

RESEARCH ARTICLE

Mixing of tree species is especially beneficial for biodiversity in fragmented landscapes, without compromising forest functioning

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Funding information

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Handling Editor: Nathalie Butt

Abstract

1. Contemporary forest management strives to satisfy contrasting demands on forest ecosystems by promoting multiple ecosystem services. These services are affected in varied manners by alternative management actions operating at local or landscape scales, potentially leading to trade-offs and synergies that may impede or encourage forest managers to change practices.
2. We here studied ecosystem functions and biodiversity across trophic levels in 53 mature forest plots varying in stand-level (tree species composition) and landscape-level (degree of fragmentation) characteristics. The consequences of tree species composition and forest fragmentation for the provision of forest ecosystem services were explored using desirability scores, contrasting two different perspectives on forest management: a conservationist perspective placing more value on biodiversity conservation and a productivist perspective attaching more value to timber production and natural forest regeneration. These scores were derived at two spatial scales distinguishing between ecosystem functions and forest biodiversity.
3. We show that more than two thirds of the 20 trade-offs and synergies between functions and diversity variables were driven by variation in tree species composition and fragmentation. While multifunctionality depended on the forest management perspective at the stand level, this dependence was no longer apparent at the landscape scale. Interestingly, more strongly fragmented landscapes had higher landscape-level multifunctionality, but this came at the expense of biodiversity across trophic levels. At the same time, mixed forest stands had higher levels of biodiversity than monocultures without affecting multifunctionality.
4. *Synthesis and applications.* In monocultures, it depends on the management perspective as to which tree species best maximizes multifunctionality. However, diversifying stands resolves this potential tension between different perspectives;

in mixtures the level of multifunctionality no longer depended on the management perspective and similar levels were reached compared to the monocultures. Tree species mixtures also maximized biodiversity across trophic levels. Diversifying forest stands thus represents a promising management strategy that resolves potential trade-offs between functioning and biodiversity.

KEYWORDS

biodiversity, ecosystem functioning, *Fagus sylvatica*, forest fragmentation, *Quercus robur*, *Quercus rubra*

1 | INTRODUCTION

Forest management has shifted from a traditional focus on optimizing economic return from timber sales towards accommodating biodiversity and multiple ecosystem functions for the provisioning of various ecosystem services (Coll et al., 2018). One strategy to achieve this objective involves forest management that promotes tree species mixtures of a particular composition. A recent study on different European forest types showed that tree species compositions associated with higher timber productivity also tend to show higher levels of other ecosystem functions, yet these most beneficial tree species compositions are currently not very common in real-world forest landscapes (Baeten et al., 2019). Choosing the most beneficial species or species mixtures for ecosystem functioning and biodiversity is complicated by the fact that there is no evidence of a super-species or super-species mixture providing high levels of functioning or diversity across multiple functions or taxa (van der Plas et al., 2016). Instead, trade-offs among or between functions and taxa seem to be more common than synergies (Gamfeldt et al., 2013), mainly driven by varying responses of individual functions and taxa to management practices (Felipe-Lucia et al., 2018; Leidinger et al., 2019; Penone et al., 2019).

Environmental drivers acting at larger spatial scales, that is, beyond the stand scale, may also affect forest functioning and biodiversity. Hertzog et al. (2019) showed that habitat fragmentation mediated tree species diversity effects on forest functioning, likely through edge and connectivity effects. Edge effects arise when abiotic conditions close to boundaries between different habitats differ from those within their cores (Schmidt et al., 2017). Edge effects may cause negative, neutral or positive responses across multiple taxa (Pfeifer et al., 2017) as well as of the storage capacity of carbon and nitrogen in the topsoil (Remy et al., 2016). Connectivity effects refer to the spatial arrangement of forest fragments within a landscape, with varying levels of isolation altering extinction–recolonization balances, and hence, biodiversity and functioning (Holyoak et al., 2005). These two aspects of fragmentation, that is, edge effects and connectivity, represent two major mechanisms through which fragmentation per se (i.e. independent of habitat loss, sensu Fahrig, 2003) affects communities and ecosystems (Fischer & Lindenmayer, 2007).

In their review on the knowledge gaps of practitioners managing mixed forests, Coll et al. (2018) identified, among others, the need for more research on the trade-offs arising from diversifying forest stands, as well as a lack of knowledge across spatial and temporal scales. Here, we aim to synthesize how forest functioning and biodiversity can be enhanced across spatial scales considering potential trade-offs, by linking stand-level effects of tree species composition with landscape-level impacts of fragmentation. Following Hooper et al. (2005), we here define ecosystem functioning as stocks (i.e. tree biomass) and fluxes (i.e. herbivory rates) of matter through the forest ecosystem. Human societies derive benefits from the natural functioning of forest ecosystems, for instance through the sale of timber products. These benefits are conceptually defined as ecosystem services and go beyond monetary benefits (timber sale) to also encompass, for instance, cultural aspects such as forest bird diversity that provide recreational services (Gaston et al., 2018). Our approach to linking forest functioning and forest biodiversity to ecosystem services is through the development of desirability scores or importance weights used to derive weighted averages across multiple functions or taxa (Allan et al., 2015; Slade et al., 2017). This approach synthesizes the responses of multiple ecosystem functions and the diversity of taxa at multiple trophic levels to changes in tree species composition and forest fragmentation. It enables contrasting different stakeholder perspectives on forest functioning and biodiversity; a ‘productivist’ perspective on forest functioning would, for instance, put more weight on wood production or tree regeneration than a ‘conservationist’ perspective, which would put more weight on biodiversity. In our analysis, services derived from forest functioning (multifunctionality) were kept separated from services derived from forest biodiversity (multidiversity). This explicit distinction between ecosystem functions and diversity allows to explore the potential tension and trade-offs between maximizing ecosystem function (i.e. provisioning ecosystem services) and conserving biodiversity (i.e. cultural services). Desirability of a particular landscape configuration can then be derived from stand-level functions and biodiversity levels (Manning et al., 2018). For instance, different tree species could each maximize a limited but different set of functions and harbour a high diversity of distinct taxa. Alternatively, mixtures of these species could compromise monoculture levels of diversity and functionality via Jack-of-all-trades mechanisms (van der Plas et al., 2016). As a

result, multiple-purpose forestry should strive to promote different forest types at the landscape scale in order to provide a wide range of ecosystem services (Simons et al., 2021).

To provide guidance on stand- and landscape-level management strategies that could maximize multiple forest functions and diversity, we studied 53 mature forest plots in 19 forest fragments with comparable soil and macroclimate but contrasting tree species composition and degree of fragmentation (De Groote et al., 2017). The expected effects of tree species composition, edge amount and connectivity on eight different ecosystem functions and taxonomic diversity of eight species groups at multiple trophic levels are summarized in Table 1 together with the relevant references. Trade-offs and synergies between these eight functions and eight diversity indices were quantified using a joint modelling approach. Next, by deriving desirability scores to quantify ecosystem services from productivist and conservationist perspectives on forest management, we evaluated optimal stand- and landscape-level management strategies under different tree species compositions, fragmentation intensities and stakeholder perspectives. A web application (available through: https://gfoe2016.shinyapps.io/treeweb_synthesis2/) was also developed for readers and practitioners to explore the impact of other perspectives of forest management on forest ecosystem services. This work builds on previous studies (Baeten et al., 2019; Hertzog et al., 2019) by explicitly considering trade-offs and synergies between multiple functions and the diversity of associated taxa at both the plot and the landscape scale, but also by confronting different stakeholder perspectives to provide direct inputs to management and policy discussions on the benefits of mixing tree species under different levels of fragmentation.

2 | MATERIALS AND METHODS

2.1 | TREEWEB design

Data were collected within the TREEWEB exploratory research platform (sensu Baeten et al., 2013), consisting of 53 mature (900 m²) forest plots scattered across 19 forest fragments in a 15 km × 30 km landscape in Belgium. The careful selection of these plots ensured that they were highly comparable in terms of soil, past land use and other site characteristics (De Groote et al., 2017). In addition, each plot has been continuously forested for at least 150 years with no evidence of management, such as thinning, in the last two decades. Three different tree species were dominant in the plots: pedunculate oak *Quercus robur*, common beech *Fagus sylvatica* and red oak *Quercus rubra*. All potential combinations of the three species were replicated between six and eight times. The plots were selected so that the relative frequencies of the different tree species were as equal as possible in mixtures. Fragmentation intensity of each plot varied from low (i.e. located in large, well-connected forests and distant from edges) to high (i.e. located in small, isolated fragments and close to edges). Fragmentation intensity was quantified using two different (and

uncorrelated) metrics: (a) amount of edge habitat and (b) proximity index. Full details can be found in De Groote et al. (2017).

2.2 | Data collection

We selected ecosystem functions (sensu Hooper et al., 2005) with direct relevance to forest management or conservation (MEA, 2005). The selected functions comprised four stocks: topsoil carbon stock, tree biomass, insect biomass (estimated through caterpillar biomass) and bird biomass (size-corrected biomass index of two dominant passerine species), and four fluxes: decomposition rate, tree regeneration rate, herbivory rate and predation rate. Community composition and abundance data of eight major taxa in forests were also gathered, including: understory vascular plants, leaf miners and leaf galls (insect herbivores hereafter), ground beetles, woodlice, millipedes, spiders, birds and bats. For all taxa we used the exponent of the Shannon index as measure of abundance-weighted true diversity. The sampling protocols for all collected variables are given in Text S1 in Supporting Information. Summary statistics of the collected variables can be found in Tables S1 and S2.

2.3 | Modelling framework

All analyses were performed using R v3.6 (R Core Team, 2019) and can be fully reproduced from an online repository: <https://doi.org/10.5281/zenodo.3516971>. All function and diversity variables were normalized prior to analyses, that is, centred on zero and scaled by their standard deviation. Normalization puts the variables on the same scale and enables more efficient model estimation. For tree regeneration, bird biomass and insect biomass, one value was missing from different plots and was replaced by the respective variable average value. A multivariate normal model was fit to the eight ecosystem functions and eight diversity indices as response variables to account for correlations among them. Tree species composition (categorical variables, seven levels), the amount of edge habitat in a 100 m buffer around each plot (continuous) and the proximity index (continuous) were used as explanatory variables. The proximity index is the sum of forest patch area (m²) divided by the nearest edge-to-edge distance squared (m²) between all forest patches and the focal forest patch (McGarigal, 2015). Given the large number of coefficients needed to test for interaction effects between tree species composition and fragmentation (21 slopes for each of the 16 variables) relative to the number of sampled plots (53), interaction terms were not included in the models. Tree species composition rather than tree species richness was used in the models to provide an applied perspective to our results, since forest manager often make management and planting decision based on tree species composition rather than tree species richness (Baeten et al., 2019).

The model was fit under a Bayesian framework with brms v2.8 (Bürkner, 2017). Following Gelman and Hill (2006), we derived the proportion of variance in the eight ecosystem functions and

Variable	Tree species composition	Fragmentation	
		Edge effect	Connectivity effect
Function			
Topsoil carbon stocks	+ ¹	± ²	No
Decomposition rate	+ ³	- ⁴	No
Tree biomass	+ ⁵	+ ⁶	No
Tree regeneration rate	+ ⁷	± ⁸	No
Insect biomass	+ ⁹	± ¹⁰	± ¹⁰
Herbivory	+ ¹¹	+ ¹¹	± ¹¹
Bird biomass	+ ¹²	+ ¹³	+ ¹³
Predation rate	No ¹⁴	+ ¹⁵	+ ¹⁵
Diversity			
Understorey vegetation	+ ¹⁶	- ¹⁷	+ ¹⁷
Insect herbivore	+ ¹⁸	± ¹⁸	+ ¹⁸
Carabid	+ ¹⁹ /No ²⁰	± ²¹	+ ²²
Araneae	+ ²³	± ²¹	+ ²⁴
Diplopod	+ ²⁵	No ²¹	+ ²⁶
Isopod	+ ²⁵	+ ²⁷	+ ²⁶
Bird	+ ²⁸ /No ¹²	± ¹³	+ ¹³
Bat	+ ²⁹	± ³⁰	+ ³⁰

Note: ¹Schulp et al. (2018; <https://doi.org/10.1016/j.foreco.2008.05.007>), ²Schmidt et al. (2017; <https://doi.org/10.1016/j.agrformet.2016.10.022>), ³Joly et al. (2017; <https://doi.org/10.1111/nph.14452>), ⁴Crockatt et al. (2014; <https://doi.org/10.1111/gcb.12676>), ⁵Baeten et al. (2019; <https://doi.org/10.1111/1365-2664.13308>), ⁶Smith et al. (2018; <https://doi.org/10.1002/fee.1793>), ⁷Dyderski et al. (2020; <https://doi.org/10.3390/f11040456>), ⁸Lohtka et al. (2013; <https://doi.org/10.1139/cjfr-2013-0231>), ⁹Schuldt et al. (2019; <https://doi.org/10.1038/s41467-019-09448-8>), ¹⁰Tscharntke et al. (2002; <https://doi.org/10.1046/j.1440-1703.2002.00482>), ¹¹van Schroyen Lantman et al. (2018; <https://doi.org/10.1016/j.baee.2018.03.006>), ¹²Castano-Villa et al. (2019; <https://doi.org/10.1016/j.foreco.2019.03.025>), ¹³Dekeukeleire et al. (2019a; <https://doi.org/10.1016/j.foreco.2019.04.023>), ¹⁴Stemmelen et al. (2021; <https://doi.org/10.1101/2021.07.05.451117>), ¹⁵Dekeukeleire et al. (2019b; <https://doi.org/10.1016/j.foreco.2019.03.055>), ¹⁶De Groote et al. (2017; <https://doi.org/10.5091/plevevo.2017.1331>), ¹⁷Govaert et al. (2019; <https://doi.org/10.1111/jvs.12844>), ¹⁸van Schroyen Lantman et al. (2020; <https://doi.org/10.1111/icad.12358>), ¹⁹Vehvilainen et al. (2008; <https://doi.org/10.1111/j.2008.0030-1299.15972.x>), ²⁰Jouveau et al. (2020; <https://doi.org/10.1111/icad.12372>), ²¹De Smedt et al. (2019; <https://doi.org/10.1111/ddi.12909>), ²²Wooscock et al. (2010; <https://doi.org/10.1016/j.agee.2010.07.018>), ²³Ampoorter et al. (2020; <https://doi.org/10.1111/oik.06290>), ²⁴Gardiner et al. (2010; <https://doi.org/10.1016/j.biocontrol.2010.06.008>), ²⁵De Smedt et al. (2016; <https://doi.org/10.1111/icad.12183>), ²⁶De Smedt et al. (2018a; <https://doi.org/10.1007/s10980-017-0607-7>), ²⁷De Smedt et al. (2018b; <https://doi.org/10.1016/j.ejsobi.2017.12.002>), ²⁸Charbonnier et al. (2016; <https://doi.org/10.1007/s00442-016-3671-9>), ²⁹Charbonnier et al. (2016; <https://doi.org/10.1007/s10980-015-0242-0>), ³⁰Froidevaux et al. (2021; <https://doi.org/10.1038/s41598-021-89660-z>).

eight biodiversity indices explained by each explanatory variable. Information on prior distributions, model settings and model checks are provided in the Text S2 in Supporting Information.

2.4 | Trade-offs and synergies

Trade-offs and synergies between the eight functions and the eight diversity indices were quantified using the residual correlation

TABLE 1 Expected relationships between tree species composition, amount of edge habitats and connectivity on the different ecosystem functions and taxa. For tree species composition a '+' identify effect of tree species composition on the variable. For edge amount and connectivity, '+' and '-' respectively identify positive or negative effect while '±' identify effect in potentially different directions. References to support the expectations are given with superscript number and are available below the table with first author, year of publication and DOI. Note that the references are given as examples supporting the expectations, a full review of available evidence for the investigated effects is beyond the scope of this article

matrices from multivariate normal models. Negative correlations imply trade-offs while positive correlations imply synergies. A two-step approach was used in order to disentangle the effect of tree species composition and forest fragmentation on trade-offs and synergies (Felipe-Lucia et al., 2018). First, a multivariate null model (intercept only) was fitted with the same settings as described above. From this model, we identified which variables showed correlation coefficients with a >90% posterior probability of being different from zero. Note that raw pairwise correlations between the

variables would be similar to the correlations derived from the null model, but we opted for a model-based approach to have consistent methodology across the two steps for the assessment of significance. In a second step, we evaluated which of the correlation coefficients identified in the first step retained a >90% posterior probability of being different from zero in a model that included the predictors tree species composition, edges and proximity as fixed effects. Trade-offs and synergies for variables for which the residual correlation was no longer different from zero in the second model were assumed to correlate principally because of their parallel (in the same or opposite direction) response to the variation in tree species composition and forest fragmentation across plots. Trade-offs and synergies for variables for which the residual correlation remained different from zero were assumed to be either driven by factors not included in the model or by direct intrinsic relationships between the respective variables, such as between insect biomass and avian body condition (Felipe-Lucia et al., 2018).

2.5 | Desirability of functioning or diversity across scales

First, we derived predictions of ecosystem functions and biodiversity measures under different tree species compositions (monocultures and three-species mixtures) and different amounts of edge habitat or different proximity (low and high levels of fragmentation) from the full model. To simplify the visualization of results, the three two-species mixtures are not shown in the main graphs; we provide the figures with all seven tree species compositions in Figure S1. Second,

each ecosystem function and diversity measure were given an importance weight and a direction (maximize or minimize) based on either a 'productivist' or a 'conservationist' perspective (see Table 2). Importance weights were derived from expertise knowledge present in the TREEWEB consortium, all five project PIs provided weights and these were then averaged for each function or diversity measure (Hertzog et al., 2019). Third, plot-level multifunctionality and multidiversity scores were calculated using the weighted average of the model predictions according to Slade et al. (2017), with higher scores reflecting more desirable levels of functioning or biodiversity across multiple ecosystem functions and multiple taxa. A web application with which users can vary the importance weights and reproduce the main figures is provided at: https://gfoe2016.shinyapps.io/treeweb_synthesis2/.

Finally, we scaled up plot-level desirability to the level of four hypothetical landscapes with 53 plots (equal sample size as in our study) in different configurations. This upscaling involved the following steps: (a) generate the tree species composition and fragmentation levels for each plot based on the particular landscape configuration, (b) derive the model predictions for the eight functions and eight diversity measures, (c) use the desirability scores to turn the model predictions into multifunctionality or multidiversity scores and (d) sum the values across the plots separately for multifunctioning and multidiversity. By using a Bayesian approach, model uncertainties could be transferred across all of these steps. The following landscapes were generated: (a) a low-fragmentation landscape (low amount of edge habitat and low proximity) with a similar proportion of the three monocultures, (b) a low-fragmentation landscape with all 53 plots being three-species mixtures, (c) a highly fragmented

TABLE 2 Importance weights (min. 0 and max. 10) and direction given to the different ecosystem functions and taxa based on a productivist and conservationist perspective of forest management. The weights were derived by averaging responses given by the five Principal Investigators of the research project, in brackets is given the coefficient of variation of the different responses, values of 0 indicate that only one response was given for the concerned variable

Variable	Productivist		Conservationist	
	Direction	Weight	Direction	Weight
Function				
C stock	Maximize	7.5 (0.13)	Maximize	8 (0.25)
Decomposition	Maximize	6 (0.33)	Maximize	4.67 (0.25)
Tree biomass	Maximize	9.5 (0.06)	Maximize	6 (0)
Regeneration	Maximize	9.33 (0.06)	Maximize	6.25 (0.27)
Insect biomass	Minimize	7 (0)	Maximize	7 (0)
Herbivory	Minimize	7.25 (0.21)	Minimize	4.67 (0.12)
Bird biomass	Maximize	3 (0.33)	Maximize	7.67 (0.2)
Predation rate	Maximize	4.5 (0.53)	Maximize	4.75 (0.36)
Diversity				
Vegetation	Maximize	5 (0.49)	Maximize	9 (0.06)
Herbivore	Maximize	2 (0)	Maximize	7 (0)
Carabid	Maximize	2 (0)	Maximize	9 (0)
Spider	Maximize	2 (0)	Maximize	9 (0)
Isopod	Maximize	2 (0)	Maximize	7 (0)
Diplopod	Maximize	2 (0)	Maximize	7 (0)
Bird	Maximize	5 (0)	Maximize	9 (0)
Bat	Maximize	3 (0)	Maximize	9 (0)

landscape (high amount of edge habitat and average proximity) with a similar proportion of the three monocultures and (d) a highly fragmented landscape with all 53 plots having three-species mixtures. Further details on the predictions derived from the fitted models are given in Text S3 in Supporting Information.

3 | RESULTS

3.1 | Responses to tree species composition and forest fragmentation

Full models explained on average 55% of the variation in the multiple indicators of functioning and diversity, ranging from 44% for millipede diversity to 70% for insect herbivore diversity (Figure 1). Tree species composition explained 32% of the variation, while both edge and proximity effects explained ca 10% each.

Tree regeneration, insect biomass and herbivory showed strong responses to variation in tree species composition, with the highest values recorded in pedunculate oak monocultures, and the lowest values in beech monocultures (Figure S2). Vegetation and herbivore diversity were higher than average in three-species mixtures, while herbivore, bird and bat diversity were higher in pedunculate oak monocultures, where vegetation diversity was lower. Herbivore and bird diversity were lower than average in common beech monocultures. Finally, in red oak monocultures herbivore diversity was lower than average.

The amount of edge habitat affected all but two ecosystem functions, with positive effects on tree biomass, decomposition rate, carbon stocks and bird biomass, and negative ones on predation and tree regeneration. Carabid beetles, diplopods and spiders showed higher-than-average levels of diversity in plots with a high amount of edge habitat, while herbivore and bat diversity were lower.

Out of the eight ecosystem functions, proximity was related to only two of them: carbon stocks and bird biomass. Both responded positively to increased proximity to other forest fragments. Out of the eight biodiversity measures, insect herbivores, carabid beetles and bird diversity were negatively related with proximity to other forest fragments, while spiders and millipede's diversity were weakly positively related.

3.2 | Trade-offs and synergies

Correlation coefficients from the null model ranged from -0.25 to 0.54 . Out of a total of 120 correlation coefficients, three correlations between biodiversity measures, seven between ecosystem functions and 12 between ecosystem functions and diversity measures had a $>90\%$ posterior probability of being different from 0 (Figure 2). Of these 22 coefficients, 16 could be partly explained by the effect of tree species composition, edges or proximity, as these coefficients did not retain significance in the full model. This means that the observed correlations between these variables can be explained

by their response to changing tree species composition and landscape fragmentation. Of the other six correlation coefficients, three indicated synergies (Insect biomass–Herbivory, Carbon stocks–Diplopod diversity and Predation–Bird diversity) and three indicated trade-offs (Decomposition–Tree biomass, Tree regeneration–Bird biomass and Carabid diversity–Tree regeneration).

3.3 | Desirability at different scales

For a given tree species composition, forest multifunctioning increased with the amount of edge habitat and proximity to other forest fragments, irrespective of management perspective (Figure 3). However, under a productivist or conservationist perspective, respectively beech or pedunculate oak monocultures showed the highest level of multifunctioning. Multidiversity showed very similar patterns under both management perspectives. Overall multidiversity was only slightly higher in more continuous landscapes, while it was highest in pedunculate oak monocultures and three-species mixtures for a given level of forest fragmentation.

Both management perspectives resulted in broadly similar patterns at the landscape scale (Figure 3). Forest multifunctioning was higher in more fragmented landscapes irrespective of whether the individual patches were all monocultures or all mixtures. This result was not affected when averaging out the effect of tree species composition (Figure S3). Multidiversity, on the other hand, was higher in landscapes composed of tree species mixtures than of different monocultures (see also Figure S4). Finally, the level of forest fragmentation had a small effect, with multidiversity only slightly higher in more continuous landscapes.

4 | DISCUSSION

New perspectives on forest management encourage managers to adapt their practices to promote both forest functioning and biodiversity (Mori et al., 2017). Despite recent evidence for higher levels of forest functioning and biodiversity in tree species mixtures than in monocultures (Baeten et al., 2019), possible drawbacks for particular ecosystem functions or biodiversity components remain unclear (Coll et al., 2018). Our study confirms that ecosystem functions and diversities of associated taxa are often correlated across sites, with synergies (reflected by positive associations) just as likely as trade-offs (negative associations; but see Felipe-Lucia et al., 2018; Penone et al., 2019). Moreover, more than two thirds of these associations were driven at least partly by variation in tree species composition and landscape fragmentation, which hence constitute potential targets for forest management. Those trade-offs and synergies not clearly related to tree species composition and fragmentation effects are possibly driven by unmeasured external drivers that affect the variables jointly, or inherent linkages between them (Felipe-Lucia et al., 2018). The synergy between insect biomass and herbivory rates is likely an

FIGURE 1 Variance explained by the different covariates included in the multivariate model. Each dot represents the median estimate and each horizontal line the 80% credible interval. The vertical dashed lines represent the overall average variance explained

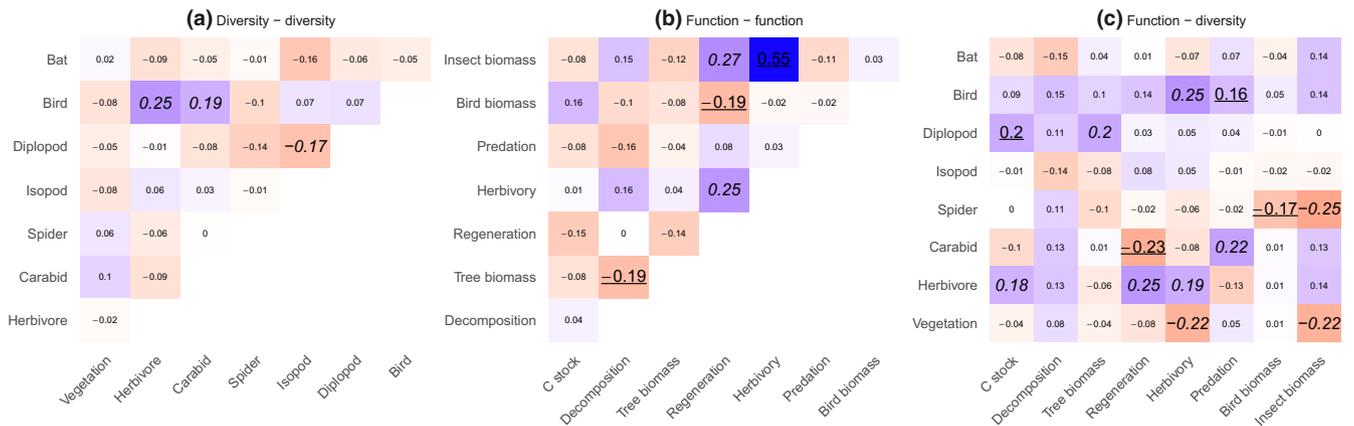
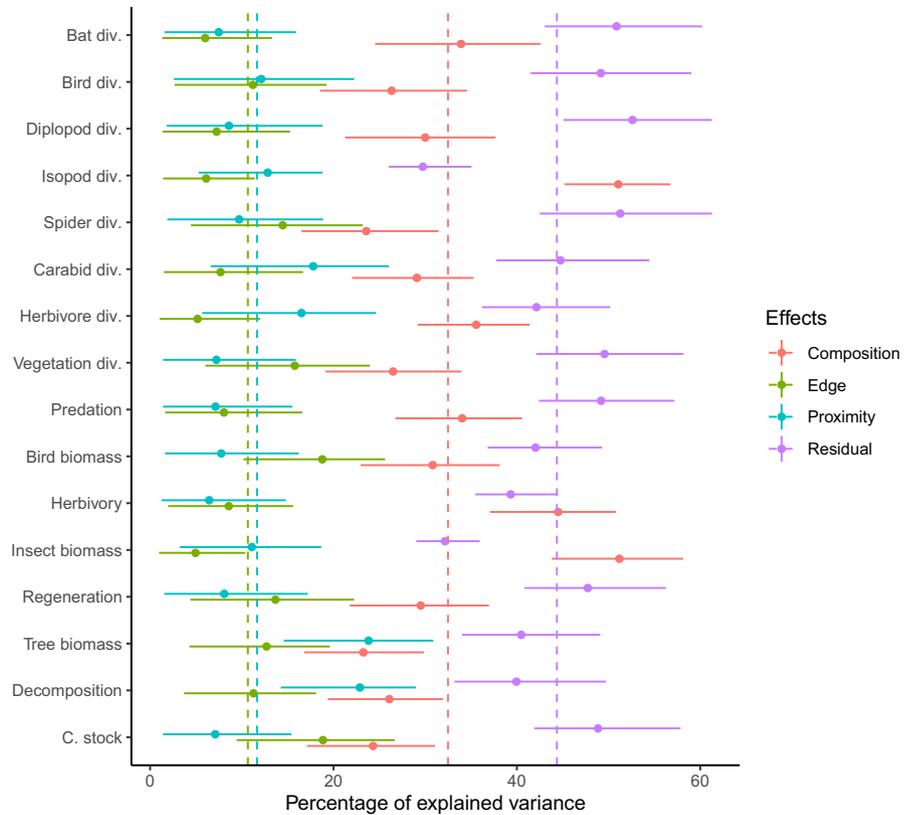


FIGURE 2 Trade-offs and synergies between the diversity of the different taxa (a), the different ecosystem functions (b) and between measures of diversity and of function (c). The values represented are the correlation coefficients as estimated from a null multivariate model. Positive values (blue) indicate synergies between two variables, negative values (red) indicate trade-offs between two variables. The italicized values represent significant trade-offs and synergies that are driven by tree species composition and fragmentation. The underlined values represent significant trade-offs and synergies driven either by direct interactions between the variables (i.e. insect biomass and herbivory) or by other unmeasured drivers

example of such an inherent mechanistic coupling, via bottom-up effects. In addition, while many relationships, such as between spider and insect biomass, were in the direction expected, some were unexpected at first sight. For instance, the negative relationship between carabid diversity and rate of tree regeneration could be due to seed predation by carabid beetles, as earlier work showed positive relationships between carabid diversity and seed predation (Gaines & Gratton, 2010). Likewise, seed predation may

also explain the observed trade-off between bird biomass and tree regeneration rates (Janzen, 1971).

Along the same lines, while many responses of individual functions to changes in tree species composition and fragmentation confirmed our a priori expectations (see Table 1; Figure S1), such as the higher topsoil carbon stocks closer to forest edges (Meeussen et al., 2021) or the strong impact of tree species composition on insect biomass, herbivory and herbivore diversity (van Schroyenstien

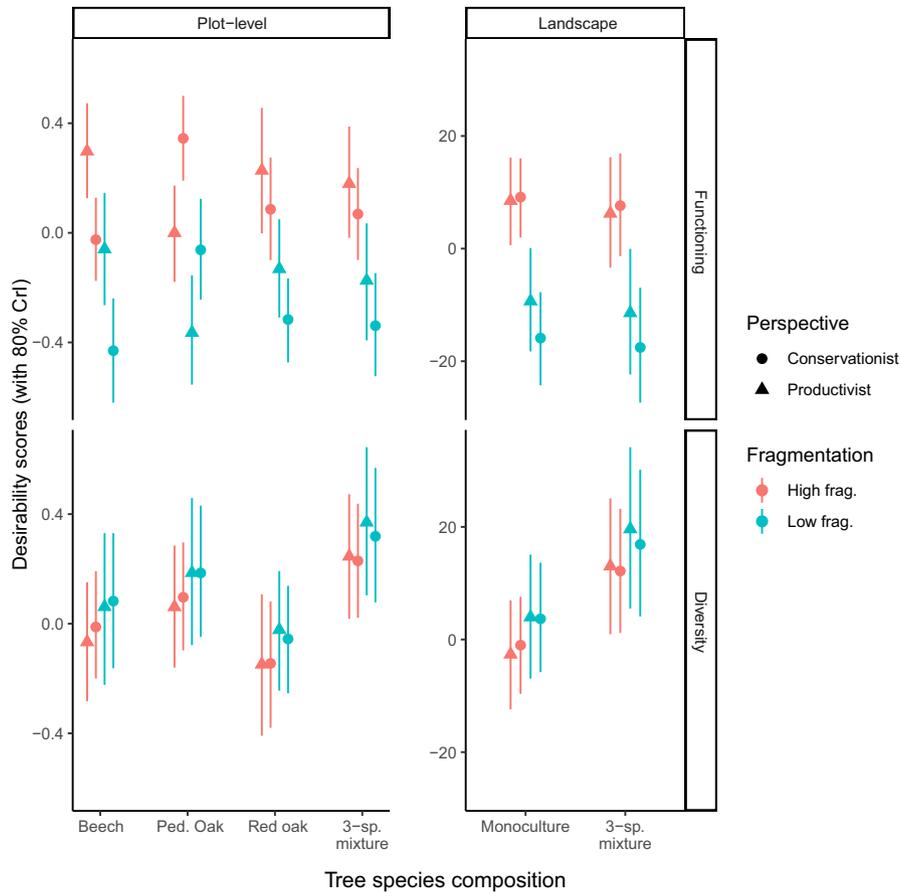


FIGURE 3 Desirability scores for forest functioning (a and b) and diversity (c and d) at the plot scale (a and c) for the three monocultures and for all tree species in a mixture at different levels of fragmentation and at the landscape level (b and d) for landscapes composed of tree monocultures or of three-species mixtures. The dots represent the posterior medians and the vertical lines the 80% credible intervals. If the credible interval (the vertical line) of a particular dot does not exceed (or falls short of) another dot, then there is a posterior probability larger than 80% that the first dot has a larger (or lower) desirability score. For instance, comparing ecosystem functioning under low fragmentation for pedunculate oak, the credible interval of the estimated median under a productivist perspective does not exceed the estimated median from a conservationist perspective. Therefore, the probability that the conservationist perspective is larger than the productivist perspective for this example is >80%

Lantman et al., 2020), other relationships were unexpected. For instance, the negative effect of connectivity to other forest fragments on herbivore, carabid and bird diversity appears to contradict classical expectations derived from the theory of island biogeography, where diversity at equilibrium increases in (habitat) islands that are closer and more connected to the mainland (MacArthur & Wilson, 2016). However, in a review paper, Bailey (2007) reported weak empirical evidence for benefits of increased connectivity on forest biodiversity in fragmented landscapes. Rather, the seemingly contradictory results in our study could be due to changes in dominance structure mediated by connectivity, for example, generalists and dominant species constrained by dispersal between forest areas displacing specialists and reducing the diversity of these groups.

The aggregation of multiple responses into desirability scores (Slade et al., 2017) further reveals effects of forest management perspective, landscape structure and tree species composition on forest multifunctioning and multidiversity. From a conservationist perspective, plot-level forest multifunctioning was highest in pedunculate oak monocultures, while under a productivist perspective beech

monocultures performed best. This pattern was in part driven by insect biomass, which peaked in pedunculate oak monocultures but was lowest in beech monoculture. Under both perspectives, plots in more fragmented forests showed higher levels of multifunctioning, mainly driven by increased tree biomass and carbon stocks near habitat edges, as previously reported (Remy et al., 2016). Multidiversity was higher in pedunculate oak monocultures, in tree species mixtures and in plots located in more continuous forest. Plot-level biodiversity may hence benefit from adding or maintaining pedunculate oak trees in mixed stands and from reducing stand isolation and the amount of edge habitat (see also Mölder et al., 2019).

Scaling up desirability scores from plot to landscape level revealed that forest multifunctioning was most strongly affected by landscape fragmentation, while overall forest multidiversity was most strongly affected by stand composition, probably due to dominant effects of tree species identity (van Schroyen Lantman et al., 2020). Indeed, the study area being fragmented for many decades already, remaining forests can be expected to mainly (or even exclusively) harbour species that are well-adapted to such

conditions. These differing responses between functioning and biodiversity at the landscape scale could potentially create trade-offs between management decisions aiming at optimizing functioning over biodiversity. Our results further show that in landscapes undergoing current habitat fragmentation, negative effects thereof on forest biodiversity could be mitigated by promoting mixed stands, as fragmentation effects per se were limited. The fact that we found landscape-level forest functioning to be higher in more strongly fragmented landscapes, does not imply that fragmentation is positive for other ecosystem aspects (Haddad et al., 2015).

Desirability scores provide a versatile tool for assessing different perspectives on forest management across spatial scales. The associated WebApp enables managers and scientists to explore which tree species composition and which levels of fragmentation maximize ecosystem functioning and biodiversity for their particular perspective and valuation system. Extrapolating these results to other tree species compositions, but also to other regions of the world, would require further research efforts. Comparable models could, for example, be applied to data collected in other forest exploratory platforms (i.e. at the European scale; Baeten et al., 2013), which could then be fed into the WebApp.

Forest managers are aware of emerging challenges when aiming to adapt forestry practices to a changing climate and new societal demands (Coll et al., 2018). Ideally, management practices should promote multiple ecosystem functions and permit multiple taxa to thrive, despite the presence of intrinsic trade-offs among them. Earlier studies already identified forest attributes that can be managed to promote multiple service provision and mitigate trade-offs: high structural heterogeneity, large trees and the presence of canopy gaps (Felipe-Lucia et al., 2018). Furthermore, sufficient forest cover configured in both large and small patches is important to support forest biodiversity at the landscape scale (Arroyo-Rodríguez et al., 2020). We here expand on these findings by demonstrating the importance of tree species mixtures in highly fragmented landscapes for boosting both forest functioning and diversity (but see Valdés et al., 2020). Specifically, the following applied implications can be derived from our results:

1. In monocultures, the tree species that maximizes forest functioning best, depends on the management perspective, particularly pedunculate oak for the conservation perspective and beech for the productivist perspective. Mixing tree species removes this incompatibility, as the two perspectives are no longer different in terms of desirability.
2. The desirability scores of the provisioning services delivered by the functions in mixtures are not significantly reduced in mixtures compared to monocultures, that is, diversification to meet the two management perspectives does not trade-off against the overall multifunctionality.
3. Highest cultural services of biodiversity are achieved in tree species mixtures, without compromising functioning.
4. Promoting local (stand-level) tree diversity is also compatible with achieving highest ecosystem services at the landscape scale, from

both management perspectives: tree species mixtures maximize biodiversity, without compromising high levels of functioning.

ACKNOWLEDGEMENTS

Financial support for this research was provided via the UGent GOA project 'Scaling up Functional Biodiversity Research: from Individuals to Landscapes and Back (TREEWEB)'. We thank the private forest owners and the Flemish Forest and Nature Agency (ANB) for granting access to their property. We thank Michael Perring and two anonymous reviewers for helpful feedback that greatly improved the text. We also wish to acknowledge the technical assistance provided by Pieter Vantieghe, Robbe de Beelde, Kris Ceunen, Luc Willems and Hans Matheve in setting up the plots, collecting the data and setting up the project database. Finally, Bram Sercu, Stefanie DeGroot, Thiebe Sleuwaert, Sanne Govaert, Manon Pien and Marc Vankerckvoorde are acknowledged for their help in collecting the data and with species identification.

CONFLICT OF INTEREST

None of the authors have a conflict of interest with the results reported here.

AUTHORS' CONTRIBUTIONS

L.B., D.B., A.M., K.V. and L.L. designed TreeWeb, the research platform used for the analysis here; L.R.H. developed the analysis approach and figure presentations, with inputs from M.L.V., L.B., D.B., A.M., K.V. and L.L.; L.R.H. performed statistical analyses and created all figures. Other authors (D.D., W.D., P.d.S., W.P. and I.v.S.L.) collected primary data or identified specimens that were analysed herein; L.R.H. wrote a first draft of the manuscript. All authors commented on further drafts.

DATA AVAILABILITY STATEMENT

Data available via Zenodo <https://doi.org/10.5281/zenodo.3516971> (Hertzog et al., 2021).

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How to cite this article: Hertzog, L. R., Vandegehuchte, M. L., Dekeukeleire, D., Dekoninck, W., de Smedt, P., van Schroyen Lantman, I., Proesmans, W., Baeten, L., Bonte, D., Martel, A., Verheyen, K., & Lens, L. (2021). Mixing of tree species is especially beneficial for biodiversity in fragmented landscapes, without compromising forest functioning. *Journal of Applied Ecology*, 58, 2903–2913. <https://doi.org/10.1111/1365-2664.14013>