

1 **Running head: biodiversity and ecosystem functioning**

2
3 **Title: Rarity and evenness are key facets of functional diversity to boost**
4 **multifunctionality**

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51 **Abstract**

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

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101 **Significance**

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

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115 **Key-words**

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117 Complex species assemblages | Litter decomposition | Nutrient cycling | Plant
118 pathogens | Trait distributions.

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147 Introduction

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

159

160 The relationship between functional traits and **multifunctionality** has been shown
161 to vary from positive to negative depending on the ecosystem, species pool and
162 biogeographical context considered (6–8). Such a high context-dependency may largely
163 depend on how functional traits are assembled within communities (9). Whilst the traits
164 of dominant species (hereafter functional dominance) can strongly determine individual
165 ecosystem functions (10), their role becomes less clear when considering
166 **multifunctionality** (7, 11). This is so because in an ecosystem, species that are functionally
167 different from the dominant ones – functional diversity – may contribute more to certain
168 key functions than their lower abundance would suggest (7, 11, 12). High functional
169 diversity – through the dispersion of trait values (hereafter functional dispersion) or the
170 presence of species with infrequent trait values (hereafter functional rarity) – for instance
171 in the case of keystone species – may enhance **multifunctionality** (9) if functionally
172 dissimilar species exploit or release contrasting resources or the same resources but at
173 different spatial or temporal scales (1). However, if species become too dissimilar, this
174 could lead to strong negative effects on ecosystems (e.g. in the case of invasive species
175 adding a new set of trait values) (6, 7, 13). In the later case, higher evenness among
176 functionally dissimilar species (hereafter functional evenness) could promote synergistic
177 interactions and counteract such negative biodiversity effects on **multifunctionality** (6, 7).
178 However, functional dominance, dispersion, rarity and evenness often co-vary in real-
179 world ecosystems (14), hindering the evaluation of their individual effect on
180 **multifunctionality** (6, 14, 15). A manipulative study revealing which trait assemblages
181 could boost positive biodiversity effects on multifunctionality across multiple ecosystems
182 is yet lacking.

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184 The distribution of trait values (trait distribution, hereafter) within complex
185 multispecies assemblages often deviates from the symmetric normal distribution,
186 classically-assumed in ecological studies (14, 15). While the mean and the variance allow
187 to characterize the functional dominance and dispersion of a normal distribution, the
188 skewness and kurtosis offer insights on the shape of the complex trait distributions
189 encountered in naturally assembled communities (6, 14, 15). The skewness represents the
190 asymmetry of the distributions. High negative or positive values of skewness occur when
191 trait distributions are strongly left- or right-tailed, as a result of rare species with
192 infrequent trait values compared with the bulk of the distribution: a definition of
193 functional rarity. Kurtosis represents the relative peakiness of trait distribution, where a
194 low kurtosis value reflects functionally even distributions. Investigating complex trait
195 distributions thus offers a unique opportunity to decipher the interplay of functional
196 dominance, dispersion, rarity and evenness in determining **multifunctionality**, and

197 represents a fundamental step towards the design and management of species
198 assemblages that could maximize biodiversity effects on ecosystems.

199
200 Here we present results from the first multi-biome experiment examining how the
201 functional dominance, dispersion, evenness and rarity of plant litter assemblages
202 influence **multifunctionality** and soil microbial communities. We manipulated complex
203 trait distributions to disentangle the influence of the four biodiversity attributes, while
204 species richness ($n = 15$ species each) and total litter biomass (1 g) were kept constant
205 among litter assemblages. We assembled 570 experimental leaf litter mixtures and
206 monocultures using 90 species from six biomes covering a wide range of the global
207 variability of two key plant functional traits (Specific Leaf Area (SLA) and lignin content)
208 (16, 17); and tracked changes in **multifunctionality** and soil microbial communities as
209 litter decomposed (Fig. 1; see also methods and *SI Appendix*, Tables S1 and S2, Figs. S1
210 and S2). Leaf litter assemblages were set-up using a set of 120,000 simulated functional
211 trait distributions (see methods; *SI Appendix*, Figs. S3 and S4). Then, we selected a subset
212 of 570 assemblages that covered the entire range of values that functional dominance and
213 diversity could take, while minimizing their correlations within and across biomes (*SI*
214 *Appendix*, Table S3, Fig. S4). **Multifunctionality** was calculated using nine functions
215 related with carbon (C), nitrogen (N) and phosphorus (P) cycling (see methods; *SI*
216 *Appendix*, Fig. S5). We also addressed the relative abundance (fungal trophic modes) and
217 diversity of soil bacteria and fungi. We tested the core hypothesis that functionally
218 dispersed, and highly even trait distributions are the litter trait assemblages to maximize
219 **multifunctionality**.

221 **Results and Discussion**

222
223 Dispersion, rarity and evenness accounted in average for 52.8 % of explained variance
224 across **multifunctionality**-thresholds (Fig. 2); although functional dominance remained an
225 important predictor. These results were robust to the statistical modeling approach used
226 (see methods; *SI Appendix*, Fig. S6). Our results highlight that the contribution of the
227 three dimensions of functional diversity to **multifunctionality** is as important as, and in
228 some cases, overwhelms that of functional dominance. Furthermore, the percentage of
229 explained variance driven by these three dimensions increased at higher
230 **multifunctionality** -thresholds (from 42 % to 66 %; Fig. 2), due to the increased effect
231 size of evenness when functions were performing at a high rate (from 9 % to 30 %).
232 Functional diversity also accounted for a fair amount of explained variance across
233 individual functions (from 18 to 67%), notably soil enzymatic activities, N transformation
234 rates and N pools (Fig.2; *SI Appendix*, Table S4). Litter assemblages with high mean-
235 lignin values decreased **multifunctionality** (standardized parameter estimate (est) = -0.136
236 ± 0.012 , $P < 0.001$; Fig. 3). This result brings new evidence supporting the role of litter
237 lignin concentration within multispecies assemblages as a key regulator of C and N
238 turnover in terrestrial ecosystems (18). Experimentally deciphering the four functional
239 attributes reveals that they all contribute to **multifunctionality** and individual functions to
240 a similar extent. Therefore, our study warns the need to consider multiple dimensions of
241 functional diversity, such as the overlooked functional rarity and evenness (14), to
242 maximize **multifunctionality**.

243
244 The functional dispersion of SLA values has a consistent and significant negative
245 effect on **multifunctionality** (est = -0.024 ± 0.008 , $P = 0.05$, Fig. 3), representing a cross-
246 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), supporting the core hypothesis that higher functional evenness in litter communities enhances **multifunctionality**. Functional diversity is increasingly used in BEF research (6, 9, 19), albeit it is often associated with dispersion. Our results clearly point to the evenness of trait assemblages, and 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 assemblage 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 relatively 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*, Table S4, Fig. S7). The lignin:N ratio of *Mabea 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, 20). 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, Fig. S7), likely due to the presence of condensed tannins forming recalcitrant complexes with proteins that are difficult to access by decomposers (21). 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 averaged leaf lignin content. Lignification is a traditional mechanism for disease resistance in plants (22). Our results

297 provide novel insights for the still debated ‘dilution effect’ (23), where higher functional
298 evenness among host species appears as a key biodiversity attribute to reduce disease risk
299 (4), independently from the average amount of lignin present in litter mixture. We also
300 observed a trend for negative relationships between kurtosis-lignin, fungal diversity and
301 saprotrophs. Soil fungal communities were dominated by taxa from the Ascomycota and
302 Basidiomycota phyla (72 % and 23 % of sequences, respectively; *SI Appendix*, Fig. S8),
303 which perform their primary ecological role as decomposers (24). Fungal saprotrophs are
304 considered the key microbial players in litter decomposition, because of their ability to
305 produce a wide range of extracellular enzymes needed to breakdown litter (25). Similarly,
306 higher evenness of SLA also promoted (positive) biodiversity effects on soil microbial
307 respiration (i.e. negative effect of kurtosis-SLA on BE_CO2; est = -0.038 ± 0.01 , $P <$
308 0.001 ; *SI Appendix*, Table S4, Fig S7), suggesting that an even array of leaf litters could
309 promote resource partitioning among soil organisms or leverage N limitation during litter
310 decomposition (26). Our results highlight a novel linkage at the interface between above
311 and belowground communities, whereby evenness in trait assemblages, independent of
312 species richness and dominant plant types, can increase soil microbial diversity and
313 activity, and reduce risks of soil fungal diseases.

314
315 We finally showed that manipulating the relative abundance of trait values in
316 multispecies assemblage can be used promote specific ecosystem function or
317 **multifunctionality as a whole**. To illustrate this finding, we first predicted the effects of
318 functional dominance and dispersion on **multifunctionality** and on soil microbial
319 respiration (Fig 4). Then, we evaluated the added value of functional evenness and rarity
320 subsequently. We found that higher functional evenness in litter assemblages increased
321 **multifunctionality** at any litter lignin value, and beyond the effects of functional
322 dominance and dispersion (Fig. 4A). Rarity further enhanced **multifunctionality** at high
323 lignin content, but the opposite was found at low lignin levels. The pattern found when
324 addressing biodiversity effects on soil microbial respiration (Fig. 4B) suggests that
325 synergistic and antagonistic biodiversity effects mediate functional rarity effects on
326 **multifunctionality**. Adding few, but functionally labile litter fragments, to recalcitrant
327 litter mixtures had a positive effect on **multifunctionality** of similar magnitude than
328 decreasing the litter lignin content from 12% (subarctic biome) to 3 % (cropland biome).
329 Our results highlight that considering multiple dimensions of functional diversity can help
330 to pinpoint the litter trait assemblages that boost positive biodiversity effects on
331 ecosystems without the need to increase the number of species, the range of trait values
332 or change the identity of dominant plant type (Fig. 4). These findings offer perspectives
333 to improve a variety of agricultural and ecosystem restoration programs to target
334 multifunctional species assemblage. For instance, incorporating functional rarity and
335 evenness into new plant breeding programs might help to offset the side effects of plant
336 domestication, that have reduced the ability of crop mixtures to benefit from biodiversity
337 effects (27) and their resistance to pathogen infection (28). Furthermore, the
338 maximization of functional evenness when restoring dryland ecosystems threatened by
339 ongoing climate change may help to prevent land degradation and desertification
340 processes (6).

341 **Conclusion**

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343
344 Using a multi-biome litter experiment covering most of the global variation in leaf trait
345 spectra, we identified functional rarity and evenness as key dimensions to maximize
346 biodiversity effects on ecosystems. Our results on the effects of litter assemblages on

347 terrestrial ecosystems pave the way for further research efforts to extending our
348 experimental framework to lived assemblages. This work highlights that trait
349 assemblages that boost biodiversity effects across biomes can be identified and managed
350 to promote specific ecosystem functions, or multifunctionality as a whole. Since more
351 than 50% of net primary production is returned to the soil via litter decomposition (29),
352 our study demonstrates that considering the complexity of trait assemblages may improve
353 our ability to anticipate the functional consequences of biodiversity loss on ecosystems.

354 355 **Methods**

356
357 **Sampling locations.** We sampled leaf litter from six biomes that are representative of a
358 wide array of climate conditions found on Earth: tropics, cropland, dryland, temperate,
359 boreal and subarctic (Fig. 1; *SI Appendix*, Table S1). Sampling was performed in 2017 in
360 five countries (Canada, France, Peru, Spain and Sweden) and a range of locations, which
361 widely differed in climate conditions (mean annual temperature and precipitation ranged
362 from 0.4°C to 18.1°C, and from 352 mm to 1840 mm, respectively).

363
364 **Leaf litter collection and trait measurements.** Freshly fallen leaf litter from 15 species
365 were collected in each biome, totalling 90 species (Fig. 1; *SI Appendix*, Table S2). The
366 species selection included the representative vegetation at each location, and comprised
367 typical grasses, shrubs and trees for each biome. Leaf litter material was air-dried for two
368 weeks and shipped to Rey Juan Carlos University for analyses and litter decomposition
369 assays. Leaf litter with signs of herbivory or disease was discarded, and all material was
370 mixed at the species level to get a homogeneous species litter pool. To characterize the
371 functional profile of litters, we focussed on the specific leaf area (SLA) and leaf lignin
372 content, which are key drivers of litter decomposability (18, 30). The SLA ($\text{cm}^2 \cdot \text{g}^{-1}$),
373 calculated as the ratio between leaf area (cm^2) and leaf dry mass (g), discriminates
374 acquisitive/conservative plants and is associated with high leaf nutrient content (16). High
375 SLA correlates with high litter decomposition(31), and with bacterial-dominated soil
376 microbial communities (32). SLA is thus a good candidate to scale up plant diversity and
377 **multifunctionality** (6, 7). Alternatively, litter lignin (% of leaf dry mass) protects labile
378 compounds from microbial attack in plant cell walls (17). Litters with high lignin content
379 are associated with low accessibility to nutrients, low litter decomposition rates, and slow
380 nutrient cycling (18). Lignified leaves are associated with fungal saprotrophs producing
381 a wide range of extracellular enzymes needed to breakdown their litter into biological
382 usable forms (33). We measured the SLA of each species on fresh green leaves of five
383 plant individuals, calculated as the ratio between leaf area (cm^2) and leaf dry mass (g).
384 Leaf lignin content (%) was analyzed following van Soest (34) using 1 g of grounded leaf
385 litter. **Using 90 species from five natural and one managed ecosystem allowed to cover a**
386 **wide range of the land spectra observed for the two traits evaluated (Fig. 1). The selected**
387 **spectrum of SLA values ranged from 23 to 373 $\text{cm}^2 \text{g}^{-1}$, approximating the range covered**
388 **by 90% of the species measured in global terrestrial systems (16). Leaf litter lignin values**
389 **ranging from 1 % to 51 %, and encompassed the classically-assumed global range of leaf**
390 **litter lignin (10 % – 40 %) and extremes (17).**

391
392 **Plant functional dominance and diversity.** We tested the effects of functional
393 dominance and diversity (dispersion, rarity and evenness) on **multifunctionality** by
394 manipulating the trait distributions of SLA and litter lignin content. To do so, we focused
395 on the four moments of the trait-abundance distributions of litter communities: the mean,
396 the variance, the skewness and the kurtosis. The mean of a trait-abundance distribution

397 reflects the trait of the dominant species while the variance quantifies the dispersion of
398 trait values, i.e. how far trait values are spread around their mean. The skewness and
399 kurtosis complement the mean and the variance by describing the shape of the
400 distribution, i.e. how species abundances are distributed within communities as a function
401 of their trait values. Skewness measures the asymmetry of the distribution. High negative
402 or positive values of skewness occur when trait–abundance distributions are strongly left-
403 or right-tailed, respectively; it highlights the presence of a few rare species with extreme
404 trait values compared with the bulk of the distribution. Kurtosis measures the relative
405 peakiness of the trait-abundance distribution and the heaviness of its tails. Low kurtosis
406 reflects an even distribution of trait values within the community.

407
408 Investigating the effect of the four moment of the trait distribution on multifunctionality
409 require rigorous experimental design because the mean variance skewness and kurtosis
410 are not entirely independent due to existing mathematical constraint among them. For
411 instance, increasing the skewness toward positive skew-values will increased the mean
412 trait value of the community when considering a fixed number of species and range of
413 trait values. Inversely, decreasing the skewness toward negative values will increase the
414 mean values of the community. Similarly, a negative correlation between the variance and
415 the kurtosis may occur when considering a fixed number of species. To overcome this
416 limitation, we considered in our experiment six contrasted species pool originated from
417 six biomes making the mean and the variance largely independent from skewness and the
418 kurtosis. Additionally, our experimental design took advantage from an existing
419 inequality between the skewness and the kurtosis that can be used to characterize complex
420 trait distributions deviating from the normal distribution (*SI Appendix*, Fig. S3). We
421 manipulated the relative abundance of each of the 15 species of each biome to simulate
422 120,000 trait-abundance distributions encompassing all types of possible trait
423 distributions (from symmetric to heavily skewed distributions, and from bimodal to
424 highly leptokurtic distributions; Step 1 in *SI Appendix*, Fig. S4). From the simulated trait-
425 abundance distributions per biome (20,000), we selected the subset of 80 that minimized
426 the correlations among all moments within and across biomes (Step 2). From the final
427 litter mixture selection (Step 3), litter weights were used to establish the relative
428 abundances of species prescribed in the simulations. The 15-species assemblages were
429 fixed at a total litter dry weight of 1,000 mg (35). We also fixed a minimum litter fragment
430 weight per species of 10 mg for the sake of litter manipulation. Litter weights thus ranged
431 between 10 mg and 860 mg (1,000 mg – 14 species * 10 mg) for all species within each
432 simulated trait-abundance distribution. The selected litter assemblages covered a wide
433 range of litter types (community mean-SLA ranged from 33.1 cm².g⁻¹ to 279.2 cm².g⁻¹;
434 community mean-lignin ranged from 2.92 g.g⁻¹ to 37.83 g.g⁻¹) and all possible types of
435 trait-abundance distributions. The final selections included 570 litter assemblages (480
436 litter mixtures of 15 species each (80-litter mixtures per biome; *SI Appendix*, Fig. S9) +
437 90 species in monocultures) and minimize the correlations between the four moment of
438 the trait-abundance distribution for SLA and lignin content making possible to
439 experimentally test their relative contribution on multifunctionality.

440
441 **Litter decomposition assay.** We set up the 570 litter assemblages + soil microcosms and
442 incubated them for 88 days in growth chambers at optimal conditions for the
443 decomposition process (darkness, 20°C and 95% air humidity). To do that, we collected
444 soil to 10 cm depth in an open grassland dominated by *Stipa tenacissima* in Central Spain.
445 The soil is a Lithic Calciorthid(36) with pH 7.6, sand content 72 %, clay content 10 %,
446 organic C 2.74 %, total N 0.27 %, NO₃⁻-N 9.37 mg N kg⁻¹ dw soil and NH₄⁺-N 14.84

447 mg N kg⁻¹ dw soil. The soil was sieved at 2 mm and homogenized to get a single pooled
448 sample across all litter assemblages. The soil was stored fresh at 4 °C for one week during
449 the set-up of microcosms. 60 g of sieved fresh soil were introduced into 250 ml plastic
450 jars (9 cm high, 6 cm diameter) and soil moisture was adjusted to 60% water-holding
451 capacity, which is favorable for microbial activity. To simulate a natural soil layer and
452 favour soil microbial colonization, leaf litter was cut in fragments if leaf size was larger
453 than microcosms area (*SI Appendix*, Figs. S1 and S2). Microcosms were incubated
454 uncapped but covered with parafilm to minimize water losses but to allow CO₂ exchange
455 with the atmosphere. To maintain a 60 % water-holding capacity, soil moisture was
456 checked every two weeks and deionized water was added when necessary two days before
457 respiration measurements were taken. The microcosms were randomly distributed across
458 four growth chambers, and their location among and within chambers was randomized
459 every two weeks to avoid potential temperature and moisture gradients within the growth
460 chamber.

461
462 Litter decomposability was estimated by monitoring microcosms' respiration rates
463 over the incubation period, as they are a good proxy of soil microbial activity (37). We
464 calculated the soil cumulative respiration as the amount of CO₂ respired by soil microbial
465 communities decomposing plant litter over the incubation period. Specifically, we
466 measured the CO₂ rates daily during the first week, once a week from weeks 2 to 5, and
467 then every two weeks until the end of the incubation. To measure CO₂ concentrations, we
468 used a high-throughput colorimetric method coupled with a 96-well microplate reader
469 (35). Absorbance at 595 nm was converted into CO₂ concentration (%) using a calibration
470 curve with gas chromatography ($R^2 = 0.86$), and then transformed into CO₂ production
471 rate ($\mu\text{g CO}_2\text{-C g}^{-1}\text{ dw soil h}^{-1}$) using gas constants, incubation temperature (20 °C),
472 headspace volume, and soil dry weight (38). We used linear interpolations between
473 sampling dates and then summed them across all dates to estimate the soil cumulative
474 respiration over the incubation period. After the last CO₂ measurement was performed,
475 the remaining litter material and the soil were retrieved from the microcosms to analyze
476 the rest of the litter and soil functions. The litter was dried at 60 °C, weighed as ash-free
477 litter mass, and ground to fine powder with a ball mill. The soil was immediately
478 separated into two different subsamples after retrieving litters: one was air-dried for two
479 weeks and stored until the analysis of soil functions, and the other was stored at -20 °C
480 until DNA extraction.

481
482 We evaluated the biodiversity effects (BE) on soil cumulative respiration and litter
483 mass loss. We calculated BE as follows:

484
485
$$\text{Mixture}_{\text{exp}} = \text{sum}(\text{Monoculture}_{\text{obs}} * \text{relative abundance of Mixture}) \quad \text{Equation (1);}$$

486
487
$$\text{BE} = (\text{Mixture}_{\text{obs}} - \text{Mixture}_{\text{exp}}) / \text{Mixture}_{\text{exp}} \quad \text{Equation (2);}$$

488
489 Where positive values of BE indicate higher soil respiration / litter mass loss than
490 expected from monocultures (synergetic biodiversity effects), and negative values
491 indicate lower soil respiration / litter mass loss than expected from monocultures
492 (antagonistic biodiversity effects)

493
494 **Litter and soil functions.** Leaf litter C and N concentrations were analysed with an
495 elemental analyser (Flash 1112 EA, Thermo-153 Finnigan, Bremen, Germany). We
496 assessed two litter functions as the major outcome of the litter decomposition process: C

497 mineralization and N immobilization/release patterns(26). To do that, we calculated litter
498 C and N loss (%) as $100 \times [(M_i \times C_{Ni}) - (M_f \times C_{Nf})] / (M_i \times C_{Ni})$, where M_i and M_f
499 are the initial and final litter dry mass, respectively, and C_{Ni} and C_{Nf} are the initial and
500 final C or N concentration (% of litter dry mass).

501

502 We analyzed multiple enzyme activity rates and N cycling rates as soil functions.
503 First, we determined the potential activity of five extracellular enzymes: β -1,4-
504 glucosidase (BG; starch degradation), β -D-cellobiohydrolase (CBH; cellulose
505 degradation), β -1,4-N-acetylglucosaminidase (NAG; chitin degradation), L-leucine
506 aminopeptidase (LAP; protein degradation) and acid phosphatase (PHOS; phosphorus
507 mineralization). Soil enzyme activities (nmol activity g^{-1} dw soil h^{-1}) were assessed
508 fluorometrically following the methods described in Bell et al. (2013) and using 4-
509 methylumbelliferone (MUB) and 7-amino-4-methylcoumarin (MUC) to produce the
510 standard curves. Integrated C and N enzyme activity were computed as BG + CBH and
511 NAG + LAP, respectively, and then multiplied by the microcosms' incubation period. To
512 determine N cycling rates, we incubated the soil samples in the laboratory for 14 days at
513 30° C. Soil samples were extracted with 0.5 M K_2SO_4 in a 1:5 ratio immediately before
514 and after the incubation period. The concentrations of ammonium ($\mu g NH_4^+-N / g^{-1}$ dw
515 soil), nitrate ($\mu g NO_3^-N / g^{-1}$ dw soil) and dissolved organic nitrogen ($\mu g DON / g^{-1}$ dw
516 soil) were measured colorimetrically in each K_2SO_4 extract using a microplate reader and
517 following Chantigny et al (2006). Total available N concentration ($\mu g TAN / g^{-1}$ dw soil)
518 was calculated as the sum of ammonium, nitrate and DON. The potential N rates (mg N
519 kg^{-1} dw soil day^{-1}) were calculated using the difference between the N concentrations
520 after and before the 14-days incubation period as follows: ammonification (NH_4^+-N) and
521 nitrification (NO_3^-N).

522

523 **Multifunctionality.** We quantified **multifunctionality** using nine litter and soil functions
524 related to the cycling of carbon (C), nitrogen (N) and phosphorous (P): litter
525 decomposability, litter C loss, litter N loss, phosphatase enzyme activity (PHOS),
526 integrated C enzyme activity, integrated N enzyme activity, total available N, potential
527 ammonification rate, and potential nitrification rate. All variables used to compute
528 **multifunctionality** represent true process rates, which has been highly recommended in
529 recent guidelines (39). This is especially important in microcosms studies, where the
530 exchange of energy and matter is limited compared to real-world ecosystems. Total
531 available N represents the pool of organic and inorganic N, but the use of the same soil
532 across all microcosms allowed us to interpret such a pool at the end of the incubation
533 period in a dynamic way adequate for inclusion in **multifunctionality** calculations.
534 Moreover, the nine variables considered are weakly correlated with each other, and
535 positively correlated to the index of **multifunctionality**, facilitating the interpretation of
536 the results (see details in *SI Appendix*, Figs S5 and S10).

537

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

541

$$542 \quad Z - score_{ij} = \frac{F_{ij} - Mean F_i}{SD F_i} \quad \text{Equation (3);}$$

543

544 where F_{ij} is the value of a function i in the community j , $Mean F_i$ and $SD F_i$ are the
545 mean and the standard deviation of the function F_i calculated for the 480 studied litter
546 mixtures, respectively. Second, we used a multiple threshold approach to evaluate

547 whether multiple functions are simultaneously performing at high levels (40). In short,
548 this approach counts the number of functions that reach a given threshold (as the % of the
549 maximum value of each of the functions observed in the dataset). This maximum is taken
550 as the top 5% values for each function observed across all study sites (41). Considering
551 multiple thresholds allows a better understanding of how biodiversity affects ecosystem
552 functioning, and to account for potential trade-offs between the functions evaluated (40).
553 We considered thresholds between 20% and 80% (every 5%), since care should be taken
554 to avoid over-interpreting results at very high or low thresholds (42). Each calculated
555 threshold (T) was smoothed by using a moving average with intervals [T-10%, T+10%]
556 (7).

557
558 **Soil microbial communities.** We randomly selected a subset of 20 microcosms out of the
559 80 available in each of the six biomes for the analysis of soil bacterial and fungal
560 communities. We ensured that the chosen subsets were representative of the full dataset.
561 Fresh soil samples harvested after microcosm incubation were defrosted and DNA was
562 extracted from 0.5 g using the DNeasy PowerSoil Kit (QIAGEN GmbH). DNA samples
563 were frozen at -20 °C and shipped to the Next Generation Genome Sequencing Facility
564 of Western Sydney University for analysis in the Illumina MiSeq platform using the
565 341F/805R (bacterial 16S-rDNA) and FITS7/ITS4 (fungal Internal Transcribed Spacer,
566 ITS) primer sets (43). The extracted DNA was of high quality, with ratios of A260/A280
567 between 1.5 and 1.9.

568
569 Sequence processing and diversity analysis were performed as follows. For raw pair-
570 end reads, primers at the beginning of each sequence were trimmed off using USEARCH
571 (44). The maximum of expected error (ee) was set as 1.0 and 0.5 for the merged reads
572 filtering in the 16S rDNA and ITS analyses, respectively. Sequence reads were binned
573 into phylotypes (i.e., operational taxonomic units; OTUs) by denoising (error-correction)
574 the sequences based on a 100% similarity threshold using UNOISE3 (45), and singletons
575 were removed. Representative sequences were annotated in QIIME (46) using UCLUST
576 (44) against the Silva database (47) for 16S rDNA and UNITE database (48) for ITS,
577 respectively. Approximately 4.3 (16S rDNA) and 9.2 (ITS) M high-quality merged-
578 sequences were mapped for all the samples, representing 23,269 (16S rDNA) and 4,563
579 (ITS) OTUs (see *SI Appendix*, Fig. S8 for the dominant taxa found). A normalization
580 procedure was performed at 10,000 (16S rDNA) and 6,000 (ITS) sequences *per* sample
581 prior to diversity analysis. Rarefaction depths were chosen to balance the number of
582 samples that could be included while maximizing the available number of sequences *per*
583 sample. Yet, the number of 16S rDNA and ITS sequences obtained from 23 microcosms
584 was still too low to estimate microbial diversity accurately, so they were not used in all
585 downstream analyses. Importantly, the number of samples removed due to low yield was
586 evenly distributed among biomes, rendering a final sample size of 95 microcosms (13
587 dryland, 14 tropical, 18 boreal, 20 subarctic, 11 cropland and 19 temperate) for whom
588 16S rDNA and ITS data were available. Resultant OTU table were converted into the
589 biom file and imported into QIIME for the calculation of the diversity metric (i.e. Simpson
590 index). FunGuild (49) was used to assign fungal phylotypes to the saprotroph trophic
591 mode, and we calculated the relative abundance (%) of saprotrophs in each soil sample.

592
593 **Data analyses.** Relationships between functional dominance, diversity (dispersion,
594 evenness and rarity), and the **multifunctionality**-index were assessed using multiple linear
595 regression models (**function *glm()*** with a poisson link in R), and run across
596 **multifunctionality**-thresholds ranging from 20% to 80%. The same models were used to

597 investigate individual functions and microbial diversity. The models included the mean,
598 variance, skewness and kurtosis for both lignin and SLA. All predictors included were
599 weakly correlated, preventing multicollinearity (*SI Appendix*, Table S3). Model residuals
600 were inspected to ensure homoscedasticity and normality. All predictors and response
601 variables were standardized before analyses using the Z-score to interpret parameter
602 estimates on a comparable scale. To ensure the robustness of our results, we repeated
603 these analyses by including “biome” as a random effect using the **function *glmer()* with a**
604 **poisson link** in the R package *lme4* (50). These two analyses provided similar results (*SI*
605 *Appendix*, Tables S4 and S5, Figs. S6 and S11).

607 We evaluated the importance of the predictors under consideration as drivers of
608 multifunctionality, individual functions and soil microbial communities. For doing so, we
609 expressed the importance of predictors as the percentage of explained variance, based on
610 the absolute value of their standardized regression coefficients in the model and compared
611 to the absolute values of all standardized regression coefficients. This method is similar
612 to a variance partition analysis because we previously transformed all predictors to Z-
613 scores (7, 51). The following identifiable variance fractions were examined: i) functional
614 dominance using mean-lignin/SLA, and ii) functional diversity using variance-
615 lignin/SLA (dispersion), skewness-lignin/SLA (rarity) and kurtosis-lignin/SLA
616 (evenness). Finally, we used standardized regression coefficients of model predictors to
617 predict multifunctionality and respiration (expressed as the relative respiration in
618 mixtures compare to monocultures) based on the additive effects of: (i) dominance +
619 dispersion; (ii) dominance + dispersion + evenness; (iii) dominance + dispersion +
620 evenness + rarity. For simplicity, we only predicted the effect of lignin content while
621 fixing the effect of SLA to its mean value. All other predictors selected in the averaged
622 model were treated as constant and fixed to their mean (i.e. 0 since all predictors were
623 transformed to Z-scores). All analyses were done in R 3.4.3(52).

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757

758 **Online Content.** Any additional Methods, Extended Data display items and Source Data
759 are available in the online version of the paper; references unique to these sections appear
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761

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781 P built the experimental microcosms and conducted leaf litter and soil analyses. YLB-P,
782 NG, HS, JW and PG-P conducted the statistical analyses. YLB-P, NG, HS and PG-P
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784

785 **Competing interests.** The authors declare no competing financial interests.

786

787 **Data availability.** All data and R codes are available on figshare:
788 <https://figshare.com/s/a73f2c4106b33f32e9c0>

789

790 **Additional information.** The *SI Appendix* is available in the online version of the paper.
791 Reprints and permissions information is available at www.nature.com/reprints.

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794

795 **Figure legends**

796

797 **Figure 1.** Experimental and analytical framework to test the effects of dominant species
798 and their traits (dominance) and of functional diversity (dispersion, rarity and evenness)
799 on multifunctionality. A. Specific leaf area (SLA) and leaf litter lignin content of 90
800 species from six biomes covering a wide array of the global variation in these traits
801 observed (see also *SI Appendix*, Table S2). B. Disentangling functional dominance,
802 dispersion, rarity and evenness by manipulating the mean, variance, skewness and
803 kurtosis of trait-abundance distributions. C. Microcosms containing the leaf litter
804 communities (photographs by JHCC, LD, NG, LD, NS and RM).

805

806 **Figure 2.** Contribution of functional diversity and dominance to multifunctionality
807 thresholds, individual (litter and soil) functions and soil communities. The importance of
808 predictors is expressed as the percentage of explained variance (model R^2 express total
809 variances), taken as the absolute value of their standardized regression coefficients. The
810 effects of the trait-abundance distribution for specific leaf area and litter lignin content
811 were summed for each predictor. T = multifunctionality-thresholds; BE_Mloss =
812 biodiversity effect on mass loss, C/N_loss = absolute litter C and N loss; CO2 =
813 cumulative soil respiration; BE_CO2 = biodiversity effect on cumulative soil respiration;
814 C/N/P_enz = soil enzymatic activities related with C, N, and P cycling; AMP/NIP = soil
815 ammonification and nitrification rates; TAN = total soil available nitrogen; B/F_div = soil
816 bacterial and fungal diversity; P/S_ab = relative abundance of soil fungal pathogens and
817 saprotrophs.

818

819 **Figure 3.** Effects of functional dominance, dispersion, rarity and evenness on
820 multifunctionality. Dark to light grey lines show model fits with increasing thresholds.
821 Dots represent model partial residuals. We provide for each predictor the averaged
822 parameter estimates (est) across thresholds \pm standard deviation and the P value.

823

824 **Figure 4.** Identifying which functional attributes of plant litter assemblages boost
825 biodiversity effects on multifunctionality. We investigated the effects of (i) functional
826 dominance and dispersion (grey dots); (ii) dominance and dispersion + evenness (blue
827 dots); (iii) dominance, dispersion, evenness + rarity (orange dots) for multifunctionality
828 and for the biodiversity effects on cumulative soil respiration (BE_CO2). Predictions are
829 based on the standardized regression coefficients of model predictors averaged across
830 thresholds (see Table SXXX). For simplicity, we only predicted the effect of lignin
831 content while fixing the effect of SLA to its mean value.

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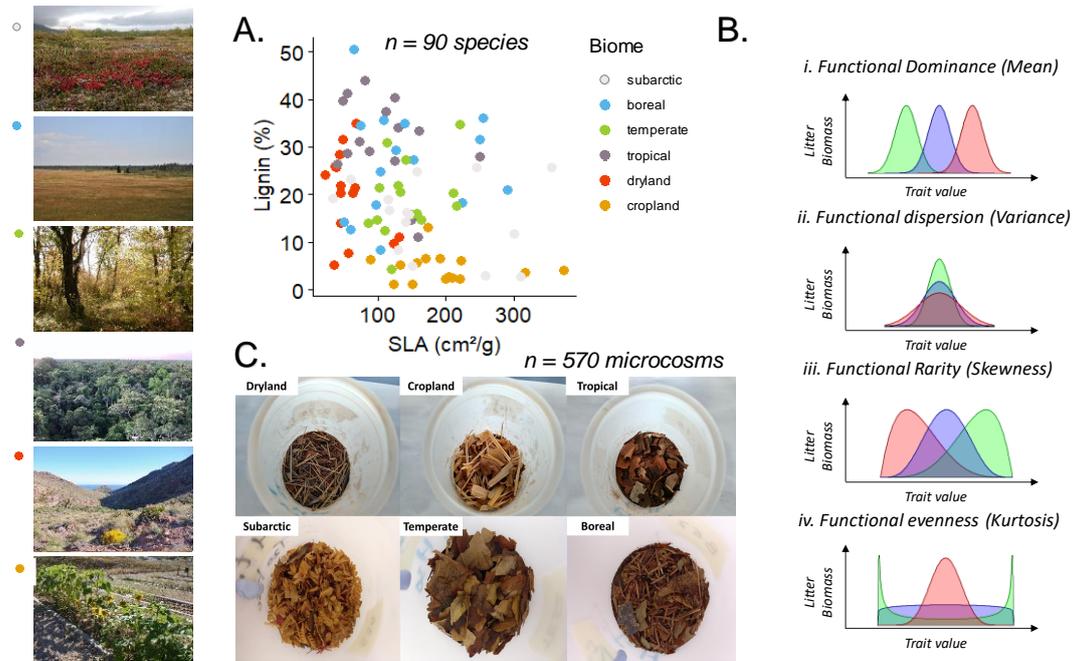
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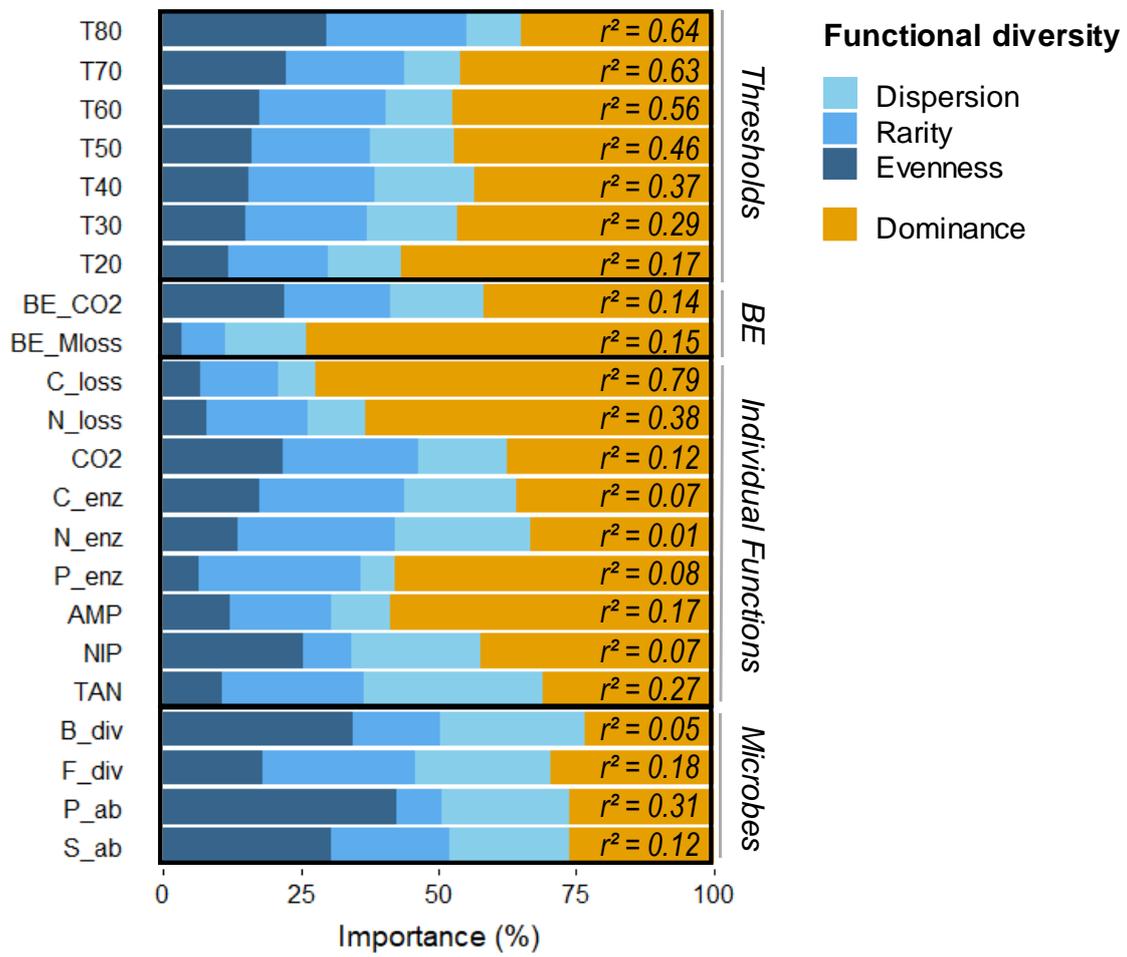
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Figure 1

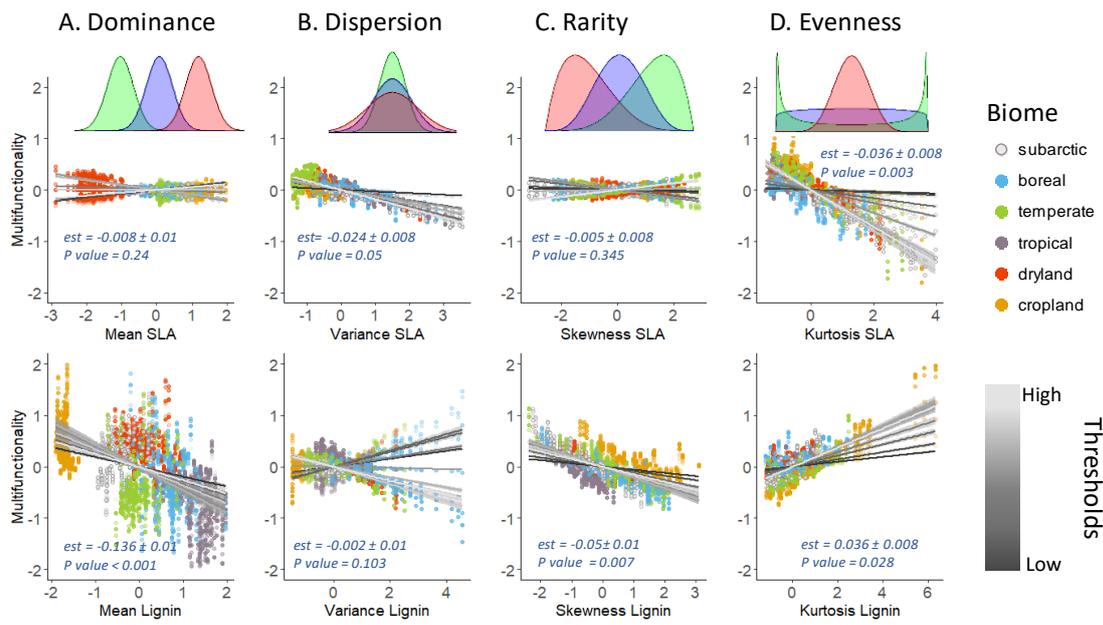
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Figure 2

Functional diversity



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Figure 3

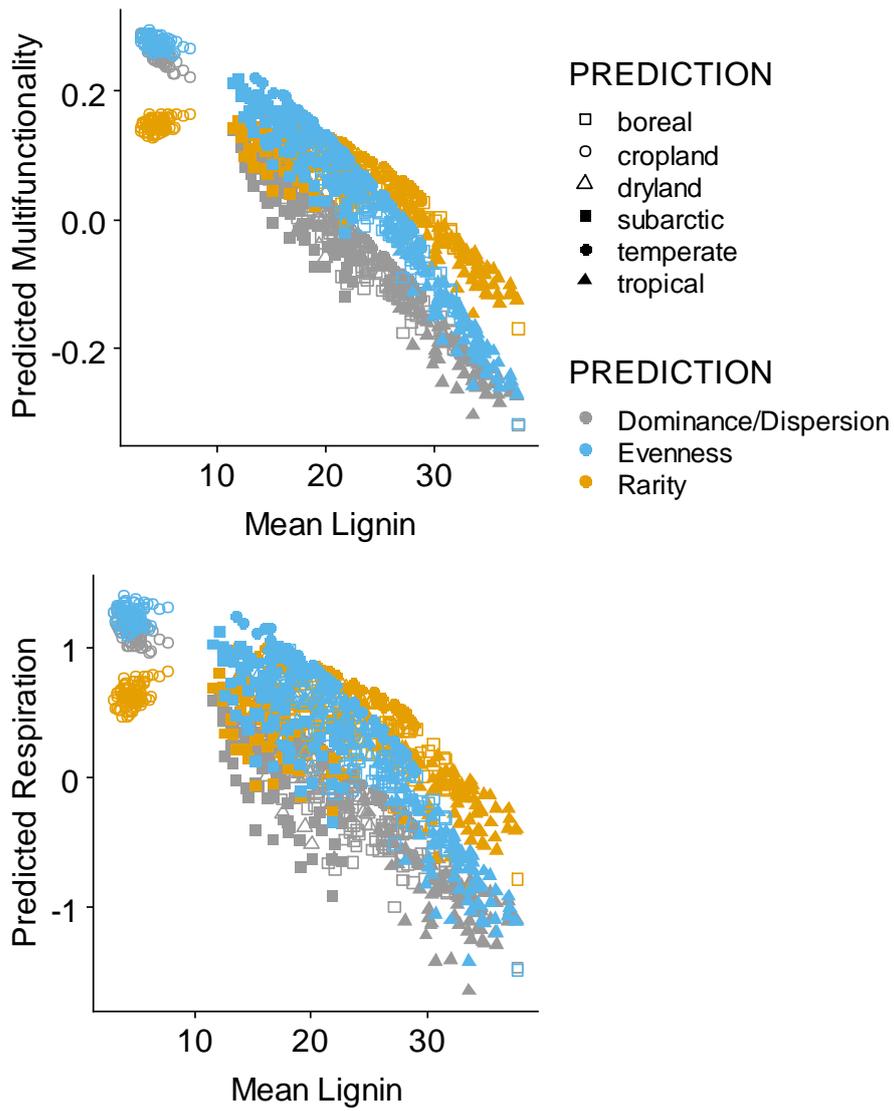


Figure 4

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914 ***SI Appendix***

915

916 **Title: Optimizing functional trait diversity to boost ecosystem multifunctionality**

917

918 Yoann Le Bagousse-Pinguet, Nicolas Gross, Hugo Saiz, Fernando T. Maestre, Sonia Ruiz,
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920 Cornelissen, Lucas Deschamps, Carlos García, Vincent Maire, Rubén Milla, Norma
921 Salinas, Brajesh K. Singh, Juntao Wang, Pablo García-Palacios

922

923 This file includes Supplementary Tables S1–5 and Supplementary Figs. S1–11.

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947 **Table S1.** Characteristics of the locations where leaf litter was collected across six contrasting biomes.

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	Tropical	Cropland	Dryland	Temperate	Boreal	Subarctic
Country	Peru	Spain	Spain	France	Canada	Sweden
Ecosystem	Tropical forest	Vegetable	Semiarid steppe	Temperate Forest	Fir - birch woodland	Tundra, birch woodland
Coordinates	12°50' S, 69°16' W	40°18' N, 3°52' W	40°22' N, 3°22' W	46°05' N, -0°48' W	47° 19'N, -71° 8'W	68°21'N, 18°49 E
Altitude (m a.s.l.)*	1690	632	750	85	750	400
MAT (°C)*	18.1	15.0	14.5	12.2 °	0.4	1.3
MAP (mm)*	1840	450	430	801	1500	352
Soil pH*	3.49	7.4	7.9	7.8	4.1	4.4
Soil organic C (%)*	14.9	5.12	2.60	NA	5.5	26
Soil total N (%)*	1.08	0.37	0.28	NA	0.23	1.05

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950 *average across locations of leaf litter collection

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953 Table S2. Species list selected per biome and corresponding trait values.
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Biome	Species	Specific leaf area (cm ² g ⁻¹)	Litter lignin content (%)
Cropland	<i>Zea mays</i>	151.15	1.14
Cropland	<i>Pennisetum glaucum</i>	123.29	1.28
Cropland	<i>Sorghum sudanense</i>	199.79	2.25
Cropland	<i>Triticum durum</i>	220.81	2.33
Cropland	<i>Avena sativa</i>	209.32	2.45
Cropland	<i>Amaranthus cruentus</i>	204.45	2.85
Cropland	<i>Hordeum vulgare</i>	315.72	3.60
Cropland	<i>Lactuca sativa</i>	373.49	4.17
Cropland	<i>Helianthus annuus</i>	133.40	5.27
Cropland	<i>Cynara cardunculus</i>	157.05	5.63
Cropland	<i>Borago officinalis</i>	222.50	6.09
Cropland	<i>Allium porrum</i>	88.53	6.44
Cropland	<i>Cichorium endibia</i>	190.62	6.48
Cropland	<i>Vigna unguiculata</i>	169.71	6.49
Cropland	<i>Sesamum indicum</i>	173.51	13.02
Dryland	<i>Stipa tenacissima</i>	35.93	5.30
Dryland	<i>Stipa offneri</i>	56.61	7.77
Dryland	<i>Brachypodium retusum</i>	123.56	9.65
Dryland	<i>Carex halleriana</i>	131.26	11.08
Dryland	<i>Globularia alypum</i>	44.67	13.99
Dryland	<i>Rosmarinus officinalis</i>	45.50	20.24
Dryland	<i>Lavandula latifolia</i>	62.86	20.42
Dryland	<i>Salvia lavandulifolia</i>	67.11	21.45
Dryland	<i>Quercus coccifera</i>	44.99	21.78
Dryland	<i>Juniperus phoenicea</i>	22.93	24.03
Dryland	<i>Quercus ilex</i>	38.70	25.73
Dryland	<i>Pinus halepensis</i>	36.71	26.02
Dryland	<i>Cistus clusii</i>	44.47	28.34
Dryland	<i>Pistacia lentiscus</i>	48.23	31.50
Dryland	<i>Cistus albidus</i>	68.66	35.01
Tropical	<i>Mabea nitida</i>	158.50	11.03
Tropical	<i>Virola calophylla</i>	149.50	14.72
Tropical	<i>Nectandra longifolia</i>	40.80	26.32
Tropical	<i>Pourouma guianensis</i>	124.40	26.98
Tropical	<i>Bixa arborea</i>	250.00	27.91
Tropical	<i>Weinmannia crassifolia</i>	55.70	28.70
Tropical	<i>Tachigali setifera</i>	87.50	29.10
Tropical	<i>Weinmannia bangii</i>	72.10	31.19
Tropical	<i>Pourouma cecropiifolia</i>	160.00	33.33
Tropical	<i>Iryanthera juruensis</i>	129.50	34.02
Tropical	<i>Pourouma minor</i>	111.40	37.47
Tropical	<i>Clusia alata</i>	49.00	39.69
Tropical	<i>Virola sebifera</i>	125.00	40.40
Tropical	<i>Hesperomeles ferruginea</i>	55.70	41.17
Tropical	<i>Perebea guianensis</i>	81.70	43.96
Boreal	<i>Kalmia angustifolia</i>	103.20	8.32

Boreal	<i>Picea glauca</i>	60.20	12.55
Boreal	<i>Picea mariana</i>	50.43	14.17
Boreal	<i>Rhododendron groenlandicum</i>	97.70	17.82
Boreal	<i>Prunus pensylvanica</i>	223.07	18.33
Boreal	<i>Sorbus americana</i>	290.33	20.93
Boreal	<i>Chamaedaphne calyculata</i>	103.76	24.73
Boreal	<i>Sambucus racemosa</i>	152.00	27.20
Boreal	<i>Populus tremuloides</i>	125.70	29.33
Boreal	<i>Alnus incana</i>	249.70	31.52
Boreal	<i>Abies balsamea</i>	74.84	34.44
Boreal	<i>Larix laricina</i>	139.22	34.96
Boreal	<i>Populus balsamifera</i>	108.35	35.55
Boreal	<i>Betula papyrifera</i>	255.21	35.99
Boreal	<i>Thuja occidentalis</i>	65.15	50.52
Temperate	<i>Cornus sanguinea</i>	119.18	4.35
Temperate	<i>Viburnum lantana</i>	109.94	12.50
Temperate	<i>Ulmus minor</i>	85.96	14.05
Temperate	<i>Fraxinus excelsior</i>	98.77	14.60
Temperate	<i>Acer campestre</i>	164.26	14.61
Temperate	<i>Prunus avium</i>	149.81	15.77
Temperate	<i>Acer pseudoplatanus</i>	156.41	16.00
Temperate	<i>Crataegus laevigata</i>	215.00	17.56
Temperate	<i>Carpinus betulus</i>	211.08	20.42
Temperate	<i>Tilia cordata</i>	133.02	20.51
Temperate	<i>Quercus petraea</i>	102.68	21.53
Temperate	<i>Prunus domestica</i>	129.71	21.83
Temperate	<i>Acer monspessulanum</i>	141.73	27.23
Temperate	<i>Corylus avellana</i>	112.76	30.97
Temperate	<i>Fagus sylvatica</i>	220.54	34.64
Subarctic	<i>Cornus suecica</i>	309.41	2.74
Subarctic	<i>Calamagrostis lapponica</i>	257.11	3.08
Subarctic	<i>Chamerion angustifolium</i>	151.05	4.99
Subarctic	<i>Populus tremula</i>	129.96	8.36
Subarctic	<i>Ribes spicatum</i>	299.68	11.74
Subarctic	<i>Rubus chamaemorus</i>	141.57	14.26
Subarctic	<i>Betula pubescens</i>	145.04	15.89
Subarctic	<i>Betula nana</i>	143.40	16.36
Subarctic	<i>Salix lapponum</i>	116.62	16.60
Subarctic	<i>Empetrum nigrum</i>	114.49	18.96
Subarctic	<i>Pinus sylvestris</i>	33.17	19.27
Subarctic	<i>Juniperus communis</i>	59.97	23.28
Subarctic	<i>Vaccinium uliginosum</i>	156.83	24.90
Subarctic	<i>Gymnocarpium dryopteris</i>	354.85	25.67
Subarctic	<i>Equisetum sylvaticum</i>	244.06	25.77

957 **Table S3.** Results of the variance inflation factor (VIF) to evaluate the risk of
 958 multicollinearity. VIFs are calculated for each predictor along the gradient of thresholds for
 959 multifunctionality. VIF values > 10 are indicative of collinearity (53). Abbreviations: SLA
 960 = specific leaf area.
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Thresholds (%)	SLA				Lignin			
	mean	variance	skewness	kurtosis	mean	variance	skewness	kurtosis
20%	1.763804	1.467449	1.571504	1.295088	2.829181	2.293307	2.289275	1.873138
25%	1.767599	1.467869	1.571259	1.291919	2.846828	2.305003	2.301037	1.878246
30%	1.771007	1.467302	1.570508	1.289179	2.864743	2.315496	2.312783	1.883176
35%	1.774379	1.466154	1.568978	1.286912	2.884149	2.325654	2.325517	1.888193
40%	1.780217	1.467395	1.569084	1.285545	2.909234	2.340553	2.340739	1.894271
45%	1.788577	1.472112	1.570077	1.28495	2.940437	2.361581	2.35797	1.900974
50%	1.799419	1.479081	1.571601	1.284869	2.975589	2.387186	2.378296	1.909986
55%	1.813201	1.487486	1.570502	1.283673	3.018834	2.417934	2.408234	1.924228
60%	1.827966	1.494494	1.564639	1.281	3.069451	2.452033	2.44641	1.941942
65%	1.843016	1.502622	1.553254	1.275941	3.127433	2.491887	2.489162	1.960545
70%	1.856414	1.509193	1.538382	1.269545	3.186564	2.531949	2.531384	1.977971
75%	1.866057	1.512451	1.5225	1.263681	3.235771	2.563123	2.567892	1.991849
80%	1.87056	1.512843	1.512774	1.260689	3.269124	2.579309	2.590692	1.997418

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963 **Table S4.** Results of the multiple regression models for each ecosystem function considered, and with and without considering “biome” as a random
964 effect. Abbreviations: CO₂ = cumulative soil respiration; BE_CO₂ = biodiversity effect on cumulative soil respiration; C/N_loss = absolute litter
965 C and N loss; BE_CO₂ = biodiversity effect on mass loss; AMP/NIP = soil ammonification and nitrification rates; TAN = total soil available
966 nitrogen; and SLA = specific leaf area.

A. With random effect		CO2			BE_CO2			Litter C Loss			Litter N Loss			BE_MLoss		
R ² conditional	0.13				0.12			0.16			0.24			0.15		
R ² marginal	0.37				0.13			0.78			0.59			0.34		
AIC	8596				-249.94			3212.7			4092.7			276.51		
	<i>Est.</i>	<i>SE</i>	<i>Pvalue</i>	<i>Est.</i>	<i>SE</i>	<i>Pvalue</i>	<i>Est.</i>	<i>SE</i>	<i>Pvalue</i>	<i>Est.</i>	<i>SE</i>	<i>Pvalue</i>	<i>Est.</i>	<i>SE</i>	<i>Pvalue</i>	
Mean SLA	11.6 ±	240.1	0.962	-0.053 ±	0.014	<0.001	1.921 ±	0.918	0.036	7.051 ±	2.25	0.002	0.145 ±	0.039	<0.001	
Variance SLA	-298.1 ±	146.6	0.042	-0.040 ±	0.012	<0.001	-0.247 ±	0.532	0.643	-1.312 ±	1.333	0.325	0.004 ±	0.024	0.879	
Skewness SLA	115.8 ±	118.2	0.327	-0.001 ±	0.011	0.901	0.239 ±	0.425	0.573	0.824 ±	1.068	0.44	-0.003 ±	0.02	0.887	
Kurtosis SLA	-308.3 ±	120.2	0.01	-0.036 ±	0.010	<0.001	0.051 ±	0.432	0.907	-0.526 ±	1.086	0.628	0.009 ±	0.02	0.667	
Mean Lignin	-860.1 ±	305.5	0.005	-0.055 ±	0.017	<0.001	-4.681 ±	1.221	<0.001	-8.790 ±	2.934	0.003	-0.044 ±	0.049	0.367	
Variance Lignin	-80.0 ±	145.8	0.583	0.004 ±	0.013	0.758	-0.385 ±	0.521	0.46	-1.361 ±	1.313	0.3	0.034 ±	0.024	0.156	
Skewness Lignin	-453.5 ±	154.6	0.003	-0.048 ±	0.013	<0.001	-1.049 ±	0.569	0.065	-3.729 ±	1.416	0.008	-0.017 ±	0.025	0.504	
Kurtosis Lignin	198.0 ±	122.5	0.106	0.021 ±	0.012	0.075	0.557 ±	0.435	0.201	1.476 ±	1.099	0.179	0.000 ±	0.02	0.989	
B. Without random effect		CO2			BE_CO2			Litter C Loss			Litter N Loss			BE_MLoss		
R ²	0.12				0.14			0.79			0.38			0.15		
AIC	8641				-250.94			3310.4			4273			280.19		
	<i>Est.</i>	<i>SE</i>	<i>Pvalue</i>	<i>Est.</i>	<i>SE</i>	<i>Pvalue</i>	<i>Est.</i>	<i>SE</i>	<i>Pvalue</i>	<i>Est.</i>	<i>SE</i>	<i>Pvalue</i>	<i>Est.</i>	<i>SE</i>	<i>Pvalue</i>	
Mean SLA	670.8 ±	121.7	<0.001	-0.060 ±	0.011	<0.001	4.496 ±	0.461	<0.001	5.787 ±	1.262	<0.001	0.138 ±	0.019	<0.001	
Variance SLA	-152.3 ±	111.4	0.172	-0.043 ±	0.010	<0.001	-0.150 ±	0.422	0.723	-0.958 ±	1.155	0.407	0.001 ±	0.018	0.958	
Skewness SLA	216.2 ±	115.4	0.062	-0.001 ±	0.011	0.890	0.636 ±	0.437	0.146	0.854 ±	1.196	0.476	-0.001 ±	0.018	0.959	
Kurtosis SLA	-0.6 ±	105.3	0.996	-0.038 ±	0.010	<0.001	0.731 ±	0.399	0.067	-4.426 ±	1.092	<0.001	-0.009 ±	0.017	0.592	
Mean Lignin	-465.7 ±	152.9	0.002	-0.060 ±	0.014	<0.001	-14.430 ±	0.579	<0.001	-8.414 ±	1.585	<0.001	0.101 ±	0.024	<0.001	
Variance Lignin	276.9 ±	138.0	0.045	0.008 ±	0.013	0.542	0.786 ±	0.523	0.133	-6.173 ±	1.431	<0.001	0.013 ±	0.022	0.546	
Skewness Lignin	-352.6 ±	138.1	0.011	-0.047 ±	0.013	<0.001	-3.219 ±	0.523	<0.001	-3.544 ±	1.432	<0.001	0.019 ±	0.022	0.392	
Kurtosis Lignin	82.8 ±	125.6	0.51	0.023 ±	0.011	0.044	1.332 ±	0.476	0.005	3.515 ±	1.302	<0.001	-0.006 ±	0.02	0.772	
Model Comparison																
With vs Without random effect																
ANOVA test	<0.001			N.S.			<0.001			<0.001			0.01			
Delta AIC (with - without Random effect)	-45			1			-97.7			-180.3			-3.68			

A. With random effect	C Enzyme			N Enzyme			P Enzyme			AMP			NIP			TAN		
R ² conditional	0.06117			0.01611			0.025			0.08283			0.05255			0.01022		
R ² marginal	0.06117			0.01611			0.35			0.17808			0.0682			0.88215		
AIC	65.807			1473.6			3876.6			-1776.2			1273.4			3851.5		
	<i>Est.</i>	<i>SE</i>	<i>Pvalue</i>	<i>Est.</i>	<i>SE</i>	<i>Pvalue</i>	<i>Est.</i>	<i>SE</i>	<i>Pvalue</i>	<i>Est.</i>	<i>SE</i>	<i>Pvalue</i>	<i>Est.</i>	<i>SE</i>	<i>Pvalue</i>	<i>Est.</i>	<i>SE</i>	<i>Pvalue</i>
Mean SLA	-0.047 ± 0.015		0.002	-0.014 ± 0.067		0.837	-1.987 ± 1.75		0.256	0.006 ± 0.004		0.117	-0.068 ± 0.072		0.346	-0.996 ± 1.796		0.579
Variance SLA	-0.044 ± 0.014		0.002	0.100 ± 0.062		0.107	0.022 ± 1.056		0.984	0.000 ± 0.003		0.866	-0.061 ± 0.057		0.286	-0.922 ± 1.035		0.373
Skewness SLA	-0.031 ± 0.015		0.033	0.011 ± 0.064		0.860	-0.454 ± 0.85		0.593	0.001 ± 0.002		0.779	0.006 ± 0.053		0.908	-1.809 ± 0.825		0.028
Kurtosis SLA	-0.039 ± 0.013		0.003	-0.039 ± 0.058		0.505	-0.329 ± 0.864		0.703	0.001 ± 0.002		0.659	-0.003 ± 0.051		0.958	0.546 ± 0.839		0.516
Mean Lignin	-0.079 ± 0.019		<0.001	-0.128 ± 0.085		0.129	-3.403 ± 2.245		0.13	-0.010 ± 0.005		0.040	-0.144 ± 0.085		0.092	2.195 ± 2.403		0.361
Variance Lignin	0.028 ± 0.018		0.113	-0.004 ± 0.076		0.955	0.568 ± 1.047		0.588	0.003 ± 0.003		0.369	0.055 ± 0.066		0.398	2.401 ± 1.011		0.018
Skewness Lignin	-0.061 ± 0.018		<0.001	-0.111 ± 0.076		0.148	-2.282 ± 1.117		0.041	-0.005 ± 0.003		0.106	0.037 ± 0.065		0.571	0.848 ± 1.11		0.445
Kurtosis Lignin	0.022 ± 0.016		0.164	0.019 ± 0.069		0.789	0.266 ± 0.879		0.762	0.002 ± 0.002		0.314	0.124 ± 0.057		0.031	0.548 ± 0.844		0.517
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B. Without random effect	C Enzyme			N Enzyme			P Enzyme			AMP			NIP			TAN		
R ²	0.06215			0.010			0.08			0.1698			0.07232			0.27		
AIC	63.807			1471.6			3937.1			-1773.8			1271.4			4584.5		
	<i>Est.</i>	<i>SE</i>	<i>Pvalue</i>	<i>Est.</i>	<i>SE</i>	<i>Pvalue</i>	<i>Est.</i>	<i>SE</i>	<i>Pvalue</i>	<i>Est.</i>	<i>SE</i>	<i>Pvalue</i>	<i>Est.</i>	<i>SE</i>	<i>Pvalue</i>	<i>Est.</i>	<i>SE</i>	<i>Pvalue</i>
Mean SLA	-0.047 ± 0.015		0.002	-0.014 ± 0.067		0.837	4.284 ± 0.888		<0.001	0.014 ± 0.002		<0.001	-0.1017 ± 0.055		0.063	-16.360 ± 1.748		<0.001
Variance SLA	-0.044 ± 0.014		0.002	0.100 ± 0.062		0.107	0.440 ± 0.813		0.589	-0.001 ± 0.002		0.559	-0.0561 ± 0.05		0.263	-5.444 ± 1.6		<0.001
Skewness SLA	-0.031 ± 0.015		0.034	0.011 ± 0.064		0.860	0.682 ± 0.842		0.418	0.002 ± 0.002		0.249	0.00066 ± 0.052		0.99	-3.645 ± 1.657		0.028
Kurtosis SLA	-0.039 ± 0.013		0.004	-0.039 ± 0.058		0.505	1.714 ± 0.769		0.026	0.002 ± 0.002		0.238	-0.0034 ± 0.047		0.943	-10.603 ± 1.513		<0.001
Mean Lignin	-0.079 ± 0.019		<0.001	-0.128 ± 0.085		0.13	-0.501 ± 1.115		0.654	-0.009 ± 0.003		<0.001	-0.2056 ± 0.069		0.003	-1.216 ± 2.196		0.58
Variance Lignin	0.028 ± 0.018		0.113	-0.004 ± 0.076		0.955	3.329 ± 1.007		<0.001	0.006 ± 0.003		0.02	0.06657 ± 0.062		0.283	-10.328 ± 1.982		<0.001
Skewness Lignin	-0.061 ± 0.018		<0.001	-0.111 ± 0.076		0.149	-1.350 ± 1.008		0.181	-0.003 ± 0.003		0.185	0.02723 ± 0.062		0.661	0.170 ± 1.983		0.932
Kurtosis Lignin	0.022 ± 0.016		0.165	0.019 ± 0.069		0.789	-0.631 ± 0.916		0.491	0.002 ± 0.002		0.358	0.13802 ± 0.056		0.015	4.262 ± 1.803		0.019
<hr/>																		
Model Comparison																		
With vs Without random effect																		
ANOVA test	N.S.			N.S.			<0.001			0.035			N.S.			<0.001		
Delta AIC (with - without Random effect)	2			2			-60.5			-2.4			2			-733		

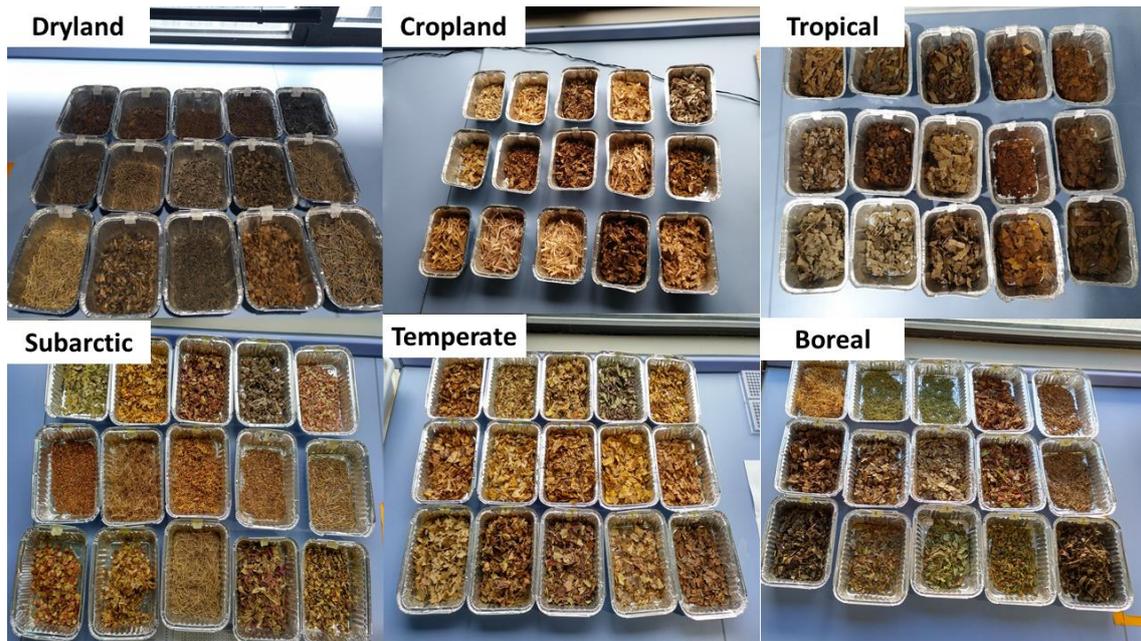
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Table S5. Results of the multiple regression models for soil bacterial and fungal diversity, and relative abundance of soil fungal pathogens and saprotrophs, with and without considering “biome” as a random effect. Abbreviations: SLA = specific leaf area.

A. With random effect	Bacterial diversity			Fungal Diversity			Pathogen			Saprotroph		
R ² conditional	0.06			0.06			0.28			0.11		
R ² marginal	0.32			0.32			0.33			0.49		
AIC	-412.27			-381.52			583.57			672.91		
	<i>Est.</i>	<i>SE</i>	<i>Pvalue</i>	<i>Est.</i>	<i>SE</i>	<i>Pvalue</i>	<i>Est.</i>	<i>SE</i>	<i>Pvalue</i>	<i>Est.</i>	<i>SE</i>	<i>Pvalue</i>
Mean SLA	0.002 ± 0.006		0.73	-0.008 ± 0.005		0.09267	-0.321 ± 0.75859		0.67	-2.046 ± 1.6342		0.211
Variance SLA	-0.001 ± 0.005		0.84	-0.008 ± 0.004		0.03575	-0.898 ± 0.63498		0.16	-0.381 ± 1.1993		0.751
Skewness SLA	0.000 ± 0.004		0.90	-0.006 ± 0.005		0.240	-0.616 ± 0.63074		0.33	-0.923 ± 0.9976		0.355
Kurtosis SLA	-0.003 ± 0.004		0.35	0.000 ± 0.004		0.86689	-1.217 ± 0.5481		0.03	0.384 ± 0.9312		0.680
Mean Lignin	0.003 ± 0.006		0.67	0.006 ± 0.006		0.22464	-1.724 ± 0.80291		0.03	0.467 ± 1.8047		0.796
Variance Lignin	0.004 ± 0.004		0.32	0.003 ± 0.005		0.381	0.919 ± 0.64937		0.16	-1.715 ± 1.0458		0.101
Skewness Lignin	0.003 ± 0.004		0.52	0.007 ± 0.005		0.09656	-0.012 ± 0.62656		0.99	1.146 ± 1.0321		0.267
Kurtosis Lignin	0.003 ± 0.003		0.31	-0.008 ± 0.004		0.064	2.087 ± 0.55156		<0.001	-2.553 ± 0.8493		0.003
B. Without random effect	Bacterial diversity			Fungal Diversity			Pathogen			Saprotroph		
R ²	0.052			0.185			0.31			0.12		
AIC	-409.52			-383.52			581.57			688.9		
	<i>Est.</i>	<i>SE</i>	<i>Pvalue</i>	<i>Est.</i>	<i>SE</i>	<i>Pvalue</i>	<i>Est.</i>	<i>SE</i>	<i>Pvalue</i>	<i>Est.</i>	<i>SE</i>	<i>Pvalue</i>
Mean SLA	0.006 ± 0.004		0.147	-0.008 ± 0.004		0.093	-0.676 ± 0.5882		0.253	-2.108 ± 1.0114		0.040
Variance SLA	0.001 ± 0.003		0.736	-0.009 ± 0.004		0.036	-0.818 ± 0.528		0.125	-0.742 ± 0.9079		0.416
Skewness SLA	-0.001 ± 0.004		0.900	-0.006 ± 0.005		0.240	-0.702 ± 0.6218		0.262	-0.719 ± 1.0691		0.503
Kurtosis SLA	0.000 ± 0.003		0.980	-0.001 ± 0.004		0.867	-1.265 ± 0.51		0.015	-0.740 ± 0.8769		0.401
Mean Lignin	0.003 ± 0.004		0.541	0.006 ± 0.005		0.225	-1.866 ± 0.6698		0.007	1.797 ± 1.1517		0.122
Variance Lignin	0.004 ± 0.004		0.354	0.004 ± 0.005		0.381	0.829 ± 0.6157		0.182	-2.167 ± 1.0587		0.044
Skewness Lignin	0.001 ± 0.004		0.819	0.008 ± 0.005		0.097	-0.116 ± 0.6045		0.848	1.306 ± 1.0395		0.212
Kurtosis Lignin	0.000 ± 0.003		0.985	-0.008 ± 0.004		0.064	2.263 ± 0.5322		<0.001	-1.438 ± 0.9152		0.120
Model Comparison												
With vs Without random effect												
ANOVA test	0.02927			N.S.			N.S.			N.S.		
Delta AIC (with - without Random effect)	-2.75			2			2			<0.001		

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Figure S1. Leaf litter from the 90 species (15 species per biome) used to build the experimental leaf litter communities.

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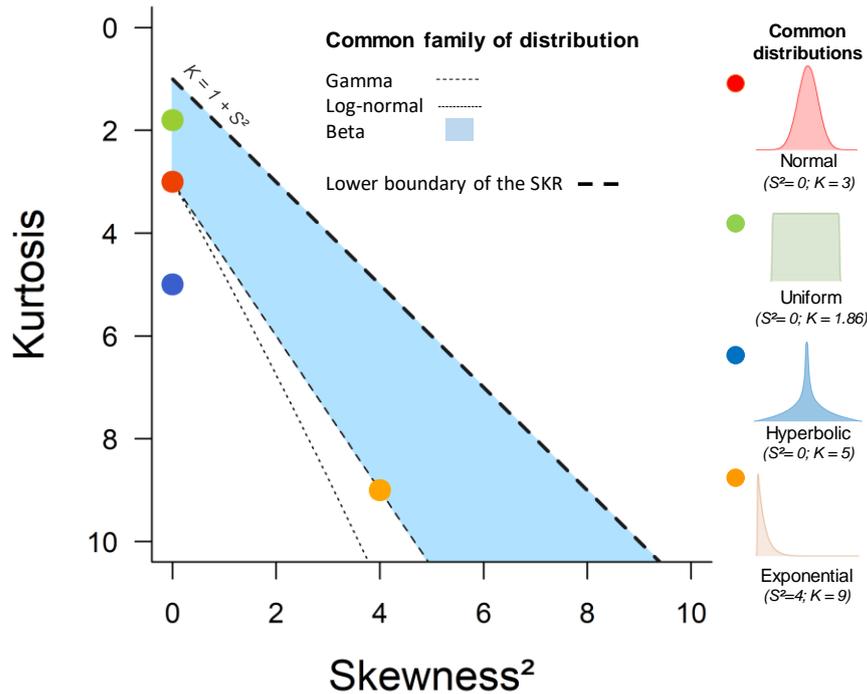
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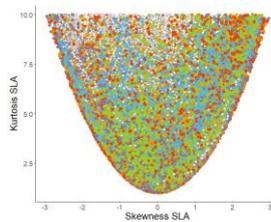
Figure S2. Examples of microcosms containing leaf litter from 15 species from each of the six biomes studied before their incubation.



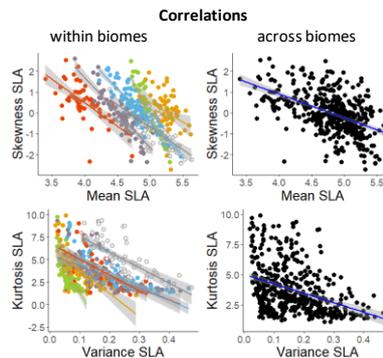
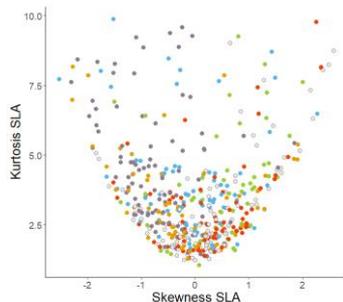
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Figure S3. The Skewness-Kurtosis Relationships (SKR) represented in the Cullen and Frey graph (54). The SKR is a common tool in statistics to assess complex distributions. We represent the location of common distributions that can be either a constant (e.g. the normal, uniform, hyperbolic secant and exponential distributions), a line (e.g. the gamma distribution, the lognormal distribution), or a surface (e.g. the beta distribution). We also indicate the location of the empirical SKRs for specific leaf area and maximum plant height (green and red dashed lines, respectively). The SKR has a lower boundary below which no kurtosis value can be observed for any degree of skewness. The lower boundary corresponds to the Bernoulli distribution.

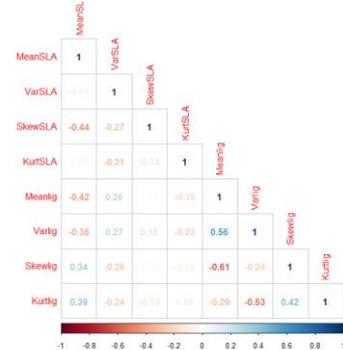
Step 1. Generating 120,000 theoretical trait distributions through the manipulation of the relative abundance of the 15 species present in each litter mixture



Step 2. Sub-setting 570 assemblages minimizing within- and across-biome correlations among moments (mean, variance, skewness, kurtosis)



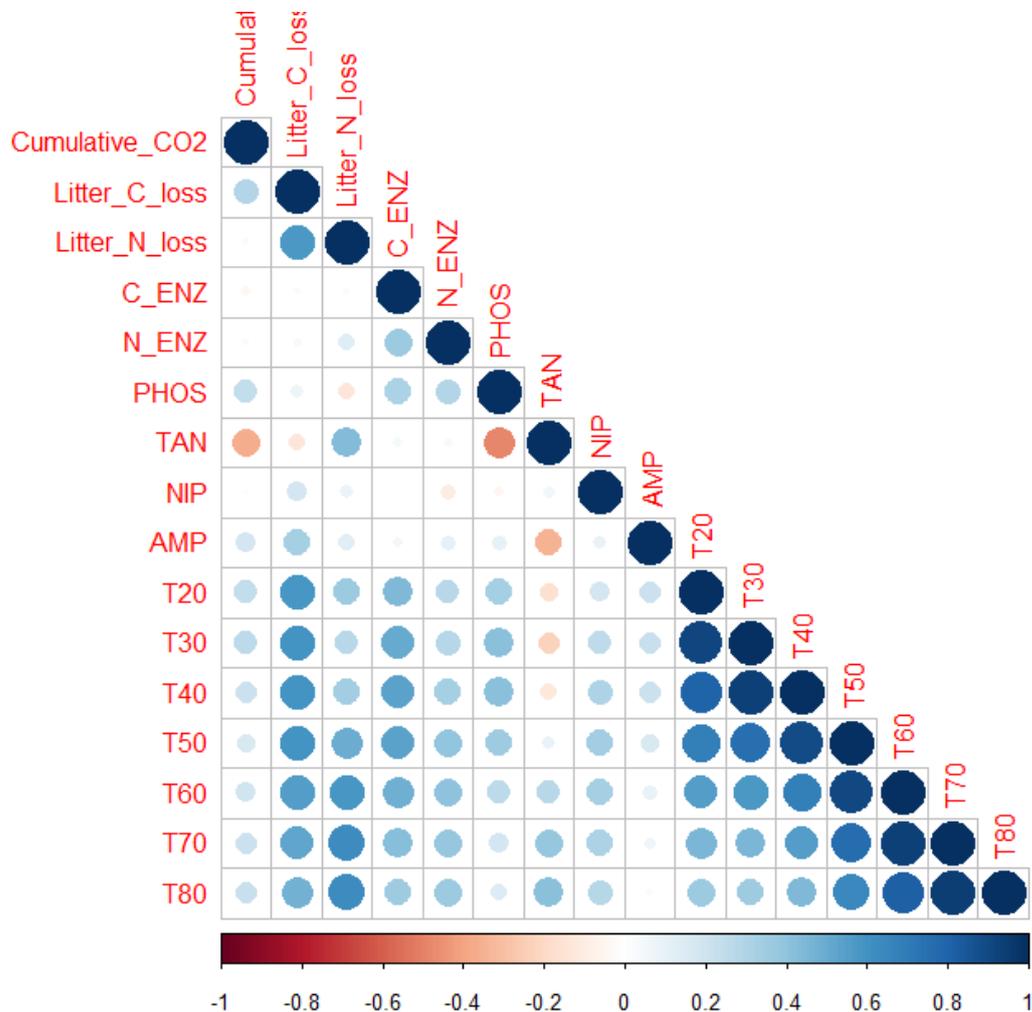
Step 3. Controlling for the across-biome correlations among moments (mean, variance, skewness, kurtosis) in the litter mixtures



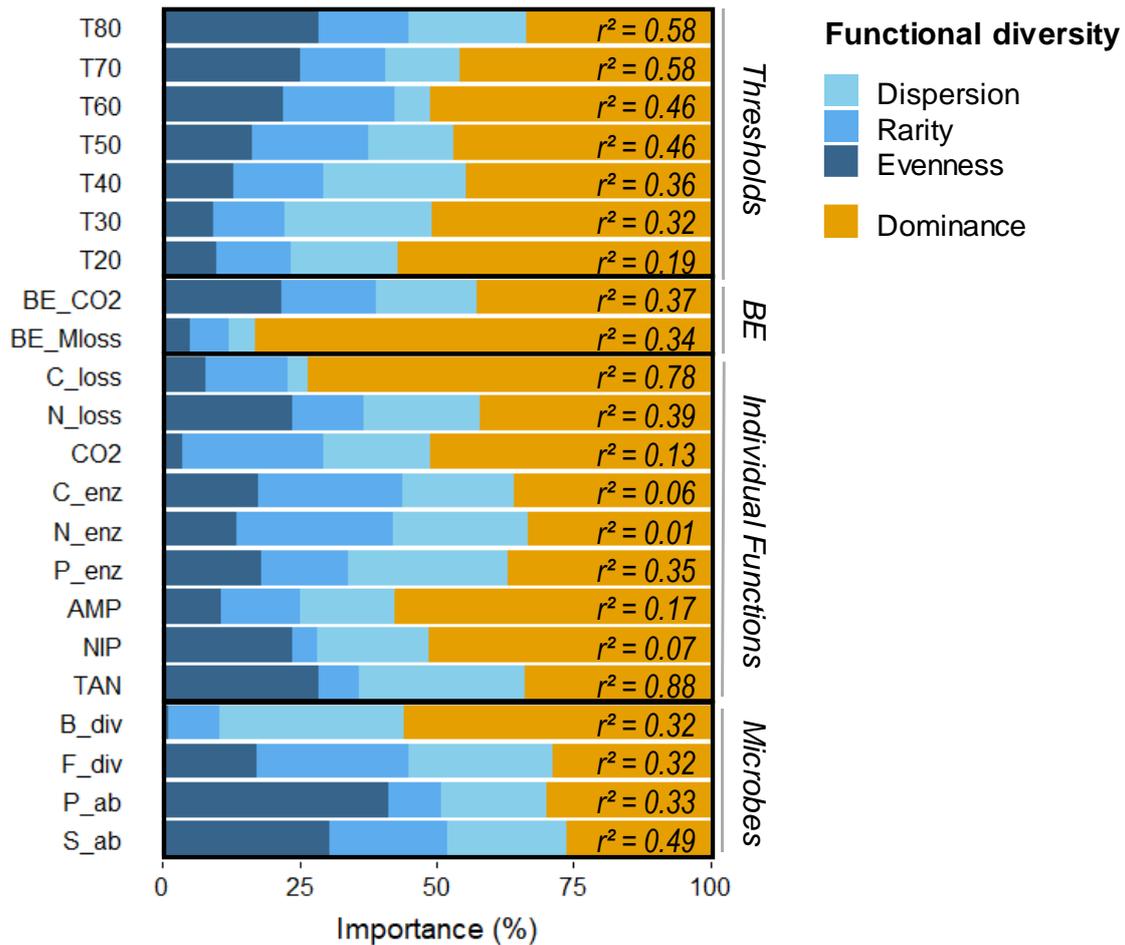
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1031 **Figure S4.** Detailed experimental and analytical framework used in the study. We present
 1032 the three steps followed to set-up the 570 leaf litter assemblages. The assemblages
 1033 covered the entire range of values that functional dominance and diversity explored by
 1034 the simulations could take, while minimizing their correlations within and across biomes.
 1035 Abbreviations: SLA = specific leaf area.

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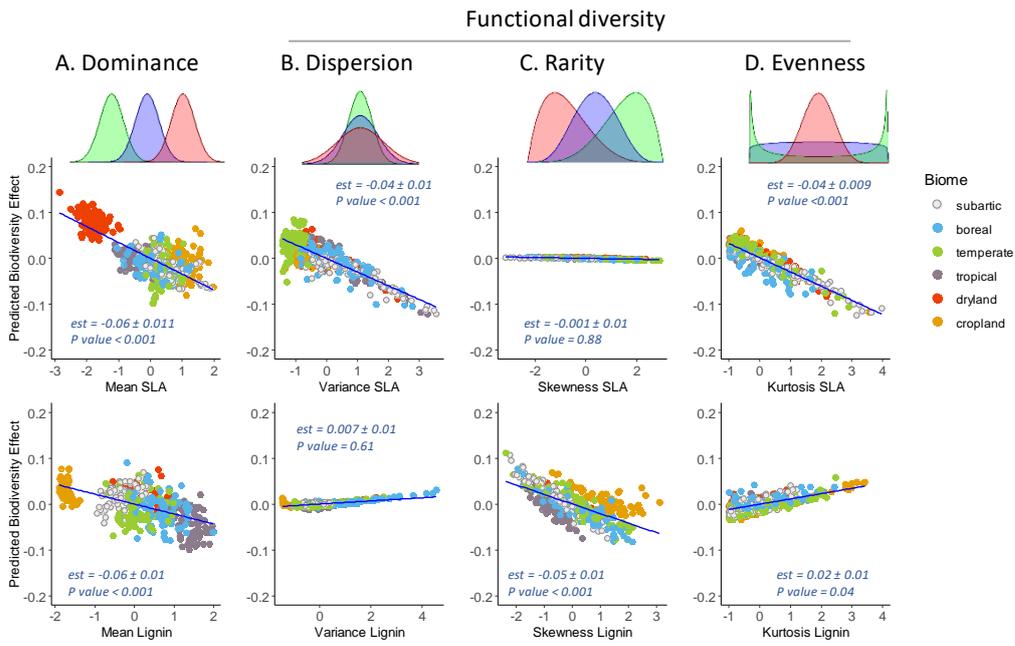


1038 **Figure S5.** Correlations among the nine functions, and with the multifunctionality-
 1039 thresholds considered. Abbreviations: T = multifunctionality thresholds; Litter C/N_loss
 1040 = absolute litter C and N loss; CO2 = cumulative soil respiration; C/N/P_enz = soil
 1041 enzymatic activities related with C, N, and P cycling; AMP/NIP = soil ammonification
 1042 and nitrification rates; TAN = total soil available nitrogen; PHOS = phosphatase.
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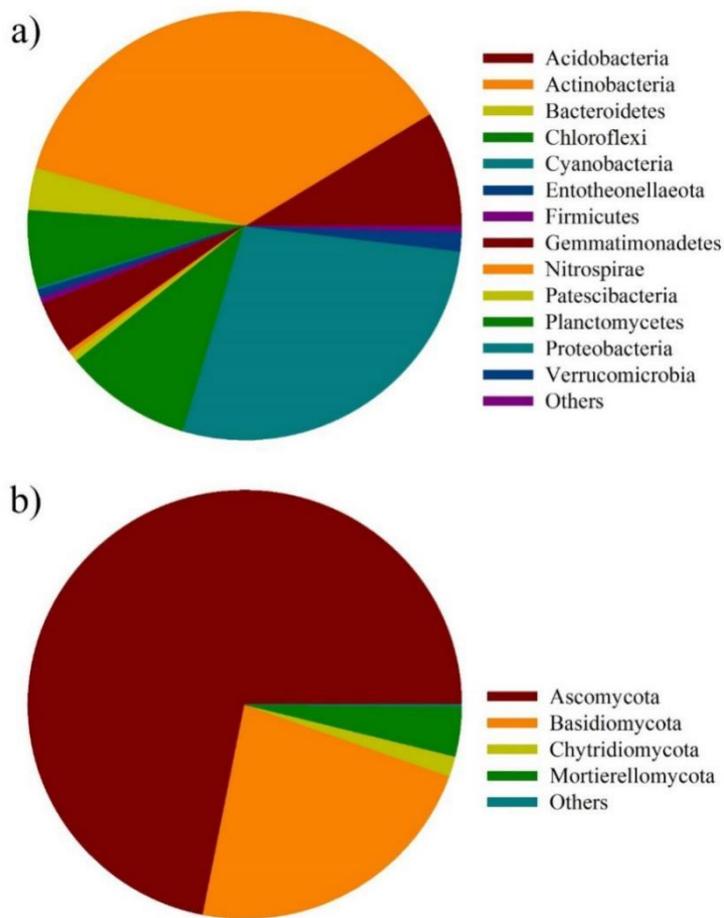
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Figure S6. Contribution of functional diversity and dominance to multifunctionality thresholds, individual (litter and soil) functions and soil communities. Models included “biome” as a random factor. The importance of predictors is expressed as the percentage of explained variance (model adj. 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; CO2 = 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; P/S_ab = relative abundance of soil fungal pathogens and saprotrophs.



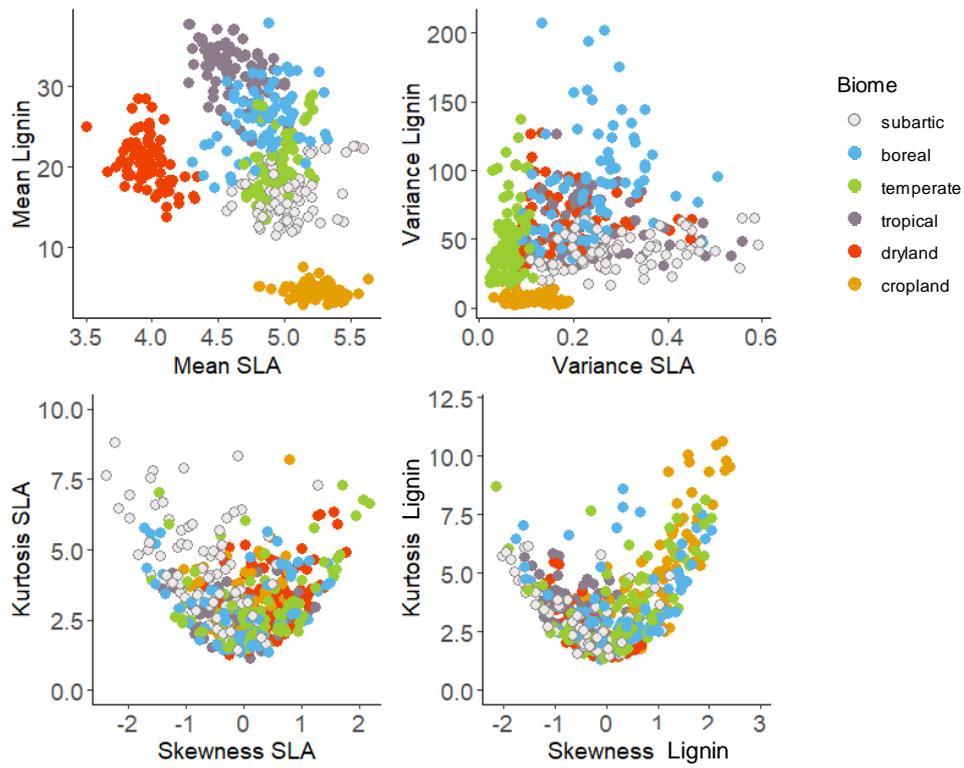
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Figure S7. Effects of functional dominance, dispersion, rarity and evenness on the biodiversity effect for soil respiration. Dots represent model partial residuals. We provide for each predictor the averaged parameter estimates (est) across thresholds \pm standard deviation and the P value. Abbreviations: SLA = specific leaf area.



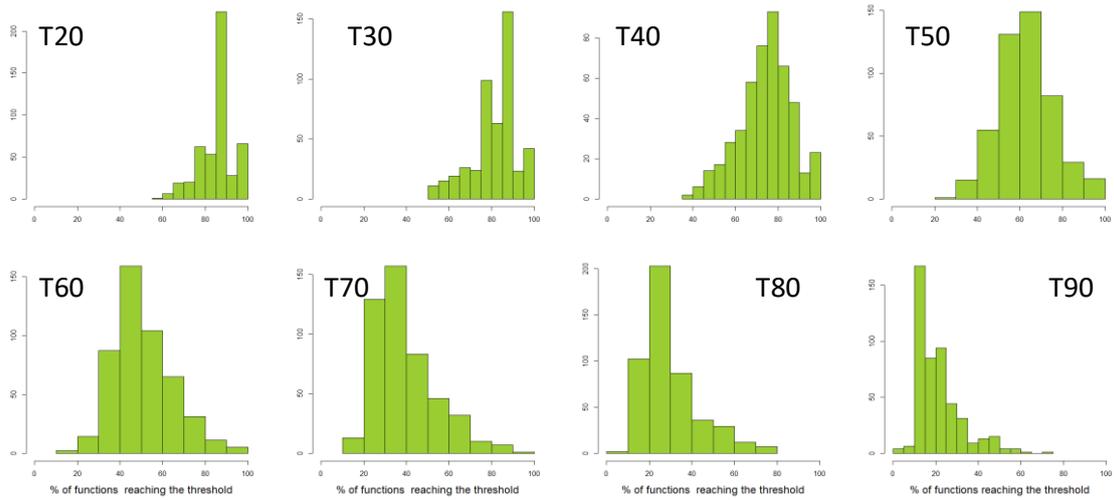
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Figure S8. Relative abundance of the soil bacterial (a) and fungal (b) phyla/classes. n = 95.



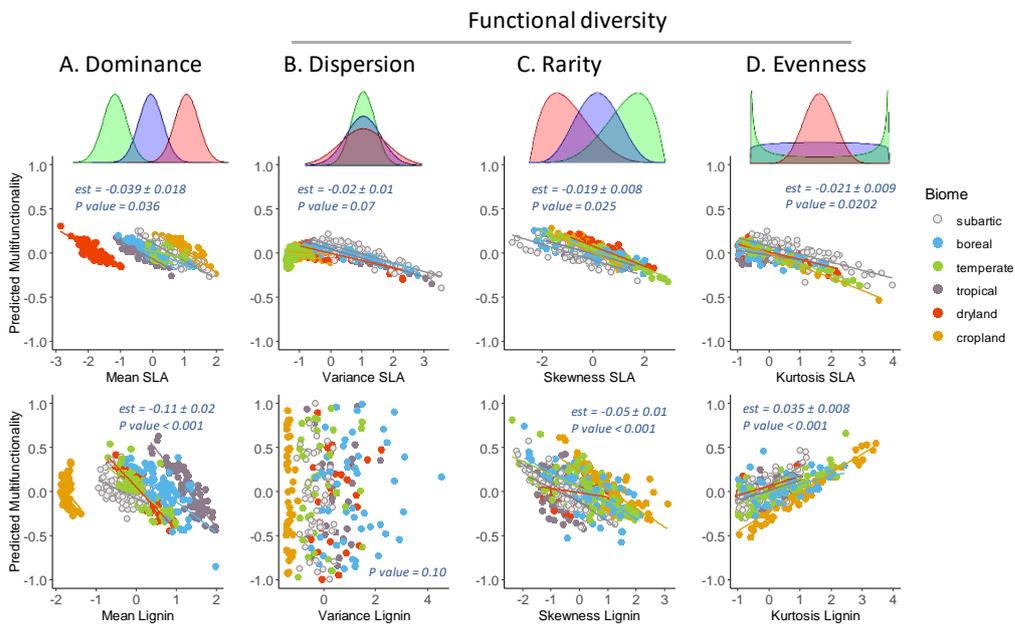
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Figure S9. Correlations among moments (mean, variance, skewness and kurtosis) for the 570 leaf litter assemblages studied. Abbreviations: SLA = specific leaf area



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Figure S10. Distribution of the threshold-based multifunctionality for thresholds between 10 and 100%. Abbreviations: T = multifunctionality thresholds.



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Figure S11. Effects of functional dominance, dispersion, rarity and evenness on ecosystem multifunctionality. Models included “biome” as a random factor. Dots represent model partial residuals. We provide for each predictor the averaged parameter estimates (est) across thresholds \pm standard deviation and the P value. Abbreviations: SLA = specific leaf area.

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