Title

Trade-offs in biodiversity and ecosystem services between edges and interiors in European forests

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Abstract

Forest biodiversity and ecosystem services are hitherto predominantly quantified in forest interiors, well away from edges. However, these edges also represent a significant proportion of the global forest cover. We quantified plant biodiversity and ecosystem service indicators in 225 plots along forest edge-to-interior transects across Europe. We found strong trade-offs: phylogenetic diversity (evolutionary measure of biodiversity), proportion of forest specialists, nutrient cycling and heatwave buffering increased towards the interior, whereas species richness, nectar production potential, stemwood biomass and tree regeneration decreased. These trade-offs were mainly driven by edge-to-interior structural differences. As fragmentation continues, recognizing the role of forest edges is crucial for integrating biodiversity and ecosystem service considerations into sustainable forest management and policy.

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 45 forest edge-to-interior transects across a 2300-km wide latitudinal gradient across Europe (**Extended Data Figure 1**, **Table S1**). We specifically investigated outer forest edges (sensu [12]), where forest patches border on large non-forest areas (e.g. arable fields or grasslands). 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 services, 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 service provisioning[19]. In addition to these biodiversity attributes, we looked at several ecosystem services covering a mixture of regulating (soil carbon storage, pollination potential, heatwave buffering and decomposition) and provisioning services (timberwood, usable plants and tree regeneration). To quantify the potential supply of these ecosystem services, different indicators were selected based on an extensive literature search (see **Extended Data Figure 2** 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, while also accounting for gradients in latitude and forest management intensity (see **Methods S1** for details on the model structure). 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, decomposition and heatwave buffering exhibited an increase towards the forest interior, other biodiversity indices and ecosystem services such as taxonomic richness, pollination potential, timberwood and tree regeneration were promoted towards the forest edge. However, functional understorey plant diversity, soil carbon storage and the amount of usable plants remained unchanged between the forest interior and the edge (**Figure 1**).

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 multiple ecosystem services in forests. Moreover, an additional analysis using a multifunctionality index revealed that there was no pattern in multiservice delivery from edge to core in the forest patches, confirming that trade-offs between ecosystem services require stand-specific management strategies to optimize forests for specific or multiple ecosystem services (**Extended Data Figure 3**).

Plant area index (PAI) is defined as the one-sided surface area of vegetation material per unit ground surface area, and is a good proxy for forest structural complexity[4,21]. We found that PAI was the predominant driver of the observed trade-offs in biodiversity and ecosystem service delivery with significant positive effects on phylogenetic and functional diversity, decomposition and microclimate buffering but a negative effect on taxonomic richness. The effects of PAI show trends very similar to the effects of the distance to the edge, suggesting that edge effects are mostly driven by forest structure (**Figure 2**). Pollination potential was higher and heatwave buffering stronger when the canopy had a higher shade-casting ability, whereas a warmer forest microclimate enhanced decomposition (**Figure 2**). At the stand level, forest management practices that manipulate the structural complexity of the canopy layer can thus play a key role in the local optimization of ecosystem services' delivery. 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 multiservice delivery[22-25]. 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 (**Extended Data Figure 4**).

Our results are relevant for forest management, nature conservation and environmental policy. 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 ecosystem service delivery of European forests. At a landscape level, 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, depend on the stakeholder's priorities and require tailored management practices. At the local scale, forest management practices can further determine the delivery of specific ecosystem services (or a combination thereof) through canopy management (e.g., opening vs. densification). Both forest edges and interiors fulfil an important role in our present-day landscapes, and this should be taken into account when designing policy instruments and management strategies that ensure their future conservation.

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 (**Extended Data Figure 1**). 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[26]). 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[27]. *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 m^2/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 three regions (Belgium, Central Italy and Central Norway), forests of contrasting management intensity were selected at three elevation levels (low, intermediate and high elevations range between 26-365 m in Belgium, 115-908 m in Italy and 21-700 m a.s.l in Norway) to include an additional macroclimatic gradient caused by elevation of 1.5-4 °C MAT. In the other six regions, only lowland forest stands were selected with elevations ranging between 7 and 451 m a.s.l. This added up to 45 forest stands in total (see **Extended Data Figure 1**, **Table S1**).

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 (**Extended Data Figure 1**, **Table S1**). Vegetation surveys in these plots took place during the peak of the vegetation season (May-June 2018) according to the local phenology. In each plot, all vascular plant species were identified and their percentage ground cover was estimated relative to the plot area. Surveys were performed for every forest stratum separately (herb layer = all vascular plant species below 1 m, including seedlings, shrubs species and lianas, shrub layer = all shrub and tree species between 1-7 m and tree layer = all shrub and tree species taller than 7 m). Furthermore, soil and litter samples were collected from each plot, the forest structure was characterized using LiDAR and soil and air temperatures were measured using microclimate loggers. More details on selection criteria and establishment of the plot network can be found below as well as in [28-30].

2. Quantifying biodiversity and the potential supply of ecosystem services

2.1. Biodiversity

For each 3 m × 3 m plot, four biodiversity metrics were quantified for the understorey plant community, i.e., taxonomic diversity, proportion of forest specialists, phylogenetic diversity and functional diversity. Our focus on understorey biodiversity is justified because the understorey harboured on average 77.6% of all vascular plant species per plot, while the shrub and tree layer contained only 10.2% and 12.2% of all species, respectively. 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 [31]. All species categorized as 1.1 and 1.2 in this Europe-wide database of forest plant species were grouped as forest specialists (see [28]). 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 [32]. Functional diversity was calculated as Rao's quadratic entropy based on relative species abundances and pairwise functional differences among species[33]. 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. Trait values were standardized to mean zero and unit variance, and subsequently used to compute a species-species Euclidean distance matrix with Cailliez correction method to account for negative eigenvalues (see [30] for more details).

2.2. Regulating services

Four regulating services were quantified per 3 m × 3 m plot, i.e., topsoil carbon storage, understorey pollination potential, heatwave buffering and litter decomposition. 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 [34]). 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 [35] as the average of their upper and lower class limits. The latter are defined in [35] 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[36], and this buffering effect, and its effects on forest biodiversity and functioning, is most pronounced during summer[37]. 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 [4]). Finally, to quantify the decomposability of understorey leaf litter we used the cover-weighted mean foliar C:N ratio of the five most abundant plant species in each plot as a proxy. Leaf traits and especially foliar-level stoichiometry are a good indicator of ecosystem elemental cycling and potential decomposition rates[38,39]. Understorey decomposability can strongly influence nutrient cycling rates in temperate forests as nutrient concentrations are on average 1.5 to 5 times higher in the herbaceous understorey compared to the canopy tree foliage, depending on the nutrient considered (see [40] for a discussion). Besides, understorey leaf litter is generally more easily decomposable than tree leaf litter, and provides a continuous input throughout the year as opposed to tree litter[41]. On top of that, spring ephemerals play a particularly important role in nutrient circulation as they capture significant amounts of nutrients from the soil in early spring when trees are still dormant, thereby preventing leakage (often referred to as the "vernal dam hypothesis"[42]).

2.3. Provisioning services

Three key provisioning services were calculated, i.e., timberwood, abundance of usable plants and tree regeneration. Timberwood was quantified by the aboveground stem biomass in circular plots with 9 m radius, which was determined per plot using multi-species biomass equations based on diameter at breast height (DBH) developed by [43]. 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 [34] 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* [43]. 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 [34] for more details). Note that the use of larger plots (necessary to accurately quantify this service) unavoidably resulted in spatial autocorrelation between the plots close to the forest edge: with centers of these plots at 1.5, 4.5 and 12.5 m from the edge, the circular 9-m plots partially overlapped. However, an additional analysis showed that the effect of distance to the forest edge on stemwood biomass was still significantly negative ($\beta = -0.154 \pm 0.059$, 95% CI = [-0.252, -0.060]) after excluding the data from the plot at 4.5 m from the edge, thereby eliminating any overlap between plots. The abundance of usable plants was assessed per 3 m x 3 m plot based on the vegetation composition. The potential use for food, medical purposes or other uses of each plant species was determined based on different bibliographical sources (**Table S2**), and their abundances were summed to obtain a total value per plot. Plants were only considered ‘usable’ when used in Europe. Tree regeneration was assessed per 3 m × 3 m plot during the time of the floristic surveys (May-June 2018) 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_2O by shaking a 1:5 ratio soil/H_2O 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). The sand fraction was negatively correlated to both the percentage of silt ($r = -0.81$; $p < 0.001$) and clay ($r = -0.80$; $p < 0.001$) in the soils. Silt and clay fractions did not show a strong correlation with each other, but for the majority of the plots, the clay fraction was rather low (<30%). Therefore, the sand fraction was used for further analysis 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[44]. The variation of the three edaphic conditions along the edge-to-interior gradient is shown in **Figure S1**.

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 m^2/m^3). 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 [30]. 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[45]. 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 [30].

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[46]) 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[47]. We use microclimate data instead of weather station data (free-air temperature or macroclimate) as this provides more ecologically relevant information for forest understories[36]. The variation of the three forest stand conditions along the edge-to-interior gradient is shown in **Figure S1**.

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 [48].

For each forest stand, drought was characterized by means of the Standardized Precipitation Evapotranspiration Index (SPEI). 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[49]. First, gridded monthly precipitation and evapotranspiration data were extracted from CRU TS v4 climate datasets[50] 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 (onset of the data collection) accounting for the water balance of the previous 21 months ($\mathrm{SPEI}_{21\text{-May2018}}$) because this value has been shown to exhibit the strongest correlation with European forest health (i.e. crown defoliation[51]). 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[52,53]. 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[54].

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 [55]. This curve was fitted based on in-situ throughfall measurements of oxidized and reduced N in oak-dominated forest edges (see [29] for more details).

4. Statistical analysis

All models were fitted with the probabilistic programming language Stan using the *brms* package in R version 4.2.1[56], and can be fully reproduced from an online repository: https://doi.org/10.6084/m9.figshare.22354069. All biodiversity and ecosystem service indices were normalized to have zero mean and unit variance (Z-scores) prior to analyses (**Table S3**). Normalization puts indices on the same scale and enables efficient model estimation. To correct for skewness in some of the scaled indices, an additional log-transformation was performed (see **Methods S1** for details). 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 intercepts to account for potential interdependence of plots located in the same transect or region.

A multivariate Bayesian model[57,58] was fit to the four Z-transformed biodiversity indices and seven Z-transformed ecosystem services as response variables to account for correlations among them (and thus for potential trade-offs and synergies). A Gaussian error distribution was assumed allowing us to estimate residual correlations in *brms*. In the first model, distance to the forest edge was included as fixed effect. We used default priors (half-Student t with three degrees of freedom) which are weakly informative, thereby having only minimal effect on the parameter estimates whilst improving sampling efficiency and model convergence. The model was run with four independent chains of 4000 iterations each after a warm-up of 2000 iterations in the Hamiltonian Markov Monte Carlo (HMC) and its extension, the No-U-Turn sampler. The maximum tree depth was set to 12 and the target average acceptance probability to 0.99 to allow proper sampling. For some biodiversity (taxonomic richness and phylogenetic diversity) and ecosystem service (nectar production) indices, we assessed whether including overstorey (shrub and tree) species influenced the observed distance to edge patterns. However, the findings were virtually similar to those with only understorey species underpinning the robustness of our analyses (see supplementary analysis in **Figure S2**).

In the second model, distance to the forest edge was substituted by a set of environmental variables as fixed effects 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 maximum microclimate temperature of warmest month 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 between environmental predictors 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[59]. For all models, VIFs were smaller than 2, indicating that no multicollinearity issues could be detected among the set of predictor variables (see [60]). All predictors were standardized to zero mean and unit variance (Z-scores), as is recommended practice when working with predictors on different scales. We used the same random effects, priors, warm-up, sampling and model settings as in the first model described above.

Convergence and mixing of chains in the two models were visually inspected using the *bayesplot* package[61] as well as the Gelman-Rubin convergence statistic (Rhat)[62]. With Rhat < 1.01, the convergence of all parameters was considered acceptable and sufficient samples were available for all of them (i.e., the ratio of effective samples over the total number of post warm-up iterations was larger than 10 %). Graphs show posterior means as well as two-sided 80 and 95 % Bayesian credible intervals (CI) for all fixed model parameters. We considered modelled parameter estimates to demonstrate an effect on the response variables if the Bayesian 95 % CIs of the posterior distribution did not overlap with zero, and a marginal effect as the 80 % CIs did not overlap with zero. Model fits were evaluated with posterior predictive checks (**Figure S3-S5**) as well as marginal and conditional R^2 using the *bayes_R2* function in brms (**Table S4-S7**). A detailed description of the models is given in **Methods S1**.

In a final analysis, we quantified a multiservice delivery index for each plot and assessed how this index varied along the edge-to-interior transects. This analysis revealed that there was no pattern in multiservice delivery from edge to core in the forest patches, confirming the trade-offs we report in this study (with the supply potential of some services being greater in the edge and others greater in the interior, hence masking a pattern in multiservice delivery). Details and results of this analysis are given in **Extended Data Figure 3**, **Figure S6** and **Table S8-S9**.

Data Availability

All data needed to reproduce the analyses and figures presented in this study are available on Figshare (https://doi.org/10.6084/m9.figshare.24559891.v1) and GitHub (https://github.com/to-vanneste/tradeoffs.git).

Code Availability

All R code needed to reproduce the analyses and figures presented in this study are available on Figshare (https://doi.org/10.6084/m9.figshare.24559891.v1) and GitHub (https://github.com/to-vanneste/tradeoffs.git).

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Author Contributions Statement

TV, LD, PDF, PV and KV conceived and designed the study. EDL, CM, SG, KDP, PS, KB, JB, KC, SAOC, MD, CG, BJG, P-OH, GI, JL, SL, AO, QP, JP, FS, FS, HV, FZ and PV collected the data. CM, SG, KDP and PS processed the data, while TV and LD performed the data analyses under supervision of PDF and KV. TV and LD drafted the manuscript and all authors contributed to later versions.

Competing Interests Statement

The authors declare no competing interests.

Tables

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Figure legends/captions

Figure 1. Effect of distance to the forest edge on biodiversity and ecosystem service indices.

(A) Distance to edge effects on the considered biodiversity and ecosystem service indices quantified for each 3 m × 3 m plot in the forest-edge-to-interior transects (n = 225 biologically independent plots). Circles represent mean standardized effect sizes with 80% (thick line) and 95% credible intervals (thin line) and distributions obtained from a multivariate Bayesian model. **(B)** Edge-to-interior gradients of biodiversity and ecosystem service indices for which 95% credible intervals don't overlap zero. All datapoints are shown as circles and represent the 3 m × 3 m plots (n = 225) in the forest-edge-to-interior transects. Lines and shading denote mean model predictions ± 95% credible intervals from Bayesian models. Colours denote biodiversity indices (green), regulating (blue) and provisioning ecosystem services (orange). The selected biodiversity indices are taxonomic richness, proportion of forest specialists, phylogenetic diversity and functional trait diversity of the forest understorey plant communities, while the ecosystem service indicators are soil carbon storage (as proxy for soil C sequestration), nectar production (as proxy for pollination potential), summer offset (as proxy for heatwave buffering capacity), foliar C:N ratio (as proxy for litter decomposition), stemwood biomass (as proxy for timberwood), abundance of usable plants and tree seedling cover (as proxy for regeneration). Given that the response variables were normalised using Z-scores in the multivariate model, a back-transformation was used in the different subpanels for a clearer visual interpretation. Icons were extracted from The Noun Project (https://thenounproject.com).

Figure 2. Effect of forest stand characteristics on biodiversity and ecosystem service indices.

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 3 m × 3 m plot in the forest-edge-to-interior transects (n = 225 biologically independent plots). Circles represent mean standardized effect sizes with 80% (thick line) and 95 % credible intervals (thin line) and distributions obtained from a multivariate Bayesian model. Colours denote biodiversity indices (green), regulating (blue) and provisioning ecosystem services (orange). The selected biodiversity indices are taxonomic richness, proportion of forest specialists, phylogenetic diversity and functional trait diversity of the forest understorey plant communities, while the ecosystem service indicators are soil carbon storage (as proxy for soil C sequestration), nectar production (as proxy for pollination potential), summer offset (as proxy for heatwave buffering capacity), foliar C:N ratio (as proxy for litter decomposition), stemwood biomass (as proxy for timberwood), abundance of usable plants and tree seedling cover (as proxy for regeneration). Effects of the other environmental drivers (edaphic and landscape conditions) are shown in **Extended Data Figure 4**.

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