Edge influence on understorey plant communities depends on forest management

Edge influence depends on management

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Abstract

Questions

Does the influence of forest edges on plant species richness and composition depend on forest management? Do forest specialists and generalists show contrasting patterns?

Location

Mesic, deciduous forests across Europe.

Methods

Vegetation surveys were performed in forests with three management types (unthinned, thinned 5-10 years ago and recently thinned) along a macroclimatic gradient from Italy to Norway. In each of 45 forests, we established five vegetation plots along a south-facing edge-to-interior gradient (n = 225). Forest specialist, generalist and total species richness, as well as evenness and proportion of specialists, were tested as a function of the management type and distance to the edge while accounting for several environmental variables (e.g. landscape composition and soil characteristics). Magnitude and distance of edge influence were estimated for species richness per management type.

Results

Highest total species richness was found in thinned forests. Edge influence on generalist plant species richness was contingent on the management type, with the smallest decrease in species richness from the edge-to-interior in unthinned forests. In addition, generalist richness increased with the proportion of forests in the surrounding landscape and decreased in forests dominated by tree species that cast more shade. Forest specialist species richness however, was not affected by management type or distance to the edge, but only increased with pH and increasing proportion of forests in the landscape.

Conclusions

Forest thinning affects the plant community composition along edge-to-interior transects of European forests with richness of forest specialists and generalists responding differently. Therefore, future studies should take the forest management into account when interpreting edge-to-interior because both modify the microclimate, soil processes and deposition of polluting aerosols. This interaction is key to predict the effects of global change on forest plants in landscapes characterized by a mosaic of forest patches and agricultural land, typical for Europe.

Keywords

Edge effects, edge influence, forest specialists, generalists, herbaceous layer, patch contrast, plant biodiversity, species richness, thinning, understorey

Introduction

Forests harbour more than two-thirds of terrestrial biodiversity (Millennium Ecosystem Assessment, 2005). In Europe, dramatic deforestation in the past has led to habitat loss and fragmentation, both being major drivers of biodiversity loss (Secretariat of the Convention on Biological Diversity (CBD), 2010). Habitat fragmentation creates new forest edges and subsequently leads to a higher edge to interior ratio (Saunders, Hobbs, & Margules, 1991). At least 20 % of the world's forest area lies within 100 m of a forest edge (Haddad et al., 2015), indicating the need to further our understanding of how edges affect forest biodiversity and functioning. Compared to forest interiors, forest edges experience more solar radiation, higher wind speeds and faster air mixing, resulting in higher light availability, decreased soil moisture, higher maximum and lower minimum temperatures, and increased diurnal and seasonal variability in temperatures (Chen et al., 1999; Gehlhausen, Schwartz, & Augspurger, 2000; Matlack, 1993; Schmidt, Lischeid, & Nendel, 2019; Tuff, Tuff, & Davies, 2016). In addition to altered microclimatic conditions, forest edges, as opposed to forest interiors, are also characterized by a higher seed influx of non-forest species (Devlaeminck, Bossuyt, & Hermy, 2005), differences in disturbance regimes, and higher nitrogen (N) and carbon (C) stocks (Remy et al., 2016). These biotic and abiotic factors all influence understorey plant communities, which contain more than 80 % of total plant species richness in temperate forests and are essential for several ecosystem functions such as nutrient cycling, carbon dynamics and tree regeneration (Gilliam, 2007; Landuyt et al., in press; Whigham, 2004).

In general, higher understorey species richness occurs at forest edges because those environmental conditions are intermediate between the forest interior and the matrix. But not all species respond similarly, and species can be grouped according to their ecological preferences (Gehlhausen et al., 2000; Guirado, Pino, & Rodà, 2006; Murcia, 1995). For example, a study in temperate forests in northern France found that edge species were more often thermophilous (warmth-loving), basophilous (alkaline-loving), nitrogen- and light-demanding, and species reproducing by seed only (and not clonally) (Pellissier et al., 2013). In contrast, interior species were more often slow-colonizing species, acidophilous and species reproducing both by seeds and vegetatively (Pellissier et al., 2013). The effect of distance to edge, hereafter also referred to as 'edge influence', on species richness has been related to mechanisms such as past land-use change (Berges et al., 2016), changes in light regime (Honnay, Verheyen, & Hermy, 2002) and altered soil moisture content (Gehlhausen et al., 2000).

While edge influence has been well studied in dense forests in single regions or landscapes, less is known on how edge influence interacts with forest management across forest types in Europe. Similar to habitat fragmentation, forest management also affects forest microclimate, and thus light availability, temperature, soil moisture and nutrient availability (Ash & Barkham, 1976; Grayson et al., 2012). Understorey plant communities respond to changes in light and soil disturbances which can be induced by forest management practices (Ash & Barkham, 1976; Aude & Lawesson, 1998; Decocq et al., 2004; Scolastri, Cancellieri, Iocchi, & Cutini, 2017; Strubelt, Diekmann, Griese, & Zacharias, 2019; Widenfalk & Weslien, 2009). It can be expected that forest management, which influences the overall forest structure and edge physiognomy, interacts with edge influence on understorey species richness and composition by reducing the edge contrast with the surrounding matrix (Cadenasso & Pickett, 2001; Harper et al., 2005; Ries, Fletcher Jr, Battin, & Sisk, 2004). For example, open, thinned forests might be more susceptible to the penetration of wind and seeds into the forest interior due to lower edge contrast. Moreover, energy exchange in open forests is also determined by the lower albedo of dark surfaces in the understorey, such as the soil surface, litter and tree trunks, instead of green leaves of the canopy cover (Wright, Kasel, Tausz, & Bennett, 2010).

Here we studied understorey vegetation biodiversity and composition responses to distance to the forest edge in ancient forest stands (i.e. continuously forested since the first available land use maps and thus never converted to another land use type ever since) with different management types (unthinned, thinned and recently thinned) in 45 edge-to-interior forest transects across Europe. Our aim was to disentangle the effects of the management type and the distance to the edge on alpha diversity of understorey plants in multiple European regions, while accounting for environmental characteristics. We expected to find (1) higher species richness at edges, with forest specialists and generalists responding differently to management intensity and (2) interactions between distance-to-edge influence and forest management on richness. For example, the edge-to-interior gradient is expected to become weaker in increasingly managed (thinned) forests and thus have less impact on understory plant diversity than in recently thinned forests.

Materials and methods

Study region and set up

Our study area includes the temperate, Mediterranean and boreonemoral forest biomes of Europe. We focus on deciduous broadleaved forests, which are hotspots of biodiversity and a widespread and ecologically important forest type in most of Europe (Brus et al., 2012). Study sites are situated in typical European fragmented landscapes, with forest patches surrounded by a matrix of arable fields and grasslands. Forest stands were selected across nine regions along a latitudinal gradient from Italy to Norway to capture much of the macroclimatic variation across Europe (**Fig. 1a**). In the south, middle and north of this latitudinal gradient, more specifically in Italy, Belgium and Norway, an elevational gradient with three levels (low, medium and high) was included to capture macroclimatic variation due to elevation. Study sites of the elevational gradient were selected to have a similar understorey composition as in the lowlands of the same region (with understorey plant species typical for Natura2000 habitat types 9120 and 9130). A total of 15 sites were thus selected: six regions without an elevational gradient, and three regions with three levels of elevation (**Fig. 1**). A study site description can be found in **Appendix S1**.

Forest stands were selected in a standardized way to increase comparability of sites. The stands, with a minimum forest area of 1 ha, were deciduous and mainly dominated by oaks (*Quercus robur*, *Q. petraea*, *Q. cerris*), *Fagus sylvatica*, *Betula pubescens*, *Populus tremula*, *Ulmus glabra*, *Alnus incana* and *Carpinus betulus*. All sites had the same type of land-use history (ancient forest) and intermediate soil moisture (mesic).

At each site, three forest stands with different forest management were selected: unthinned (1), thinned (2) and recently thinned (3) (**Fig. 1b**) (see **Appendix S2**: site selection protocol).

1. The first type (unthinned) is typically a dense forest, with a well-developed shrub layer, 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 densitometer measurements, **Appendix S3**), and not recently thinned for at least 10 years and mostly > 30 years ago , indicated by e.g. the absence of cut tree stumps.
2. The second type is intermediate to types one and three (openness 6.5 ± 0.6 %, basal area 31.4 ± 1.9 m^2/ha; **Appendix S3**); even-aged and regularly thinned, but not recently (probably 5-10 years ago).
3. The third type is typically an open, even-aged and recently thinned forest (probably within 4 years of sampling), indicated by the presence of cut tree stumps, and characterised by the absence of a shrub and subdominant tree layer, with low basal area (21.6 ± 1.3 m^2/ha) and low canopy cover (mean openness 14.8 ± 2.1 %, **Appendix S3**).

We established 100 m transects from the southern forest edge to the forest interior of each forest stand at each site. We thus established 45 transects in total (15 sites x 3 management types). The transect started at the hypothetical line of tree stems at the edge of the forest stand (0 m). These edges are outer edges, bordering a matrix of agricultural land and were created by ancient deforestations (**appendix S1**). Because edge orientation affects understorey species richness and microclimatic conditions (Didham & Lawton, 1999; Honnay et al., 2002; Matlack, 1993; Orczewska & Glista, 2005), we standardized this by only locating the transects at the south-facing edge (or south-western or south-eastern), bordering with either grassland or arable land (**appendix S1**). The transect was installed perpendicular to the edge and at least 100m from any another edge. Elements that affect the microclimate at the edge or along the transect (such as water bodies, buildings and wide, tarmacked roads) were avoided.

Along each transect, five 3 by 3 m² quadrats were installed at an exponentially increasing distance from the forest edge because of the exponential change in microclimatic condition close to the edge (Chen et al., 1999; Didham & Lawton, 1999), resulting in a total of 225 plots. The centres of the plots were thus at distances of 1.5 m, 4.5 m, 12.5 m, 35.5 m and 99.5 m from the edge (**Fig. 1c**). However, in six plots the centres were located at different distances (for example at 18m instead of 12.5m), for instance, to avoid the influence of forest paths on the vegetation.

Plant biodiversity variables: understorey

Vegetation surveys were conducted at the peak of vegetation biomass from May until early July 2018, depending on the regional phenology (**Appendix S1**). All vascular plant species were identified and their percentage ground cover visually estimated in teams of two persons. The herb layer included all vascular species, both woody plants smaller than 1 m and non-woody plants, as well as lianas. The shrub layer was defined as all woody species with a height between 1 and 7 m and the tree layer as all trees reaching heights more than 7 m. *Corylus avellana* was always classified into the shrub layer, regardless of its height. Species nomenclature follows Euro+Med (2006).

Plant species of the herb layer were assigned to five forest guilds following Heinken et al. (2019): species which can be mainly found in the closed forest (1.1); species which occur typically along forest edges and in forest openings (1.2); species which can be found in both forest and open vegetation (2.1); species which can be found partly in forest, mainly in open vegetation (2.2); and true open habitat species (O) (**Appendix S4**). In our data set, few species belonged to forest guilds 1.2, 2.2 and O (with 70, 45 and 86 % the plots containing zero species of these guilds, respectively), and therefore all species belonging to 1.1 and 1.2 were grouped as forest specialists and those belonging to 2.1, 2.2 and O as generalists. Hereinafter, forest guild 1.2 will be referred to as closed forest species. According to Heinken et al. (2019) species can shift forest guilds over the geographical gradient, and thus the forest guild a certain species was assigned dependent on the region it was observed in. Individuals only determined to the genus level were excluded from this categorisation, as well as seven species (out of 383 taxa) for which no data was available to classify them as forest specialists or generalists (**Appendix S4**).

Environmental predictor variables

Light transmission differences due to overstorey species identity were accounted for by means of the shade casting ability (SCA) index. The SCA index is a species-specific, expert-based index that varies from 1 to 5, indicating low to high shade casting ability of the canopy species (Verheyen et al., 2012). The SCA of the canopy (the shrub and tree layer combined) was calculated as a cover weighted mean of the scores listed in **Appendix S5**.

In all 225 plots, topsoil samples (0-10 cm depth, diameter 30mm) were collected for chemical analyses (pH and soil nutrient concentration) and between 10-20 cm depth for texture analysis (% silt, clay and sand). Within each plot, five random subsamples were taken after removal of the litter layer, and pooled together. The 0-10 cm soil samples were dried to constant weight at 40 °C for 48 h, ground and sieved over a 2 mm mesh. These samples were analysed for pH-H_2O by shaking a 1:5 ratio soil/H_2O mixture for 5 min at 300 rpm and measuring with a pH meter Orion 920A with pH electrode model Ross sure-flow 8172 BNWP, Thermo Scientific Orion, USA. To measure the total concentration of C and N in the soil, subsamples were combusted at 1200 °C and the gases were measured by a thermal conductivity detector in a CNS elemental analyzer (vario Macro Cube, Elementar, Germany). Bioavailable phosphorus (P) which is available for plants within one growing season (Gilbert, Gowing, & Wallace, 2009) was measured by extraction in $NaHCO_3$ (P_{Olsen}; according to ISO 11263 (1994)) and colorimetric measurement according to the malachite green procedure (Lajtha, Driscoll, Jarrell, & Elliott, 1999). Total calcium (Ca), potassium (K) and magnesium (Mg) were measured by atomic absorption spectrophotometry (AA240FS, Fast Sequential AAS) after complete destruction of the soil samples with $HClO_4$ (65 %), HNO_3 (70 %) and H_2SO_4 (98 %) in teflon bombs for 4 h at 150 °C. Texture analysis was performed by sieving and sedimentation with a Robinson-Köhn pipette according to ISO 11277 (2009).

Landscape and topographic characteristics were derived from satellite-based global tree cover data with a spatial resolution of 30 m (Hansen et al., 2013) and a pan-European digital elevation model (DEM) with a spatial resolution of 25 m, using Copernicus data and information from the European Union (EU-DEM, 2018). The proportion of forest cover, hereafter proportion forest, was assessed within a circular buffer area with a radius of 500 m and measured as the percentage of area covered by a minimum tree cover of 20 % (Hansen et al., 2013). Forest edge density was computed by transforming the forest cover mask into contour lines and summing up their length within the 500 m buffer area, using the *rasterToContour* function in the R package *raster* (Hijmans, 2019).

The mean annual temperature (°C) and De Martonne's aridity index were used to take into account macroclimatic variation from latitudinal and elevational differences. De Martonne's aridity index was calculated by dividing the mean annual precipitation (mm) by mean annual temperature plus 10°C (de Martonne, 1926). Temperature and precipitation data were extracted for each plot from the CHELSA database for 1979-2013 (Karger et al., 2017).

Data analysis

In total, six response variables were tested comprising measurements for alpha diversity of the understorey layer. The number of forest specialist species (1), as well as generalist richness (2) and total species richness (3) per plot, were calculated. In addition, Pielou's evenness index (4) (Pielou, 1966) and the proportion of forest specialists compared to the total number of species (5) were also determined. As two forest guilds (1.1 and 1.2) were grouped as forest specialists, the number of closed forest species (6) was also calculated to be able to compare the closed forest species and forest specialists.

Two out of 225 plots did not contain any understorey species. These two plots were omitted for the analysis on evenness and proportion of specialists.
To take into account the hierarchical structure of the data, (generalized) linear mixed-effects models were used with transect nested within region as random effect (random intercepts). Poisson error distributions were applied for the count data (such as species richness), while a binomial distribution was used for the proportion of forest specialists. Evenness was initially modelled with a binomial distribution as well, but this models had convergence issues, and therefore a Gaussian error distribution was applied for the model presented here.
Models were built in a two-step process (Perring et al., 2018). First, a model including latitude, elevation (as continuous variables), soil variables (pH, C:N ratio, % silt, % clay, Olsen-P and K), SCA, the proportion of forest and edge density was assessed for each of the eight response variables. Mg, Ca and sand (%) were highly correlated with other explanatory variables and thus left out of the analysis (**Appendix S6**). Olsen-P and K were log-transformed to symmetrize the skewed distribution and eradicate influential outliers. For the sake of simplicity, quadratic terms were not included to keep the number of explanatory variables as low as possible. The most parsimonious model (single best model) was selected based on the Akaike Information Criterion (AIC) with the *dredge*-function of the package *MuMIn* (Barton, 2018). Second, the focal explanatory variables, that is, the distance to the edge and the forest management type, were added to the simplified model as a two-way interaction, resulting in the final model. Parallel to these analyses, the same procedure was followed for analyses taking macroclimatic variables into account by replacing latitude and elevation with the mean annual temperature and De Martonne's aridity index.

The distance to the edge was log-transformed to linearize the relationship. The figures presented show the back-transformed results. All continuous explanatory variables were scaled (z-transformation) to facilitate comparisons. A protocol for data exploration and model evaluation was followed precisely (Zuur, Ieno, & Elphick, 2010). All analyses were performed in R (R Core Team, 2018), with packages *lme4* (Bates, Machler, Bolker, & Walker, 2015) and *MuMIn* (Barton, 2018).

In addition, the magnitude of edge influence (MEI) and distance of edge influence (DEI) were calculated per management type for specialists, generalist and total species richness. For each transect, MEI was estimated for the four edge plots as $(e - i)/(e + i)$ where e is the response value at the edge (either at 1.5 m, 4.5 m, 12.5 m or 35.5 m), and i the response value at the forest interior (99.5 m), resulting in four MEI values per transect. We report the mean and standard error of MEI calculated per management type. Next, we calculated the distance at which MEI was significantly different from zero per management type (this is the DEI), by means of a randomization test of edge influence (RTEI) with blocking (Harper & Macdonald, 2011). A routine provided by Dodonov, Harper, & Silva-Matos (2013) was used: (1) For each distance to the edge, the observed MEI was calculated relative to the interior plot (99.5m). (2) A data-set was created with the edge and interior values. (3) One value was randomly assigned to be the new edge value, and the leftover as the interior value. (4) We calculated randomized MEI based on the randomized edge and interior values. (5) Steps 3-4 were repeated 5000 times for a significance level of 1%, resulting in a distribution of randomized MEI values. (6) Two times the percentile of the observed MEI within the distribution of the randomized MEIs was used as the p-value (alpha = 0.01) for this distance. This routine was repeated per distance to the edge per management type. DEI was estimated as the farthest distance from the edge that was preceded by no more than one non-significant value (Dodonov et al., 2013).

Results

In total, 351 understorey plant species were identified to the species level, and 32 only to the genus level. Of all species, 97 were forest specialists across all regions and 224 generalists, while 23 species switched forest guilds across regions (**Appendix S4**). Recently thinned forest stands were in general richer in generalists compared to unthinned forest stands (on average 13.3 and 11.4 species, respectively) (**Fig. 2**). The total number of species as well as the number of generalists decreased from the edge to the interior (**Fig. 2**), but for generalists this pattern was dependent on the management type: in unthinned forests, no effect of the distance to the edge was detected (**Fig. 2c**). However, in thinned and recently thinned forests, the number of generalist species was highest at the edge, and declined exponentially towards to forest interior. Generalist richness decreased more strongly from edge to interior in thinned than in recently thinned forests. In thinned (and recently thinned) forests, on average 8.3 (8.3) generalist species were found at the edge, compared to only 4.5 (5.7) generalist species at the forest interior. Because of the decreasing generalist and stagnant specialist numbers from the edge to interior, the proportion of specialist species increased (**Table 1**). Neither the distance to the edge nor the management type influenced the number of forest specialists (**Fig. 2b)**.

Richness of forest specialists, generalists and total species richness increased with the increasing proportion of forest in a radius of 500 m (**Fig. 3a**). Furthermore, the community-weighted SCA of the tree and shrub layer positively affected the proportion of forest specialists, but negatively affected total species richness and generalist richness (**Fig. 3c**). In contrast, soil pH was positively correlated with the total number of plant species as well as with the species richness of forest specialist (**Fig. 3b**). Finally, the proportion of forest specialists was the highest when the amount of edge in a radius of 500 m was minimal (**Table 1**). Evenness increased with percentage silt in the topsoil (**Table 1**). Analysing the closed forest species richness alone resulted in the same findings as the results on specialist richness (**Appendix S7**).The macroclimatic analysis, with mean annual temperature and De Martonne's aridity index replacing latitude and elevation, did not differ much with the initial analysis (reported in **Appendix S8)**.

The MEI and DEI results were in line with the outcomes of the previous results. MEI and DEI varied across management types and species richness variables (**Fig. 4**). MEI was greatest in (recently) thinned forests for generalists and total richness, while it was close to zero for forest specialist richness (**Fig. 4a**). The edge influence was not significant for forest specialists in all three management types (**Fig. 4b**). Total species and generalist richness were significantly higher at the first 1.5-4.5 m and 18-35.5 m respectively in (recently) thinned forests. In unthinned forests, the MEI was not significantly different from zero for any of the three response variables.

Discussion

Forest management interacted with edge-to-interior gradients on generalist species richness in ancient forests along a latitudinal gradient across Europe. Contrary to our hypothesis, the edge-to-interior gradient in (generalist) species richness was stronger in thinned forests than in unthinned forests, where richness gradients were weaker. Forest edges in unthinned forests were likely more densely vegetated along the entire vertical gradient compared to those in thinned and recently thinned forest. This 'vegetation wall' may thus have served as an effective barrier that buffered the forest interior from seed inflow from the matrix (Devlaeminck et al., 2005), from wind and solar radiation (Honnay et al., 2002; Matlack, 1993), and the influx from warm air thereby preserving the microclimatic conditions typical of the forest interior. In this study, edge sealing might have occurred at the non-forest side of the 0 m edge plot, as the detected MEI was close to zero. In recently thinned forests, forest edge and interior microclimates did probably not contrast much due to more incoming solar radiation in the forest interior, also resulting in a more gradual gradient which levels off more quickly in species richness. For example, sparse Mediterranean temperate forests in southern Australia are found to have less pronounced edge influence on the microclimate than in closed forests, with even reversed patterns being recorded (e.g. warmer and drier forest interiors compared to edges) (Wright et al., 2010). In thinned forests, however, interior and edge conditions were presumably most dissimilar, and edges relatively open, resulting in steep edge-to-core gradients in species richness penetrating 35.5 m into the forest. Hence, forest management modifies the contrast in structure and composition, which in turn determines the magnitude and distance of edge influence (Harper et al., 2005).

The distance to the edge had the most significant effects on species richness. Indeed, the decline of total species richness from edge to interior corroborates the findings of Fraver (1994), Gehlhausen et al. (2000), Guirado et al. (2006), Honnay et al. (2002), Pellissier et al. (2013), Vallet, Beaujouan, Pithon, Roze, and Daniel (2010) and Willi, Mountford, and Sparks (2005). Higher species richness at forest edges compared to forest interiors was mostly driven by increased generalist richness at the edge, while forest specialists richness was constant along the edge-to-interior transects. Forest specialists thrive best in spatially/temporal varying intermediate light conditions and are characterized by a slow demography (Whigham, 2004), and can thus persist at the edge. At the same time, many generalists can opportunistically colonize edge habitats characterized by increased disturbance regimes (Godefroid & Koedam, 2003), warmer temperatures and a relatively higher amount of available resources, such as light and nutrient inputs (Brunet et al., 2011; Thimonier, Dupouey, & Timbal, 1992). As a result, forest edges were more species-rich compared to interiors in our study (respectively 14 and 11 species per plot, on average), and the proportion of forest specialists was highest in the forest interior, and lowest at the edge. Conversely, some studies also detected decreasing richness from edge to interior for forest specialists, for instance, in oak (*Q. robur*) and chestnut (*Castanea sativa*) dominated forests in northern France (Vallet et al., 2010).

However, their study was performed at a smaller, regional scale and forests were not selected to be continuously forested since the last available land use maps. In addition, Guirado et al. (2006) observed higher forest species richness at the edge compared to the interior over a distance of 500 m in oak and pine dominated Mediterranean forests in Spain, indicating that distance-to-edge influence is dependent on the specific condition of the studied system.

Furthermore, forest management also influenced species diversity patterns. Recently thinned forest stands harboured overall higher generalist diversity compared to thinned and unthinned stands. In contrast, forest specialist as well as total species richness did not consistently differ between the three tested forest management. Forest management practices, such as thinning, indeed can strongly modify the understorey environmental conditions by enhancing the amount of solar radiation penetrating the canopy, increasing disturbances and modifying resource availability and microclimatic conditions (e.g. light, temperature, humidity and soil moisture) (Ash & Barkham, 1976; Grayson et al., 2012). Changes in the amount of light along with microclimatic stability and soil disturbance are the most important drivers of understory plant diversity following forest management practices (Ash & Barkham, 1976; Aude & Lawesson, 1998; Brunet, FalkengrenGrerup, & Tyler, 1996; Decocq et al., 2004; Scolastri et al., 2017; Strubelt et al., 2019; Widenfalk & Weslien, 2009), which explains why light-demanding generalists can thrive in thinned, open forests. Forest specialists, on the contrary, can tolerate the changed environmental conditions. Forest specialists often lag behind environmental drivers (Hermy, 2015), requiring them to cope with altered environmental conditions (Decocq et al., 2004), and show extinction debts (Vellend et al., 2006). On the other hand, most forest specialists depend on intermediate disturbance for long-term survival.

While we focussed on the effects of forest edges, forest management and their interaction, we also took into account environmental variables that potentially influence understorey species richness and composition. The amount of forest in the surrounding landscape was important to predict the number of total species, specialists and generalists. Specialist richness was associated with the forest cover. High forest cover in the landscape may positively influence dispersal and colonisation of forest specialists, as obligate forest specialists are poor colonizers (Ehrlen & Eriksson, 2000). What is intriguing is that generalist richness increased similarly with the amount of forest cover in the landscape. This pattern might be associated with land use intensity, as more forest at the landscape level gives an indication about the (semi-)naturalness of the environment, and is likely negatively related to the amount of intensive agriculture and nitrogen input (Jamoneau et al., 2011; Paal, Kuett, Lohmus, & Liira, 2017; Takkis et al., 2018). Alternatively, high forest cover in the surrounding landscape is also linked to a higher availability of forest edges (at least in fragmented landscapes), and thus perhaps to more available habitat for generalists. However, the density of forest edge in the landscape, a measure of fragmentation, did not explain additional variability in generalist richness. The density of forest edges did affect the proportion of forest specialists negatively, although this model explained little variation in response, and the numbers of generalists and specialists were not impacted significantly (**Table 1**). This indicates that the amount of forest in the landscape has positive effects on understorey species richness, while the density of forest edge in the surrounding landscape is of minor importance.

High community-weighted SCA (shade casting ability), a measure for light transmission differences due to overstorey composition, resulted in lower total and generalist species richness. Thus, in our study, highest species richness was detected in forest stands dominated by *Betula pubescens*, *Quercus robur* and *Populus tremula*, species with relatively low SCA. In contrast, understorey species richness was lowest under canopies dominated by species with relatively high SCA such as *Fagus sylvatica*, *Carpinus betulus* and *Ulmus glabra*. Shade-intolerant generalists were suppressed by a lack of light, as the proportion of specialist species increased slightly with increasing SCA levels. The composition of the overstorey has been shown to be important to explain compositional shifts in understorey communities, by changing the availability of light (Baeten et al., 2009).

Of all measured soil variables, only soil pH had a significant influence. Specialist richness increased with increasing soil pH resulting in increasing total species richness, consistent with literature (Borchsenius, Nielsen, & Lawesson, 2004; De Keersmaeker et al., 2004). However, the true relationship between pH and richness of total species and generalists is may be more hump-shaped, with an optimum around pH 5.5 (**Fig. 3b**) (Schuster & Diekmann, 2003). Our results are in agreement with Brunet et al. (2011), who found that forest specialists are not affected by light (measured as the tree and shrub cover), but by soil pH, while the opposite was found for generalist species. On acidic soils, the share of forest specialists is generally lower (and thus the share of forest generalists higher) than on base-rich soils, because there is a very limited species pool of forest specialists on acidic soils (Schmidt, Kriebitzsch, & Ewald, 2011).

We have shown over a large geographic gradient that thinning as forest management does not affect forest specialist species richness negatively in ancient forests, while generalists showed a contrasting pattern. Our results underpin how forest management affects edge influences on forest plant biodiversity. We recommend to take this interaction between forest management and edge-to-interior gradients better into account in future research as well as in conservation decisions because both modify the microclimate, soil processes and deposition of polluting aerosols. Therefore, this interaction is key to predict the effects of global change on forest plants in landscapes characterized by a mosaic of forest patches and agricultural land, now typical for many parts of Europe.

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Author contributions

PDF, SG, PVG, CM and KV designed the research; all authors collected data; SG performed statistical analyses; SG, with contributions from PDF, PVG and FZ, wrote the paper; all authors discussed the results and commented on the manuscript drafts.

Data accessibility

Raw data and R code is available at Figshare. doi: 10.6084/m9.figshare.c.4665125.v1

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List of appendices

S1: Study site description per transect

S2: Protocol for site selection

S3: Quantification of the forest management types

S4: List of species observed per region with forest guild association

S5: SCA scores per species

S6: Correlation between variables

S7: Closed forest species richness results

S8: Parameter estimates

Table 1. Effects of forest management type, distance to the forest edge, the interaction between the distance to the edge and forest management, the proportion of forest in a radius of 500 m, soil potassium concentration (K), soil pH, SCA (shade casting ability), soil texture (clay and silt percentage), elevation and forest edge density on species richness, evenness and species composition of forests across Europe. Environmental variables not shown in the table were not included in any final model (latitude, Mg, P and C:N ratio). Values here are χ^2 of the (generalized) linear mixed models. Symbols denote significance levels ($p < 0.05$ *, $p < 0.01$ **, $p < 0.001$ ***), arrows denote the direction of the continuous effects (positive ↑, negative ↓). The marginal r^2 is the proportion of variance explained by the fixed factors alone, while the conditional r^2 is the proportion of variance explained by both the fixed and random factors.

	Management type	Distance to edge (m)		Interaction (management	Proportion forest (%)		Potassium (K) (%)	pH		SCA		Clay (%)	Silt (%)		Elevation (m.a.s.)		Forest edge density (m/ha)		Variation explained	
																			Marginal r^2 (%)	Conditional r^2 (%)
Total species richness	7.96	**27.05*****	↓	5.35	**5.91***	↑	0.69	**4.84***	↑	**11.99****	↓								22	72
Specialist richness	1.81	0.91		0.71	**5.14***	↑	2.32	**6.55****	↑										16	49
Generalist richness	**10.41***	**10.41***	↓	**7.35***	**6.06***	↑	0.51			**13.68*****	↓								17	73
Proportion specialists	7.61	**20.09*****	↑	4.45						**7.27****	↑	1.12			**4.9***	↑	**5.34***	↓	3	7
Evenness	1.14	2.59		0.91			1.01						**5.75***	↑					7	46

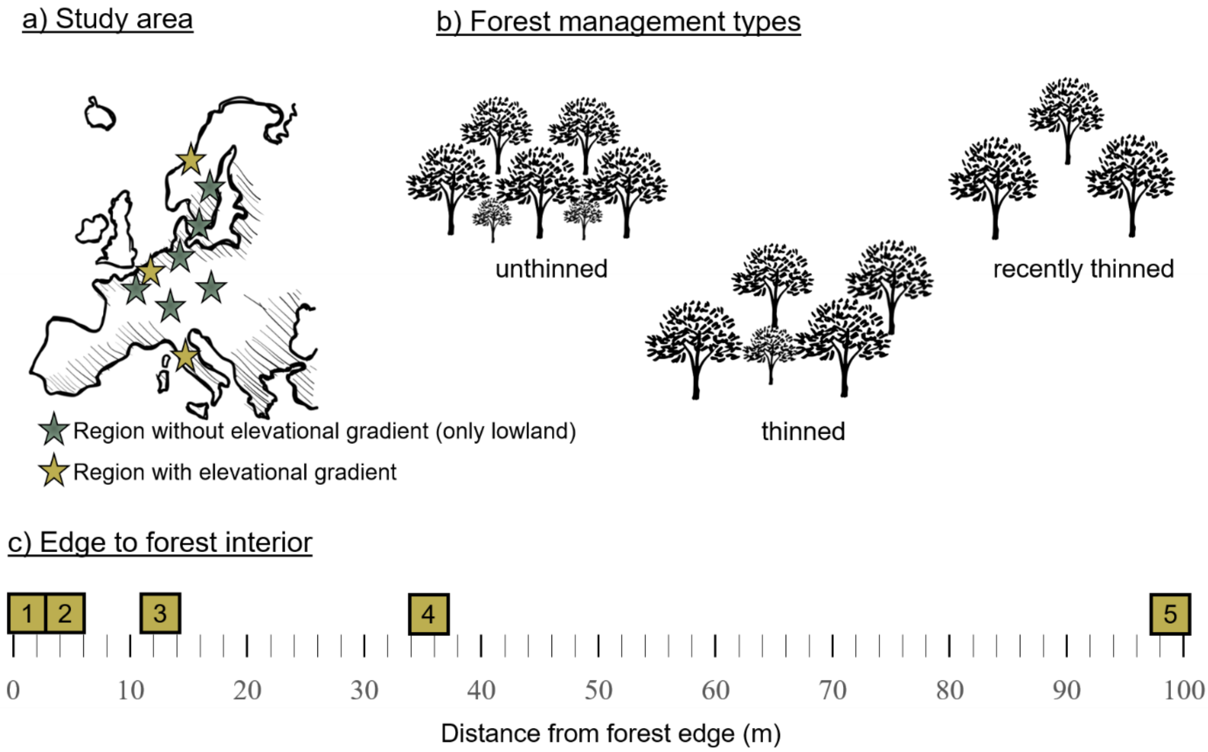

Figure 1. Study set up. Nine regions were selected across a latitudinal gradient in Europe (a). To study the effect of forest management, we compared unthinned, thinned and recently thinned forests (b). Study plots were distributed with an exponentially increasing distance from the south-facing forest edge to the interior (c)

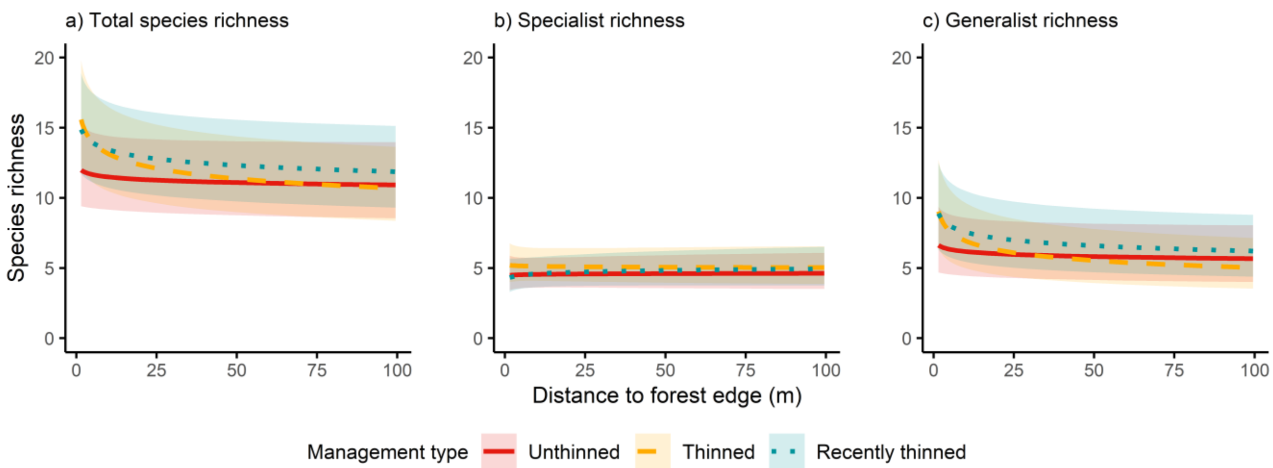

Figure 2. **Effects of the distance to the forest edge on generalist richness depend on the forest management type.** Effects of the distance to the forest edge on species richness (a-c) in forests with different forest management types. The interaction effect is significant at the 0.05 level for total species richness (a), and the main effect of distance to edge is significant for generalist richness (c). Lines represent model estimates of the effects, with other continuous variables set at their observed mean. Shaded areas indicate 95 % confidence intervals.

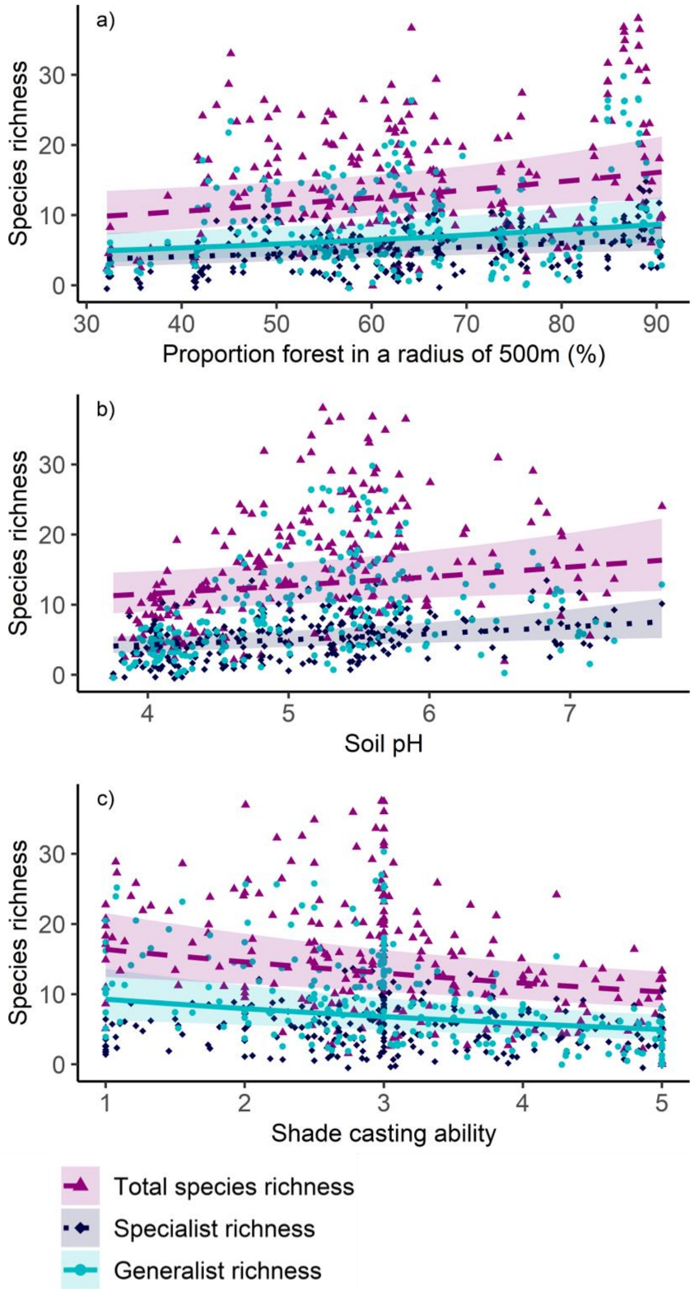

Figure 3. **Understorey species richness increases with the proportion of forest cover in the landscape (a), soil pH (b) and decreasing SCA of the overstorey (c).** Lines represent model estimates with the other continuous variables set at their observed mean and with forest management set to thinned. Shaded areas indicate 95 % confidence intervals. A small amount of random variation is added to the location of each point along the y-axis of panel c to avoid overplotting (jittering).

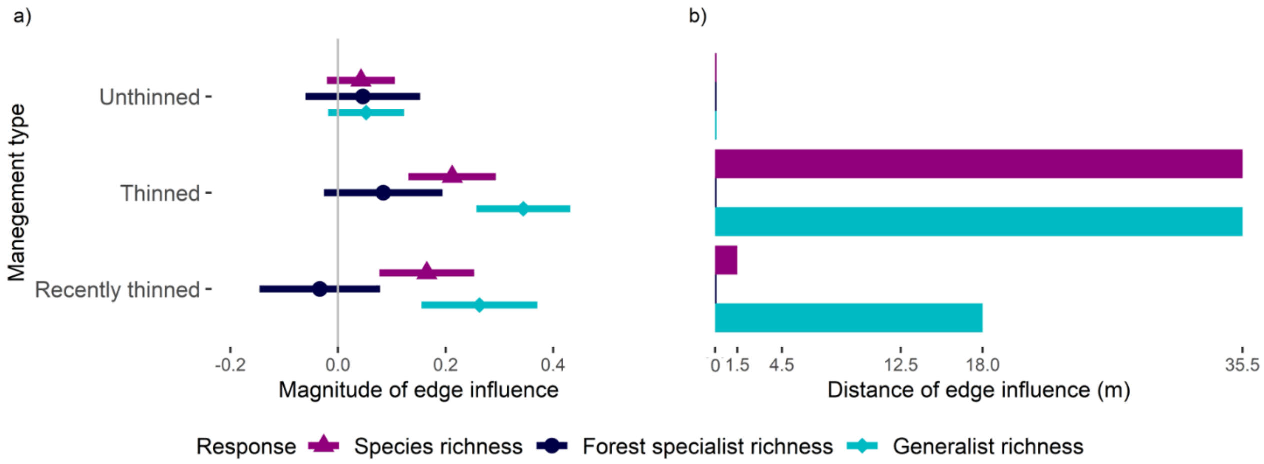

Figure 4. Magnitude of edge influence (MEI) (a) and distance of edge influence (DEI) (b) per management type per response variable. In (a) the mean is depicted with error bars indicating 95% confidence intervals.