

Most studies on understorey biodiversity rely on taxonomic species richness due to its simplicity and convenience. However, during the last two decades, the focus has changed from number of species towards their ecological diversity, i.e. the degree to which species differ in terms of their function, niche or evolutionary history (Cadotte et al. 2013). The ecological diversity can be assessed with a functional approach, based on functional traits, and with a phylogenetic approach, based on species' genealogies. Both approaches can add complementary information for conservation (Carvalho et al. 2017, Cadotte and Tucker 2018). The functional diversity metrics can provide important information regarding ecosystem functioning (Cadotte et al. 2011, Flynn et al. 2011), whereas phylogenetic diversity relates to genetic variability, which is believed to improve the communities' adaptability to future change (Cavender-Bares et al. 2009).

Functional and phylogenetic metrics can provide insight in the community assembly of forest understorey communities (Gerhold et al. 2013, Thorn et al. 2016, Vanneste et al. 2019). At the finest spatial resolution of forest plant communities (usually 400 m^2), community assembly is often attributed to the *limiting similarity* and *competitive exclusion* mechanisms (Webb et al. 2002, Cavender-Bares et al. 2009). These

mechanisms suggest that closely related (e.g. sister species) or functionally similar species compete more intensely than phylogenetically or functionally distant species. Consequently, the chance of co-existence is higher for distant-related or functionally divergent species (Webb et al. 2002). On a larger scale involving landscape or regional extents and coarser spatial resolutions (between 400 m^2 and 1 km^2), the *environmental filtering* mechanism limits the diversity of communities, filtering for species adapted to the specific environment through similar ecological strategies and/or phylogenetic histories (Cavender-Bares et al. 2009, Laliberte et al. 2014).

When species retain their niche and related ecological traits over time, with niche defined as the set of biotic and abiotic conditions where a species can persist (Holt 2009), this can be described as niche conservatism (Wiens et al. 2010). Phylogenetic niche conservatism then expands this concept to related species (Wiens et al. 2010). The degree of phylogenetic conservatism of functional traits and the shape of the phylogenetic tree thus determine the correspondence of phylogenetic and functional diversity approaches (Mazel et al. 2017). They might result in contrasting plant diversity patterns and therefore, contribute different important information to provide a more general view on the communities' biodiversity (Cadotte et al. 2013, Thorn et al. 2020). While numerous studies have unravelled how taxonomic and compositional diversity are affected in deciduous forests by environmental drivers (Van Calster et al. 2008, Price and Morgan 2010, Depauw et al. 2019, Macek et al. 2019), only few studies have simultaneously assessed taxonomic, functional and phylogenetic diversity of the understorey (e.g. Wasof et al. (2018) and Closset-Kopp et al. (2019)) and never before at the continental scale.

Here we assessed different metrics of taxonomic, phylogenetic and functional diversity of understorey herb communities in 225 plots spread along edge-to-interior gradients in deciduous forests across Europe. We capitalized on large-scale macroclimatic latitudinal and altitudinal gradients in combination with fine-grain management and edge-to-core gradients in microclimate. We specifically assessed the following hypotheses for the understorey biodiversity in European forest edges:

H1: We expected different responses to environmental predictors, in terms of magnitude and direction, between the taxonomic, phylogenetic and functional diversity metrics that we derived in our study.

H2: We expected taxonomic diversity to increase with higher light availability and less buffered microclimates, in contrast to functional and phylogenetic diversity, which we expected to decrease due to the increased presence and dominance of generalist species: i.e. local functional and phylogenetic homogenization.

H3: We expected a higher importance of edaphic and stand conditions than landscape conditions for phylogenetic and functional diversity, as edaphic and stand conditions strongly influence community assembly processes such as environmental filtering and species' competitive ability.

Methods

Study area and experimental set-up

We selected European broadleaved forests with a dominance of oak species (mainly *Quercus robur*, *Q. petraea* and *Q. cerris*) locally complemented with *Fagus sylvatica*, *Betula pubescens*, *Populus tremula*, *Ulmus glabra, Alnus incana* and *Carpinus betulus*, because these are important for conservation as biodiversity 'hotspots'. All forests had a minimal area of 4 ha and were ancient forests; they have been continuously forested and were not converted to other land use since at least the oldest available maps, which is typically at least 150-300 years. We specifically did not include post-agricultural forests, to rule out any possible effect of past land-use history. To increase comparability, all forests had loamy soils with an intermediate moisture content.

We selected forests in nine regions spanning a 2000-km long latitudinal gradient across Europe (from south to north): Italy, Switzerland, France, Belgium, Poland, Germany, southern Sweden, central Sweden and Norway. This latitudinal gradient includes a change in mean annual temperature (MAT) of > 10°C and a variation in annual precipitation from approximately 550 to 1250 mm (data retrieved from CHELSA database for 1979 – 2013 (resolution of ~ 1 km^2) (Karger et al. 2017)). The latitudinal range of the broadleaved temperate forest biome, as given by Olson et al. (2001), was covered completely. In three of these regions (Italy, Belgium and Norway), an additional elevational gradient was established; forests were selected at low, intermediate and high elevations (ranging from 21 to 908 m above sea level, corresponding to a smaller macroclimate gradient of 1.5 to 4 °C MAT). In the other six regions, only lowland forests were selected with elevations between 7.5 and 451 m above sea level (Fig. SI.D1).

In each of these regions, and at each elevation, forest stands with three different management types were selected. The first type were '*dense forests*', which were not thinned for at least 10 to 30 years. Additional criteria for this forest type were a well-developed shrub layer and a complex vertical structure. These forests generally had low canopy openness (5.8 ± 0.6%, mean of three densiometer measurements (Baudry et al. 2014)) and high basal area (mean and standard error of 28.8 ± 1.5 m^2/ha). The second forest type, referred to as *'intermediate forests'*, were forests that were regularly thinned with the most recent thinning ideally 5 to 10 years ago. For this forest type, we looked for sparser shrub layers and a less complex vertical structure (canopy openness of 6.5 ± 0.6% and mean basal area of 31.4 ± 1.9 m^2/ha). The third forest type were '*open forests*', which were regularly thinned and most recently within 4 years before sampling. Additionally, the shrub layer and subdominant tree layer of these forests were ideally sparse or lacking and the vertical structure comprised only the dominant tree layer. These forests were generally characterised by high canopy openness values (14.8 ± 2.1%) and low basal area values (21.6 ± 1.3 m^2/ha).

In each forest stand, a transect was established perpendicular to the forest edge. Forest edge was defined as the outer edge of the forest stand that borders a matrix of open land. All forest edges were south-facing to

ensure comparability since edge orientation can affect forest microclimate and herbaceous vegetation considerably (Matlack 1993, Honnay et al. 2002, Orczewska and Glista 2005). Five plots of 3 by 3 m were installed, with their plot centre on an exponentially increasing distance from the forest edge, respectively 1.5, 4.5, 12.5, 35.5 and 99.5 m. All plots were at least 100 m away from any forest edge other than the studied forest edge, to avoid interference with effects from other forest edges. Thus, in total 45 forest edge-interior transects were sampled ((6 lowland regions + 9 from 3 regions with elevation gradient) x 3 forest types), totalling 225 plots (45 forest edges x 5 plots per edge-interior transect). More detailed descriptions of the selection criteria and structural characteristics of the different management types can be found in Govaert et al. (2020) and Meeussen et al. (2020).

Trait and phylogeny data

Vegetation surveys were performed during peak of the vegetation season (May – July 2018) according to the local phenology. In each 3 x 3 m plot, all vascular plant species were identified and their percentage ground cover was estimated (n = 353 species in total). The herb layer comprised all vascular plants smaller than 1m, including woody, non-woody plants and lianas. Vegetation surveys are also described in detail by Govaert et al. (2020). Seedlings, shrub species and lianas in the herb layer were excluded from this analysis (n = 62 species), since they do not remain in the herb layer throughout their lifecycle and their trait values from most online databases do not represent the juveniles encountered in the herb layer (Table SI.D1).

Three key functional traits were chosen based on the leaf-height-seed plant ecology strategy scheme: seed mass, specific leaf area (SLA) and plant height. SLA informs on the plant's acquisition and conservation of resources as it represents a trade-off between photosynthetic rate and leaf lifespan (Wright et al. 2004). Plant height strongly determines the plant's competitiveness for light and the dispersal of its seeds, whereas seed mass reflects the trade-off between seed output and seedling survival (Westoby 1998, Westoby and Wright 2006, Diaz et al. 2016). We assessed the variation of traits in our study species with a principal component analysis (PCA). A parallel analysis for determining significant principal components (method developed by Franklin et al. (1995)) showed that two significant principal components are necessary to represent the variation in the trait data (Fig. SI.D2a). The first two axes comprise 40.9 and 34.4% of the trait variation and the biplot shows the separate factor loading of functional traits on these axes (Fig. SI.D2b). The plot shows a broad spread of species, representing different plant strategies in three major trait domains informing on species' resource use, competition and reproduction (Westoby 1998, Westoby et al. 2002, Pierce et al. 2014, Diaz et al. 2016) (Fig. SI.D2b). Species-specific trait values were derived from several databases including the LEDA trait database (Kleyer et al. 2008), BiolFlor (Kuhn et al. 2004) and the Kew Seed Information Database (KEW 2017) (Table SI.D4). For 60 species, no or insufficient trait data was present, these species were excluded from the analysis (Table SI.D4). However, trait values were

available for all species that occurred in more than 5% of the plots with a mean cover value of more than 2% (Table SI.D2**).**

We chose to extract a phylogenetic tree from the dated molecular phylogeny for land plants constructed by Zanne et al. (2014), because this tree included plants from the entire study region, including Mediterranean species. The extraction was done with the '*brranching*' package in R (Chamberlain 2019). Two species were omitted from further analysis due to their absence in the phylogenetic tree of Zanne et al. (2014) (*Phegopteris connectilis* and *Polypodium interjectum*). Both species occurred in less than 3% of the plots. The resulting final vegetation matrix of the herb layer contained 229 species (Fig. 1**)**, which represented on average 93.7% of the total herbaceous cover in the plots (Table SI.D3). The final tree counted 229 tips, one for each species in the final vegetation matrix, and had 221 internal nodes (Fig. 1).

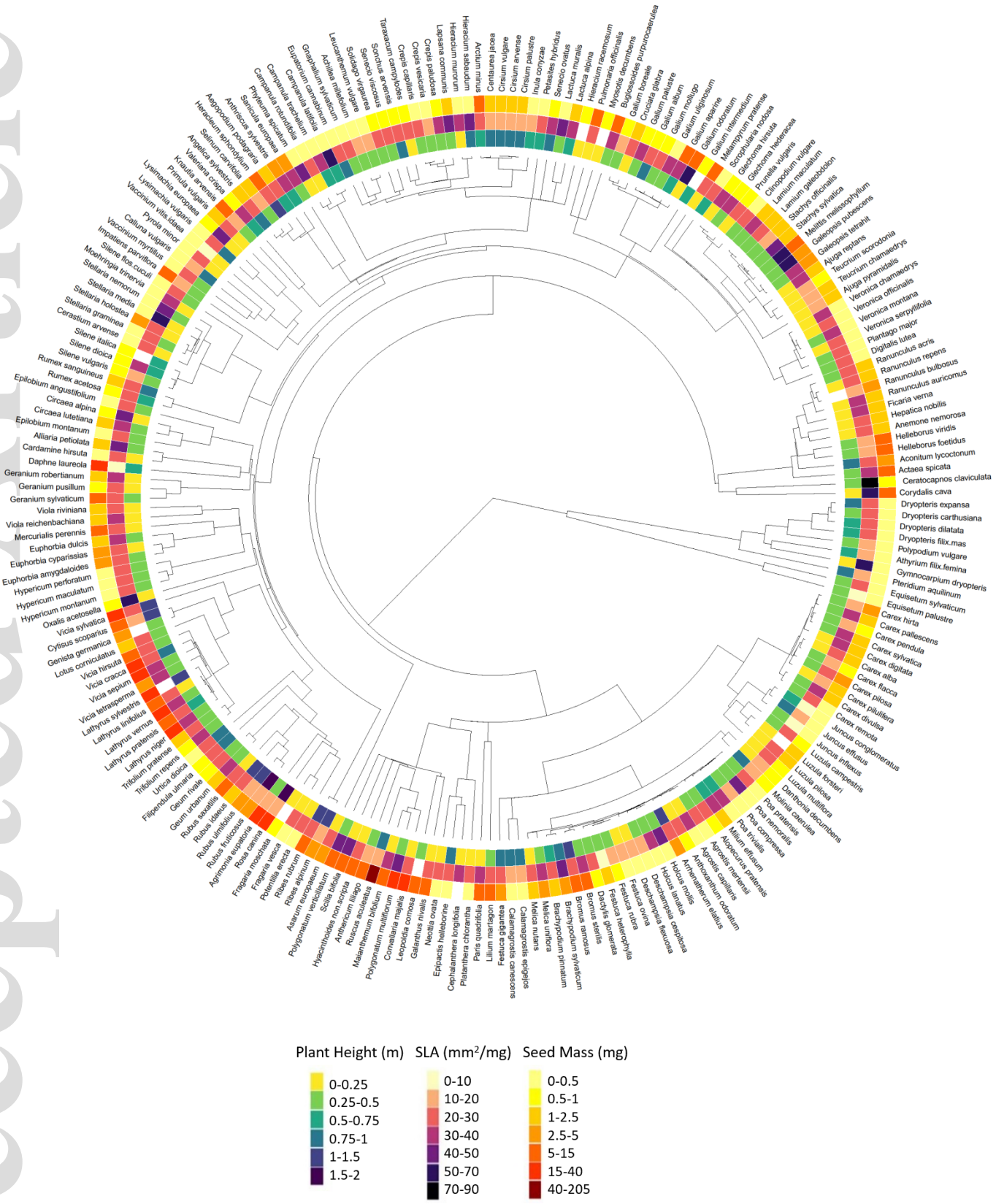


Figure 1. Phylogenetic tree of species included in this study. This tree was standardised taxonomically with The Plant List (2013) and visualized with *ggtree* and *gheatmap* in R (Yu et al. 2017). Functional traits

are represented with a colour scale around the tree, plant height (m) on the inner circle, SLA (mm^2 mg^{-1}) on the middle circle and seed mass (mg) on the outer circle.

Diversity metrics

Traditionally, the diversity concept includes two components: species richness and evenness. Species richness gives the number of species, and species evenness the equitability of their relative abundances. Generally, species diversity is defined as a metric including both species richness and species evenness (Smith and Wilson 1996). However, based on phylogeny or function, diversity can also be regarded as a measure of variation in the community, irrespective of species richness. Therefore, we always calculated three metrics, i.e., richness, evenness and diversity or variability metrics, and this based on taxonomy, phylogeny or function to come to nine response variables (Table 1).

Regarding taxonomy, we calculated **species richness (Tax.rich)** (number of species per plot) and the **Evar evenness index (Tax.even),** proposed by Smith and Wilson (1996). This evenness index ranges from zero to one, is independent from species richness and was calculated with the '*codyn'* R package (Hallett et al. 2016). As diversity metric we calculated the **Shannon diversity index (Tax.div)** (Shannon 1948).

Phylogenetic diversity metrics were calculated, using the '*pez*' R package (Pearse et al. 2015). First, the **phylogenetic species variability (Phy.div)** of the community indicates the variation in evolutionary history of the species. The metric ranges between zero and one and is independent of the community's species richness. A value of one characterizes a community in which none of the species has a lineage in common, and a value close to zero indicates a community of species, which share large parts of their lineages in the phylogenetic tree (Helmus et al. 2007). Secondly, **phylogenetic species richness (Phy.rich)** was calculated by multiplying Phy.div with species richness values (Helmus et al. 2007). Thirdly, **phylogenetic species evenness (Phy.even)** was calculated by adapting Phy.div to take the abundances of species into account, as such it combines evenness in abundance and phylogeny (Helmus et al. 2007).

Finally, functional metrics were calculated using the '*FD*' package in R (Laliberté and Legendre 2010). Traits were standardized to mean zero and unit variance and a species-species Euclidian distance matrix was computed. The 'Cailliez' correction method was used to correct for negative eigenvalues (Cailliez 1983) and a Principal Coordinates Analysis (PCA) was performed with the resulting species-species distance matrix. The axes obtained from the PCA were used to compute **functional richness (Fun.rich)** and **functional evenness (Fun.even)** indices (Villéger et al. 2008). **Functional richness** reports on the trait-space volume, whereas **functional evenness** assesses simultaneously the evenness of species distribution in trait-space and evenness of their abundances. Finally, the **Rao's quadratic entropy (Fun.div)** was calculated based on relative species abundances and pairwise functional differences between species (Botta-Dukat 2005, Laliberté and Legendre 2010). This distance-based metric is frequently used to

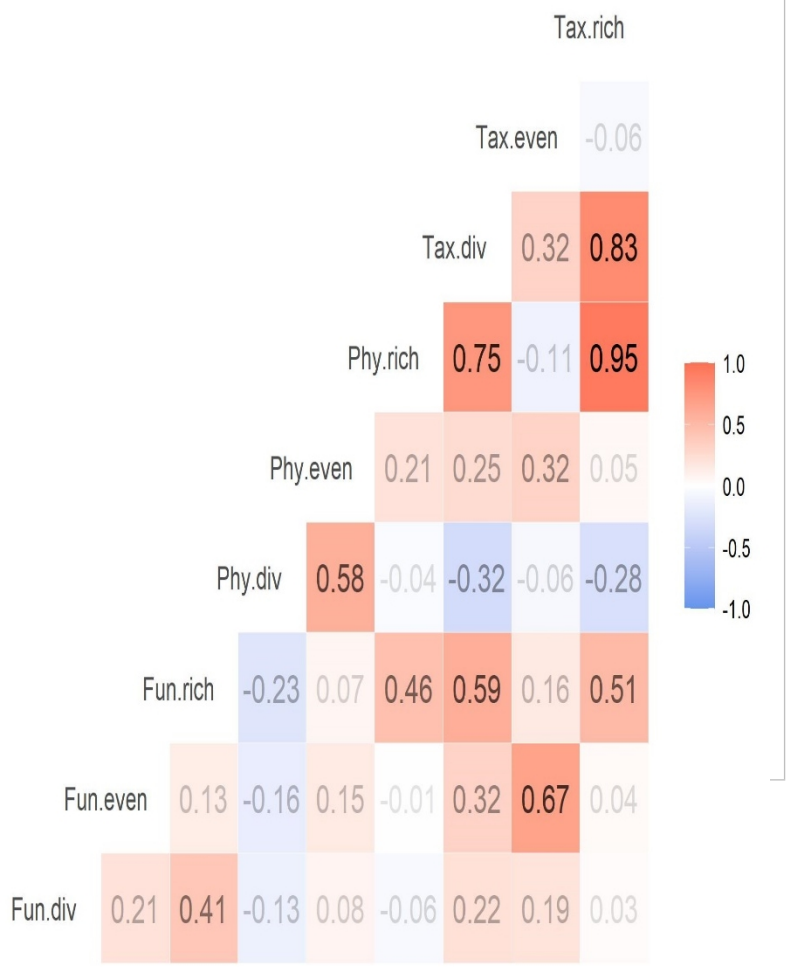
quantify functional diversity and is independent of species richness (Botta-Dukat 2005, Laliberté and Legendre 2010).

Mean and standard deviations of the nine diversity metrics are given for the nine study regions in Table SI.D6.

Table 1. **Overview of the diversity metrics used to assess the diversity of understorey plants in 225 plots in the forest edges of European deciduous forests.** A richness, evenness and diversity or variability metric (.rich, .even, .div respectively) were calculated based on taxonomy, phylogeny or function (Tax., Phy., Fun. respectively). In the formulas, p_i, p_j = relative abundance of species i, j, S = total number of species in community and d_{ij} = difference between species i, j. The value of the Pearson correlation is given as a number and indicated by the colour in the Pearson correlation

Diversity metric		Meaning	Formula (if appropriate)
Taxonomic diversity metrics (Shannon 1948, Smith and Wilson 1996)			
Tax.rich	Species richness	Number of species present	$Tax.rich = count\ (species)$
Tax.even	Species evenness	Equality of species' abundances, calculated based on the variance of species' abundances	$Tax.even = 1 - \frac{2}{\pi} arctan\left(\sum_{i}^{S}\left(\ln(p_i) - \sum_{j}^{S}\ln(p_j)/S\right)^2/S\right)$
Tax.div	Shannon diversity index	Diversity in terms of richness and evenness	$Tax.div = -\sum_{i}^{S} p_i * \ln(p_i)$
Phylogenetic diversity metrics (Helmus et al. 2007)			
Phy.rich	Phylogenetic species richness	Species richness taking into account phylogenetic relatedness	$Phy.rich = Phy.div * Tax.rich$
Phy.even	Phylogenetic species evenness	Combined evenness of species abundances and evenness of phylogeny	
Phy.div	Phylogenetic	Measure for phylogenetic	

Pearson correlation matrix of diversity metrics matrix



	species variability	relatedness		
Functional diversity metrics (Botta-Dukat 2005, Villéger et al. 2008)				
Fun.rich	Functional richness	Volume of trait-space		
Fun.even	Functional evenness	Evenness of species distribution within trait-space		
Fun.div	Rao's quadratic entropy	The mean pairwise functional difference between species in the community, weighted by their abundance.	$Fun.div = \sum_{i}^{S-1} \sum_{j}^{S} d_{ij} p_i p_j$	

Environmental predictor variables

Edaphic conditions

In each plot of 3 × 3 m, the forest floor or organic soil horizon (i.e. litter, humus and fragmentation layer) was sampled in a 20 × 20 cm subplot from its surface to the mineral soil layer underneath, after removal of the herb layer. These samples were dried to constant weight at 65 °C for 48 h and then, the organic soil layer mass was determined (mass OS). This variable was used as indicator for litter quality, thickness and nutrient availability since low-degradable litter tends to accumulate on the forest floor and results in slower nutrient turnover and lower nutrient availability (Scott and Binkley 1997). Additionally, dense litter layers may pose a physical barrier for germination of forest species or reduce germination through phytotoxic components (Facelli and Pickett 1991). Texture analysis (% sand, silt and clay) was performed by sieving and sedimentation of mineral soil samples of 10-20 cm depth, whereas soil pH was determined for mineral soil samples of 0-10 cm depth. For these analyses, five subsamples were taken per plot and pooled (detailed description in Suppl. Information A).

Stand conditions

In each plot, the microclimate temperature was recorded hourly at 1 m height using a temperature data logger (Lascar EL-USB-1, range of -30 to +80 °C, resolution of 0.5 °C) covered by a radiation shield (Fig. SI.D3). For each of the nine regions and for each of the three elevation levels, the temperature was also measured in an identical set-up in an open field close to the forest stands (‘reference’ sensor). The temperature measurements of these ‘reference’ sensors were used to calculate temperature offset values (offset = sub-canopy temperature – free air temperature = plot sensor – ‘reference’ sensor). Positive and negative offset values represent warmer and cooler forest microclimates, respectively, compared to the macroclimate temperature. Typically, the forest microclimate is buffered from temperature extremes and this buffering is largest during the summer months, when understorey plants are most likely to experience extreme heat and drought stress (Zellweger et al. 2019). Also cold temperatures and frost are limiting factors regarding plant survival and distributions (Sakai and Larcher 1987, Woodward 1990, Svenning et al. 2008, Bucher et al. 2019). For these reasons, we focused on the effect of cooling of maximum temperatures in summer and warming of minimum temperatures in winter. During winter (from October 2018 to March 2019), the offset was calculated for the mean daily 5th percentile temperature (‘winter offset’) and during summer (from April to September 2019) for the mean daily 95th percentile temperatures (‘summer offset’).

The three forest management types are expected to impact microclimate and light availability at the forest floor, since they differ in density and complexity. We quantified forest structural differences using Plant Area Index (PAI), which is half of the surface area of all aboveground vegetation matter (including stems, branches and leaves) per unit surface area. PAI was calculated as the integral of vertically resolved plant

area per volume density ($m^2\ m^{-3}$) profiles derived from single-scan position terrestrial laser scanning (TLS) using a RIEGL VZ-400 (RIEGL Laser Measurement Systems GmbH, Horn, Austria) in the centre of each plot. PAI thus gives an indication of the denseness and complexity of the forest structure and is negatively related to light availability at the forest floor. We chose to apply TLS, since the technique is highly reproducible and more direct compared to conventional forest surveys (Calders et al. 2015, Liang et al. 2016, Calders et al. 2018). The TLS method was described in detail by Meeussen et al. (2020).

Landscape conditions

The macroclimate was taken into account as mean annual temperature and annual precipitation, which were retrieved for the coordinates of each plot from the CHELSA database for 1979 – 2013 (resolution of ~ 1 km^2) (Karger et al. 2017). Plots from one edge-to-interior transect might be located within the same or neighbouring 1 km^2 grid cells and thus have very similar macroclimatic conditions, whereas microclimatic conditions will vary depending on the forest edge distance and structure. To incorporate the amount of habitat in the 'local landscape', the percentage area with a tree cover >20% was calculated within a radius of 500 m based on satellite-based global tree cover data with a spatial resolution of 30 m (Hansen et al. 2013).

Mean and standard deviations of the nine predictor variables (mass OS, sand fraction, pH, plant area index, winter offset, summer offset, mean annual temperature, annual precipitation, forest cover) are given for the nine study regions in Table SI.D5.

Data analyses

We used generalized linear mixed-effects models (GLMM) to infer responses of the nine diversity metrics (Table 1) to environmental drivers and performed all analyses in R (R Development Core Team 2020). Due to the hierarchical nature of the data, GLMMs with transect ID (45 levels corresponding to 45 edge-to-interior transects) as random effect (random intercept) nested within region (nine levels corresponding to 9 regions) were used (225 plots nested in 45 transect nested in 9 regions). For models with species richness as response variable, a Poisson error distribution was used with a log link function since these are count data, and, as a consequence, these models can be nonlinear. For all other models a Gaussian error distribution was applied, resulting in strictly linear models. Correlations between predictor variables were assessed with Pearson correlation coefficients before modelling (Fig. SI.D4). Multicollinearity of the predictor variables in the models was assessed using variance inflation factors (VIFs) with the vif function from the package '*cars' (Fox and Weisberg 2019)*. For all models, VIFs were smaller than 3.1 and thus no strong multi-collinearity issues were detected among the set of predictor variables we used (Neter et al. 1990, Zuur et al. 2009). The models were fitted with the '*lme4'* package (Bates et al. 2015).

To explore the effects of latitude, elevation, forest structure type and the distance to the edge (the design variables of the experimental set up) on the diversity metrics, GLMM were performed with these design variables as fixed effects, including all two-way interactions. The distance to the edge was log-transformed to meet model assumptions ($\log_e$).

Furthermore, we included continuous environmental variables in the models. To represent the edaphic conditions, we included sand fraction, pH of the mineral soil and mass of the organic soil layer (mass OS). Mass OS was log-transformed due to its skewed distribution ($\log_e$). For forest structure, we used the PAI (Plant Area Index), summer offset and winter offset. For landscape conditions, we included two macroclimate variables, mean annual temperature (MAT) and annual precipitation, and percentage forest cover. No interactions were taken into account to avoid too much predictor terms and complexity. Equation 1 represents the model structure of the global model.

$$y \sim \%\, sand + pH + \log(mass\ OS) + summer\ offset + winter\ offset + PAI + MAT + annual\ precipitation + \%\, forest\ cover + (1|region/transect) \quad \textit{Eq. 1}$$

Starting from the global model with all predictor variables, model selection was performed based on the lowest corrected Akaike Information Criterion (AICc), testing all possible combinations of predictor variables with the dredge function from the package '*MuMin'* (Barton 2019). During model selection, maximum likelihood was used to fit models, whereas afterwards, the restricted maximum likelihood approach was used to obtain model estimates of the best model. *P*-values were obtained with the '*lmerTest'* package (Kuznetsova et al. 2017) and corrected for multiple testing with false discovery rates based on Pike (2011). All continuous predictor variables were scaled to unit variance and mean zero.

As second step in the analysis, we performed a variation partitioning to assess the importance of the predictor variables of edaphic, stand and landscape conditions, following the procedure of Legendre and Legendre (1983). This second step was only performed for Tax.rich, Phy.div and Fun.div, as we chose to focus further analysis on this set of three independent metrics to obtain comparable and independent results regarding taxonomic, phylogenetic and functional diversity (Table 1) (Botta-Dukat 2005, Helmus et al. 2007, Schleuter et al. 2010). First, the global model was produced, including all nine predictors (Eq. 1), and then models were produced with only one or two out of three groups (edaphic – stand – landscape conditions). Each group had three predictor variables to balance the variation partitioning. For all models we obtained the proportion of variance explained by the fixed factors of the model (marginal R^2, R^2_m), according to Nakagawa and Schielzeth (2013). Finally, we calculated the amount of variation explained by each group and combination of groups by subtracting R^2_m from the R^2_m of the global model. The variation explained by each group and intersection is reported as percentage of variation explained by the global

model.

Results

The results that we highlight here are strongly focused on taxonomic richness (Tax.rich), phylogenetic diversity (Phy.div) and functional diversity (Fun.div) because they are most widely used and independent from changes in species number (Botta-Dukat 2005, Helmus et al. 2007, Schleuter et al. 2010).

Diversity patterns with latitude, forest type and distance to forest edge

We found that latitude, forest type and the distance to the forest edge, as well as the interaction between forest type and the edge distance, significantly explained variation in several biodiversity metrics (Table SI.B1). Tax.rich decreased towards the forest interior, especially strong close to the edge (estimate ± standard error: -0.096 ± 0.022, $p < 0.001$). Contrastingly, Phy.div decreased towards the forest edge and this gradient was the steepest for the intermediate forest type, whereas dense forests had a higher Phy.div overall and the smallest edge-to-interior gradient (interaction estimate ± se: -0.045 ± 0.017, $p = 0.029$). While Tax.rich and Phy.div showed no latitudinal gradient, Fun.div decreased towards the north (estimate ± se: -0.005 ± 0.001, $p = 0.005$). Simultaneously, there was a significant difference between the forest management types, with the intermediate type showing the highest Fun.div (open compared to intermediate type estimate ± se: -0.009 ± 0.003, $p = 0.03$) (Fig. 2).

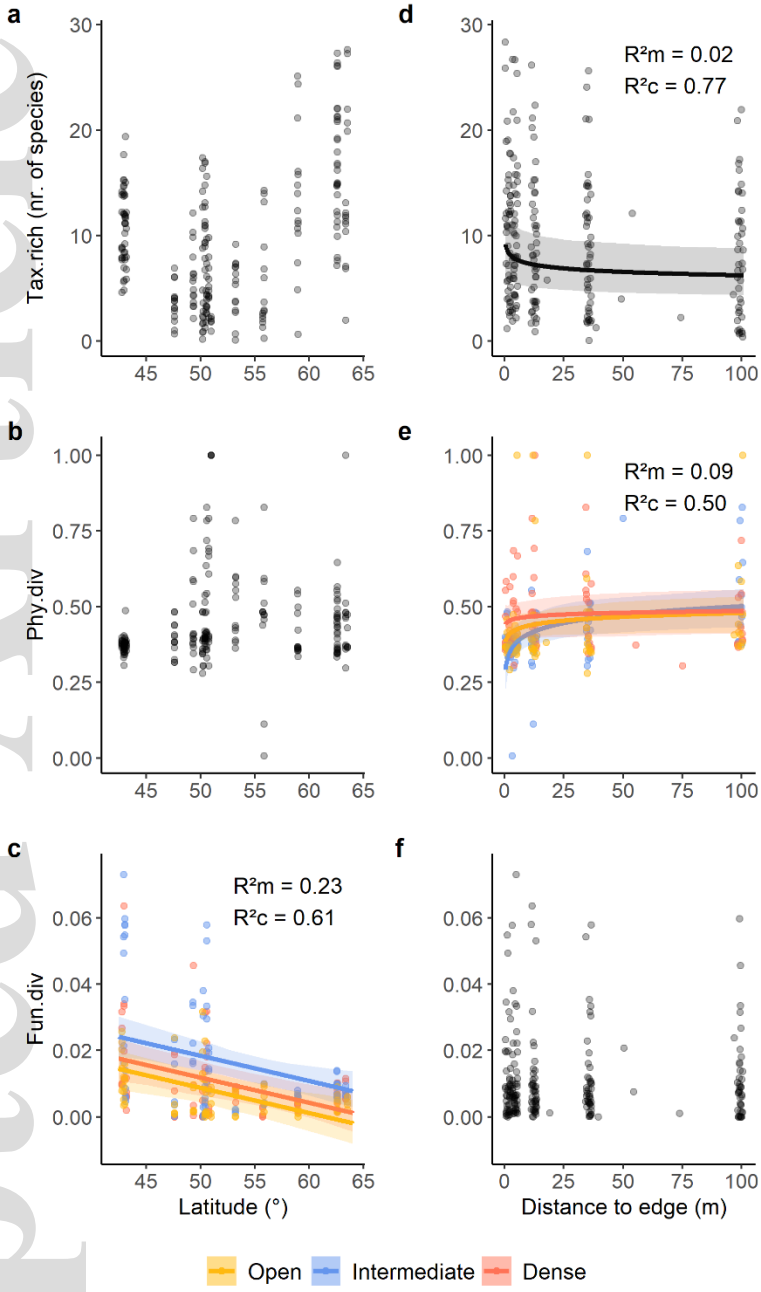


Figure 2. **Taxonomic richness, phylogenetic diversity and functional diversity as a function of the latitude (a-c), distance to the forest edge (d-f) and the interaction with forest management type (c, e).** The lines show model predictions for significant effects based on the generalized mixed effect models (Table SI.B1) and shading corresponds to 95% confidence intervals. Yellow, blue and red colours in d and e indicate significant (interactive) effects of forest management type (see legend). Jittering on the X axis was added for clarity, as well as transparency of points, darker areas thus indicate several overlapping points. Model fit is shown in the panels with significant predictor as marginal R^2 (R^2_m) and conditional R^2 (R^2_c), following Nakagawa and Schielzeth (2013). We highlight results for Tax.rich combined with Phy.div and Fun.div because of their wide use and independence from species number (Botta-Dukat 2005, Helmus et al. 2007, Schleuter et al. 2010).

Diversity patterns with landscape, stand and edaphic environmental conditions

In general, we found four out of nine environmental predictors having a significant impact on multiple diversity metrics: soil pH, Plant Area Index (PAI), summer offset and mean annual temperature (MAT). From these, only summer offset explained variation for taxonomic, phylogenetic and functional diversity metrics. Annual precipitation and winter offset were not retained for any of the biodiversity metrics after model selection. The percentage forest cover in the surrounding landscape, mass of the organic soil layer and sand fraction showed no significant effects after correcting for multiple testing (Table 2). Furthermore, none of the environmental predictors significantly explained variation in functional richness and functional evenness, neither for taxonomic and phylogenetic evenness after *p*-value correction (Table 2).

Tax.rich decreased with decreasing light availability (increasing PAI) and stronger microclimatic buffering of summer maximum temperature (more negative summer offset), whereas Fun.div increased when microclimatic buffering was stronger (Fig. 3 b and h, Table 2). Additionally, Tax.rich increased for higher pH values, whereas Phy.div decreased with increasing pH values (Fig. 3 c and f, Table 2). Furthermore, Fun.div increased with increasing MAT, while Tax.rich and Phy.div showed no significant response to MAT (Fig. 3 a, d and g, Table 2). Tax.rich, Phy.div and Fun.div thus exhibited contrasting responses to stand and edaphic conditions (Fig. 3).

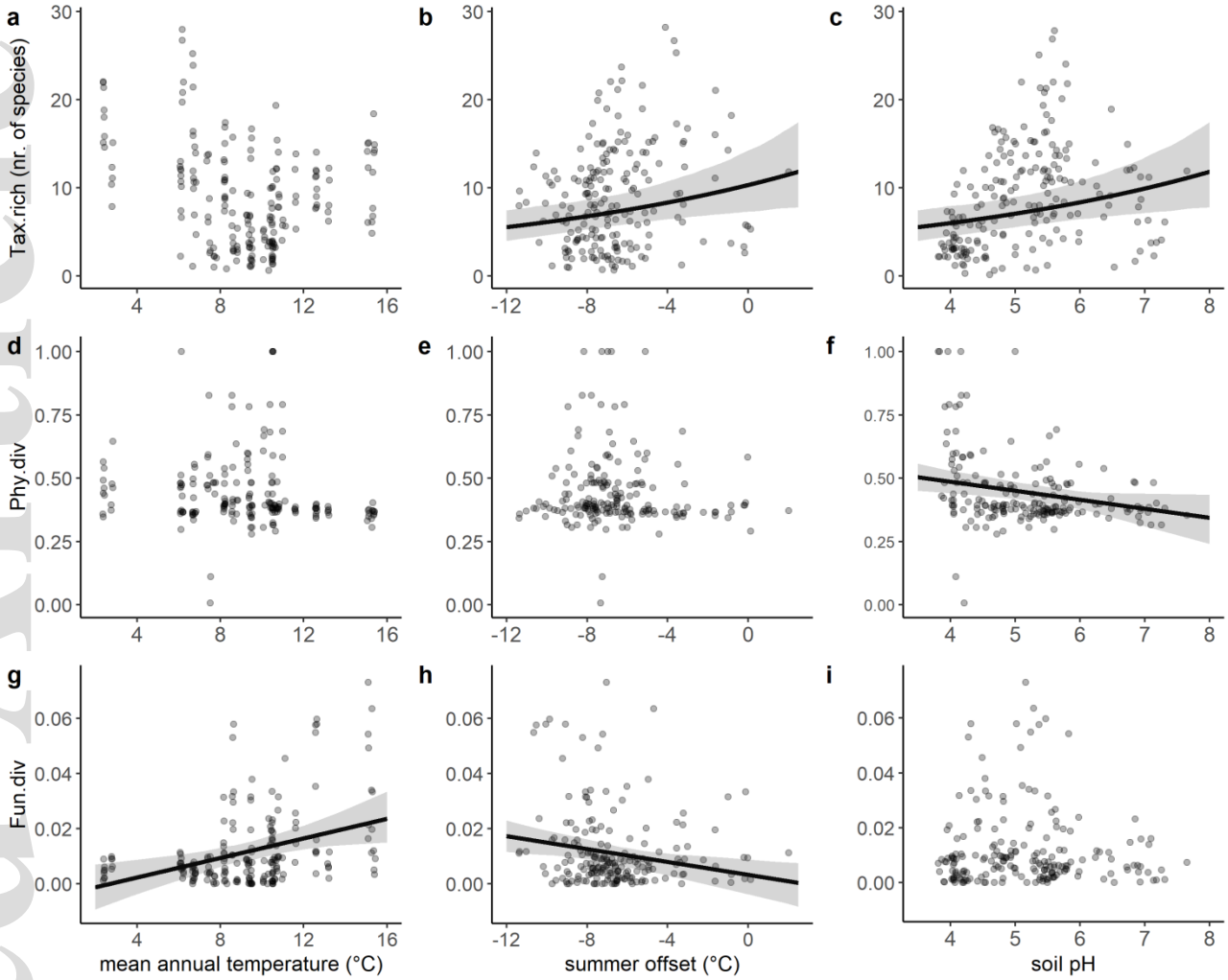


Figure 3. **The relationship of taxonomic richness, phylogenetic and functional diversity with landscape, stand and edaphic conditions as predictors (Table 2).** Taxonomic richness (Tax.rich), phylogenetic diversity (Phy.div) and functional diversity (Fun.div) as a function of mean annual temperature (a,d,g), summer offset (b,e,h) and soil pH (c,f,i). The lines show model predictions for significant parameter estimates based on the generalized mixed effect models and shading corresponds to 95% confidence intervals. Jittering was added for clarity, as well as transparency of points, darker areas thus indicate several accumulated points at the same or overlapping location. We highlight results for Tax.rich combined with Phy.div and Fun.div because of their wide use and independence from species number (Botta-Dukat 2005, Helmus et al. 2007, Schleuter et al. 2010).

Variation partitioning: landscape, stand and edaphic conditions

For Tax.rich, all three variable groups (landscape, stand and edaphic conditions) explained large parts of the variation (42.8%, 52.4% and 34.1% respectively). For both Phy.div and Fun.div we did find large differences between proportions of variation explained by the different groups. Most of the variation in

Phy.div was explained by edaphic conditions (52.6%), followed by stand conditions (24.1%) and only a small amount of variation was explained by the landscape conditions (8.5%). For Fun.div, the variation partitioning resulted in an opposite pattern. Landscape conditions explained most of the variation in Fun.div (60.2%), followed by the stand conditions (23.6%) and only a small amount of variation was explained by edaphic conditions (3.2%) (Fig. 4, Fig. SI.D5).

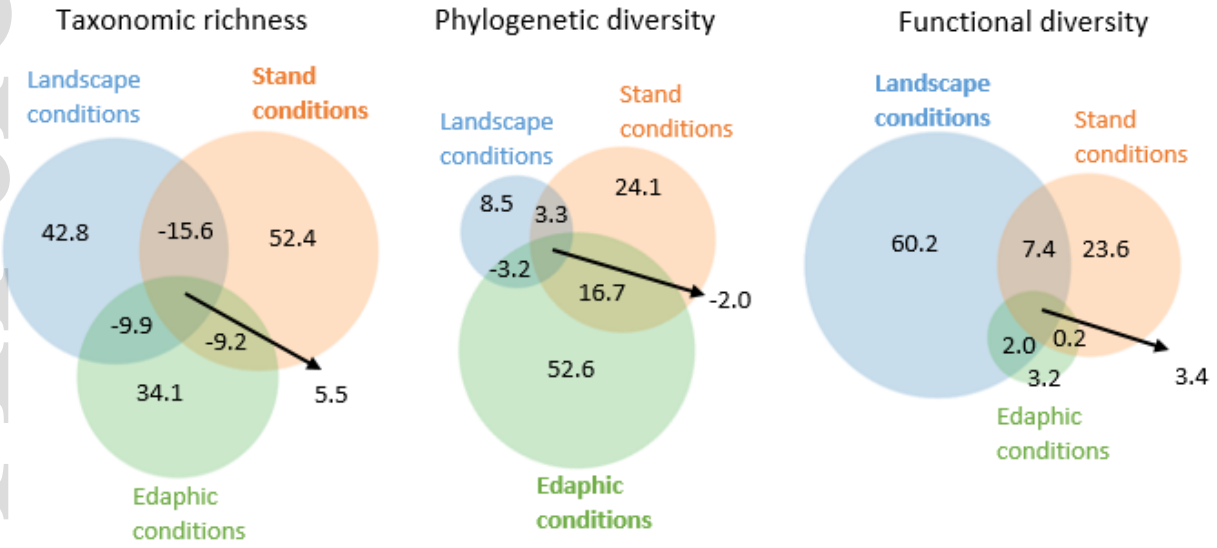


Figure 4. **Variation partitioning**. Venn-Euler diagrams for variation partitioning of taxonomic richness, phylogenetic and functional diversity. These diagrams show the proportion of explained variation (marginal R^2) by three variable groups (landscape, stand and edaphic conditions) and the shared proportion of group combinations (intersection of circles) compared to the explained variation of the global model including all nine predictors. The size and numbers within the circles correspond to the proportion of explained variation. The proportion shared by all three groups is indicated with an arrow.

Table 2. **Summary of the results of the generalized linear mixed-effect models of the nine diversity metrics with landscape, stand and edaphic conditions as predictors.** Models were run for taxonomic, phylogenetic and functional richness (Tax.rich, Phy.rich, Fun.rich), evenness (Tax.even, Phy.even, Fun.even) and diversity metrics (Tax.div, Phy.div, Fun.div). Model fit was assessed based on marginal R^2 (R^2_m), the proportion of variation explained by the fixed effects, and conditional R^2 (R^2_c), the proportion of variation explained by both random and fixed effects (Nakagawa and Schielzeth 2013). Parameter estimates are given for the model with lowest corrected AIC value after model selection with the *dredge* function. *P*-values corrected for false discovery rates are given following Pike (2011), those estimates with a *p*-value below 0.05 are given in bold. The significance of the original *p*-values is given within brackets with '***' for p <0.001, '**' for p <0.01, '*' for p <0.05. Positive and negative significant parameter estimates are respectively red and blue coloured, with darker hues for significant terms after correction.

Predictor		Landscape conditions			Stand conditions			Edaphic conditions			Model fit	
Response		Mean annual temperature	Ann Prec	Forest cover	Summer offset	Winter offset	Plant area index	Sand fraction	Soil pH	Log (mass organic soil)	R^2_m	R^2_c
Tax.rich	Mean ± SE	- 0.200±0.099		0.129±0.071	**0.116±0.040**		**-0.132± 0.043**	-0.092± 0.06	**0.142± 0.051**	-0.063± 0.035	0.28	0.72
	p corrected (original)	0.073 (*)		0.109	**0.020 (**)**		**0.014 (**)**	0.166	**0.025 (**)**	0.114		
Tax.even	Mean ± SE						0.037±0.02	-0.056±0.02			0.09	0.41
	p corrected (original)						0.076 (*)	0.059 (*)				
Tax.div	Mean ± SE				**0.100±0.042**			-0.142±0.067	**0.141±0.055**	-0.063±0.042	0.10	0.66
	p corrected (original)				**0.047 (*)**			0.069 (*)	**0.041 (*)**	0.177		
Phy.rich	Mean ± SE	**-1.060±0.371**		0.565±0.251	**0.475±0.118**				**0.372±0.155**	-0.207±0.119	0.29	0.79
	p corrected (original)	**0.041 (*)**		0.060 (*)	**0.002 (***)**				**0.047 (*)**	0.119		
Phy.even	Mean ± SE						0.028±0.012		-0.028±0.013		0.07	0.16
	p corrected (original)						0.055 (*)		0.069 (*)			
Phy.div	Mean ± SE						0.024±0.011	0.033±0.014	**-0.032±0.013**		0.13	0.47
	p corrected (original)						0.062 (*)	0.060 (*)	**0.047 (*)**			
Fun.rich	Mean ± SE								0.029±0.017		0.03	0.49

	p corrected (original)				0.132		
Fun.even	Mean ± SE			0.021±0.014	-0.026±0.017	0.05	0.27
	p corrected (original)			0.166	0.177		
Fun.div	Mean ± SE	**0.005±0.002**	**-0.003±0.001**			0.18	0.62
	p corrected (original)	**0.014 (**)**	**0.020 (**)**				

Discussion

Responses differ between taxonomic, phylogenetic and functional diversity metrics (H1)

The use of phylogenetic and functional diversity metrics along taxonomic metrics provided different, complementary information on community assembly mechanisms in forest understorey plant communities across Europe. From the Pearson correlation matrix, it was clear that some metrics were strongly correlated, such as taxonomic and phylogenetic richness, but that others were not (Table 1). Both phylogenetic and functional diversity were independent of taxonomic richness, showing that in this study, plots with higher species numbers in the understorey did not necessarily have higher phylogenetic or functional understorey diversity.

Furthermore, we found different responses in both magnitude and direction to gradients of the experimental design of the study (Fig. 2, Table SI.B1) and to other environmental predictors (Table 2). Low mean annual temperatures (e.g. at high latitudes) led to lower functional diversity, whereas taxonomic richness and phylogenetic diversity showed no clear pattern driven by the macroclimate (Table 2, Fig. 2, Fig. 3). At high latitudes, environmental filtering probably led to a plant community with restricted variation in functional traits, enabling the plants to survive longer and colder winters. For example, the community weighted mean of plant height tended to be smaller and SLA tended to be higher in plots with lower mean annual temperatures. Additionally, colder, more northern regions needed to be recolonized after the last glaciation period, causing a convergent functional composition regarding functional traits linked to dispersal, such as lower seed mass values (Pinto-Ledezma et al. 2018).

Also soil pH caused contrasting responses; species richness decreased with a lower pH, possibly due to higher soluble aluminium in acidic soils, which decreases plant root growth (Kopittke et al. 2015, Bojórquez-Quintal et al. 2017), in combination with the toxic effect of a low pH itself (Falkengrengrerup and Tyler 1993, Falkengren-Grerup 1995). Phylogenetic diversity, on the other hand, increased when the soil became more acidic, corroborating the findings of Piwczynski et al. (2016), which might be due to environmental filtering for acidophilous species. Most often, environmental filtering leads to phylogenetic clustering, as was found in the understorey of Mediterranean oak forests (Selvi et al. (2016)). This pattern can arise when the ability to cope with a particular environmental filter is shared in more closely related species of the community. In our study, however, these acidophilous communities often contained a mixture of forbs, graminoids and ferns (for example, *Stellaria holostea* and *Pteridium aquilinum* co-occurring with *Molinia caerulea* in plots with low pH). Species from different phylogenetic lineages acquired the ability to grow in acidic soils independently, leading to phylogenetic variability instead. Clearly, the effect of environmental filtering on phylogenetic diversity depends strongly on the degree of phylogenetic conservatism of the traits which are favoured by the environmental filter. These results suggest that in this situation niche conservatism might be the case within species but not phylogenetically,

among related species.

There was no clear effect of soil pH on functional diversity. Plants might cope with acidity in different ways, which are not necessarily directly related to their general ecological strategy in terms of resource use, competition and reproduction (represented by SLA, plant height and seed mass). Mechanisms to deal with acidity are often related to root traits, such as the secretion of organic acid anions or associations with mycorrhiza (Marschner 1991, Chen et al. 2013). Furthermore, root traits provide highly useful information on, for example, velocity of resource turn-over and the association with mycorrhiza (Bergmann et al. 2020). Whereas some categorical root traits are becoming increasingly available (such as mycorrhiza type), quantitative root traits are not yet available for many understorey herbs. For example, specific root length data was only available for 37% of the species studied here, whereas this is one of the most studied belowground traits (Table SI.D7). In the future, root traits could greatly increase our understanding of biodiversity responses to environmental conditions, especially to edaphic factors such as soil pH.

Effect of light availability and microclimatic buffering (H2)

Higher taxonomic richness was found in plots with higher light availability, a pattern clearly driving the increase towards the forest edges through a gradual decrease in plant area index (Table 2, Fig. 2, Fig. SI.D6) (Gehlhausen et al. 2000, Honnay et al. 2002, Vallet et al. 2010). The higher understorey species richness at the forest edge in this study is predominantly driven by an increase of forest generalist species (Govaert et al. 2020). Furthermore, the generalist richness was lower beneath canopy tree species casting more shade (Govaert et al. 2020). The lower light availability in the forest interior poses an environmental filter for the light demanding generalist edge species (Pellissier et al. 2013). The increasing availability of a limiting resource, such as light, can remove an environmental filter, increasing the number of species, but this process can lead to different edge-to-interior patterns depending on the context and land-use history (e.g. Hofmeister et al. (2013)).

We also detect higher species richness in the less microclimatically buffered forest edge plots (Fig. 2, Fig. SI.D7). Strikingly, the functional diversity was lower in plots that are less buffered (Fig. 3). Similarly, the plots in the open forest management type had lower functional diversity and less buffered summer temperatures (Fig. 2, Fig. SI.D7). It is possible that reduced microclimatic buffering due to less dense tree canopies made the forest understorey more susceptible to spring frost and summer drought (von Arx et al. 2013, Zellweger et al. 2019), acting as an environmental filter and favouring plants adapted to higher temperatures and lower soil moisture. Additionally, it is known that thermophilization of understorey communities (the process in which warm-adapted species gain abundance over more cold-adapted species over time) occurs more in forest stands with less microclimatic buffering, especially when light availability is high (De Frenne et al. 2013). Thermophilization can be driven by tall and competitive species (De

Frenne et al. 2015), which could suppress smaller, less competitive plants and drive a loss of functional diversity through competitive exclusion. To assess this hypothesis, resurveyed vegetation studies are needed (De Frenne et al. 2013, Feeley et al. 2020, Zellweger et al. 2020). Nevertheless, in an additional analysis we calculated the floristic temperature of the understorey communities and assessed its relationship with microclimate. The floristic temperature increased when minimum winter temperatures were more buffered (less cold in winter), but we did not detect a link with the buffering of summer maximum temperatures (SI.C).

Besides, forest microclimates are more buffered in warmer regions (Fig. SI.D7, De Frenne et al. (2019)), and functional diversity increased with warmer macroclimate temperatures; this association could thus have contributed indirectly to the higher functional diversity in strongly buffered forest plots.

Conversely, unmanaged forests often have a high basal area, high PAI and a complex forest structure providing strongly buffered microclimates (Frey et al. 2016) and low light levels on the forest floor (Hardwick et al. 2015). Higher functional diversity is often found in dense, unmanaged forests with low light levels (Liu et al. 2015, Closset-Kopp et al. 2019, Lelli et al. 2019). In such conditions, the proportion of generalist species is lower (Govaert et al. 2020) and the less competitive forest specialists shape the understorey communities (Honnay et al. 2002).

Chesson's framework states that coexistence mechanisms can result from stabilizing or equalizing processes. Stabilising niche differences are crucial; niche differences among co-occurring species (often inferred from species traits; but see HilleRisLambers et al. (2012)) can be ensured, if biotic and abiotic factors force species to experience stronger intraspecific than interspecific competition (Chesson 2000). Equalizing niche differences, on the other hand, are processes that suppress fitness inequality between species resulting from many ecological and evolutionary factors, which fundamentally contributes to stable multispecies coexistence. Low light availability can function as an equalizing mechanism, decreasing the growth of the most competitive species. Most forest specialist species might be quite similar in having low competitive abilities, e.g. lower plant height than forest generalist species (Marinšek et al. 2015). As a result, the interspecific competition can be low and thus small niche differences could already cause larger intraspecific competition and stabilize the coexistence between these species. This is supported by the tendency of evenness metrics to increase with lower light availability.

Furthermore, stronger microclimatic buffering is often related to a higher complexity of the forest structure (Frey et al. 2016, Kovacs et al. 2017), which enhances heterogeneity in forest stratification and in forest-floor conditions. This could also increase the coexistence of species with different abiotic preferences and explain the increased functional diversity. Further research might look deeper into the link between microclimatic buffering, thermophilization, functional diversity in forests and possible consequences for ecosystem functioning, such as nutrient cycling and litter decomposition.

We hypothesised that increased light and reduced microclimatic buffering could lead to local functional or phylogenetic homogenization due to the increased presence of generalist species. Contrary to our expectation, we did not find lower functional diversity in forest edges or with more light (Fig.SI.B1, Table 2). However, weaker buffering of the microclimate did decrease functional diversity (Fig. 3, Table 2). Further research might elucidate the different roles of light and microclimate in shaping the diversity of the forest understorey through controlled experimental set-ups separating both factors.

Regarding the phylogenetic diversity, we detected a significant interaction of the forest management type and distance to the edge (Fig. 2). For the intermediate forest type, the phylogenetic diversity decreased towards the forest edge, whereas it was more stable for the dense and open forest type. Both the increase of generalist species and the decrease of Plant Area Index at the forest edge were steepest and most abrupt for the intermediate forest types (Govaert et al. 2020, Meeussen et al. 2020). Abrupt changes in forest structure could thus be related to changes in phylogenetic diversity in the understorey. Stand characteristics did account for 24% of explained variation of phylogenetic diversity in the variation partitioning, however, no strong direct linear responses to microclimate or plant area index were found after model selection (Fig. 4, Table 2).

Varying importance of landscape, stand and edaphic conditions (H3)

Landscape, stand and edaphic conditions were of relatively similar importance for Tax.rich. This could be expected from the well-known influence of edaphic and stand conditions on species richness (Van Calster et al. 2008, Vanhellemont et al. 2014, Govaert et al. 2020) in combination with the large spatial gradient of the study, covering important changes in landscape conditions (Bernhardt-Römermann et al. 2015). The phylogenetic and functional diversity metrics showed very different results. For Phy.div, the importance of the landscape conditions was negligible compared to the influence of stand and edaphic conditions. However, Li et al. (2018) reported a high impact of macroclimatic factors for phylogenetic diversity but, in contrast to our study, their study extended to all ecosystem types and covered a larger spatial gradient, with larger variation in macroclimate. For the functional diversity, the macroclimatic temperature gradient explained most of the variation, acting as a strong overarching environmental filter, followed by the forest microclimate. We expected also a strong impact of edaphic conditions, similar to phylogenetic diversity, but this was not confirmed. The recurring difference between functional and phylogenetic diversity responses indicates that the conservation of plant height, SLA and seed mass through the phylogenetic tree of the understorey species is not very strong (Fig. 1), challenging the niche conservatism concept and the notion of functional and phylogenetic diversity as substitutes. Furthermore, it also shows that the evolutionary history indeed comprises much more information about a species than three key functional traits, even though they represent the main plant strategies regarding resource acquisition, competitiveness and reproduction.

Stand conditions were important for the three diversity metrics through regulation of light at the forest floor and microclimatic buffering. Nevertheless, the directions of responses were different. Trade-offs between diversity aspects are clearly present in deciduous forests. It is thus essential to look beyond species counts when studying forest understorey plant diversity, certainly when interested in community assembly mechanisms.

Conclusions

Combining taxonomy, phylogeny and functional traits proved to be important when assessing plant diversity of understorey communities in forest edges of temperate deciduous forests. We show that different diversity aspects can be driven by contrasting environmental conditions and in different directions, leading to trade-offs between diversity metrics. It was clear that also for forest understorey species, the reality is more complex than environmental filtering and competitive exclusion leading unequivocally to less and more diverse communities respectively. Diversity is an outcome of many different, interacting and context-dependent processes. Functional and phylogenetic diversity were no mere substitutes for each other, but revealed complementary and important insights. Future studies could acknowledge this complexity more by including intraspecific trait variation, an aspect which we did not consider here, but could help to understand functional biodiversity patterns and community assembly mechanisms (Siefert 2012, Violle et al. 2012, Des Roches et al. 2018). Furthermore, we suggest to measure and study belowground traits of understorey herbs to enable a clearer understanding of functional diversity responses to edaphic conditions. We detected no significant local functional or phylogenetic homogenization close to forest edges in general. However, we did find a decrease of phylogenetic diversity in forest edges for forests of intermediate and high openness and we did find a decreasing functional diversity in plots with less buffered microclimates. In the context of climate change, with increasing frequency of extreme summer temperatures (IPCC 2018) and canopy disturbances due to drought, heat stress and insect attacks (Allen et al. 2010, Anderegg et al. 2015), it would be highly valuable to further investigate this relationship and possible consequences of functional homogenization in the understorey for forest ecosystem functioning.

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Authors' contributions

PDF, SG, CM, PVa, KDP and KV conceived the ideas and designed methodology; all authors, including TV, MB, KB, JB, KC, SC, MD, PH, GI, JL, SL, AO, QP, JP, FSe, FSp, HV, PVe and FZ collected data; KDP analysed the data and led the writing of the manuscript, in close collaboration with PDF, PVa, PS, SG, CM, and KV. All authors contributed critically to the drafts and gave final approval for publication.

Data availability

Data is available on Figshare. https://doi.org/10.6084/m9.figshare.c.5176136.v1

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Figure legends

Figure 1. Phylogenetic tree of species included in this study. This tree was standardised taxonomically with The Plant List (2013) and visualized with *ggtree* and *gheatmap* in R (Yu et al. 2017). Functional traits are represented with a colour scale around the tree, plant height (m) on the inner circle, SLA (mm^2 mg^{-1}) on the middle circle and seed mass (mg) on the outer circle.

Figure 2. **Taxonomic richness, phylogenetic diversity and functional diversity as a function of the latitude (a-c), distance to the forest edge (d-f) and the interaction with forest management type (c, e).** The lines show model predictions for significant effects based on the generalized mixed effect models (Table SI.B1) and shading corresponds to 95% confidence intervals. Yellow, blue and red colours in d and e indicate significant (interactive) effects of forest management type (see legend). Jittering on the X axis was added for clarity, as well as transparency of points, darker areas thus indicate several overlapping points. Model fit is shown in the panels with significant predictor as marginal R^2 (R^2_m) and conditional R^2 (R^2_c), following Nakagawa and Schielzeth (2013). We highlight results for Tax.rich combined with Phy.div and Fun.div because of their wide use and independence from species number (Botta-Dukat 2005, Helmus et al. 2007, Schleuter et al. 2010).

Figure 3. **The relationship of taxonomic richness, phylogenetic and functional diversity with landscape, stand and edaphic conditions as predictors (Table 2).** Taxonomic richness (Tax.rich), phylogenetic diversity (Phy.div) and functional diversity (Fun.div) as a function of mean annual temperature (a,d,g), summer offset (b,e,h) and soil pH (c,f,i). The lines show model predictions for significant parameter estimates based on the generalized mixed effect models and shading corresponds to 95% confidence intervals. Jittering was added for clarity, as well as transparency of points, darker areas thus indicate several accumulated points at the same or overlapping location. We highlight results for Tax.rich combined with Phy.div and Fun.div because of their wide use and independence from species number (Botta-Dukat 2005, Helmus et al. 2007, Schleuter et al. 2010).

Figure 4. **Variation partitioning**. Venn-Euler diagrams for variation partitioning of taxonomic richness, phylogenetic and functional diversity. These diagrams show the proportion of explained variation (marginal R^2) by three variable groups (landscape, stand and edaphic conditions) and the shared proportion of group combinations (intersection of circles) compared to the explained variation of the global model including all nine predictors. The size and numbers within the circles correspond to the proportion of explained variation. The proportion shared by all three groups is indicated with an arrow.

Table legends

Table 1. **Overview of the diversity metrics used to assess the diversity of understorey plants in 225 plots in the forest edges of European deciduous forests.** A richness, evenness and diversity or variability metric (.rich, .even, .div respectively) were calculated based on taxonomy, phylogeny or function (Tax., Phy., Fun. respectively). In the formulas, p_i, p_j = relative abundance of species i, j, S = total number of species in community and d_{ij} = difference between species i, j. The value of the Pearson correlation is given as a number and indicated by the colour in the Pearson correlation matrix.

Table 2. **Summary of the results of the generalized linear mixed-effect models of the nine diversity metrics with landscape, stand and edaphic conditions as predictors.** Models were run for taxonomic, phylogenetic and functional richness (Tax.rich, Phy.rich, Fun.rich), evenness (Tax.even, Phy.even, Fun.even) and diversity metrics (Tax.div, Phy.div, Fun.div). Model fit was assessed based on marginal R^2 (R^2_m), the proportion of variation explained by the fixed effects, and conditional R^2 (R^2_c), the proportion of variation explained by both random and fixed effects (Nakagawa and Schielzeth 2013). Parameter estimates are given for the model with lowest corrected AIC value after model selection with the *dredge* function. *P*-values corrected for false discovery rates are given following Pike (2011), those estimates with a *p*-value below 0.05 are given in bold. The significance of the original *p*-values is given within brackets with '***' for p <0.001, '**' for p <0.01, '*' for p <0.05. Positive and negative significant parameter estimates are respectively red and blue coloured, with darker hues for significant terms after correction.