Tree species identity outweighs the effects of tree species diversity and forest fragmentation on understorey diversity and composition

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Background & aim – In general, biodiversity has positive effects on ecosystem functioning. In forests, understorey vegetation is influenced by both the composition and species richness of the overstorey through species-specific effects on environmental conditions at the forest floor. Forest fragmentation is also known to influence understorey vegetation composition and richness. However, the combined effects of tree species diversity and forest fragmentation have not been studied yet. With the TREEWEB research platform, consisting of 53 forest plots along a tree species diversity and forest fragmentation gradient, we aim to unravel the combined effects of tree species diversity, tree species identity and forest fragmentation on the understorey composition and diversity.

Methods – The TREEWEB platform includes forest plots of three tree species richness levels, containing all possible species combinations of *Quercus robur*, *Quercus rubra* and *Fagus sylvatica*. Complete dilution is avoided in the design, allowing separation between tree species identity and diversity effects. Vegetation surveys were conducted in all plots to investigate the species richness, species diversity, compositional turnover and cover of the herb layer as well as the shrub layer cover.

Key results – Within the TREEWEB platform, overstorey-understorey diversity relationships were mainly characterised by tree species identity effects. No clear effects of tree species diversity and forest fragmentation on understorey composition and diversity were found.

Conclusion – Tree species identity effects were most important in explaining the observed patterns in the understorey vegetation. Further in-depth research will allow us to disentangle which mechanisms underlie these patterns and whether effects of fragmentation are more pronounced at higher trophic levels.

Key words – TREEWEB, tree species diversity, identity effects, forest fragmentation, understorey vegetation.

INTRODUCTION

Most evidence for functional biodiversity effects has been derived from experiments or theoretical studies, and there is an urgent need for functional biodiversity research (FBR) in real-world landscapes, where the effects of biodiversity are interacting with other environmental drivers (De Laender et al. 2016). In this context, a recently established network of tree species diversity plots in existing forests across Europe has provided valuable new insights into the significance of biodiversity across multiple ecosystem functions (FunDivEUROPE; e.g. van der Plas et al. 2016). The FunDivEUROPE platform was intentionally designed to represent major forest types across Europe, while keeping within-region variation in environmental drivers other than tree species diversity and composition at a minimum (Baeten et

al. 2013). Such research allows quantifying how biodiversity effects differ between forest types along extensive environmental gradients. Yet, a next important step in forest FBR is studying the degree to which biodiversity effects depend on the local context of forest patches (e.g. fragmentation), that is, accounting for the within-region variation in environmental drivers. Habitat fragmentation has long been recognized as a prime driver of ecosystem composition and function; it is known to affect the diversity and abundance of species and ecosystem processes (e.g. Billings & Gaydess 2008). According to the island biogeography theory, the species richness in a fragment can be seen as a dynamic balance between immigration and extinction (MacArthur & Wilson 1963). More isolated fragments typically have lower immigration rates than fragments closer to the source of colonisation, and smaller fragments have higher species extinction rates than bigger ones. Tree species diversity can affect habitat heterogeneity by providing more niches and diverse ways of exploiting environmental resources (Bazzaz 1975), and could affect extinction rates by changing the biotic and abiotic conditions. Thus, increased habitat heterogeneity in mixtures of different tree species could counteract higher extinction rates in smaller fragments. Despite this potential interaction, fragmentation has rarely been integrated in functional biodiversity studies (Kaartinen & Roslin 2011, Macfadyen et al. 2011).

The diversity and composition of the understorey vegetation in forests show clear tree species identity effects (e.g. Barbier et al. 2008), caused by, for instance, differences in litter quality (e.g. Augusto et al. 2003) or shade-casting ability (e.g. Reich et al. 2012) between tree species. Reported effects of tree species diversity on the understorey community are less consistent, as both increases and decreases in understorey diversity with increasing tree species diversity have been observed, as well as absence of any relationship (e.g. Vockenhuber et al. 2011, Ampoorter et al. 2015, 2016). Based on ecological theory, tree species diversity may affect the understorey in two different ways. On the one hand, the presence of multiple tree species may induce environmental heterogeneity at the forest floor, e.g. in light availability or litter quality. Such environmental heterogeneity is expected to promote the coexistence of more understorey species compared with the more homogenous forest floor environment in monocultures. On the other hand, different tree species growing together may interact and create new environmental conditions at the forest floor, such as positive effects of litter mixing on the decomposition and nutrient availabilities that are beyond the (additive) contributions of individual tree species (Gartner & Cardon 2004). In addition to tree species identity and diversity, forest fragmentation has also been shown to affect the understorey vegetation. Generally, a lower plant species diversity is found in smaller or more isolated patches (e.g. Damschen et al. 2006, Rogers et al. 2009). The effect of forest fragmentation is typically strongest for forest specialist species, whereas less clear patterns are found for generalist species that are not strictly bound to forest (e.g. Guirado et al. 2006, Jamoneau et al. 2011).

To date, the joint effects of forest fragmentation and the composition and diversity of the overstorey on the understorey vegetation have not been tested. Triggered by this gap in the current knowledge on the possible mutual effects of fragmentation and local tree biodiversity on forest ecosystem functioning, we set up the TREEWEB research platform. The platform consists of an exploratory network of 53 research plots in mature forests, situated in a 450 km² window in northern Belgium. The design largely follows the European-scale FunDivEUROPE research platform (Baeten et al. 2013), but we explicitly added between-plot variation in forest fragmentation as a design element. Hence, the TREEWEB design allows unravelling the effects of tree species diversity, tree species composition and fragmentation on ecosystem composition and functioning. We expected:

1) a strong impact of tree species identity on understorey diversity and composition, given that tree species can differ considerably in their effect on the environmental conditions;
2) positive tree species diversity effects on understorey diversity and heterogeneity because of increased environmental heterogeneity or the creation of new environmental conditions;
3) lower understorey diversity in smaller, more isolated forest patches because of increased extinction risk of local populations and reduced colonisation of isolated fragments.

## MATERIALS AND METHODS

The TREEWEB research platform

The TREEWEB research platform is situated in northern Belgium (fig. 1). The temperate climate is characterized by a mean annual temperature of 9.5 °C and an annual precipitation of 726 mm distributed evenly over the year (1980–2010, Royal Meteorological Institute of Belgium). The 15 km × 30 km study window has a total forest cover of c. 3 000 ha (forest index 6.8 %), covering both larger forest patches (> 80 ha) as well as many small forest patches (< 1 ha). The 53 selected study plots have a similar land-use history (continuously forested since at least 1850) and developmental stage (mature stands) (see electronic appendix 1 for a detailed description).

All plots are located on a similar relatively dry, sandy loam soil located outside river valleys with the soil parent material varying from light sandloam to sandloam (electronic appendix 2). This way, potential confounding between tree species diversity effects and soil or land-use legacy effects are minimized. A pool of three tree species was a priori selected to construct a diversity gradient: all forest stands are monocultures or mixtures of the three target species pedunculate oak (*Quercus robur* L.), common beech (*Fagus sylvatica* L.) and red oak (*Q. rubra* L.). These species are regionally economically important and *Q. robur* and *F. sylvatica* harbour an important associated biodiversity (e.g. Brändle & Brandl 2001). By contrast, the non-native *Q. rubra* is locally invasive and therefore of concern to both forest managers and policy makers, although it can be locally important for some taxonomic groups (e.g. bats, Dekeukeleire & Janssen 2014). As red oak is often present in managed forests, i.e. it is the second most present non-native tree species in Flanders (northern Belgium) according to the forest inventory, red oak is part of real-world forests in Flanders. Each of the seven possible tree species combinations is included in the platform: three monocultures, three mixtures of two-species, and one three-species mixture. A complete dilution

design, i.e. a design in which one species is present at all diversity levels, was avoided since all tree species are included as monocultures, all species are represented at all tree diversity levels, and a single tree species is not present in each species mixture. Therefore, the design allows to distinguish tree diversity from tree identity effects (Baeten et al. 2013). By implementing all tree species combinations along a forest fragmentation gradient (fig. 1, electronic appendix 1), inter-

actions between local variables such as tree species identity and diversity and landscape features such as connectivity can also be studied.

The 30 m × 30 m plots were established in early 2014 and marked with wooden poles. Plots were small enough to avoid a complete dilution design yet reached the minimum size for several measurements (e.g. herbivory, litter input) to be ecologically meaningful (Baeten et al. 2013). The location of a
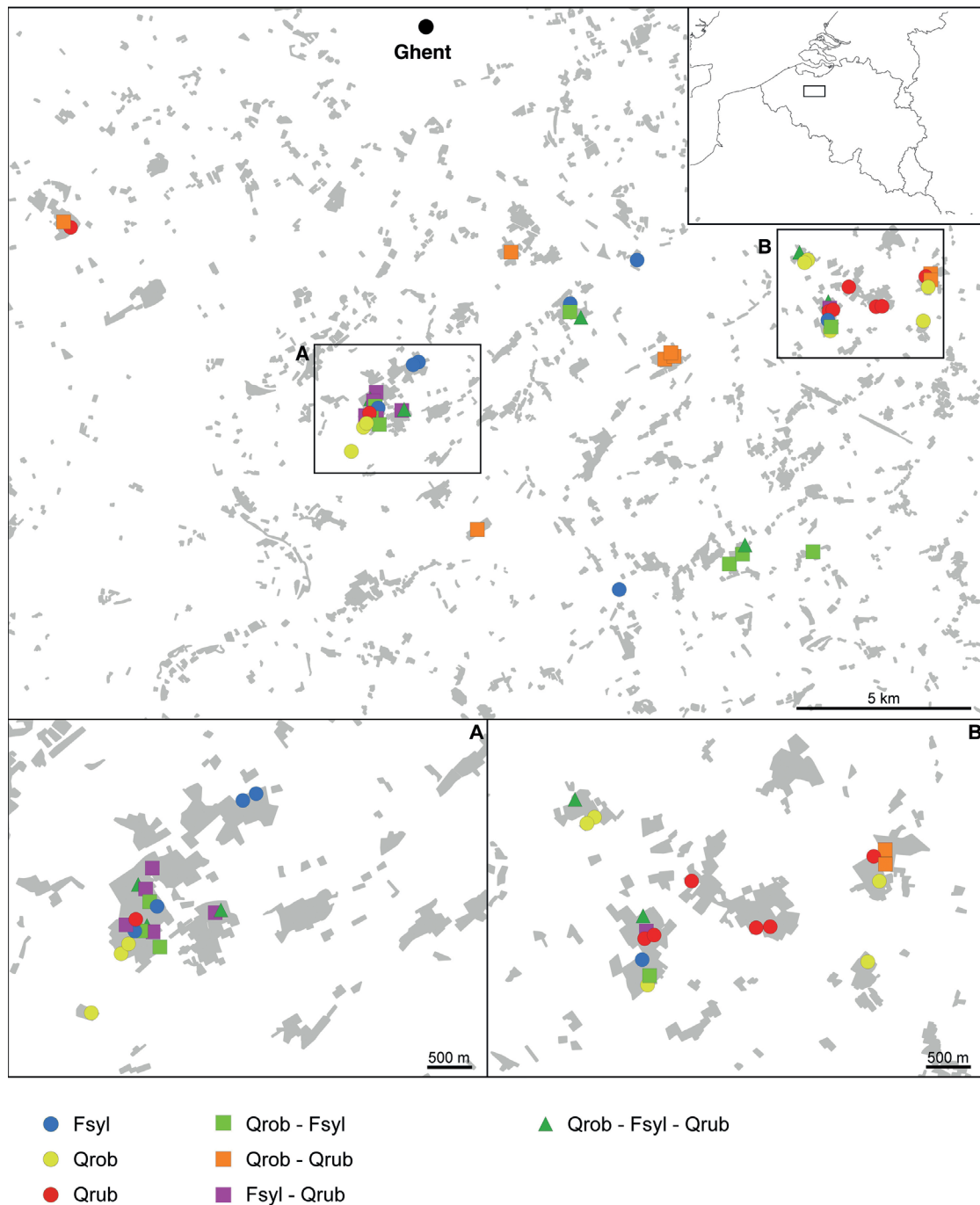
Figure 1 – Map of the study area in northern Belgium. Grey patches represent forest fragments, and the 53 TREEWEB plots are indicated by coloured symbols, showing plot-level tree species diversity and composition (*Quercus robur* = Qrob, *Fagus sylvatica* = Fsyl and *Quercus rubra* = Qrub).

plot within a forest stand was chosen in a way that minimized the admixture of non-target tree species (< 5 % of the basal area) and maximized the evenness of the target tree species in mixtures (> 60 % of maximum evenness based on basal area) (Baeten et al. 2013). The latter is important because tree species that are present in low numbers or as small individuals are unlikely to contribute much to ecosystem processes, either directly or through interspecific interactions (Mulder et al. 2004). Besides, every target species needed to be represented by at least two trees per plot to make sure that measurements using individuals as the level of observation have replicates of species identity. To avoid edge effects of adjacent, different stands, we aimed for a buffer zone of minimum 10 m wide around the plots (selected zone 50 m × 50 m). For the buffer zone, the evenness and admixture criteria were less strict, but the tree species composition and structure of the buffer zone needed to be comparable to the plots.

Plot characteristics

During February–March 2015, we mapped the position of each tree with a diameter at breast height (dbh) larger than 15 cm using the Field-Map system (Institute of Forest Ecosystem Research (IFER) – Monitoring and Mapping Solutions, Ltd., Jílové u Prahy, Czech Republic; www.field-map.com). For all the trees of which the crown covered part of the plot, we measured the dbh, height, crown base height and crown projection. Based on these data, we drew plot-specific maps (fig. 2). The study plots had a mean stem number of 17 (min 9 – max 40) and a mean basal area of 39.04 m²/ha (25.09–55.28 m²/ha) (table 1). Non-target species were present in 23 study plots; only seven plots exceeded the 5 % admixture criterion and one plot had an admixture of 12 %. The most common admixed species were ash (*Fraxinus excelsior* L.), sweet chestnut (*Castanea sativa* Mill.) and sycamore maple (*Acer pseudoplatanus* L.). The evenness based on basal area of the target tree species in mixtures was on average 96.8 % of maximum evenness (86.8–99.9 %). In a two-species mixture, evenness is at its maximum if the basal area of both species is the same. For two species with a basal area of 22.36 m²/ha and 17.11 m²/ha, for example, the evenness is 98.7 % of the maximum evenness.

Two fragmentation measures were calculated for every study plot. *Forest fragment area* is defined as the area of the forest fragment in which the plot is situated and ranged between 1.3 ha and 90.4 ha; *Distance to the closest edge* is defined as the shortest Euclidian distance from the centre of the plot to the closest forest edge and ranged between 7.0 m and 215.5 m (table 1). Distance to forest edge was used as fragmentation measure since this measure has been identified as determinant of herb layer diversity (Harper et al. 2005, Gonzalez et al. 2009). While distance to forest edge can be seen as a local fragmentation measure, considering forest fragment area allows to take into account fragmentation in a landscape context. However, since both fragmentation measures were positively correlated ($r_{pearson}$ = 0.46, p < 0.001), all models were run with only one fragmentation measure at the time.

Vegetation data

Each plot was subdivided into four 15 m × 15 m squares. Five subplots of 5 m × 5 m were established, one in the centre of each square and one in the centre of the plot (fig. 2). Within each of these subplots, we identified all species in the tree (height > 7 m), shrub (1 m < height < 7 m) and herb layer (height < 1 m) and estimated the percentage cover of each species during August 2015. The herb layer species richness per plot was calculated as the number of different herb layer species found across the five subplots. Likewise, the herb layer species diversity was calculated as the exponent of the Shannon diversity index, using the mean cover values of each species over the five subplots per plot. For each plot, we also quantified the compositional variation within the plot, using the species composition of the five subplots per plot, with a multiple-site dissimilarity measure accounting for species turnover only (β_{SIM}, Baselga 2010). Finally, total cover of the herb and shrub layer were estimated at plot level.

Statistical analyses

To explore which variables drive the understorey community composition, a redundancy-analysis (RDA) was performed (function *rda* from library *vegan* in R version 3.2.5, R Core Team 2016). We chose RDA as the gradient in species turnover was expected to be small. As response variable, we used a matrix containing the mean plot-level abundances of each understorey species. The explanatory variables were true tree

5 m

□ *Quercus robur* ■ *Fagus sylvatica* ■ *Quercus rubra*
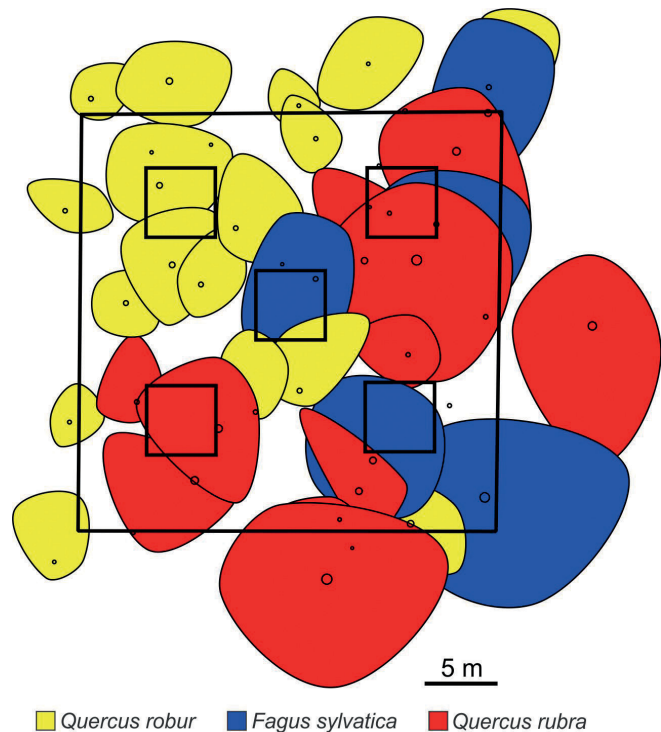
Figure 2 – A detailed plot map. The big square is the 30 m × 30 m plot, dots represent trees, polygons are tree crown projections (different colours for different tree species). Small squares indicate the 5 m × 5 m subplots in which vegetation surveys took place.

Table 1 – Stem density (N), basal area (BA), forest fragment area (fragment area) and distance to closest edge (closest edge) of the 53 TREEWEB plots with *Quercus robur* (Qrob), *Fagus sylvatica* (Fsyl) and *Quercus rubra* (Qrub) as target tree species. Values are mean with [min–max].

Tree species composition	Qrob	Fsyl	Qrub	Qrob-Fsyl	Qrob-Qrub	Fsyl-Qrub	Qrob-Fsyl-Qrub
no. plots	8	8	8	8	8	6	7
BA (m²/ha)	37 [26–51]	41 [33–52]	39 [25–55]	38 [33–44]	39 [32–44]	41 [37–46]	39 [35–46]
N (/ha)	186 [133–233]	122 [100–156]	236 [111–444]	183 [133–300]	207 [178–311]	163 [133–278]	184 [122–289]
BA % Qrob	98.8 [95–100]	–	–	45.3 [33.8–57.4]	46.5 [27.6–59.9]	–	27.5 [17.9–38.7]
BA % Fsyl	–	99.6 [96.9–100]	–	53.8 [42.6–65.2]	–	47 [35.8–59.3]	33.7 [24.1–44.8]
BA % Qrub	–	–	98.1 [92.1–100]	–	49.7 [36.7–67.5]	53 [40.7–64.2]	35.9 [25.3–49.4]
BA % other species	1.2 [0–5]	0.4 [0–3.1]	1.9 [0–7.9]	0.9 [0–5.4]	3.7 [0–9.3]	0	2.9 [0–12]
Fragment area (ha)	39.1 [3–90.4]	46.1 [3.5–90.4]	55.9 [35.5–90.4]	48 [1.3–90.4]	30.7 [19.3–53.4]	73 [29.8–90.4]	47.3 [10.7–90.4]
Closest edge (m)	52.1 [21.6–101.4]	75.7 [43–215.5]	92.2 [7–200]	87 [33.6–196.6]	75 [12.9–199.4]	104.4 [53.1–171.6]	70.5 [25.9–135.7]

species diversity (calculated as the exponent of the Shannon diversity index based on basal area of all the tree species present in a plot), distance to forest edge, forest fragment area and the total basal areas of *Q. robur*, *F. sylvatica* and *Q. rubra* at plot level.

To test for overall effects of tree species diversity and forest fragmentation on the understorey, we used linear models (see electronic appendix 3 for details about the used models). We included true tree species diversity, a measure of forest fragmentation and plot-level total basal area as predictor variables. We fitted different models for the different response variables: plot-level species richness, species diversity and compositional turnover of the herb layer within the plot, and cover of the herb and shrub layer.

Next, to investigate how the identity and diversity of the tree species affect the different understorey-related response variables, we used a set of diversity-interaction models (Kirwan et al. 2009) (electronic appendix 3). A first null model assumes that all the tree species have a similar, non-interactive effect on the understorey. The species identity model assumes that the tree species have a different, purely additive effect (i.e. no interactive effect). The pairwise interaction model assumes that the tree species have a different effect and their interaction further contributes to patterns in the understorey. The interaction between the tree species is described as interactions between the species pairs. Each model was fitted with the *lm* function in R. AIC (Akaike's information criterion; Akaike 1973) was used to compare the different models and the model with the lowest AIC was regarded as most consistent with the data. However, models that differed < 2 in AIC were considered equivalent (Burnham & Anderson 2004) and in this case, preference was given to the simplest model.

RESULTS

The herb layer was in general relatively poor in species, with *Rubus* sp., *Pteridium aquilinum* and saplings of *Quercus rubra* as the most common species. In total, 56 different plant species were recorded in the herb layer (electronic appendix 4). The understorey community at plot level was correlated with the different tree species in the overstorey (fig. 3). Only three understorey species showed clear relationships with specific overstorey species or forest fragmentation. Cover values of *Rubus* sp. increased with increasing basal area of *Q. robur* in the overstorey. *P. aquilinum* cover was more abundant in plots situated in larger forest fragments and also showed a positive relationship with the basal area of *F. sylvatica* in the overstorey. *Q. rubra* saplings were more abundant with increasing basal area of *Q. rubra* in the overstorey.

When distance to edge was included as fragmentation measure in the linear models, none of the predictor variables was significant in explaining the different understorey response variables (results not shown). When forest fragment area was included, we found a significant negative effect of forest fragment area ($p = 0.004$) and a significant positive interaction ($p = 0.02$) between tree species diversity and fragment area on the species richness of the herb layer. However, this model was only marginally significant ($p = 0.056$, $r^2 = 0.17$).

For the set of diversity-interaction models, both fragmentation measures gave similar results, and further only results with forest fragment area as fragmentation measure are discussed. None of the diversity-interaction models explained herb layer species richness ($p = 0.15$, $r^2 = 0.07$ for the null model) or herb layer species diversity ($p = 0.91$, $r^2 =$

0.003). Thus, tree species identity had no significant effect on herb layer species richness (fig. 4A) and diversity (fig. 4B). The identity models provided the best fit for the compositional turnover of the herb layer between subplots (p < 0.001, r² = 0.74), herb cover (p < 0.001, r² = 0.84), and shrub cover (p < 0.001, r² = 0.79). Species turnover was highest under *F. sylvatica*, followed by *Q. robur*, and then *Q. rubra* (fig. 4C). Herb and shrub cover were highest under *Q. robur*, followed by *Q. rubra* and *F. sylvatica* (fig. 4D & E).

DISCUSSION

Effects of tree species diversity and forest fragmentation

True species diversity effects emerge when the effects of mixing tree species on ecosystem properties or processes are beyond what one may expect based on purely additive species identity effects. Within the TREEWEB platform, the overstorey-understorey diversity relationships were mainly characterised by tree species identity effects. No tree species diversity effects on the understorey, nor interactions between tree species diversity and forest fragmentation were found. The herb layer species richness was the only response variable that tended to show a relationship with fragmentation (i.e. fragment area). The absence of clear effects of fragmentation (distance to forest edge, fragment area) on the understorey may be due to the overall historical fragmentation, degradation and homogenisation of forests which has resulted in more generalist plant species in the understorey, tolerant to various soil, nutrient and light conditions. The minor influence of landscape context on the understorey is consistent with the results of Guirado et al. (2007), who found that local site conditions were more important than forest
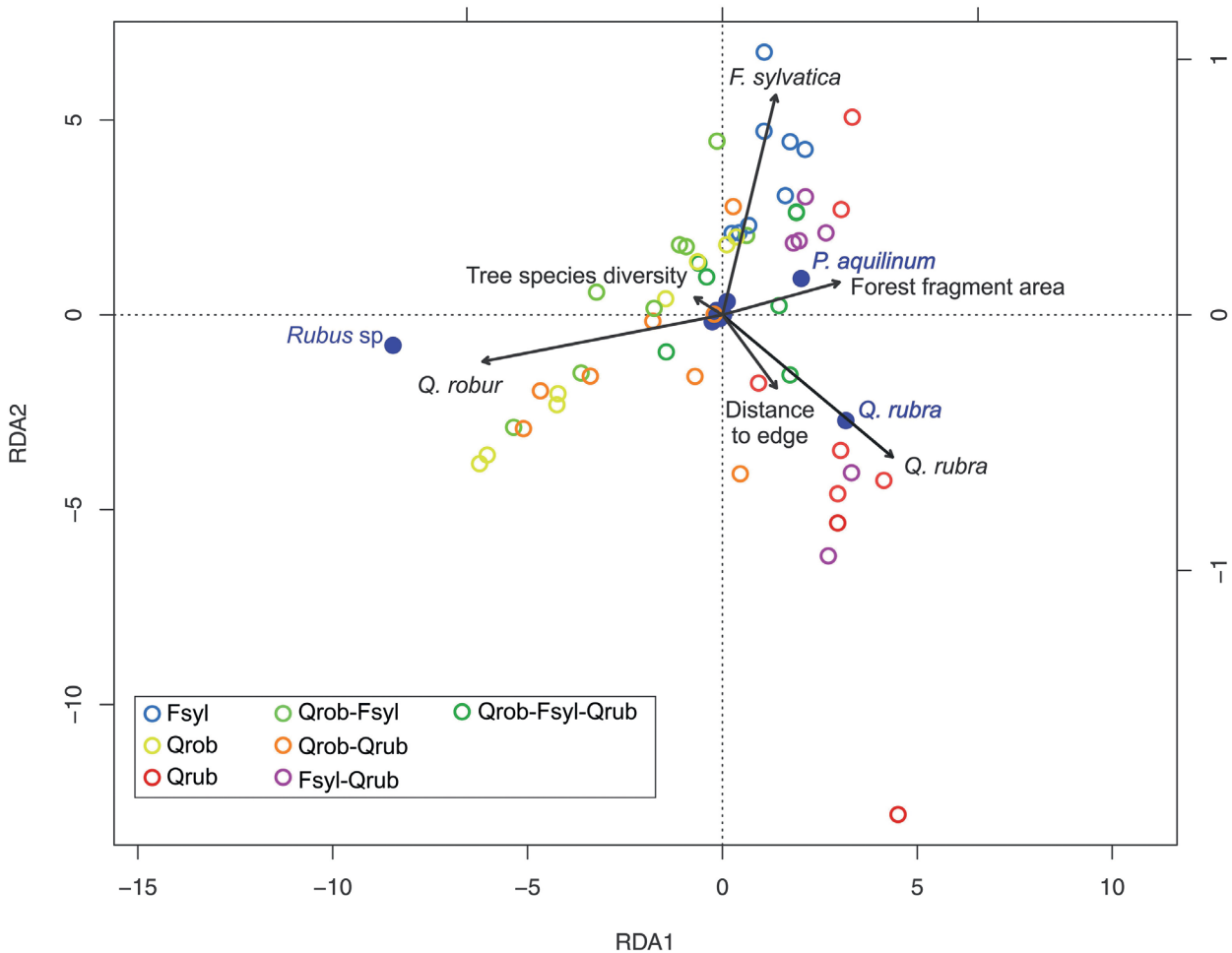
Figure 3 – Redundancy analysis of the understorey vegetation data. Coloured circles represent the plots with different tree species composition (*Quercus robur* = Qrob, *Fagus sylvatica* = Fsyl and *Quercus rubra* = Qrub). Blue filled circles represent the understorey species with outliers captioned. Explanatory variables (indicated on the arrows) are the basal area of *Quercus robur*, *Q. rubra* and *Fagus sylvatica*, tree species diversity and the fragmentation measures distance to edge and forest fragment area. Tree species diversity is calculated as the exponent of the Shannon diversity index based on the basal area of all the trees in a plot.

patch size and connectivity in explaining understorey composition. In addition, landscape ecology theory predicts that habitat loss and fragmentation mainly affect species at high trophic levels (Holt et al. 1999, Davies et al. 2004, Cagnolo et al. 2009), while our study is considering the understorey consisting of species from the lowest trophic level. The generalist species composition of the understorey may also be a reason for the absence of a clear relationship between tree species diversity and the understorey in the TREEWEB platform. When considering generalist species, heterogeneity in tree species composition will not necessary lead to increased niche heterogeneity or decreased plant species performance due to positive or negative complementarity effects. Our findings are similar to those of Ewald (2002), Borchsenius
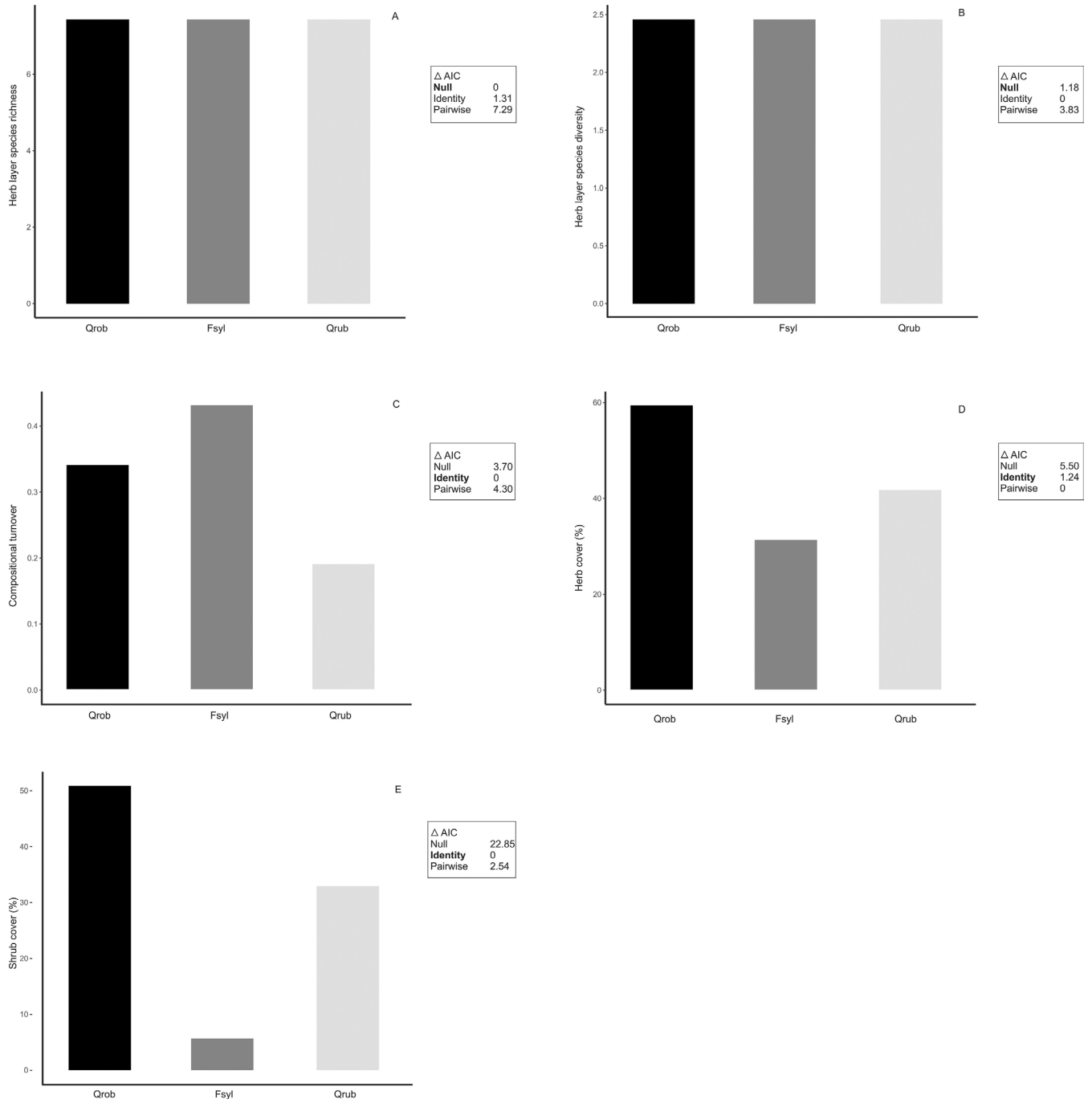
Figure 4 – The results of the diversity-interaction modelling for the five understorey response variables: herb layer species richness (A), herb layer diversity as the exponent of Shannon (B), compositional turnover of the herb layer (C), the total cover of the herb (D) and shrub (E) layer. The models with the lowest AIC (indicated in bold) were used to predict the different responses for hypothetical forest plots consisting of monocultures of each target species at average basal area and average level of fragmentation. Δ AIC represents the differences in AIC between the best model and the remaining models.

et al. (2004), Houle (2007) and Ampoorter et al. (2016), but others detected positive relationships between tree and herb layer diversity (Ingerpuu et al. 2003, Aubert et al. 2004, Mölder et al. 2008, Vockenhuber et al. 2011), while Barbier et al. (2008) even found a negative effect. As we sampled the understorey in August, this might have influenced the understorey species composition since early-flowering geophytic herbs such as *Anemone nemorosa* L. are no longer visible in summer. If some of these herbs were influenced by tree species diversity, we might have missed the effect due to the late sampling season.

Effects of tree species identity

We found no significant difference in herb layer species richness between tree species, contradictory to Brunet et al. (1996) and Skov (1997), who reported a higher herb layer species richness in stands of oak compared to beech, and Chmura (2013), who found that the species richness of the herb layer was negatively correlated with the cover of *Q. rubra* in the overstorey. The diversity of the herb layer seemed also not affected by the identity of the tree species in the overstorey, consistent with Augusto et al. (2003), who did not find clear tree species identity effects on understorey vegetation diversity, and other studies that have shown relatively weak tree species identity effects on understorey vegetation diversity (Whitney & Foster 1988, Qian et al. 1997). This absence of response may be due to the generalist species composition of the understorey vegetation, being tolerant to various soil, nutrient and light conditions. The late sampling season may also have influenced these results as some herb species are no longer visible in August. However, we did find clear tree species identity effects on the compositional turnover of the herb layer as well as the covers of both herb and shrub layer. Species-specific influences of the overstorey on shrub and herb cover were also noticed by Klinka et al. (1996) and Augusto et al. (2003).

Summarizing per tree species, we found that *Quercus robur* was related with the highest cover values for both the herb and the shrub layer and a medium species turnover within plots. Under *Fagus sylvatica*, we found the lowest cover values and the highest turnover: few individuals of understorey species occurring locally. *Quercus rubra* showed medium cover values and the lowest turnover: a spatially uniform herb layer, with numerous *Q. rubra* saplings. The observed differences in understorey cover might be the result of differences in light transmittance between the three tree species. Light is often considered a major limiting factor of understorey vegetation cover and richness (Kirby 1988, Jennings et al. 1999). In trees, light transmittance is closely correlated with shade tolerance and successional status, with the most shade-tolerant species casting the deepest shade (Canham et al. 1994). Of our study species, *Q. robur* is the least shade-tolerant species and *F. sylvatica* the most shade-tolerant species (Niinemets & Valladares 2006, Ellenberg 2009), while *Q. rubra* is classified as intermediate (Rebbeck et al. 2012). Hence, light transmittance was probably highest under *Q. robur*, leading to the highest understorey cover. Within the TREEWEB platform, a lower crown cover was found in *Q. robur* and *Q. rubra* stands compared to *F. sylvatica* stands, indicating higher light avail-

ability under *Q. robur* and *Q. rubra* (B. Sercu, Ghent University, Belgium, unpubl. res.). Härdtle et al. (2003) also found a lower canopy cover with increasing proportion of *Quercus* in mixed *F. sylvatica* – *Quercus* species (*Q. robur*, *Q. petraea* (Matt.) Liebl.) stands. In addition, as these two *Quercus* sp. leaf out rather late in spring and have a low crown density, the light regime is favourable for the understorey vegetation (see Heinken 1995, Pallas 2000). Low light availability is characteristic for *F. sylvatica*, but the species is also known for its dense fine roots near the soil surface. Leuschner et al. (2001), for instance, found denser fine roots under *F. sylvatica* compared to *Q. petraea*. Strong root competition between trees and the herb layer may result in a lower availability of water and nutrients for the understorey species (Coomes & Grubb 2000), and a lower understorey cover. Barbier et al. (2008) also attributed low understorey cover under *F. sylvatica* to the strong competition for water between the dense superficial tree roots and the understorey vegetation. The intermediate cover under *Q. rubra* might be caused by its litter. The large, tough leaves with low litter quality (S. De Groote, Ghent University, Belgium, unpubl. res.) decompose slowly and accumulate on the soil (Dobrylovska 2001), creating a physical barrier for the understorey vegetation and causing low germination and establishment success (Facelli & Pickett 1991). In addition, the growth inhibitors (mainly phenolics) in the leaves may reduce germination of several herbaceous species (Lodhi 1976). Seedlings and saplings of *Q. rubra* were omnipresent under *Q. rubra*, which might explain the low spatial diversity of the associated herb layer. As a non-native, invasive tree species in Belgium, we expected *Q. rubra* to have a negative impact on understorey biodiversity (cf. Branquart et al. 2007, Chmura 2013). Yet, we did not find a clear effect on species richness or diversity of the herb layer.

CONCLUSION

Within the TREEWEB research platform, consisting of monoculture plots up to three-species mixtures of *Quercus robur*, *F. sylvatica* and *Q. rubra*, we found no clear effects of tree species diversity and forest fragmentation on understorey diversity and composition; tree species identity was more important for explaining patterns in the understorey vegetation. Understorey cover was highest under *Q. robur*, *F. sylvatica* was characterised by a sparse herb layer with high turnover, while the herb layer was spatially homogenous under *Q. rubra*. Differences in light transmittance, root density, and litter quality between the tree species might play a role in explaining these identity effects. The TREEWEB research platform will be further used to study the combined effects of tree diversity and forest fragmentation at different trophic levels, with fragmentation effects expected to be more pronounced at higher trophic levels.

SUPPLEMENTARY DATA

Supplementary data are available at *Plant Ecology and Evolution*, Supplementary Data Site (http://www.ingentaconnect.com/content/botbel/plecevo/supp-data) and consist of the following: (1) plot selection procedure of the TREEWEB research platform (pdf); (2) soil characteristics of the TREE-

WEB plots (pdf); (3) detailed model descriptions (pdf); and (4) species list of the herb layer within the 53 TREEWEB plots (Excel spreadsheet).

ACKNOWLEDGEMENTS

REFERENCES

Akaike H. (1973) Information theory as an extension of the maximum likelihood principle. In: Petrov B.N., Csaki F. (eds) Second international symposium on information theory: 267–281. Budapest, Akademiai Kiado.

Ampoorter E., Baeten L., Vanhellemont M., Bruelheide H., Scherer-Lorenzen M., Baasch A., Erfmeier A., Hock M., Verheyen K. (2015) Disentangling tree species identity and richness effects on the herb layer: first results from a German tree diversity experiment. Journal of Vegetation Science 26: 742–755. https://doi.org/10.1111/jvs.12281

Ampoorter E., Selvi F., Auge H., Baeten L., Berger S., Carrari E., Coppi A., Fotelli M., Radoglou K., Setiawan N.N., Vanhellemont M., Verheyen K. (2016) Driving mechanisms of overstorey-understorey diversity relationships in European forests. Perspectives in Plant Ecology, Evolution and Systematics 19: 21–29. https://doi.org/10.1016/j.ppees.2016.02.001

Aubert M., Bureau F., Alard D., Bardat J. (2004) Effect of tree mixture on the humic epipedon and vegetation diversity in managed beech forests (Normandy, France). Canadian Journal of Forest Research 34: 233–248. https://doi.org/10.1139/x03-205

Augusto L., Dupouey J.-L., Ranger J. (2003) Effects of tree species on understory vegetation and environmental conditions in temperate forests. Annals of Forest Science 60: 823–831. https://doi.org/10.1051/forest:2003077

Baeten L., Verheyen K., Wirth C., Bruelheide H., Bussotti F., Finér L.,Jaroszewicz B., Selvi F., Valladares F., Allan E., Ampoorter E., Auge H., Avăcăriei D., Barbaro L., Bărnoaiea I., Bastias C.C., Bauhus J., Beinhoff C., Benavides R., Benneter A., Berger S., Berthold F., Boberg J., Bonal D., Brüggemann W., Carnol M., Castagneyrol B., Charbonnier Y., Chećko E., Coomes D., Coppi A., Dalmaris E., Dănilă G., Dawud S.M., de Vries W., De Wandeler H., Deconchat M., Domisch T., Duduman G., Fischer M., Fotelli M., Gessler A., Gimeno T.E., Granier A., Grossiord C., Guyot V., Hantsch L., Hättenschwiler S., Hector A., Hermy M., Holland V., Jactel H., Joly F.-X., Jucker T., Kolb S., Koricheva J., Lexer M.J., Liebergesell M., Milligan H., Müller S., Muys B., Nguyen D., Nichiforel L., Pollastrini M., Proulx R., Rabasa S., Radoglou K., Ratcliffe S., Raulund-Rasmussen K., Seiferling I., Stenlid J., Vesterdal L., von Wilpert K., Zavala M.A., Zielinski D., Scherer-Lorenzen M. (2013) A novel comparative research platform designed to determine the functional significance of tree species diversity in European forests. Perspectives in Plant Ecology, Evolution and Systematics 15: 281–291. https://doi.org/10.1016/j.ppees.2013.07.002

Barbier S., Gosselin F., Balandier P. (2008) Influence of tree species on understory vegetation diversity and mechanisms involved – A critical review for temperate and boreal forests. Forest Ecology and Management 254: 1–15. https://doi.org/10.1016/j.foreco.2007.09.038

Baselga A. (2010) Partitioning the turnover and nestedness components of beta diversity. Global Ecology and Biogeography 19: 134–143. https://doi.org/10.1111/j.1466-8238.2009.00490.x

Bazzaz F.A. (1975) Plant species diversity in old-field successional ecosystems in southern Illinois. Ecology 56: 485–488. https://doi.org/10.2307/1934981

Billings S.A., Gaydess E.A. (2008) Soil nitrogen and carbon dynamics in a fragmented landscape experiencing forest succession. Landscape Ecology 23: 581–593. https://doi.org/10.1007/s10980-008-9218-7

Borchsenius F., Nielsen P.K., Lawesson J.E. (2004) Vegetation structure and diversity of an ancient temperate deciduous forest in SW Denmark. Plant Ecology 175: 121–135. https://doi.org/10.1023/B:VEGE.0000048095.29961.c5

Brändle M., Brandl R. (2001) Species richness of insects and mites on trees: expanding Southwood. Journal of Animal Ecology 70: 491–504. https://doi.org/10.1046/j.1365-2656.2001.00506.x

Branquart E., Vanderhoeven S., Van Landuyt W., Van Rossum F., Verloove F. (2007) Invasive species in Belgium: Quercus rubra – Red Oak [online]. Available from http://ias.biodiversity.be/species/show/87 [accessed 17 Aug. 2016].

Brunet J., Falkengren-Grerup U., Tyler G. (1996) Herb layer vegetation of south Swedish beech and oak forests – Effects of management and soil acidity during one decade. Forest Ecology and Management 88: 259–272. https://doi.org/10.1016/S0378-1127(96)03845-5

Burnham K.P., Anderson R.P. (2004) Multimodel inference: understanding AIC and BIC in model selection. Sociological Methods & Research 33: 261–304. https://doi.org/10.1177/0049124104268644

Cagnolo L., Valladares G., Salvo A., Cabido M., Zak M. (2009) Habitat fragmentation and species loss across three interacting trophic levels: effects of life-history and food-web traits. Conservation Biology 23: 1167–1175. https://doi.org/10.1111/j.1523-1739.2009.01214.x

Canham C.D., Finzi A.C., Pacala S.W., Burbank D.H. (1994) Causes and consequences of resource heterogeneity in forests: interspecific variation in light transmission by canopy trees. Canadian Journal of Forest Research 24: 337–349. https://doi.org/10.1139/x94-046

Chmura D. (2013) Impact of alien tree species Quercus rubra L. on understorey environment and flora: a study of the Silesian upland (Southern Poland). Polish Journal of Ecology 61: 431–442.

Coomes D.A., Grubb P.J. (2000) Impacts of root competition in forests and woodlands: a theoretical framework and review of experiments. Ecological Monographs 70: 171–207. https://doi.org/10.1890/0012-9615(2000)070[0171:IORCIF]2.0.CO;2

Damschen E.I., Haddad N.M., Orrock J.L., Tewksbury J.J., Levey D.J. (2006) Corridors increase plant species richness at large scales. Science 313: 1284–1286. https://doi.org/10.1126/science.1130098

Davies K.F., Margules C.R., Lawrence J.F. (2004) A synergistic effect puts rare, specialized species at greater risk of extinction. Ecology 85: 265–271. https://doi.org/10.1890/03-0110

De Laender F., Rohr J.R., Ashauer R., Baird D.J., Berger U., Eisenhauer N., Grimm V., Hommen U., Maltby L., Meliàn C.J.,

Pomati F., Roessink I., Radchuk V., Van den Brink P.J. (2016) Reintroducing environmental change drivers in biodiversity-ecosystem functioning research. Trends in Ecology & Evolution 31: 905–915. https://doi.org/10.1016/j.tree.2016.09.007

Dekeukeleire D., Janssen R. (2014) A large maternity colony of 85 Bechstein' s bats (Myotis bechsteinii) in an invasive tree, the red oak (Quercus rubra). Lutra 57: 49–55.

Dobrylovska D. (2001) Litter decomposition of red oak, larch and lime tree and its effect on selected soil characteristics. Journal of Forest Science 47: 477–485.

Ellenberg H. (2009) Vegetation ecology of Central Europe. Cambridge, Cambridge University Press.

Ewald J. (2002) Multiple controls of understorey plant richness in mountain forests of the Bavarian Alps. Phytocoenologia 32: 85–100. https://doi.org/10.1127/0340-269X/2002/0032-0085

Facelli J.M., Pickett S.T.A. (1991) Plant litter: light interception and effects on an old-field plant community. Ecology 72: 1024–1031. https://doi.org/10.2307/1940602

Gartner T.B., Cardon Z.G. (2004) Decomposition dynamics in mixed-species leaf litter. Oikos 104: 230–246. https://doi.org/10.1111/j.0030-1299.2004.12738.x

Gonzalez M., Deconchat M., Balent G. (2009) Woody plant composition of forest layers: the importance of environmental conditions and spatial configuration. Plant Ecology 201: 305–318. https://doi.org/10.1007/s11258-009-9572-9

Guirado M., Pino J., Rodà F. (2006) Understory plant species richness and composition in metropolitan forest archipelagos: effects of forest size, adjacent land use and distance to the edge. Global Ecology and Biogeography 15: 50–62. https://doi.org/10.1111/j.1466-822X.2006.00197.x

Guirado M., Pino J., Rodà F. (2007) Comparing the role of site disturbance and landscape properties on understory species richness in fragmented periurban Mediterranean forests. Landscape Ecology 22: 117–129. https://doi.org/10.1007/s10980-006-9009-y

Härdtle W., von Oheimb G., Westphal C. (2003) The effects of light and soil conditions on the species richness of the ground vegetation of deciduous forests in northern Germany (Schleswig-Holstein). Forest Ecology and Management 182: 327–338. https://doi.org/10.1016/S0378-1127(03)00091-4

Harper K.A., Macdonald S.E., Burton P.J., Chen J., Brosofske K.D., Saunders S.C., Euskirchen E.S., Roberts D., Jaiteh M.S., Esseen P.-A. (2005) Edge influence on forest structure and composition in fragmented landscapes. Conservation Biology 19: 768–782. https://doi.org/10.1111/j.1523-1739.2005.00045.x

Heinken T. (1995) Naturnahe Laub- und Nadelwälder grundwasserferner Standorte im niedersächsischen Tiefland: Gliederung, Standortsbedingungen Dynamik. Dissertationes Botanicae 239: 1–311.

Holt R.D., Lawton J.H., Polis G.A., Martinez N.D. (1999) Trophic rank and the species-area relationship. Ecology 80: 1495–1504. https://doi.org/10.1890/0012-9658(1999)080[1495:TRATSA]2.0.CO;2

Houle G. (2007) Determinants of fine-scale plant species richness in a deciduous forest of northeastern North America. Journal of Vegetation Science 18: 345–354. https://doi.org/10.1111/j.1654-1103.2007.tb02546.x

Ingerpuu N., Vellak K., Liira J., Pärtel M. (2003) Relationships between species richness patterns in deciduous forests at the north Estonian limestone escarpment. Journal of Vegetation Science 14: 773–780. https://doi.org/10.1658/1100-9233(2003)014[0773:rbsrpi]2.0.co;2

Jamoneau A., Sonnier G., Chabrerie O., Closset-Kopp D., Saguez R., Gallet-Moron E., Decocq G. (2011) Drivers of plant species assemblages in forest patches among contrasted dynamic agricultural landscapes. Journal of Ecology 99: 1152–1161. https://doi.org/10.1111/j.1365-2745.2011.01840.x

Jennings S.B., Brown N.D., Sheil D. (1999) Assessing forest canopies and understorey illumination: canopy closure, canopy cover and other measures. Forestry 72: 59–73. https://doi.org/10.1093/forestry/72.1.59

Kaartinen R., Roslin T. (2011) Shrinking by numbers: landscape context affects the species composition but not the quantitative structure of local food webs. Journal of Animal Ecology 80: 622–631. https://doi.org/10.1111/j.1365-2656.2011.01811.x

Kirby K.J. (1988) Changes in the ground flora under plantations on ancient woodland sites. Forestry 61: 317–338. https://doi.org/10.1093/forestry/61.4.317

Kirwan L., Connolly J., Finn J.A., Brophy C., Lüscher A., Nyfeler D., Sebastià M.-T. (2009) Diversity-interaction modeling: estimating contributions of species identities and interactions to ecosystem function. Ecology 90: 2032–2038. https://doi.org/10.1890/08-1684.1

Klinka K., Chen H.Y.H., Wang Q., DeMontigny L. (1996) Forest canopies and their influence on understory vegetation in early-seral stands on west Vancouver Island. Northwest Science 70: 193–200.

Leuschner C., Hertel D., Coners H., Büttner V. (2001) Root competition between beech and oak: a hypothesis. Oecologia 126: 276–284. https://doi.org/10.1007/s004420000507

Lodhi M.A.K. (1976) Role of allelopathy as expressed by dominating trees in a lowland forest in controlling the productivity and pattern of herbaceous growth. American Journal of Botany 63: 1–8. https://doi.org/10.2307/2441664

MacArthur R.H., Wilson E.O. (1963) An equilibrium theory of insular zoogeography. Evolution 17: 373–387. https://doi.org/10.2307/2407089

Macfadyen S., Gibson R.H., Symondson W.O.C., Memmott J. (2011) Landscape structure influences modularity patterns in farm food webs: consequences for pest control. Ecological Applications 21: 516–524. https://doi.org/10.1890/09-2111.1

Mölder A., Bernhardt-Römermann M., Schmidt W. (2008) Herb-layer diversity in deciduous forests: raised by tree richness or beaten by beech? Forest Ecology and Management 256: 272–281. https://doi.org/10.1016/j.foreco.2008.04.012

Mulder C.P.H., Bazeley-White E., Dimitrakopoulos P.G., Hector A., Scherer-Lorenzen M., Schmid B. (2004) Species evenness and productivity in experimental plant communities. Oikos 107: 50–63. https://doi.org/10.1111/j.0030-1299.2004.13110.x

Niinemets Ü., Valladares F. (2006) Tolerance to shade, drought, and waterlogging of temperate Northern Hemisphere trees and shrubs. Ecological Monographs 76: 521–547. https://doi.org/10.1890/0012-9615(2006)076[0521:TTSDAW]2.0.CO;2

Pallas J. (2000) Zur Synsystematik und Verbreitung der europäischen bodensauren Eichenmischwälder. Abhandlungen aus dem Westfälischen Museum für Naturkunde 62: 1–125

Qian H., Klinka K., Sivak B. (1997) Diversity of the understory vascular vegetation in 40 year-old and old-growth forest stands on Vancouver Island, British Columbia. Journal of Vegetation Science 8: 773–780. https://doi.org/10.2307/3237021

R Core Team (2016) R: a language and environment for statistical computing. Vienna, R Foundation for Statistical Computing. Available from https://www.r-project.org [accessed 27 Jun. 2017].

Rebbeck J., Scherzer A., Gottschalk K. (2012) Do chestnut, northern red, and white oak germinant seedlings respond similarly to light treatments? II. Gas exchange and chlorophyll responses. Canadian Journal of Forest Research 42: 1025–1037. https://doi.org/10.1139/x2012-057

Reich P.B., Frelich L.E., Voldseth R.A., Bakken P., Adair E.C. (2012) Understorey diversity in southern boreal forests is regulated by productivity and its indirect impacts on resource availability and heterogeneity. Journal of Ecology 100: 539–545. https://doi.org/10.1111/j.1365-2745.2011.01922.x

Rogers D.A., Rooney T.P., Hawbaker T.J., Radeloff V.C., Waller D.M. (2009) Paying the extinction debt in southern Wisconsin forest understories. Conservation Biology 23: 1497–1506. https://doi.org/10.1111/j.1523-1739.2009.01256.x

Skov F. (1997) Stand and neighbourhood parameters as determinants of plant species richness in a managed forest. Journal of Vegetation Science 8: 573–578. https://doi.org/10.2307/3237209

van der Plas F., Manning P., Allan E., Scherer-Lorenzen M., Verheyen K., Wirth C., Zavala M.A., Hector A., Ampoorter E., Baeten L., Barbaro L., Bauhus J., Benavides R., Benneter A., Berthold F., Bonal D., Bouriaud O., Bruelheide H., Bussotti F., Carnol M., Castagneyrol B., Charbonnier Y., Coomes D., Coppi A., Bastias C.C., Muhie Dawud S., de Wandeler H., Domisch T., Finér L., Gessler A., Granier A., Grossiord C., Guyot V., Hättenschwiler S., Jactel H., Jaroszewicz B., Joly F.-X., Jucker T., Koricheva J., Milligan H., Müller S., Muys B., Nguyen D., Pollastrini M., Raulund-Rasmussen K., Selvi F., Stenlid J., Valladares F., Vesterdal L., Zielínski D., Fischer M. (2016) Jack-of-all-trades effects drive biodiversity-ecosystem multifunctionality relationships in European forests. Nature Communications 7: 11109. https://doi.org/10.1038/ncomms11109

Vockenhuber E.A., Scherber C., Langenbruch C., Meißner M., Seidel D., Tscharntke T. (2011) Tree diversity and environmental context predict herb species richness and cover in Germany's largest connected deciduous forest. Perspectives in Plant Ecology, Evolution and Systematics 13: 111–119. https://doi.org/10.1016/j.ppees.2011.02.004

Whitney G.G., Foster D.R. (1988) Overstorey compostition and age as determinants of the understorey flora of woods of central New England. Journal of Ecology 76: 867–876. https://doi.org/10.2307/2260578