Trade-offs of biodiversity and ecosystem services in European forest edges vs interiors

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Abstract

Forest biodiversity and ecosystem services have been predominantly quantified in forest interiors, well away from edge influences. However, edges represent a significant portion of the forest cover in many regions world-wide. We quantified a broad set of plant biodiversity and ecosystem service indicators in 225 plots along forest edge-to-interior transects across Europe. We found strong trade-offs: while phylogenetic diversity (evolutionary measure of biodiversity), the proportion of forest specialists, nutrient cycling and heatwave buffering increased towards the forest interior, species richness (taxonomic measure of biodiversity), nectar production potential, stemwood biomass and overall tree regeneration were promoted towards the forest edge. These trade-offs were mainly driven by forest structural complexity differences from edge to interior. As fragmentation continues, forest edges increasingly reshape biodiversity and ecosystem service provisioning, which is yet to be integrated in forest management and policy to ensure sustainability in ecosystem services delivery.

Main Text

Forests harbor the majority of terrestrial species on earth and provide a multitude of ecosystem services to humans, including carbon sequestration, timber production, nutrient cycling, water cycling and climate buffering[1]. However, most forest biodiversity and ecosystem service assessments report data from forest interiors, well away from edges and their complex influences on biodiversity (see e.g. [2,3]). This is most often done intentionally, to avoid complex interactions and exclude the environmental differences between forest edges and interiors including edges' warmer microclimates[4], higher light availability[5] and enhanced soil nutrient inputs from adjacent land-use[6]. Ongoing forest fragmentation, however, increases the relative amount of the area covered by forest edges and causes edge effects to penetrate more frequently and deeply into the forest interior. Edge effects can potentially reach the core in small forest fragments[7,8]. Up to 70% of the world's remaining forest is now found within 1 km of a forest edge and 20% is even closer than 100 m[9]. In fact, recent global inventories have shown that the loss of forest interior area is at least twice as high as the net loss of forest area[10]. In Europe, the situation is even more precarious with 40% of forests lying within 100 m of the edge[11]. As fragmentation persists globally, edges will play an increasingly important role in future forest functioning and service provisioning, and can no longer be ignored in conservation decision-making, forest policies, and management planning. In spite of the urgency, no continental-scale study to date has quantified edge vs. interior patterns of the potential supply in terms of forest ecosystem services and biodiversity.

Here we quantified a broad range of biodiversity indicators and ecosystem services in 225 plots along forest edge-to-interior transects across a 2300-km wide latitudinal gradient across Europe (**Figure S1**, **Table S1**). We specifically investigated outer forest edges (sensu [12]), where forests border large non-forest areas. To quantify biodiversity, we focused on understorey plants as they represent the majority of plant biodiversity in temperate forests and play a crucial role for temperate forest functioning[13]. Understorey plants are directly linked to several forest ecosystem functions, for instance via their impact

on water cycling[14], nutrient dynamics[15] and forest regeneration[16], and may strongly shape forest ecosystem responses to global change[17,18]. Multiple facets of biodiversity were considered including taxonomic (total richness of species and relative amount of forest specialists), phylogenetic (variety of evolutionary lineages) and functional diversity (presence of different growth forms and resource use strategies) of the understorey plant community because of their simultaneous but often contrasting influence on ecosystem functioning[19]. In addition to these biodiversity attributes, we looked at several ecosystem services covering a mixture of regulating and provisioning services that act across various spatial scales, i.e., from local (e.g., usable plants) to global services (e.g., carbon sequestration). To quantify the potential supply of these ecosystem services, different indicators were selected based on an extensive literature search (see Fig. 1 and *Materials and Methods* for more details). Using a multivariate Bayesian modeling framework, specifically suited to study trade-offs, we then assessed how the selected biodiversity and ecosystem service indicators changed with increasing distance to the forest edge. Next, we evaluated the effects of several environmental drivers on biodiversity and ecosystem service delivery potential, ranging from edaphic properties (soil texture, soil acidity and leaf litter quality) over forest stand characteristics (forest structural complexity, tree species composition and microclimate) to landscape-scale conditions (forest cover, drought and nitrogen deposition).

We found complex trade-offs in biodiversity indices and ecosystem service delivery along forest edge-to-interior transects across Europe. While phylogenetic diversity, proportion of forest specialists, nutrient cycling and heatwave buffering exhibited a significant increase towards the forest interior, other biodiversity indices and ecosystem services such as taxonomic richness, nectar production potential, stemwood biomass and tree regeneration were promoted towards the forest edge. However, functional understorey plant diversity, belowground carbon storage and the amount of usable plants remained steady between the forest interior and the edge (Fig. 2, **Figure S2**).

The trade-offs we found among ecosystem services also represent important trade-offs for management and conservation assessments. Promoting landscapes with large, continuous forest cover or a few large patches would maximize the delivery of some ecosystem services that prevail in forest interiors, at the expense of other services that reach their highest level in forest edges. On the contrary, complex heterogeneous landscapes with a mixture of both small and large forest patches, and thus a well-balanced mixture of forest edge and interior area, are most likely to deliver, at least, moderate levels of a broad array of ecosystem services. The latter echoes perfectly the principle of *"a jack of all trades is a master of none, but oftentimes better than a master of one"* which was already introduced as a mechanism underlying biodiversity-ecosystem multifunctionality relationships in forest interiors[20]. Here we show that, from a landscape point of view, the complementarity of edge and interior area is also needed to ensure the simultaneous delivery of ecosystem services by forests.

Plant area index, as a proxy for forest structural complexity, was the predominant driver of the observed trade-offs in biodiversity and ecosystem service delivery with significant positive effects on phylogenetic and functional diversity, nutrient cycling and microclimate buffering but a negative effect on taxonomic richness. The effects of plant area index show trends very similar to the effects of the distance to the

edge, suggesting that edge effects are mostly driven by plant area index (Fig. 3). Nectar production was higher and heatwave buffering stronger when the canopy had a higher shade-casting ability, whereas a warmer forest microclimate enhanced nutrient cycling (Fig. 3). At the stand level, forest managers can thus play a key role in the local optimization of ecosystem services' delivery by their forests through manipulating structural complexity of the canopy layer. Indeed, management actions that increase variability in canopy density and promote heterogeneity in tree sizes and crown morphologies will result in a higher variety of resources and microhabitats thereby promoting species coexistence and enhancing ecosystem multifunctionality[21–24]. The most important edaphic condition was soil pH, having a positive effect on the proportion of forest specialists, taxonomic richness and stemwood biomass. None of the landscape conditions had a strong effect on multiple biodiversity indices or ecosystem services (**Figure S3**).

Our results are of central concern to forest managers, conservation practitioners and policymakers. We recommend that future policies and strategy documents (e.g. the EU Biodiversity Strategy and Forest Strategy) consider the importance of edges in maintaining and fostering the biodiversity and functioning of European forests. In particular, we show that both forest interiors as well as forest edges, preferably with a contrasting structural complexity, are needed to guarantee the simultaneous delivery of multiple ecosystem services rather than maximizing a few target services at the expense of others. These trade-offs, however, depends on the stakeholder's priorities. On a local scale, foresters can determine the delivery of specific ecosystem services (or a combination thereof) through their canopy management (e.g., opening vs. densification).

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Materials And Methods

1.   Study area and experimental set-up

Our study was conducted in broadleaved forests in nine regions spanning a ±2300-km wide latitudinal gradient across the European sub-Mediterranean and temperate forest biomes (**Figure S1**). This latitudinal gradient covers a mean annual temperature (MAT) range of >10 °C, while mean annual precipitation (MAP) varies between 550 and 1250 mm (long-term average values for 1979-2013 retrieved from the CHELSA database; Karger et al. 2017). In each region, broadleaf forest stands larger than 4 ha were selected with a dominance of oak species (chiefly) as these are important forest stands for biodiversity in Europe (Brus et al. 2012). *Quercus robur*, *Q. petraea* and *Q. cerris* were the dominant species, but locally complemented by *Alnus incana*, *Betula pubescens*, *Carpinus betulus*, *Fagus sylvatica*, *Populus tremula* and *Ulmus glabra.* Specifically, three forest stands were selected per region with contrasting management intensity: (1) 'dense forests' that were not thinned over the past 10-30 years, with a high basal area (mean ± SE was here 28.8 ± 1.5 m²/ha) and high canopy cover (openness 5.8 ± 0.6%, mean of three densiometer measurements); (2) 'medium dense forests' with frequent thinning and most recent thinning about 5-10 years ago (basal area 31.4 ± 1.9 m²/ha, openness 6.5 ± 0.6%); and (3)

'open forests' with the most recent thinning less than 4 years before sampling, with a low basal area (21.6 ± 1.3 m²/ha) and low canopy cover (mean openness 14.8 ± 2.1%).

In each forest stand, a 100-m transect was then established perpendicular to the south-facing forest edge. Five plots of 3 m × 3 m were installed along each transect, with their plot centers at an exponentially increasing distance from the focal forest edge (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 focal forest edge (**Figure S1**, **Table S1**). More details on selection criteria and establishment of the plot network can be found in Govaert et al. (2020), Meeussen et al. (2020) and De Pauw et al. (2021).

2.   Quantifying biodiversity and the potential supply of ecosystem services

2.1.   Biodiversity

For each plot, four biodiversity metrics were quantified for the understorey plant community, i.e., taxonomic diversity, proportion of forest specialists, phylogenetic diversity and functional diversity. Taxonomic diversity was quantified as the total number of plant species per plot in the forest understorey. The relative number of forest specialists in the understorey was calculated based on the forest affinity categories defined in Heinken et al. (2022). All species categorized as 1.1 and 1.2 in this Europe-wide database of forest plant species were grouped as forest specialists (see Govaert et al. 2020). Phylogenetic diversity was quantified as the phylogenetic species variability (i.e. variation in evolutionary history) of the herb community, and based on the molecular megaphylogeny of land plants constructed by Zanne et al. (2014). Functional diversity was calculated as Rao's quadratic entropy based on relative species abundances and pairwise functional differences among species (Laliberté and Legendre 2010). Three key functional traits were selected following the leaf-height-seed scheme for plant ecological strategies, i.e., seed mass, specific leaf area (SLA) and plant height (see De Pauw et al. 2021 for more details).

2.2.   Regulating services

Four regulating services were quantified per plot, i.e., topsoil carbon storage, pollination, heatwave buffering and nutrient cycling. The soil carbon stock (Mg/ha) in the combined litter layer and mineral topsoil (0-20 cm) of each plot was used as a measure of the potential topsoil carbon storage (see Meeussen et al. 2021). Pollination was assessed by the abundance-weighted average nectar production potential of the understorey plant community per plot. Potential nectar production was extracted per species from Tyler et al. (2021) as the average of their upper and lower class limits. The latter are defined in Tyler et al. (2021) using a seven-degree logarithmic scale: 1 = no nectar production (0 g sugar m^{-2} year^{-1}) and no collectable pollen; 2 = nectar production insignificant (<0.2 g), or absent but with low but significant amounts of collectable pollen; 3 = nectar production small (0.2−5 g), or lower but with copious collectable pollen; 4 = nectar production modest (5−20 g); 5 = rather large (20−50 g); 6 = large (50−200 g); and 7 = very large (>200 g) (**Table S2**). The maximum summer temperature offset was used as a proxy for the heatwave buffering (or 'cooling') capacity of the forest stands. Forest understorey

microclimates are generally buffered against severe temperature extremes (De Frenne et al. 2019), and this buffering effect, and its effects on forest biodiversity and functioning, is most pronounced during summer (Zellweger et al. 2019). Microclimate temperature was recorded hourly at 1 m above the soil surface in each vegetation plot using miniature data loggers covered by radiation shields (type: Lascar EL-USB-1, range: -30 to 80 °C, resolution: 0.5 °C). Temperature offsets were calculated for each plot by subtracting sub-canopy temperatures (plot sensor) with temperature measured in open field close to each corresponding forest stand (reference sensor). Positive (negative) offset values thus denote warmer (cooler) sub-canopy temperatures compared to macroclimate temperatures. Maximum summer temperature offsets were computed per plot as mean daily 95th percentile temperature during the summer months (April to September 2019) (see Meeussen et al. 2021). Finally, to quantify the nutrient cycling potential we used the cover-weighted mean foliar nitrogen concentration of the five most abundant plant species in each plot as a proxy (see Landuyt et al. 2019 for a discussion).

2.3. Provisioning services

Three key provisioning services were calculated per plot, i.e., above ground stem biomass (timber wood), abundance of usable plants and tree regeneration. Stem biomass was determined per plot using multi-species biomass equations based on diameter at breast height (DBH) developed by Jenkins et al. (2003). This generic equation was used because species-specific or local allometric equations were not always available in the literature, and because the tree species pool was especially large in this dataset (i.e. more than 40 different tree species across each of nine geographical regions). Moreover, a validation by Meeussen et al. (2021) using only the Belgian plots in this dataset showed that local and species-specific equations produced highly comparable biomass estimations (R^2 = 0.98). First, the DBH of all standing trees within 9-m radius of each plot center was measured with a caliper. Two perpendicular measurements per stem were performed and averaged. For multi-stemmed trees, all individual stems (with DBH ≥ 7.5 cm) were measured and treated as separate trees in the calculations. Next, all tree species were classified by expert knowledge into the ten multi-species biomass groups *sensu* Jenkins et al. (2003). Each group represents a unique allometric equation based on DBH. As a final step, the stem biomass estimations of all trees per plot were summed and converted to Mg per ha (see Meeussen et. al. 2021 for more details). The abundance of usable plants was assessed per plot based on different bibliographical sources (**Table S2**). For each plant species per plot, its potential use for food, medical purposes or other uses was determined. Plants were only considered 'usable' when used in Europe. Tree regeneration was assessed per plot as the total abundance of tree seedlings across all tree species in the understorey community of each plot.

3. Environmental predictor variables

3.1. Edaphic conditions

In each plot, five random subsamples of mineral topsoil were taken at 0-10 cm and 10-20 cm depth (30 mm diameter), and subsequently pooled per depth horizon. Samples were dried to constant weight at 40

°C for 48 h, ground and sieved over a 2 mm mesh. Then, they were analyzed for pH-H$_2$O by shaking a 1:5 ratio soil/H$_2$O mixture for 5 min at 300 r.p.m. and measuring with an Orion 920A pH meter with a Ross sure-flow 8172 BNWP pH electrode model (Thermo Scientific Orion, USA).

The same sampling procedure was followed for the soil samples taken between 10-20 cm depth for texture analysis (% sand, silt and clay), which was performed by sieving and sedimentation with a Robinson-Köhn pipette according to ISO 11277 (2009). We selected the percentage of sand as a proxy for soil texture.

The organic soil horizon (litter, humus and fragmentation layer) was sampled in a 20 cm × 20 cm subplot from its surface to the mineral soil horizon underneath, after removal of the herb layer. These samples were subsequently dried to constant weight at 65 °C for 48h to determine the total mass of the organic forest floor. This variable gives an indication of the quality and thickness in the litter layer as well as nutrient availability because low-quality litter tends to degrade slowly and accumulates at the forest floor resulting in slower nutrient turnover and lower nutrient availability. Moreover, thick litter layers (e.g., in beech forests) may strongly impede emergence of tree saplings or forest herbs, while germination can also be hampered through phytotoxic components (Dzwonko and Gawronski 2002).

3.2. Stand conditions

Plant area index (PAI) was used as a proxy for forest structure. It is defined as half of the surface area of all aboveground plant parts (stems, branches and leaves) per unit surface area. Here PAI was computed per plot as the integral of the vertically resolved plant area per volume density profiles (in m²/m³). The latter were obtained from single-scan position terrestrial laser scanning (TLS) stationed in the center of each plot using a RIEGL VZ-400 (RIEGL Laser Measurement Systems GmbH, Horn, Austria), described in more detail in Meeussen et al. (2020). The PAI can be used as an indicator for forest structural complexity and denseness of the canopy layer, and is thus negatively correlated to light availability at the forest floor.

To characterize the composition of the overstorey (tree and shrub canopy), the average shade-casting ability (SCA) was used. This variable was calculated per plot as the cover-weighted average of species-specific SCA indices (Verheyen et al. 2012). These indices range from 1 (very low SCA, e.g. *Betula pubescens*) to 5 (high ability of mature trees to cast shade, e.g. *Fagus sylvatica*), and are listed for all canopy species in De Pauw et al. (2021).

To quantify the microclimate in each plot, the air temperature was recorded at 1 m above the forest floor using miniature temperature sensors (see Section 2.2). For each sensor, the absolute maximum temperature of the warmest month (microclimate alternative for BIO5 in WorldClim; Fick and Hijmans 2017) was calculated as mean daily 95th percentile of maximum temperatures recorded underneath the canopy during the warmest month of the measuring period. Such local temperature extremes are disproportionately important for the response of organisms to climate warming since a species' relative fitness is strongly determined by its heat tolerance (Huey et al. 2012). We use microclimate data instead

of weather station data (free-air temperature or macroclimate) as this provides more ecologically relevant information for forest understories (De Frenne et al. 2019).

3.3. Landscape conditions

The amount of forest habitat in the landscape surrounding each forest stand was characterized by the percentage area with a tree cover >20 % within a 500-m buffer zone. This variable was calculated based on GIS analyses using a satellite-based global tree cover map with spatial resolution of 30 m developed by Hansen et al. (2013).

For each forest stand, drought was characterized by means of the Standardized Precipitation Evapotranspiration Index (SPEI) index. The SPEI is a multi-scalar drought index based on macroclimatic data, and can be used to identify the onset, duration and severity of drought conditions based on the precipitation deficit and evaporative demand. The SPEI was calculated using the SPEI-package in R (Beguería and Vicente-Serrano 2017). First, gridded monthly precipitation and evapotranspiration data were extracted from CRU TS v4 climate datasets (Harris et al. 2020) for the period 1901-2019. This data was used to calculate the monthly climatic water balance (precipitation − evapotranspiration) for each site. Based on this water balance, monthly SPEI values can be computed at time scales between 1 and 24 months prior to the survey (i.e. accounting for the water balance of the previous 1 to 24 months). In this study, we specifically focused on the SPEI index of May 2018 accounting for the water balance of the previous 21 months ($SPEI_{21\text{-}May2018}$) because this value has been shown to exhibit the strongest correlation with European forest health (i.e. crown defoliation; Sousa-Silva et al. 2018). Drought-induced defoliation of the tree canopy is predicted to have important consequences for forest ecosystem functioning, e.g., by reducing productivity and carbon sequestration but at the same time also stimulating tree regeneration (Grossiord et al. 2014, Guada et al. 2016). Positive values of SPEI indicate a wet period, while negative values represent dry conditions relative to the reference period of 1980-2015. Note that SPEI values ranging between -0.67 and 0.67 are considered normal, while drought and severe drought are characterized by SPEI values below -0.67 and -1.28, respectively (Isbell et al. 2011).

Atmospheric pollution via nitrogen (N) deposition was estimated using modeled atmospheric N deposition data from the European Monitoring and Evaluation Program (EMEP). Data was extracted for the year 2016 at a resolution of 50 km × 50 km. For each forest stand, the total atmospheric N deposition rate was calculated by summing the modeled rates of wet and dry oxidized and reduced N. To account for higher N deposition rates in forest edges, values were corrected using a decreasing exponential curve developed by Wuyts et al. (2008). This curve was fitted based on in-situ throughfall measurements of oxidized and reduced N in oak-dominated forest edges (see Meeussen et al. 2020 for more details).

4. Data analysis

As a first step, the effect of latitude, forest management type and distance to edge (that is, the main gradient on which the study design was based) was tested for each of the biodiversity indices and ecosystem services separately using univariate Bayesian regression models (Bürkner 2017, 2021). For

phylogenetic diversity, functional diversity, nutrient cycling and soil carbon stock, a Gaussian error distribution was used, while for taxonomic diversity (count data), a Poisson distribution with a log link function was applied. The proportion of forest specialists, abundance of usable plants and tree seedling cover are typically zero-inflated and bounded between 0 and 1. Analyzing this data with classical linear models would therefore be sub-optimal (see Damgaard 2009). Instead, a zero-inflated beta distribution was applied, which first models the probability of absence (zero-inflation part, ZI) and then models the rest of the data using a beta-distribution (i.e., the proportion or cover of a species or species group conditional on it being present in that particular plot). For both the zero-inflated and beta part, a logit link function was used, whereas for the precision parameter a log link function was adopted (see Damgaard 2014, Herpigny and Gosseslin 2015). Potential nectar production was modeled with a gamma hurdle distribution, using a log link function for the shape parameter and a logit link function for the hurdle part. This is a two-component model consisting of a binomial mixed part based on presence/absence of understorey plant species per plot and a zero-truncated gamma model for the positive nectar production values. This analysis showed strong trade-offs in edge-to-interior patterns of the considered biodiversity and ecosystem service indices, with some increasing towards the forest interior and others increasing towards the edge (results are only available in Supporting Information **Figure S2**).

To account for these trade-offs, we repeated this analysis using a multivariate mixed-effect Bayesian modeling framework. First, we combined all biodiversity and ecosystem service indices into one multivariate multilevel model, which again assessed the effect of latitude, forest management type and distance to edge. Next, the design variables were substituted by the set of environmental predictors in the multivariate model. To represent edaphic conditions in each plot, sand fraction as a proxy for soil texture, pH and organic layer mass as proxy for litter quality was used. For forest structure and canopy composition, PAI, SCA and summer offset was included. To characterize landscape conditions, the percentage forest cover, SPEI (drought) index and N deposition were used. The organic layer mass and N deposition were log-transformed due to their skewed distribution. No interaction terms were considered to reduce complexity and avoid overparameterization of the model. Prior to running the model, multicollinearity among the nine predictor variables was assessed using variance inflation factors (VIFs) through the *vif* function in the *car* package (Fox and Weisberg 2019). For all models, VIFs were smaller than 2, indicating that no multicollinearity issues could be detected among the set of predictor variables (see Zuur et al. 2009).

All models were fitted with the probabilistic programming language Stan using the *brms* package in R version 4.2.1 (R core Development Team 2022). Due to the hierarchical nature of the dataset, all models were fit with transect ID (levels corresponding to the 45 edge-to-interior transects) nested within region (levels corresponding to nine regions) as random intercept. Default priors were used and all models were ran with four chains of thousand iterations each after a warm-up of thousand iterations. Convergence and mixing of chains were visually inspected using the *bayesplot* package (Gabry and Mahr 2018). Graphs show posterior means as well as 80 and 95 % credible intervals (CI) for the considered model parameters.

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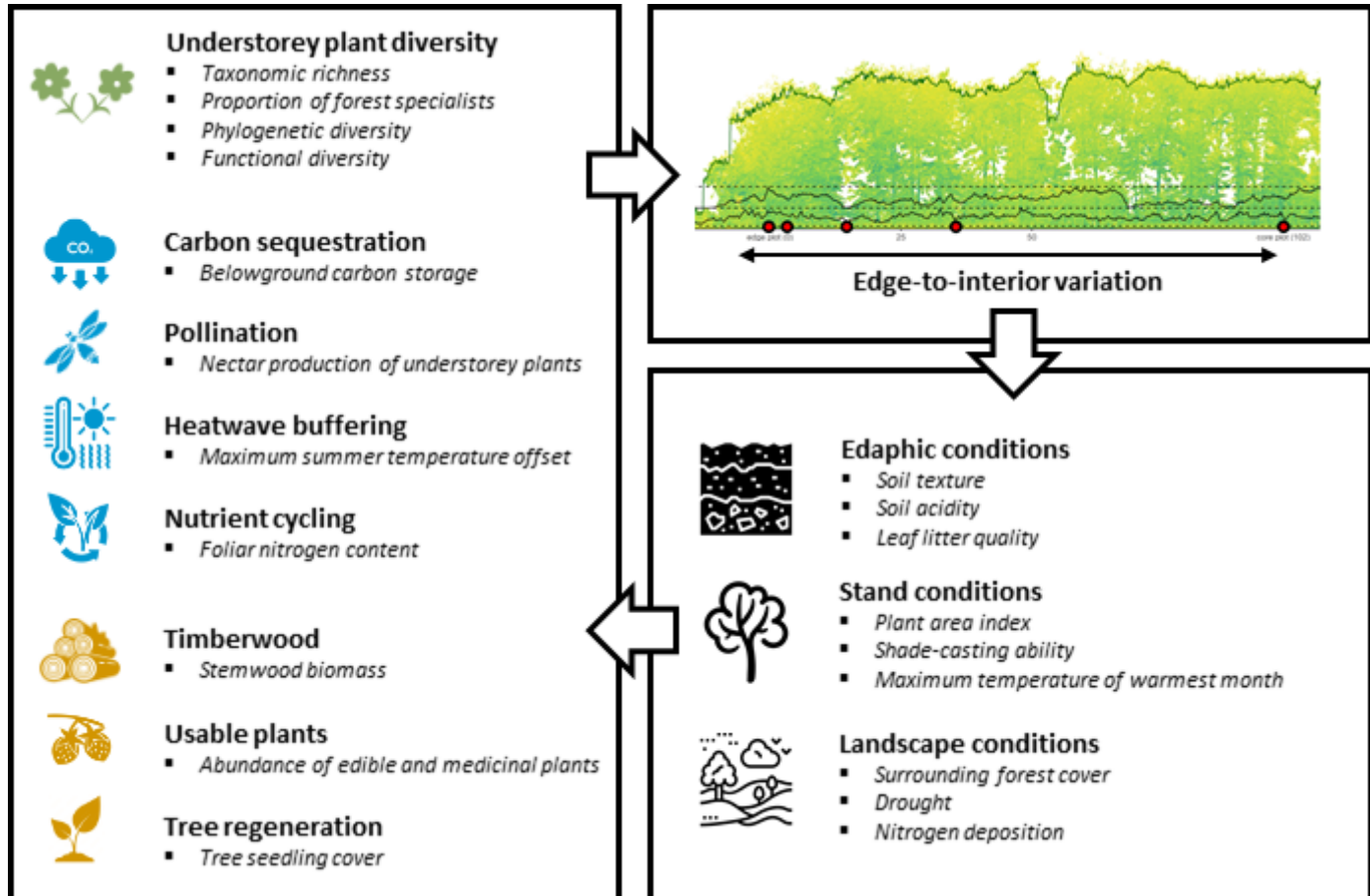
Figures

Figure 1

Selection of biodiversity and ecosystem service indices for which edge-to-interior patterns were investigated in deciduous forest stands across temperate Europe. Subsequently, the underlying effect of several environmental drivers acting across three biogeographical scales on these indicators was assessed to explain the observed edge-to-interior variation.
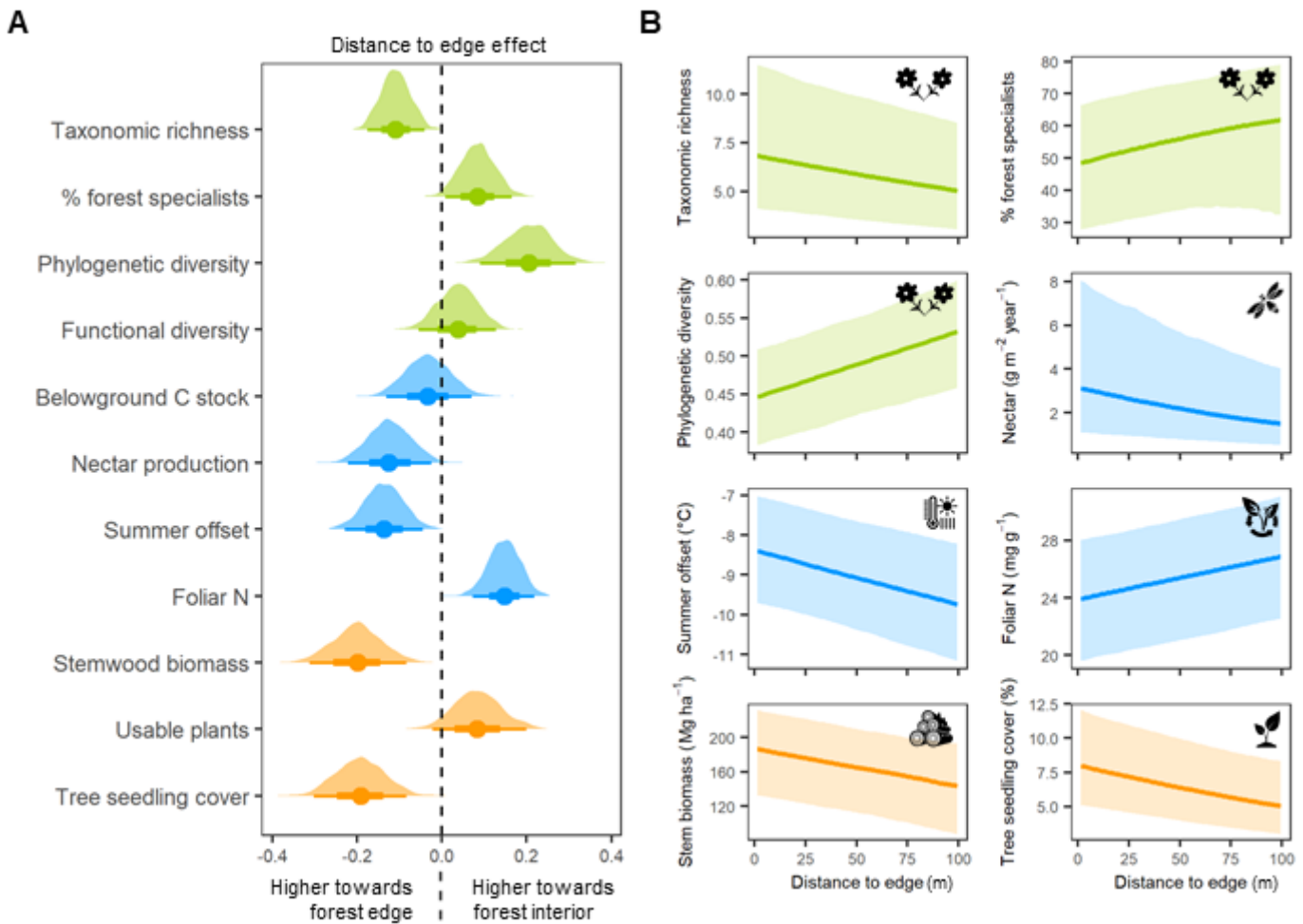
Figure 2

(A) Distance to edge effects on the considered biodiversity and ecosystem service indices. Circles represent mean standardized effect sizes with 80% (thick line) and 95% credible intervals (thin line) and distributions obtained from a multivariate Bayesian mixed-effect model. (B)Edge-to-interior gradients of biodiversity and ecosystem service indices for which 95% credible intervals don't overlap zero. Lines and 95% credible intervals are from Bayesian mixed-effect models. Colors denote biodiversity indices (green), regulating (blue) and provisioning ecosystem services (orange).
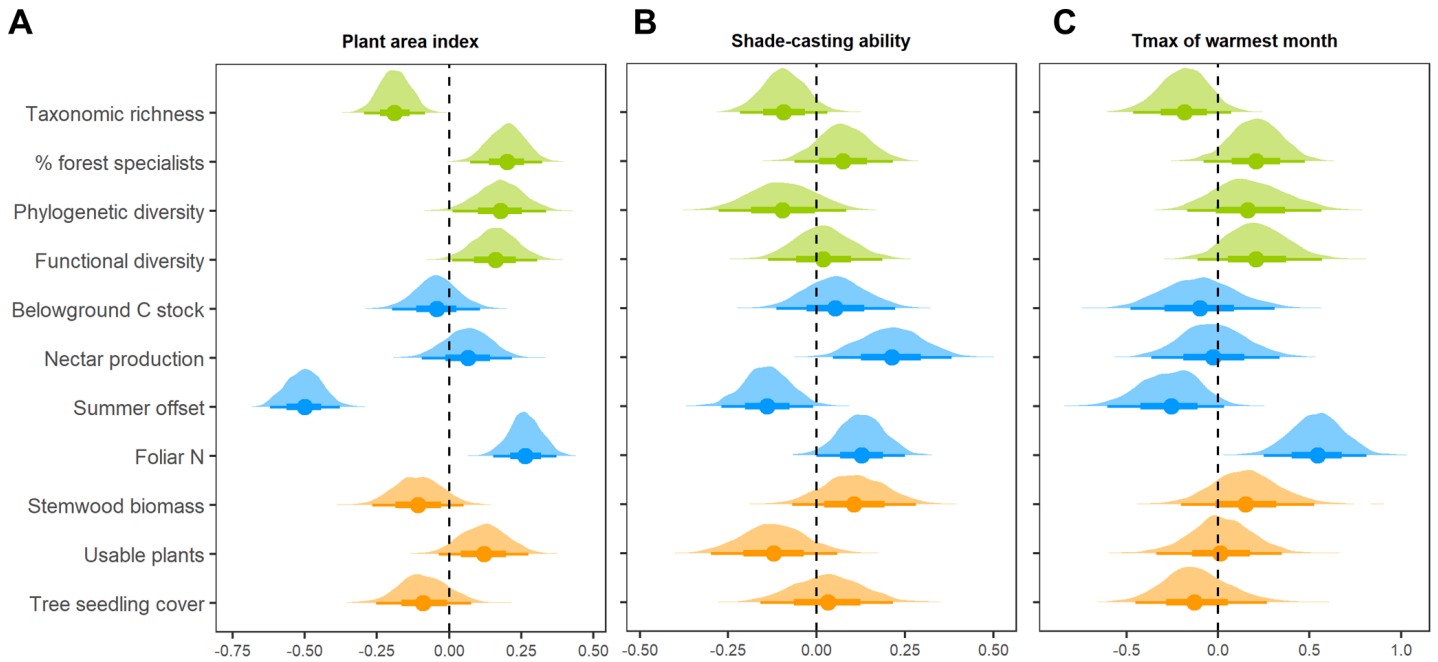
Figure 3

Effect of plant area index **(A)**, shade-casting ability **(B)** and maximum understorey (microclimate) temperature of the warmest month **(C)** on the biodiversity and ecosystem service indices quantified for each plot in the forest-edge-to-interior transects. Circles represent mean standardized effect sizes with 80% (thick line) and 95 % credible intervals (thin line) and distributions obtained from a multivariate Bayesian mixed-effect model. Colors denote biodiversity indices (green), regulating (blue) and provisioning ecosystem services (orange). Effects of the other environmental drivers (edaphic and landscape conditions) are shown in Figure S3.

Supplementary Files

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