

Tree species with limited geographical ranges show extreme responses to ectomycorrhizas

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Abstract

Aim: At continental scales, abiotic factors such as climate are typically used to explain differences in plant ranges. Although biotic interactions also underlie the biogeography of plants, the importance of plant-associated microbes is often overlooked when predicting ranges. In particular, symbiotic microbes may influence the distribution of plants that engage in strong interactions with them. We tested whether seedling response to inoculation by ectomycorrhizal fungi explains range size of trees. To examine mechanisms underlying the relationship between range size and response to inoculation, we also examined to what extent sympatry between host and fungi influenced this relationship.

Location: Global.

Time period: Contemporary.

Major taxa studied: Trees and fungi forming ectomycorrhizas.

Methods: Using a dataset of 1,275 observations from 126 papers, we calculated mean biomass response (effect size) of 59 tree species to fungal inoculation. We extracted host range area from digitized maps of native distributions, and determined whether hosts were naturally sympatric with fungal species used as inoculum by searching herbaria databases with geospatially referenced data.

Results: Tree species with seedling effect sizes falling above or below the average response tended to have small ranges and those with average responses, large ranges. Moreover, hosts inoculated with fungi whose ranges were allopatric to their own had higher biomass compared to those that were inoculated by sympatric fungi, suggesting that the extent of geographical overlap between trees and symbiotic fungi may attenuate the mutualism.

Main conclusions: We demonstrate that mycorrhizas may underlie host biogeographical patterns at the continental scale. Our study is novel in the scope of species and scale tested, and points to a possible mechanism underlying this pattern related to the process of mutualism breakdown accruing over time at local geographical scales. For ectomycorrhizal tree species, performance may increase when exposed to fungal partners without a recent shared evolutionary history.

KEYWORDS

allopatry, enemy release hypothesis, fungi, geographical overlap, inoculation, mutualism breakdown, MycoDB, plant–soil feedback, sympatry

1 | INTRODUCTION

Many mechanisms have been proposed to explain variation in geographical range size (Brown, Stevens, & Kaufman, 1996; Gaston, 1996, 1998, 2003; Sexton, McIntyre, Angert, & Rice, 2009; Stevens, 1989). At large spatial scales, the main determinant of range sizes in trees is assumed to be abiotic conditions, in particular, climate or some derivative thereof (Morin & Lechowicz, 2011, 2013; Pither, 2003). Although the importance of biotic interactions in controlling species ranges has a long history in biogeography (Gaston, 2003), how they shape the geography of tree species is rarely investigated. This omission may be due to our poor understanding of coevolutionary processes and the scale of spatial and temporal variation that structures biotic interactions. That is, biotic conditions are believed to be highly variable across large scales and it is unclear whether an aggregate of interconnected local interactions could determine geographical range size in trees. In addition to mismatches in spatial scale between biotic interactions and range sizes of trees, temporal mismatches are also implied. Specifically, it is often assumed that biotic interactions change over shorter time-scales than those needed to link outcomes of coevolution and range size. How natural selection influences range size in a shifting and unpredictable biotic environment is unclear.

Plants that engage in strong interactions with symbiotic organisms ought to be sensitive to their occurrence and distribution. The majority of trees form symbioses with microbes, such as endophytic fungi, nitrogen-fixing bacteria and mycorrhizal fungi. However, these types of microbes are typically ignored when predicting tree ranges. With growing recognition that microbes in soils affect plant health (Berendsen, Pieterse, & Bakker, 2012), growth (Kulmatiski, Beard, Stevens, & Cobbold, 2008) and fitness (Vandenkoornhuysse, Quaiser, Duhamel, Le Van, & Dufresne, 2015), increasing attention has focused on their role in influencing the distribution of plants. At local scales, soil microbes have explained patterns in plant density (Bennett et al., 2017; Reinhart, Packer, Van der Putten, & Clay, 2003), abundance (Klironomos, 2002), species coexistence (Bever, 2003; Teste et al., 2017) and invasion (Reinhart & Callaway, 2006), but little research has been done to test their role underlying range patterns at the continental scale.

The potential for microbial symbionts to have either positive or negative effects on the distribution of host plants is underscored by recent research that considers the reciprocal relationships within these symbioses, that is, plant–soil feedbacks (PSFs). Extending this framework, predictions emerge for shifts in range size of trees. Specifically, under conditions of negative PSFs, migration may be promoted so that trees escape microbial enemies and in consequence, host ranges increase. Conversely, under conditions of positive PSFs, migration deprives trees of mutualistic organisms and in consequence, host ranges decrease. These hypotheses, however, are predicated on the assumption that enemy-release and mutualist-deprivation are predictable outcomes upon host dispersal. Where the outcome of interactions between partners is unpredictable by geography, tree species with little response to microbial symbionts may have fewer limits on range size. That is, in unpredictable biotic environments, hosts with conservative responses to microbial symbionts may have larger ranges than hosts that have extreme positive or negative responses to symbionts.

For at least 90 million years, and most likely longer, trees have co-evolved with ectomycorrhizal (EM) fungi (Sánchez-Ramírez, Wilson, & Ryberg, 2017). Despite this ancient partnership, the role of EM fungi in determining host range size has been mostly ignored. Mycorrhizal fungi colonize tree roots, provisioning nutrients acquired from soils in exchange for sugars photosynthesized by hosts. Of the several types of mycorrhizas, ectomycorrhizas are present on many shrub and tree species including aggressive invaders [e.g. *Pinus contorta* (Richardson, 1998)], and those with high timber value and potential sources of bio-fuel (e.g. *Pinus radiata*). Ectomycorrhizas are a widespread mutualism in that EM trees dominate the boreal forest, the most widely distributed forest type worldwide, and are dominant associations in most other forests, with the exception of some tropical forest types (Smith & Read, 2008). Ectomycorrhizal fungi vary in their distributions; a few EM fungi are widespread and others less so (Peay, Kennedy, & Talbot, 2016; Tedersoo et al., 2014). Although ectomycorrhizas are typically viewed as mutualisms, host response occurs along a continuum ranging from positive to negative (Egger & Hibbett, 2004; Hoeksema et al., 2010; Karst, Marczak, Jones, & Turkington, 2008), and hosts show a range of specificity for EM fungi (Molina, Massicotte, & Trappe, 1992). Importantly, the majority of evidence indicates that the composition of fungal communities is predictable (i.e. spatially autocorrelated) only at relatively small geographical distances (Bahram, Kõljalg, Courty, et al., 2013; Bahram, Peay, & Tedersoo, 2015; Bahram et al., 2016; Lilleskov, Bruns, Horton, Taylor, & Grogan, 2004; Pickles et al., 2010). This means that trees cannot rely on the same fungal associates from place to place, nor will the same associates necessarily function similarly from place to place.

We posit that it is precisely the distance decay in similarity of fungal community composition that may lead some tree hosts to evolve conservative responses to EM fungi. Range expansion of tree species with conservative responses should be less limited by fungal abundance or changes in the species composition of fungal communities compared with trees sensitive to EM fungi. Given the wide taxonomic and geographical scope required to test this prediction, field surveys are of limited use. However, there have been decades of research testing the response of hosts to EM fungal inoculation, yielding a wealth of studies available for synthesis. Using a comprehensive dataset synthesizing results across existing experiments, we tested whether growth responses of seedlings to EM fungal inoculation explain the variation in range size of trees. Here, we show that extreme (i.e. positive or negative) responses of seedlings to EM fungi are associated with smaller range sizes in trees, and moreover, that the extent of geographical overlap between partners may attenuate the mutualism.

2 | METHODS

2.1 | Quantifying response to ectomycorrhizal inoculation

Our analysis expands an existing database, MycoDB, which contains studies where plants were inoculated with mycorrhizal fungi and plant growth was measured (Chaudhary et al., 2016). Prior to this effort,

MycoDB contained 1026 EM observations from 86 papers. On 8 March 2016 we conducted a literature search of the ISI Web of Science database using the keywords *ectomyc**, *inocul** AND 2010–2016 to identify recent published papers not included in the most recent version of MycoDB (Chaudhary et al., 2016). This search yielded 494 papers. Most experiments used fungal mycelia, followed by spores, field soils, and roots to inoculate seedlings. The sources of inoculum were mostly unknown (Rúa et al., 2018), and the most common growth medium was sand. Most experiments were done in the greenhouse and lasted for approximately 7 months. All papers were initially screened for the inclusion of a comparison of mycorrhizal inoculation treatment to a non-inoculated control (i.e. an 'observation'). We then extracted information on whole plant biomass when available, and shoot biomass only if whole plant biomass was not available. This screen yielded 566 new observations from 86 papers. In combination with previous studies found in MycoDB, the new database contains 1578 observations from 172 papers. All data were deposited into the Dryad Digital Repository (<https://dx.doi.org/10.5061/dryad.723m1.2>; Chaudhary et al., 2016).

For each observation, we extracted information on plant biomass with and without EM inoculation. The effect size of EM inoculation was quantified using a standardized, unitless measure of performance, the log response ratio of inoculated to non-inoculated plants. For each host species, we then calculated the mean effect size.

2.2 | Quantifying range sizes of trees

We extracted range area (km²) from digitized maps of native distributions (Supporting Information Table S1). Most of these data originated from shapefiles provided by the U.S. Geological Survey (1999) and to a lesser extent, EUFORGEN (2009). All shapefiles were imported using ArcGIS version 10.4.05524 (Environmental Systems Research Institute Inc., Redlands, California). Shapefiles from the U.S. Geological Survey (1999) were not originally assigned a coordinate system. However, as the metadata indicated these were mapped in a North American 1927 Datum with a Clarke 1866 ellipsoid, semi-major axis of 6378206.4, ellipsoid flattening of 1/294.98, latitude and longitude in decimal degrees and to the nearest 0.01, this coordinate system and units were then assigned to the shapefiles. To calculate the area of the polygons, the data frame was adjusted to a North America Albers Equal Area Conic projection, with a 'NAD_1927_To_WGS_1984_3 + NAD_1983_To_WGS_1984_1' geographical coordinate system transformation. Shapefiles from the U.S Geological Survey (1999) came with attribute data, including a binary 'CODE' field in which 1 denoted the presence of the species and 0 denoted the absence of a species for a particular polygon. Only polygons with a 'CODE' of 1 were included and these polygons were summed and total area collected.

Shapefiles from the EUFORGEN (2009) dataset came with a custom coordinate system known as 'EF1' and were mapped in Lambert Azimuthal Equal-Area Projection. As this dataset already came in a projection with a linear unit (m), no geographical coordinate system transformations were made. The EUFORGEN (2009) dataset contained two feature classes, continuous polygons and fragmented population

occurrences in XY point data; only the polygons were used for the total range area for species in this dataset.

For species whose range size could not be determined from the U.S. Geological Survey or EUFORGEN datasets, ranges were extracted from images of published maps (Supporting Information Table S1). Only maps that featured a scale bar were included. These maps were imported into the GNU Image Manipulation Program version 2.8.16 (Mattis & Kimball, 2015) and the 'select by color' feature was used to extract the layer of the respective species' distribution and exported into a new layer. Layers were then exported into ImageJ version 1.50i (Rasband, 2016) and the scale bars were measured to create a pixel/km ratio. Subsequently, the images were transformed into eight-bit images and the threshold was adjusted to allow for the program to calculate the area of particles. The sum of each particle grouping was then summed to acquire the total area for species distribution.

For *Ostryopsis davidiana* (Liu, Abbott, Lu, Tian, & Lu, 2014), *Pinus tecunumanii* (Brawner, Hodge, Medder, & Dvorak, 2014; Hodge & Dvorak, 2012) and *Betula pubescens* (Chukhina & Bagmet, 2007) we used spatially referenced point data to create range maps. Liu et al. (2014) provided coordinates for species occurrences of *Ostryopsis davidiana*. These coordinates were imported into ArcGIS as XY point data and assigned a 'WGS 1984' coordinate system as specified by the authors' metadata. These point data were then exported and made into a single polygon with the aggregation distance set at 6.5 decimal degrees. The data frame was assigned the North Asia Albers Equal Area Conic projection to maintain accuracy when calculating the area of the polygon. Hodge and Dvorak (2012) along with Brawner et al. (2014) provided coordinates for provenance locations of *Pinus tecunumanii* in its native distribution. Spatial coordinates obtained from Hodge and Dvorak (2012) and Brawner et al. (2014) were imported into ArcGIS; the coordinate system was not specified in the latter. Both datasets were mapped in 'WGS 1984'. The point data were grouped into a convex hull polygon, trimming portions that extended into ocean. Chukhina and Bagmet (2007) provided downloadable GIS layers in which the *Betula pubescens* range was calculated using only the polygon layer and the provided Albers Equal-Area Conic Projection for Russia. Of the initial 1563 observations, 1275 were retained; these observations represent those for which we could find range data on hosts (59 of 110 tree species).

2.3 | Data analysis

Prior to testing the relationship between host response to EM fungal inoculation and range size, we tested for phylogenetic non-independence among tree species in response to inoculation. To create a phylogeny for data analysis, we used the fossil calibrated seed plant phylogeny from Zanne et al. (2014), which contained 53 of the 59 species used in this study. For three of the missing species (*Alnus incana*, *Pinus tecunumanii* and *Pinus caribaea*), we substituted the nearest congeneric species (*Alnus rubra*, *Pinus teocote* and *Pinus palustris*) (Chen & Li, 2004; Hernandez-Leon, Gernandt, de la Rosa, & Jardon-Barbolla, 2013). Phylogenetic information for the remaining species, *Acacia*

mangium, *Eucalyptus miniata* and *Pinus tabulaeformis*, could not be found; however, the effect sizes for these species fell within the range of those for congeners. To determine a phylogenetic signal in response to inoculation, we measured phylogenetic signal as Pagel's λ on the mean values for response to inoculation using the R package 'phytools' (Revell, 2012). There was no significant phylogenetic signal ($\lambda = .000066$, $p = 1$), thus phylogeny was not used in subsequent models. Of note, this latter result indicates that the response of conifers to EM fungal inoculation was similar to that of angiosperms.

Using nonlinear quantile regression, we estimated the conditional quantiles of range sizes associated with mean effect size for host species. Specifically, we compared the range sizes of adult trees to the magnitude of seedling growth response to fungal inoculation. The approach of using seedling growth responses to infer mechanisms underlying adult tree distributions is standard (Bennett et al., 2017; Mangan et al., 2010; Nunez, Horton, & Simberloff, 2009; Reinhart et al., 2003; Teste et al., 2017). Regression quantile estimates are an ascending sequence of planes that are above an increasing proportion of sample observations with increasing values of tau, that is, the quantiles (Cade & Noon, 2003). When predictor variables exert both a change in means and a change in variance on the distribution of the response, the regression model has unequal variances, and thus quantile regressions are preferred over ordinary least squares regression, which models only a mean response curve (Cade & Noon, 2003). If extreme responses to EM fungal inoculation – whether positive or negative – limit host range sizes, we expected a bell-shaped distribution for range size as a function of effect size. Therefore, we fit a Gaussian function (Equation 1) and estimated model parameters for a range of quantiles (tau of .10 to .99) of the data, where y is the predicted range size, μ is the mean effect of EM fungal inoculation on plant biomass, σ is the standard deviation and k is the height of the Gaussian curve. When μ differs from 0, this indicates that tree species overall tend to respond positively to EM fungal inoculation. When σ differs from 0, the response of most tree species to EM fungal inoculation is different than the mean, specifically, extreme responses to EM fungal inoculation become more prevalent as σ increases. And as k depends on σ , the height of the curve (i.e. $k > 0$) necessarily increases with lower values of σ . Together, σ and k capture the strength of the relationship between range size of adult trees and seedling response to EM fungal inoculation, and μ represents its central tendency.

$$y = ke^{-\frac{(x-\mu)^2}{2\sigma^2}} \quad (1)$$

To determine whether range size is a function of the strength of the mutualism, that is, the extent to which seedling biomass increases with EM fungal inoculation, we also re-ran the quantile regression using a simple linear model. The linear model tested the prediction that enemy-release or mutualist-deprivation influences range size. Statistical analyses were conducted within the R software environment version 3.3.2 (R Core Team, 2016). Functions provided in R package 'quantreg' version 5.29 (Koenker, 2016) were used to perform the nonlinear quantile regression.

To examine possible mechanisms underlying the relationship between range size and seedling response to EM fungal inoculation, we compared how effect sizes calculated for each observation varied by extent of sympatry between host and fungi. Using observations representing inoculated seedlings with only one fungal species ('single inoculum experiments'), and that identified fungi to species ($n = 975$), we investigated whether hosts were naturally sympatric with fungi by searching herbaria databases with geospatially referenced data. Here, we define sympatry as any population of fungi from anywhere in the range of a tree hosts. Nomenclature of fungi was checked for consistency with Index Fungorum (<http://www.indexfungorum.org/>), and we subsequently visually compared ranges of hosts and fungi using The Global Biodiversity Information Facility (<https://demo.gbif.org>). From this database, point occurrences are displayed on a map based on observations and living and preserved specimens. In some cases, the Atlas of Living Australia (<http://www.ala.org.au/>) was used to map point occurrences of hosts. Although some tree species have been widely cultivated around the world (e.g. *Eucalyptus globulus* and *Pinus radiata*), we restricted our investigation of sympatry to native host ranges. We categorized range overlap into two categories: (a) clear or possible overlap, where the ranges touched borders, or the data were more limited (< 100 occurrences total); and (b) no or unlikely overlap, where no points occurred within geographical proximity and a search of the literature failed to show any records of co-occurrence, or, where only a few locations of the fungal species occurred near the range of the host tree and/or the literature was comprised solely of inoculation experiments. We used a Welch's t test to test the relationship between effect size and extent of host-symbiont geographical range overlap.

We tested for sampling artefacts in several ways. First, we tested whether tree species with large ranges were included in the database more extensively than those with small ranges by using a correlation between the number of inoculation experiments performed on a host species (i.e. observations) and its range size. Second, we tested whether species with large ranges have been subject to inoculations by a greater number of fungal species than those with small ranges by a correlation between range size and the overall number of fungal species used across experiments for a given host species. Similarly, we also tested for a correlation between mean effect size and the overall number of fungal species used across experiments for a given host species. These latter two analyses were constrained to single inoculum experiments. We tested for a taxonomic bias (see Results) by re-running nonlinear quantile regressions using the upper values of tau (.99, .90, .80) on subsets of the data. Tree species belonging to *Pinus* were the most frequent host (48%) in the database and *Pisolithus* was the most commonly used fungal inoculant (34% of studies). We re-ran the analysis on the following subsets of data: (a) *Pinus* species only, (b) tree species excluding *Pinus*, (c) studies using *Pisolithus* as an inoculant, and (d) studies excluding *Pisolithus* as an inoculant. Parsing the data in this way enabled us to test whether the results were the product of the response of a single common genus (*Pinus*) to EM fungal inoculation, or alternatively, the effect of a single frequently used fungal genus (*Pisolithus*) as inoculum across experiments.

3 | RESULTS

Across 59 tree species (14 genera), range size varied by six orders of magnitude (Supporting Information Table S1). *Eucalyptus dunnii* had the smallest range area (8 km²) and *Picea abies* the largest (12,093,500 km²). Mean effect sizes across the tree species ranged from negative (minimum: -0.55, *Pinus caribaea* var. *hondurensis*) to positive (maximum: 1.12 *Pinus patula*), reflecting a continuum of host responses to EM fungal inoculation (Figure 1). In total, 52 genera of fungi were represented across the inoculation experiments (Supporting Information Table S2). The most commonly used genera for inoculum

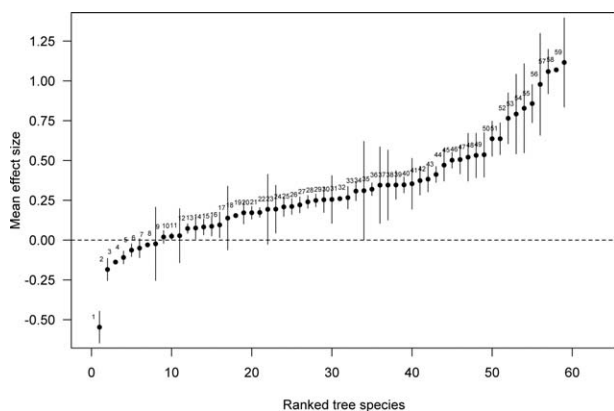


FIGURE 1 Distribution of host responses to inoculation by ectomycorrhizal fungi. Effect sizes were calculated as log response ratios of inoculated to non-inoculated plant biomass and pooled for each tree species: (1) *Pinus caribaea* var. *hondurensis* ($n = 3$), (2) *Castanopsis fissa* ($n = 7$), (3) *Arbutus unedo* ($n = 1$), (4) *Pinus lambertiana* ($n = 10$), (5) *Pinus pinea* ($n = 44$), (6) *Quercus rubra* ($n = 6$), (7) *Quercus faginea* ($n = 1$), (8) *Eucalyptus urophylla* ($n = 96$), (9) *Pinus pinaster* ($n = 166$), (10) *Tilia cordata* ($n = 2$), (11) *Pinus tabulaeformis* ($n = 6$), (12) *Picea mariana* ($n = 23$), (13) *Pinus jeffreyi* ($n = 13$), (14) *Pinus radiata* ($n = 22$), (15) *Populus trichocarpa* ($n = 5$), (16) *Quercus ilex* ($n = 12$), (17) *Betula pendula* ($n = 5$), (18) *Pinus elliotii* ($n = 2$), (19) *Pinus banksiana* ($n = 35$), (20) *Quercus alba* ($n = 5$), (21) *Pinus nigra* ($n = 10$), (22) *Alnus incana* ($n = 6$), (23) *Picea koraiensis* ($n = 3$), (24) *Pinus tecunumanii* ($n = 7$), (25) *Pinus oocarpa* ($n = 7$), (26) *Pseudotsuga menziesii* ($n = 33$), (27) *Eucalyptus dunnii* ($n = 72$), (28) *Pinus taeda* ($n = 31$), (29) *Pinus halepensis* ($n = 27$), (30) *Pinus densiflora* ($n = 18$), (31) *Quercus petraea* ($n = 1$), (32) *Picea abies* ($n = 50$), (33) *Quercus robur* ($n = 18$), (34) *Betula pubescens* ($n = 4$), (35) *Quercus velutina* ($n = 7$), (36) *Pinus virginiana* ($n = 2$), (37) *Acacia mangium* ($n = 13$), (38) *Picea glauca* ($n = 14$), (39) *Pinus wallichiana* ($n = 4$), (40) *Pinus resinosa* ($n = 15$), (41) *Pinus clausa* ($n = 2$), (42) *Eucalyptus diversicolor* ($n = 92$), (43) *Betula lenta* ($n = 6$), (44) *Eucalyptus miniata* ($n = 16$), (45) *Eucalyptus globulus* ($n = 153$), (46) *Quercus variabilis* ($n = 3$), (47) *Populus deltoides* ($n = 8$), (48) *Ostryopsis davidiana* ($n = 10$), (49) *Pinus sylvestris* ($n = 105$), (50) *Pinus rigida* ($n = 6$), (51) *Eucalyptus marginata* ($n = 4$), (52) *Pinus strobus* ($n = 8$), (53) *Fagus sylvatica* ($n = 2$), (54) *Pinus contorta* ($n = 10$), (55) *Eucalyptus tetrodonta* ($n = 8$), (56) *Pinus ponderosa* ($n = 7$), (57) *Pinus pseudostrobus* ($n = 12$), (58) *Pinus greggii* ($n = 1$), (59) *Pinus patula* ($n = 16$). The dotted line indicates no response, values above the line indicate positive response to ectomycorrhizal fungal inoculation (mutualism), and values below the line indicate negative response to inoculation (parasitism)

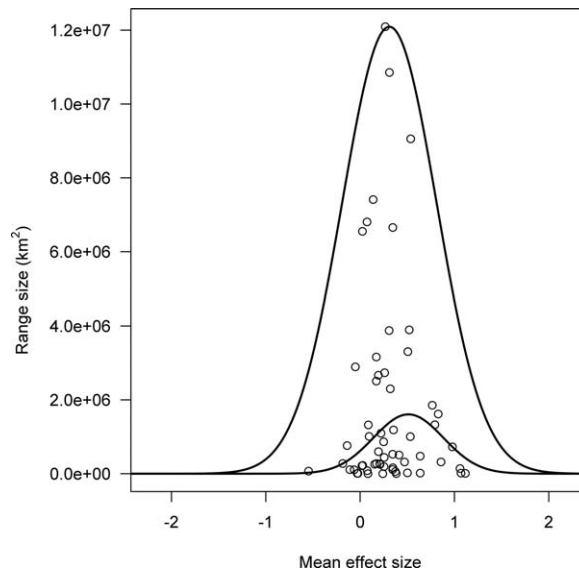


FIGURE 2 Seedlings of tree species with extreme responses to ectomycorrhizal fungal inoculation tend to have small range sizes. Modeled Gaussian relationships between mean effect size (log response ratios of inoculated to non-inoculated seedling biomass) of seedling biomass and tree range area. Each point is a tree species; the upper and lower curves represent the 99th and 60th percentile of points fitting a Gaussian model

were *Pisolithus* (34%), *Laccaria* (11.2%), *Scleroderma* (8.8%), *Suillus* (6.7%), *Rhizopogon* (4.9%) and *Hebeloma* (4.7%) (Supporting Information Table S2). The vast majority of studies (96.9%) used a single species of fungus as inoculum. The number of studies for each tree species ranged from 1 to 166; however, there was no correlation between range size and the number of experiments performed ($r^2 = .041$; $p = .76$). That is, widespread tree species were not present in the database more than species with small ranges. The mean number of fungal species used as inoculum across studies for a given tree species was 4.7 (minimum: 1, maximum: 41). There was no confounding effect of the number of fungal species used as inoculum on host range size ($r^2 = .06$; $p = .66$) or mean effect size ($r^2 = .14$; $p = .32$).

Across tree species, the overall response to EM fungal inoculation was positive; the mean of the Gaussian curve, μ , differed from zero for most values of τ (Supporting Information Table S3, Figures S1 and S2). On average, inoculation with EM fungi resulted in a nearly 40% increase in seedling biomass. Tree species with effect sizes deviating from μ tended to have small ranges and species with average responses tended to have large ranges (Figure 2). For τ greater than .70, k was significantly different than zero (Supporting Information Figures S1 and S2, Table S3). For the parameters μ and σ of the Gaussian model, there was high variation at low values of τ , validating the need for quantile regression (Supporting Information Figure S1). While the μ and σ estimated for the quantiles tended not to differ from those parameters estimated by the ordinary least squares (OLS) model, k parameter estimates for large ($\tau > .90$) quantiles significantly differed from those estimated by OLS (Supporting Information Figure S1). Most species had effect sizes close to the mean; for quantiles below .5, σ did not differ from zero (Supporting Information Table S3, Figure S1). Taken

together, at the upper boundary of range sizes (99–70th percentile), the unimodal response of seedlings to EM fungal inoculation is clearly observed. However, other unmeasured factors become limiting at lower quantiles, expressed as higher heterogeneity of tree species response to EM fungal inoculation. Range size was not predicted by the strength of the mutualism (linear quantile regression: minimum $\rho = .24$ across taus).

The extent of sympatry between hosts and fungi had a significant influence on the response of tree species to EM fungal inoculation ($t_{(227)} = 3.65$; $p < .0001$). Host species inoculated with fungi whose ranges were likely allopatric to their own had a higher positive response (mean = $.43 \pm .047$ SE) than those that were inoculated by sympatric fungi (mean = $.23 \pm .024$ SE).

We did not detect a taxonomic bias in our results (Supporting Information Figure S2, Table S4). Specifically, the relationship between the response to EM fungal inoculation and range size was not solely driven by pines; μ , σ and k were significant at tau of $.99$ for the subset of data analysed on pines only, and all three parameters were significant when the analysis was run on tree species excluding pines ($p < .01$, across the majority of tested values of tau; Supporting Information Table S4). Similarly, the results were not driven by the singular effect of *Pisolithus* on hosts. The relationship between range size and response to inoculation was significant in the subset of studies using fungi other than those species belonging to *Pisolithus*, and non-significant in the subset of studies including *Pisolithus*.

4 | DISCUSSION

Not only do soil microbes influence local and regional patterns of tree distributions (Bennett et al., 2017; Reinhart et al., 2003), but we show that they may also underlie biogeographical patterns at the continental scale. Here, we document that tree species with extreme responses to EM fungal inoculation have small range sizes. This finding is important as it broadens perspectives on factors controlling range sizes beyond abiotic conditions, such as climate. While other research has focused on the role of soil microbes in range shifts of select tree species (Dickie, Bolstridge, Cooper, & Peltzer, 2010; Gundale et al., 2014; Lankau, Zhu, & Ordonez, 2015; McCarthy-Neumann & Ibanez, 2012; Van Nuland, Bailey, & Schweitzer, 2017), ours is novel in the scope of species and the scale tested. Our study also points to a possible mechanism underlying this pattern related to the process of mutualism attenuation with extent of geographical overlap between partners.

As mycorrhizas are generally considered a nutritional mutualism, the presence of different species of fungi may be viewed as a resource for host trees (Peay, 2016). Hosts that benefit more from EM fungal inoculation ought to outperform plants receiving less benefit and in consequence, occupy a large range. However, we found no linear relationship between range size and the strength of mutualism. One explanation for this result is that the range expansion of hosts that have a very positive response to EM fungi is limited by the absence of these fungal species. Similarly, the range expansion of hosts that have a negative response to EM fungi would be limited by the presence of these

fungal species. Our results suggest that tree species that avoid large investments, and as a trade-off, forgo large returns of interacting with EM fungi may have fewer limits on range size (i.e. a unimodal relationship) as this strategy renders hosts less sensitive to unpredictable changes with distance in the species composition of EM fungal communities. This finding is akin to models predicting intermediate levels of virulence in parasites and pathogens once feedbacks between ecological and evolutionary processes are incorporated (Lenski & May, 1994). Recent studies have reported that flexibly mycorrhizal plants (i.e. the ability to grow both with and without mycorrhizal symbiosis) have wider niches (Gerz, Bueno, Ozinga, Zobel, & Moora, 2017), and facultative mycorrhizal plants (i.e. those that are colonized under some conditions but not others) have more success in invading new regions (Menzel et al., 2017). In our study, a conservative response to EM fungi was still a sizeable increase relative to non-inoculated plants. Our results suggest that a conservative response by hosts to EM fungi may be an important factor in defining a species' realized niche. Given that species of EM fungi are patchy and unpredictable in their distributions at local and regional scales, this conservative strategy may have evolved among some tree hosts to manage uncertainty upon dispersal.

In our study, the mean seedling response to EM fungal inoculation is positive; however, the strength of the mutualism declines as the geographical overlap between partners increases. Specifically, tree species inoculated with fungi with overlapping distributions had relatively less growth compared with those inoculated by fungi with distributions that do not overlap the host tree. Allopatric partners presumably represent combinations of hosts and fungi that are novel, and sympatric partners, experienced. From this perspective, our finding aligns with predictions from the enemy-release hypothesis that plant species in 'home' environments suffer from natural enemies more than those in 'foreign' environments (Gundale et al., 2014; Mitchell & Power, 2003). In the present case, 'home' and 'foreign' environments may describe sympatric and allopatric occurrences of partners, respectively. What sets our results apart from those previous is that enemies need not be pathogens; rather, they may reflect the attenuation of a mutualism (Sachs & Simms, 2006; Seifert, Bever, & Maron, 2009). The role of novel associations in promoting the spread and in some cases, invasion, of EM trees has been well documented (Dickie et al., 2017). For instance, *Eucalyptus*, *Pinus* and *Pseudotsuga* formed novel associations with native fungi when planted in new regions (Bahram, Kõljalg, Kohout, Mirshahvaladi, & Tedersoo, 2013; Moeller, Dickie, Peltzer, & Fukami, 2015; Tedersoo, Suvi, Beaver, & Kõljalg, 2007). Our results suggest that trees with conservative responses to fungi that move into new areas with pre-existing EM fungi could be potentially aggressive invaders. Alternatively, our results may reflect a potentially positive mutualism not yet reached between novel partners. Elsewhere, the dynamic nature of species interactions has been demonstrated by the increase of negative PSFs with time since introduction (Diez et al., 2010; Lau & Suwa, 2016). That is, the advantages conferred under conditions of novel species interactions may wane as species share ecological and evolutionary history.

The potential attenuation of the EM mutualism as novel partnerships become experienced may partly underlie differences in range

sizes among tree species. Shifts in range sizes have been cast as the outcomes of biotic forces (Jones & Gilbert, 2016; Levine, Pachepsky, Kendall, Yelenik, & Lambers, 2006). Extending this framework, ranges may expand for tree species that have higher growth when colonized by novel rather than experienced fungi (i.e. positive PSFs) as dispersal of trees is rewarded through interactions with more beneficial fungal partners. However, as the interaction between the partners persists, the reduction of host growth may cause ranges to contract or fragment as these trees are outcompeted. If the rate of expansion at the leading range edge is matched by the rate of contraction at the trailing edge, the entire range may shift. If, however, the relative strength of the mutualism is asymmetrical across the range, this may alter range sizes depending on which process dominates. The strength and direction of the mycorrhizal mutualism depend on both the abiotic and biotic context, and soil conditions may be an important factor underlying these asymmetries (Hoeksema et al., 2010; Kiers et al., 2011). Alternatively, having a conservative response to EM fungi would render hosts insensitive to partner status and perhaps lead to an overall increase in range size. The lack of strict dependence on mutualisms has been recognized as a characteristic that increases resilience in times of rapid environmental change (Kiers, Palmer, Ives, Bruno, & Bronstein, 2010). The high spatial heterogeneity in the composition of EM fungal communities may be precisely the factor underlying the large range sizes of tree species that are relatively insensitive to EM inoculation. To address this hypothesis, further research, especially experimentation, is required on the evolution and ecology of the dynamic nature of mutualisms and their relation to geographical ranges.

We show that tree seedlings can benefit from novel interactions with EM fungi, which appears in conflict with studies on the importance of local adaptation. However, support for local adaptation between EM fungi and their hosts is generally weak, and where strong, the effect of EM fungi is coupled with home soils. For instance, in comparing allopatric and sympatric combinations of three pine species and *Rhizopogon occidentalis* in a pot experiment, Hoeksema and Thompson (2007) did not find support for discrete local adaptation or host-specificity across several measures of pine performance. When examined as a clinal pattern, pine growth did not vary with distance between host and fungal populations of origin. In another pot experiment, Hoeksema, Hernandez, Rogers, Mendoza, and Thompson (2012) found no evidence for local adaptation of *Pinus radiata* populations to soils; in fact, plant relative growth rate was lower in sympatric combinations of plants and soils (suggesting possible maladaptation), although the precise characteristics of soils (chemical properties or composition of pathogenic or EM fungi) underlying this pattern could not be ascertained. Across 32 combinations of soil origin and seedling response of *Pseudotsuga menziesii*, only six showed local adaptation mediated by soil fungi alone (Pickles, Twieg, O'Neill, Mohn, & Simard, 2015). Of the tests performed in the field, different genotypes of *Populus angustifolia* did not vary with EM fungal communities; however, the climate transfer functions of *Pseudotsuga menziesii* populations responded to the combined effects of soil fertility and local EM fungal communities (i.e. soils were coupled with soil biota; Kranabetter, Stoehr, & O'Neill, 2015). Although the evidence for local adaptation between hosts and EM fungi is not

strong, there may be components of the process missed in past experiments. For instance, a host may show a degree of local adaptation to one fungus and not another, or to the community as a whole, or to a particular fungus in a particular soil, or any combination of interactive effects. Similarly, local adaptation might be evident in survival and seed production, but not in growth, and in consequence, local adaptation may be present in the population but unmeasured in existing experiments. In summary, the overall lack of empirical support for local adaptation in EM symbioses does not disagree with our results, but this is an area that needs more research.

While our findings are novel, there are several limitations to the study. First, the majority of experiments included in our analysis were not performed in the field and were on seedlings. Thus, the response to EM fungal inoculation was measured under artificial environments and in a narrow ontogenetic window. However, given the longevity of trees and the difficulty maintaining inoculation treatments in the field, these types of experiments are the only tractable way to circumvent these issues. Second, only a handful of fungal genera have been used as inoculum across the majority of experiments and these have been applied as single species inoculum. Approximately 20,000 species of fungi are estimated to form ectomycorrhizas (Rinaldi, Comandini, & Kuyper, 2008), and a community of these fungi regularly colonizes roots of individual mature trees, sometimes with a high degree of host specificity. In consequence, empirical patterns emerging from these types of experiments lack a community context and miss a large fraction of diversity underlying ectomycorrhizas. These limitations in our synthesis underscore the need to build complexity and ecological relevance into future experimental work, and investigate controls on host specificity. Similarly, nearly half of the tree species included in the database were pines. Although we did not find evidence of taxonomic bias underlying our results, performing experiments with other EM hosts will be important to broaden generalizations. Third, the methods used to assess the extent of range overlap between hosts and fungi are coarse. Sympatric fungi in our study are defined as any population of fungi from anywhere in the range of a tree host. However, the effects of sympatric fungi may be fine-tuned to the local abiotic environment and tree host genetics (Gehring, Sthultz, Flores-Rentería, Whipple, & Whitham, 2017; Kranabetter et al., 2015), while allopatric fungi provide broad advantages to the host. And although there are notable developments in identifying, surveying and cataloguing the biogeography of fungi (Glassman et al., 2015; Peay et al., 2016; Tedersoo et al., 2012, 2014), these attempts lag behind those for plants. One easy solution to this issue would be for researchers to report the geographical origin of plants, fungi and soils used in experiments to enable subsequent meta-analysis on this topic (Rúa et al., 2018). Finally, an important finding revealed by quantile regression is that for tree species with small ranges, their response to EM fungal inoculation poorly accounted for the heterogeneity in outcomes. For these species, unmeasured ecological and evolutionary factors likely play a role in range size and deserve further attention.

Much attention has focused on the detrimental effects arising from when co-evolved partners are uncoupled, but the co-evolutionary process may produce maladaptation more often than not (Thompson,

Nuismer, & Gomulkiewicz, 2002). Here we show that for seedlings of EM tree species, growth may, in fact, increase when exposed to fungal partners lacking recent co-evolutionary interactions. Importantly, it appears that host species that have evolved conservative responses to EM fungi also have larger geographical ranges. Based on these findings, our research has several broad implications. First, it demonstrates the need and validity of incorporating biotic interactions, notably those involving microbes, into tree species distribution models. Second, it necessitates a wider view on how species become invasive or fragmented in distribution. Finally, it reinforces the dynamic nature of mutualisms with space and time.

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DATA ACCESSIBILITY

Data supporting the results can be found on the Dryad Digital Repository (<https://dx.doi.org/10.5061/dryad.723m1.2>).

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REFERENCES

- Bahram, M., Kohout, P., Anslan, S., Harend, H., Abarenkov, K., & Tedersoo, L. (2016). Stochastic distribution of small soil eukaryotes resulting from high dispersal and drift in a local environment. *ISME Journal*, 10(4), 885–896. <https://dx.doi.org/10.1038/ismej.2015.164>
- Bahram, M., Kõljalg, U., Courty, P.-E., Diédhiou, A. G., Kjølner, R., Põlme, S., ... Tedersoo, L. (2013). The distance decay of similarity in communities of ectomycorrhizal fungi in different ecosystems and scales. *Journal of Ecology*, 101(5), 1335–1344. <https://doi.org/10.1111/1365-2745.12120>
- Bahram, M., Kõljalg, U., Kohout, P., Mirshahvaladi, S., & Tedersoo, L. (2013). Ectomycorrhizal fungi of exotic pine plantations in relation to native host trees in Iran: Evidence of host range expansion by local symbionts to distantly related host taxa. *Mycorrhiza*, 23(1), 11–19. <https://doi.org/10.1007/s00572-012-0445-z>
- Bahram, M., Peay, K. G., & Tedersoo, L. (2015). Local-scale biogeography and spatiotemporal variability in communities of mycorrhizal fungi. *New Phytologist*, 205(4), 1454–1463. <https://doi.org/10.1111/nph.13206>
- Bennett, J. A., Maherali, H., Reinhart, K. O., Lekberg, Y., Hart, M. M., & Klironomos, J. (2017). Plant-soil feedbacks and mycorrhizal type influence temperate forest population dynamics. *Science*, 355(6321), 181–184. <https://doi.org/10.1126/science.aai8212>
- Berendsen, R. L., Pieterse, C. M. J., & Bakker, P. (2012). The rhizosphere microbiome and plant health. *Trends in Plant Science*, 17(8), 478–486. <https://doi.org/10.1016/j.tplants.2012.04.001>
- Bever, J. D. (2003). Soil community feedback and the coexistence of competitors: Conceptual frameworks and empirical tests. *New Phytologist*, 157(3), 465–473. <https://doi.org/10.1046/j.1469-8137.2003.00714.x>
- Brawner, J., Hodge, G., Medder, R., & Dvorak, W. (2014). Visualising the environmental preferences of *Pinus tecunumanii* populations. *Tree Genetics and Genomes*, 10, 1123–1133.
- Brown, J. H., Stevens, G. C., & Kaufman, D. M. (1996). The geographic range: Size, shape, boundaries, and internal structure. *Annual Review of Ecology and Systematics*, 27, 597–623. <https://doi.org/10.1146/annurev.ecolsys.27.1.597>
- Cade, B. S., & Noon, B. R. (2003). A gentle introduction to quantile regression for ecologists. *Frontiers in Ecology and the Environment*, 1(8), 412–420. <https://doi.org/10.2307/3868138>
- Chaudhary, V. B., Rúa, M. A., Antoninka, A., Bever, J. D., Cannon, J., Craig, A., ... Hoeksema, J. D. (2016). MycoDB, a global database of plant response to mycorrhizal fungi. *Scientific Data*, 3, 160028. <https://doi.org/10.5061/dryad.723m1.2>
- Chen, Z. D., & Li, J. H. (2004). Phylogenetics and biogeography of *Alnus* (Betulaceae) inferred from sequences of nuclear ribosomal DNA ITS region. *International Journal of Plant Sciences*, 165(2), 325–335. <https://doi.org/10.1086/382795>
- Chukhina, I., & Bagmet, L. (2007). Range of distribution of *Betula pubescens* Ehrh. (Downy birch, white birch). In A. N. Afonin, S.L. Greene, N.I. Dzyubenko, & A.N. Frolov (Eds.), *Interactive agricultural and ecological atlas of Russia and neighboring countries: Economic plants and their diseases, pests and weeds*. AgroAtlas. Retrieved from <http://www.agroatlas.ru>
- Dickie, I. A., Bolstridge, N., Cooper, J. A., & Peltzer, D. A. (2010). Co-invasion by *Pinus* and its mycorrhizal fungi. *New Phytologist*, 187(2), 475–484. <https://doi.org/10.1111/j.1469-8137.2010.03277.x>
- Dickie, I. A., Bufford, J. L., Cobb, R. C., Desprez-Loustau, M.-L., Grelet, G., Hulme, P. E., ... Williams, N. M. (2017). The emerging science of linked plant-fungal invasions. *New Phytologist*, 215(4), 1314–1332. <https://doi.org/10.1111/nph.14657>
- Diez, J. M., Dickie, I., Edwards, G., Hulme, P. E., Sullivan, J. J., & Duncan, R. P. (2010). Negative soil feedbacks accumulate over time for non-native plant species. *Ecology Letters*, 13(7), 803–809. <https://doi.org/10.1111/j.1461-0248.2010.01474.x>
- Egger, K. N., & Hibbett, D. S. (2004). The evolutionary implications of exploitation in mycorrhizas. *Canadian Journal of Botany*, 82(8), 1110–1121. <https://doi.org/10.1139/b04-056>
- European Forest Genetic Resources Programme (EUFORGEN). (2009). *Distribution maps Biodiversity International*. Retrieved from <http://www.euforgen.org/distribution-maps/>
- Gaston, K. J. (1996). Species-range-size distributions: Patterns, mechanisms and implications. *Trends in Ecology and Evolution*, 11(5), 197–201. [https://doi.org/10.1016/0169-5347\(96\)10027-6](https://doi.org/10.1016/0169-5347(96)10027-6)
- Gaston, K. J. (1998). Species-range size distributions: Products of speciation, extinction and transformation. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 353(1366), 219–230. <https://doi.org/10.1098/rstb.1998.0204>
- Gaston, K. J. (2003). *The structure and dynamics of geographic ranges*. UK: Oxford University Press.
- Gehring, C. A., Sthultz, C. M., Flores-Rentería, L., Whipple, A. V., & Whitham, T. G. (2017). Tree genetics defines fungal partner communities that may confer drought tolerance. *Proceedings of the National Academy of Sciences USA*, 114(42), 11169–11174. <https://doi.org/10.1073/pnas.1704022114>
- Gerz, M., Bueno, C. G., Ozinga, W. A., Zobel, M., & Moora, M. (2017). Niche differentiation and expansion of plant species are associated with mycorrhizal symbiosis. *Journal of Ecology*, 106, 6–19.

- Glassman, S. I., Peay, K. G., Talbot, J. M., Smith, D. P., Chung, J. A., Taylor, J. W., ... Bruns, T. D. (2015). A continental view of pine-associated ectomycorrhizal fungal spore banks: A quiescent functional guild with a strong biogeographic pattern. *New Phytologist*, 205(4), 1619–1631. <https://doi.org/10.1111/nph.13240>
- Gundale, M. J., Kardol, P., Nilsson, M. C., Nilsson, U., Lucas, R. W., & Wardle, D. A. (2014). Interactions with soil biota shift from negative to positive when a tree species is moved outside its native range. *New Phytologist*, 202(2), 415–421. <https://doi.org/10.1111/nph.12699>
- Hernandez-Leon, S., Gernandt, D. S., de la Rosa, J. A. P., & Jardon-Barbolla, L. (2013). Phylogenetic relationships and species delimitation in *Pinus* section *trifoliae* inferred from plastid DNA. *PLoS One*, 8(7), e70501. <https://doi.org/10.1371/journal.pone.0070501>
- Hodge, G., & Dvorak, W. (2012). Growth potential and genetic parameters of four Mesoamerican pines planted in the Southern Hemisphere. *Southern Forests*, 74, 27–49.
- Hoeksema, J. D., Chaudhary, V. B., Gehring, C. A., Johnson, N. C., Karst, J., Koide, R. T., ... Umbanhowar, J. (2010). A meta-analysis of context-dependency in plant response to inoculation with mycorrhizal fungi. *Ecology Letters*, 13(3), 394–407. <https://doi.org/10.1111/j.1461-0248.2009.01430.x>
- Hoeksema, J. D., Hernandez, J. V., Rogers, D. L., Mendoza, L. L., & Thompson, J. N. (2012). Geographic divergence in a species-rich symbiosis: Interactions between Monterey pines and ectomycorrhizal fungi. *Ecology*, 93(10), 2274–2285.
- Hoeksema, J. D., & Thompson, J. N. (2007). Geographic structure in a widespread plant-mycorrhizal interaction: Pines and false truffles. *Journal of Evolutionary Biology*, 20(3), 1148–1163. <https://doi.org/10.1111/j.1420-9101.2006.01287.x>
- Jones, N. T., & Gilbert, B. (2016). Biotic forcing: The push-pull of plant ranges. *Plant Ecology*, 217(11), 1331–1344. <https://doi.org/10.1007/s11258-016-0603-z>
- Karst, J., Marczak, L., Jones, M. D., & Turkington, R. (2008). The mutualism-parasitism continuum in ectomycorrhizas: A quantitative assessment using meta-analysis. *Ecology*, 89(4), 1032–1042. <https://doi.org/10.1890/07-0823.1>
- Kiers, E. T., Duhamel, M., Beesetty, Y., Mensah, J. A., Franken, O., Verbruggen, E., ... Bucking, H. (2011). Reciprocal rewards stabilize cooperation in the mycorrhizal symbiosis. *Science*, 333(6044), 880–882. <https://doi.org/10.1126/science.1208473>
- Kiers, E. T., Palmer, T. M., Ives, A. R., Bruno, J. F., & Bronstein, J. L. (2010). Mutualisms in a changing world: An evolutionary perspective. *Ecology Letters*, 13(12), 1459–1474. <https://doi.org/10.1111/j.1461-0248.2010.01538.x>
- Klironomos, J. N. (2002). Feedback with soil biota contributes to plant rarity and invasiveness in communities. *Nature*, 417(6884), 67–70. <https://doi.org/10.1038/417067a>
- Koenker, R. (2016). *Quantreg: Quantile regression* (R package version 5.29). Retrieved from <https://CRAN.R-project.org/package=quantreg>
- Kranabetter, J. M., Stoehr, M., & O'Neill, G. A. (2015). Ectomycorrhizal fungal maladaptation and growth reductions associated with assisted migration of Douglas-fir. *New Phytologist*, 206(3), 1135–1144. <https://doi.org/10.1111/nph.13287>
- Kulmatiski, A., Beard, K. H., Stevens, J. R., & Cobbold, S. M. (2008). Plant-soil feedbacks: A meta-analytical review. *Ecology Letters*, 11(9), 980–992. <https://doi.org/10.1111/j.1461-0248.2008.01209.x>
- Lankau, R. A., Zhu, K., & Ordóñez, A. (2015). Mycorrhizal strategies of tree species correlate with trailing range edge responses to current and past climate change. *Ecology*, 96(6), 1451–1458. <https://doi.org/10.1890/14-2419.1>
- Lau, J. A., & Suwa, T. (2016). The changing nature of plant-microbe interactions during a biological invasion. *Biological Invasions*, 18(12), 3527–3534. <https://doi.org/10.1007/s10530-016-1245-8>
- Lenski, R. E., & May, R. M. (1994). The evolution of virulence in parasites and pathogens - reconciliation between 2 competing hypotheses. *Journal of Theoretical Biology*, 169(3), 253–265. <https://doi.org/10.1006/jtbi.1994.1146>
- Levine, J. M., Pachepsky, E., Kendall, B. E., Yelenik, S. G., & Lambers, J. H. R. (2006). Plant-soil feedbacks and invasive spread. *Ecology Letters*, 9(9), 1005–1014. <https://doi.org/10.1111/j.1461-0248.2006.00949.x>
- Lilleskov, E. A., Bruns, T. D., Horton, T. R., Taylor, D. L., & Grogan, P. (2004). Detection of forest stand-level spatial structure in ectomycorrhizal fungal communities. *FEMS Microbiology Ecology*, 49(2), 319–332. <https://doi.org/10.1016/j.femsec.2004.04.004>
- Liu, B., Abbott, R., Lu, Z., Tian, B., & Lu, J. (2014). Diploid hybrid origin of *Ostryopsis intermedia* (Betulaceae) in the Qinghai-Tibet Plateau triggered by quaternary climate change. *Molecular Ecology*, 23, 3013–3027.
- Mangan, S. A., Schnitzer, S. A., Herre, E. A., Mack, K. M. L., Valencia, M. C., Sanchez, E. I., & Bever, J. D. (2010). Negative plant-soil feedback predicts tree-species relative abundance in a tropical forest. *Nature*, 466(7307), 752–755. <https://doi.org/10.1038/nature09273>
- Mattis, P., & Kimball, S. (2015). *GNU Image Manipulation Program (GIMP)*. Boston, MA. Retrieved from <https://www.gimp.org/>
- McCarthy-Neumann, S., & Ibanez, I. (2012). Tree range expansion may be enhanced by escape from negative plant-soil feedbacks. *Ecology*, 93(12), 2637–2649.
- Menzel, A., Hempel, S., Klotz, S., Moora, M., Pyšek, P., Rillig, M. C., ... Kühn, I. (2017). Mycorrhizal status helps explain invasion success of alien plant species. *Ecology*, 98(1), 92–102. <https://doi.org/10.1002/ecy.1621>
- Mitchell, C. E., & Power, A. G. (2003). Release of invasive plants from fungal and viral pathogens. *Nature*, 421(6923), 625–627. <https://doi.org/10.1038/nature01317>
- Moeller, H. V., Dickie, I. A., Peltzer, D. A., & Fukami, T. (2015). Mycorrhizal co-invasion and novel interactions depend on neighborhood context. *Ecology*, 96(9), 2336–2347. <https://doi.org/10.1890/14-2361.1>
- Molina, R., Massicotte, H. B., & Trappe, J. M. (1992). Specificity phenomena in mycorrhizal symbioses: Community-ecological consequences and practical implications. In M. F. Allen (Ed.), *Mycorrhizal Functioning* (pp. 357–423). New York: Chapman and Hall.
- Morin, X., & Lechowicz, M. J. (2011). Geographical and ecological patterns of range size in North American trees. *Ecography*, 34(5), 738–750. <https://doi.org/10.1111/j.1600-0587.2010.06854.x>
- Morin, X., & Lechowicz, M. J. (2013). Niche breadth and range area in North American trees. *Ecography*, 36(3), 300–312. <https://doi.org/10.1111/j.1600-0587.2012.07340.x>
- Nunez, M. A., Horton, T. R., & Simberloff, D. (2009). Lack of below-ground mutualisms hinders Pinaceae invasions. *Ecology*, 90(9), 2352–2359. <https://doi.org/10.1890/08-2139.1>
- Peay, K. G. (2016). The mutualistic niche: Mycorrhizal symbiosis and community dynamics. *Annual Review of Ecology, Evolution, and Systematics*, 47, 143–164.
- Peay, K. G., Kennedy, P. G., & Talbot, J. M. (2016). Dimensions of biodiversity in the Earth mycobiome. *Nature Reviews Microbiology*, 14(7), 434–447. <https://doi.org/10.1038/nrmicro.2016.59>
- Pickles, B. J., Genney, D. R., Potts, J. M., Lennon, J. J., Anderson, I. C., & Alexander, I. J. (2010). Spatial and temporal ecology of Scots pine ectomycorrhizas. *New Phytologist*, 186(3), 755–768. <https://doi.org/10.1111/j.1469-8137.2010.03204.x>

- Pickles, B. J., Twieg, B. D., O'Neill, G. A., Mohn, W. W., & Simard, S. W. (2015). Local adaptation in migrated interior Douglas-fir seedlings is mediated by ectomycorrhizas and other soil factors. *New Phytologist*, 207(3), 858–871. <https://doi.org/10.1111/nph.13360>
- Pither, J. (2003). Climate tolerance and interspecific variation in geographic range size. *Proceedings of the Royal Society B: Biological Sciences*, 270(1514), 475–481. <https://doi.org/10.1098/rspb.2002.2275>
- R Core Team. (2016). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. Retrieved from <https://www.R-project.org/>
- Rasband, W. (2016). *ImageJ*. Bethesda, MD: U.S. National Institutes of Health. Retrieved from <https://imagej.nih.gov/ij>
- Reinhart, K. O., & Callaway, R. M. (2006). Soil biota and invasive plants. *New Phytologist*, 170(3), 445–457. <https://doi.org/10.1111/j.1469-8137.2006.01715.x>
- Reinhart, K. O., Packer, A., Van der Putten, W. H., & Clay, K. (2003). Plant-soil biota interactions and spatial distribution of black cherry in its native and invasive ranges. *Ecology Letters*, 6(12), 1046–1050. <https://doi.org/10.1046/j.1461-0248.2003.00539.x>
- Revell, L. J. (2012). phytools: An R package for phylogenetic comparative biology (and other things). *Methods in Ecology and Evolution*, 3(2), 217–223. <https://doi.org/10.1111/j.2041-210X.2011.00169.x>
- Richardson, D. (1998). *Ecology and Biogeography of Pinus*. UK: Cambridge University Press.
- Rinaldi, A. C., Comandini, O., & Kuyper, T. W. (2008). Ectomycorrhizal fungal diversity: Separating the wheat from the chaff. *Fungal Diversity*, 33, 1–45.
- Rúa, M. A., Lamit, L. J., Gehring, C., Antunes, P. M., Hoeksema, J. D., Zabinski, C., ... Woods, M. J. (2018). Accounting for local adaptation in ectomycorrhizas: A call to track geographical origin of plants, fungi, and soils in experiments. *Mycorrhiza*, 28, 187–195.
- Sachs, J. L., & Simms, E. L. (2006). Pathways to mutualism breakdown. *Trends in Ecology and Evolution*, 21(10), 585–592. <https://doi.org/10.1016/j.tree.2006.06.018>
- Sánchez-Ramírez, S., Wilson, A. W., & Ryberg, M. (2017). Overview of phylogenetic approaches to mycorrhizal biogeography, diversity and evolution. In L. Tedersoo (Ed.), *Biogeography of mycorrhizal symbiosis: Ecological studies (Analysis and synthesis)* (Vol. 230, pp. 1–37). Cham, Switzerland: Springer.
- Seifert, E. K., Bever, J. D., & Maron, J. L. (2009). Evidence for the evolution of reduced mycorrhizal dependence during plant invasion. *Ecology*, 90(4), 1055–1062.
- Sexton, J. P., McIntyre, P. J., Angert, A. L., & Rice, K. J. (2009). Evolution and ecology of species range limits. *Annual Review of Ecology Evolution and Systematics*, 40, 415–436.
- Smith, S., & Read, D. (2008). *Mycorrhizal Symbiosis*. Great Britain: Elsevier Ltd.
- Stevens, G. C. (1989). The latitudinal gradient in geographical range - How so many species coexist in the tropics. *The American Naturalist*, 133(2), 240–256. <https://doi.org/10.1086/284913>
- Tedersoo, L., Bahram, M., Polme, S., Koljalg, U., Yorou, N. S., Wijesundera, R., ... Abarenkov, K. (2014). Global diversity and geography of soil fungi. *Science*, 346(6213), 1256688. <https://doi.org/10.1126/science.1256688>
- Tedersoo, L., Bahram, M., Toots, M., Diédhiou, A., Henkel, T., Kjøller, R., ... Koljalg, U. (2012). Towards global patterns in the diversity and community structure of ectomycorrhizal fungi. *Molecular Ecology*, 21(17), 4160–4170. <https://doi.org/10.1111/j.1365-294X.2012.05602.x>
- Tedersoo, L., Suvi, T., Beaver, K., & Koljalg, U. (2007). Ectomycorrhizal fungi of the Seychelles: diversity patterns and host shifts from the native *Vateriopsis seychellarum* (Dipterocarpaceae) and *Intsia bijuga* (Caesalpiniaceae) to the introduced *Eucalyptus robusta* (Myrtaceae), but not *Pinus caribea* (Pinaceae). *New Phytologist*, 175(2), 321–333. <https://doi.org/10.1111/j.1469-8137.2007.02104.x>
- Teste, F. P., Kardol, P., Turner, B. L., Wardle, D. A., Zemunik, G., Renton, M., & Laliberté, E. (2017). Plant-soil feedback and the maintenance of diversity in Mediterranean-climate shrublands. *Science*, 355(6321), 173–176. <https://doi.org/10.1126/science.aai8291>
- Thompson, J. N., Nuismer, S. L., & Gomulkiewicz, R. (2002). Coevolution and Maladaptation1. *Integrative and Comparative Biology*, 42(2), 381–387. <https://doi.org/10.1093/icb/42.2.381>
- U.S. Geological Survey (1999). Digital representation of “Atlas of United States Trees” by Elbert L. Little, Jr. Retrieved from <http://gec.cr.usgs.gov/data/little>
- Van Nuland, M. E., Bailey, J. K., & Schweitzer, J. A. (2017). Divergent plant-soil feedbacks could alter future elevation ranges and ecosystem dynamics. *Nature Ecology and Evolution*, 1, 0150. <https://doi.org/10.1038/s41559-017-0150>
- Vandenkoornhuysen, P., Quaiser, A., Duhamel, M., Le Van, A., & Dufresne, A. (2015). The importance of the microbiome of the plant holobiont. *New Phytologist*, 206(4), 1196–1206. <https://doi.org/10.1111/nph.13312>
- Zanne, A. E., Tank, D. C., Cornwell, W. K., Eastman, J. M., Smith, S. A., FitzJohn, R. G., ... Beaulieu, J. M. (2014). Three keys to the radiation of angiosperms into freezing environments. *Nature*, 506(7486), 89. <https://doi.org/10.1038/nature12872>

BIOSKETCH

Our group studies the ecology and evolution of ectomycorrhizas and uses this information to inform basic and applied ecology.

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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