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Identifying the tree species compositions that maximize ecosystem functioning in European forests

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Abstract

1. Forest ecosystem functioning generally benefits from higher tree species richness, but within richness levels variation is typically large, mostly due to the contrasting performances of communities with different compositions. Evidence-based understanding of composition effects on forest productivity as well as on multiple other functions has large practical relevance, because forest managers are more likely to be concerned with the selection of species that maximize functioning rather than with diversity *per se*.
2. Here we used a dataset of thirty ecosystem functions measured in stands with different species richness and composition in six European forest types. First, we quantified whether the compositions that maximize annual aboveground wood production (productivity) generally also fulfil the multiple other ecosystem functions (multifunctionality). Then, we quantified the species identify effects and strength of interspecific interactions, to identify the "best" and "worst" species composition for multifunctionality. Finally, we evaluated the real-world frequency of occurrence of best and worst mixtures, using harmonized data from multiple national forest inventories.
3. The most productive tree species combinations also tended to express relatively high multifunctionality, although we found a relatively wide range of compositions with high or low average multifunctionality for the same level of productivity. Monocultures were distributed among the highest as well as the lowest performing compositions. The variation in functioning between compositions was generally driven by differences in the performance of the component species and, to a lesser extent, by particular interspecific interactions. Finally, we found that the most frequent species compositions in inventory data were monospecific stands and that the most common compositions showed below-average multifunctionality and productivity.
4. *Synthesis and applications*. While a management focus on productivity does not necessarily trade-off against other ecosystem functions, it matters considerably which particular tree species and

combinations are promoted. These identity and composition effects are essential in the context of developing high-performing production systems, for instance in forestry and agriculture, and deserve much more attention in the analysis and design of functional biodiversity studies if the aim is to inform ecosystem management.

Keywords: forest management, FunDivEUROPE, multifunctionality, overyielding, species interactions, tree species mixtures

1 Introduction

During the last 25 years, a wealth of studies aimed to answer the question: does plant biodiversity matter for the functioning of ecosystems and for their potential to deliver services to humanity? In essence, these studies showed that changes in species diversity usually result in changes in multiple ecosystem processes, including those related to productivity, nutrient cycling, and stability, as well as to trophic interactions and associated biodiversity (e.g., Schulze & Mooney 1993; Tilman et al. 2014; Isbell et al. 2017). These general patterns were mainly derived from comparisons of mean values of ecosystem functioning among different levels of species richness. However, within each level of richness, there is typically a high variation in functioning, mostly due to different species composition providing different levels of functioning. This compositional variation may have a similar or even greater impact on ecosystem functioning compared with variation in diversity (Hector et al., 2011; Ratcliffe et al., 2017), but it is often overlooked or even considered to be unwanted noise. Species differ strongly in their functional effects, meaning that compositions containing different species provide different levels of function ("species identity effect"; Kirwan et al. 2009). In addition, functional effects of mixtures may differ from the expected effects of the individual species monocultures due to interspecific interactions ("species interaction effect"), which can be synergistic, neutral, or antagonistic depending on the particular species involved. If we can identify which identity and interaction effects provide highest function, then we could deliberately select certain species combinations that optimize one or multiple ecosystem functions (Storkey et al., 2015). In this context, biodiversity-ecosystem functioning research could help to develop high-performing production systems, for instance in multifunctional low-input agriculture (Barot et al. 2017), in carbon plantings (Hulvey et al. 2013) and in the context of sustainable forest management (Mori, Lertzman & Gustafsson 2017).

By favouring different tree species through management (e.g., selective thinning), foresters have been following this approach for centuries. However, forestry has traditionally focused on wood production as the main management goal, rather than on the simultaneous provision of multiple ecosystem functions or services (ecosystem function or service “multifunctionality”; Manning et al. 2018). It is often assumed that a focus on wood production will, *quasi* automatically, fulfil all other functions as well. This reasoning even has its own name in German forestry (the "Kielwassertheorie" or "wake theory"; Rupf 1961), where habitat, regulation, and recreation functions are assumed to be boosted in the “wake” of use functions, i.e. wood production. Yet, this premise has been challenged by studies showing trade-offs between different functions or services. For example, a focus on tree biomass production was found to be detrimental for dead wood occurrence, bilberry production and food for game in boreal and temperate production forests (Gamfeldt et al., 2013). In general, species effects on different functions are not well correlated, so that no “super-species” fulfils many functions at the same time and under all conditions (van Der Plas et al., 2016). In sum, there is a need for evidence-based understanding of how different tree species compositions promote multiple ecosystem functions and services, including, but not restricted to, wood production. Such insights will help to bridge the gap between fundamental biodiversity-functioning theory and ecosystem management and could, for instance, better inform forest managers about which trees should be planted together in order to maximize forest multifunctionality within stands.

Research on biodiversity-ecosystem functioning relationships, as well as on tree species mixture effects in forestry (reviewed in Pretzsch, Forrester & Bauhus 2017), still often relies on single-site experiments or case-studies, limiting our capacity for synthesis and generalisation across spatial and temporal scales. The FunDivEUROPE exploratory platform was established as a network of research plots in six European forest types, selected to differ in tree species richness and different species compositions (Baeten et al., 2013). The platform provided a common hypothesis-driven design in different geographical locations, used standardised methodology and measurements protocols and coordinated data acquisition and management. Using data on thirty ecosystem functions measured in this platform, we can perform an indepth analysis of tree composition effects on forest ecosystem multifunctionality. We aim to (i) assess to what degree a management focus on tree productivity also boosts other ecosystem functions or whether there are trade-offs between production and other functions; (ii) quantify the individual species effects and strength of interactions among particular species and species groups to identify the “best” and “worst” species compositions for multifunctionality; and (iii) evaluate the frequency of occurrence of best and worst mixtures based on National Forest Inventories. We hypothesize that (i) tree productivity is not strongly positively related with ecosystem multifunctionality, refuting the wake theory; (ii) interspecific interactions can explain ecosystem functioning better than species identity effects alone, and that these interactions are species specific; (iii) tree compositions supporting high ecosystem multifunctionality are rare in European forests due to the historical focus on production forests.

2 Methods

2.1 FunDivEUROPE exploratory platform design

The FunDivEUROPE exploratory platform is a coordinated network of 209 forest plots in six European regions, covering a gradient of different climates and forest types (Fig. S1.1 in Appendix S1). It was established in 2011 to study the effect of tree diversity on ecosystem multifunctionality (www.fundiveurope.eu). The field sites include boreal forests in Finland, hemi-boreal forests in Poland, beech forests in Germany, mountainous beech forests in Romania, thermophilous deciduous forests in Italy and Mediterranean mixed forests in Spain. In each forest type, plots with locally dominant and economically important tree species were selected to cover a range in species richness from 1 to 3 in boreal (number of plots: 28), 1 to 4 in mountainous beech (28), beech (38) and Mediterranean mixed (36), and 1 to 5 in thermophilous deciduous (36) and hemi-boreal (43) (Table S1.1). Each richness level was replicated with different species compositions. Furthermore, the tree species had similar abundances in mixtures (high evenness), all species were represented in all species richness levels, and none of the species was present in every plot so that species identity and diversity effects could be separated. The study plots were located in mature forests stands and shared similar environmental conditions within forest types (e.g., geology, soil type, topography), so that covariation between these factors and species richness levels was minimized. Thus, the diversity gradient mainly resulted from historical management or stochastic events. More details about the study sites, the selection procedure, and plot-level information can be found in Baeten et al. (2013).

2.2 Ecosystem property and function measurements

We used plot-level measurements of 30 ecosystem properties, functions or service proxies, which for simplicity we refer to as "functions" or properties hereafter (Table S1.2). These include the set of 26 functions analysed in a previous study looking at the relative importance of composition versus diversity effects (Ratcliffe et al. 2017). Four additional functions, representing diversity measurements of four taxonomic groups, were added to the data set: bat, bird, earthworm, and understorey plant diversity. As a measure of tree productivity, we used the mean annual aboveground wood production estimated from wood cores (Jucker, Bouriaud, Avacaritei, & Coomes, 2014). To aid in the interpretation, the functions were *a priori* classified into six groups reflecting basic ecological processes (Table S1.2): nutrient and carbon cycling related drivers (e.g., earthworm biomass, microbial biomass), nutrient cycling related processes (e.g., litter decomposition, nitrogen resorption efficiency), primary production (including tree productivity, but also photosynthetic efficiency and tree biomass), regeneration (e.g., tree seedling regeneration, sapling growth), resistance to disturbance (e.g. resistance to drought, resistance to insect damage), and the value of the forest stands as habitat for other species (e.g., bat and bird diversity). A major strength of the FunDivEUROPE project was the general philosophy to measure all ecosystem functions in all plots, following the same protocol by the same observers across the six forest types. Measurements are thus directly comparable across plots and show high coverage; 24 functions were measured in at least 207 of the 209 plots. Details on the measurements of the various functions can be found in previous synthesis papers of the FunDivEUROPE project (e.g., van der Plas et al., 2016; Ratcliffe *et al.,* 2017).

2.3 National Forest Inventory Data

Within the FunDivEUROPE project we compiled harmonised forest plot data from the national forest inventories of Finland, Sweden, Germany, Belgium (Wallonia) and Spain (for details see Ratcliffe *et al.* 2016). These inventories included three forest types from the exploratory platform: boreal forest, beech(-dominated) forest, and Mediterranean mixed forest (which comprised Mediterranean coniferous, broadleaved evergreen, and thermophilous deciduous forest). Determination of the forest type was based on the EEA Technical Report 9 (Barbati, Corona & Marchetti 2017). In each inventory, we used the two most recent surveys and extracted basal area (BA, m^2 ha^{-1}) for all trees with a diameter at breast height of more than 10 cm. Plots with single measurements or any indication of harvest activities between surveys were omitted from the dataset. For each of the remaining plots, we calculated the proportional BA per tree species. Tree species names were harmonized following the Atlas Florae Europapeae. In order to identify the species composition of a plot, we adopted the following approach: only species with a BA exceeding 10 % were considered and only plots in which the summed proportion of all component species exceeded 90% were included. Plots that did not meet these criteria were discarded from the dataset. This approach is in agreement with the selection criteria of the FunDivEUROPE exploratory platform. Furthermore, we only retained the plots with compositions that could be assigned to one of the three forest types mentioned above. No distinction was made between planted and spontaneously regenerated stands. Our final dataset included 64.8% (boreal), 22.3% (beech) and 70.8% (Mediterranean mixed) of the available NFI plots.

2.4 Data analyses

2.4.1 Quantifying multifunctionality and its relationship with productivity across different species compositions

We quantified the multifunctionality of each tree species composition with a model-based approach. In each plot, we have a value for each of the 30 functions. These estimates were modelled together in a hierarchical meta-analytic model with group-level effects for plot identity (209 plots) and species composition (103 compositions). We considered species combinations occurring in multiple forest types as different compositions, because the same species combination may have different functioning when growing on different soils or in different climates and we wanted to account for the fact that the same composition may behave differently among forest types. In addition, compositions within the same forest type were related to each other because they were measured more closely together in time and space. However, only eight out of 92 unique species compositions occurred in multiple forest types: six were represented in two forest types and monocultures of *Pinus sylvestris* and *Picea abies* were present in three and four types, respectively.

The estimated effects of composition from the hierarchical model were used here as measure of multifunctionality for a given tree species composition. The effect quantifies the degree to which the functioning of a particular composition deviates from the average, taking all functions into account. Positive and negative values express above-average and below-average functioning of that species combination, respectively. An alternative, single threshold approach (Byrnes et al., 2014) provided a very similar measure of multifunctionality, so we expect qualitatively similar results when using alternative measures (Fig. S2.1). The model-based approach was preferred here because it directly quantifies the dependency of functioning on composition (without the need to derive a metric first) and allows us to extend the analyses to diversity-interaction models (see below *Diversity interaction models*). A full model description is given in Appendix S2 and additional sensitivity analyses are provided in Appendix S4 (e.g., reducing the number of functions to calculate the multifunctionality measure, either randomly or by ecosystem function group).

We related the multifunctionality to the mean productivity of each composition with a linear regression model, to test whether selecting composition for high productivity also ensures high multifunctionality. In this analysis, we quantified the measure of multifunctionality after excluding productivity, i.e. multifunctionality was calculated with 29 functions. This analysis was first performed on the full data set and then for each forest type separately. Differences in productivity and multifunctionality between compositions with different species richness values (monoculture *vs* mixed) or different leaf phenologies (pure evergreen, pure deciduous or mixed) were tested with an analysis of variance.

2.4.2 Diversity interaction models

To identify the individual species and pairs of species that increased functioning, we used a diversity-interaction modelling framework (Kirwan et al., 2009). This tests how the abundance of individual tree species, and the interactions between them, affect ecosystem functioning. The approach uses a linear model of the form $f = ID + DE + BA + residual$, with f an estimate of functioning in a plot, ID the species identity effects, DE the diversity effects, BA the effect of variation in plot-level basal area (average centred to zero within forest types), and a residual error term. The species identity effects equal the average monoculture performances, weighted by the species' relative abundances. The diversity effects result from species interactions, which causes mixture functioning to differ from that expected from monoculture functioning. Kirwan et al. (2009) proposed alternative patterns of interactions based on different ecological assumptions, corresponding to different formulations of the diversity effects term. See Appendix S2 for a full model description and explanation of the alternative diversity terms.

We confronted five alternative models with the data. A first null model assumes that all species identity effects are equal (model 0), while a second assumes that monoculture functioning differs and only the relative abundances of the species influence functioning in mixtures (identity-effect model; model 1). Three additional models combine the identity effect with different diversity effects, corresponding to the alternative types of species interactions: a pairwise-interactions effect (model 2), an additive species-specific contributions effect (model 3), or a functional-group effect (model 4). The importance of the different types of interactions was then explored by comparing the models differing in their ecological assumptions (Kirwan et al., 2009). We used AIC values and likelihood ratio tests to compare models. Firstly, we fitted the alternative models for each ecosystem function and forest type separately. Secondly, we modelled the 30 functions together, using a similar meta-analytic model described above (§2.4.1), replacing the composition effect with the identity and diversity effects of the diversity-interaction models. The values for each function were normalized before modelling.

2.4.3 Relationship between multifunctionality and frequency of occurrence of tree species compositions

We calculated the frequency of occurrence of all tree species compositions for each of the three forest types (boreal, beech, and Mediterranean mixed forest) from the national forest inventory data. So, for each of the compositions of these three forest types studied in the exploratory platform, we have a measure of their frequency among all other compositions in the same forest type. We drew graphs ranking compositions by frequency, multifunctionality, and productivity to explore whether compositions supporting high ecosystem multifunctionality were rare in a given forest type. We are aware that the species combinations encountered in the exploratories may have different effects on multifunctionality in the different contexts (e.g., climates, soil types or stand development stages) encountered in the inventories (Ratcliffe et al., 2017). Nevertheless, our assessment provides an indication of whether compositions likely to promote high multifunctionality occur more often in the inventories than those with low multifunctionality.

3 Results

3.1.1 Relationship between productivity and ecosystem multifunctionality

Across all plots, the multifunctionality (excluding productivity) of tree species compositions was positively related to their mean productivity (Fig. 1; slope = 0.028, $P < 0.001$, $R^2 = 0.22$), although for a given level of productivity there was a considerable range in multifunctionality between compositions. Within the forest types, the productivity-multifunctionality relationship was significantly positive in three types (beech, thermophilous deciduous, Mediterranean mixed) and positive but non-significant in the three others (Fig. S3.1). Patterns at the level of individual ecosystem functions were consistent: in beech, thermophilous deciduous and Mediterranean mixed forest, the most productive compositions also had above-average (within region) values of the majority of the other functions (> 20 out of 29 functions), whereas less than half of the functions exceeded the average in the least productive compositions (Fig. S3.2 and S3.3). Monocultures were not consistently different from mixtures: they were distributed among the highest as well as the lowest performing compositions, both in terms of productivity ($F = 0.62$, $P = 0.43$) and multifunctionality ($F = 2.19$, $P = 0.14$). Similarly, the leaf phenology (evergreen, deciduous or mixed) was not important in explaining differences in productivity ($F = 1.83$, $P = 0.17$) or multifunctionality ($F = 1.09$, $P = 0.34$).

Sensitivity analyses showed that the tree productivity – multifunctionality relationship did not change when we classified all species combinations occurring in different forest types as the same, e.g. rather than considering *P. abies* monocultures as being four separate compositions because they occurred in four forest types, we regrouped them as a single composition (Fig. S4.1). While the productivity-multifunctionality relationship remained the same if we randomly excluded functions from our multifunctionality measure (Fig. S4.2), when we excluded particular ecosystem function groups then the strength of the relationship altered (Fig. S4.3). For instance, excluding all functions supporting primary production weakened the productivity – multifunctionality relationship, however it remained significantly positive.

3.1.2 Identifying the best mixtures

Looking at individual functions, diversity-interaction models showed that pairwise species interactions often influenced functioning, positively as well as a negatively (Fig. 2). Interactions indicate, for particular species pairs, whether growing the two species in a mixture increased or decreased functioning compared with growing them in separate monocultures. Ecosystem function groups did not show consistent patterns: production-related functions were more often found to benefit from mixing (26 positive versus 11 negative interaction effects) and positive interactions also outnumbered negative interactions in resistance- and regeneration-related functions (27 versus 17 and 10 versus 3, respectively). Interactions tended to be positive in thermophilous deciduous and Mediterranean mixed and negative in boreal forest. Results for the individual functions are shown in Fig. S3.4.

When multifunctionality was modelled with all 30 functions together, including productivity, we often found tree species to have very different effects on functioning (identity-effects model; Fig. S3.5). Furthermore, functioning levels generally also increased with plot-level basal area. We also looked at variation in functioning across forest types, for the small number of composition present in multiple types. We found that *Picea abies* had higher functioning, compared with the average monoculture, in hemi-boreal and mountainous beech forest, but below average functioning in boreal and beech forests (Fig. S3.5). *Pinus sylvestris* had higher (Mediterranean mixed), lower (boreal) or average (hemi-boreal) monoculture performance. In contrast, monocultures of *Quercus robur/petraea* tended to have consistently lower multifunctionality than other monocultures, across forest types (hemi-boreal, beech, thermophilous deciduous).

Species interactions were important in explaining multifunctionality in all forest types except for mountainous beech (likelihood ratio tests of models with interaction effects versus identity-effects models; $P < 0.05$). We found that mixing evergreen and deciduous species reduced functioning in boreal (functional group versus identity model; $P = 0.029$) but increased functioning in hemi-boreal forest ($P = 0.025$). In boreal forests, the negative effect was mainly because of an antagonistic interaction between *Picea abies* and *Betula pendula* leading to lower multifunctionality than expected based on their monoculture functioning. In beech, thermophilous deciduous and Mediterranean mixed forest, there was no such functional group effect, as here the species interacted similarly with all others, illustrating that the main effect of mixing was the contrast between intra- and interspecific interactions (additive contributions versus identity model; $P < 0.05$).

The list of top five compositions in each forest type in terms of their multifunctionality (Table 1), reflected this: only six out of the total 28 best compositions listed in Table 1 were monocultures. Some of the best compositions included up to four species and in some types none of the five best compositions were monocultures (hemi-boreal and thermophilous deciduous). Finally, the compositions with the highest multifunctionality were also not dominated by pure evergreen or deciduous compositions and 15 out of the 22 multi-species compositions were mixtures of deciduous and evergreen species. The species combinations with the highest multifunctionality were also among the most productive ones.

3.1.3 Frequency of the best mixtures in forest inventory data

The species compositions studied in the exploratory platform were also well represented in the national forest inventories of the three studied forest types (boreal, beech, and Mediterranean mixed forest) (Fig. 3). In all three types, the most widely occurring tree species compositions were monospecific stands. Furthermore, the most frequent compositions had below-average multifunctionality scores, that is, below zero. Especially in beech forest, the compositions with above-average multifunctionality were rare (frequency < 1 %). We found essentially the same pattern when focussing on productivity rather than multifunctionality (Fig. S3.6): the most productive compositions were not the most frequent ones.

4 Discussion

Despite the importance of species composition in explaining variation in ecosystem functioning (Hector et al., 2011; Ratcliffe et al., 2017), species identity effects are generally not the focus of biodiversity and ecosystem functioning studies, where they are instead treated as a nuisance variable to be accounted for. Here we aimed to unpack the variation in functioning between compositions and to understand which particular species or species pairs sustained the highest multifunctionality. Our findings show that it matters considerably which particular combinations are promoted within a given richness level. This is critical from an applied perspective, as forest managers are much more likely to focus on species selection (e.g., when replanting after a regeneration cut) rather than diversity *per se*.

4.1 Managing for productivity can also promote multifunctionality

A fundamental management goal in forestry is to produce wood, and so, many studies looking at the functional importance of mixing tree species focused on tree productivity. There is evidence that tree species diversity increases the productivity of forests globally (Piotto 2008; Liang et al., 2016). In closed canopy forests, this is primarily due to more efficient light use when species with contrasting canopy traits co-occur (Fichtner et al., 2017; Pretzsch, 2014; Zhang, Chen, & Reich, 2012). These insights provide relevant information for making informed tree species choices in forestry but they do not indicate whether selecting species to maximize high productivity also benefits multiple other functions. While trade-offs between productivity and other functions have previously been reported in boreal forests (Gamfeldt et al., 2013), our study evaluated a greater number of functions across a broad range of forest types, and showed that the most productive tree species combinations also tend to provide relatively high multifunctionality. In the context of recent discussions about the sensitivity of multifunctionality measures to the number and identity of their component functions (e.g. Gamfeldt & Roger 2017; Meyer et al. 2018), we showed that our findings were robust when randomly reducing the number of functions considered. Deleting particular groups of functions did change the strength of the relationship between productivity and multifunctionality, although it was always positive. Since previous analyses of our data showed few trade-offs between a range of multifunctionality measures reflecting alternative stakeholder objectives (*sensu* Allan et al. 2015; van der Plas et al. 2018), changing our multifunctionality measure to represent specific management scenario's is also unlikely to change the conclusions.

Ranking the species compositions within forest types, based on either productivity or multifunctionality, resulted in a similar set of best compositions (Table 1, Fig. S3.1). A notable pattern to emerge from our analysis is that for four of the six forest types we identified at least one species that repeatedly occurred across the best compositions that characterise that particular forest type (hemi-boreal: *Picea abies*, beech: *Fraxinus excelsior*, thermophilous deciduous: *Quercus ilex* and *Quercus cerris*, Mediterranean mixed: *Pinus sylvestris*) (Table 1). In beech forests, the combination *F. excelsior – A. pseudoplatanus* even appeared four times in this top five. At the same time, mixtures containing these particular species were not always the most productive ones. This information may already provide useful empirical evidence when deciding among several management options, such as the selection (or exclusion) of species when planting or regenerating new stands.

We do not propose to use tree productivity as an integrated measure of forest performance in a general way, because for the same level of productivity we found a relatively wide range of compositions with high or low average performance across functions. For instance, in Mediterranean mixed forest, monocultures of *P. sylvestris* and *Pinus nigra* had nearly the same productivity, but varied strongly in multifunctionality. Furthermore, the most productive compositions had above-average values for many, but certainly not all functions (Fig. S3.2, S3.3). The relative importance of these existing trade-offs between individual ecosystem functions need to be evaluated based on socio-ecological perspectives, including the desired management goals and land-use schemes (Mori, Lertzman & Gustafsson 2017), and in this respect our data can help inform these decisions. Thus, our results should not be used as a general confirmation of the "wake theory" that all forest functions are automatically fulfilled by a focus on timber production only. Rather, we conclude that a management focus on productivity does not necessarily trade-off against other ecosystem functions and high productivity and multifunctionality can be combined with an informed selection of tree species combinations.

4.2 The identity of co-occurring tree species matters

We found that the variation in functioning between compositions was generally driven by identify effects and, to a lesser extent, by particular interspecific interactions. In trying to explain what makes up a high-performing species combination, we looked at differences between pure deciduous, pure evergreen and mixed deciduous-evergreen mixtures. While heterogeneity of canopy traits related to light capture and use, including leaf phenology, is often found to increase productivity (Jucker, Bouriaud, Avacaritei, Dănilă, et al., 2014; Lu, Mohren, den Ouden, Goudiaby, & Sterck, 2016; Zhang, Chen, & Taylor, 2015), mixing species from these broad functional groups did not always increase multifunctionality. Many of the ecosystem properties included here are not directly related to light availability (e.g., nutrient cycling related drivers or processes; Rothe & Binkley 2001) and our findings show that the mechanisms responsible for overyielding of mixtures (for an overview see Forrester & Bauhus 2016), do not necessarily increase other functions. More generally, while studies on identity effects have mostly looked at community-weighted means of traits as a way of generalizing results (Ratcliffe et al., 2016), such an approach is not the best choice when searching for high performing tree species compositions because we lack theory linking traits to multifunctionality. In addition, many species interactions are not related to commonly measured traits (such as pathogens or herbivory), and it would be difficult to translate trait-based identity effects into concrete management decisions with real species.

Our study was designed using a pool of regionally abundant and economically important tree species (Baeten et al., 2013) and therefore provides comprehensive data on multifunctionality values in many relevant species combinations. A next step would be to explore when and where specific combinations of interest provide maximum multifunctionality, so that managers can make informed decisions as to which combinations of species to favour on their land. This requires determining the variation in multifunctionality for particular species compositions across different environments (e.g., climates, soil types) and trying to explain the principal environmental drivers of this variation. Another comprehensive analysis in our study plots showed that tree diversity effects on various ecosystem functions are highly context dependent: stronger diversity effects on multifunctionality were found in forest types in drier climates, with longer growing seasons, and more functionally diverse tree species pools (Ratcliffe et al., 2017). A similar analysis of the context dependency of species composition effects is not straightforward because compositions are not easily replicated in very different environments and forest types, unlike diversity gradients that can be replicated with very different species pools. Focusing on productivity, Pretzsch et al. (2010, 2013) already showed that specific two-species combinations (oak-beech, spruce-beech) change from overyielding, due to facilitation, to underyielding, driven by competitive interference, along a gradient from poor to rich soils across central Europe. Focusing on multiple other functions, here we showed that for the subset of species that occurred in multiple types, that their identity effects on multifunctionality tended to vary considerably. The presence of *Picea abies* and *Pinus sylvestris*, for instance, increased or decreased mixture performance, depending on the forest type.

This calls for a new generation of forestry-oriented scientific experiments or silvicultural trials tailored to study species identity and composition effects in different environments (e.g., Paquette et al. 2018), especially focusing on the drivers of the context dependency in diversity effects (water availability, growing season length; Ratcliffe et al. 2017). Compositions can be replicated within forest types under different soil conditions and levels of water supply, but also across different forest types to cover regional-scale gradients such as climate (see Bruelheide *et al.* 2014 for a diversity-oriented example). Of course, the geographic scope of a multi-site experiment will not be global and should stay within the current or predicted distributional range of the species involved (e.g., Verheyen et al. 2013), as studying functioning well outside the species range is probably not relevant for foresters. Setting up practical trials obviously requires the involvement of foresters, policy makers, resource managers, and conservationists. They can use our identification of the best species combinations as a good starting point to carefully select compositions from the large pool of available species.

4.3 Low multifunctionality of the most common species compositions

By ranking tree species compositions of three forest types according to how often they occurred in inventory data, we showed that the most frequent compositions were monospecific stands and that the most frequent species combinations mostly showed below-average performance in terms of multifunctionality and productivity based on the exploratory platform data. Several mixtures with high performance were very rare in the national inventories or even absent from our selection. We should acknowledge, however, that the inventory data span much larger environmental gradients than the exploratory platform and that the same mixture may perform differently under different environmental conditions. Compositions showing poor performance in the exploratory platform may thus perform better in different climatic or soil conditions. While this may limit the generality of any conclusions regarding specific mixtures, the under-representation of numerous above-average performing mixtures in today’s forests and the high proportion of monocultures is a clear indication that the potential of mixing different tree species in forest stands has not yet have been fully realized in Europe.

Authors' contributions

LB, HB, FVDP, and MSL conceived the ideas and analysed the data; LB led the writing of the manuscript, together with HB, FVDP, SK, SR, TJ, and MSL. All authors collected the data, contributed critically to the drafts and gave final approval for publication.

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Data accessibility

The data of the ecosystem property and function measurements used in Ratcliffe *et al.* (2017) is available at https://doi.org/10.6084/m9.figshare.5368846.v1

Information on the availability of the National Forest Inventory datasets can be found on the following websites: http://www.magrama.gob.es/es/desarrollo-rural/temas/politica-forestal/inventario-cartografia/inventario-forestal-nacional/ (Spain); https://bwi.info/?lang=en (Germany); http://iprfw.spw.wallonie.be (Wallonia); http://www.metla.fi/ohjelma/vmi/info-en.htm (Finland); http://www.slu.se/nfi (Sweden)

Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. FunDivEurope exploratory platform: study locations, tree species, and functions

Appendix S2. Quantifying multifunctionality and species identity and diversity effects

Appendix S3. Supplementary results

Appendix S4. Results sensitivity analyses

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Tables

Table 1 Top five species composition for each forest type, ranked according to decreasing multifunctionality (from the top down). Compositions with an asterisk were also identified among the best five in case ranking was done based on productivity only. Underlined species are evergreen trees. The number of different compositions studied in each type is given in brackets. In boreal forest, only seven compositions were studied, so that only three performed above average.

boreal (7)	hemi-boreal (25)	beech (18)	mountainous beech (14)	thermophilous deciduous (27)	Mediterranean mixed (12)
*P. abies	*C. betulus, P. abies	A. pseudoplatanus, F. sylvatica, F. excelsior	P. abies	*C. sativa, O. carpinifolia, Q. cerris, Q. ilex	*P. nigra, P. sylvestris
B. pendula	B. pendula, C. betulus, P. abies, Q. robur	A. pseudoplatanus, F. sylvatica, F. excelsior, Q. petraea	A. alba, A. pseudoplatanus, F. sylvatica, P. abies	*Q. cerris, Q. ilex	*P. sylvestris, Q. faginea
*B. pendula, P. abies, P. sylvestris	*P. abies, P. sylvestris	*F. excelsior	*F. sylvatica, P. abies	O. carpinifolia, Q. cerris, Q. ilex	*P. sylvestris
	*C. betulus, P. abies, Q. robur	*A. pseudoplatanus, F. excelsior, Q. petraea	*A. alba	*C. sativa, Q. cerris	*P. nigra, P. sylvestris, Q. faginea
	B. pendula, P. abies, P. sylvestris, Q. robur	*A. pseudoplatatnus, F. syvaltica, F. excelsior, P. abies	A. pseudoplatanus, F. sylvatica	C. sativa, O. carpinifolia, Q. ilex, Q. petraea	*P. nigra, P. sylvestris, Q. faginea, Q. ilex

Full species names. **Coniferous species**: *Abies alba, Picea abies, Pinus nigra, Pinus sylvestris*. **Broadleaved species**: *Acer pseudoplatanus, Betula pendula, Carpinus betulus, Castanea sativa, Fagus sylvatica, Fraxinus excelsior, Ostrya carpinifolia, Quercus robur, Quercus petraea, Quercus cerris, Quercus faginea, Quercus ilex*

Figures

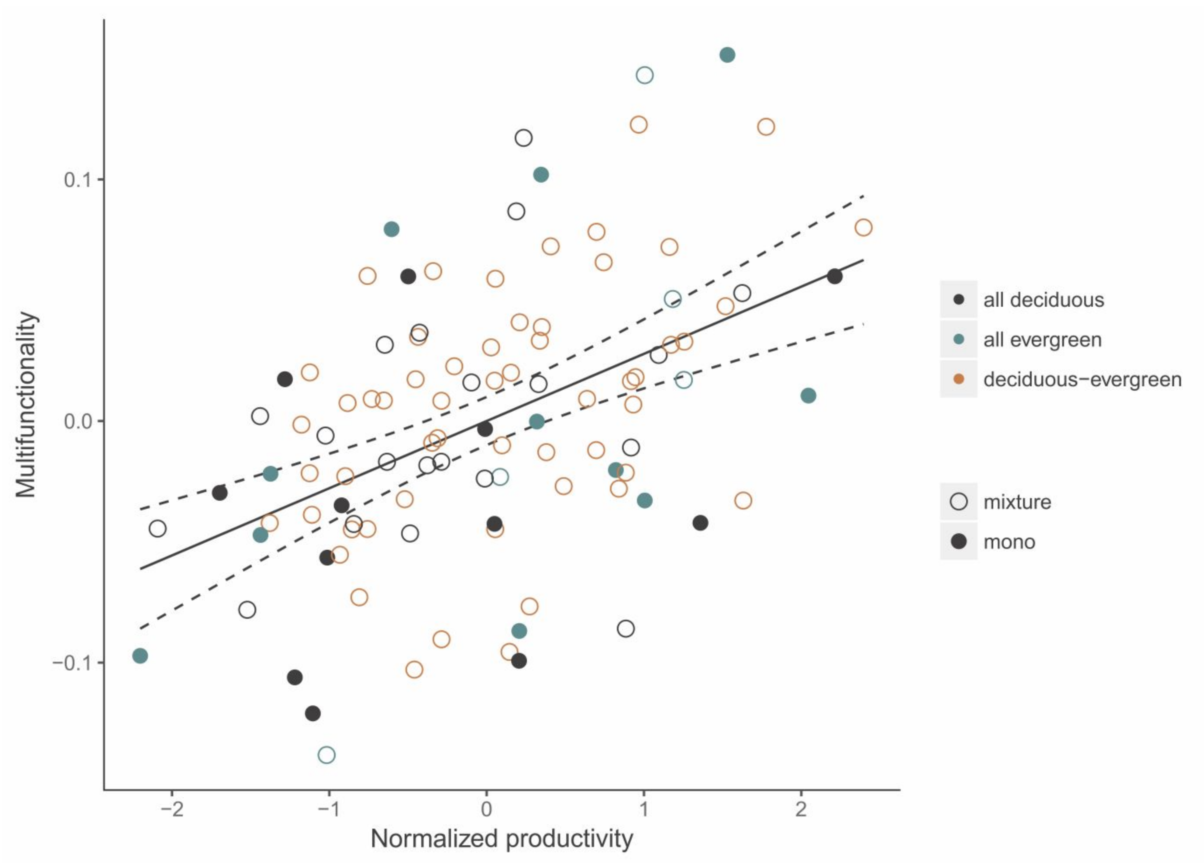
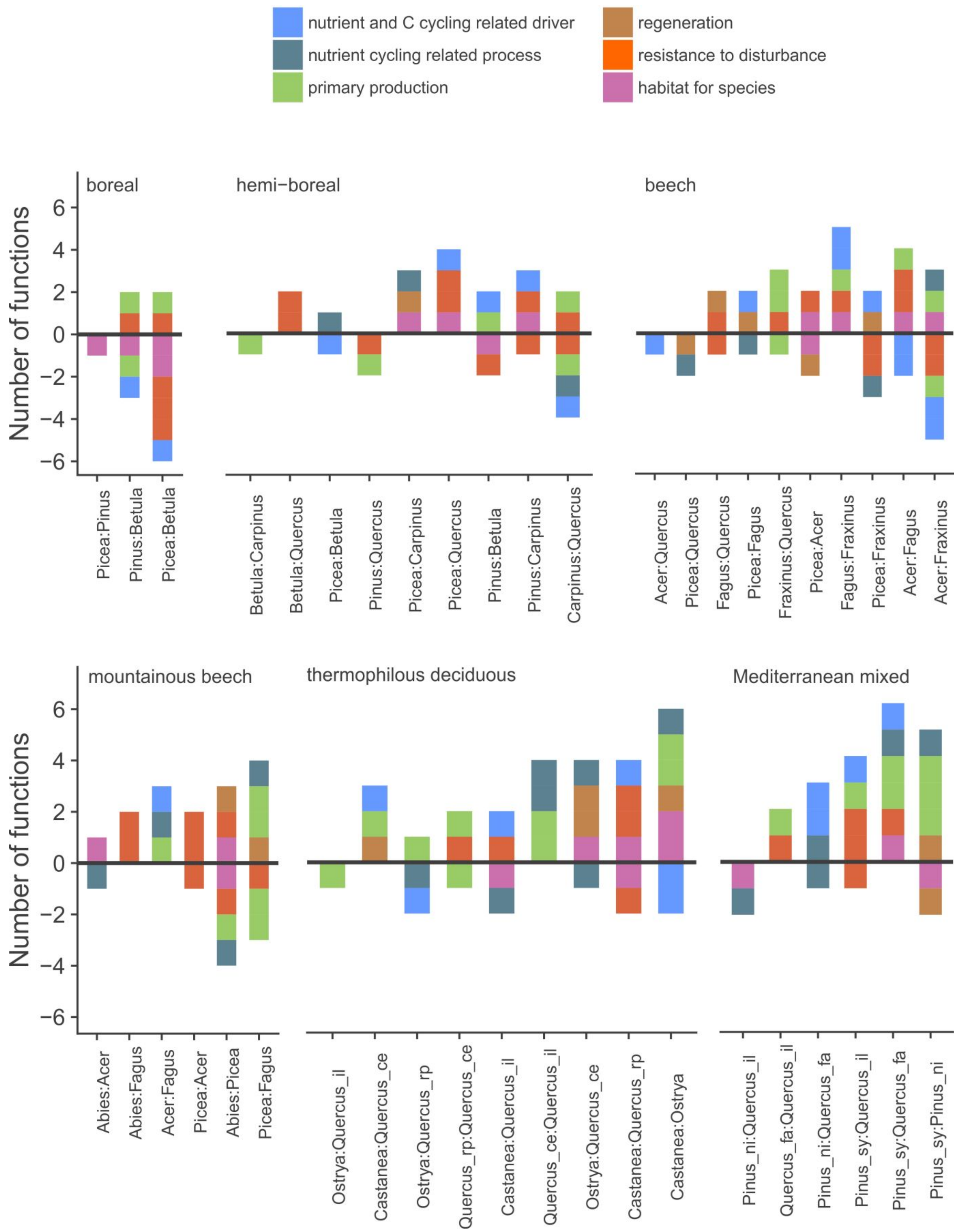


Fig. 1 Relationships between the tree productivity and multifunctionality of different tree species compositions across six European forest types. Points show the performance of individual compositions (N = 103): filled points represent monocultures and colouring represents functional composition in terms of leaf phenology (only deciduous species, only evergreen species, or a mixture of both). The full line shows the fit of a linear model, with the dashed lines delimiting the 95% confidence interval. Productivity corresponds to the annual aboveground wood production and was normalized within forest types to allow for a cross-regional comparison; absolute mean productivity values are presented in Fig. S3.1. The multifunctionality expresses the degree to which the functioning of a particular composition deviates from the average, taking all functions into account (positive values indicate above-average performance). For this analysis, the productivity was excluded from the multifunctionality measure.



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607 **Fig. 2** Synthesis of tree species interaction effects on ecosystem functioning (30 functions) in six

608 European forest types. For each function, pairwise species interaction models were fitted to quantify the

degree to which tree species interactions cause mixture performance to differ from that expected from the monoculture species performances. For each species pair, the graph shows the total number of positive (and negative) effects, indicating the number of times the species mixture is providing more (or less) functioning than the corresponding monocultures (only effects with $P < 0.1$ were counted). Functions were grouped into a priori classes to aid in the interpretation; see methods and Table S1.2. For results for single functions, see Fig. S3.4. Note that the graph compares within tree species combinations (performance of mixtures versus the monocultures of two particular species) and does not allow a direct comparison between compositions, because the species identity effects were not accounted for in this analysis. Full species names are given below Table 1.

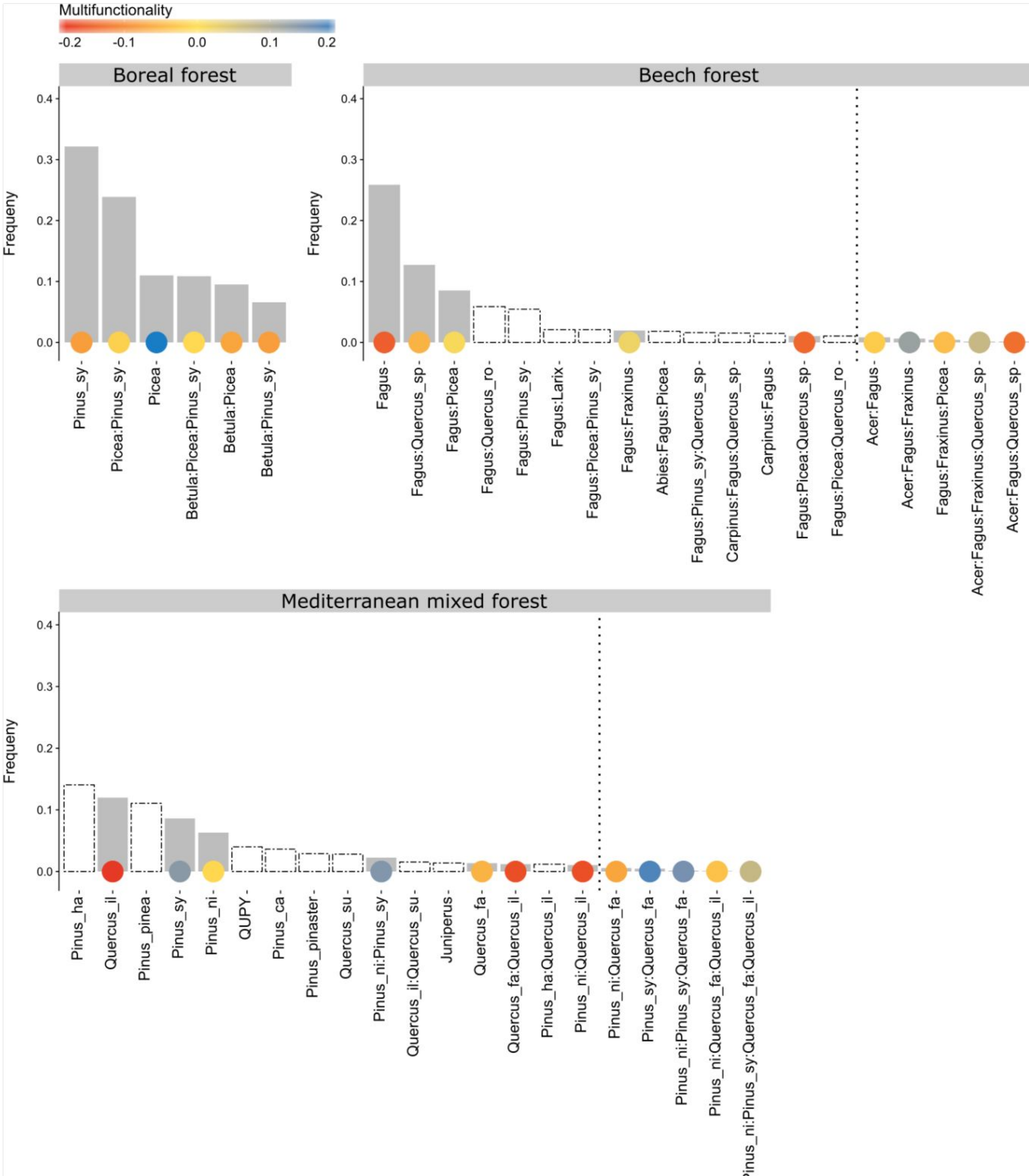

Fig. 3 Frequency of occurrence of particular tree species compositions in national forest inventory data for boreal forests, beech forest, and Mediterranean mixed forests. Grey bars indicate the compositions that were also studied in the corresponding forest types in the FunDivEUROPE exploratory platform; the white bars represent compositions that were not included in the exploratory platform. The coloured

circles indicate the degree of multifunctionality of the compositions based on the estimates in the exploratory platform (so only for grey bars). This multifunctionality expresses the degree to which the functioning of a particular composition deviates from the average, taking all 30 functions into account (positive values indicate above average performance). The dotted lines indicate a threshold frequency of 0.01 below which rare combinations of tree species are not shown, unless they were studied in the exploratory platform.

Supporting information to the paper
Baeten *et al.* Identifying the tree species compositions that maximize ecosystem functioning in European forests. *Journal of Applied Ecology*

Appendix S1 – FunDivEurope exploratory platform: study locations, tree species, and functions

Figure S1.1. Location and local names of the six forest types included in the FunDivEUROPE exploratory platform. The study locations were selected to represent six major European forest types: boreal (North Karelia, Finland, *N* = 28 research plots), hemi-boreal (Białowieza, Poland, *N* = 43), beech (Hainich, Germany, *N* = 38), mountainous beech (Râsca, Romania, *N* = 28), thermophilous deciduous (Colline Metallifere, Italy, *N* = 36), Mediterranean mixed (Alto Tajo, Spain, *N* = 36). Details on the design can be found in Baeten *et al.* (2013).

Table S1.1. Overview of the study species for each of the six forest types of the FunDivEUROPE exploratory platform. The last three rows provide summaries of the number of species richness levels, total number of plots, and number of plots per richness level. See Baeten et al. (2013) for additional environmental variables.

	boreal (North Karelia)	**hemi-boreal** (Białowieza)	**beech** (Hainich)	**mountainous beech** (Râsca)	**thermophilous deciduous** (Colline Metallifere)	**Mediterranean mixed** (Alto Tajo)
Study species in each forest type (indicated with "x")						
(1) Coniferous						
Abies alba				×		
Picea abies	×	×	×	×		
Pinus nigra						×
Pinus sylvestris	×	×				×
(2) Broadleaved						
Acer pseudoplatanus			×	×		
Betula	×	×				
pendula/pubescens		×				
Carpinus betulus					×	
Castanea sativa			×	×		
Fagus sylvatica			×			
Fraxinus excelsior					×	
Ostrya carpinifolia		×	×		×	
Quercus robur/petraea					×	
Quercus cerris						×
Quercus faginea					×	×
Quercus ilex						
(evergreen)						
Species richness levels	3	5	4	4	5	4
Number of plots	28	43	38	28	36	36
Plots per richness level	12/12/4	10/10/11/10/2	6/10/16/6	8/10/7/3	10/9/9/7/1	12/15/6/3

Table S1.2. Overview of the 30 ecosystem functions and their classification into a priori groups. For full details on their measurement see Ratcliffe *et al.* (2017) and van der Plas *et al.* (2018). Table adapted from Ratcliffe *et al.* (2017).

Ecosystem function	Description
Nutrient and carbon cycling related drivers	
Earthworm biomass	Biomass of all earthworms (g m^{-2})
Fine woody debris	Snags and standing dead trees shorter than 1.3 m and thinner than 5 cm DBH, and all stumps and other dead wood pieces lying on the forest floor
Microbial biomass	Mineral soil (0-5cm layer) microbial biomass carbon (mg C kg^{-1})
Soil carbon stock	Total soil carbon stock (Mg ha^{-1}) in forest floor and 0-10 cm mineral soil layer combined
Nutrient cycling related processes	
Litter decomposition	Decomposition of leaf litter using the litterbag methodology (% daily rate)
Nitrogen resorption efficiency	Difference in N content between green and senescent leaves divided by N content of green leaves (%)
Soil C/N ratio	Soil C/N ratio in forest floor and 0-10 cm mineral soil layer combined
Wood decomposition	Decomposition of flat wooden sticks placed on forest floor (% daily rate)
Primary production	
Fine root biomass	Total biomass of living fine roots in forest floor and 0-10 mineral soil layer combined (g m^{-2})
Photosynthetic efficiency	Chlorophyll fluorescence methodology (ChlF)
Leaf mass	Leaf Area Index (LAI)
Litter production	Annual production of foliar litter dry mass (g)
Tree biomass	Aboveground biomass of all trees (Mg C ha^{-1})
Tree productivity	Annual aboveground wood production (Mg C ha^{-1} yr^{-1})
Understorey biomass	Dry weight of all understorey vegetation in a quadrant (g)
Regeneration	
Sapling growth	Growth of saplings up to 1.60 m tall (cm)
Tree juvenile regeneration	Number of saplings up to 1.60 m tall
Tree seedling regeneration	Number of tree seedlings less than a year old

Resistance to disturbance	
Resistance to drought	Difference in carbon isotope composition in wood cores between dry and wet years (‰)
Resistance to insect damage	Foliage not damaged by insects (%)
Resistance to mammal browsing	Twigs not damaged by browsers (%)
Resistance to pathogen damage	Foliage not damaged by pathogens (%)
Tree growth recovery	Ratio between post-drought growth and growth during the respective drought period
Tree growth resilience	Ratio between growth after and before the drought period
Tree growth resistance	Ratio of tree growth during a drought period and growth during the previous five year high-growth period
Tree growth stability	Mean annual tree growth divided by standard deviation in annual tree growth between 1992 and 2011
Habitat for species	
Bird diversity	Shannon-Wiener diversity of bird species estimated with standardized point-counts
Bat diversity	Total number of species (or species pairs) of bats per forest plot recorded with an automatic bat recorder
Earthworm richness	Total number of earthworm species in the litter and 20 cm topsoil (mustard extraction and hand sorting)
Understorey plant diversity	Mean Shannon-Wiener diversity of plants in the understorey community

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Appendix S2 – Quantifying multifunctionality and species identity and diversity effects

A MODEL-BASED MEASURE OF MULTIFUNCTIONALITY

We quantified the multifunctionality of each tree species composition with a model-based approach. In each of the 209 plots, we have a quantitative estimate for each of the 30 functions. These estimates were modelled together in a hierarchical meta-analytic model $f_i = \mu + ef_{j[i]} + s_{k[i]} + c_{l[i]} + \varepsilon_i$ (Nakagawa & Santos 2012). In this model, f_i is an estimate of a function in a plot, μ is the global intercept, $ef_{j[i]}$ denotes the effect of the j^{th} function (j = 1, …, 30 functions), $s_{k[i]}$ is an effect of plot (k = 1, …, 209 plots), and $c_{l[i]}$ is the effect of tree species composition (l = 1,…, 103). Species combinations occurring in multiple forest types were considered different compositions. These effects were assumed to come from a zero-mean normal distribution with group-specific variance (e.g., between-plot variance ${\sigma_s}^2$). The residual term ε_i was also assumed to be normally distributed around zero with variance σ^2. To remove the differences in measurement scale, the values for each function were normalized before modelling by subtracting the mean and dividing by the standard deviation. In this case, the effect $ef_{j[i]}$ becomes redundant, because functions are centred on zero. Models were fitted with the *lmer* function in the *lme4* package called from R3.4.1 (Bates *et al.* 2015; R Core Team 2017).

We used the composition effect c_l as a measure of multifunctionality for each tree species composition. This effect quantifies the degree to which the functioning of a particular composition deviates from the average, taking all functions into account. Positive values express above-average performance of that species combination and negative values show below-average performance. Note that this approach is related to an unweighted averaging approach to quantify multifunctionality (Byrnes *et al.* 2014). We also calculated an alternative threshold-based measure according to the approach described in Byrnes et al. (2014). Here we used a threshold of 50 % of the maximum observed value of each function. The model-based and threshold-based approach were clearly related (Fig. S2.1), so that the rankings of the compositions according to the two multifunctionality measures were quite similar. We can therefore assume that the results presented in the main text are robust to the choice for a particular multifunctionality measure.

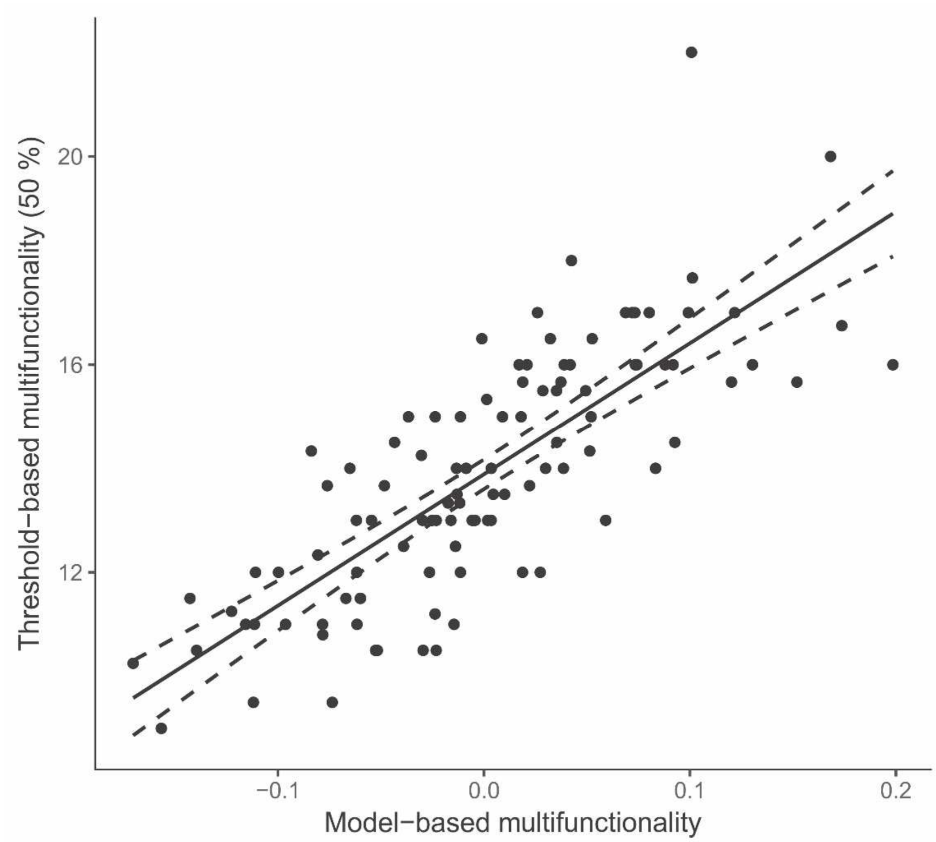

Fig. S2.1. Relationship between a model-based measure of forest multifunctionality and a threshold-based measure of multifunctionality. The measures were calculated for each of the different tree species compositions (combinations within forest types), expressing the performance of each composition when considering all 30 functions together. The regression line shows the linear regression (± 95 % CI) between the two measures and shows that they are clearly related ($R^2 = 0.62$; regression slope 25.3, $P < 0.001$). We can therefore assume that the results presented in the main text are robust to the choice for a particular multifunctionality measure.

DIVERSITY INTERACTION MODELS: SPECIES IDENTITY AND DIVERSITY EFFECTS

We used a diversity-interaction modelling framework (Kirwan *et al.* 2009) to quantity species identity and diversity effects. The approach uses a linear model of the form $f_i = ID + DE + \alpha BA_i + \varepsilon_i$, with f_i an estimate of functioning in a plot i, ID the species identity effects, DE the diversity effects, α the effect of variation in plot-level basal area (BA; average centred to zero within forest types), and a normally distributed residual error term ε_i. The species identity effects equal the average monoculture performances, weighted by the species' relative abundance: $ID = \sum_m \beta_m P_m$, where β_m is the estimated performance of species m in a monoculture and P_m its relative basal area in a plot. The diversity effects results from species interactions, which causes mixture performance to differ from that expected from monoculture species performances. Kirwan et al. (2009) proposed alternative patterns of interactions based on different biological assumptions, corresponding to different formulations of the diversity effects term. Firstly, pairwise interactions between species m and n lead to a diversity effect: $DE =$

$\sum_{m<n} \delta_{mn} P_m P_n$, with δ_{mn} the strength of the interspecific interaction (*pairwise interactions* assumption). Positive interaction terms indicate higher performance than expected based on the abundance-weighted average of the monoculture performance (overyielding in the context of productivity). Negative values similarly indicate antagonistic effects and thus lower performance than expected (underyielding). Secondly, under the assumption that species interact similarly with any other species and that the main effect of mixing is the contrast between intra- and interspecific interactions, the diversity effects can be simplified: $DE = \sum_m \lambda_m P_m (1 - P_m)$, with λ_m the interaction effect of species m with any other species (*additive contribution* assumption). Thirdly, interactions between trees from different functional groups may principally cause the diversity effect. Here we analysed the interaction between deciduous versus evergreen tree species: $DE = \delta_{de} P_d P_e$, with δ_{de} the interaction between deciduous and evergreen species when they co-occur in a mixture, with relative basal areas P_d and P_e, respectively (*functional group* assumption). The within functional-group interaction effects were assumed to be zero here.

We confronted five alternative models with the data to explore the importance of the identity effects and the different types of interactions. Combining the variables and effects described above, this resulted in the following models:

Null model; identity effects are equal (model 0)

$$f_i = \beta + \alpha BA_i + \varepsilon_i$$

Identity-effects model, no species interactions (model 1)

$$f_i = \sum_m \beta_m P_{im} + \alpha BA_i + \varepsilon_i$$

Pairwise-interactions effect model (model 2)

$$f_i = \sum_m \beta_m P_{im} + \alpha BA_i + \sum_{m<n} \delta_{mn} P_{im} P_{in} + \varepsilon_i$$

Additive contributions model (model 3)

$$f_i = \sum_m \beta_m P_{im} + \alpha BA_i + \sum_m \lambda_m P_{im}(1 - P_{im}) + \varepsilon_i$$

Functional-groups effect model (model 4)

$$f_i = \sum_m \beta_m P_{im} + \alpha BA_i + \delta_{de} P_{id} P_{ie} + \varepsilon_i$$

All models were fitted in R3.4.1 (R Core Team 2017) and model comparisons were performed based on AIC and likelihood ratio tests.

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Appendix S3 – Supplementary results

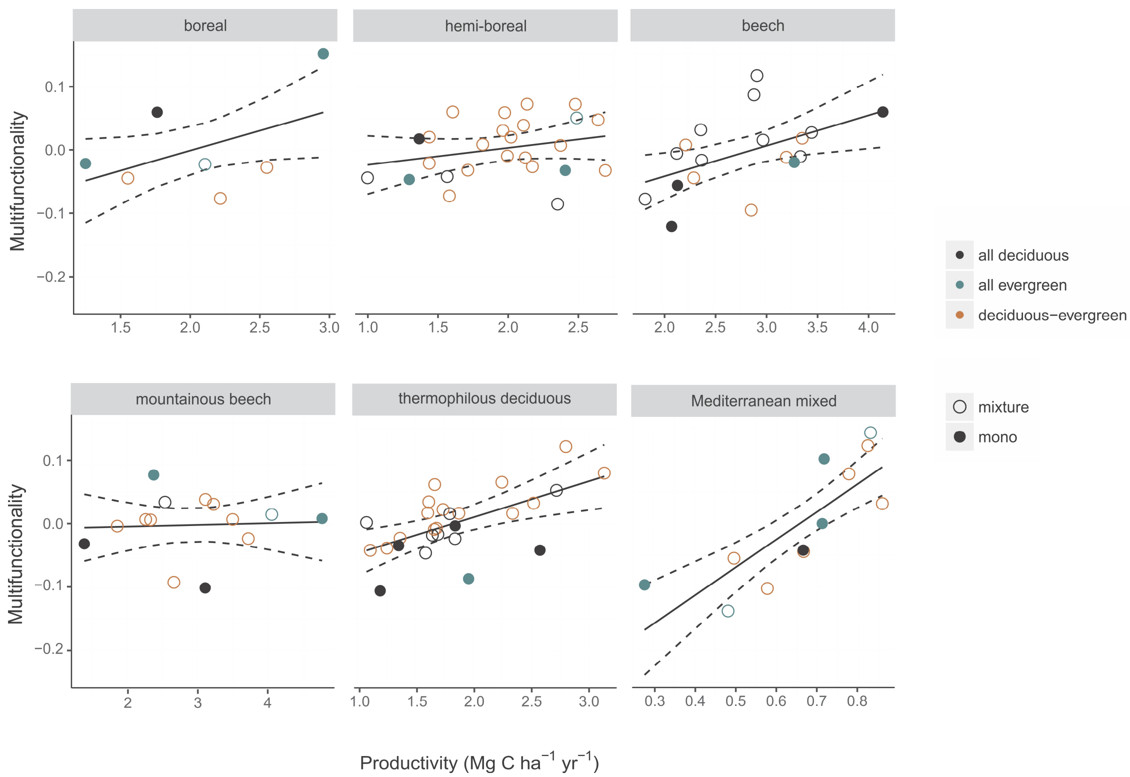

Fig. S3.1. Relationship between the mean productivity and multifunctionality of each composition in the six forest types. The productivity is derived from the annual aboveground wood production and conversion of 0.5 g C per gram of biomass (Jucker *et al.* 2014). A tree productivity of 1 Mg C ha^{-1} yr^{-1} thus corresponds to an annual production of two tons of aboveground woody biomass per hectare. The regression line shows the linear relationship (± 95 % CI) between the two measures of composition performance for each forest type. Slopes were significantly positive ($P < 0.05$) for beech, thermophilous deciduous, and Mediterranean mixed forest. For this analysis, the function productivity was excluded from the multifunctionality measure. Results for the global model are shown in the main text.

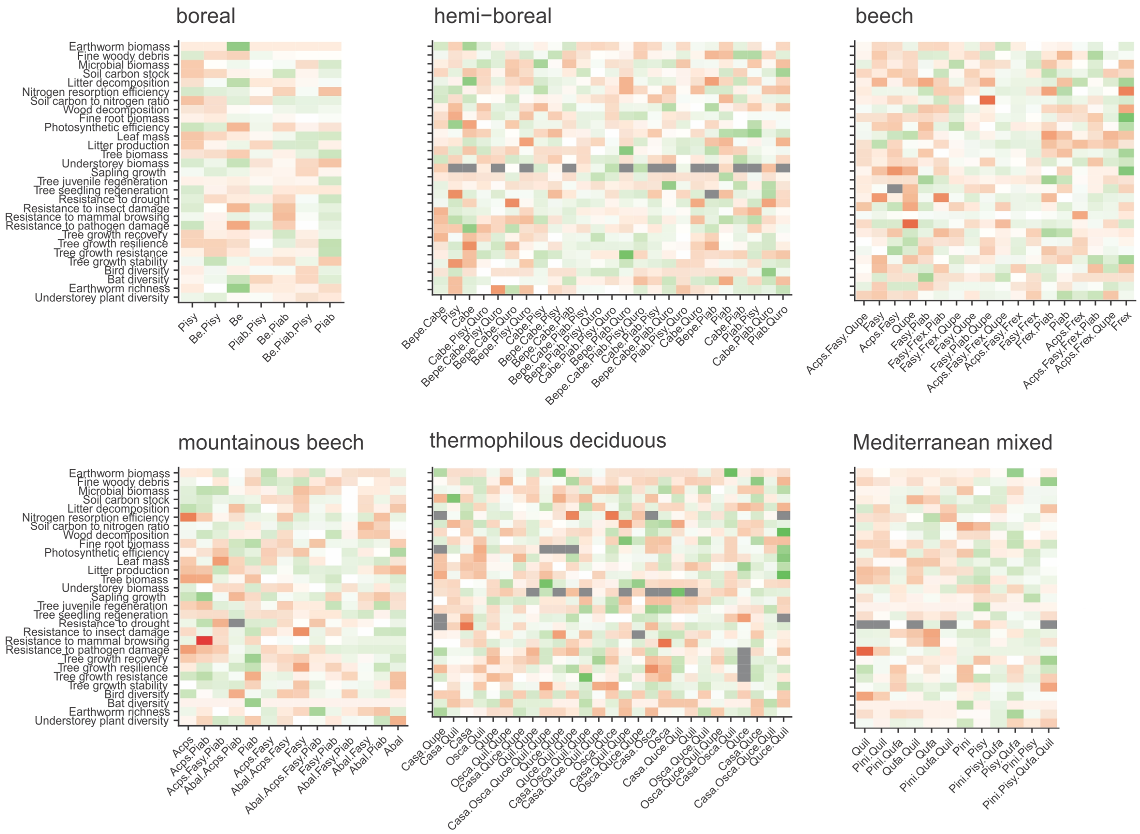

Fig. S3.2. Mean performance of each tree species composition for the 29 individual ecosystem functions (excluding tree productivity). Within each forest type, the species compositions were ranked from the lowest (left) to the highest (right) mean productivity. Measurements of each funtion were normalized within forest types and are represented on a colour scale: green values represent compositions that show above-average (within forest types) performance for a particular function (values > 0). Red values are for compositions with below-average performance (values < 0). The darker the colour the stronger the deviation from the average; maximum values were ±4 and represent ecosystem functions with a performance of four standard deviations higher or lower compared with the average. The general pattern across forest types (except mountainous beech) are prevailing green colours on the right-hand side and red colours on the left-hand side, showing that compositions with higher productivtiy on the right are also associated with high levels of other functions.

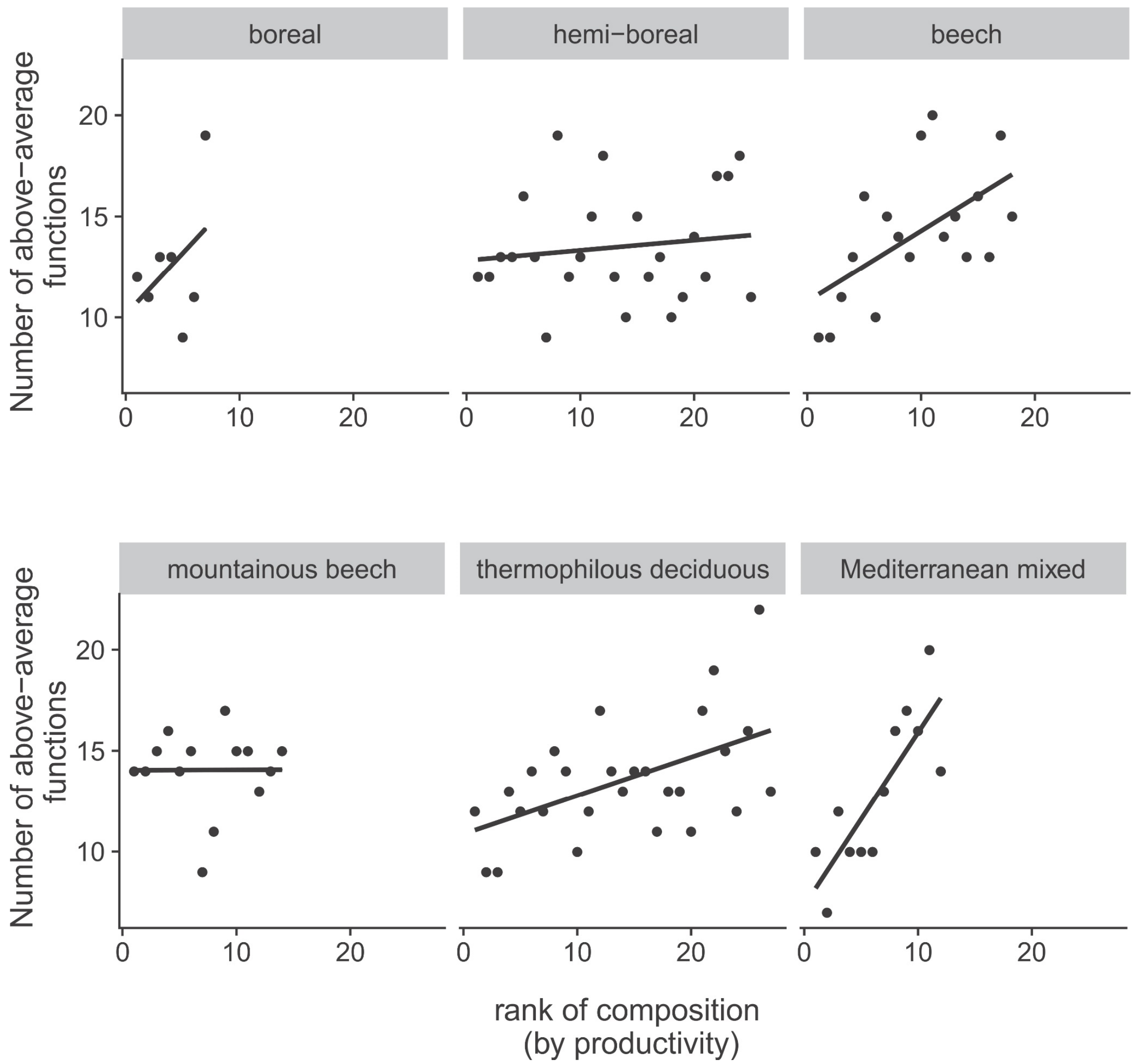

Fig. S3.3. Relationship showing for each species composition (ranked from lowest to highest productivity within forest types) the total number of ecosystem functions with above-average performance (total 29 functions). The lines are fitted values from linear models; slopes were significant for beech, thermophilous deciduous and Mediterranean mixed forest ($P < 0.05$; consistent with Fig. S3.1). The present graph is actually a condensed representation of Fig. S3.2: the ranking of compositions on the x-axis is the same and the response on the y-axis equals the number of colums in Fig. S3.2 with values > 0.

Fig. S3.4. Overview of tree species interaction effects on the 30 individual ecosystem functions in six European forest types. For each function, pairwise species interaction models were fitted to quantify the degree to which tree species interactions cause mixture performance to differ from that expected from the monoculture species performances. For each species pair and function, the graph shows the significant ($P < 0.1$) positive (green) or negative (red) effects, indicating whether the species mixture is doing better or worse than expected. The summary of this graph is shown in the main text (Fig. 2). Note that the graph compares within tree species combinations (performance of mixtures versus the monocultures of two particular species) and does not allow a direct comparison between compositions, because the species identity effects were not accounted for in this analysis. Full species names are given below Table 1.

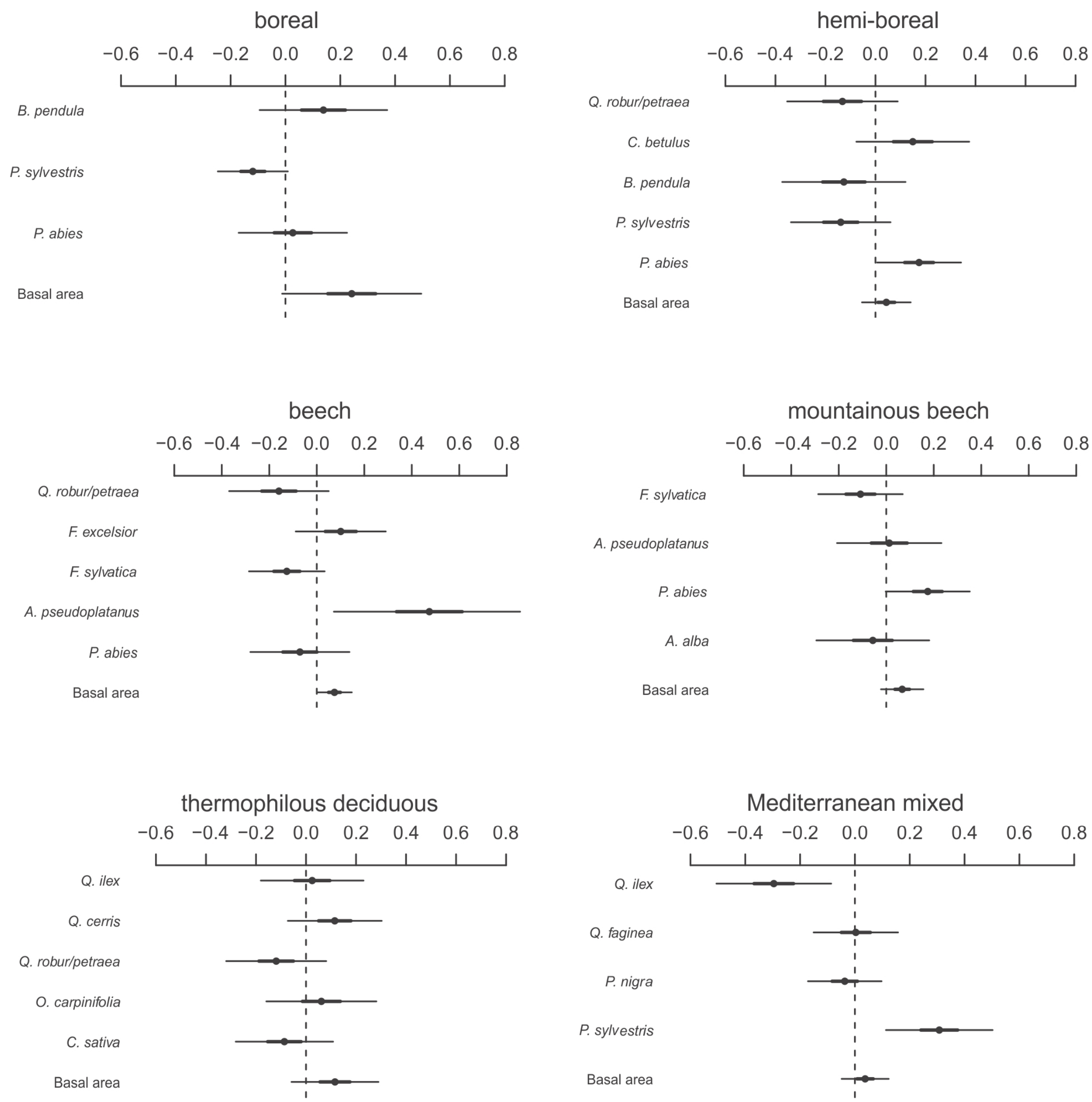

Fig. S3.5. Estimated coeficients (± 50% and 95% confidence interval) for the identity effects model quantifying differences in species monoculture multifunctionality in each forest type (model 1; species performance across 30 ecosystem functions). Positive and negative estimates represent higher and lower monoculture performance compared with the average within a forest type, respectively. These are considered significant in the main text if the 95% intervals do not overlap with zero. Note that the ecosystem functions were normalized, so that a one-unit change corresponds to a change from one standard deviation below/above the mean. The basal area effect quantifies how functioning changes with increasing stand density. Basal area was centred to average to zero within forest types, so that species effects are estimated at average basal area. See main text for more details on the identity model.

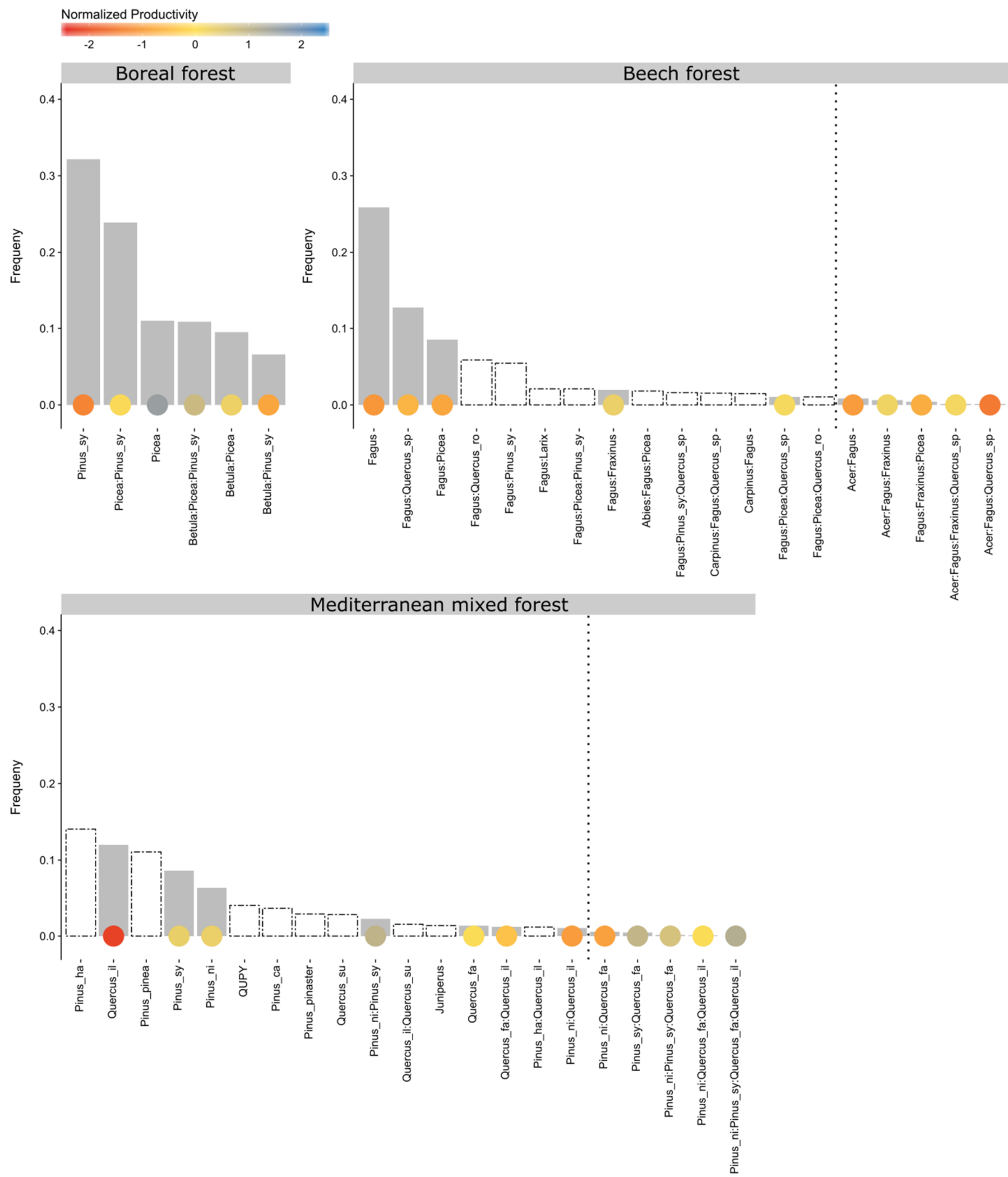

Fig. S3.6. Frequency of occurrence of particular tree species compositions in national forest inventory data for boreal forests, beech forest, and Mediterranean mixed forests. Grey bars indicate the compositions that were also studied in the corresponding forest types in the FunDivEUROPE exploratory platform; the white bars represent compositions that were not included in the exploratory platform. The degree of productivity of the compositions is indicated by coloured circles, based on the estimates in the exploratory platform (so only for grey bars). The dotted lines indicate a threshold frequency of 0.01 below which rare combinations of tree species are not shown, unless they were studied in the exploratory platform.

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Appendix S4 – Results sensitivity analyses

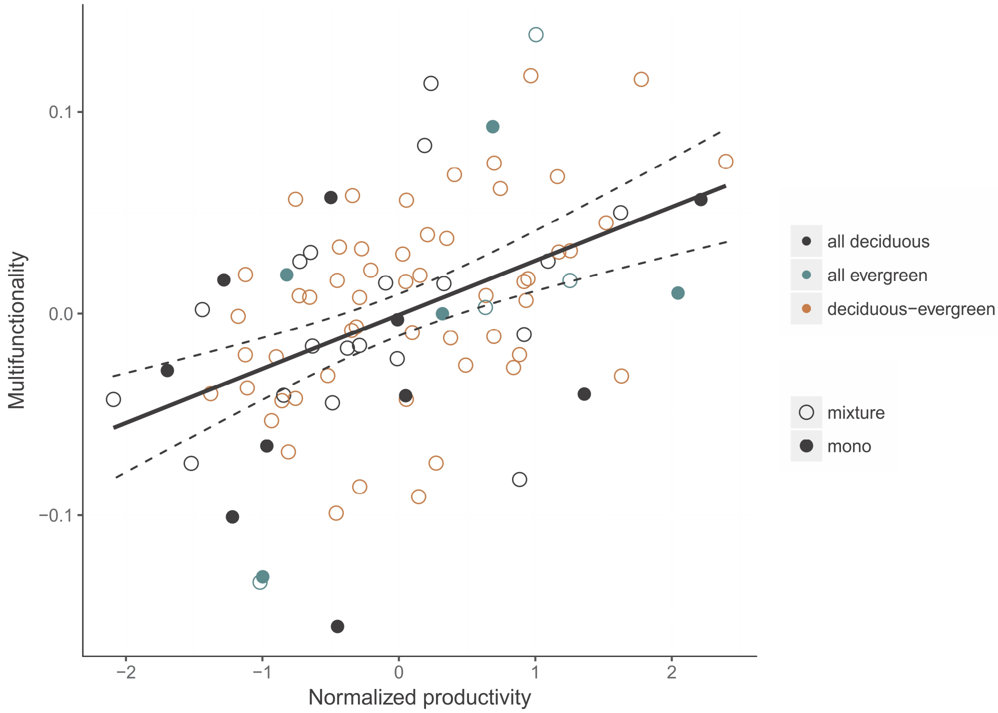

Fig. S4.1. Relationships between the tree productivity and multifunctionality of different tree species compositions across six European forest types. This is a reanalysis of Fig. 1 in the main text, but we now assume a particular species mixture occurring in multiple regions to be the same composition (N = 92 compositions instead of 103). For instance, *Picea abies* monocultures were studied in four forest types and were therefore represented as four different points (compositions) in Fig. 1. The present graph only includes one point for *P. abies* monocultures, because its multifunctionality and mean productivity was calculated across types. The multifunctionality was calculated based on 29 functions, that is, excluding tree productivity. The slope of the relationships now equals 0.027 ($P <$ 0.001, $R^2 = 0.20$), which is nearly identical to the slope in Fig. 1. The caption of Fig. 1 provides more information on the axes and legends.

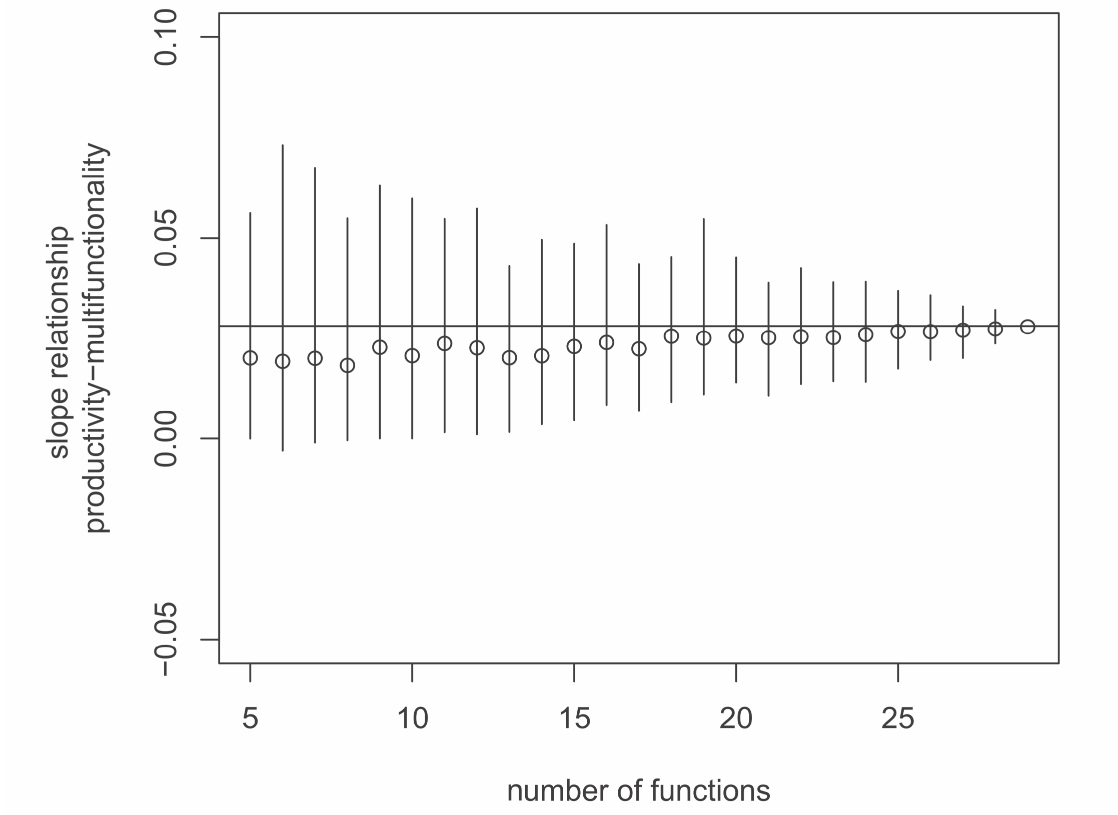

Fig. S4.2. Change in the slope of the relationships between the tree productivity and multifunctionality when the number of ecosystem functions considered in the multifunctionality measure was reduced from 29 to 5 (from right to left). The slope at 29 functions, that is, considering all functions except tree productivity, corresponds to the relationship shown in Fig. 1 and is indicated by the horizontal line. For each number of functions, we randomly selected functions, calculated the model-based multifunctionality, and fitted the slope of a linear producitivity-multifunctionality relationship. This was done 100 times for each number of functions; the points show the averages and the vertical lines mark the range between the 2.5% and 97.5% quantiles. While the relationship becomes slightly lower when fewer functions are considered, it is consistently positive (95% intervals only start to include zero when <10 functions are considered).

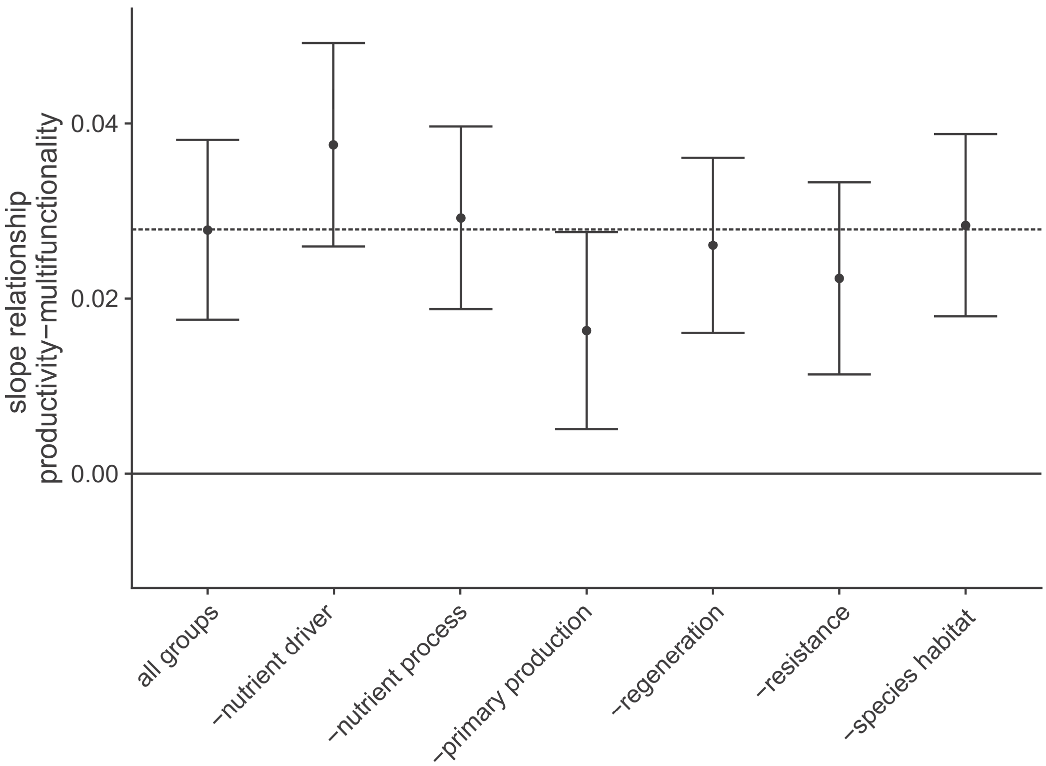

Fig. S4.3. Differences in the slope of the relationship between the tree productivity and multifunctionality when excluding one of the ecosystem function groups (Table S1.2) from the multifunctionality measure. For example, the '- nutrient driver' category shows the relationship in case no functions from the 'Nutrient and carbon cycling related drivers' group were used for calculating the multifunctionality measure. The 'all groups' category considers all 29 functions and corresponds to the slope of the relationship shown in Fig. 1 (dashed horizontal line). The tree productivity was always excluded from the multifunctionality measure. Points are the estimates of the slopes ± 95 % confidence intervals.