Title: Mixing tree species is especially beneficial for biodiversity and forest functioning in highly fragmented landscapes

Short title: Tree species mixtures promote functioning and diversity

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Abstract

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. We here studied ecosystem functions and biodiversity data across ecosystem compartments in 53 mature forest plots varying in stand-level (tree species composition) and landscape-level (degree of fragmentation) characteristics. 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. Interestingly, more fragmented landscapes had higher landscape-level forest functioning, but this came at the expense of forest biodiversity. At the same time, mixed forest stands had higher levels of biodiversity than monocultures without affecting forest functioning. Diversifying forest stands thus represents a potential management strategy that promotes both ecosystems functioning and biodiversity in fragmented landscapes.

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 (Leidinger et al. 2019, Felipe-Lucia et al. 2018, 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).

Here we aim to synthesize how forest functioning and biodiversity can be enhanced across spatial scales, by linking stand-level effects of tree species diversity and composition with landscape-level impacts of fragmentation. Our approach is to develop desirability scores, based on weighted averages, (Allan et al 2015, Slade et al. 2017) to synthesize the responses of multiple ecosystem functions and the diversity of taxa at multiple trophic

levels to changes in tree species composition and forest fragmentation. This approach can accommodate contrasting 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. 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 harbor a high diversity of distinct taxa, while mixtures of these species could compromise monoculture levels of diversity and functionality (van der Plas 2016). This therefore means that the optimal landscape-level strategy would be to promote different tree monocultures rather than mixtures.

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 (DeGroote et al. 2017). Trade-offs and synergies between eight different ecosystem functions and taxonomic diversity of eight species groups at multiple trophic levels were quantified using a joint modeling approach. Next, by deriving desirability scores for forest functioning and diversity 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. This work builds on previous studies (Hertzog et al 2019, Baeten 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.

Methods

TREEWEB design

Data were collected within the TREEWEB exploratory research platform (sensu Baeten et al. 2013), consisting of 53 mature (900 m^2) forest plots scattered across 19 forest fragments in a 15 x 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 (DeGroote 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: (i) amount of edge habitat and (ii) proximity index. Full details can be found in DeGroote et al. (2017).

Data collection

Ecosystem functions (sensu Hooper et al 2005) comprised four stocks: topsoil carbon stock, tree biomass, insect biomass, and avian body condition (size-corrected biomass index), 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: understorey vascular plants, leaf miners and leaf galls (insect herbivores hereafter), carabid 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 potential contributions of the different functions and diversity indices to the desirability scores are given in Table 1. Sampling protocols are given in Appendix Text S1 together with summary statistics in Appendix Table S1 and S2.

Modeling framework

All analyses were performed using R v3.6 (R CoreTeam 2019) and can be fully reproduced from an online repository: 10.5281/zenodo.3516972. All function and diversity variables were normalized prior to analyses, that is, centered 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, avian body condition, 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, and the proximity index were used as explanatory variables. The proximity index is the sum of forest patch area (m^2) divided by the nearest

edge-to-edge distance squared (m^2) between all forest patches and the focal forest patch (McGarigal 2015).

The model was fit under a Bayesian framework with brms v2.8 (Brückner 2017). Following Gelman et al. (2006), we derived the proportion of variance in the eight ecosystem functions and eight biodiversity indices explained by each explanatory variable. Information on prior distributions, model settings, and model checks are provided in the Appendix Text S2.

Trade-offs and synergies

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

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 Appendix Figure S2. 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 1). Importance weights were derived from expertise knowledge present in the TREEWEB consortium, all project PIs provided weights and these were then averaged for each function or diversity measure (Hertzog et al. 2019). Third, plot-level multifunctionality 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: (i) generate the tree species composition and fragmentation levels for each plot based on the particular landscape configuration, (ii) derive the model predictions for the eight functions and eight diversity measures, (iii) use the desirability scores to turn the model predictions into multi-functionality or multi-diversity scores and (iv) sum the values across the plots separately for multi-functioning and multi-diversity. By using a Bayesian approach, model uncertainties could be transferred across all of these steps. The following landscapes were generated: (i) a low-fragmentation landscape (low amount of edge habitat and low proximity) with a similar proportion of the three monocultures, (ii) a low-fragmentation landscape with all 53 plots being three-species mixtures, (iii) a highly fragmented landscape (high amount of edge habitat and average proximity) with a similar proportion of the three monocultures and (iv) 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 Appendix Text S3.

Results

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, five between ecosystem functions, and 12 between ecosystem functions and diversity measures had a >90% posterior probability of being different from 0 (Figure 1). Of these 20 coefficients, 14 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).

Response 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 2). 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 S3). 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, bird, and woodlouse diversity were lower than average in common beech monocultures. Finally, in red oak monocultures, woodlouse diversity was higher, and 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 and spiders showed higher-than-aver-

age levels of diversity in plots with a high amount of edge habitat, while herbivore and bird diversity were lower.

Out of the eight ecosystem functions, proximity was related to only two: carbon stocks and bird body condition. Out of the eight biodiversity measures, insect herbivore, carabid beetle, millipede and bird diversity were negatively related with proximity to other forest fragments, while spider and woodlouse diversity were weakly positively related.

Desirability at different scales

For a given tree species composition, forest functioning 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 functioning. Desirability scores for biodiversity showed very similar patterns under both management perspectives. Overall diversity 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 functioning was higher in more fragmented landscapes irrespective of whether the individual patches were all monocultures or all mixtures. Overall diversity, on the other hand, was higher in landscapes composed of tree species mixtures than of different monocultures. Finally, the level of forest fragmentation had a small effect, with overall diversity only slightly higher in more continuous landscapes.

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, 2019 Penone et al 2019). Moreover, about two-thirds of these associations are 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 example of such an inherent mechanistic coupling, via bottom-up effects.

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 functioning and biodiversity. From a conservationist perspective, plot-level forest functioning 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 functioning, mainly driven by increased tree biomass and carbon stocks near habitat edges, as previously reported (Remy et al. 2016). Biodiversity 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 functioning was most strongly affected by landscape fragmentation, while overall forest biodiversity was most strongly affected by stand composition, probably due to dominant effects of tree species identity (van Schrojenstein Lantman et al. 2019). These differing response between functioning and biodiversity at the landscape scale could potentially create trade-offs. Moreover, the study area has been fragmented for many decades already, so that forests mainly (or even exclusively) harbor species that are well-adapted to such conditions. 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 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 between 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) but also the importance of sufficient forest cover configured in both large and small patches to support forest biodiversity at the landscape scale (Arroyo-Rodriguez et al 2020). We here expand on this by demonstrating the importance of tree species mixtures in highly fragmented landscapes for boosting both forest functioning and diversity (but see Valdes et al. 2020). Our results suggest that diversifying forest stands benefits forest biodiversity, both at the plot and landscape scale, without compromising the level of ecosystem functioning. Furthermore, converting monoculture stands into mixed stands in landscapes undergoing fragmentation appears to compensate for negative fragmentation effects on biodiversity.

Acknowledgments

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Tables

Table 1: Importance weights (min. 0 and max. 10) and direction given to the different ecosystem functions and taxa based on a productivist and conservationist perspective.

	variable	forest manager		conservationist	
		direction	weight	direction	weight
function	C stock	maximize	8.00	maximize	8.00
	Decomposition	maximize	6.00	maximize	4.67
	Tree biomass	maximize	9.50	maximize	6.00
	Regeneration	maximize	9.30	maximize	6.25
	Herbivory	minimize	7.25	minimize	4.67
	Predation	maximize	4.50	maximize	4.75
	Bird biomass	maximize	3.00	maximize	7.67
	Insect biomass	minimize	7.00	maximize	7.00
diversity	Vegetation	maximize	5.00	maximize	9.00
	Herbivore	maximize	2.00	maximize	7.00
	Carabid	maximize	2.00	maximize	9.00
	Spider	maximize	2.00	maximize	7.00
	Isopod	maximize	2.00	maximize	7.00
	Diplopod	maximize	2.00	maximize	7.00
	Bird	maximize	5.00	maximize	9.00
	Bat	maximize	3.00	maximize	9.00

Figures

Figure 1: Trade-offs and synergies between the diversity of the different taxa (a), the different ecosystem functions (b) and between the diversity and the function (c). The values represented are the correlation coefficient as estimated from a null multivariate model. Positive values (blue) indicate synergies between two variables, negative values (red) indicates 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 tradeoffs and synergies driven either by direct interactions between the variables (i.e. insect biomass and herbivory) or by other unmeasured drivers

(a) Diversity - Diversity

	Vegetation	Herbivore	Carabid	Spider	Isopod	Diplopod	Bird
Bat	0.02	−0.08	−0.04	−0.01	−0.16	−0.06	−0.05
Bird	−0.08	0.25	0.19	−0.1	0.06	0.07	
Diplopod	−0.05	−0.01	−0.08	−0.14	−0.17		
Isopod	−0.07	0.05	0.02	−0.01			
Spider	0.06	−0.06	0				
Carabid	0.1	−0.09					
Herbivore	−0.01						

(b) Function - Function

	C stock	Decomposition	Tree biomass	Regeneration	Herbivory	Predation	Bird biomass
Insect biomass	−0.09	0.15	−0.12	0.27	0.55	−0.12	0.03
Bird biomass	0.16	−0.1	−0.08	−0.19	−0.02	−0.02	
Predation	−0.08	−0.16	−0.04	0.08	0.02		
Herbivory	0.01	0.16	0.04	0.24			
Regeneration	−0.14	0	−0.14				
Tree biomass	−0.08	−0.19					
Decomposition	0.04						

(c) Function - Diversity

	C stock	Decomposition	Tree biomass	Regeneration	Herbivory	Predation	Bird biomass	Insect biomass
Bat	−0.08	−0.15	0.04	0	−0.08	0.06	−0.04	0.14
Bird	0.09	0.15	0.11	0.13	0.26	0.17	0.05	0.14
Diplopod	0.2	0.11	0.2	0.03	0.04	0.03	−0.01	0
Isopod	−0.01	−0.14	−0.08	0.08	0.05	0	−0.02	−0.02
Spider	0	0.1	−0.1	−0.02	−0.06	−0.02	−0.16	−0.25
Carabid	−0.1	0.13	0.01	−0.24	−0.08	0.22	0.01	0.13
Herbivore	0.18	0.14	−0.06	0.25	0.19	−0.14	0.01	0.15
Vegetation	−0.04	0.08	−0.05	−0.08	−0.22	0.05	0.01	−0.23

Figure 2: 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.
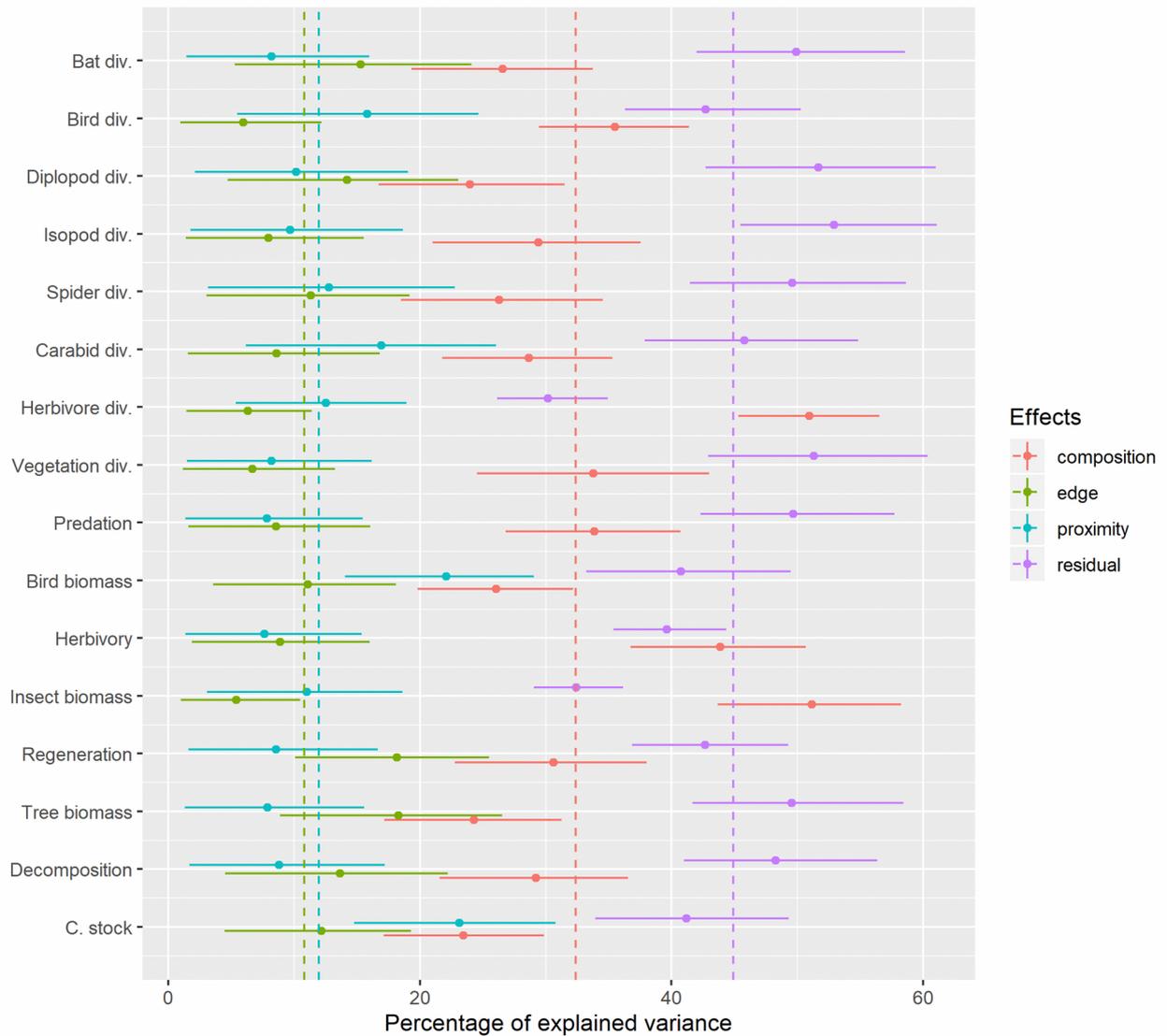
Figure 3: Desirability score for forest functioning (**a-b**) and diversity (**c-d**) at the plot scale (**a** and **c**) for the three monocultures (beech: fsyl, pedunculate oak: qrob, red oak: qrub) and for all tree species in a mixture (all) at different levels of fragmentation and at the landscape level (**b** and **d**) for landscapes composed of tree monocultures or of tree species mixtures. The dot represents the posterior median 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 greater than 80%.