Overstorey composition shapes across-trophic level community relationships in deciduous forest regardless of fragmentation context

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Abstract

1. Communities across trophic levels, and the functional roles they play, are vital for the sustained provision of ecosystem services. In forest systems, diversification of overstorey composition has been shown to be a key driver of biodiversity, but its influence on across-trophic level relationships remains scarcely known. Species across trophic levels in varied overstorey compositions are also differentially susceptible to fragmentation context. We hypothesise that fragmentation will disrupt community relationships associated with particular overstorey compositions.

2. We test this hypothesis using a tree diversity research platform across 53 deciduous woodland plots in central Belgium. We estimate species' abundances within nine, generally taxonomic, community groups across trophic levels: understorey vegetation; leaf miners and gall formers; woodlice, millipedes; carabid beetles, harvestmen, spiders, birds, bats. We use multiple co-inertia analyses to examine how taxonomic and trophic role community matrices covary across gradients of overstorey composition, via three different tree species diversification pathways, and fragmentation.

3. For all trophic role groups, across all plots, there was at least one significant pairwise comparison. Apart from comparisons involving bats, there was at least one significant pairwise correlation between taxonomic groups too. These results indicate correlated community matrices across trophic levels. Overstorey composition related to community tightness, that is, the level of co-ordinated change among taxonomic and/or trophic role groups as revealed by multiple co-inertia analyses. Notably, diversifying woodlands of beech *Fagus sylvatica* or red oak *Quercus rubra*

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with pedunculate oak *Quercus robur* correlated with increased taxonomic community tightness. Diversifying pedunculate oak forest stands with other overstorey species related to unchanged community tightness. Evidence was lacking for fragmentation affecting community tightness, singly or by interacting with overstorey composition.

4. *Synthesis*. Overall, changing tree species composition and fragmentation level affected across-trophic level community relationships differently. Yet, we demonstrated a clear signal that diversifying monoculture stands with particular species correlated with greater community tightness, and co-ordinated change among sets of community groups, across trophic levels and regardless of fragmentation context. We postulate that having tighter community relationships suggests that measures to improve biodiversity at one trophic level (i.e. trees) could affect other groups, and their associated roles, in a co-ordinated manner.

1 | INTRODUCTION

There is heightened awareness that greater biodiversity within ecosystems can support the increased delivery of multiple ecosystem functions, which in turn underlie the supply of ecosystem services that are vital for human well-being (IPBES, 2019). Although much early research focussed on single trophic levels in grassland systems and single functions, that is, diversity of herbaceous plants and primary productivity (Cardinale et al., 2012), recent work has demonstrated the importance of tree species richness and composition in determining multiple ecosystem functions in forest systems in different environmental contexts, for example, specific overstorey compositions (Baeten et al., 2019; Hertzog et al., 2019; Ratcliffe et al., 2017). Emergent functional properties (such as nutrient cycling rates, productivity, herbivory) depend on more than just tree species though. Relationships among community groups across trophic levels, and the connections and networks driving energy and matter flux among organisms (decomposers, primary producers, herbivores, predators), are vital (Barnes et al., 2018; Schuldt et al., 2018). Indeed, evidence is accumulating for the coupled change of community compositions across trophic levels in forest systems in different climate and forest management contexts (Schall et al., 2018; Vleminckx et al., 2019). Moreover, and across systems, there is evidence for the importance of well-connected multi-trophic relationships for efficient energy transfer and multi-functionality (Buzhdygan et al., 2020; Delgado-Baquerizo et al., 2020). However, multi-trophic community compositions, that is, the relationships among trophic levels, have scarcely been revealed, particularly in forest systems of different overstorey composition.

The degree to which the effect of tree species diversity and composition cascades across trophic levels is likely affected by the process of fragmentation (by which we mean the loss and associated splitting apart of habitat area, as opposed to fragmentation per se, Fahrig, 2003, 2019). This expectation arises because various groups of organisms are differentially susceptible to habitat loss, and the changed environmental conditions associated with different landscape configurations and patch dimensions (Ewers & Didham, 2006). For instance, higher trophic level organisms, for example, predators, are likely more dependent on the overall amount of habitat in an area, and thus likely prey resource base, than on the overstorey composition of specific forest patches. As predators are typically more mobile than other organisms, such as plants, this means predators can more easily get to different fragments, and within large fragments can reach the most suitable stands thus meaning that landscape context, for example, habitat area, can have a larger influence than local contexts. Indeed, loss of habitat area would tend to favour generalist predators with low exploration costs (Melián & Bascompte, 2002). When other species depend on fragmentation-sensitive taxa, species changes could propagate across trophic levels, leading to changed links and altered composition (Dunne et al., 2002). As well as internal drivers of change in community composition, through, for example, disruption of food web links, there may also be external drivers of change, via, for example, environmental filtering, dispersal and drift (Guzman et al., 2019; Jabot et al., 2020). For instance, different taxonomic groups may generally have different dispersal capabilities and tolerance of altered environmental conditions, such that fragmentation can change across-taxa community relationships.

Although evidence exists for the combined and/or interactive effect of tree composition and patch-scale fragmentation metrics on functional outcomes, for example, topsoil carbon storage, herbaceous plants of potential use to humans such as for medicine (Hertzog et al., 2019; Valdés et al., 2020), changes in community composition,

across trophic levels, in response to these drivers in forest systems is unknown. Earlier work has investigated questions of how overstorey composition and/or fragmentation context can affect the biodiversity in forests for multiple taxa. However, investigations typically investigate single community groups, taxonomic and/or functional, such as herbivores (e.g. Peter et al., 2014; Savilaakso et al., 2009), understorey vegetation (e.g. Normann et al., 2016; Pasion et al., 2018) and birds (e.g. Batáry et al., 2014). When single studies do examine multiple taxa, they do not explicitly analyse the possibility for co-ordinated community change in relation to putative drivers (a classic being Middleton & Merriam, 1983; more recent examples being Penone et al., 2019; Schuldt et al., 2015, 2019). In contrast, recent investigations into multi-trophic community composition relationships (e.g. Schuldt et al., 2017) tend not to consider potential drivers of differences in relationships (although note Vleminckx et al., 2019) and have been focussed on intact tropical forests.

Many forests though, especially in parts of Europe, exist in a fragmented landscape (Estreguil et al., 2013). In these landscapes, there is more and more impetus for forest managers to diversify their forest estates for multiple goals, away from an emphasis on even-aged, monoculture production plantations (Forest Europe, 2015; Puettmann et al., 2015; although note Schall et al., 2018, 2020). Indeed, management interventions for biodiversity may be more effective in relatively simplified landscapes (Mori et al., 2017); for instance, diversifying monoculture plantations with a few additional species. However, we do not know how such interventions (i.e. changing overstorey composition) will affect community relationships across trophic levels, especially in different fragmentation contexts. Co-ordinated change could imply that as one group of organisms respond, others will too. In addition, it may imply that one group of organisms could be used to indicate biodiversity responses more generally. Given across-trophic level relationships can also underlie the delivery of ecosystem functions, it is vital that we elucidate these ecological connections. This elucidation will advance knowledge on fundamental ecological relationships but also inform sustainable management.

Here, we reveal how a known driver (i.e. overstorey composition) of within-trophic level community change relates to networks of correlative relationships *among* functionally important taxa across trophic levels (hereafter 'taxonomic groups'). We investigated nine taxonomic groups comprising (trophic role in brackets): understorey plants (primary producers); woodlice, millipedes (decomposers); leaf miners and leaf gall formers (as one taxonomic group: herbivores); and carabid beetles, harvestmen, ground-dwelling spiders, birds and bats (predators). Using a tree diversity-oriented observational platform (sensu Baeten et al., 2013), of 53 mature woodland plots situated in a fragmented temperate deciduous forest landscape, we investigate whether fragmentation context changes relationships among groups in three different tree species 'diversification pathways'. These diversification pathways, not to be confused with evolutionary diversification, represent overstorey species richness trajectories from monocultures to three-species mixtures of economically (and socially) important species commonly planted

in European forests: *Quercus robur* L. (hereafter, pedunculate oak), *Quercus rubra* L. (red oak) and *Fagus sylvatica* L. (beech). In other words, one diversification pathway represents going from a given monoculture, that is, a stand dominated by one particular species, to either of the two-species mixtures that involve the monoculture species and one other species, and finally all three species together. Our study species are also associated with varied levels of biodiversity (e.g. Brändle & Brandl, 2001; Kennedy & Southwood, 1984). However, given the limited knowledge on multi-trophic compositional responses, we have limited expectations as to the correlation of a given diversification pathway with community patterns, except for the likely importance of pedunculate oak being linked to responses given its importance for different elements of biodiversity (Penone et al., 2019).

We ask whether taxonomic group relationships across trophic levels within diversification pathways relate to the fragmentation context. Our main expectation is that fragmentation disrupts the connections across taxonomic groups, and that this may depend on the specific overstorey species 'diversification pathway'. Although unable to test the mechanism directly due to using correlative analyses, we expect this disruption because organisms at different trophic levels are differentially susceptible to fragmentation. On the other hand, changing environmental conditions due to fragmentation may lead to high congruence among taxonomic group matrices due to environmental filtering (i.e. strict species sorting), while community divergence may be more related to drift and mass effects (Jabot et al., 2020).

To test our expectation, we use multiple co-inertia analyses for taxonomic group matrices, and take account of the spatial dependence among plots. To assess the network of connections, we compute a novel across-trophic level metric: 'community tightness' (Figure 1). Tight communities show co-ordinated change among groups across the different plots, are highly congruent, and thus exhibit low community distances from their plot centroid in multivariate space. In contrast, loose communities have a low degree of co-ordinated change, and thus have low congruence and a higher overall distance from the plot centroid. Importantly, plots that are shown to have tight communities represent a situation where within and across- group correlations, positive or negative, are strong, whereas large across-trophic level community distances can be derived even when there are tight correlations within a group, but not among groups (Figure S1, Appendix A). Prior to our main analysis, we also tested whether individual taxonomic group compositions relate to overstorey diversification and/or fragmentation context using redundancy analyses (RDAs) that take account of spatial relationships among plots. We would expect at least some individual group relationships with fragmentation to be necessary if fragmentation was to disrupt across-trophic level connections. To complement our main focus, we also tested whether our results were robust to grouping of species into trophic roles alone (i.e. primary producers, herbivores, detritivores, predators and omnivores, regardless of the taxonomic group they belonged to). We discuss the potential implications for biodiversity and ecosystem functioning where our correlative
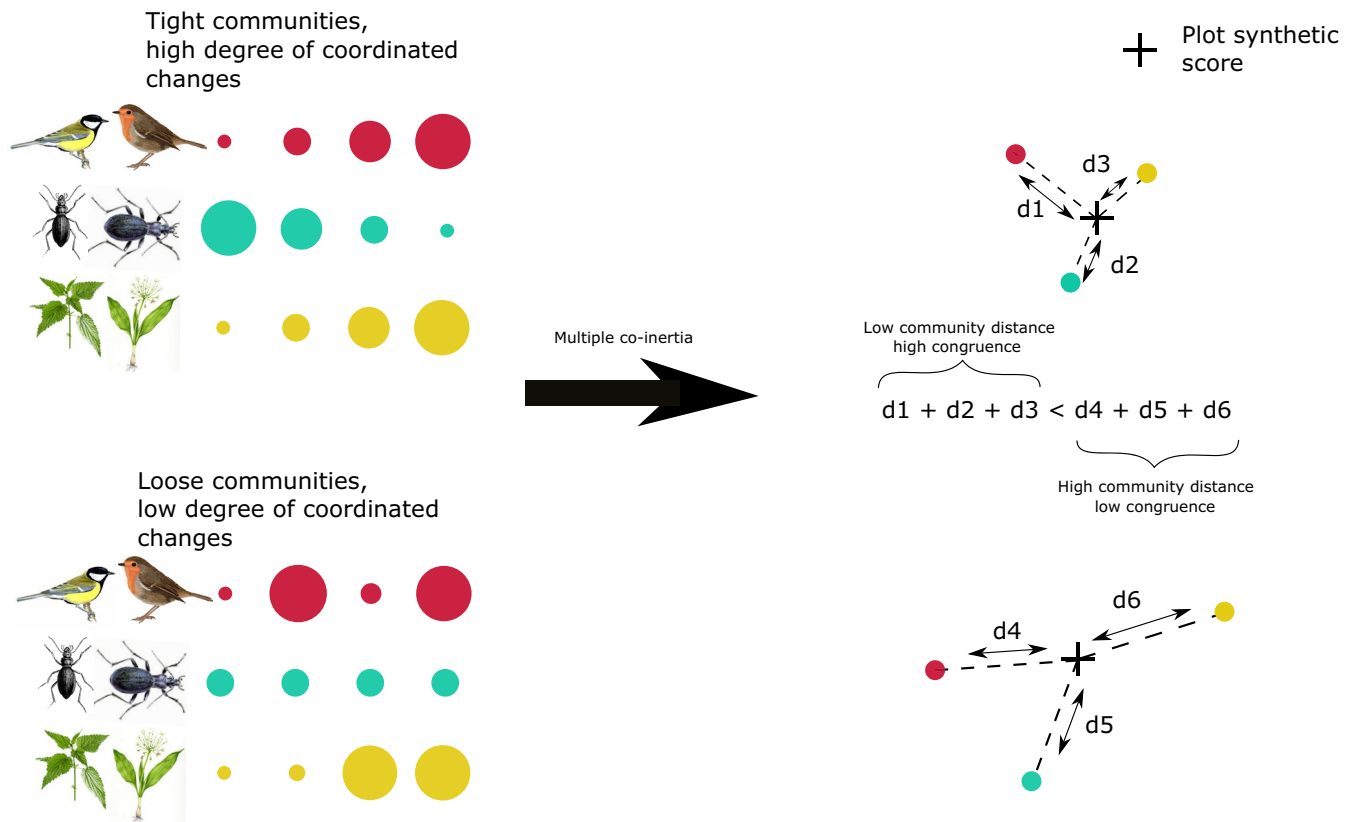
FIGURE 1 The visualisation of community tightness. Taxonomic communities across trophic levels can exhibit a high (top) or low (bottom) degree of co-ordinated change across plots (bubble size indicates abundance of species in a taxonomic group; one set of bubbles per taxonomic group per level of co-ordinated change is shown for clarity). When this covariation (across multiple species within and across groups) is visualised in two-dimensional space after multiple co-inertia analyses, tight communities show a low summed distance (i.e. high congruence) from the plot synthetic score while loose communities show a high summed distance (i.e. low congruence). The plot synthetic score represents the location of a given plot on the first two axes in multiple co-inertia analysis space, based on a compromise between all considered groups, with each group weighted by their inertia (see Section 2 for details). Simulation analyses show that high distances from the plot synthetic score can be derived when across-group correlation is low, even if within-group correlations are high (Figure S1)

analyses reveal greater or lesser amounts of organised across-trophic level community structure.

2 | MATERIALS AND METHODS

2.1 | Study design

We used community composition data from nine taxonomic groups surveyed in 53 woodland plots scattered across 19 forest fragments in northern central Belgium. The careful selection of these 30 × 30 m plots allowed us to estimate the effect of overstorey composition on multi-trophic community relationships, via three overstorey 'diversification pathways', in different fragmentation contexts. This platform represents an 'exploratory platform design' (sensu Baeten et al., 2013) and is a unique resource, as it allows the disentangling of overstorey composition and fragmentation effects from each other, while controlling for potential confounding factors. For instance, we situated all plots in mature forest stands that have been continuously forested for at least 150 years and are on similar

soil type (De Groote et al., 2017), as well as being located in similar agricultural/built environment landscape contexts. In addition, no large-scale management activities (e.g. tree felling) have taken place within the last 20 years. This latter criterion minimises the possibility of confounding post-disturbance dynamics with focal variables, although we cannot rule out long-lasting legacies of historic management practices on community relationships (e.g. Perring et al., 2018).

In the 53 plots, we represented all possible combinations of three site-adapted species: beech, pedunculate oak and red oak. We had six to eight replicates of each of the seven possible combinations: all three monocultures, three two-species mixtures and all species together. We chose these particular species and their constituent mixtures because of their importance to forestry, both in the study area and more widely in Europe (Nicolescu et al., 2018; Schelhaas et al., 2018), and because of the drive to manage the forestry estate sustainably. It is thus particularly relevant to understand how multi-trophic community composition changes for different mixtures of these species. Of particular note is that red oak is a non-native species sometimes considered problematic for biodiversity (Campagnaro et al., 2018; Chmura, 2013; Dyderski et al., 2020).

In marked contrast, pedunculate oak is considered a useful reservoir for multiple aspects of biodiversity (Böhm et al., 2011; Penone et al., 2019; Southwood et al., 2004). Dense beech stands, because of low light availability at the forest floor, can be considered less 'wildlife-friendly' as there may be limited habitat niches for other organisms.

We made our initial plot choice so that we could design a classic biodiversity–ecosystem function 'experiment' in mature forest plots. In other words, relative frequencies of the different species were as equal as possible in the different mixtures, and having all possible mixtures avoided dilution effects in the overall design. Thus, diversity effects could be disentangled from a dilution of a given species in monoculture by other species, because other species' monocultures were available for comparison (Baeten et al., 2013). However, the overall design can also be regarded as three dilution experiments side-by-side, that is, dilution of constituent monocultures (e.g. species X) to two different two-species mixtures (e.g. species X and Y, species X and Z), and then to a three-species mixture (species X, Y and Z). We use this property (of three separate diversification pathways via a dilution gradient), which is also of direct relevance to forest managers considering diversifying their estate, for subsequent analyses.

To understand whether the fragmentation context of the diversification pathway related to multi-trophic relationships, we derived plot-based indices of fragmentation. We used geographical information systems to derive data on variables such as fragment size, shape and isolation, as well as plot distance to nearest edge and forest area in the surrounding landscape. Using QGIS and FragStats (McGarigal et al., 2012), we computed 12 fragmentation indices for each plot, for example, fragment area, fragment edge density (see Table S1). We then used a principal component analysis (PCA) to extract uncorrelated axes of variation from these indices; we used plot scores from the first axis (51% of total variation) as an index of fragmentation (Figure S2, Appendix B). Given the correlations of the different fragmentation variables with the first axis, low plot scores along this axis denote plots found in relatively large, contiguous forest habitat while high plot scores denote plots found in small, isolated fragments. The second axis, though with non-random relationships (according to parallel analysis), was most related to fragment shape, and explained limited variation (17%). Since we did not expect fragment shape to influence across-trophic level community relationships, we only used plot scores from the first axis, given the large amount of variation it explains across the 12 fragmentation variables, and due to its interpretability. It should be noted that there is a general tendency, in our landscape, for large fragments to be better connected, so scores midway along this gradient do not represent a situation of small fragments with low isolation, nor an isolated large fragment, instead they represent medium-sized fragments of medium isolation. We emphasise that in using the term 'fragmentation', we mean the *process* of splitting contiguous habitat into habitat patches with accompanying loss of area (Ewers & Didham, 2006), such that we can estimate fragmentation at the patch level. This is opposed to the *pattern* of habitat for a given amount of total habitat area, with a

comparison among different landscapes, that is, habitat fragmentation per se (Fahrig, 2017).

Importantly, most diversification pathways occupy a similar range, and have a similar distribution, across the fragmentation gradient (Figure S3, Appendix B). This enables us to disentangle the influence of fragmentation from that of overstorey composition, and robustly examine the potential for fragmentation to disrupt across-trophic level community relationships in the different diversification pathways. However, the fewer replicates in the red oak and beech mixture have a more limited fragmentation gradient, while the beech and pedunculate oak mixtures extend the fragmentation gradient, compared to other compositions. In addition, beech–red oak mixture plots tend to be found at closer distances to each other within the study landscape, than plots of the other overstorey compositions (Figure S4, Appendix B). We bear these properties in mind when interpreting the results.

2.2 | Response variables: Community compositions across trophic levels

In each of the plots, we estimated the community composition of eight taxonomic groups, with well-defined functional roles across trophic levels. These groups were: primary producers (represented by the understorey [<1 m in height] vegetation); predators (separately, for carabid beetles [*Coleoptera*], ground-dwelling spiders [*Araneae*], harvestmen [*Opiliones*], breeding birds and bats); and, decomposers (separately, for woodlice [*Isopoda*] and millipedes [*Diplopoda*]). We included a ninth 'taxonomic' grouping, of leaf miners and leaf gall formers of overstorey trees. Most of the species included are, among others, representatives of the *Diptera* and *Hymenoptera* orders. Although these orders represent a wide array of functional groups (e.g. pollinators, predators, parasitoids), we only sampled herbivorous larvae via the mines and galls on overstorey leaves. We therefore categorised them as herbivores in relation to their trophic role. Furthermore, since estimations of abundance were done on the same leaves, we merged these taxa to create this 'taxonomic category' that we refer to as gall formers/miners hereafter. Our generally taxonomic classification also considered other factors, beyond the trophic role played by organisms. For instance, the decomposers of woodlice and millipedes have differing sensitivities to soil moisture (De Smedt et al., 2018) and thus have potentially different responses to our focal variables of overstorey composition and fragmentation. We considered species that ate seeds (e.g. carabids) as predators because this (usually) leads to the death of the individual organism being 'preyed' upon (notwithstanding passage through the gut required for some plant species to germinate). We did not separately classify omnivores within these taxonomic groups, instead considering all species to be predators that are known to consume live prey, even as a minor part of their diet. However, in Supplementary Analyses (Appendix G) to test the robustness of our findings, we grouped species in community matrices according to their presumed trophic role, and including omnivores as separate

from pure predators (i.e. a grouping of primary producers, herbivores, decomposers, predators, omnivores).

We measured proxies of abundance of representatives of each of these groups using appropriate methods, as explained in Appendix C, for example, activity–abundance of carabids via pitfall traps, herbaceous community cover via plot surveys. Since we were assaying a large number of groups, and given logistical constraints, confidence in some methods to generate robust abundance patterns was relatively low. For instance, we only sampled bats on one night per plot, although previous work has shown that a single night of records can reveal differences in bat communities among forests (e.g. Charbonnier et al., 2016; Fuentes-Montemayor et al., 2017), and we also found all bat species known to occur in the region. Importantly, sampling effort for each group was constant across plots, thus satisfying a key assumption in our later statistical analyses, while plots were sampled in a random order for any given taxon to prevent bias. In addition, sample coverage, as based on equations from Chao et al. (2014), and implemented in the iNEXT R package (Hsieh et al., 2020), was between 66% for birds and 99% for herbivores. Sample coverage could not be assessed for bats and understorey vegetation, but local experts considered that these communities were also sampled close to completely in any given plot. Our later analyses therefore assume we sampled each of the taxonomic groups, for their assumed trophic role, completely. Most importantly, estimates among forest fragments and in different overstorey compositions are comparable since we conducted surveys, within a taxon, at essentially the same time.

These taxonomic groups of species occupy different trophic levels (Table S2, Appendix C). However, given that we did not analyse ecological interactions directly, we analyse all possible pairwise community relationships. Indeed, it may be the case that there are important relationships that structure communities that are not driven directly by trophic relationships, including through environmental filtering, variation in spatial use properties, and dispersal (Guzman et al., 2019; Jabot et al., 2020). We would overlook such relationships with a network analysis type of approach (see also Section 4, and arguments in Schuldt et al., 2017). Our approach thus allows us to investigate community congruence in taxonomic groups across trophic levels, and in poorly known food webs, in these fragmented forest patches. However, to help organise the presentation of cross-taxa relationships, we assume trophic roles and distances between the different taxonomic groups as explained in Appendix C and Table S2.

2.3 | Statistical analysis

Prior to all statistical analyses, community data were Hellinger-transformed to prevent overabundant species influencing results (Legendre & Gallagher, 2001). We conducted all analyses in R (R Core Team, 2020), using packages VEGAN (Oksanen et al., 2019), ADE4 (Bougeard & Dray, 2018; Dray & Dufour, 2007; Dray et al., 2007) and ADESPATIAL (Dray et al., 2020). Code and data to reproduce the

analysis and results are stored in an open online repository: https://doi.org/10.5281/zenodo.3921936.

2.3.1 | Within-trophic level analyses

Prior to testing our main expectation (that across community group relationships in different diversification pathways are disrupted by fragmentation), we checked whether each of the nine taxonomic groups were affected by overstorey composition in each diversification pathway and/or by fragmentation, acting alone or interactively. We ran separate RDAs for each taxonomic grouping and each diversification pathway, that is, $9 \times 3 = 27$ RDAs. In these RDAs, the response was species' abundance in cells of a given taxonomic group's plot $\times$ species matrix, and the covariates were: (a) the tree species composition as a categorical variable; (b) the fragmentation index plot score (see above for definition); (c) the interaction between tree composition and fragmentation; and (d) the principal coordinates of neighbourhood matrix (PCNM) scores, to account for potential spatial non-independence among plots. The effect of each covariate on taxonomic group community composition was assessed by permutational ANOVA, with 9999 permutations (see Appendix D). Results from these RDAs confirmed that the various groups are affected to different extents by overstorey composition in different fragmentation contexts (Table S3). Explained variation in significant models ranged from 12% (millipedes in the pedunculate oak diversification pathway) to 72% (herbivores in the red oak pathway). In general, fragmentation had larger effects than overstorey composition on within-group community relationships in the different diversification pathways (cf. Figure S6 with Figure S7), while interactive effects were extremely rare (Table S3). There was limited predictability in the movement of communities in the constrained RDA space from monocultures to two-species mixtures, and thence to three-species mixtures (Figure S6). Considering diversity metrics for the groups separately (Appendix E) also showed large ranges in total species richness (i.e. gamma diversity: 7 (bats)—88 (spiders) species) and average plot-based species richness (alpha diversity: 2.9 (harvestmen) to 18.4 (spiders) species), while for all groups, beta diversity was dominated by turnover rather than nestedness (sensu Baselga, 2010; Table S4).

These findings confirm that within these taxonomic groups, and in terms of their community composition, they are differentially susceptible to overstorey composition, and to fragmentation, confirming the premise of our main expectation. Given this confirmation, we may therefore expect that fragmentation context can influence the across-trophic level relationships found in each of the diversification pathways. The remainder of our manuscript now focuses on investigating this expectation.

2.3.2 | Across-trophic level community relationships

First, we used traditional co-inertia analysis (COIA) to examine whether there were any pairwise community relationships among

the taxonomic group abundance matrices. We analysed all possible pairwise comparisons including all plots. COIA extracts the common structure in two community matrices using a symmetric coupling method; this approach provides more flexibility than RDA or co-correspondence analysis (CCA; Dray et al., 2003). For each community matrix pair (36 pairs in total), we ran a COIA using uniform row weights and unit column weights (which reflects the equal sampling effort applied in all plots). We retained the first two axes from each analysis, which explained between 30% (spider–millipede pair) and 80% (bat–leaf miner/gall forming pair) of the covariation in paired community matrices. We extracted the congruence coefficient (RV), which is akin to a squared Pearson's correlation coefficient for multivariate data (Robert & Escoufier, 1976), from each pairwise analysis. Larger RV denotes tighter links between community pairs.

To assess the significance of each pairwise congruence, and to account for any potential spatial effect in structuring the communities, we used Moran spectral randomisation to generate 9999 simulated communities for each taxonomic group, based on the spatial connection between plots (see also Vleminckx et al., 2019). We defined the spatial connection between plots by the forest fragments in which they were located: we considered plots in the same fragment to be neighbours. We assumed that the strength of the connection between plots was inversely related to their Euclidean distance. For pairs of matrices from the 9999 simulated communities for each taxon (e.g. matrix 1 of birds, and matrix 1 of carabids), we ran COIA to get a distribution of null congruence coefficients for a given pairwise relationship. In other words, this gives the congruence distribution that we would expect between communities based on spatial location alone. We then compared the observed RV to this null RV distribution. We considered the observed RV coefficients to be significant if more than 95% of the null congruence values were lower than, or equal to, the observed values. Comparing these raw correlations to a null distribution allows us to investigate what drives observed correlations in a robust manner. Significance therefore implies that pairwise community relationships appear to be driven by more than spatial location alone; for instance by overstorey composition, unmeasured drivers or direct/indirect interactions among taxa.

In a next step, we asked whether the overall tightness of these significant pairwise relationships across taxonomic groups (Figure 1) depended on the diversification pathways, and whether fragmentation disrupted the across-trophic level taxonomic group relationships in the different diversification pathways. To assess sensitivity of our results to the choice of included taxonomic groups, we also repeated analyses with all taxonomic groups (i.e. including those without any significant pairwise relationships) and a set of taxonomic groups with significant, and highly congruent, pairwise relationships.

This community tightness assessment required a two-step approach. In the first step, we analysed the chosen taxonomic groups with multiple COIA, retaining the first two axes, as with the pairwise COIA. Thus, the analysis extends pairwise COIA to more than two community matrices, but the derivation of congruence in PCA axes remains. We weighted each group by their inertia (proportion of variation explained by the first two axes), to ensure that the plot synthetic score location (compromise) between all groups will represent all the groups as closely as possible (Thioulouse, 2011). From the multiple COIA we extracted this plot synthetic score, that is, the average plot position across all groups in the co-inertia space (based on the first two axes). Per taxonomic group, we then calculated the Euclidean distance between their group-level normed score and the plot synthetic score (Figure 1). We then summed these distances across all included groups to arrive at an estimate of how congruent the given taxonomic groups are in a given plot: the community tightness. The smaller this summed community distance, the more closely related communities are, as all communities in total are closer to the plot-level normed score. We have introduced a new term 'community tightness' despite the superficial appearance of relationships to existing concepts, for instance connectivity and multivariate homogeneity of group dispersion (e.g. betadisper in VEGAN R package). Connectivity refers to the number of nodes that need to be removed to isolate sub graphs in a given network (Diestel, 2005), which is different than the concept here, which works on relationships among community compositions across trophic levels. Multivariate homogeneity of group dispersion works on one community table (one taxon) and tests for deviation in the distance between plots with different grouping variables, while our approach accommodates multiple taxa and works per plot to return a vector. In addition, betadisper can only test for the effect of categorical grouping variables while the effect of both continuous and categorical variables on community tightness can be investigated here.

The second step of our analysis capitalises on these metric properties, and asks whether community tightness in each plot depended on overstorey composition (expressed as a categorical variable, with seven levels, in the model), the position of the plot along the fragmentation gradient, or their interaction. To do this, we used a generalised linear model with Gamma distribution and log link, in the BASE package of R. No spatial autocorrelation was present in model residuals, after checking with the package DHARMA (Hartig, 2020). We interpreted these overall results in the frame of each diversification pathway and its associated fragmentation context.

3 | RESULTS

Analyses of all possible pairs of community taxonomic matrices showed that congruence (RV) values vary between 0.12 (bats–harvestmen pair) and 0.60 (carabids–spiders pair). There were 14 significant tests, based on comparisons to null distributions and taking account of spatial relationships among plots, out of a possible 36. Interestingly, there was no pattern of increased covariation (i.e. matrix congruence), or increased likelihood of significance for tests, in pairs across neighbouring trophic levels. Instead, 71%, 28%, 33% and 50% of pairwise relationships were significant in the classes of assumed trophic distances of 0 ($n = 7$ comparisons), 1 (18 comparisons), 2 (9 comparisons) and 3 (2 comparisons) respectively (Figure 2).

Closer inspection of these results showed that all analysed groups, except bats, had at least one significant pairwise interaction
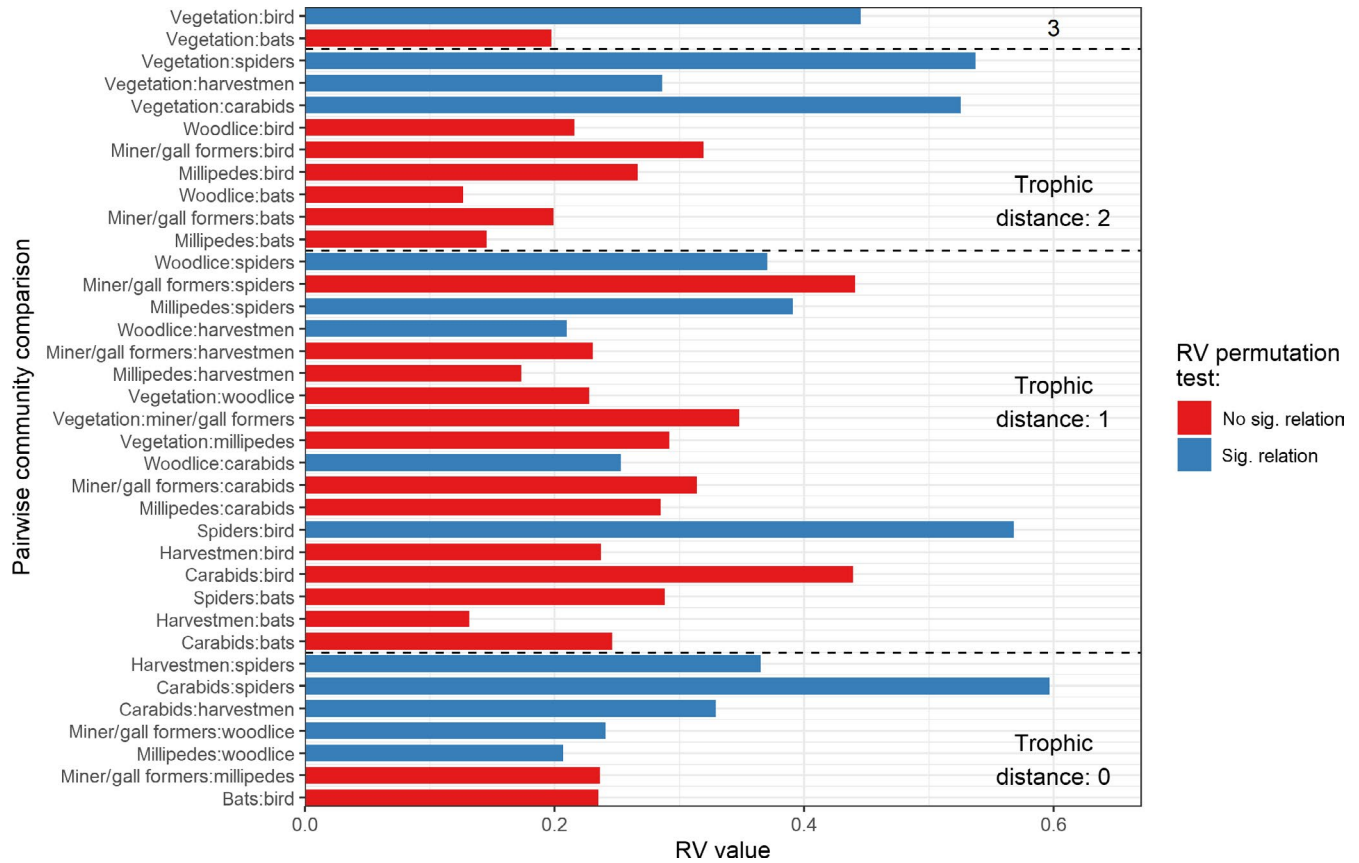
FIGURE 2 Pairwise community relationships in the nine taxonomic groups examined, as assessed by the community congruence coefficient (RV value). A high RV value denotes correlated relationships between community matrices. Significant relationships (at 5% level), based on comparison of the observed values to a null distribution from Moran Spectral Randomisation tests, are shown in blue; significant results based on this test imply that factors beyond spatial relationships between plots (e.g. due to an underlying environmental factor, interactions among groups) underlie the observed co-ordinated change in community matrices. Bars are ordered on the assumed trophic distance between the different taxonomic groups we examined (Appendix C)

TABLE 1 Results from a GLM of the effect of overstorey species composition, fragmentation, and their interaction on community tightness, as computed according to Figure 1 with inertia weighting. Significant values ($p < 0.05$) are indicated in bold. The taxonomic groups considered were: understorey vegetation, leaf miners/gall formers, woodlice, millipedes, carabids, spiders, harvestmen and birds, that is, all taxa with at least one significant pairwise interaction with another taxon (bats were omitted)

Variable	df	Deviance	Residual degrees of freedom	Residual deviance	Pr (>Chi)
Fragmentation	1	0.00	51	2.59	0.842
Species composition	6	0.66	45	1.93	**0.016**
Fragmentation: species composition	6	0.29	39	1.64	0.347

with another taxonomic group, that is, representing the following set: 'understorey vegetation–leaf miners/gall formers–woodlice–millipedes–carabids–spiders–harvestmen–birds'. All congruence coefficients were >0.2 for pairwise relationships among these groups, except for harvestmen and millipedes. Interestingly, some relatively high coefficients (>0.4) were not significant (i.e. birds and carabids, spiders and leaf miners/gall formers) indicating that spatial relationships among plots could be related to these community relationships. In contrast, four pairwise groups had significantly congruent relationships, of a value >0.5 (spiders and understorey vegetation,

carabids and understorey vegetation, birds and spiders, spiders and carabids). In such significant cases, strong pairwise community congruence was driven by more than spatial relationships among plots, suggesting other underlying factors for relationships, that is, due to responses to focal variables, direct/indirect interactions among communities, and/or relationships with unmeasured variables.

Analysing the tightness of relationships across these taxonomic groups, by totalling each group's distance from the normed plot score in multi co-inertia space, indicated that tree composition is significant in determining community distance ($p = 0.016$; Table 1). There
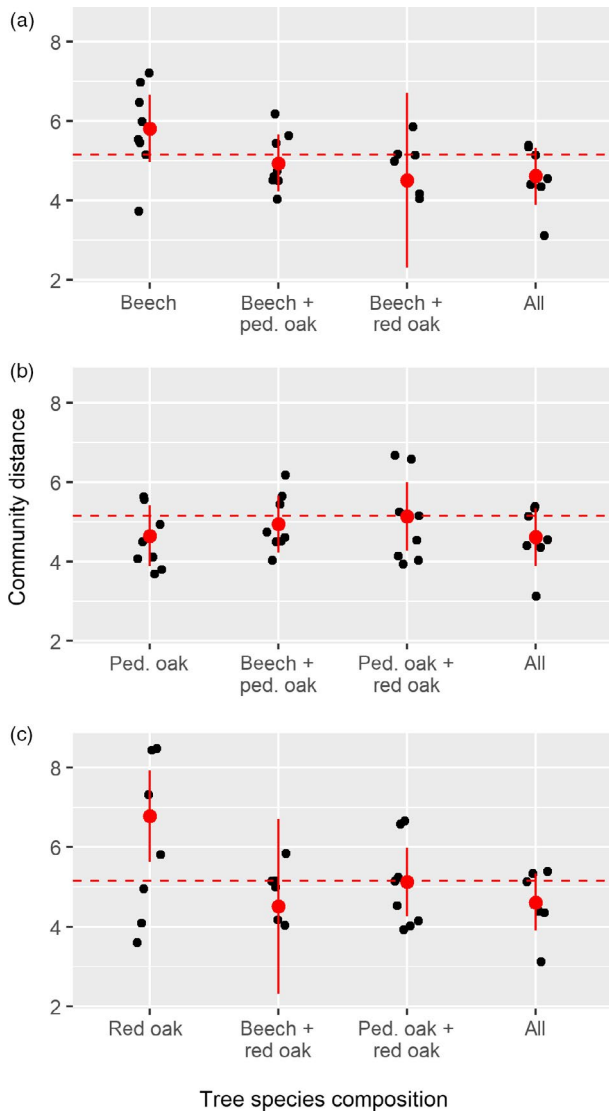
FIGURE 3 Taxonomic community distance across trophic levels as a function of overstorey tree species composition, plotted for each of (a) beech, (b) pedunculate oak and (c) red oak diversification pathways. We computed distances according to each taxonomic group's position in relation to the plot synthetic score on the first two axes from a multi co-inertia analysis, as conceptualised in Figure 1. Black dots represent observed individual-plot community distances in the given overstorey compositions, while the red dot gives the model prediction of total community distance for a given overstorey composition at an average level of fragmentation, with 95% confidence intervals. The red dotted line represents the average community distance across all overstorey compositions at an average level of fragmentation. Shown are results from the eight groups that exhibited at least one significant pairwise congruence coefficient (Figure 2), that is, excluding bats. Qualitative results are robust to the number of taxonomic groups included (Figures S18 and S19; Tables S6 and S7) but differ slightly when groups comprise community matrices of trophic roles, regardless of taxonomic group (Figure S21; Table S8; see also main text and Appendix G)

was no evidence for fragmentation acting alone or interactively with tree composition to disrupt this community distance ($p = 0.84$ and $p = 0.35$ respectively). These insights were qualitatively unchanged

when we analysed all (i.e. including bats), or a restricted set (i.e. 'understorey vegetation–carabids–spiders–birds'), of the taxonomic groups (Tables S6 and S7). Quantitatively, and unsurprisingly, the total community distance decreased the fewer the groups we considered. Analysing community matrices that account for trophic role only showed at least one significant pairwise relationship in all groups; the importance of overstorey composition, and not fragmentation, in determining community tightness remained (Table S8; Appendix G).

Regardless of the taxonomic groups we included in the community tightness analyses, diversifying a pedunculate oak monoculture, which already has tight linkages between the across-trophic level communities, tended to leave community tightness unchanged, that is, community distance was relatively low (Figure 3; Figures S18 and S19). In contrast, beech and red oak monocultures tended to have loosely connected taxonomic communities across trophic levels, that is, relatively high community distances, although this loose connection was not apparent for beech monocultures when trophic roles alone were considered (Figure S21, Appendix G). This increased distance was significant in the case of red oak, when compared to the average community distance across all seven possible overstorey compositions (red dotted line in Figure 3; Figures S18, S19 and S21). Diversifying red oak and beech monocultures with the other overstorey species did not correlate with predictable changes in community tightness. Adding pedunculate oak to either of the other monocultures related to increased taxonomic community tightness but the mix of red oak and beech was more variable (Figure 3).

4 | DISCUSSION

Our correlative analysis of taxonomic groups across trophic levels in fragmented temperate deciduous forests indicates that overstorey composition potentially plays a crucial role in determining the tightness of relationships among these groups. In particular, the even presence of pedunculate oak in forest stands related to relatively congruent (tight) across-trophic level community relationships compared to compositions without pedunculate oak. Stands without pedunculate oak (i.e. red oak, beech and their two-species mixture) have a tendency, with taxonomic grouping, for higher, and more variable, across-community distances from plot centroids, indicating less co-ordinated and more diverging relationships between the different species assemblages. Contrary to our initial expectation, fragmentation context was not related to the tightness of these relationships, either alone or via an interaction with overstorey composition. This is despite the fact that fragmentation and overstorey composition have important relationships with within-group assemblage composition (Table S3). Together, these results could imply that fragmentation can affect species' relative abundances within groups across trophic levels, but across-trophic level relationships are maintained due to co-ordinated change in species (Figure 1; Figure S1). As we go on to discuss, our novel findings, if indeed shown to be causal rather than merely correlative,

can have implications for understanding biodiversity dynamics in response to different overstorey compositions. In addition, disruption of (relatively) tight across-trophic level community relationships may have important consequences for ecosystem functioning and thence delivery of ecosystem services.

4.1 | Going beyond biodiversity metrics: Across-trophic level community composition responses

Substantial research efforts have gone into understanding diversity responses, from different trophic levels, in forests with varying overstorey composition, sometimes in alternative fragmentation contexts (e.g. Schall et al., 2018; Valdés et al., 2020). However, multi-diversity analyses typically ignore the explicit community compositions in these different groups, concentrating instead on diversity metrics (e.g. species richness or beta diversity), as noted in the Introduction. However, the abundance of species in different groups (via mass-ratio effects; Grime, 1998) and the relationships among species across trophic levels can drive energy and nutrient flows (Buzhdygan et al., 2020; Schuldt et al., 2018). It is thus important to begin to understand how community compositions can vary in response to drivers, that is, taking account of abundance and relationships among, as well as identity of, species, across trophic levels. Co-inertia analyses offer this opportunity, especially in complex systems where we do not know all trophic, or non-trophic, interactions. Such analyses offer the opportunity to consider co-ordinated responses across groups, going beyond the typical within-community analyses (Jabot et al., 2020).

Previous studies contributing to the endeavour of understanding co-ordinated change have used similar analytical techniques to us, but in intact tropical forests (Schuldt et al., 2017; Vleminckx et al., 2019) as compared to the fragmented temperate forests here. Schuldt et al. (2017) used Procrustes analysis rather than COIA, precluding direct comparison of the pairwise relationships we found among the functionally important groups (Figure 2), although their correlation coefficients ranged from 0.36 to 0.9. Vleminckx et al. (2019) on the other hand, found a slightly smaller range and higher pairwise RV values (0.37–0.75) compared to our analysis (0.12–0.6). They examined taxonomic groups of trees, ants, spiders and fungi. Interestingly, all Vleminckx et al.'s (2019) pairwise relationships were statistically significant, while we found some insignificant pairwise relationships (as did Schuldt et al., 2017), especially involving bat communities. Although not all relationships structuring communities may be due to direct trophic links (Schuldt et al., 2017), and bat community sampling was necessarily restricted (see Section 2), it is possible that bats were unrelated to other communities in our results due to foraging preferences for unmeasured groups and/or their different activity times (although this may also apply to carabids), low species numbers coupled with a generalist profile, and their ability to roam widely. Indeed, we observed virtually all bat species in virtually all overstorey compositions (Figure S9).

The evidence we have uncovered (Figure 3) that taxonomic groups across trophic levels can exhibit co-ordinated change, especially in overstorey compositions with pedunculate oak, suggests that measures to improve biodiversity at one trophic level (i.e. in trees) may lead to biodiversity change at other trophic levels. The effects this has on overall biodiversity (e.g. does it improve?) depends on the changes invoked, but co-ordinated change implies that as one group of species will respond, others, on different trophic levels, will also respond. For instance, one could speculate that if across-trophic level community relationships are tight, then as one group at one trophic level increases in abundance because of some conservation measure, we can expect another group to track this increase—this could lead to larger population size, increased stability and potentially larger biodiversity depending on effects such dynamics have on other organism groups. The strength of the relationships we have observed may be due to the deliberate manipulation of overstorey composition; whether deliberate variation in the composition of another trophic group (if achievable) leads to such co-ordinated change across trophic levels would require further investigations. Additionally, it would be good to consider whether any changed diversity is desirable (for instance, in a conservation context (cf. Tylianakis et al., 2010)), and the actual species involved, but such considerations are beyond the scope of this paper.

On the other hand, a relatively large (or variable) taxonomic community distance metric (i.e. loose correlation; as shown for red oak and beech monocultures and their two-species mixtures) implies little covariation among species and groups such that a single species (or group) may respond to a management measure to improve biodiversity without response across other trophic levels. This may arise because individual species groups (or even individual species) respond to different drivers. However, the sequence of RDAs we undertook (Appendix D) shows that individual taxonomic groups can respond differentially to potential underlying drivers, without losing co-ordinated change among groups. Such responses may at first appear surprising, and are exemplified by the millipede-spider significant pairwise relationship which was moderately strong (RV ≈ 0.4) yet individual groups showed contrasting responses to potential drivers in the RDA (Appendix D). It may be that the significant pairwise relationship arose due to similar responses to unmeasured drivers (between 46% and 73% of the composition change in spiders was unexplained, and 88%–91% in millipedes). We could also posit that it is due to direct interactions between the two, that is, spiders predating on the millipedes. Further insight into how these within-taxon community responses scale to across-taxa relationships could be garnered by considering how properties such as dispersal ability, body size and forest affinity relate to organism responses to fragmentation and overstorey composition, as well as through direct observations of interactions, but such analyses were beyond the scope of this paper.

Differential responses within groups did though generally match with expectations, adding justification to our novel findings on community tightness. For instance, woodlice, which are sensitive to humidity, responded to fragmentation while millipedes,

which are considered less sensitive (De Smedt et al., 2018), did not. Forest floor predators also responded to fragmentation in the manner expected given their mobility (Appendix D; De Smedt et al., 2019) while detritivores may exhibit even stronger responses to diversification if litter quality differences between overstorey species were greater. Researchers would usually conclude that differential responses to underlying drivers between groups in within-group analyses would preclude the use of particular species, or species groups, as indicator taxa for biotic responses in general (e.g. Filgueiras et al., 2019). Indeed, multi-taxon patterns could be influenced by particularly strong responses of some taxa to tree composition, and this could mean that within-taxon drivers are masked within multi-taxa analyses. However, we did not observe evidence for particular taxa having a large distance to plot centroids across the tree composition gradient in our analyses (Figure S17). Thus, our results on community tightness suggest that any conclusion on the restricted use of indicator taxa given differential responses to underlying drivers may be premature; co-ordinated change among groups within mixtures containing pedunculate oak can be observed, despite differential within-group responses to potential underlying drivers.

The importance of pedunculate oak in apparently driving this across-trophic level covariation in taxonomic groups is perhaps not surprising. Through its provision of energy/nutrient resources as well as habitat, it is widely acknowledged as being important for biodiversity in different trophic groups (e.g. Böhm & Kalko, 2009; Brändle & Brandl, 2001; Koch Widerberg et al., 2018), especially in mature forests and in comparison to other overstorey species (Penone et al., 2019). Given the greater number of species, the opportunity for co-evolutionary relationships on oak may be greater than on red oak or beech, and thus be related to greater taxonomic community congruence and co-ordinated change. On the other hand, with a greater number of associated species, there may have been more opportunity for drift and thence divergent community relationships in pedunculate oak, which we did not observe.

We did observe greater, and more variable, community distances in the red oak diversification pathway, except when including pedunculate oak. This tendency is particularly marked in red oak monocultures, and the greater community distances may be related to the non-native status of *Q. rubra*. Non-nativeness could prevent the co-evolution of tight relationships among communities, which can characterise some well-characterised and well-developed (mutualistic) networks (Bascompte et al., 2006). However, a meta-analysis of insect species that have expanded their host range on to non-natives showed that red oak has a high relative number with a large proportion of generalists, likely because of the congeneric status of the species with native oaks (Branco et al., 2015). The con-familial status of all overstorey species may also explain the relatively small differences in across-trophic level community distances we observe among the various diversification pathways, although the novel nature of our metric, to our knowledge, makes it impossible to compare the magnitudes seen here to other contexts. The lower certainty of community distance estimation in the red oak–beech mixture as

indicated by the larger confidence interval width, despite their tendency to be more spatially clustered than other overstorey compositions, is likely related to the lower number of sample plots in this particular overstorey composition.

4.2 | Functional implications of co-ordinated change

Co-ordinated change, that is, a (relatively) small community distance metric, may also imply more regulated ecosystem dynamics. For instance, in its absence, there is the potential for pest-species outbreaks. As one group or individual species responds to changing conditions through a rapid increase, loose connections would imply there is not a concomitant response from other groups, that is, predator species. In other words, loose community metrics imply there is the potential for a species to increase rapidly in abundance without response from other species. However, the asynchrony in species response could also have a positive effect on the stability of the system by ensuring the persistence of at least some of the species under changing conditions (Loreau & de Mazancourt, 2013). Thus, synchronous changes across communities could actually lead to a diminution of functional response over time. These speculations require testing through further observational and experimental research.

Despite our sampling of (generalist) organisms without measurement of specific interactions, co-ordinated change may also imply an overall cohesive web of interactions. Such cohesion, in an explicit food web without measurement of interaction strengths, has been demonstrated to decrease the probability of trophic network fragmentation when species are removed (Melián & Bascompte, 2004). Omnivory is also important for the persistence of networks in the face of fragmentation, and associated habitat loss. Webs that contain omnivorous species are theoretically expected to persist at a greater level of habitat fragmentation (Melián & Bascompte, 2002) while Stouffer and Bascompte (2010) showed that food web persistence over time is most strongly correlated with a greater frequency of omnivorous modules within the web. Such properties (omnivory and cohesion) may explain why there is a lack of an effect of physical fragmentation on our metric of community tightness: our results could suggest that a cohesive web of taxonomic groups, consisting of some omnivores, persists in this particular fragmented landscape providing pedunculate oak is part of the overstorey composition. Indeed, our trophic role analysis showed that omnivores were only significantly related to the detrivore community while significant pairwise interactions, although large in magnitude, were absent with the other groups and could be related to spatial structure alone rather than measured variables such as fragmentation (Figure S20). It may also be that pedunculate oak provides the opportunity for strong species sorting (i.e. environmental filtering) while the other overstorey species, with fewer species and thus potentially more marginal habitat for some organisms, are driven by mass effects and/or drift (Jabot et al., 2020). Future analyses

could try to disentangle these meta-community processes (Jabot et al., 2020) from internal food web drivers, while also considering whether omnivorous species feature more or less often than would be expected by chance alone given co-ordinated change. An alternative explanation for the lack of response to fragmentation would be that vital connections have already been lost in forests with a low fragmentation index score in our landscape, and thus additional fragmentation has limited effects. However, as noted above, individual taxonomic groups still respond to the fragmentation gradient, suggesting this explanation, while plausible, is less supported by the evidence. Interestingly, our results (Appendix E) also suggest that links are maintained despite species turnover, rather than nestedness, characterising differences in diversity between plots (i.e. β-diversity).

Importantly, the tighter community compositional relationships that we found in overstorey compositions comprising pedunculate oak is suggestive of more efficient energy and matter (e.g. nutrient) transfer (i.e. transfer of biomass). Such efficiency will ultimately lead to improved ecosystem functioning (Buzhdygan et al., 2020; Delgado-Baquerizo et al., 2020). Loose correlations imply fewer direct and indirect interactions among species, and likely less efficient biomass transfer. However, in some instances, interference among species can lead to greater energy flows in communities with fewer interactions (Zhao et al., 2019). Given the critical importance of direct and indirect interactions for predicting the ecosystem consequences of, among others, habitat loss during the process of fragmentation (Melián & Bascompte, 2002), our metric of community tightness may be a useful indicator of ecosystem functioning in the absence of known species interaction networks.

4.3 | Synthesis

Understanding how communities across trophic levels relate to each other is important, given across-community effects on the delivery of ecosystem functions and the maintenance of biodiversity. Coupling methods across groups of community matrices are a particularly promising approach, especially when complex systems do not allow the ready specification of well-resolved interaction networks, and given that non-trophic interactions can also structure community relationships. Furthermore, assessing synthetic metrics along environmental gradients could allow the investigation of whether across-trophic level community relationships can be stabilised or diverge with management interventions. Here, we show that diversifying monocultures of red oak and beech, or their two-species mixture, with pedunculate oak correlates with greater co-ordinated change of species across taxonomic groups with varied trophic roles. This co-ordinated change (or lack thereof) has potential implications for biodiversity dynamics and ecosystem functions, and is, surprisingly, unaffected by the fragmentation process. Future research could target comparative approaches across different environmental gradients (Tylianakis & Morris, 2017), while expanding the range

of tree species and organism groups/functional roles investigated (e.g. soil fungi and bacteria, small mammals, adult butterflies and moths (as pollinators) and their larval stage (as herbivores)) and estimation methods used. Adopting a trait-based focus and considering appropriate resource comparisons, with an individual level focus, may be especially beneficial (Ings et al., 2009; Pellissier et al., 2018).

Over 20 years ago, John Lawton provocatively said that community ecology was a mess (Lawton, 1999) and that if general rules emerged from community-level investigations, we should treasure them. Further research is required to reveal the generality of our results and ascertain whether we should treasure what we have revealed here. However, our novel metric of community tightness suggests that adding pedunculate oak (likely among other species we have at our disposal) to certain forest stands, regardless of fragmentation context, could affect relationships among communities across trophic levels. Any impact these co-ordinated changes in communities have on functional interactions and biodiversity metrics at higher trophic levels, and the implications for energy and matter transfer, processes at the core of ecosystem service delivery, requires further investigation.

AUTHORS' CONTRIBUTIONS
L.B., D.B., A.M., K.V. and L.L. designed TreeWeb, the research platform used for the analysis here; M.P.P. and L.R.H. developed the analysis approach and figure presentations, in conjunction with L.B., D.B., A.M., K.V. and L.L.; L.R.H. performed statistical analyses and created all figures; Other authors (S.R.E.D.G., D.D., W.D., P.D.S., W.P., B.K.S., T.S., J.V.K., I.M.v.S.L. and P.V.) collected primary data or identified specimens that were analysed herein; M.P.P. wrote a first draft of the manuscript, with extensive input from L.R.H. All authors commented on further drafts.

PEER REVIEW
The peer review history for this article is available at https://publons.com/publon/10.1111/1365-2745.13580.

DATA AVAILABILITY STATEMENT
Data and code to reproduce the analyses herein can be found at https://doi.org/10.5281/zenodo.3921936 (Perring et al., 2020).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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