A trait-based understanding of wood decomposition by fungi

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As the primary decomposers of organic material in terrestrial ecosystems, fungi are critical agents of the global carbon cycle. Yet our ability to link fungal community composition to ecosystem functioning is constrained by a limited understanding of the factors accounting for different wood decomposition rates among fungi. Here we examine which traits best explain fungal decomposition ability by combining detailed trait-based assays on 34 saprotrophic fungi from across North America in the laboratory with a 5-y field study comprising 1,582 fungi isolated from 74 decomposing logs. Fungal growth rate (hyphal extension rate) was the strongest single predictor of fungal-mediated wood decomposition rate under laboratory conditions, and accounted for up to 27% of the in situ variation in decomposition in the field. At the individual level, decomposition rate was negatively correlated with moisture niche width (an indicator of drought stress tolerance) and with the production of nutrient-mineralizing extracellular enzymes. Together, these results suggest that decomposition rates strongly align with a dominance-tolerance life-history trade-off that was previously identified in these isolates, forming a spectrum from fast-growing, stress-tolerant fungi that are poor decomposers to slow-growing, highly competitive fungi with fast decomposition rates. Our study illustrates how an understanding of fungal trait variation could improve our predictive ability of the early and midstages of wood decay, to which our findings are most applicable. By mapping our results onto the biogeographic distribution of the dominance-tolerance trade-off across North America, we approximate broad-scale patterns in intrinsic fungal-mediated wood decomposition rates.

Fungi differ vastly in their decomposing ability. Here, we examine which traits explain fungal-mediated wood decomposition. In a laboratory study of 34 fungal isolates, we found that decomposition ability varies along a spectrum from stress-tolerant, poorly decomposing fungi to fast-growing, competitively dominant individuals to slow-growing stress-tolerant fungi, a trade-off that might underpin the spatial distribution of these organisms. The next critical step to comprehend the functional relevance of these community-level patterns is to link these key fungal traits to wood decomposition rates across a wide range of taxa (3, 20, 29). Such insight will allow predicting these forecasts urgently requires a tangible, empirically tested link between fungal characteristics and their contribution to ecosystem function across landscapes (7, 14, 15).

Significance

Fungi play a key role in the global carbon cycle as the main decomposers of litter and wood. Although current climate models reflect limited functional variation in microbial groups, fungi differ vastly in their decomposing ability. Here, we examine which traits explain fungal-mediated wood decomposition. In a laboratory study of 34 fungal isolates, we found that decomposing ability varies along a spectrum from stress-tolerant, poorly decomposing fungi to fast-growing, competitive fungi that rapidly decompose wood. We observed similar patterns in a 5-y field experiment, in which communities of fast-growing fungi more rapidly decomposed logs in the forest. Finally, we show how linking decomposition rates to known spatial patterns in fungal traits could improve broad-scale predictions of wood decomposition by fungi.


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us to translate physiological life-history trade-offs into predictions of ecosystem function.

Several hypotheses have been proposed to explain which fungal traits should predict fungal-mediated wood decomposition rates. At the phenotypic level, it has long been assumed that slow-growing fungi with a high hyphal density may decompose wood faster than thin fungi with a rapid outward extension rate (30). In contrast, the first studies incorporating the microbial community into decomposition models assumed that the rate of decay increases with the growth rate of the decomposers (3, 31, 32). At the genetic level, Treseder and Lennon (26) concluded that several functional genes regulating decomposition (specifically, breakdown of cellulose and lignin) were negatively associated with genes promoting stress tolerance. However, it remains unclear whether these genetic patterns relate to phenotypic trait expression (33). To test these hypothesized relationships between fungal traits and decomposition, empirical studies of a range of fungal taxa are needed that bridge the historical gap between the ecological focus of single-species studies and the greater taxonomic breadth of community-level sequencing efforts.

Here, we explore which fungal characteristics predict wood decomposition rate across a range of common wood decomposer fungi. First, we use a database of 22 fungal traits previously measured in each of 34 wood rot fungi collected from a wide geographic range across North America (25, 34–36) to identify potential drivers of wood decomposition. Specifically, we measured the mass loss of wood blocks when colonized by each fungus to estimate a standardized wood decomposition rate, and examined which fungal traits in the database best explained the variation in wood decomposition across fungal isolates. Second, to evaluate the relevance of these trait measurements under complex natural conditions, we isolated 1,582 fungi from logs in a large field decomposition experiment (37) and tested whether these best-fitting traits likewise help us to explain the variation in mass loss of logs in situ. Finally, we combine our results with existing maps of fungal trait expression (25) to approximate the functional biogeography of fungal wood decomposition across North America.

To evaluate which characteristics of our fungi may predict wood decomposition, we considered a broad range of traits that influence different aspects of fungal ecology and physiology. A wide variety of trait definitions exist in the literature, ranging from physiological to performance-oriented properties of organisms (21, 23, 38, 39). Some can be linked directly to the expression of specific genes, while others are emergent properties that arise as a result of multiple genetic mechanisms. For the purposes of this study, we define a fungal trait as any characteristic of an individual fungus that can be measured under standardized growth conditions and compared across individuals. Specifically, we focused on three groups of traits for which previous work had demonstrated that they vary in consistent patterns across our fungal taxa: hyphal extension rate and hyphal density reflect hyphal morphology and growth strategy, ecological performance traits (11 in total) relate to competitive ability and tolerance of a range of temperature and moisture conditions (25), and finally, the production of oxidative and hydrolytic enzymes (9 traits) promotes nutrient acquisition from organic resources (26). All traits were measured directly on fungi growing on agar. Consistent with the positive relationship between community-weighted intrinsic hyphal extension rate and decomposition under the complex natural conditions of forest ecosystems, we quantified hyphal extension rates at the community level in logs of 20 woody plant species that had been decomposing for 3 or 5 y in a landscape-scale field experiment in a temperate oak-hickory forest (37). Specifically, we cultivated 14 fungal isolates from each of 113 samples collected from 74 unique logs at the field site (1,582 isolated fungi in total) and estimated the intrinsic extension rate of each isolate when growing on agar. Consistent with the positive relationship between extension and decomposition rate found in our laboratory cultures, community-weighted hyphal extension rate also was a strong predictor of wood mass loss (representing cumulative decay) in the field (Fig. 2). That is, communities composed of fungi with high intrinsic hyphal extension rates were associated with more rapidly decomposing logs than those composed of slow-growing fungi. We found the strongest relationship between extension rate and wood mass loss after 3 y of decay (log-log scale, slope = 0.32 ± 0.04 SE; F1,30.3 = 50.7; P < 0.001), with the slope of the relationship attenuating at the 5-y point (0.09 ± 0.04 SE; F1,32.5 = 4.21; P = 0.048). Although there were differences in the physical and chemical properties of wood (30, 42), tree species explained a large proportion of the variance in wood mass loss (57% and 31% after 3 and 5 y, respectively). Yet the intrinsic hyphal extension rate of the community explained an additional 27% (3 y) or 10% (5 y) of the variance in mass loss. This distinct relationship between community-weighted intrinsic growth rate in the laboratory and decomposition rate under field conditions after 3 y of decay provides one of the first tangible links between fungal community composition and wood decay, supporting growing calls to incorporate fungal community characteristics into broad-scale carbon cycling models (3, 4, 10, 14).

In our laboratory assays, fungal growth traits of the 34 isolates were not the only characteristics to predict intrinsic fungal-mediated wood decomposition. In particular, several physiological and biochemical traits correlated negatively with decomposition rate. Fungi that were tolerant of a wider range of moisture conditions (i.e., those with wide moisture niche widths) had lower decomposition rates (Fig. 1A), matching the genetic association between stress tolerance and wood decomposition ability found in previous work (26). In addition, the production of hydrolytic extracellular enzymes that release macronutrients from decaying organic material (acid phosphatase, P; chitinase, N; β-glucosidase, C; Fig. 1B) came at the cost of faster decomposition. Of all enzymes, acid phosphatase had the strongest negative relationship with decomposition rate (log-log scale, slope = –0.50 ± 0.10; F1,30 = 9.66; P = 0.004; R2 = 0.31; Fig. 1D).

**Results and Discussion**

**Fungal Traits Predicting Decomposition Rate.** Of all 22 traits measured across our 34 fungal isolates, the strongest individual predictor of fungal-mediated wood decomposition was the hyphal extension rate of the fungal colony on 2% malt agar (ρ = 0.67; P < 0.001; Fig. 1A). Extension rate explained 19% of the variance in decomposition rate across our fungi (F1,49.2 = 18.9; P < 0.001; semipartial R2 = 0.19; Fig. 1C) across three different temperatures (no significant interaction effect, F1,69.6 = 0.07; P = 0.79). The positive relationship between extension rate and decomposition rate eventually leveled off for the fastest-growing isolates (slope = 0.59 ± 0.09 SEM on a log-log scale). In direct contrast to extension rate, hyphal density was negatively correlated with decomposition (ρ = –0.61; P < 0.001; Fig. 1A), which reflects the well-supported trade-off between colony density and extension rate (18). These results contradict the hypothesis that dense colonies should achieve higher intrinsic wood decomposition rates (30) and instead support models assuming that decomposition is positively related to growth or extension rate (31).

Indeed, previous efforts to apply allometric scaling theory to fungi suggest that colonies with a higher extension rate capture and consume resources more rapidly and efficiently (40, 41). Our results provide strong empirical support for this hypothesis and suggest that hyphal extension rate could serve as an easily measurable proxy for the wood decay ability of fungi, as determined over a 4- to 5-mo period under standardized laboratory conditions.

To evaluate the strength of the relationship between extension rate and decomposition under the complex natural conditions of forest ecosystems, we quantified hyphal extension rates at the community level in logs of 20 woody plant species that had been decomposing for 3 or 5 y in a landscape-scale field experiment in a temperate oak-hickory forest (37). Specifically, we cultivated 14 fungal isolates from each of 113 samples collected from 74 unique logs at the field site (1,582 isolated fungi in total) and estimated the intrinsic extension rate of each isolate when growing on agar. Consistent with the positive relationship between extension and decomposition rate found in our laboratory cultures, community-weighted hyphal extension rate also was a strong predictor of wood mass loss (representing cumulative decay) in the field (Fig. 2). That is, communities composed of fungi with high intrinsic hyphal extension rates were associated with more rapidly decomposing logs than those composed of slow-growing fungi. We found the strongest relationship between extension rate and wood mass loss after 3 y of decay (log-log scale, slope = 0.32 ± 0.04 SE; F1,30.3 = 50.7; P < 0.001), with the slope of the relationship attenuating at the 5-y point (0.09 ± 0.04 SE; F1,32.5 = 4.21; P = 0.048). Although there were differences in the physical and chemical properties of wood (30, 42), tree species explained a large proportion of the variance in wood mass loss (57% and 31% after 3 and 5 y, respectively). Yet the intrinsic hyphal extension rate of the community explained an additional 27% (3 y) or 10% (5 y) of the variance in mass loss. This distinct relationship between community-weighted intrinsic growth rate in the laboratory and decomposition rate under field conditions after 3 y of decay provides one of the first tangible links between fungal community composition and wood decay, supporting growing calls to incorporate fungal community characteristics into broad-scale carbon cycling models (3, 4, 10, 14).
The primary role of this enzyme is to convert organic phosphorus compounds into soluble inorganic forms, increasing phosphorus availability in the soil for both microorganisms and plants (43).

**Broad-Scale Patterns in Fungal Decomposition.** We have thus far considered each trait in our laboratory database in isolation, with our primary aim being to identify simple predictors of intrinsic decay rate across our fungal taxa. Together, these traits represent an apparent trade-off between competitive dominance and moisture stress tolerance in fungi, which was recently demonstrated by Maynard et al. (25) for the same trait dataset (a dataset that did not include decomposition rate). To evaluate the functional consequences of this physiological trade-off in terms of wood decay, we mapped intrinsic decomposition rate onto the trait space, using a principal component analysis (Fig. 3). We found that across our fungi, decomposition rate strongly aligns with the dominance-tolerance trade-off, parallel to extension rate (along axis PC1, which explains 31% of variation; Fig. 3). At one end of this spectrum, highly competitive fungi with high hyphal extension rates have high intrinsic rates of wood decomposition. At the other end of this spectrum, dense fungi that tolerate a wide range of moisture conditions and produce large quantities of N- and P-mineralizing enzymes were associated with slower rates of wood decomposition (Figs. 1 and 3).

Throughout the fungal literature, a range of contrasting theories has been proposed to link fungal communities to ecosystem functioning (e.g., refs. 27 and 44–46). Our trait-based data support conceptual models (14, 29, 47, 48) and genetic studies (26) in suggesting that fungal-mediated decomposition rates might be governed by a fundamental trade-off between stress tolerance and competitive dominance. In his classic CSR framework of competitive (C), stress-tolerant (S), and ruderal (R) plant ecological strategies, Grime (49) originally proposed that the distinction between fast-growing competitors and slow-growing stress-tolerant individuals may also apply to fungi and relate to changes in decomposer ability through successional time. More recently, this framework has been expanded with the hypothesis that producing specific extracellular enzymes or cell damage repair compounds should be beneficial for fungi living in nutrient-limited or stressful environments (14, 44, 47). Indeed, genetic studies show a positive association between genes regulating acid phosphatase or chitinase production and genes promoting stress tolerance (26). Our results indicating that decomposition is negatively associated with production of nutrient-mineralizing enzymes and with moisture stress tolerance (Fig. 1 A, B, and D), while showing a positive relationship with combative ability (Fig. 1D) and extension rate (Figs. 1C and 2), support this framework at the phenotypic level.

![Fig. 1.](image-url) Traits explaining wood decomposition across 34 fungal isolates under laboratory conditions. Decomposition was positively correlated with extension rate and combative ability, but negatively with hyphal density, moisture niche width, and the production of various enzymes (A and B). Bars represent Spearman's rank correlation coefficients (\(\rho\)) between the geometric mean rate of decomposition (percentage mass loss over 122 d, measured at 10 °C, 16 °C, and 22 °C) and each trait, with dark shading indicating statistically significant correlations at \(\alpha = 0.05\). Extension rate (mm day\(^{-1}\)) was a strong predictor of decomposition across all three temperatures (C), and acid phosphatase production (D) had the strongest relationship with decomposition of all enzymes (measured at 22 °C). Points in C and D represent individual fungal isolates (each occurring 3 times in [C]), and lines and shading indicate model predictions ± SEM (full model details in Materials and Methods).
Because all fungi in our database are dominant species in the early to midstages of wood decay, our laboratory measurements are most informative about fungal dynamics during this phase of the decomposition process. Other studies suggest that fungal interactions may change at later stages of decay, affecting wood decomposition rates (reviewed in ref. 50). For example, Holmer and Stenlid (51) found that late-successional species outcompeted fungi from the earlier stages of wood decay in 6-mo laboratory trials on wood. It is possible that our fast-growing fungi with high intrinsic decay abilities best represent a ruderal, high-yield life history (sensu ref. 14) that is advantageous at early decay stages, while late-stage specialists could outcompete them by being able to access more complex substrates as wood decomposition progresses. This hypothesis is consistent with our result that oxidative enzymes necessary to break down lignin [biochemically the most complex step in wood decomposition (26)] were not significantly correlated with wood decay rates in our laboratory experiment (neutral and positive trends in Fig. 1B). Future studies could run fungal combat trials under less favorable nutrient conditions to test how competitive hierarchies change over the course of wood decay. Successional changes in the fungal community might also explain why the relationship between hyphal extension rate and decomposition rate leveled off between 3 and 5 y of decay in the field (refs. 42 and 50 and Fig. 2). In contrast to our laboratory study, field logs did reach the later stages of decay. The fungal community will likely have changed substantially over this time, although molecular data would have been necessary to confirm fungal identities genetically. As fungal communities become more complex during succession, higher investment into combat could reduce wood decay rates (52) and lessen the impact of fungal traits such as extension rate. Finally, changes in the relationship between extension rate and wood decay over time could also reflect the temporally variable nature of the wood decay process itself (53). Taking into account these constraints of our study system, we conclude that the dominance-tolerance trade-off (25) may play a key role in shaping the functional capacity of fungal communities, specifically in the early to midstages of wood decay.

Our results directly build on previous findings obtained using these fungal isolates showing how the dominance-tolerance trade-off predicts their broad-scale biogeographic distributions (25). Here, we demonstrate that this same trade-off also governs intrinsic wood decay ability (slope = 0.82 ± 0.28; F1, 30 = 8.37; P = 0.007; R2 = 0.42; Fig. 4A), and thereby provides a link between community ecology and ecosystem function in wood decay fungi. By projecting this relationship onto the biogeographic distribution of the dominance-tolerance trade-off estimated previously (25), we can approximate the spatial variation of fungal-mediated wood decomposition rates across North American forests (Fig. 4B, map adapted from ref. 25). In essence, this map suggests that the slow-growing, stress-tolerant fungi that are more likely to exist in drier forests with high precipitation seasonality are likely to have poor intrinsic wood decay abilities. In contrast, the fast-growing, highly competitive fungi that are favored in more favorable environments are more likely to decompose wood more quickly, irrespective of the local microclimate. Thus, broad-scale environmental filters may select for fungal communities with certain traits that are in turn strongly linked to decomposition (54, 55). The direction of these indirect effects aligns with the direct effect of the climate on decomposition rate, which is higher in warm, moist environments for any given fungus (ref. 2 and Fig. 1C). Consequently, the biogeographic distribution of fungal traits may reinforce the climate-induced differences in wood decay rates, as fast-decomposing fungi exist in environments that are also conducive to high decomposer activity (as suggested by ref. 56).

Notwithstanding these general patterns, it is widely acknowledged that local decomposition rates will be contingent upon microclimatic conditions, legacy effects, and nutrient quality (2), as observed in the deadwood decay field assays from which we cultured fungi (37). Although decay rates in the field will likely deviate substantially from the standardized rates estimated in the laboratory with pure isolates, the community-weighted means of hyphal extension rates for the field isolates helped explain observed wood decomposition in the field. Thus, our coupled laboratory and field approaches support the value of studying fungal activity in isolation under controlled laboratory conditions, in order to quantify and compare a large number of traits for a tractable number of fungi (57). The field experiment allowed us to demonstrate the validity of extrapolating our findings to field conditions, although our inference is constrained by the limited number of fungi studied in the laboratory (full variable names for V2, V3, etc., listed in SI Appendix, Table S1). The PC1 axis (explaining 31% of variation) represents a dominance-tolerance trade-off across taxa, ranging from fast-growing, highly competitive isolates to stress-tolerant isolates with wide moisture niches and high enzyme production. Decomposition rate (red, PC1 loading = 0.25) strongly aligns with extension rate and competitive ability along this trade-off axis. Results therefore closely match a previous principal component analysis of the trait dataset only (25), with small differences due to the added variable of decomposition rate.
Because the traits predicting decomposition are associated with tal conditions, highlights the predictive strength of the mechanism. with hyperdiverse natural communities and variable environmen-
could be discerned within the complexity of the field environment,
apparent trade-offs in extension rate and decomposition ability
into spatial patterns of intrinsic functional capacity. That these
us to translate previously documented physiological trade-offs (25)
slower-growing, stress-tolerant fungi. This close association be-
simply information about hyphal extension rate, as faster-growing,
predicting fungal-mediated wood decomposition, a critical driver
of trait expression, genetic diversity, and community structure as
capacity of wood decay fungi. Disentangling the relative importance
based approach, our results demonstrate that community-weighted
trait expression rather than the taxonomic identities of the field-
zyme production and competitive ability (9, 42, 48). By focusing on
cay rates for phylogenetically diverse fungi that vary widely in en-
fungal community composition has been associated with wood de-
Most importantly, the phylogenetic range should be expanded to
broad-scale biogeographic distributions of wood-decomposer fungi,
provide unique insight into their functional biogeography.
We hope that our results motivate broad-scale efforts to vali-
date these patterns using fungal isolates sampled across the globe
from a wide variety of environments. Future studies should in-
clude taxonomically diverse fungi from all stages of the decay
process, to further elucidate how the relationships between fungal
traits and decomposition rates change over time. If the patterns we
observed among our North American fungi hold across taxa and
ecosystems, then this research may prove to be a useful step to-
ward the meaningful incorporation of fungal processes into global
biogeochemical models. For example, it is expected that we can
currently account for ~50% of spatial variation in wood decom-
position rates by considering the extrinsic drivers (climate and
plant traits) of soil organic matter turnover (2, 7). Our analysis
suggests that accounting for the intrinsic variation in wood decay
ability of fungi in the field (10) might ultimately enhance our
ability to predict broad-scale variation in wood decomposition
rates to a great degree (in our field study, by up to 10% to 27%).
The next key steps in this regard will be to incorporate continuous
fungal trait variation into spatially explicit models of wood decay,
alogous to recent models of litter decomposition (13, 58). Be-
cause each additional biotic layer of a biogeochemical model can
introduce new model uncertainty (59), field validation of model
outputs (14) and model sensitivity analyses (7) will be needed to
determine the optimal level of ecological detail at which the
functional biogeography of fungi should be represented.

Materials and Methods
Fungal Isolates. Our database comprises 34 saprotrophic basidiomycete fungi
from 20 unique species (SI Appendix, Fig. S1 and Table S3), previously de-
scribed in refs. 25, 34, 35, and 36. All fungal isolates were obtained from the
US Forest Service culture collection at the Center for Forest Mycology Re-
search (Madison, WI). They were collected from fruiting bodies on dead
wood in mixed-hardwood forests across North America and stored in liquid
nitrogen without serial transfer. All species are dominant decomposers
during the early to midstages of wood decay, from newly fallen logs to the
point where cellulose and labile carbon compounds have largely been
decomposed and the wood has started to disintegrate (60, 61). Thus, our
fungi cover a wide taxonomic and geographic range, but have similar eco-
roles (34), allowing us to examine general patterns in fungal traits
and decomposition rates change over time. If the patterns we
observe among our North American fungi hold across taxa and
ecosystems, then this research may prove to be a useful step to-
ward the meaningful incorporation of fungal processes into global

Conclusion and Future Directions. Our study reveals key traits
predicting fungal-mediated wood decomposition, a critical driver of the
global carbon cycle (3). Specifically, intrinsic decay ability under standardized laboratory conditions can be predicted from simple information about hyphal extension rate, as faster-growing, more competitive fungi have higher decomposition rates than slower-growing, stress-tolerant fungi. This close association between decomposition rates and fungal life-history strategies allows us to translate previously documented physiological trade-offs (25) into spatial patterns of intrinsic functional capacity. That these apparent trade-offs in extension rate and decomposition ability could be discerned within the complexity of the field environment, with hyperdiverse natural communities and variable environmental conditions, highlights the predictive strength of the mechanism. Because the traits predicting decomposition are associated with
carbon pools.}

**Fig. 4.** The relationship between decomposition rate (percentage mass loss over 122 d, log-transformed) and the dominance/moisture tolerance trade-off (A), projected across North America (B). The moisture trade-off (x axis in A) is the difference between each isolate's competitive ranking and their moisture niche width, both scaled to [0,1], as calculated by Maynard et al. (25). Points in A represent fungal isolates, the line and shading indicate predictions ± SEM from a general linear model (overall slope excluding species indicator effects of *Armillaria gallica* and *Merulius tremellosus*). Color shading in both A and B indicates decomposition rate, increasing along the fitted line in A. Thus, the map in B represents predicted decomposition rates, as projected onto the previously published spatial distribution of the moisture trade-off (25). Points in B indicate sampling locations of fungal isolates (n = 34). The sampling location of one isolate (~146.69, 60.73) falls outside the spatial extent of the map.
measured on single isolates growing on artificial media. Because these sys-
tems are structurally different from all other substrates, they provide a non-
ological approach to characterize trait variation or comparison across species
(29, 57). Fungi were grown in deep-well, 10-cm-diameter Petri dishes with 2%
malt extract agar, sealed with Petri-Seal (full experimental protocol in ref. 34).
All trait measurements were carried out at 22 °C and ~0.5 MPa moisture
potential, unless otherwise noted. This design provides near-
optimal growth conditions for all fungal isolates in our study and resem-
bles the nutrient conditions of decaying wood.

Physiological growth rates of each isolate were determined at 5 °C, 15 °C,
and 20 °C, as previously described. For each temperature, we determined
an extension rate and hyphal density (presented in ref. 34). In brief, we
inoculated the center of five replicate Petri dishes (plates) per isolate with
a 5-mm-diameter plug of sample culture. Plates were incubated for 2 wk
or until the growing isolate reached the edge of the plate. Hyphal extension
rate was quantified as the linear extension rate in millimeters per day.
Hyphal density was measured using a similar design with media covered
by a layer of cellophane, which allowed us to remove and weigh the my-
celium (as described in ref. 34, following refs. 62 and 63). We quantified
hyphal density as micrograms dry mass per cubic centimeter at 1 cm from
the edge of the growing front.

Temperature and moisture niche. Physiological response curves have previously
been described for our fungi in ref. 25. Skew-normal distribution models
were used to quantify the niche of each isolate across a temperature range
from 40 °C, five replicates per isolate) and moisture (water potentials
−0.5 to −4.5 MPa, three replicates) gradient, with extension rate measured at six
values along each gradient. To quantify temperature and moisture niche
traits of each isolate based on these response curves (full methods in ref. 25,
based on ref. 23), we derived the niche width, minimum, and maximum
(maximizing the range of conditions that supports at least half the maximum
extension rate, such that both species formed a hyphal front across half the
center of the plate. Inoculation time was adjusted to known differences in
inoculation, until one fungus completely displaced the other (competitive exclusion),
and preserved for cultivation of fungi (full details of sample preparation in
refs. 37 and 33). The eight sawdust subsamples from each side of a log were
pooled as top and bottom samples and shipped to the laboratory. Samples
were refrigerated until freeze-dried, and moisture and temperature and
moisture conditions (where maximum extension rate is reached).

Combative ability. To quantify the ability of our fungal isolates to displace
other isolates in direct combat, we conducted pairwise competition trials with
all 20 species, excluding intraspecific interactions (presented in ref. 34,
methods following ref. 64). We inoculated plates with two straight lines
composed of three plugs per isolate, facing each other at 2 cm from the
center. The extension rate was measured at each temperature, such that both species formed a hyphal front across half the plate 1 cm apart at the start of the trial. Plates were incubated for up to 8 wk,
until one fungus completely displaced the other (competitive exclusion),
or when no displacement was observed for 3 wk (deadlock). Based on the
outcome of 615 unique trials, we quantified three traits at the species level.
“Competitive ranking” is the position of a species in the overall competitive
hierarchy among our fungi, calculated using the Elo ranking system (34, 65).
“Offensive ability” is the average extension rate of a fungus when displacing
its competitor, divided by its extension rate in monoculture. Finally, “de-
fensive ability” is the average rate at which a fungus is overgrown, divided
by the competitor’s extension rate in monoculture (25).

Enzyme production. For each fungal isolate, we quantified the production of
five hydrolytic and four oxidative enzymes (described in ref. 34, following
refs. 66, 67, and 68). We determined the extension rate of each isolate (unit:
β-glucosidase, N-acetyl-β-1-glucosaminidase (a chitinase, substrate: N-acetyl-
β-glucosaminide), β-glucosidase (substrate: β-d-glucopyranoside), celluloh-
drolase (a cellulase, substrate: β-d-celllobiose), leucine aminopeptidase
(substrate: L-leucine), two peroxidases (substrates 0.3% hydrogen peroxide
and tetramethylbenzidine, referred to as peroxidase I and II, respectively), and
two phenol oxidases (substrates L-3,4-dihydroyphenylalanine (I-DOPA)
and 2,2’-azino-bis (3-ethylbenzothiazoline-6-sulfonic acid) (ABTS), referred
to as phenol oxidase I and II). Fungal isolates were cultured over a period of 7 d,
after which enzyme activity was measured per unit biomass for 4 plugs
of agar (diameter 7 mm) sampled 1 cm behind the growing front of each isolate.
Hydrolytic enzyme activity was assayed using fluorescence methods,
and oxidative enzyme activity using absorbance methods (following ref. 68).

Laboratory Decomposition Experiment. Decomposition measurements in the
laboratory at 10 °C, 16 °C, and 22 °C are newly presented in this study.
To obtain a standardized estimate of the decomposition rate for each fungal isolate, we
quantified their ability to decompose blocks of maple wood (Acer spp.) in the laboratory. The experiment (full methodological details provided in ref. 34) was conducted on similar plates as the trait assay. Pre-
liminary experiments showed that maple wood supports the growth of all fungal taxa in our study. Thus, fungi could obtain carbon from both the
wood and the medium. We inoculated the center of each plate with a 5-mm-
plug of sample culture. Three sterilized wood blocks (10 mm × 10 mm × 5
mm) were placed 15 mm from the plug and equidistant from each other,
secured between two squares of stainless-steel micro mesh. Plates were
sealed with Parafilm and incubated for 14 to 18 wk. To measure de-
composition, we quantified marker traits (14). For each fungal isolate, we incubated
plates at 10 °C, 16 °C, and 22 °C, with six replicate wood blocks (distributed
over two plates) per isolate and temperature. After incubation, any fungal
residues were carefully scraped from the surface of each block with a razor
blade. Wood blocks were dried at 40 °C to constant mass. We quantified
decomposition rate as the average mass loss (percentage dry weight) of the six replicate blocks over a period of 122 d. To examine the relationship be-
tween extension rate and decomposition for each fungal isolate, we incubated
plates at 10 °C, 16 °C, and 22 °C, as previously described. Hyphal
extension rate at 22 °C was highly consistent (r = 0.95; P < 0.001) with our
earlier measurements at this temperature (34).

Field Decomposition Experiment. To evaluate whether intrinsic extension rate
measured under laboratory conditions could predict wood decomposition by
natural communities of fungi in the field, we sampled the fungal commu-
nity from wood logs in a 7-y decomposition study in a temperate deciduous
oak-hickory forest at Tyson Research Center in Missouri (37). We established
common garden decay sites with logs (22 cm long and 5 to 9 cm φ) from 21
woody species widely spread across seed plant families, deployed in two
cohorts: one beginning in 2009 and the another in 2011 (SI Appendix, Table
55). We present here data from 2014, when we harvested subsamples for
analyzing fungal communities. In the field, the extension rate of each isolate
was measured at 10 °C, 16 °C, and 22 °C, as previously described. Hyphal
extension rate at 22 °C was consistently measured (r = 0.95; P < 0.001) with our
earlier measurements at this temperature (34).

Statistical Analysis. All statistical analyses were conducted in R v.3.5.1 (69). As
a general measure of decomposition under standardized conditions, we used
the mass loss (percentage) of each log as a measure of cumulative decay over a
3- or 5-y period, noting that our samples represent a snapshot of a decay process
that may change through time (53).

To further explore the relationship between decomposition rate and
extension rate (both in the laboratory and in the field) and between de-
composition rate and acid phosphatase activity, we first log-transformed all
these rates and analyzed the relationships between them using general
linear (mixed) models. The slope of the relationship at a log-log scale cor-
responds to the exponent of a power-law relationship at a linear scale,
which was used for graphical representation. Where necessary due to very
small data values, we used an offset of +1 for the log-transformation to
satisfy assumptions of normality. To account for species identity effects in
our laboratory data, we included a species indicator variable for each species
with more than one isolate. Only significant species indicators (α = 0.05, two-
sided) were retained in the model, with the exception of the indicator for
Armillaria gallica, which was always retained because of the high number of
isolates for this species. Plotted regression lines show the predicted mean
regression trend, with the indicators set to zero.

To test whether the relationship between decomposition and extension rate
was consistent across the three temperatures, we fitted a mixed-effects model with extension rate, temperature, and their interaction as fixed ef-
fects (in addition to the species indicators) and fungal isolate as a random

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effect (imw package, ref. 70). Main and interaction effects were evaluated using Type II Wald F tests with Kenward-Roger degrees of freedom (df) (car package, ref. 71). We used a similar approach to analyze the field decomposition data, with extension rate, years decayed (three or five) and their interaction as fixed effects and plant species as a random effect. Because the interaction was significant, we then fitted separate models for each decay period. R²-values for the mixed models were estimated following Nakagawa and Schielzeth (72), using the packages r2glmm (73) and MuMIn (74). Finally, we analyzed the relationship between acid phosphatase activity and T. L. Boddy, Saprotrophic cord-forming fungi: Warfare strategies and other ecological strategies. Soil Biol. Biochem. 42, 529–535 (2010).


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