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Diversity begets diversity in competition for space

Daniel S. Maynard[1]*, Mark A. Bradford[1], Daniel L. Lindner[2], Linda T. A. van Diepen[3], Serita D. Frey[4], Jessie A. Glaeser[2] and Thomas W. Crowther[1,5]

Competition can profoundly affect biodiversity patterns by determining whether similar species are likely to coexist. When species compete directly for space, competitive ability differences should theoretically promote trait and phylogenetic clustering, provided that niche differences are otherwise minimal. Yet many sessile communities exhibit high biodiversity despite minimal reliance on niche differentiation. A potential explanation is that intransitive competition ('rock–paper–scissors' competition) not only promotes species richness but also fosters coexistence among highly dissimilar species with different competitive strategies. Here, we test this hypothesis using a combination of empirical and analytical approaches. In an experimental system comprising 37 wood-decay basidiomycete fungi grown in nutrient-rich agar media, pairwise displacement was maximized when species had widely different competitive traits and divergent evolutionary histories. However, when these interactions were embedded in models of species-rich communities, high levels of intransitivity ultimately overwhelmed the pairwise relationships, allowing the weakest and most dissimilar species to survive. In line with theoretical expectations, these multispecies assemblages exhibited reduced functional and phylogenetic diversity, yet the smallest losses were likewise observed in species-rich communities. By demonstrating that species richness can act as a self-reinforcing buffer against competitive exclusion, these results contribute to our understanding of how biodiversity is maintained in natural systems.

Many natural communities exhibit higher levels of biodiversity than can seemingly be explained by ecological theory[1–3]. 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 species[4]. In most of these frameworks, the continued persistence of individuals in communities is attributed either to the interplay between extinction and migration[1], or to the presence of negative density-dependence (for example, niche differentiation), which stabilizes communities against fluctuations in the abundances of species[5]. Yet in spatially structured populations where competitive exclusion is determined by direct displacement or overgrowth (that is, by interference competition), the patterns that emerge can be starkly different from those in well-mixed systems[6–8]. In particular, the survival of species 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 ('rock–paper–scissor' competition)[9–11]. In sufficiently complex spatial systems, even the weakest species may persist in patches where they are surrounded by species that cannot displace them[7,10]. 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'[7].

The effect of intransitive competition on species richness depends heavily on the traits of the species in the community[12,13], yet there is little overarching expectation of how species dissimilarity mediates the relationship between intransitivity and coexistence[2]. Under modern theory, coexistence of species is determined by the interplay between equalizing and stabilizing forces[5]. Equalizing forces typically promote similarity by reducing competitive ability differences, whereas stabilizing forces typically promote dissimilarity by ensuring that species limit themselves more than do competitors[2,5]. Thus, although competition is typically expected to increase functional and phylogenetic diversity owing to the 'limiting similarity' principle[14,15], it can alternatively promote trait clustering or phylogenetic clustering in communities strongly structured by competitive ability differences[16,17]. If there is otherwise minimal opportunity for niche differentiation over small temporal and spatial scales, then direct competition for space should reduce dissimilarity by allowing only dominant species near the top of the competitive hierarchy to persist[17–20]. However, intransitivity should, to some extent, foster dissimilarity by negating hierarchical or asymmetrical competition, thereby allowing multiple species with different competitive strategies and traits to persist[11,21]. Despite the fact that these two competing forces (competitive ability differences and intransitivity) can operate simultaneously, the extent to which they interactively determine biodiversity patterns under competition for space remains largely unexplored.

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 our understanding of biodiversity and complex network dynamics[13,22,23]. Competitive exclusion in microbes operates over small temporal or spatial scales, and therefore it is often determined by interference competition (for example chemical allelopathy, overgrowth or displacement) rather than by exploitative competition or the drawing-down of limiting resources[24,25]. 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 ability differences and intransitive relationships

[1]School of Forestry and Environmental Studies, Yale University, 370 Prospect Street, New Haven, Connecticut 06511, USA. [2]US Forest Service, Northern Research Station, Center for Forest Mycology Research, 1 Gifford Pinchot Drive, Madison, Wisconsin 53726, USA. [3]Department of Ecosystem Science and Management, University of Wyoming, 1000 East University Avenue, Laramie, Wyoming 82071, USA. [4]Department of Natural Resources and the Environment, University of New Hampshire, Durham, New Hampshire 03824, USA [5]Netherlands Institute of Ecology (NIOO-KNAW), Droevendaalsesteeg 10, 6708 PB Wageningen, The Netherlands. *e-mail: daniel.maynard@yale.edu

relate to effective coexistence, independent of niche differentiation and other stabilizing forces[13]. 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 coexistence[4]. Rather, the model system used here is intended to explore how complex patterns arise from simple pairwise interactions.

We grew each of 37 wood-decay basidiomycete fungi, representing 23 unique species, against each other in all pairwise competitions (Fig. 1a), with the outcome (deadlock versus competitive exclusion) tracked over the course of 7 weeks ($N = 615$; see Methods for specifics). 'Competitive exclusion' was defined by one of the two species displacing the other, whereas 'deadlock' was defined by neither species overtaking any territory previously colonized by the other, with both species thus persisting over the full course of the experiment. A suite of competition-related traits (*sensu* ref. [26]) was first measured on each isolate growing in isolation in agar media under standard conditions. The traits used in this analysis (Fig. 2) were selected because they were *a priori* hypothesized to be important drivers of competitive interactions among these fungi. For example, growth rate is potentially indicative of overgrowth ability and overall metabolic activity[27]; the production of dense hyphae can protect against overgrowth by serving as a physical barrier[28]; and extracellular enzymes can damage competitors' cells and protect against combat-induced chemical stress[29]. Following established approaches[11,13,30], 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. By providing spatially uniform environmental conditions, this experimental system allowed us to quantify the influence of interference competition on competitive exclusion, independent of what might arise through environmental heterogeneity[31].

To investigate how these pairwise patterns scaled to species-rich communities, we then used these experimental observations as baseline data to parameterize analytical models of complex networks (see Methods, Analytical models). We used a patch-occupancy, Markov-chain modelling approach[32], intended to capture metacommunity dynamics in which different subsets of species colonize different patches nested within a larger landscape. Using the pairwise competitive outcomes, we calculated the steady-state equilibrium abundances of >7,000 randomly selected communities, with initial species richness ranging from two to nine unique species. We then calculated the proportional change in species diversity, functional dissimilarity and phylogenetic dissimilarity by comparing the steady-state abundances to the initial community composition. Given that these steady-state abundance distributions relied solely on the pairwise competition matrix, this approach allowed us to isolate how direct competition for space affects biodiversity patterns in the absence of ancillary stabilizing forces or fitness differences.

Results and discussion

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 individuals lost or became deadlocked in ~30% of their competitions (Fig. 1b; Supplementary Table 1). The community exhibited consistent evidence of asymmetric competition, with competitive exclusion most likely when species had maximal differences in enzymatic profile, growth rate, density, decomposition rate and phylogenetic distance (Fig. 2; Supplementary Tables 2 and 3). Nevertheless, variation

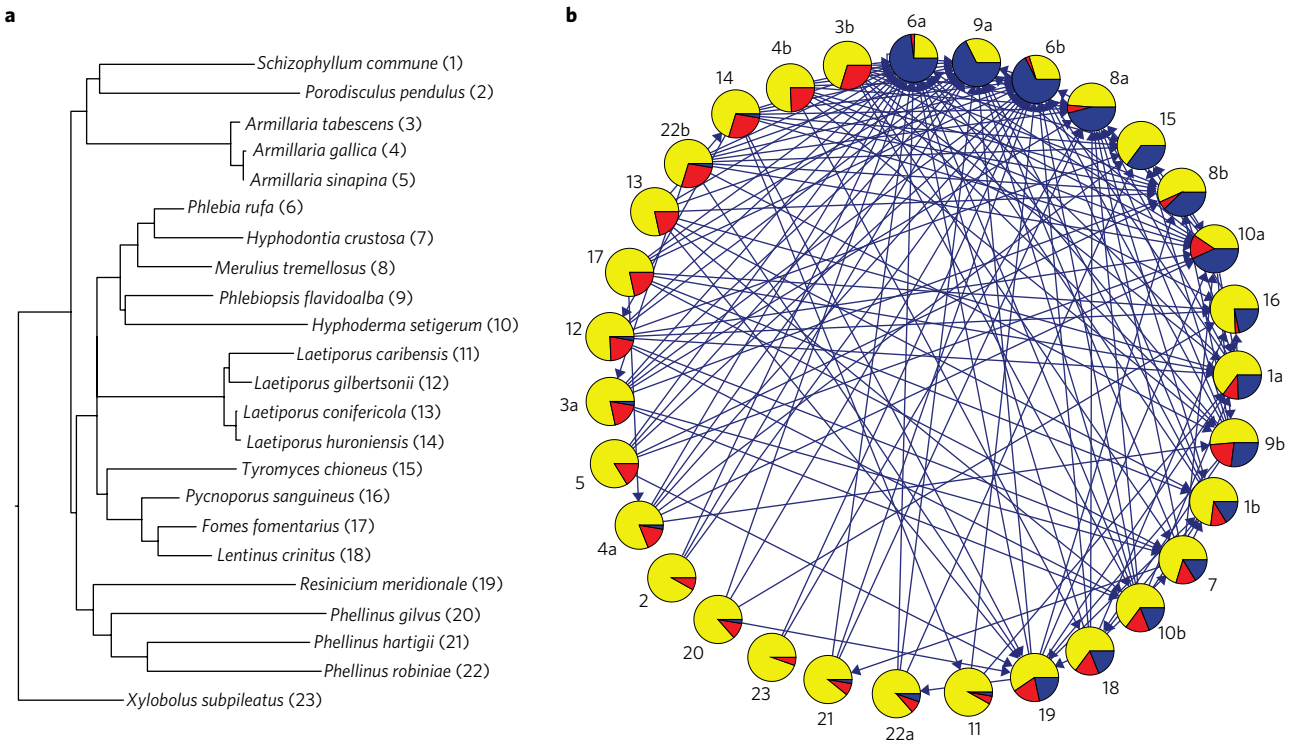

Figure 1 | The 23 fungal species used in the pairwise competition experiments. a, The molecular phylogenetic tree including all species. **b**, The competitive network structure for 31 of the 37 colonies (not shown are six *Armillaria gallica* colonies). Blue arrows point to the winner of each competition, 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 (6a) at the top, moving clockwise towards the least dominant species (3b). Pie charts indicate the proportion of wins (blue), losses (red) and deadlocks (yellow) for each isolate.

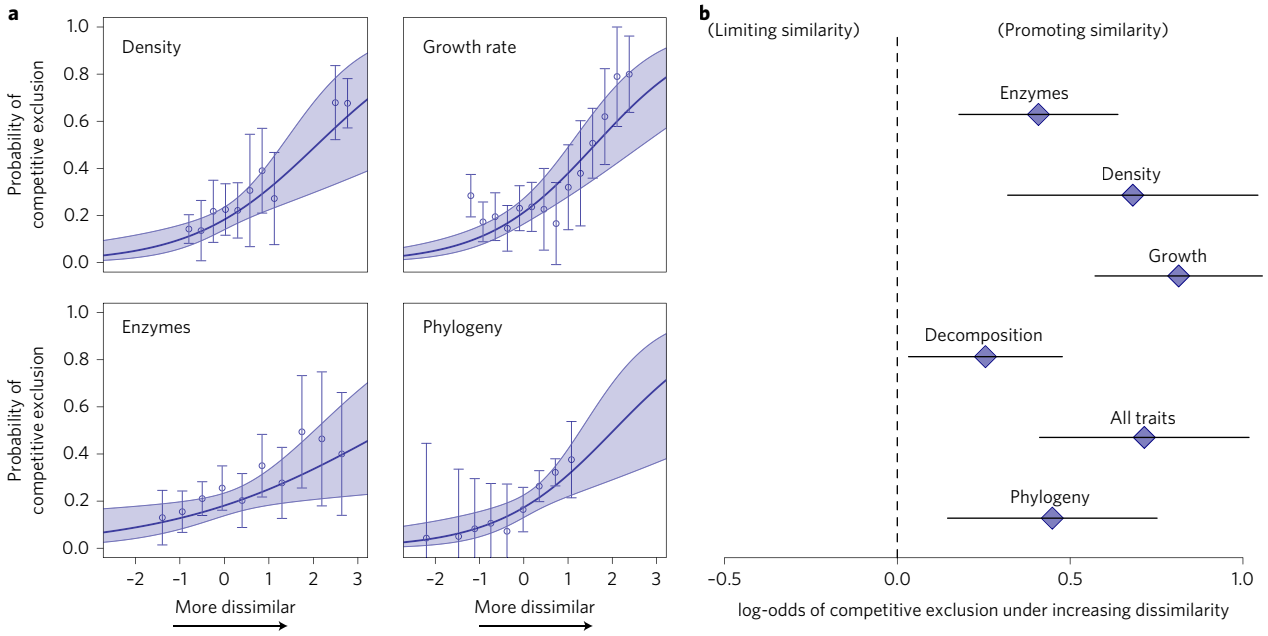

Figure 2 | Pairwise competitive exclusion was most likely when species were functionally and phylogenetically dissimilar. a, Regression lines and blue confidence bands show the overall trend after adjusting for species-specific effects ($N = 615$). Points and vertical lines give the approximate mean frequency (± standard error) of competitive exclusion within each interval (see Methods). All variables were standardized using z-scores to allow 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.

in outcomes was high, with traits and phylogeny combined explaining only 24% of the variance in competitive exclusion, whereas species-specific effects explained 38%. These pairwise results demonstrate that the full system exhibits moderate levels of asymmetric competition, but that unexplained variation and the ubiquity of deadlocks may promote intransitive loops at higher levels of species richness.

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 (Supplementary Tables 4–6). 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; Supplementary Table 4). 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; Supplementary Fig. 1). 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 seem 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.

Despite the fact that intransitivity protected against losses in species richness, competitive interactions strongly altered the relative abundances of species that persisted, ultimately reducing trait and phylogenetic dissimilarity in comparison with fully even communities (Fig. 4; Supplementary Table 7). Although competition is typically expected to increase species dissimilarity (the limiting similarity hypothesis[15]), our results align with modern coexistence theory, which highlights that competition should promote trait or phylogenetic clustering when competitive ability differences (that is, equalizing forces) rather than niche differences ultimately dictate survival[16,17,33]. Notably, however, the relative losses in functional and phylogenetic dissimilarity were highest at low levels of species richness (~40% reductions), with this level dropping to ~10% losses in the most species-rich communities (Fig. 4). These results demonstrate that complex networks may be unable to buffer completely against losses in functional or phylogenetic dissimilarity as a by-product of equalizing forces, but that high levels of species richness likewise provide the strongest protective effects against losses in biodiversity.

We observed an intransitivity threshold of approximately 0.4, above which an increase in intransitivity did little to protect further against loss of species (Fig. 3c). These results mirror previous work on intransitive competition in plant communities[34], where moderate intransitivity values were found to be the most frequently observed. Whether or not these two results are directly linked is unclear. It may be the case that totally intransitive communities are ultimately more sensitive to destabilizing forces, because they rely on perfectly offsetting pairwise interactions that may easily be disrupted by other processes such as the addition of a new species or by spatial or temporal heterogeneity[35]. Conversely, if indeed moderate intransitivity is sufficient for survival—as is also suggested by previous research[10]—then there should be negligible selection for highly intransitive communities across the landscape, such that other ecological forces (such as exploitative competition or trophic interactions) may ultimately override the benefit of high intransitivity. Exploring how intransitive competition interacts with these other community-assembly processes for *in situ* communities is a critical next step.

Even in the absence of outside ecological forces, the combined effects of species richness, intransitivity, hierarchical ranking, and functional and phylogenetic dissimilarity accounted for only ~50% of the total variability in species loss. Thus, much of the protective

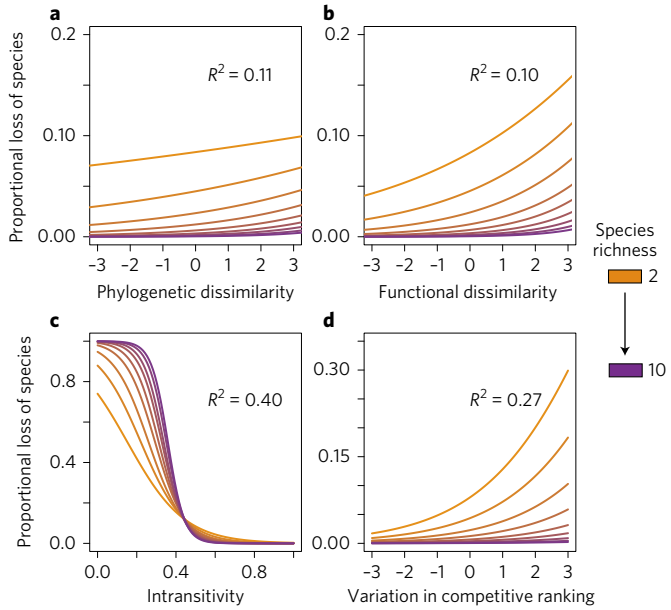

Figure 3 | Patch-occupancy model results linking community characteristics to losses in species richness. Orange-to-purple lines represent increasing levels of species richness (2 to 10 species). **a**,**b**, Higher levels of phylogenetic and functional dissimilarity both led to higher rates of species 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 dissimilarity, highlighting that hierarchical competition drives competitive exclusion only at low richness levels ($N = 7{,}263$ for all analyses).

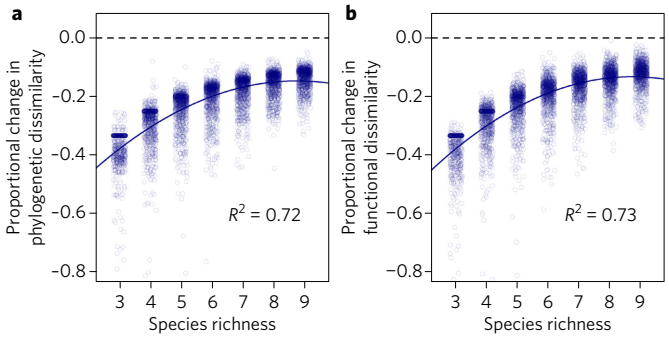

Figure 4 | Relationships between species richness and losses in phylogenetic dissimilarity and functional dissimilarity. a,**b**, Losses in both dissimilarity metrics decrease (become less negative) as species richness increases, highlighting that the network structure protects against losses in diversity 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.

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 to disentangle underlying trends, although subsequent analysis revealed that many of the common metrics likewise explained less than 15% of the variation in species loss (for example phylogenetic evenness, mean-nearest-taxon distance, functional dispersion or functional divergence). Intransitivity is likewise only one metric for quantifying competitive network structure[36], and more complex measures may yield a better understanding of the drivers behind competitive exclusion in spatial competitive networks[37,38].

Much debate exists over the relative merit of phylogenetic and functional metrics to infer community assembly mechanisms[17]. Here, traits and phylogeny exhibited similar patterns across all analyses, despite the fact that less than half of the traits showed strong evidence of phylogenetic conservatism (Supplementary Table 8) and that trait differences were only weakly correlated (Supplementary Table 9). The finding that trait dissimilarity was slightly more predictive of competitive exclusion than phylogeny (Figs 2,3; Supplementary Tables 2,4) is likely to arise because the specific traits that we quantified are directly linked to combative fitness differences, whereas phylogeny reflects multiple interacting evolutionary and ecological pressures beyond displacement ability (for example abiotic tolerances[39]). In communities in which resource-mediated niche differentiation is also an important structuring force, the linkages between phylogenetic dissimilarity and coexistence should be particularly complex, and ultimately driven by which traits (for example niche-related traits or competitive traits) have stronger phylogenetic signals[16], and whether these pairwise relationships ultimately scale to community-level outcomes[2,40].

Our findings support observation-based inferences that intransitivity in sessile communities may play a significant role in fostering local biodiversity[9,34,41]. Further, our results highlight that complex competitive networks may allow species to persist in communities for long periods of time ('effective coexistence'), even when there are minimal opportunities for niche differentiation or life-history trade-offs. We therefore provide an alternative mechanism by which multiple species can coexist when competing for a single limiting resource. Previous research has shown that 'competitive chaos' and species oscillations can support dozens of species on only a handful of unique resources[42,43]. Alternatively, environmental stochasticity can prevent a single species from becoming competitively dominant[35], and trade-offs between resource exploitation and interference competition can allow for stable coexistence of multiple species[31,44–46]. Notably, our results suggest that coexistence under spatial competition need not rely on stochasticity or heterogeneity, and may instead be a quantifiable and deterministic property of the competitive network structure.

There are several important considerations about our analytical results. First, the specific patch-occupancy modelling approach does not incorporate aspects of competitive ability beyond direct displacement ability. The experimental microcosms were constructed so that competitors occupied equal areas before interacting; this allowed us to isolate each species' relative displacement ability, but also prevented us from exploring the importance of colonization differences. Faster-growing species should acquire territory more rapidly, potentially strengthening the hierarchical structure of the community (Fig. 1b); conversely, differences in dispersal rates between fast- and slow-growing species (or between strong and weak competitors) may provide an additional mechanism by which weak competitors persist across the landscape[31,46]. Our theoretical results thus provide testable hypotheses of how spatial competition can structure communities, but whether or not these patterns are ultimately found in any particular community will depend on the importance of intransitive spatial competition relative to other ecological processes[34].

An additional consideration is that our results extend most naturally to sessile or clonal organisms in which individuals (or colonies) compete with a finite set of neighbours in their immediate vicinity. Indeed, the distinction between our findings and previous work

into competitive network dynamics—for example, the expectation that only an odd number of species can coexist[21]—is at least partially due to the fact that the patch-occupancy model does not assume a well-mixed system (and hence why it best approximates spatially structured organisms). Additionally, the model we use allows for probabilistic or stochastic outcomes (rather than binary win–loss), such that an even number of species can coexist, for example, if they all have a 0.5 chance of displacing each other in pairwise competitions. A final important note is that our analytical model assumes that these pairwise interactions are relevant to how species behave in multispecies communities[32,47]. Indeed, this is a core assumption in nearly all modern coexistence theory[5], and our approach is no exception. Investigating how and when these pairwise outcomes fail to inform multispecies outcomes is a foundational question in ecology[47], and is a particularly challenging and important next step for coexistence theory[2,48–50].

How biological diversity arises and how it is maintained in natural systems are critical ongoing questions. Our results suggest that initially high levels of species richness can promote positive-feedback loops that increase network complexity and minimize subsequent losses in functional, phylogenetic and species diversity. Further, our analysis shows that the forces structuring pairwise competitive exclusion (that is, asymmetric competition) may break down at higher levels of species richness. Finally, we present a potential mechanistic explanation as to why some communities that are structured by intransitive competitive relationships (for example coral reef communities) exhibit higher biodiversity than can be attributed solely to niche differences[9,41]. By showing that species richness, diversity and intransitivity are fundamentally interlinked, our results contribute to basic understanding of the mechanisms that protect and promote biodiversity in natural systems.

Methods

Experimental design and measurements. *Fungal isolates.* Thirty-seven wood-decay basidiomycete fungi, comprising 23 unique species, were obtained from the US Forest Service, Center for Forest Mycology Research (CFMR) culture collection (Supplementary Table 1), which is maintained by the Northern Research Station and located at the Forest Products Laboratory, Madison, Wisconsin (USA). All isolates were collected from fruiting bodies in early-to-mid-stage dead wood (decay stages 1–2.5) throughout North American mixed forests. Since original collection, isolates have been stored in liquid nitrogen at the CFMR and were not serially transferred at any point.

DNA-based measures. Isolation and sequencing of DNA from fungal isolates followed ref. [51] for live cultures on 2% malt extract agar (MEA), with the exception that only the internal transcribed spacer (ITS) and large subunit (LSU) regions were amplified and sequenced. All 37 ITS sequences and 34 of the 37 LSU sequences were generated for this study and deposited in GenBank (accession numbers KX065932–KX065968 and KX065969–KX066002). One LSU sequence was obtained from GenBank for isolates sequenced previously (*Laetiporus caribensis*; collection GDL-1). Generalized LSU sequences were used for one of the *Armillaria tabescens* isolates (collection FP-102622-T) and one of the *Armillaria gallica* isolates (collection HHB-12551 (T-1)). We subsequently used the combined LSU and ITS regions to construct the molecular phylogenetic tree and the pairwise phylogenetic distance matrix (see Phylogenetic analysis, below).

Trait measurements. All trait measurements and competitive outcomes were assayed at 22 °C, which initial analyses showed to be near-optimal for fungal growth across all isolates. Unless otherwise noted, all microcosms were constructed of 30 ml of 2% (w/v) MEA in 10-cm-diameter deep-well Petri dishes ('plates'), sealed with Petri-Seal (Sigma-Aldrich, Z376922) to prevent moisture loss. All trait measurements were taken on fungi growing in monoculture.

Growth rate. We inoculated the fungi into each plate by placing a 5-mm-diameter plug of previously colonized MEA onto the centre of each plate using a sterilized cork borer. Linear hyphal extension rate, relative to the inoculum plug, was measured daily for 2 weeks, or until the isolate reached the edge of the plate. Growth rate was calculated as the average distance per day[52,53]. Each assay was replicated five times per isolate.

Density. Following previous methods[54,55], we collected mycelia from each dish by overlaying the MEA with cellophane (Fischer Scientific, NC9823382), which allows uptake of nutrients and water, but prevents mycelia from burrowing into the agar. Cellophane disks (10 cm diameter) were cut, submerged in a flask of DI water and autoclaved for 5 min. A sterile disk was placed in each plate, and isolates were inoculated as above. We incubated the plates at 22 °C for 2 weeks, or until the colonies reached the edge of the plate. Subsequently, a 1 cm × 1 cm square of colonized cellophane was cut from each plate at a distance of 1 cm from the edge of the growing front. The squares were dried at 60 °C and weighed. We scraped the dried mycelia off each square with a small aluminium spatula, and re-weighed the cellophane square. We calculated the density (dry mass per square centimetre) as the average difference in the mass of the cellophane squares before and after removing the mycelia. Each assay was replicated five times per isolate.

Wood decomposition rate. We placed maple wood blocks (10 mm × 10 mm × 5 mm) in a 45 °C oven until dry. They were then weighed, placed in numbered tubes and sterilized for 30 minutes in an autoclave. Stainless-steel micro mesh ('Gutter Guard', Amerimax, Lancaster, PA) was used to keep the wood blocks off the immediate surface of the MEA to prevent saturation and to aid removal. We cut the mesh into 60 mm × 60 mm squares, which were then weighted under a flask full of water and autoclaved for 20 minutes to sterilize and flatten them. A square piece of mesh was placed on each MEA plate, and a 5-mm-diameter plug of the sample culture was placed in the centre. Next, we placed three wood blocks 15 mm from the plug and equidistant from one another. A second square of mesh was placed on top to secure the wood blocks. The plates were sealed with ParaFilm (Bemis NA, Neenah, WI) and incubated for 12 weeks. We subsequently harvested the blocks and gently scraped any fungal remnants from the surface of each block with a razor blade. The blocks were weighed and dried at 40 °C to constant mass. We calculated wood decomposition for each isolate as the average mass loss (as percentage dry-mass) across all blocks. Each assay was replicated six times per isolate.

Enzymes. We conducted enzyme analysis of fungal cultures following previously established methods[56,57]. Colonies were cultured for 7 days, or until they reached a minimum diameter of 2 cm. We took four circular agar plugs (7 mm diameter each, ~1.5 cm^2 total) from 1 cm behind the growing front, replicated four times for each isolate. These plugs were added to 40 ml of 50-mM sodium acetate buffer solution (pH = 5.0) in plastic centrifuge tubes. Tube contents were homogenized for 30 s and agitated for 2 h at 4 °C under constant mixing. We used the filtered extracts for enzyme assays (five hydrolytic and three oxidative enzymes).

We measured the hydrolytic enzymes as follows: leucine aminopeptidase (LAP) was measured by using a 7-amido-4-methylcoumarin (AMC)-linked substrate L-leucine; and cellobiohydrolase, acid phosphatase, *N*-acetyl-β-glucosaminidase and β-glucosidase were measured by using the methylumbelliferyl-linked substrates β-D-cellobioside, phosphate, *N*-acetyl-β-D-glucosaminide, and β-D-glucopyranoside, respectively. Activities of the two phenol oxidases (phenox1 and phenox2) and one peroxidase (perox1) were assayed using the substrates L-3, 4-dihydroxyphenylalanine (L-DOPA, 25 mM), 2,2′-azino-bis(3-ethylbenzothiazoline-6-sulfonic acid) (10 mM) and L-DOPA+H_2O_2 (0.3% hydrogen peroxide), respectively. We assessed enzyme potential by using fluorescence (hydrolytic enzymes) and absorbance (perox1, perox2, phenox1), following previously published methods[58].

Competitive outcomes. Each competitive microcosm was constructed as above, using 2% MEA in deep-well, 10-cm-diameter Petri dishes. Following previous methods[59], we inoculated three 5-mm-diameter plugs on one side of the dish, 1 cm apart in a straight line, about 2 cm from the centre of the dish. The use of three plugs rather than a single plug allowed fungi to form a relatively straight and uniform hyphal front across half of the plate, preventing fast-growing fungi from circumventing the other fungus and immediately acquiring more territory and a larger resource base[59]. The slower-growing fungus (as determined from baseline growth-rate measurements of the fungi in monoculture) in each pairing was plated proportionately before the faster-growing fungus so that they were projected to be 5 mm from the centre of the dish (10 mm apart) at the start of the experiment. Because fungi can inhibit growth by volatile production and the secretion of antifungal compounds through the substrate[25,28,29,60], this 1-cm distance between fungi at the start of the study allowed fungi to participate in some degree of 'combat-at-a-distance', while also minimizing the resource-capture rate advantage for the faster-growing fungi.

After both fungi were inoculated in each plate, we sealed the microcosms and incubated them at 22 °C for up to 8 weeks. Plates were tracked until one fungus completely displaced the other or until no displacement was observed for 3 weeks. Plates were checked daily for the first week, and twice-weekly thereafter. The location of each fungus at each date was marked on the bottom of each dish, and measurements were taken at the end of the study. Plates remained sealed throughout the study to prevent moisture loss. Competitive outcomes were scored as a win, loss or draw.

We used a total of 23 unique fungal species in the competition assays. Given that the variation in competitive outcomes across pairings was considerably greater than the variation in repeated measurements within pairings (that is, within pseudo-replicates), we used a continuous regression design to capture the maximum variation across all species. All isolates were competed against all other isolates (within-isolate and intraspecific competitions omitted), and plates

in which species did not directly interact (that is, did not meet and showed no signs of retreat or gains in territory) were discarded from the statistical analyses. Thus, from the initial 666 pairings ('37 choose 2'), 35 of these were omitted owing to intraspecific competition (eight isolates of the same species, giving '8 choose 2' = 28 intraspecific pairings omitted; plus seven additional intraspecific pairings omitted for the seven species with two isolates each; Supplementary Table 1), and an additional $n = 16$ additional pairings were discarded due to lack of adequate growth by the isolates. This gave a final sample size of $N = 615$ unique pairings in the analysis (666 minus 35 intraspecific interactions minus 16 missing).

Statistical and analytical methods. *Trait differences.* We calculated pairwise differences in growth rate, density and decomposition rate by using the Euclidean distance in trait expression between each pairing of isolates. Enzymatic dissimilarity and overall trait dissimilarity were calculated using 'Rao's quadratic entropy'[61] (Rao's *Q*) in the FD package in the statistical R freeware[62] (see Analytical models, below, for more details). To calculate this metric for each pairing, all traits were standardized to have a mean of 0 and variance of 1, thus assigning equal *a priori* weights to each trait. We calculated functional dissimilarities by assuming equal abundance weighting, thus reflecting the initial pairwise differences among isolates.

Phylogenetic analysis. Generally followed a previously reported method[63]. First the LSU and ITS were analysed separately. DNA sequences were aligned using MAFFT v6[64] with the Q-INS-I algorithm for the alignment of ITS and the G-INS-I algorithm for LSU sequences. We identified significant conflict between the LSU and ITS datasets by comparing the phylogenetic trees from both datasets. Because no strongly supported conflicts were detected, a combined LSU+ITS dataset was constructed by concatenating both alignment files.

We inferred the evolutionary history by using the maximum likelihood method based on the data-specific model[65]. The bootstrap consensus tree inferred from 500 replicates is taken to represent the evolutionary history of the taxa analysed[66]. Branches corresponding to partitions reproduced in fewer than 50% bootstrap replicates are collapsed. When the number of common sites was <100 or less than a quarter of the total number of sites, we used the maximum parsimony method; otherwise the BIONJ method[67] with the maximum composite likelihood distance matrix was used. A discrete gamma distribution was used to model evolutionary rate differences among sites (five categories (+*G*, parameter = 0.4207)). The tree is drawn to scale, with branch lengths measured in the number of substitutions per site. The analysis involved 23 nucleotide sequences. All positions with less than 95% site coverage were eliminated. There were a total of 1,313 positions in the final dataset. A DNA-based distance matrix was calculated for all 37 isolates using MEGA v5[68]. We calculated pairwise distances for all 37 sequences using the number of differences for all nucleotide positions with greater than 95% site coverage; the final dataset for the full distance matrix included 1,213 positions. Using the resulting tree, we calculated the phylogenetic signal of each trait by using Blomberg's *K* (ref. [69]).

We calculated three additional phylogenetic distances to test the robustness of these results to the choice of phylogenetic distance metric. First, using the 'TimeTree' function in MEGA[68], a molecular clock was estimated for the data by using the above tree as a guide tree, and using an independent, distantly related basidiomycete fungus, *Asterostroma muscicola* (Berk. & M.A. Curtis), as the outgroup. Second, an ultrametric tree was estimated using the 'chronos' function in the *ape* package[70] in R, which uses semiparametric rate-smoothing to transform the phylogeny into an ultrametric tree[71,72]. Following refs [73,74], this function was iterated across a range of rate smoothing parameters[75], with a value of 0 found to maximize the log-likelihood. Finally, the original distance matrix was directly converted to an ultrametric tree by using a naive bottom-up hierarchical clustering method, UPGMA[76], which makes a constant-rate assumption across taxa. Pairwise distances using the resulting trees were calculated as the sum of the branch lengths between taxa. These three additional results are reported in the Supplementary Material (Supplementary Tables 3,6; Supplementary Fig. 1) and do not differ appreciably from the results obtained using pairwise substitutions as the measure of pairwise distances.

Competitive rankings. Some isolates were strongly defensive, neither winning nor losing against otherwise strongly combative fungi. Others were strongly offensive, rarely deadlocking but having high rates of wins and losses (Fig. 1b). To capture this variation in combative strategies, we used the Elo ranking system[77] in the *PlayerRatings* package in R. As opposed to standard rankings, Elo penalizes a highly ranked competitor if it loses against a weak competitor, and assigns a higher rank to a weak competitor if it draws or wins against stronger competitors. Whereas a simple hierarchy based on win percentage would assign a low rank to a species with a high number of draws but no wins, the Elo system ranks these species closer to the middle of the hierarchy (for example *Xylobolus subpileatus*; Fig. 1b). This approach better captured variation among 'defensive' competitors and 'weak' competitors in our study system. Elo rankings were subsequently standardized so that the lowest-ranking species (weakest competitor) had a value of 0, and the highest-ranked species (strongest competitor) had a value of 1. We also explored the use of an alternative ranking method, in which isolates were ranked solely on the proportion of wins (that is, the method did not penalize losses against weak competitors), but the results in Fig. 3d were qualitatively the same. However, the Elo ranking method resulted in a higher overall R^2 (0.27 versus 0.21 using the simple ranking), and so the Elo ranking was used throughout. An important additional note is that, regardless, these competitive rankings do not consider additional intraspecific or interspecific effects beyond direct overgrowth ability, such that the hierarchical ranking of species (Fig. 1b) only relates to overgrowth ability and not necessarily to the species' competitive fitness, which may ultimately strengthen or negate the observed hierarchical structure (see Discussion).

Statistical modelling. We used generalized linear mixed-effect models to link trait distances and phylogenetic distances to competitive outcomes. Outcomes across plates were correlated because of replication across isolates and species. To account for this, we used a random-intercept approach, with each microcosm receiving a random effect term for each species in the plate. The outcome for each pairwise competition was modelled as a Bernoulli random variable (competitive exclusion versus deadlock) using logistic regression via the logit link function. All trait and phylogenetic distances were analysed separately and included in each model as a fixed effect, with initial differences in starting positions (that is, deviation from the centre of the Petri dish when first meeting) also included as a fixed effect to control for slight discrepancies in colonization rates.

All variables were standardized across all pairings to have a mean of 0 and a standard deviation of 1, aiding comparisons of effect sizes across models. Results thus reflect the relative change in probability of deadlock for a 1 s.d. increase in distance. Confidence bands in Fig. 2 were estimated using standard regression models, with species included as fixed rather than random effects. Raw mean-adjusted probabilities and standard errors in Fig. 2a were approximated by dividing the *x*-axis into 15 quantiles and calculating the average number of trials in each interval that ended in deadlock. To account for the importance of species differences, these raw probabilities were then adjusted upward or downward by subtracting the average species-specific effects within each interval, as calculated for each difference metric using the full regression models. To quantify the relative explanatory power of the traits versus species-specific effects, we refitted the models using standard logistic regression, with species-specific indicator variables included as fixed effects rather than random effects. Pseudo-R^2 values were then calculated using 'Nagelkerke's R^2' in the *fmsb* package in R.

Analytical models. We investigated the link between diversity and competition in species-rich communities by using a simple Markov chain patch-occupancy model[32,34,78]. The competitive outcomes (win, loss, tie) for all pairings were converted into a pairwise competition matrix, with a value of 1 representing a win and a value of 0 representing a loss. Isolates ending in a draw were assigned a value of 0.5, representing only stochastic fluctuations in outcomes when interacting. For each randomly selected community, the corresponding competition matrix was converted to a transition matrix following ref. [32], thus giving the probability that species *i* is displaced by species *j* in each time step of the model. The dominant eigenvector of each transition matrix was then calculated, giving the predicted relative equilibrium abundances of each species in the community[32].

There are four key assumptions of this approach[32]: first, only one species occupies any given patch at any given time; second, at each time-step of the model, this species is either displaced by a single competitor or retains ownership of that patch; third, the patches are not spatially related to each other; and fourth, all species have equal demographic and dispersal rates, such that life-history differences (competition–colonization trade-offs)—which have otherwise been shown to promote coexistence in similar systems[11,31,46,79,80]—are removed as potential stabilizing effects. Thus, intraspecific competitive effects and ancillary fitness differences beyond direct displacement ability (for example that higher growth rate may confer higher colonization ability) are likewise omitted, such that the models results capture how direct spatial competition affects biodiversity patterns in the absence of ancillary ecological forces.

For each species richness of $S = 2$ to 9, we randomly selected 1,000 communities and trimmed them to remove duplicates, resulting in $N = 7{,}263$ unique communities. Species richness was limited to <10 species to represent common diversity of dominant wood-decay fungi in a single log[81–83]. For each community, only one isolate of each species was allowed to be selected, precluding communities with multiple isolates of the same species. Those communities that contained paired isolates with missing outcomes were excluded from the analysis, which ultimately excluded only one of the unique 253 species-by-species interactions from the analytical models because only one of the 16 missing pairings included two species that lacked multiple isolates (*Laetiporus caribensis* versus *Phellinus gilvus*).

For each sampled community, we calculated the predicted steady-state relative abundances of each species. Initial trait and phylogenetic dissimilarity were calculated for each community assuming all species were initially equally abundant; and final trait and phylogenetic dissimilarity were calculated using the steady-state equilibrium abundances. Proportional changes in species richness and dissimilarity for each community were calculated based on the relative change between initial and final values. The measure of intransitivity of each randomly selected community was calculated by first sorting the pairwise competitive matrix such that it had the maximum number of 1s in the upper right triangle, and then

taking 1 minus the proportion of matrix entries for which $A_{ij} < A_{ji}$ (for $i < j$)[32,84]. The value ranges from 0 (completely hierarchical) to 1 (completely intransitive).

Functional trait dissimilarity and phylogenetic dissimilarity were both calculated using abundance-weighted mean pairwise distances:

$$D = \sum_{i \neq j} d_{ij} p_i p_j$$

where d_{ij} is the distance metric between two species (either functional or phylogenetic) and the p_i and p_j are the proportional abundances of species i and j in the community. For functional dissimilarity, d_{ij} was calculated by using Euclidean distance among all traits, with each trait standardized to have a mean of 0 and a variance of 1, so as to assign equal *a priori* weighting to all traits. Note that this measure is equivalent to abundance-weighted Rao's quadratic entropy across trait space[61,85]. For phylogenetic dissimilarity, the d_{ij} were obtained from the pairwise phylogenetic distance matrix (described above). In reference to phylogenetic dissimilarity, this measure is equivalent to abundance-weighted 'mean pairwise distance'[86–88]. Although more complex dissimilarity metrics exist[85,89], mean pairwise distances are useful in this setting because they allow for direct comparisons to the experimental results (which necessarily use pairwise distances), and, in contrast to many other common diversity metrics, mean pairwise distances can be abundance-weighted to capture relative shifts in trait distributions.

For each level of initial species richness, we standardized the resulting dissimilarity values to have mean of 0 and variance of 1, thus accounting for autocorrelation between richness and dissimilarity and allowing them to be directly overlaid on the same scale (for example Fig. 3a,b). Using standard logistic regression, the change in species richness was modelled as a function of initial dissimilarity (functional or phylogenetic), intransitivity or mean competitive ability (that is, mean ranking), with initial species richness included as an interaction term with these independent variables. An additional model was run that included all pairwise interactions among these variables (Supplementary Table 5). To account for species-specific effects, each unique species was included as an indicator variable in the model, and the predicted values in Fig. 3 and Fig. 4 were calculated by taking the average marginal response across all species combinations. To model proportional change in functional and phylogenetic dissimilarity (Fig. 4), the same process was repeated using standard linear regression, with initial species richness as the independent variable. Because functional and phylogenetic dissimilarity are not defined for $S = 1$, the proportional change in dissimilarity is likewise undefined; communities that contained only one species were thus omitted from this analysis, resulting in $N = 6{,}763$.

Data availability. Experimental data in support of these findings and the R code for the analytical models are available at https://github.com/dsmaynard/diversity_begets_diversity.

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Author contributions

D.S.M. conceived the study, collected and analysed the data, and prepared the manuscript. T.W.C. and M.A.B. contributed equally to the study; T.W.C. helped to design the experiments, collect data and assist with manuscript preparation; M.A.B. assisted with the study design, conceptual advances and manuscript preparation; L.T.A.v.D. and S.D.F. performed enzyme analyses and supplied analytical tools; J.A.G. and D.L.L. provided fungal cultures, collected fungal trait data, and conducted DNA and phylogenetic analyses. All authors discussed the results and commented on the manuscript.

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Competing interests

The authors declare no competing financial interests.