Competitive network determines the direction of the diversity–function relationship

Daniel S. Maynard\textsuperscript{a,b,1}, Thomas W. Crowther\textsuperscript{c,d}, and Mark A. Bradford\textsuperscript{b}

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 (4–6). 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 insights as to how and when losses in biodiversity will impact ecosystem function.

---

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.

Author contributions: D.S.M., T.W.C., and M.A.B. designed research; D.S.M. and T.W.C. performed research; M.A.B. contributed new reagents/analytic tools; D.S.M. analyzed data; and D.S.M. wrote the paper.

The authors declare no conflict of interest.

This article is a PNAS Direct Submission. Published under the PNAS license.

1To whom correspondence should be addressed. Email: dmaynard@uchicago.edu.

This article contains supporting information online at www.pnas.org/cgi/doi/10.1073/pnas.1712211114/DCSupplemental.
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
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, intraspecifically, strongly competitive communities had a neutral richness relationship ($\beta = 0.001$, $P = 0.273$; Fig. 4D), 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 intraspecific, 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. 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 (~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).

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, strongly a decrease in functioning; and blue, correspondingly, 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 functional traits (18), with these behaviors heavily influenced 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.
Materials and Methods

Fungal isolates. The 18 wood decay basidiomycete fungal isolates used in this study have been previously discussed in detail (15, 31) (see SI Materials and Methods, Table S1, Fig. S1, and Dataset S1). All were obtained from the US Forest Service Center for Forest Mycology Research, and were originally collected from fruiting bodies on dead wood in the early to middle stages of decay. All species are endemic to mixed-hardwood forest throughout North America, with most having widespread global distributions. These 18 species were selected to capture a range of taxonomic, phylogenetic, and functional diversity values, while also ensuring that all species are prominent decomposers of dead wood during at least a portion of their life cycle. The original species pool included 23 unique species and 37 total unique isolates (15). Eighteen of these species were selected for inclusion here, based on those that showed adequate growth over the course of 20 d (at least 2-cm-diameter radial expansion). Large subunit (LSU) and internal transcribed spacer (ITS) sequences for these 18 isolates are available in GenBank (accession numbers KK065932–KK065968 and KK065969–KK066002), as submitted in ref. 15.

Community Selection. Following the approach outlined in Dias et al. (43), communities were selected from among the ~37,000 possible combinations using a stratified random sampling scheme to ensure that each richness level included a range of competitive abilities and intransitivity values. Specifically, for each richness level, communities were divided into high vs. low competitive ability crossed with high vs. low intransitivity, and communities were selected at random from each of these four quadrants (~12 communities for each combination for each richness level). The benefit of this approach is that it has the statistical power to identify underlying mechanistic relationships; the drawback is that it may not necessarily reflect which relationships (and functional outcomes) are most common across the metacommunity. Thus, we subsequently conducted a simulation experiment to explore how these model-based relationships scale to a fully random selection of communities (Quantifying Patterns Across Communities).

Microcosm Design. Following traditional diversity-function study designs (41, 44, 45), all microcosms, including the monocultures, were “seeded” with the same initial number of fungal colonies, regardless of richness level, thus ensuring that any resulting effects were not confounded by differing colony densities among treatments. All plugs of each species were taken from a single colony, such that, after meeting other genetically identical individuals, they would fuse to form a single cohesive colony. However, some degree of “intraindividual” aggression is expected (e.g., a time delay before fusion), so that our design should be interpreted as quantifying the effect of species richness after accounting for intraindividual effects (31). Previous work showed that 10 d was sufficient for identifying the costs of competing communities (31). We extended this time period to 20 d to better capture complex community dynamics that may not manifest over shorter time periods (e.g., combative species overgrowing close neighbors but then deadlock after species on the other side of the dish). To account for this longer time period, we increased the C in the media (2% vs. 4% malt extract agar) to ensure that C was nonlimiting over the course of the experiment.

Biomass Harvesting. After 20 d, a total of 40 plugs, 7 mm diameter each, were subsampled from each dish using a sterilized cork borer (11% of the plate subsampled by area) and used to estimate the 13C present in the biomass plus agar media. The plugs were placed in a preweighed tin and dried at 65 °C to constant mass. Fungal biomass in the remaining media was recovered using standard approaches (26, 31). Briefly, the remaining media was heated to 121 °C for 5 min to melt the agar. The solution was filtered through a 53-µm sieve and rinsed with 1 L of 90 °C deionized water, agitating slightly to remove residual agar, and subsequently rinsed for 2 min with 20 °C deionized water. The resulting biomass was dried at 65 °C to constant mass and weighed. The dried biomass and the dried plugs (agar + biomass) were milled with a mortar and pestle into a fine powder, and analyzed for total %C and atm% 13C content (ESC0410; Costech Analytical Technologies Inc.).

Quantifying Community Function. Community function was quantified three ways, via net productivity (biomass production), net respiration, and CUE, all of which were measured using the 13C label. Total biomass in the dish was estimated by scaling the recovered biomass by the inverse proportion of the dish that was subsampled for biomass (31, 46). Variance was included as a potential confounder variable in the statistical analysis, although it is not otherwise a primary variable of interest in this analysis (Table S2).

Model Estimation. Separate regression models were fit for biomass, respiration, and CUE. All models included species richness, mean competitive ability, intransitivity, and secondary confounding variables (variation in competitive ability, functional dissimilarity, and phylogenetic dissimilarity). Also included were the pairwise interactions among richness, intransitivity, and competitive ability. Species-specific effects were taken into account two ways. First, the community-specific average monolute performance (e.g., average monolute respiration) was included as a predictor for each outcome, thus accounting for baseline differences in communities’ functioning based solely on differences in community composition. Second, the relative proportions of each species in each community (i.e., 0, 1/3, 1/6, or 1/12) were included as fixed effects in all models to account for species-specific effects and autocorrelation among communities with shared species. Richness, intransitivity, and mean competitive ability—as well as their pairwise interactions—were included in all models regardless of significance; otherwise, variables were included in the final model only if they had a P value of <0.10. Note that potential confounding variables (phylogenetic and functional dissimilarity, variation in competitive ability) are not discussed in detail further, given that they were not the main variables of our hypothesis-testing (but see Table S2 for the full model results). All P values were adjusted for multiple comparisons (49).

Estimating Marginal Effects. In the presence of strong interactions, individual coefficients are difficult to interpret, even after standardizing variables. Therefore, to illustrate the marginal effect of each variable (richness, intransitivity, competitive ability), we plotted the model-based coefficients (i.e., slopes) for each variable across a grid of values. Thus, for example, we calculated the regression coefficient corresponding to species richness across a grid of intransitivity and competitive ability values (with all other values


