Functional rarity and evenness are key facets of biodiversity to boost multifunctionality

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The functional traits of organisms within multispecies assemblages regulate biodiversity effects on ecosystem functioning. Yet how traits should assemble to boost multiple ecosystem functions simultaneously (multifunctionality) remains poorly explored. In a multibiome litter experiment covering most of the global variation in leaf trait spectra, we showed that three dimensions of functional diversity (dispersion, rarity, and evenness) explained up to 66% of variations in multifunctionality, although the dominant species and their traits remained an important predictor. While high dispersion impeded multifunctionality, increasing the evenness among functionally dissimilar species was a key dimension to promote higher multifunctionality and to reduce the abundance of plant pathogens. Because too-dissimilar species could have negative effects on ecosystems, our results highlight the need for not only diverse but also functionally even assemblages to promote multifunctionality. The effect of functionally rare species strongly shifted from positive to negative depending on their trait differences with the dominant species. Simultaneously managing the dispersion, evenness, and rarity in multispecies assemblages could be used to design assemblages aimed at maximizing multifunctionality independently of the biome, the identity of dominant species, or the range of trait values considered. Functional evenness and rarity offer promise to improve the management of terrestrial ecosystems and to limit plant disease risks.

complex species assemblages | litter decomposition | nutrient cycling | plant pathogens | trait distributions

Biodiversity is of pivotal importance for maintaining ecosystem functions, such as primary productivity, litter decomposition, or soil nutrient cycling, and for preventing disease risks (1–4). Despite the important advances in our understanding of the role of biodiversity in natural and managed ecosystems, we still ignore how the physiological, morphological, and biochemical characteristics of species—their functional traits—should assemble to boost multiple functions simultaneously [multifunctionality (5)]. Uncovering the trait assemblages that promote high multifunctionality is critical to identify baselines that track the consequences of biodiversity loss on ecosystems, to undertake effective restoration actions, or to engineer the species assemblages of managed ecosystems that promote biodiversity and high multifunctionality in a changing world.

The relationship between functional traits and multifunctionality has been shown to vary from positive to negative depending on the ecosystem, species pool, and biogeographical context considered (6–8). Such a high context dependency may largely depend on how functional traits are assembled within communities (9). While the traits of dominant species (hereafter referred to as functional dominance) can strongly determine individual ecosystem functions (10), their role becomes less clear when considering multifunctionality (7, 11). This is so because in an ecosystem, species that are functionally different from the dominant ones—functional diversity—may contribute more to certain key functions than their lower abundance would suggest (7, 11, 12). High functional diversity—through the dispersion of trait values (hereafter referred to as functional dispersion) or the

Significance

Identifying species assemblages that boost the provision of multiple ecosystem functions simultaneously (multifunctionality) is crucial to undertake effective restoration actions aiming at simultaneously promoting biodiversity and high multifunctionality in a changing world. By disentangling the effect of multiple traits on multifunctionality in a litter decomposition experiment, we show that it is possible to identify the assemblages that boost multifunctionality across multiple species mixtures originating from six biomes. We found that higher evenness among dissimilar species and the functional attributes of rare species as key biodiversity attributes to enhance multifunctionality and to reduce the abundance of plant pathogens. Our study identifies those species assemblages needed to simultaneously maximize multifunctionality and limit plant disease risks in natural and managed ecosystems.

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presence of species with infrequent trait values (hereafter referred to as functional rarity)—for instance, in the case of keystone species—may enhance multifunctionality (9) if functionally dissimilar species exploit or release contrasting resources or the same resources but at different spatial or temporal scales (1). However, if species become too dissimilar, this could lead to strong negative effects on ecosystems (e.g., in the case of invasive species adding a new set of trait values) (6, 7, 13). In the later case, higher evenness among functionally dissimilar species (hereafter referred to as functional evenness) could promote synergistic interactions and counteract such negative biodiversity effects on multifunctionality (6, 7). However, functional dominance, dispersion, rarity, and evenness often covary in real-world ecosystems (14), hindering the evaluation of their individual effect on multifunctionality (6, 14, 15). A manipulative study revealing which trait assemblages could boost positive biodiversity effects on multifunctionality across multiple ecosystems is yet lacking.

The distribution of trait values (hereafter referred to as trait distribution) within complex, multispecies assemblages often deviates from the symmetric normal distribution, classically assumed in ecological studies (14, 15). While the mean and the variance allow for characterization of the functional dominance and dispersion of a normal distribution, the skewness and kurtosis offer insights on the shape of the complex trait distributions encountered in naturally assembled communities (6, 14, 15). The skewness represents the asymmetry of the distributions. High negative or positive values of skewness occur when trait distributions are strongly left or right tailed as a result of rare species with infrequent trait values compared with the bulk of the distribution: a definition of functional rarity. Kurtosis represents the relative peakiness of trait distribution, where a low kurtosis value reflects functionally even distributions. Investigating complex trait distributions thus offers a unique opportunity to decipher the interplay of functional dominance, dispersion, rarity, and evenness in determining multifunctionality and represents a fundamental step toward the design and management of species assemblages that could maximize biodiversity effects on ecosystems.

Here, we present results from a multibiome experiment examining how the functional dominance, dispersion, evenness, and rarity of plant litter assemblages influence multifunctionality and soil microbial communities. We manipulated complex trait distributions to disentangle the influence of the four biodiversity attributes, while species richness (n = 15 species each) and total litter biomass (1 g) were kept constant among litter assemblages. We assembled 570 experimental leaf litter mixtures and monocultures using 90 species from six biomes covering a wide range of the global variability of two key plant functional traits (Specific Leaf Area [SLA] and lignin content) (16, 17) and tracked changes in multifunctionality and soil microbial communities as litter decomposed (Fig. 1; see also *Methods* and *SI Appendix*, Tables S1 and S2 and Figs. S1 and S2). We used a single decomposition environment (i.e., one soil type and controlled climatic condition) to avoid variations due to differences in decomposer communities, soil parameters, and climate. Leaf litter assemblages were set up using a set of 120,000 simulated functional trait distributions (see *Methods* and *SI Appendix*, Figs. S3 and S4). Then, we selected a subset of 570 assemblages that covered the entire range of values that functional dominance and diversity could take while minimizing their correlations within and across biomes (*SI Appendix*, Table S3 and Fig. S4). We calculated multifunctionality using nine litter and soil functions related to carbon (C), nitrogen (N), and phosphorus (P) cycling (see *Methods* and *SI Appendix*, Fig. S5). We also addressed the relative abundance (fungal trophic modes) and diversity of soil bacteria and fungi. Monitoring changes in litter decomposition, soil processes, and microbial communities thus allowed us to consider a part—albeit a functionally important part—of whole ecosystem functioning. We tested the core hypothesis that functionally dispersed and highly even trait distributions are the litter trait assemblages to maximize multifunctionality.

Results and Discussion

Dispersion, rarity, and evenness accounted for, on average, 52.8% of explained variance across multifunctionality thresholds (Fig. 2), although functional dominance remained an important predictor. These results were robust to the statistical modeling approach used (see *Methods* and *SI Appendix*, Fig. S6). Our results highlight that the contribution of the three dimensions of functional diversity to multifunctionality is as important as, and in some cases, overwhelms that of functional dominance. Furthermore, the percentage of explained variance driven by these three dimensions increased at higher multifunctionality thresholds (from 42 to 66%; Fig. 2) due to the increased effect size of evenness when functions were performing at a high rate (from 9 to 30%). Functional diversity also accounted for a fair amount of explained variance across individual functions (from 18 to 67%), notably soil enzymatic activities, N transformation rates, and N pools (Fig. 2 and *SI Appendix*, Table S4). Litter assemblages with high mean lignin values decreased multifunctionality (standardized parameter estimate [est] = -0.136 ± 0.012, $P < 0.001$; Fig. 3). This result brings evidence supporting the role of litter lignin concentration within multispecies assemblages as a key regulator of C and N turnover in terrestrial ecosystems (18). Experimentally deciphering the four functional attributes reveals that they all contribute to multifunctionality and individual functions to a similar extent. Therefore, our study warns of the need to consider multiple dimensions of functional diversity, such as the overlooked functional rarity and evenness (14), to maximize multifunctionality.

The functional dispersion of SLA values has a consistent and significant negative effect on multifunctionality (est = -0.024 ± 0.008, $P = 0.05$, Fig. 3), representing a cross-biome experimental validation of the results previously observed in real-world dryland ecosystems (6, 7). In contrast, we observed a negative relationship between kurtosis SLA and multifunctionality (est = -0.036 ± 0.007, $P = 0.003$; Fig. 3). This supports the core hypothesis that higher functional evenness in litter communities enhances multifunctionality and reminds of the role of species evenness for litter decomposition [e.g., (2, 19)]. Functional diversity is increasingly used in biodiversity and ecosystem functioning research (6, 9, 20), albeit it is often associated with dispersion. Our results clearly point to the evenness of trait assemblages, not dispersion, as the key functional diversity dimension promoting positive effects on multifunctionality. Overall, we found that higher evenness of functionally dissimilar species can boost ecosystem functioning, but too dissimilar species assemblages can strongly impede multifunctionality. Our findings suggest that trait differences can be optimized in multispecies assemblages by simultaneously managing the dispersion and evenness of trait distributions, and this could aid in maximizing multifunctionality.

We also observed a strong negative effect of skewness lignin on multifunctionality (est = -0.049 ± 0.01, $P = 0.007$; Fig. 3). The presence of functionally rare species—those with infrequent litter lignin content—can thus either positively or negatively influence multifunctionality. On the one hand, the presence of rare but highly decomposable species with low lignin content relative to the bulk of the assemblages (negatively skewed distributions of lignin) promoted multifunctionality. These species also promoted positive biodiversity effects on soil microbial respiration (*SI Appendix*, Fig. S7). For instance, tropical assemblages were dominated by species with highly recalcitrant litter (Fig. 1, mean litter lignin = 31%). In this biome, the presence of litter from functionally rare species such as *Mabea nitida* (litter lignin = 11%) promoted soil microbial respiration through significant positive synergetic effects and litter C and N loss (*SI Appendix*,

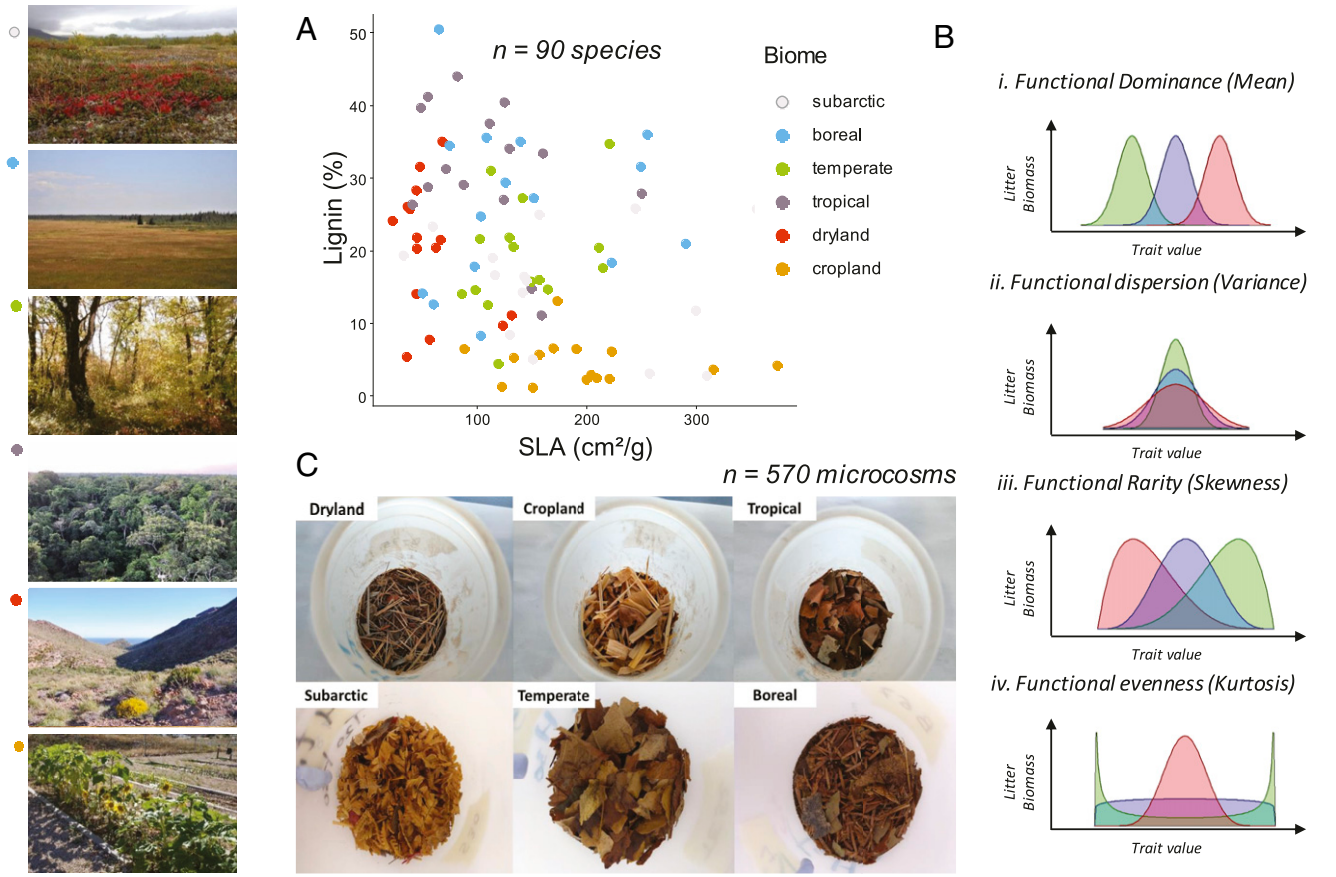

Fig. 1. The experimental and analytical framework to test the effects of dominant species and their traits (dominance) and of functional diversity (dispersion, rarity, and evenness) on multifunctionality. (*A*) The SLA and leaf litter lignin content of 90 species from six biomes covering a wide array of the global variation in the traits observed (see also *SI Appendix*, Table S2). (*B*) Disentangling functional dominance, dispersion, rarity, and evenness by manipulating the mean, variance, skewness, and kurtosis of trait-abundance distributions. (*C*) The microcosms containing the leaf litter communities (photographs by J.H.C.C, L.D., N.G., N.S., and R.M.).

Table S4 and Fig. S7). The lignin:N ratio of *M. nitida* (4.26), which is the lowest among the studied tropical species (mean lignin:N ratio = 22.44), suggests that priming effects and/or litter nutrient transfer are potential mechanisms driving the observed effects of skewness lignin in microcosms from the tropical biome (3, 21). On the other hand, the presence of litter from rare but highly recalcitrant species with high lignin content (positively skewed distributions of lignin) significantly reduced multifunctionality (Fig. 3). For example, cropland litter assemblages were dominated by highly decomposable species (Fig. 1, mean litter lignin = 5%). In this biome, functionally rare species such as *Sesamum indicum* (litter lignin = 13%) inhibited soil microbial respiration and multifunctionality (*SI Appendix*, Table S4 and Fig. S7), likely due to the presence of condensed tannins forming recalcitrant complexes with proteins that are difficult to access by decomposers (22). Beyond illustrating the contribution of functionally rare species to litter decomposition rates and soil nutrient cycling across biomes, our study shows that it is the functional profile of rare species compared to that of dominant ones that plays a key role in regulating rarity effects on multifunctionality.

The three dimensions of litter functional diversity accounted for >70% of explained variance in soil fungal diversity and the relative abundances of soil fungal pathogens and saprotrophs (Fig. 2). However, soil bacterial diversity was unaffected by litter functional diversity (*SI Appendix*, Table S5), which may be the result of the less-efficient colonization of heterogeneous environments such as litter mixtures by bacteria compared with fungal mycelial networks. Interestingly, lower-kurtosis lignin decreased fungal pathogens (est = 2.263 ± 0.532, $P < 0.001$; *SI Appendix*, Table S5). This result indicates that higher functional evenness in leaf litter lignin content drastically reduced the abundance of plant pathogens, irrespective of the average leaf lignin content. Lignification is a traditional mechanism for disease resistance in plants (23). Our results provide insights for the still-debated "dilution effect" (24), where higher functional evenness among host species appears as a key biodiversity attribute to reduce disease risk (4) independently from the average amount of lignin present in litter mixture. We also observed a trend for negative relationships between kurtosis lignin, fungal diversity, and saprotrophs. Soil fungal communities were dominated by taxa from the Ascomycota and Basidiomycota phyla (72 and 23% of sequences, respectively; *SI Appendix*, Fig. S8), which perform their primary ecological role as decomposers (25). Fungal saprotrophs are considered the key microbial players in litter decomposition because of their ability to produce a wide range of extracellular enzymes needed to breakdown litter (26). Similarly, higher evenness of SLA also promoted (positive) biodiversity effects on soil microbial respiration (i.e., negative effect of kurtosis SLA biodiversity effect on cumulative soil respiration [BE_CO2)]; est = −0.038 ± 0.01, $P < 0.001$; *SI Appendix*, Table S4 and Fig. S7), suggesting that an even array of leaf litters could promote resource partitioning among soil organisms or leverage N limitation during litter decomposition (27). Our results highlight a linkage at the interface between

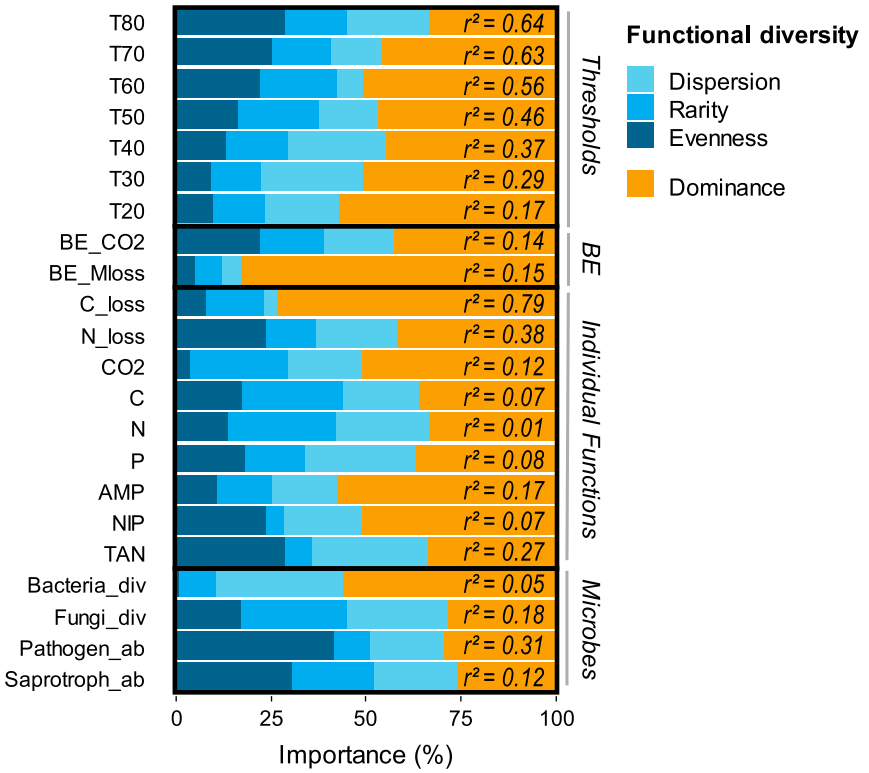

Fig. 2. The contribution of functional diversity and dominance to multifunctionality thresholds, individual (litter and soil) functions, and soil communities. The importance of predictors is expressed as the percentage of explained variance (model R^2 express total variances), taken as the absolute value of their standardized regression coefficients. The effects of the trait-abundance distribution for specific leaf area and litter lignin content were summed for each predictor. T = multifunctionality-thresholds; BE_Mloss = biodiversity effect on mass loss, C/N_loss = absolute litter C and N loss; CO_2 = cumulative soil respiration; BE_CO2 = biodiversity effect on cumulative soil respiration; C/N/P_enz = soil enzymatic activities related with C, N, and P cycling; AMP/NIP = soil ammonification and nitrification rates; TAN = total soil available nitrogen; B/F_div = soil bacterial and fungal diversity; and P/S_ab = relative abundance of soil fungal pathogens and saprotrophs.

above and belowground communities, whereby evenness in trait assemblages, independent of species richness and dominant plant types, can increase soil microbial diversity and activity and reduce risks of soil fungal diseases.

We finally showed that manipulating the relative abundances of trait values in multispecies assemblages can be used to promote a specific ecosystem function or multifunctionality as a whole. To illustrate this finding, we first predicted the effects of functional dominance and dispersion on multifunctionality and soil microbial respiration (Fig. 4). Then, we quantified the effect of adding functional evenness and rarity to this prediction. We found that higher functional evenness in litter assemblages increased multifunctionality at any litter lignin value and beyond the effects of functional dominance and dispersion (Fig. 4, Top). Rarity further enhanced multifunctionality at high lignin content, but the opposite was found at low lignin levels. The pattern found when addressing biodiversity effects on soil microbial respiration (Fig. 4, Bottom) suggests that synergistic and antagonistic biodiversity effects mediate functional rarity effects on multifunctionality. Adding few, but functionally labile, litter fragments to recalcitrant litter mixtures had a positive effect on multifunctionality of a similar magnitude as decreasing the litter lignin content from 12 (subarctic biome) to 3% (cropland biome). Our results highlight that considering multiple dimensions of functional diversity can help to pinpoint the litter trait assemblages that boost positive biodiversity effects on ecosystems without the need to increase the number of species, the range of trait values, or change the identity of dominant plant type (Fig. 4). These findings offer perspectives to improve a variety of agricultural and ecosystem restoration programs by means of promoting multifunctional species assemblages. For instance, incorporating functional rarity and evenness into new plant breeding programs might help to offset the side effects of plant domestication that have reduced the ability of crop mixtures to benefit from biodiversity effects (28) and their resistance to pathogen infection (29). Furthermore, the maximization of functional evenness when restoring dryland ecosystems threatened by ongoing climate change may help to prevent land degradation and desertification processes (6).

Conclusion

Using a multibiome litter experiment covering most of the global variation in leaf trait spectra, we identified functional rarity and evenness as key dimensions to maximize biodiversity effects on ecosystems. Our results on the effects of litter assemblages on terrestrial ecosystems pave the way for further research efforts to extend our experimental framework to living assemblages. This work highlights that trait assemblages that boost biodiversity effects across biomes can be identified and managed to promote specific ecosystem functions or multifunctionality as a whole. Since more than 50% of net primary production is returned to the soil via litter decomposition (30), our study demonstrates that considering the complexity of trait assemblages may improve our ability to anticipate the functional consequences of biodiversity loss on ecosystems.

Methods

Sampling Locations. We sampled leaf litter from six biomes that are representative of a wide array of the following climate conditions found on Earth:

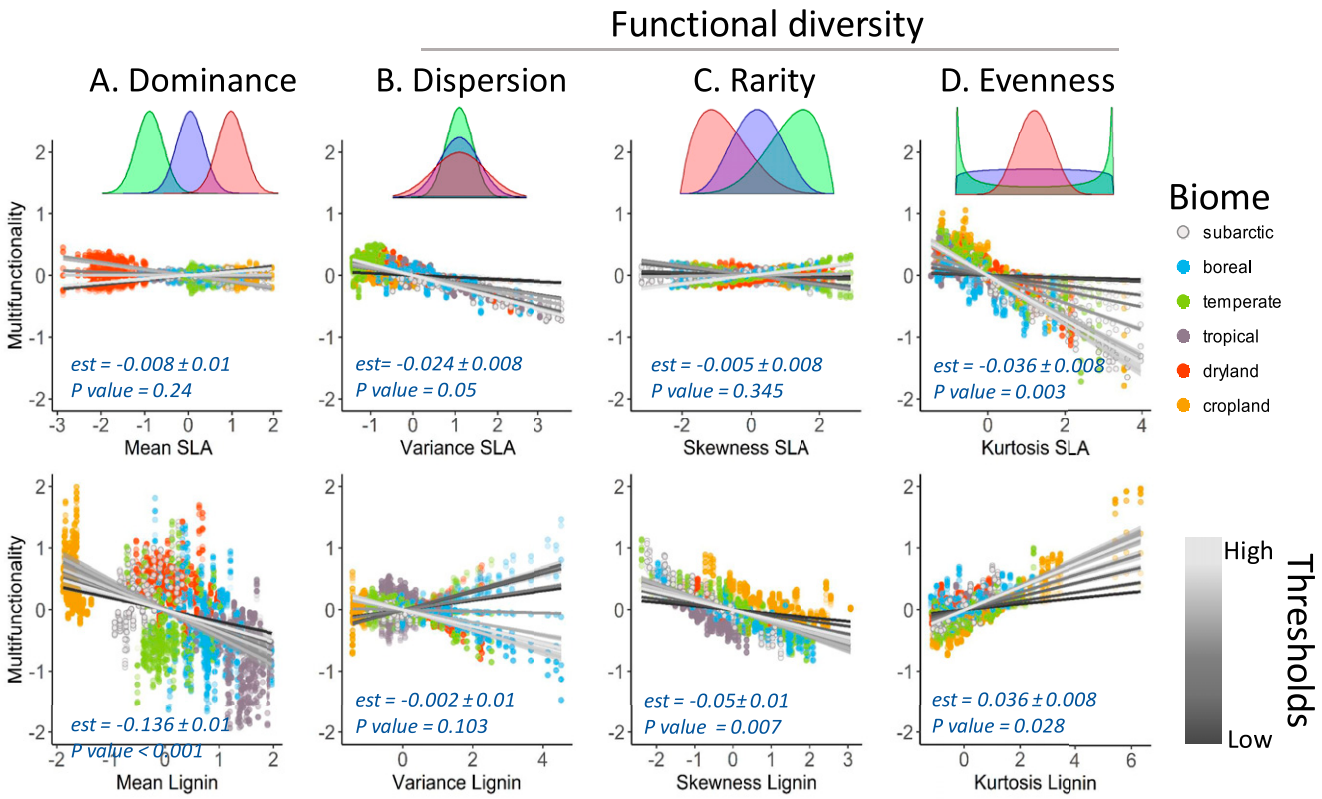

Fig. 3. The effects of functional dominance (*A*), dispersion (*B*), rarity (*C*), and evenness (*D*) on multifunctionality. The dark to light gray lines show model fits with increasing thresholds. The dots represent model partial residuals. We provide for each predictor the averaged parameter estimates (est) across thresholds ±SD and the *P* value.

tropics, cropland, dryland, temperate, boreal, and subarctic (Fig. 1 and *SI Appendix*, Table S1). Sampling was performed in 2017 in five countries (Canada, France, Peru, Spain, and Sweden) and a range of locations, which widely differed in climate conditions (mean annual temperature and precipitation ranged from 0.4 to 18.1 °C and from 352 to 1,840 mm, respectively).

Leaf Litter Collection and Trait Measurements. Freshly fallen leaf litter from 15 species was collected in each biome, totalling 90 species (Fig. 1 and *SI Appendix*, Table S2). The species selection included the representative vegetation at each location and comprised typical grasses, shrubs, and trees for each biome. Leaf litter material was air dried for 2 wk and shipped to Rey Juan Carlos University for analyses and litter decomposition assays. Leaf litter with signs of herbivory or disease was discarded, and all material was mixed at the species level to get a homogeneous species litter pool. To characterize the functional profile of litters, we focused on the SLA and leaf lignin content, which are key drivers of litter decomposability (18, 31). The SLA ($cm^2 \cdot g^{-1}$), calculated as the ratio between leaf area (cm^2) and leaf dry mass (g), discriminates acquisitive/conservative plants and is associated with high leaf nutrient content (16). High SLA correlates with high litter decomposition (32) and bacterial-dominated soil microbial communities (33). SLA is thus a good candidate to scale up plant diversity and multifunctionality (6, 7). Alternatively, litter lignin (% of leaf dry mass) protects labile compounds from microbial attack in plant cell walls (17). Litters with high lignin content are associated with low accessibility to nutrients, low litter decomposition rates, and slow nutrient cycling (18). Lignified leaves are associated with fungal saprotrophs producing a wide range of extracellular enzymes needed to breakdown their litter into biologically usable forms (34). We measured the SLA of each species on fresh green leaves of five plant individuals, calculated as the ratio between leaf area (cm^2) and leaf dry mass (g). Leaf lignin content (%) was analyzed following van Soest (35) using 1 g of grounded leaf litter. Using 90 species from five natural and one managed ecosystem allowed us to cover a wide range of the land spectra observed for the two traits evaluated (Fig. 1). The selected spectrum of SLA values ranged from 23 to 373 $cm^2 \cdot g^{-1}$, approximating the range covered by 90% of the species measured in global terrestrial systems (16). Leaf litter lignin values ranged from 1 to 51% and encompassed the classically assumed global range of leaf litter lignin (10 to 40%) and extremes (17).

Plant Functional Dominance and Diversity. We tested the effects of functional dominance and diversity (dispersion, rarity, and evenness) on multifunctionality by manipulating the trait distributions of SLA and litter lignin content. To do so, we focused on the four moments of the trait-abundance distributions of litter communities: the mean, the variance, the skewness, and the kurtosis. The mean of a trait-abundance distribution reflects the trait of the dominant species while the variance quantifies the dispersion of trait values (i.e., how far trait values are spread around their mean). The skewness and kurtosis complement the mean and the variance by describing the shape of the distribution (i.e., how species abundances are distributed within communities as a function of their trait values). Skewness measures the asymmetry of the distribution. High negative or positive values of skewness occur when trait-abundance distributions are strongly left or right tailed, respectively; it highlights the presence of a few rare species with extreme trait values compared with the bulk of the distribution. Kurtosis measures the relative peakiness of the trait-abundance distribution and the heaviness of its tails. Low kurtosis reflects an even distribution of trait values within the community.

Investigating the effect of the four moments of the trait distribution on multifunctionality require rigorous experimental design because the mean, variance, skewness, and kurtosis are not mathematically independent (6, 36, 37). For instance, the mean trait value increases when a trait distribution becomes positively skewed for a given number of species and range of trait values. Similarly, a negative correlation between the variance and the kurtosis of trait distributions can occur when considering a fixed number of species. To overcome these mathematical constraints, we selected six species pools originating from six biomes, rendering the mean and the variance independent from skewness and the kurtosis. Additionally, our experimental design took advantage of the existing inequality between the skewness and the kurtosis that can be used to characterize complex trait distributions deviating from the normal distribution (*SI Appendix*, Fig. S3).

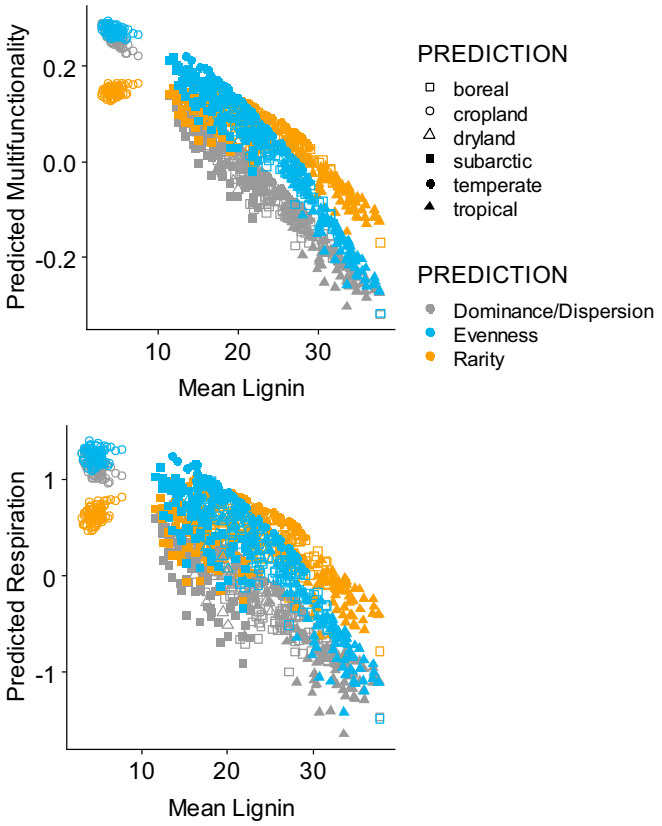

Fig. 4. Identifying which functional attributes of plant litter assemblages boost biodiversity effects on multifunctionality. We investigated the effects of the following: 1) functional dominance and dispersion (gray dots); 2) dominance and dispersion + evenness (blue dots); and 3) dominance, dispersion, evenness + rarity (orange dots) for multifunctionality and for the biodiversity effects on BE_CO2. The predictions are based on the standardized regression coefficients of model predictors averaged across thresholds. For simplicity, we only predicted the effect of lignin content while fixing the effect of SLA to its mean value.

We manipulated the relative abundances of each of the 15 species of each biome to simulate 120,000 trait-abundance distributions encompassing all types of possible trait distributions (from symmetric to heavily skewed distributions and from bimodal to highly leptokurtic distributions; Step 1 in *SI Appendix*, Fig. S4). From the simulated trait-abundance distributions per biome (20,000), we selected the subset of 80 that minimized the correlations among all moments within and across biomes (Step 2). From the final litter mixture selection (Step 3), litter weights were used to establish the relative abundances of species prescribed in the simulations. The 15-species assemblages were fixed at a total litter dry weight of 1,000 mg (38). We also fixed a minimum litter fragment weight per species of 10 mg for the sake of litter manipulation. Litter weights thus ranged between 10 and 860 mg (1,000 mg – 14 species × 10 mg) for all species within each simulated trait-abundance distribution. The selected litter assemblages covered a wide range of litter types (community-mean SLA ranged from 33.1 to 279.2 $cm^2 \cdot g^{-1}$ and community-mean lignin ranged from 2.92 to 37.83 $g \cdot g^{-1}$) and all possible types of trait-abundance distributions. The final selections included 570 litter assemblages (480 litter mixtures of 15 species each [80 litter mixtures per biome; *SI Appendix*, Fig. S9] + 90 species in monocultures). The selection of litter assemblages minimized the correlations between the four moments of the trait-abundance distributions for SLA and lignin content and allowed us to experimentally test their relative contribution to multifunctionality.

Litter Decomposition Assay. We set up the 570 litter assemblages + soil microcosms and incubated them for 88 d in growth chambers at optimal conditions for the decomposition process (darkness, 20 °C, and 95% air humidity). To do that, we collected soil to 10-cm depth in an open grassland dominated by *Stipa tenaccisima* in Central Spain. The soil is a Lithic Calciorthid (39) with pH = 7.6, sand content = 72%, clay content = 10%, organic C = 2.74%, total N = 0.27%, NO_3^- –N = 9.37 mg · N · kg^{-1} dry weighted (dw) soil, and NH_4^+ –N = 14.84 mg · N · kg^{-1} dw soil. The soil was sieved at 2 mm and homogenized to a get a single pooled sample across all litter assemblages. The soil was stored fresh at 4 °C for 1 wk during the setup of microcosms. A total of 60 g of sieved fresh soil were introduced into 250-mL plastic jars (9 cm high, 6-cm diameter) and soil moisture was adjusted to 60% water-holding capacity, which is favorable for microbial activity. To simulate a natural soil layer and favor soil microbial colonization, leaf litter was cut in fragments if leaf size was larger than the microcosm's area (*SI Appendix*, Figs. S1 and S2). Microcosms were incubated uncapped but covered with parafilm to minimize water losses but to allow CO_2 exchange with the atmosphere. To maintain a 60% water-holding capacity, soil moisture was checked every 2 wk, and deionized water was added when necessary 2 d before respiration measurements were taken. The microcosms were randomly distributed across four growth chambers, and their location among and within chambers was randomized every 2 wk to avoid potential temperature and moisture gradients within the growth chamber.

Litter decomposability was estimated by monitoring the microcosms' respiration rates over the incubation period, as they are a good proxy of soil microbial activity (40). We calculated the soil cumulative respiration as the amount of CO_2 respired by soil microbial communities decomposing plant litter over the incubation period. Specifically, we measured the CO_2 rates daily during the first week, once a week from weeks 2 through 5, and then every 2 weeks until the end of the incubation. To measure CO_2 concentrations, we used a high-throughput colorimetric method coupled with a 96-well microplate reader (38). Absorbance at 595 nm was converted into CO_2 concentration (%) using a calibration curve with gas chromatography (R^2 = 0.86) and then transformed into CO_2 production rate (μg CO_2-C · g^{-1} dw soil h^{-1}) using gas constants, incubation temperature (20 °C), headspace volume, and soil dry weight (41). We used linear interpolations between sampling dates and then summed them across all dates to estimate the soil cumulative respiration over the incubation period. After the last CO_2 measurement was performed, the remaining litter material and the soil were retrieved from the microcosms to analyze the rest of the litter and soil functions. The litter was dried at 60 °C, weighed as ash-free litter mass, and ground to fine powder with a ball mill. The soil was immediately separated into two different subsamples after retrieving litters: one was air dried for 2 wk and stored until the analysis of soil functions, and the other was stored at −20 °C until DNA extraction.

We evaluated the biodiversity effects (BE) on soil cumulative respiration and litter mass loss. We calculated BE as follows:

$$\text{Mixture}_{exp} = \text{sum}\left(\text{Monoculture}_{obs} * \text{relative abundance of Mixture}\right) \quad [1]$$

$$\text{BE} = \left(\text{Mixture}_{obs} - \text{Mixture}_{exp}\right)/\text{Mixture}_{exp} \quad [2]$$

where positive values of BE indicate higher soil respiration/litter mass loss than expected from monocultures (synergetic biodiversity effects), and negative values indicate lower soil respiration/litter mass loss than expected from monocultures (antagonistic biodiversity effects)

Litter and Soil Functions. Leaf litter C and N concentrations were analyzed with an elemental analyzer (FlashEA 1112, Thermo-153 Finnigan). We assessed two litter functions as the major outcome of the litter decomposition process: C mineralization and N immobilization/release patterns (27). To do that, we calculated litter C and N loss (%) as 100 × [(Mi × CNi) − (Mf × CNf)]/(Mi × CNi)], where Mi and Mf are the initial and final litter dry mass, respectively, and CNi and CNf are the initial and final C or N concentration (% of litter dry mass).

We analyzed multiple enzyme activity rates and N cycling rates as soil functions. First, we determined the potential activity of five extracellular enzymes: β-1,4-glucosidase (BG; starch degradation), β-D-cellobiohydrolase (CBH; cellulose degradation), β-1,4-*N*-acetylglucosaminidase (NAG; chitin degradation), L-leucine aminopeptidase (LAP; protein degradation), and acid phosphatase (PHOS; phosphorus mineralization). Soil enzyme activities (nanomol [nmol] activity g^{-1} dw soil h^{-1}) were assessed fluorometrically and using 4-methylumbellfferone and 7-amino-4-methylcoumarin to produce the standard curves. Integrated C and N enzyme activity were computed as BG + CBH and NAG + LAP, respectively, and then multiplied by the microcosms' incubation period. To determine N cycling rates, we incubated the

soil samples in the laboratory for 14 d at 30 °C. Soil samples were extracted with 0.5 M K_2SO_4 in a 1:5 ratio immediately before and after the incubation period. The concentrations of ammonium (μg NH_4^+–N/g^{-1} dw soil), nitrate (μg · NO_3^-–N/g^{-1} dw soil), and dissolved organic nitrogen (μg dissolved organic N [DON]/g^{-1} dw soil) were measured colorimetrically in each K_2SO_4 extract using a microplate reader. Total available N concentration (μg · TAN/g^{-1} dw soil) was calculated as the sum of ammonium, nitrate, and DON. The potential N rates (mg · N kg^{-1} dw soil day^{-1}) were calculated using the difference between the N concentrations after and before the 14-d incubation period as follows: ammonification (NH_4^+–N) and nitrification (NO_3^-N).

Multifunctionality. We quantified multifunctionality using nine litter and soil functions related to the cycling of C, N, and P as follows: litter decomposability, litter C loss, litter N loss, PHOS, integrated C enzyme activity, integrated N enzyme activity, total available N, potential ammonification rate, and potential nitrification rate. All variables used to compute multifunctionality represent true process rates, which has been highly recommended in recent guidelines (42). This is especially important in microcosm studies, where the exchange of energy and matter is limited compared to real-world ecosystems. Total available N represents the pool of organic and inorganic N, but the use of the same soil across all microcosms allowed us to interpret such a pool at the end of the incubation period in a dynamic way adequate for inclusion in multifunctionality calculations. Moreover, the nine variables considered are weakly correlated with each other and positively correlated to the index of multifunctionality, facilitating the interpretation of the results (see *SI Appendix*, Figs. S5 and S10).

We calculated the index of multifunctionality based on all measured functions as follows. First, we separately standardized the nine functions measured (F) using the following Z-score transformation:

$$Z - score_{ij} = \frac{F_{ij} - MeanF_i}{SDF_i}, \quad [3]$$

where F_{ij} is the value of a function i in the community j, Mean F_i, and $SD\ F_i$ are the mean, and the SD of the function F_i calculated for the 480 studied litter mixtures, respectively. Second, we used a multiple-threshold approach to evaluate whether multiple functions are simultaneously performing at high levels (43). In short, this approach counts the number of functions that reach a given threshold (as the % of the maximum value of each of the functions observed in the dataset). This maximum is taken as the top 5% values for each function observed across all study sites (44). Considering multiple thresholds allows a better understanding of how biodiversity affects ecosystem functioning and to account for potential trade-offs between the functions evaluated (43). We considered thresholds between 20 and 80% (every 5%) since care should be taken to avoid overinterpreting results at very high or low thresholds (45). Each calculated threshold (T) was smoothed by using a moving average with intervals [T−10%, T+10% (7)].

Soil Microbial Communities. We randomly selected a subset of 20 microcosms out of the 80 available in each of the six biomes for the analysis of soil bacterial and fungal communities. We ensured that the chosen subsets were representative of the full dataset. Fresh soil samples harvested after microcosm incubation were defrosted and DNA was extracted from 0.5 g using the DNeasy PowerSoil Kit (QIAGEN GmbH). DNA samples were frozen at −20 °C and shipped to the Next Generation Genome Sequencing Facility of Western Sydney University for analysis in the Illumina MiSeq platform using the 341F/805R (bacterial 16S ribosomal DNA [rDNA]) and FITS7/ITS4 (fungal Internal Transcribed Spacer, ITS) primer sets (46). The extracted DNA was of high quality, with ratios of A260:A280 between 1.5 and 1.9.

Sequence processing and diversity analysis were performed as follows. For raw pair-end reads, primers at the beginning of each sequence were trimmed off using USEARCH (47). The maximum of expected error (ee) was set as 1.0 and 0.5 for the merged reads filtering in the 16S rDNA and ITS analyses, respectively. Sequence reads were binned into phylotypes (i.e., operational taxonomic units [OTUs]) by denoising (error-correction) the sequences based on a 100% similarity threshold using UNOISE3 (48) and singletons were removed. Representative sequences were annotated in QIIME (49) using UCLUST (47) against the Silva database (50) for 16S rDNA and UNITE database (51) for ITS, respectively. Approximately 4.3 (16S rDNA) and 9.2 (ITS) M high-quality merged sequences were mapped for all the samples, representing 23,269 (16S rDNA) and 4,563 (ITS) OTUs (see *SI Appendix*, Fig. S8 for the dominant taxa found). A normalization procedure was performed at 10,000 (16S rDNA) and 6,000 (ITS) sequences per sample prior to diversity analysis. Rarefaction depths were chosen to balance the number of samples that could be included while maximizing the available number of sequences per sample. Yet, the number of 16S rDNA and ITS sequences obtained from 23 microcosms was still too low to estimate microbial diversity accurately, so they were not used in all downstream analyses. Importantly, the number of samples removed due to low yield was evenly distributed among biomes, rendering a final sample size of 95 microcosms (13 dryland, 14 tropical, 18 boreal, 20 subarctic, 11 cropland, and 19 temperate) for which 16S rDNA and ITS data were available. Resultant OTU tables were converted into the Biological Observation Matrix file and imported into QIIME for the calculation of the diversity metric (i.e., Simpson index). FunGuild (52) was used to assign fungal phylotypes to the saprotroph trophic mode, and we calculated the relative abundance (%) of saprotrophs in each soil sample.

Data Analyses. Relationships between functional dominance, diversity (dispersion, evenness, and rarity), and the multifunctionality index were assessed using multiple linear regression models (function *glm()* with a poisson link in R) and run across multifunctionality thresholds ranging from 20 to 80%. The same models were used to investigate individual functions and microbial diversity. The models included the mean, variance, skewness, and kurtosis for both lignin and SLA. All predictors included were weakly correlated, preventing multicollinearity (*SI Appendix*, Table S3). Model residuals were inspected to ensure homoscedasticity and normality. All predictors and response variables were standardized before analyses using the Z-score to interpret parameter estimates on a comparable scale. To ensure the robustness of our results, we repeated these analyses by including "biome" as a random effect using the function *glmer*() with a poisson link in the R package *lme4* (53). These two analyses provided similar results (*SI Appendix*, Tables S4 and S5 and Figs. S6 and S11).

We evaluated the importance of the predictors under consideration as drivers of multifunctionality, individual functions, and soil microbial communities. For doing so, we expressed the importance of predictors as the percentage of explained variance based on the absolute value of their standardized regression coefficients in the model and compared to the absolute values of all standardized regression coefficients. This method is similar to a variance partition analysis because we previously transformed all predictors to Z-scores (7, 54). The following identifiable variance fractions were examined: 1) functional dominance using mean-lignin/SLA and 2) functional diversity using variance-lignin/SLA (dispersion), skewness-lignin/SLA (rarity), and kurtosis-lignin/SLA (evenness). Finally, we used standardized regression coefficients of model predictors to predict multifunctionality and respiration (expressed as the relative respiration in mixtures compare to monocultures) based on the additive effects of the following: 1) dominance + dispersion; 2) dominance + dispersion + evenness; and 3) dominance + dispersion + evenness + rarity. For simplicity, we only predicted the effect of lignin content while fixing the effect of SLA to its mean value. All other predictors selected in the averaged model were treated as constant and fixed to their mean (i.e., 0 since all predictors were transformed to Z-scores). All analyses were done in R 3.4.3 (55).

Data Availability. All data and R codes are available on Figshare: https://figshare.com/s/a73f2c4106b33f32e9c0.

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