Biotic homogenization can decrease landscape-scale forest multifunctionality

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ECOLOGY

Many experiments have shown that local biodiversity loss impairs the ability of ecosystems to maintain multiple ecosystem functions at high levels (multifunctionality). In contrast, the role of biodiversity in driving ecosystem multifunctionality at landscape scales remains unresolved. We used a comprehensive pan-European dataset, including 16 ecosystem functions measured in 209 forest plots across six European countries, and performed simulations to investigate how local plot-scale richness of tree species (α-diversity) and their turnover between plots (β-diversity) are related to landscape-scale multifunctionality. After accounting for variation in environmental conditions, we found that relationships between α-diversity and landscape-scale multifunctionality varied from positive to negative depending on the multifunctionality metric used. In contrast, when significant, relationships between β-diversity and landscape-scale multifunctionality were always positive, because a high spatial turnover in species composition was closely related to a high spatial turnover in functions that were supported at high levels. Our findings have major implications for forest management and indicate that biotic homogenization can have previously unrecognized and negative consequences for large-scale ecosystem multifunctionality.

β-diversity | biodiversity | ecosystem functioning | FunDivEUROPE | spatial scale

Significance

Numerous studies have demonstrated the importance of biodiversity in maintaining multiple ecosystem functions and services (multifunctionality) at local spatial scales, but it is unknown whether similar relationships are found at larger spatial scales in real-world landscapes. Here, we show, for the first time to our knowledge, that biodiversity can also be important for multifunctionality at larger spatial scales in European forest landscapes. Both high local (α-) diversity and a high turnover in species composition between locations (high β-diversity) were found to be potentially important drivers of ecosystem multifunctionality. Our study provides evidence that it is important to conserve the landscape-scale biodiversity that is being eroded by biotic homogenization if ecosystem multifunctionality is to be maintained.

It is widely established that high local-scale biodiversity increases levels of individual ecosystem functions in experimental ecosystems (1–4), and that biodiversity is even more important for the simultaneous maintenance of multiple functions at high levels (i.e., ecosystem multifunctionality) (5–8). Because the capacity of natural ecosystems to maintain multiple functions and services is crucial for human well-being (9), the positive

diversity–multifunctionality relationship is often used as an argument to promote biodiversity conservation (6, 10). However, although society seeks to maximize the delivery of potentially conflicting ecosystem services, such as food production, bioenergy generation, and carbon storage at the landscape scale (11–13), research into the relationship between biodiversity and ecosystem multifunctionality has been largely limited to local-scale studies, where diversity is manipulated in experimental plant communities. Although some studies have focused on more natural communities distributed over larger spatial extents (e.g., 14–16), they examined relationships between local-scale biodiversity and local-scale multifunctionality. The only previous study to investigate multifunctionality at larger scales (17) simulated artificial landscapes using data from experimental grassland communities. It showed that although different aspects of biodiversity affected multifunctionality, local-scale (α-) diversity was a much stronger driver than the turnover of species between sites (β-diversity). However, whether those findings can be extrapolated to real-world (i.e., natural, seminatural) ecosystems, such as forests, is unknown. As a result, we have a poor understanding of how multifunctionality relates to biodiversity at the larger spatial scales that are most relevant to ecosystem managers. This question is of particular concern, given recent findings suggesting that human-driven homogenization of communities [loss of β-diversity (18–21)] may be just as widespread as α-diversity declines (22, 23).

Multifunctionality can be measured by a variety of methods, and the most appropriate means of doing so remains unresolved (24–27), particularly at larger scales, where the desired distribution of ecosystem function across the landscape has not been quantified. At local scales, one can quantify ecosystem multifunctionality as the number of ecosystem functions that exceed a given threshold value, where the threshold equals a certain percentage of the maximum observed value of each function (10, 24) (hereafter "threshold-based multifunctionality"; Fig. 1B). This threshold reflects the minimum value of ecosystem functioning that is deemed satisfactory. Because trade-offs between ecosystem functions or services are commonplace (5, 7, 28, 29), it is often impossible to maximize all of the desired functions in a local community (6). However, when different species provide different functions (5, 7) at larger spatial scales, a high spatial turnover in community composition (i.e., a high β-diversity) across the landscape can cause different parts of the landscape to provide different functions at high levels (defined as high threshold-based β-multifunctionality; Fig. 1B). Therefore, high β-diversity might cause all desired ecosystem functions to be provided at high levels in at least one patch within a landscape [and hence promote threshold-based landscape-scale or γ-multifunctionality (30)] (Fig. 1B), but only if

(i) species differ in the functions they support and (ii) there is no "superspecies" that supports the majority of functions. This threshold-based γ-multifunctionality may be relevant for cases where forest landscapes are managed for many different services (e.g., timber production, limitation of nutrient runoff, ecotourism), but where each of these services only needs to be provided at high levels in a part of the landscape, not everywhere (31). Alternatively, a manager may seek to promote the total delivery of many summed individual ecosystem functions across a landscape. We define this total delivery as sum-based γ-multifunctionality (Fig. 1B). This metric may be a more appropriate measure of multifunctionality in cases where the benefits of ecosystem services are manifested at large scales, such as carbon sequestration or water purification (32). In this case, β-diversity might only promote sum-based γ-multifunctionality if nonadditive diversity effects, such as resource partitioning, species-environment matching, or spillover effects, operate at relatively large spatial scales (33, 34). It is therefore likely that the importance of β-diversity for γ-multifunctionality varies depending on the desired pattern of ecosystem service provision.

Forests provide many ecosystem services, including wood production, regulation of water quality and climate, and recreation (35, 36). Most present-day European forests and almost all forest plantations worldwide are dominated by only one or a few tree species (15, 37), although their diversity could be promoted relatively easily by planting more species or by encouraging natural regeneration. This fact makes the understanding of diversity–multifunctionality relationships in these ecosystems highly relevant for forest management.

We therefore assessed the importance of α- and β-diversity of tree species in driving γ-multifunctionality in mature European forests. To do so, we used data taken from a pan-European forest dataset consisting of 209 forest plots, specifically selected to investigate relationships between tree diversity and ecosystem functioning by maximizing variation in dominant "target" species richness and minimizing (i) variation in other potential drivers of ecosystem function (e.g., soil and climatic conditions) and (ii) covariation between tree α-diversity, species composition, and environmental variables as much as possible (38). Our plot selection therefore aimed to mimic biodiversity experiments to investigate relationships between biodiversity and ecosystem functioning in mature forests, which are difficult to undertake with manipulative approaches due to the longevity of tree species. The plots were widely distributed across six European countries, spanning boreal to Mediterranean zones and representing six major European forest types (38). In each plot, 16 ecosystem processes, functions, or properties (termed "functions" hereafter) were measured. These functions represented a wide range of

Fig. 1. Quantifying biodiversity and multifunctionality across spatial scales. The light yellow areas represent hypothetical landscapes, consisting of (white) local communities. In these communities, some species are present (colored icons in A and C), whereas others are absent (gray icons). Similarly, some functions are performing above a hypothetical threshold of 0.5 (colored icons in B), whereas others are not (gray icons). Diversity and threshold-based multifunctionality are quantified at (i) the local plot (α-) scale as the number of species present (two and three in A) or functions performing above a given threshold (two and three in B), (ii) the β-scale as the turnover in species composition [$= 1 - \log((a + b + 2c)/(a + b + c)) = 1 - \log((1 + 2 + 2)/(1 + 2 + 1)) = 0.90$ in A (49)] or functions [$= 1 - \log((a + b + 2c)/(a + b + c)) = 1 - \log((1 + 2 + 2)/(1 + 2 + 1)) = 0.90$ in B (49)] across plots, and (iii) the landscape (γ-) scale as the number of functions (four in B) present in at least one plot. Sum-based γ-multifunctionality is defined as the sum of all standardized ecosystem values in a landscape ($= 0.8 + 0.2 + 0.7 + 0.4 + 0.9 + 1.0 + 0.1 + 0.6 = 4.7$). In contrast to threshold-based multifunctionality, sum-based multifunctionality is not analogous to biodiversity (where species are either present or absent), and can therefore not be partitioned into α- or β-components. (C) This framework allows investigation of whether γ-multifunctionality is promoted by α- and/or β-diversity.
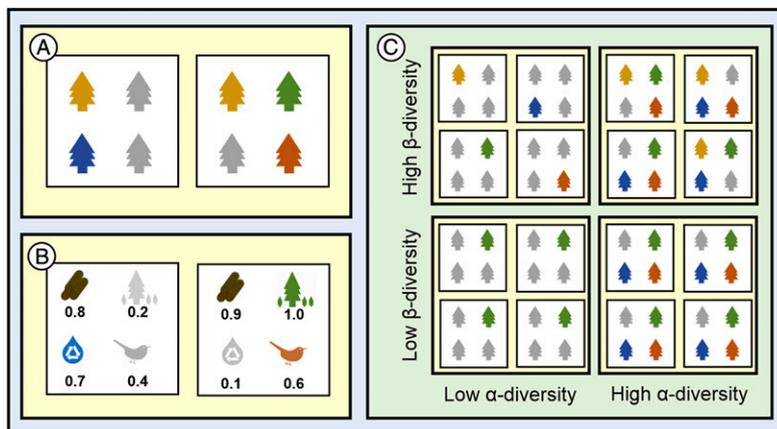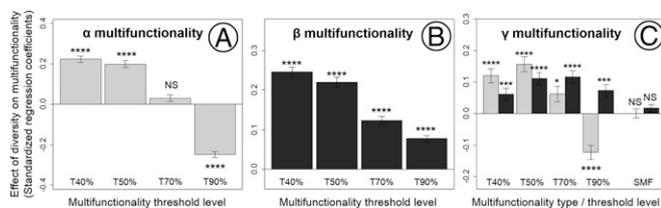
Fig. 2. Scale-dependent effects of biodiversity on forest ecosystem multifunctionality. Bars represent the standardized regression coefficients of α-diversity (light gray) and β-diversity (dark gray) in generalized LMMs explaining α- (*A*), β- (*B*), or γ- (*C*) multifunctionality. Multifunctionality was quantified at different scales using a threshold approach, with thresholds of 40%, 50%, 70%, and 90%. In addition, sum-based γ-multifunctionality was calculated as the sum of scaled (between 0 and 1) individual function values. Diversity measures were calculated based on individuals of target tree species. *$P < 0.05$; ***$P < 0.001$; ****$P < 0.0001$. NS, not significant.

supporting, provisioning, regulating, and cultural ecosystem services (*sensu* 9) (*SI Appendix*, Table S3). Next, we created simulated landscapes by randomly drawing plots from a country to generate a "landscape" of five plots, from which γ-multifunctionality was calculated. We then explored relationships between α- and β-diversity and different measures of γ-multifunctionality: threshold-based γ-multifunctionality, quantified as the number of functions with levels above a threshold [a certain percentage of maximum functioning observed across all plots (10)] in at least one plot of the landscape (quantification is shown in Fig. 1*B*), and sum-based γ-multifunctionality, quantified as the sum of scaled values of all functions across all plots within a landscape (quantification is shown in Fig. 1*B*). To demonstrate how α- and β-diversity can promote threshold-based γ-multifunctionality, we also measured the relationships between both α- and β-diversity and threshold-based α- and β-multifunctionality (quantification is shown in Fig. 1*B*).

Results and Discussion

Our analyses show that relationships between α-diversity and threshold-based γ-multifunctionality varied from positive, when moderate levels of ecosystem functioning were desired (40–70% thresholds), to negative, when very high levels (90% threshold) of ecosystem functioning were required (Fig. 2*C*; all $P < 0.05$). In contrast, relationships between β-diversity and threshold-based γ-multifunctionality were, when significant, always positive, irrespective of the level of functioning desired (Fig. 2*C*; all $P < 0.05$). These positive relationships with β-diversity were generally consistent throughout countries (Fig. 3*C*) and largely independent of whether diversity was measured as total species richness or richness of abundant target species (*SI Appendix*, Fig. S3 and Tables S5–S7) and the statistical approach used to investigate diversity–multifunctionality relationships (*SI Appendix*, Figs. S5–S9). Thus, landscapes with a high spatial turnover in species composition had consistently more functions at high levels in at least some plots than more biotically homogeneous landscapes. This finding indicates that biotic homogenization can have detrimental consequences for threshold-based γ-multifunctionality of ecosystems, whereas management that promotes a higher spatial turnover in species composition may reverse these detrimental effects. In contrast, sum-based γ-multifunctionality was related to neither α- nor β-diversity (Fig. 2*C* and *SI Appendix*, Fig. S3).

Next, we investigated the mechanisms by which α- and β-diversity may affect threshold-based γ-multifunctionality by investigating relationships between α- and β-diversity and threshold-based α- and β-multifunctionality (i.e., local multifunctionality and turnover in functioning across plots; Fig. 1*B*). These analyses showed that the aforementioned relationships between α-diversity and threshold-based γ-multifunctionality were mediated by effects on threshold-based α-multifunctionality: α-Diversity was positively related to threshold-based α-multifunctionality when moderate levels (40–50%) of functioning were desired [similar to most experimental

studies (8)], but negatively related when high levels (90%) of functioning were required (Fig. 2*A*; all $P < 0.001$), a finding that was largely consistent throughout countries (Fig. 3*A*) and largely independent of whether the richness of the dominant species or the richness of all species (*SI Appendix*, Fig. S3) was used as an α-diversity measure. This pattern may have been caused by "statistical averaging" effects similar to the portfolio effects that drive diversity–stability relationships (39): Without strong selection or complementarity effects (40), mixed species plots will tend to have intermediate, but never extremely high or low, ecosystem function levels due to the averaging of individual species effects on function. In line with this mechanism, α-diversity did not have significant effects on sum-based γ-multifunctionality (Fig. 2*C*). These results suggest that although function values were, on average, not higher or lower in diverse communities than in monocultures, they tended to be less extreme (never extremely high or low) (41). This result contrasts with the results of other studies focusing on more diverse and/or experimental grassland, aquatic, or soil communities. In these studies, higher α-diversity enhances α-multifunctionality even at very high thresholds (8, 24), possibly due to strong complementarity effects. However, the diversity-ecosystem functioning literature has tended to concentrate on particular ecosystems and study designs. As a result, it is difficult to infer whether these contrasting results are caused by biological or methodological differences. In any case, our results indicate that in European forests at least, the relationship between α-diversity and both α- and γ-multifunctionality strongly depends on the desired level of functioning.

In our next analysis, we investigated the relationship between β-diversity and γ-multifunctionality. In contrast to α-diversity, the positive relationship between β-diversity and threshold-based γ-multifunctionality was independent of the desired level of ecosystem functioning. In almost all countries (Figs. 2*B* and 3*C*), and irrespective of whether target or total species richness was the diversity metric used (*SI Appendix*, Fig. S3), β-diversity was positively related to threshold-based β-multifunctionality when moderate or high levels of ecosystem functioning were desired, thereby increasing the number of functions that were provided at high levels in at least one part of the landscape (threshold-based γ-multifunctionality; Fig. 2*B*). However, we did not detect a significant relationship between β-diversity and sum-based γ-multifunctionality (Fig. 2*B*). This finding was likely due to trade-offs between ecosystem functions: Of the 120 possible pairwise correlations among functions, 50 were negative. This result made it impossible to
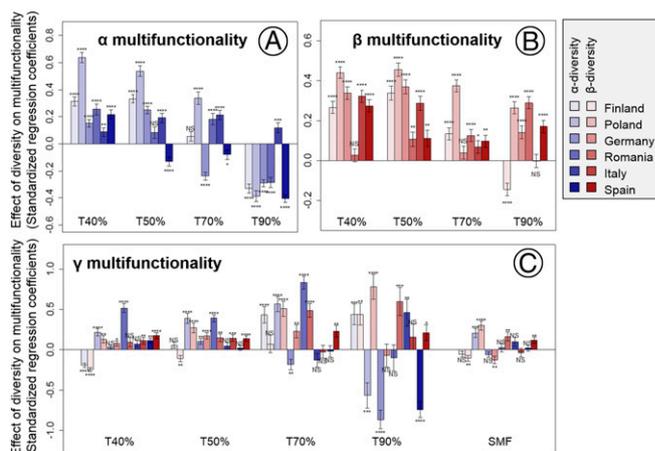
Fig. 3. Scale-dependent effects of biodiversity on forest ecosystem multifunctionality are generally consistent across countries. Bars represent the standardized regression coefficients of α-diversity (blue) and β-diversity (red) in LMMs explaining α- (*A*), β- (*B*), or γ- (*C*) multifunctionality. Multifunctionality was quantified at different scales using a threshold approach, with thresholds of 40%, 50%, 70%, and 90%. In addition, sum-based γ-multifunctionality was calculated as the sum of scaled (between 0 and 1) individual function values. Diversity measures were calculated based on individuals of target tree species.

achieve very high levels of all functions across the entire landscape. These results thus indicate that although β-diversity is not related to higher average levels of ecosystem functions, it is positively related to the number of functions that perform at high levels in at least part of the landscape. Hence, positive relationships between β-diversity and threshold-based β-multifunctionality (and hence threshold-based γ-multifunctionality) are caused by the fact that different species support different functions (5, 7). For example, in Polish forests, monoculture plots of the conifer *Picea abies* are related to high levels of many functions relating to the production of quality timber (e.g., timber quality, biomass production), whereas plots of the deciduous tree *Carpinus betulus* were of higher recreational and conservation value due to a high diversity of bats and understory plants (*SI Appendix*, Table S8). Hence, forest landscapes where some locations were dominated by *P. abies* and others by *C. betulus* provided more functions at high levels than those forest landscapes where all plots had the same tree species composition.

Our finding that the relationship between biodiversity and European forest γ-multifunctionality depends strongly on the way that multifunctionality is quantified has important implications for European forest management. In short, our results suggest that different patterns of tree species distribution would achieve different management goals (or "landscape multifunctionality scenarios"). The results of the threshold-based γ-multifunctionality analysis would be most relevant to situations where managers sought to promote forest landscapes with very high levels of ecosystem functioning in at least some (but not necessarily all) local patches (*sensu* 30). As described earlier, this situation may occur when managers seek to provide different ecosystem services in different localities. An example of such a landscape is one where some localities provide recreation or cultural services, such as aesthetic beauty and a diversity of charismatic taxa (31) (*SI Appendix*, section S3), whereas other localities maximize provisioning services that are only cost-effective when delivered at very high levels, such as production of high-value timbers (42), or form hotspots of certain biogeochemical functions that need to be strategically located, such as the minimization of nutrient runoff close to water bodies. In such scenarios, threshold-based γ-multifunctionality could be promoted in forest landscapes that possess a high turnover in community composition, but a low α-diversity (top left landscape in Fig. 1*C*), by promoting a range of different monocultures across the landscape. When the delivery of provisioning services is cost-effective at lower levels or when cultural or regulating services do not need to be at extremely high levels, one could aim to promote landscapes with moderate levels of many functions (40% or 50% threshold γ-multifunctionality). In this scenario, threshold-based γ-multifunctionality is highest in forests with both a high spatial turnover in community composition and a high local diversity of tree species (top right landscape in Fig. 1*C*). This finding is in line with Gamfeldt et al. (15), who hypothesized, based on local-scale analyses, that "adjacent stands, each with multiple species but in different combinations, might be the best way to provide multiple ecosystem services at the landscape scale." A third hypothetical scenario would be to maximize total delivery of services across the landscape (high sum-based γ-multifunctionality), rather than having highly localized specialist patches that deliver a limited number of services at very high levels. This scenario may be most relevant to cases where the primary goal of ecosystem management is to provide ecosystem services whose benefits are manifested at large scales, such as carbon sequestration (43). We found that neither α-diversity nor spatial turnover in community composition (β-diversity) had significant detectable relationships with γ-multifunctionality under this scenario. In summary, we demonstrate that the importance of different components of diversity for promoting γ-multifunctionality is likely to depend on management goals. Accordingly, stakeholder engagement is required to see where these situations apply in real forested landscapes. Further studies are also required to confirm that tree α- and β-diversity are causal drivers of the observed relationships and to see how important they are in comparison to

other potentially important factors in driving ecosystem multifunctionality in representative European forests.

In this study, some of the benefits of biodiversity for γ-multifunctionality may have been underestimated. Our study did not consider some of the spatiotemporal processes that occur in real forest landscapes [e.g., dispersal and movement of ecosystem service providers, species-environment matching, large-scale resource partitioning, spillover and subsidy of ecosystem services between neighboring patches (13, 44)]. These processes could promote ecosystem functioning in landscapes that possess a high spatial turnover in species composition even more than was detected here. For example, a forest resistant to herbivory might also reduce pest damage in adjacent forests by lowering populations of herbivores and preventing their movement into more vulnerable areas, thus strengthening the relationship between β-diversity and forest γ-multifunctionality. Future studies could explore these ideas by studying ecosystem multifunctionality in landscapes where ecological interactions between patches of differing diversity and composition are quantified.

Previous studies have demonstrated that local-scale (α-) biodiversity can boost multifunctionality in the real world, in addition to experimental ecosystems (8, 14–16). Here, we add evidence that both α- and β-diversity can also drive ecosystem multifunctionality at the landscape scale, and that the desired distribution of ecosystem functions across the landscape influences the importance of this relationship. Biotic homogenization is occurring worldwide at local, regional, and global scales (19–21). Similarly, current forest management often results in large areas of low species turnover. Our study is an important step forward in exploring the importance of this biotic homogenization for γ-multifunctionality. It shows that biotic homogenization may have negative, strong, far-reaching, and so far overlooked impacts upon the ecosystem services on which humanity depends, and that these impacts may be as strong as, or even stronger than, the impacts of local diversity loss.

Methods

Plot Selection. In total, 209 forest plots (each measuring 30 × 30 m) were established within the European FunDivEUROPE project (fundiveuropektp. boku.ac.at/). Because we were interested in the effects of tree species diversity on ecosystem functioning in mature forests (38), plot selection was aimed at mimicking the design of a biodiversity experiment, in which variation in environment is minimized and diversity is not confounded with composition, as in most observational studies of diversity. Hence, the design aimed to bridge the gap between controlled but very young tree diversity experiments and observational studies, where diversity can be strongly confounded with other factors.

Plots were located in six European countries, ranging from boreal to Mediterranean zones, and with each representing a major European forest type (38): Finland (28 plots, boreal forest), Poland (43 plots, hemiboreal forest), Germany (38 plots, temperate deciduous forest), Romania (28 plots, mountainous deciduous forest), Italy (36 plots, thermophilous deciduous forest), and Spain (36 plots, Mediterranean mixed forest) (*SI Appendix*, Fig. S1). Within countries, plots were located in a single region ranging in size from 5 × 5 km (Romania) to 150 × 150 km (Finland). In each country, between three and five regionally common target species were selected, 15 in total (*SI Appendix*, Table S1). Plots were then selected to differ as much as possible in richness of target species and so that almost all possible combinations of these target species were realized, a design that emulates the designs of biodiversity experiments (38). Richness levels of one, two, three, four, and five target species were replicated 56, 67, 54, 29, and 3 times, respectively, across countries, and most possible target species compositions were realized [additional details on the selection procedure are provided in the study by Baeten et al. (38)]. To achieve this goal, some admixture of nontarget species was unavoidable. However, on average, target species accounted for 93.75% of the individuals and 91.39% of the basal area, and they were always represented by more than two individuals (*SI Appendix*, Fig. S2). We therefore focus on using the richness of target species in our analyses, but we also tested for the effect of total (target + admixed) species richness (*SI Appendix*). Plot selection strictly avoided correlations between tree species richness and soil factors, as well as any spatial autocorrelation in diversity (38), by choosing plots that differed as little as possible in environmental factors (soil texture, depth, pH, and altitude) that could potentially confound diversity effects on multifunctionality. The diversity gradient

was therefore most likely a result of stochastic factors or differences in past management between plots.

Tree Diversity and Community Composition Data. Within each plot, all tree stems ≥7.5 cm in diameter at breast height were identified to the level of species and mapped (12,939 stems in total). Species richness was defined as the number of target species (*SI Appendix*, Table S1) with at least two individuals in a plot. We also calculated Pielou's evenness (45) for target tree species and the proportion of coniferous target trees. Because plots were specifically selected to have similar abundances of the target species, variation in evenness values across plots was low, with values above 0.6 in >90% of plots. In addition to richness, evenness, and the proportion of coniferous individuals of target species, we calculated richness, evenness, and proportion of coniferous individuals of all tree species for the purpose of sensitivity analyses.

We recorded diameter to the nearest 0.1 cm of each individual tree stem and measured height to the nearest 0.1 m. We used these diameter and height measurements to estimate the aboveground biomass of each individual tree, based on published allometric functions (ref. 46 and references therein). These functions were species-specific, and, whenever possible, functions developed for trees growing in forests similar to the forests of our study were used. Plot-level biomass estimates were calculated by summing the biomass of all individuals of the target tree species within a plot.

Environmental Data. We recorded the altitude of each plot as a proxy for variation in local climate. Soil pH was also measured because it is an important driver of numerous other soil properties (47). Between May and October 2012, forest floor litter (in nine 25 × 25-cm patches) and mineral soil (using a cylindrical metal corer from 0–10 cm in all countries and from 10–20 cm in all countries except Spain) were sampled for pH measurements, which were then measured using standard protocols (*SI Appendix*). Soil texture was also estimated using expert assessment as the abundance of sand (size), silt (size), and clay (size) content. Measurements were done on an ordinal scale, with values ranging from 1 (absent) to 3 (very common). Finally, soil depth (centimeter depth to bedrock) was measured in each plot using a soil auger.

Measurement of Ecosystem Functions and Properties. In each plot, 16 ecosystem processes, functions, or properties (termed functions hereafter) were measured between 2012 and 2014: timber quality, timber production, tree regeneration, root biomass, litter decomposition, wood decomposition, microbial biomass, soil carbon stock, resistance to drought, resistance to insect herbivory, resistance to mammal browsing, resistance to pathogens, bird diversity, bat diversity, understory plant diversity, and earthworm biomass. All measured ecosystem functions have established links to supporting, provisioning, regulating, or cultural services (*sensu* 9). Details about function measurements are available in *SI Appendix*, section S2, and details on the services they provide are available in *SI Appendix*, section S3. To allow comparison of the different ecosystem functions, they were scaled between 0 and 1:

$$SEF_i = \frac{EF_i - \min(EF)}{\max(EF) - \min(EF)},$$

with *SEF* indicating the final (scaled) ecosystem value; *EF* indicating raw (unscaled) ecosystem function values; and min/max(*EF*), respectively, indicating the minimum/maximum raw values of the ecosystem function.

Simulating Artificial Forest Landscapes. To analyze diversity and multifunctionality at different spatial scales, ranging from plots (α), to species turnover between plots (β), to landscape scales (γ), we simulated artificial forest landscapes from the observed forest plots. Within each country, we randomly selected, without replacement, five plots to create an artificial landscape and repeated this process 1,000 times. With six countries, we therefore created 6,000 artificial forest landscapes, with 5,981 unique plot combinations. The number of unique dominant tree species within countries was relatively small (up to five), and few plots contained all of these species; hence, creating landscapes from a relatively low number of plots ensured that landscapes varied as much as possible in both α- and β-diversity. Additional analyses showed that the compositions of these simulated landscapes are likely to be realized at the local regional scale (*SI Appendix*, section S5). Within each of these 5,981 unique landscapes, we then calculated tree diversity at two spatial scales. α-Diversity was defined as the average target species richness value across the plots. Turnover in tree community composition [i.e., β-diversity (48)] was calculated for each of the 10 pairs of plots within a landscape as follows: $\beta_{div} = 1 - (\log((A + B + 2C)/(A + B + C))/\log(2))$, where *A* and *B* are the number of target species unique to each plot and *C* is the number of target species shared by the plots (49). This measure is bound between 0 (no turnover) and 1 (complete turnover).

Landscape-level β-diversity was then calculated as the average of all 10 β-diversity values of pairwise plot combinations. γ-Diversity was calculated as the richness of all the target species present in at least one plot within the landscape. Note that γ-diversity (or threshold-based γ-multifunctionality; see below) is not strictly additively or multiplicatively partitioned into α- and β-diversity (or threshold-based α- or β-multifunctionality; see below), so that α-, β-, and γ-diversity can, to some extent, vary independent of one another. For sensitivity analyses, we also calculated α-, β-, and γ-diversity based on all tree species present (rather than target species only).

In the 5,981 artificial landscapes, we used two approaches to calculate multifunctionality measures, which correspond to different hypothetical management objectives. We calculated threshold-based α-, β-, and γ-multifunctionality in a way that is analogous to calculating α-, β-, and γ-diversity (Fig. 1) and also broadly analogous to a recent method for quantifying the temporal stability of ecosystem functioning at different spatial scales (50). Within plots, threshold-based multifunctionality was defined as the number of ecosystem function values that exceeded a minimum threshold:

$$MF = \sum_{i=1}^{n} \begin{cases} 1 \; SEF_i \geq T \\ 0 \; SEF_i < T \end{cases}$$

(10), in which *n* is the number of functions and *T* is the performance threshold value. Threshold values were defined as a certain percentage of the 95th percentile of maximum functioning (10) from the country in which plots were located. We chose to investigate diversity–multifunctionality relationships at four different multifunctionality thresholds: 40%, 50%, 70%, and 90%. In plots with one ($n = 28$), two ($n = 1$), or three ($n = 1$) missing ecosystem function values, threshold-based multifunctionality scores were corrected by accounting for the proportion of nonmissing functions:

$$TMF = \left(\sum_{i=1}^{n} \begin{cases} 1 \; SEF_i \geq T \\ 0 \; SEF_i < T \end{cases} \right) \cdot \frac{n}{n\_c},$$

where *TMF* is threshold-based multifunctionality, n_c is the number of nonmissing functions, and *n* is the total number of functions measured in this study. Threshold-based α-multifunctionality was then calculated as the average *TMF* value across the five plots comprising a landscape. Threshold-based β-multifunctionality was calculated as the turnover in ecosystem functions present (i.e., exceeding a threshold) across plots comprising a landscape, with the same formula as was used for β-diversity (see above), but this time with *A* and *B* representing functions exceeding the threshold in either the first or second plot and *C* representing the ecosystem functions that exceed the threshold in both plots. Lastly, threshold-based γ-multifunctionality was measured as the number of ecosystem functions exceeding a 40%, 50%, 70%, or 90% threshold value in at least one of the five plots within each landscape.

In addition to the threshold-based approach, we calculated γ-multifunctionality based on a summing approach [broadly similar to the approach used by Maestre et al. (14)]. To calculate sum-based γ-multifunctionality, we first summed the five plot-level values for each function. These summed landscape-level function values were then scaled between 0 and 1 ($[(EF - \min(EF))/(\max(EF) - \min(EF))]$). To calculate sum-based γ-multifunctionality, we then summed the scaled values of the 16 functions. In contrast to biodiversity and threshold-based multifunctionality, sum-based multifunctionality is quantified using continuous variation in function values, rather than "presence/absence data" (of species or functions passing a threshold), making it impossible to partition it into α- and β-components.

In the landscapes, we also quantified factors that potentially affect relationships between diversity and multifunctionality: average values of target species evenness, the proportion of coniferous tree individuals, sand content, clay content, soil depth, soil pH, and altitude. In addition, we calculated environmental heterogeneity in two steps. First, we quantified the heterogeneity of individual abiotic factors (altitude, pH, and soil texture) as the coefficient of variation (CV) of values across plots within a landscape. In the case of soil texture, heterogeneity was quantified as the sum of CV values of clay, silt, and sand content. Next, these three heterogeneity measures were Z-transformed and summed to produce a single measure of environmental heterogeneity. By using Z-scores, we ensured that each abiotic variable had an equal impact on total environmental heterogeneity. All analyses were done with R version 3.0.2 (48).

Statistical Analyses. We first investigated whether α- and β-diversity in simulated forest landscapes was associated with γ-multifunctionality using linear mixed models (LMMs). Although we designed our study to minimize variation in environmental factors, completely eliminating any variation in these environmental factors was impossible (*SI Appendix*, section S3). Hence, to avoid the detection of spurious diversity–multifunctionality relationships, we included these

environmental factors as covariates in the LMMs. We performed three different LMM analyses. In the first, we investigated how α-multifunctionality was driven by α-diversity, using an LMM with α-multifunctionality as the response variable, species richness as the focal fixed factor, species evenness, proportion of evergreen trees, altitude, soil depth, soil pH, soil sand and clay content, and their two-way interactions as covariates, and with country as a random factor. In the second analysis, we investigated the relationship between β-multifunctionality and β-diversity, using an LMM with β-multifunctionality as the response variable, β-diversity as the focal fixed factor, environmental heterogeneity as a covariate, and country as a random factor. In the third analysis, we investigated how γ-multifunctionality was affected by both α- and β-diversity, by first constructing a full LMM with γ-multifunctionality as the response variable; α- and β-diversity as the focal fixed factors; species evenness, proportion of evergreen trees, altitude, soil depth, soil pH, soil sand and clay content, environmental heterogeneity, and their bivariate interactions as covariates; and country as a random factor. As a result of the careful study design, diversity measures were largely independent of the covariates (38): Correlations between focal predictors and covariates were always <0.230, whereas the correlation between α- and β-diversity was moderate ($R^2 = 0.316$, $P < 0.0001$); hence, there was no strong indication of multicollinearity. In all three analyses, we used a backward model-selection analysis to remove covariates sequentially (based on ratio-likelihood tests with a Bonferroni correction) until we reached a final model with only the focal fixed factor(s) and significant covariates. From this final model, we quantified the significance of α- and β-diversity in driving multifunctionality using likelihood ratio tests, and we also quantified their standardized regression coefficients. All analyses were performed for all different threshold-based and sum-based multifunctionality variables. As a robustness check, we also repeated all these analyses with predictors and covariates based on all tree species, rather than on target species only (*SI Appendix*). In addition, to investigate how general the main patterns were across countries, we ran linear models for each country separately, with the same fixed factors in models as in the finally selected LMMs. All analyses were performed using R version 3.0.2 (51). LMMs were fitted using the "lmer" function of the "lme4" library (52). Given that effects of covariates were variable and complex, and that the main focus of this study was on biodiversity effects, the effects of covariates are not presented here (effect sizes of all covariates are shown in *SI Appendix*, Tables S2–S4).

In addition to LMMs, we used structural equation models to investigate relationships between biodiversity and multifunctionality, to test the sensitivity of our results to the statistical method used, and to test for indirect relationships between biodiversity and multifunctionality (*SI Appendix*, section S4).

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