Diversity begets diversity in competition for space

Daniel S. Maynard^{1*}, Mark A. Bradford¹, Daniel L. Lindner², Linda T.A. van Diepen³, Serita D. Frey⁴, Jessie A. Glaeser², Thomas W. Crowther^{1,5}

1. Yale School of Forestry and Environmental Studies, Yale University, New Haven, CT, USA

2. US Forest Service, Northern Research Station, Center for Forest Mycology Research, Madison, WI, USA

3. Department of Ecosystem Science and Management, University of Wyoming, Laramie, WY, USA

4. Department of Natural Resources and the Environment, University of New Hampshire, Durham, NH, USA

5. Netherlands Institute of Ecology (NIOO-KNAW), Wageningen, Netherlands

*Correspondence: Daniel Maynard
Yale School of Forestry and Environmental Studies
370 Prospect St.
Yale University
New Haven, CT, 06511 USA

E-mail: daniel.maynard@yale.edu

Phone: +1 508 463 5939

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Competition can profoundly affect biodiversity patterns by determining whether similar species are likely to coexist¹⁻³. In communities where competitive exclusion is driven primarily by competition for space rather than by niche differentiation, theory suggests that equalizing forces (i.e., ‘hierarchical competition’) should reduce diversity by allowing only highly-competitive species with similar traits to survive⁴⁻⁷. Yet this expectation does not match patterns observed in many sessile communities, which can exhibit high biodiversity despite minimal reliance on niche differentiation⁸⁻¹¹. A potential mechanistic explanation is that intransitive competitive networks (i.e., ‘rock-paper-scissor’ dynamics) offset hierarchical competition and maintain species richness¹²⁻¹⁴, thereby fostering coexistence among highly-dissimilar species with different competitive traits. Here, we use a combination of empirical and analytical approaches to test whether spatial competitive networks promote coexistence among similar or dissimilar species. In an experimental fungal system, pairwise competitive outcomes were strongly hierarchical, with displacement maximized when species had different traits and divergent evolutionary histories. Yet when these pairwise interactions were embedded in spatial models of species-rich communities¹⁵, high levels of intransitivity ultimately overwhelmed the hierarchical structure, minimizing losses in species richness and allowing even the weakest, most dissimilar competitors to survive. Although competition decreased functional and phylogenetic diversity, the smallest losses were likewise observed in species-rich communities. By demonstrating that species richness can act as a self-reinforcing buffer against diversity loss, these results contribute to our fundamental understanding of how biodiversity is maintained in spatially-structured communities.

Many natural communities exhibit higher levels of biodiversity than can seemingly be explained by ecological theory^{11,16,17}. Various biotic and abiotic factors, such as environmental heterogeneity, niche differentiation, competition-colonization trade-offs, and neutral dynamics have been invoked to explain the co-occurrence of species¹⁸. In most of these frameworks, the continued persistence of individuals in communities is attributed either to the interplay between extinction and migration¹¹, or to the presence of negative density-dependence (e.g., niche differentiation), which stabilizes communities against fluctuations in species' abundances¹⁹. Yet in spatially structured populations where competitive exclusion is determined by direct displacement or overgrowth (i.e., via interference competition), the patterns that emerge can be starkly different from well-mixed systems²⁰⁻²⁴. In particular, species' survival may have little to do with niche overlap or resource uptake, and instead be driven by intransitive, non-hierarchical competitive relationships in which no single species outcompetes all others (i.e., 'rock-paper-scissor' competition)^{13,14,25,26}. In sufficiently complex spatial systems, even the weakest species may persist in patches where they are surrounded by species that cannot displace them^{13,20}. Although these intransitive competitive networks are not always sufficient to ensure stable coexistence, they may still allow for long-term persistence of co-occurring species over many generations; a phenomenon that has been termed 'effective coexistence'²⁰.

Intransitive competitive networks have been shown to promote species richness, regardless of whether the community is spatially-structured or well-mixed^{12,13}, yet there is comparatively little theory to predict how species similarity mediates these relationships. Under modern theory, coexistence of species is determined by the interplay between equalizing and stabilizing forces¹⁹. Equalizing forces typically promote similarity by reducing competitive ability differences, whereas stabilizing forces typically promote dissimilarity by ensuring that

species limit themselves more than competitors^{16,19}. When long-term persistence is instead determined by intransitive relationships rather than negative density-dependence, there is little expectation of how species similarity should alter coexistence patterns. Theory suggests that, in the absence of niche differentiation, equalizing forces should reduce dissimilarity by allowing only dominant species at the top of the competitive hierarchy to persist over long time scales^{4-7,27}. In contrast, intransitivity should, to some extent, foster dissimilarity by allowing multiple species with different competitive strategies (and traits) to persist^{12,26}. However, it remains largely unexplored how these two opposing forces (i.e., hierarchical competition versus intransitivity) determine species survival and biodiversity patterns in spatially structured populations.

Here, we use a model microbial system in tandem with analytical models to explore the links between species richness, species dissimilarity, and competitive intransitivity. Microbial systems have been instrumental in elucidating our understanding of biodiversity and complex network dynamics²⁸⁻³⁰. Competitive exclusion over small temporal or spatial scales is often determined by interference competition (e.g., chemical allelopathy, overgrowth, or displacement) rather than by exploitative competition or the drawing-down of limiting resources^{31,32}. Because interference competition typically involves the release of allelopathic compounds targeted to harm interspecific competitors, it is unlikely to produce the niche differences that stabilize competition between species pairs. This system thus allows us to explore how competitive fitness differences and subsequent intransitive relationships relate to effective coexistence, independent of niche differentiation and other stabilizing forces²⁸. Importantly, these systems are not intended to mimic the *in situ* dynamics of a specific microbial community, particularly since competitive outcomes are highly context dependent and are only one of the many ecological processes

determining species coexistence¹⁸. Rather, the model system used here is intended to explore how complex patterns arise from simple pairwise interactions.

We grew each of 37 fungal colonies, representing 23 unique species, against each other in all pairwise competitions (Fig. 1a), with the outcome (deadlock vs. competitive exclusion) tracked over the course of seven weeks (N=615). A suite of functional traits was first measured on each colony growing in isolation in agar media under standard conditions. The traits used in this analysis (Fig. 2) were selected because they capture various aspects of organismal performance, fitness, and competitive ability (see Methods). Following established approaches^{26,28,33}, we used standardized, near-optimal environmental conditions for all trait and competitive assays to ensure that abiotic stress was minimal and to avoid progressive nutrient limitation. Further, this experimental system provides spatially homogenous environmental conditions, permitting us to quantify the influence of interference competition on competitive exclusion, independent of what might arise through environmental heterogeneity²².

The pairwise competitive outcomes suggested a highly complex network structure (Fig. 1b). Seventeen of the 23 species were able to invade another species' territory, yet even the most combative species lost or deadlocked in ~30% of their competitions (Fig. 1b; Table S1). The community exhibited consistent evidence of hierarchical competition, with competitive exclusion most likely when species had maximal dissimilarity in enzymatic profile, growth rate, density, decomposition rate, and phylogenetic distance (Fig. 2; Table S2). Nevertheless, variation in outcomes was high, with traits and phylogeny explaining only 24% of the variance in competitive exclusion combined; whereas species-specific effects explained 38%. These pairwise results demonstrate that the full system exhibits moderate levels of hierarchical

competition, but that unexplained variation and the ubiquity of deadlocks may promote intransitive loops at higher species richness levels.

To investigate how these pairwise patterns scaled to species-rich communities, we used these experimental observations as baseline data to parameterize analytical models of spatially-structured competitive networks. We used a patch-occupancy, Markov-chain modeling approach¹⁵, intended to capture spatial dynamics in which different subsets of species colonize different patches nested within a larger landscape. Using the pairwise competitive outcomes, we first calculated the steady-state equilibrium abundances of 8000 randomly selected communities, with initial species richness ranging from three to ten unique species (see Methods, Analytical models). We then calculated the proportional changes in species richness, functional dissimilarity, and phylogenetic dissimilarity, relative to the initial pool of species. Importantly, there are two key assumptions of this approach: first, only one species occupies any given patch at any given time, and that at each time-step of the model this species is either displaced by a single competitor or retains ownership of that patch; second, it assumes that all species have equal demographic and dispersal rates, such that life-history trade-offs – which have otherwise been shown to promote coexistence in similar systems^{22,26,34,35} – are removed as potential stabilizing effects. Thus, this approach allows us to explore the potential for competitive interactions to affect biodiversity patterns in the absence of ancillary stabilizing forces.

When the pairwise results were embedded in models of complex communities, the proportion of species excluded from any randomly assembled community depended on complex interactions that only emerged in these more diverse competitive networks. High levels of phylogenetic dissimilarity, functional dissimilarity, and variation in competitive ranking remained significant predictors of competitive exclusion at low richness levels, mirroring the

pairwise results (Fig. 3; Table S3). However, as species richness increased, these relationships quickly deteriorated, with the probability of any one species being excluded from the community rapidly dropping to less than 1%, regardless of functional or phylogenetic dissimilarity (Fig. 3). Competitive intransitivity – which measures the degree of nonhierarchical competition in the community (see Methods, Analytical Models) – was the strongest single predictor of competitive exclusion in the diverse communities (pseudo- $R^2=0.40$, $p<0.001$), with proportional losses dropping to near-zero at higher levels (Fig. 3c). Competitive asymmetry, hierarchical competition, and trait dissimilarity therefore appear to play strong roles in structuring species-poor communities, but at high species-richness, the intransitive network that emerges dampens their effects, such that they ultimately become disassociated from species survival.

Nevertheless, competitive interactions strongly altered the relative abundances of species that persisted, clustering phylogenies and traits around the most dominant species in the community (Fig. 4; Table S4). Since hierarchical ranking (i.e., Fig. 1b) was directly linked to trait expression and phylogeny, the most abundant (and competitively dominant) individuals in each community shared similar traits and phylogenetic histories. As with competitive exclusion, the relative losses in functional and phylogenetic dissimilarity were highest at low species richness (~40% reductions), with this level dropping to <10% losses in the most species-rich communities (Fig. 4). These results suggest that complex networks are less able to buffer against losses in functional or phylogenetic dissimilarity as a byproduct of hierarchical competition, but that high levels of species richness likewise provide the strongest protective effects.

The combined effects of species richness, intransitivity, hierarchical ranking, and functional and phylogenetic dissimilarity could only explain ~50% of the total variability in species loss. Thus, much of the protective ability of the competitive network to buffer against

competitive exclusion remains unexplained, suggesting that other emergent properties of the network have yet to be elucidated. Certainly, more complex metrics of species dissimilarity may help disentangle underlying trends, although subsequent analysis revealed that many of the common metrics likewise explained less than 15% of the variation in species loss (e.g., phylogenetic evenness, mean-nearest-taxon-distance, functional dispersion, functional divergence). Similarly, intransitivity is only one metric for quantifying competitive network structure³⁶, and more complex measures may yield a better understanding of the drivers behind competitive exclusion in spatial competitive networks. Our results highlight that, even in the absence of environmental heterogeneity or demographic trade-offs, competitive intransitivity and species richness can, in part, interactively protect against competitive exclusion by increasing the probability that weak competitors persist in low abundances across the landscape.

These findings support observation-based inferences that intransitivity in sessile communities may play a significant role in fostering local biodiversity^{8,14,25,37,38}, and our results highlight that complex competitive networks may allow species to persist in communities for long periods of time (i.e., ‘effective coexistence’), even when there are minimal opportunities for resource differentiation. There are, however, three important considerations. First, these results only inform the potential for long-term persistence, but they in no way guarantee stable coexistence, in that they do not ensure that a species can recover (i.e., avoid local extinction) if perturbed to low abundances¹⁹. Yet high levels of complexity have been shown to promote stability in other complex systems^{39–41}, and previous work has illustrated that competitive networks can exhibit neutral stability, in which species’ abundances oscillate around their equilibrium values when perturbed¹². Second, the patch-occupancy model used here extends most naturally to sessile organisms – such as corals, wood-decay fungi, or plant communities –

in which individuals compete with a finite set of neighbors in their immediate vicinity. It thus remains to be tested if these patterns hold for well-mixed systems, such as aquatic invertebrate communities. A final important note is that the analytical approach used here assumes that species behave identically in complex communities as they do in pairwise interactions¹⁵. Indeed, this is a core assumption in nearly all modern coexistence theory¹⁹, and our approach is no exception. Investigating how and when these pairwise outcomes break down and fail to inform multispecies outcomes is a particularly challenging and important next step in ecology^{16,41–43}.

Understanding how biological diversity arises and is maintained in natural systems are critical ongoing questions^{2,17,44}. Our results suggest that initially high levels of species richness can promote a positive-feedback loop that increases network complexity and minimizes the subsequent exclusion of species. Further, our analysis shows that the forces structuring pairwise competitive exclusion (i.e., hierarchical competition) may break down at higher species richness levels. Lastly, we present a potential mechanistic explanation as to why some communities strongly structured by intransitive competitive relationships (e.g., corals^{8,25}) may have reduced trait and genetic diversity, yet simultaneously exhibit relatively high species richness⁴⁵. By showing that species richness, diversity, and intransitivity are fundamentally interlinked, these results contribute to our basic understanding of the mechanisms that protect and promote biodiversity in natural systems.

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Figure 1 | The 23 fungal species used in the pairwise competition experiments. a, The molecular phylogenetic tree all species. **b,** The competitive network structure for 31 of the 37 colonies (not shown are six *Armillaria gallica* colonies). Blue arrows point to the winner of each competition and a lack of an arrow indicates deadlock. Numbers in **b** correspond to species' numbers in **a**, and letters denote different isolates within species. Species are ranked in order of competitive ability (see Methods), with the most dominant species (i.e. 6a) at the top, moving clockwise toward the least dominant species (i.e. 3b). Pie charts indicate the proportion of wins (blue), losses (red), and ties (yellow) for each colony.

Figure 2 | Pairwise competitive exclusion was most likely when species were functionally and phylogenetically dissimilar. a, Regression lines and blue confidence bands show the overall trend after adjusting for species-specific effects (N=615). Points and vertical lines given the approximate mean frequency (+/- S.E) of competitive exclusion within each interval (see Methods). All variables were standardized using z-scores to allow for meaningful comparisons of effect sizes. **b,** Standardized coefficients and 95% confidence intervals for the mean log-odds of competitive exclusion. All coefficients are positive, highlighting that all variables reflect pairwise hierarchical competition.

Figure 3 | Patch-occupancy model results linking community characteristics to losses in species richness. Orange-to-purple lines represent increasing levels of species richness (2 to 10 species). **a-b**, Both phylogenetic and functional diversity show high rates of species loss at low richness levels, indicated by the positive slope of the orange lines, thereby mirroring the experimental results; yet these relationships quickly flatten as richness increases (purple lines). **c**, Intransitivity is the strongest single predictor of species loss, with a clear inflection point around 0.4 that becomes increasingly defined at high richness levels. **d**, Variation in competitive ranking mirrors trends for functional and phylogenetic diversity, highlighting that hierarchical competition drives competitive exclusion only at low richness levels.

Figure 4 | Relationships between species richness and losses in phylogenetic dissimilarity and functional dissimilarity. a-b, Losses in both dissimilarity metrics decrease (i.e., become less negative) as species richness increases, highlighting that the network structure protects against losses in diversity beyond just species richness. Nevertheless, communities experience reductions in functional and phylogenetic dissimilarity of 10-15%, even at the highest richness levels, with the most abundant (and most competitive) individuals in each community sharing similar traits and evolutionary histories.