



Competitive network determines the direction of the diversity–function relationship

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The structure of the competitive network is an important driver of biodiversity and coexistence in natural communities. In addition to determining which species survive, the nature and intensity of competitive interactions within the network also affect the growth, productivity, and abundances of those individuals that persist. As such, the competitive network structure may likewise play an important role in determining community-level functioning by capturing the net costs of competition. Here, using an experimental system comprising 18 wood decay basidiomycete fungi, we test this possibility by quantifying the links among competitive network structure, species diversity, and community function. We show that species diversity alone has negligible impacts on community functioning, but that diversity interacts with two key properties of the competitive network—competitive intransitivity and average competitive ability—to ultimately shape biomass production, respiration, and carbon use efficiency. Most notably, highly intransitive communities comprising weak competitors exhibited a positive diversity–function relationship, whereas weakly intransitive communities comprising strong competitors exhibited a negative relationship. These findings demonstrate that competitive network structure can be an important determinant of community-level functioning, capturing a gradient from weakly to strongly competitive communities. Our research suggests that the competitive network may therefore act as a unifying link between diversity and function, providing key insight as to how and when losses in biodiversity will impact ecosystem function.

competitive intransitivity | basidiomycete | interference | community assembly | ecosystem function

The relationship between biological diversity and ecosystem functioning is a central question in ecology and conservation, providing tangible links between natural systems and the provision of ecosystem services to humans. In recent decades, a wealth of studies have explored how ecosystem functioning responds to changes in various types of diversity (e.g., species, trait, or phylogenetic diversity), revealing the highly idiosyncratic nature of this relationship across systems (1). Functionally unique species with mutually exclusive resource requirements can exhibit greater productivity in diverse communities (2), whereas highly similar species with overlapping niches exhibit minimal increases in functioning as diversity increases (1, 3). Although the field of biodiversity–ecosystem function (BEF) research continues to gain momentum, the sheer complexity of ecological communities complicates the search for unifying patterns (1). As such, in most systems, we still lack the ability to predict a priori how changes in biodiversity will alter ecosystem function.

The BEF relationship is often linked to the degree of functional redundancy, complementarity, or niche overlap among species (4–6). Yet this relationship can alternatively be formulated in terms of the nature, variability, and intensity of competitive interactions among species (7–9). Competitive dynamics and competitive relationships among species can attenuate or reverse BEF relationships (10–13), driven by both the direct effects of competition (e.g., reductions in per capita growth rate) and indirect effects (e.g., community turnover or overyielding

of dominant species). Thus, the structure of the competitive network—that is, the complete set of pairwise competitive outcomes among species (14)—should play an important role in the BEF relationship by dictating the nature and intensity of competitive interactions (and corresponding functional costs) exhibited across species in the community. Although the structure of the competitive network is increasingly acknowledged as an important driver of biodiversity and coexistence in competitive communities (14–16), whether or not the competitive network likewise affects ecosystem function remains largely untested.

Here, we explore how the competitive network interacts with species richness to determine the BEF relationship in competitive fungal communities. We focus on two measures of the competitive network: (i) competitive intransitivity (a continuous measure of the extent to which the community exhibits rock–paper–scissors relationships) and (ii) mean competitive ability (a continuous measure of how competitive the individuals in the community are, based on fully factorial pairwise interactions). These two properties were selected because of their importance in determining biodiversity and coexistence patterns across systems (15–17). We use a saprotrophic basidiomycete fungal community for several reasons. First, these organisms provide a tractable means of measuring the full set of pairwise competitive outcomes among species, thereby allowing us to precisely quantify the full competitive network (15). Second, our knowledge of the mechanisms underlying the BEF relation remains particularly elusive in fungal and bacterial systems (18–20), in part due to complex competitive dynamics that drive both positive and

Significance

Diverse communities typically have higher functional potential (e.g., biomass production) because species use different resources and respond to different environmental cues. Yet, in highly competitive communities, individuals often grow less efficiently together due to intense competition for shared resources. Here, we show that the structure of the competitive network (i.e., who beats who) ultimately determines whether an increase in diversity leads to an increase or a decrease in functioning. The diversity–function relationship depended both on whether communities exhibited “rock–paper–scissors” (i.e., intransitive) dynamics, and whether they comprised strong versus weak competitors. These results highlight that knowledge of the competitive network may be integral for predicting when losses in biodiversity will have positive or negative effects on ecosystem function.

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negative BEF relationships (21–25). Last, basidiomycete fungi comprise an important functional guild from a carbon cycle perspective, being the dominant decomposers of recalcitrant organic material in forested ecosystems (26–29). Understanding how and when diversity affects function in basidiomycete communities therefore has important secondary implications for terrestrial carbon storage (30).

Using a set of 18 unique fungal species with previously measured traits, phylogenies, and competitive hierarchies (15, 31) (Table S1, Fig. S1, and Dataset S1), we explored how increasing levels of species richness interacted with the competitive network structure to determine community function. We selecting 150 unique communities comprising 3, 6, or 12 unique fungal species, with 50 unique communities per richness level (Materials and Methods and Dataset S2). Functioning was measured via biomass production, respiration, and carbon use efficiency (CUE; the ratio of carbon allocated to biomass vs. respiration), and we focus predominantly on CUE throughout, given its central role as a net measure of overall organismal function in fungi and bacteria (32). To capture the structure of the competitive network, we first competed all fungi against each other in all pairwise combinations (Dataset S1) (15). These outcomes were then used to calculate continuous measures of “average competitive ability” and “competitive intransitivity.” Both of these metrics vary between 0 and 1: A value of 0 indicates a community that is perfectly hierarchical or comprises the weakest competitors, and a value of 1 indicates a community that is perfectly intransitive or comprises the strongest competitors (Fig. S2; see also Materials and Methods and SI Materials and Methods). Using these network metrics, we quantified how species richness, intransitivity, and competitive ability interactively determine biomass production, respiration, and CUE.

Due to inherent relationships among network properties, some network structures and corresponding diversity–function patterns may be exceedingly rare in natural systems. For example, at high richness levels, it is increasingly unlikely that communities comprising weak competitors will, by chance alone, happen to exhibit a perfectly hierarchical structure, since these weak competitors, by definition, have low rates of overgrowth. Alternatively, because of the law of large numbers, the average competitive ability of species in a community should start to converge to 0.5 at high richness levels (e.g., Fig. S2). Such phenomena are not otherwise reflected in statistical models. Thus, to gain insight into how such constraints might alter the “realized” diversity–function patterns across the landscape, we secondarily used a simulation approach to quantify the BEF patterns that emerge across a broad set of communities. We randomly selected 20,000 unique communities comprising the 18 fungal isolates (richness ranging from 3 to 12), and used the statistical models to calculate the CUE of each community (Materials and Methods). By reflecting the underlying relationships and constraints between competitive network properties, this complementary approach allows us to explore how the statistical patterns scale to larger metacommunities.

Results and Discussion

Without accounting for competitive network properties, an increase in species richness was not correlated with changes in biomass (Fig. 1A; $\beta = 0.001$, $P = 0.37$), nor with respiration (Fig. 1B; $\beta = 0.002$, $P = 0.10$), or CUE (Fig. 1C; $\beta = -0.0002$, $P = 0.83$), such that richness explained <1% of the variation in each of these functional outcomes. These same fungal species were previously found to exhibit reductions in biomass and CUE in mixtures relative to monoculture (31), such that our expectation was that increases in diversity would lead to further reductions in functioning. Yet the null effect of richness instead suggests that the induced costs of competition at the individual level are relatively fixed, regardless of the number of competitors present. Conversely, the fact that these communities likewise failed to exhibit a positive BEF relationship is in line with traditional BEF theory, given that the microcosms were intentionally designed to provide minimal opportunities for niche differentiation, facilitation, or environmentally driven species averaging, which can otherwise drive significant positive BEF relationships (7, 24, 25).

However, once the competitive network variables were included in the model, there emerged strong pairwise interactions among intransitivity, competitive ability, and richness (Fig. 2 and Table S2). The coefficients for CUE largely mirrored the net response of the biomass and respiration functional endpoints (Fig. 2), reflecting the fact that CUE is calculated as the net allocation of carbon (C) to growth versus respiration. CUE was affected by a significant negative interaction between richness and competitive ability ($\beta = -0.27$, $P = 0.006$), driven by their positive interactive effects on respiration and null interactive effect on biomass. CUE was likewise influenced by a significant richness-by-intransitivity interaction due to the positive interactive effects of these variables on biomass and null interactive effect on respiration. With all other variables held constant at their mean (including species richness), more competitive communities exhibited significantly lower CUE ($\beta = -0.39$, $P < 0.001$), whereas more intransitive communities exhibited higher CUE ($\beta = 0.37$, $P = 0.03$). These results suggest that the links between diversity and function differ markedly in communities with different competitive network structures, with both competitive intransitivity and mean competitive ability being significant drivers of community functioning.

Most strikingly, when plotted against a range of intransitivity and competitive ability values, the slope of the diversity–function relationship depended on the interactions between intransitivity and mean competitive ability (Fig. 3). Among highly intransitive communities, an increase in richness increased biomass production, with this effect tapering off for more competitive communities at high intransitivity (Fig. 3A, blue portion). In contrast, the effect of richness on respiration was more strongly influenced by the average competitive ability of the community, such that highly competitive communities exhibited higher respiration in response to increasing richness (Fig. 3B, red portion), whereas weakly competitive communities exhibited lower respiration with

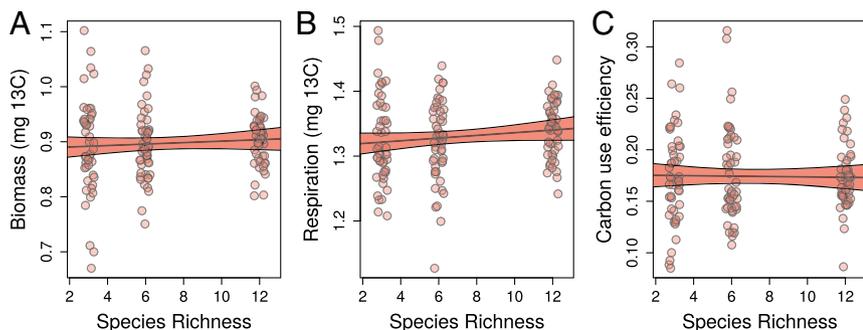


Fig. 1. The mean relationships between species richness and biomass, respiration, and CUE. Without accounting for competitive network properties, an increase in species richness was unrelated to (A) biomass, (B) respiration, or (C) CUE. Richness explained <1% of the variation in each of these functional outcomes ($n = 46$).

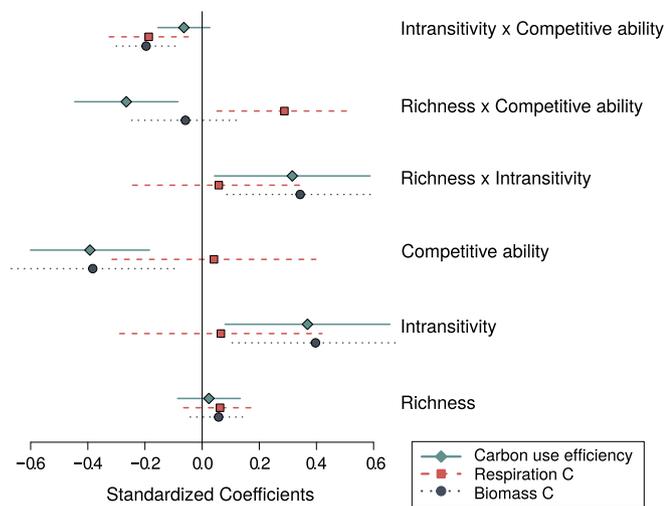


Fig. 2. Standardized effect sizes linking richness, intransitivity, and competitive ability to biomass, respiration, and CUE. Shown are the effect sizes with corresponding 95% CIs. Variables were standardized to have a mean of 0 and an SD of 1, such that the main effects are interpretable as the change in the outcome with all other variables held constant at their mean. The full regression models explained 68% of the variation in biomass, 47% of the variation in respiration, and 58% of the variation in CUE. Biomass and CUE largely showed matching trends, driven by the fact that biomass was more closely linked to CUE than to respiration (Fig. S3). Both biomass and CUE showed significant relationships with competitive ability, intransitivity, and richness. Respiration responded most strongly to the interaction between richness and competitive ability, and the interaction between intransitivity and competitive ability ($n = 146$).

increasing richness (Fig. 3B, blue portion). Combined, the contrasting interactions with intransitivity (for biomass) and competitive ability (for respiration) led to a positive diversity effect on CUE only among highly intransitive communities comprising weak competitors ($\sim 10\%$ absolute increase, Fig. 3C, blue portion). In all other settings, an increase in richness led to an absolute decrease in CUE of as much as 5% (Fig. 3C, red portion), with this reduction being strongest in highly competitive communities with low intransitivity (Fig. 3C, upper left corner).

These results illustrate that the impact of diversity on fungal function exists along a continuum of competitive dynamics. In the absence of other ecological forces, communities strongly structured by competition may exhibit negative diversity–function relationships, due to greater investment in competitive activities with the addition of more competitors. Conversely, communities minimally structured by competition may instead exhibit positive diversity–function relationships. These positive relationships might arise because of negligible negative effects of competitive interactions on individual productivity, or, in fungal-specific cases, potentially due to greater investment in defensive activities that increase biomass [i.e., defensive wall building to prevent overgrowth by competitors (31)]. Quantifying the relative influences of exploitative versus interference competition may help to resolve why such a broad range of diversity–function relationships is observed for fungal communities (22, 24, 25, 33).

An often overlooked aspect of competitive network theory is that some competitive network structures are correlated with species richness, and should therefore become more or less likely to occur in diverse communities. Indeed, when our results were applied to 20,000 randomly selected communities, clear patterns emerged between CUE and richness (Fig. 4) that were not otherwise evident from the statistical models. In line with our empirical results, intransitive, strongly competitive communities had a neutral richness relationship ($\beta = 0.001$, $P = 0.273$; Fig. 4A), and hierarchically structured, weak competitors had a slightly positive relationship between CUE and richness ($\beta = 0.004$, $P < 0.001$; Fig. 4B). However, both of these community types became increasingly rare at higher richness levels—reflecting inherent constraints between network properties—such that they comprised less than 1% of the communities with more than 10 species. The low abundance of hierarchically structured, weak competitors is presumably due to the fact that weak competitors, by definition, have poor displacement ability, such that a random assemblage of weak competitors is unlikely to exhibit sufficient displacement to establish a perfectly hierarchical community. Conversely, the low abundance of intransitive, strong competitor communities is likely because strong competitors have high displacement ability, such that it becomes increasingly unlikely that a random assemblage of these species will exhibit perfect rock–paper–scissors relationships as the number of species increases. Collectively, these results suggest that these two network structures and their corresponding BEF relationships should be exceedingly rare in natural systems.

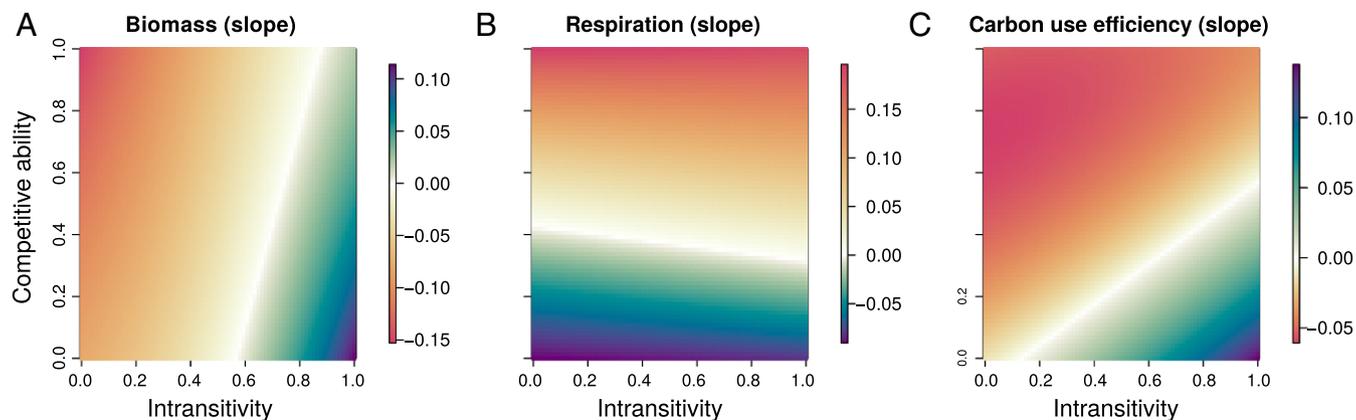


Fig. 3. The effect of diversity on function. Shown are the marginal coefficients (slopes) denoting the change in functional outcomes for an increase in richness of three species, plotted across the full range of intransitivity and competitive ability values. Red denotes a decrease in functioning, and thus corresponds with a decrease in biomass and CUE in A and C, but an increase in respiration in B. (A) Increasing richness corresponds to a decrease in biomass for everywhere except highly intransitive communities, where the increase in biomass is stronger at lower levels of competitive ability. (B) Highly competitive communities (> 0.4) exhibited an increase in respiration with the addition of more species (red), with this effect negligibly modified by intransitivity ($P > 0.10$ for the interaction). (C) An increase in richness corresponds to a decrease in CUE for all but the least competitive communities. Among weak competitors, an increase in richness translates to an increase in CUE (blue portion, lower right), with this effect being more pronounced at high intransitivity levels ($n = 146$).

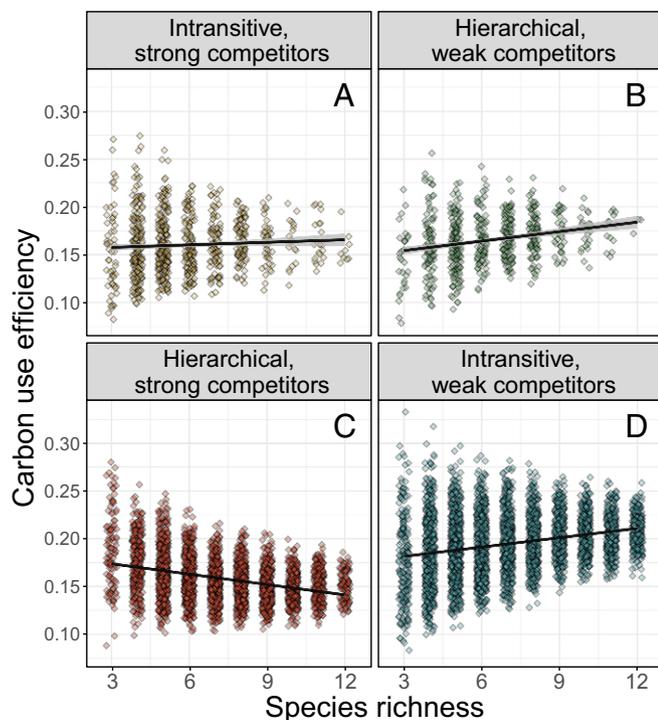


Fig. 4. The realized patterns between richness and CUE across a random sample of communities: 20,000 randomly sampled communities were divided into high vs. low intransitivity and high vs. low competitive ability based on the 33rd and 66th percentiles across all communities. In line with the model predictions, (A) intransitive communities comprising strong competitors and (B) hierarchical communities comprising weak competitors showed moderate positive relationships. However, these two types of communities became increasingly rare as richness increased, ultimately comprising <1% of all communities with 10 or more species. At these higher richness levels, three clear groups emerged, each with pronounced differences in the slope of the BEF response: (C) Hierarchical communities comprising strong competitors exhibited a negative diversity–function relationship; (D) highly intransitive communities comprising weak competitors exhibited a positive diversity–function relationship; and, last, communities that fell into none of these four categories (data shown in Fig. S4) exhibited a null relationship between diversity and function. Thus, although on aggregate there appears to be no link between diversity and function (Fig. 1 and Fig. S4), this result can be attributed to offsetting BEF relationships between these different network structures (see *SI Discussion*).

At higher richness levels, the two most common network structures were intransitive communities comprising weak competitors and hierarchical communities comprising strong competitors (Fig. 4 C and D). The markedly different diversity–function relationships between these two groups highlights that the competitive network has the potential to promote fundamentally different diversity–function relationships across the landscape. Nevertheless, if we ignore the differential responses of these four groups, the overall relationship between diversity and function across all 20,000 communities is negligible (Fig. S4)—as seen in the experimental results (Fig. 1)—highlighting that these offsetting BEF patterns essentially negate each other when taken on aggregate (see *SI Discussion*). Thus, at the landscape level, these findings illustrate that knowledge of the competitive network can help to disentangle underlying BEF relationships by identifying which subsets of communities are likely to display significant positive or negative diversity–function responses.

These results suggest that intransitivity is not only critical for maintaining diversity (14, 15), but is also a key driver of productivity and efficiency in competitive communities. Yet exactly how intransitivity affects community-level functioning is not immediately apparent. From a coexistence perspective, intransitive loops

can provide a type of indirect benefit (or harm) to species by reducing the importance of direct pairwise outcomes (i.e., “the enemy of my enemy is my friend”) (15, 34). Analogous to indirect interactions in food webs (35), species’ abundances in competitive communities can thus be an emergent byproduct of the full set of interactions within the community (14, 36). From a functional perspective, it is therefore plausible that intransitivity predicts functional outcomes because it captures the net costs of these indirect interactions, and thereby reflects the average intensity of competition perceived by each individual. If indeed this is the case, then, as with trophic systems (37), the importance of intransitivity as a driver of functioning will likely depend on the relative importance of direct vs. indirect interactions in the system.

Intransitive competition and competitive hierarchies are important drivers of coexistence and biodiversity in nonfungal communities [e.g., grassland plant communities (16, 38)]. Nevertheless, an important outstanding question is whether or not these results extend to other systems. Indeed, the observed patterns among richness, intransitivity, competitive ability, and functioning are certain to be context-dependent, even among fungal communities. Some fungi (e.g., basidiomycetes, as used here) are known to prioritize competitive behaviors relative to other fungi (28), with these behaviors heavily modified by environmental conditions (18, 31, 39, 40). Alternately, in communities where interspecific interactions alter functioning predominantly via indirect changes in community composition or by differential responses to environmental variability—rather than via direct competitive interactions—the links between diversity and function should depend more strongly on the correlations between competitive ability and functioning (11, 12).

Over long timescales, or in the presence of environmental variability, various ecological processes such as species averaging, overyielding, or selection effects may overwhelm the short-term relationships observed here (4, 5, 25, 41). Such long-term processes should be particularly relevant in systems where the functional endpoint of interest (e.g., plant primary productivity) correlates strongly with competitive ability or environmental conditions, such that changes in community composition or environmental conditions correlate with predictable changes in community functioning (41). Disentangling the importance of direct effects (induced changes in functioning) vs. indirect effects (changes in functioning due to community turnover) is therefore an important next step for identifying when and where induced competitive costs scale to long-term patterns (42). Nevertheless, by showing that the competitive network structure has the potential to play a key role in linking diversity to function, we demonstrate a mechanism by which species interactions directly determine the strength and direction of the BEF relationship. The relative importance of this mechanism in situ will only be revealed by exploring its context dependency and its importance in relation to other biotic and abiotic controls.

Conclusion

We demonstrate that two key aspects of the competitive network structure—intransitivity and average competitive ability—interactively determine the direction and magnitude of the diversity–function relationship in a competitive fungal system. Our results suggest that the competitive network structure captures a continuum from highly competitive communities to minimally competitive communities, with these groups having widely different functional responses to increasing richness. In communities strongly structured by competitive activities (highly competitive, weakly intransitive assemblages), diversity had a negative effect on functioning, whereas, in communities with minimal investment in competition (weakly competitive, highly intransitive assemblages), diversity had a positive effect. By demonstrating that intransitivity can dictate functioning as well as diversity, our results identify a potential mechanism underpinning diversity–function relationships in competitive communities.

held constant at their mean), which gives the slope of the diversity–function relationship (or “diversity effect”) for any given competitive network structure.

Quantifying Patterns Across Communities. Some competitive network structures are more likely than others to occur in a random sample of communities, due to correlations among variables and species. Thus, we used a simulation approach to explore how the relationships identified in our statistical models might translate to patterns in functioning across a much larger random sample of communities. We selected, at random, 20,000 unique communities from among the ~350,000 possible, with species richness ranging from 3 to 12 species, and each community combination drawn from the 18 species used in the experiment. We then used the model-derived parameters to predict the CUE of each community. To explore the relative contribution of intransitivity and competitive ability, the communities were then split into high vs. low intransitivity and high vs. low mean

competitive ability based on the <33rd and >66th percentiles of each of these values across all 20,000 communities. These four groups (low intransitivity and low competitive ability, low intransitivity and high competitive ability, high intransitivity and low competitive ability, and high intransitivity and high competitive ability) were then plotted, and simple linear regression was used to capture the resulting relationship between diversity and function among these four groups. This approach therefore reflects how innate relationships among variables among and between species can constrain or modulate the metacommunity patterns, thus capturing the “average” relationships that might be likely to occur under random community assembly.

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