



# More closely related species are more ecologically similar in an experimental test

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**The relationship between phylogenetic distance and ecological similarity is key to understanding mechanisms of community assembly, a central goal of ecology. The field of community phylogenetics uses phylogenetic information to infer mechanisms of community assembly; we explore, the underlying relationship between phylogenetic similarity and the niche. We combined a field experiment using 32 native plant species with a molecular phylogeny and found that closely related plant species shared similar germination and early survival niches. Species also competed more with close relatives than with distant relatives in field soils; however, in potting soil this pattern reversed, and close relatives might even have more mutualistic relationships than distant relatives in these soils. Our results suggest that niche conservatism (habitat filtering) and species interactions (competition or facilitation) structure community composition, that phylogenetic relationships influence the strength of species' interactions, and that conserved aspects of plant niches include soil attributes.**

Darwin's naturalization hypothesis | phylogenetic signal

A primary goal of ecology is to understand the processes governing species coexistence and how species are assembled into communities. As Donoghue (1) notes, "As we proceed to predict responses to global change, I believe it will be necessary to acknowledge and more finely characterize the spectrum that exists in the evolutionary lability of ecologically relevant traits" (1). Models of community assembly make predictions about how species' differences affect the likelihood of coexistence (2–6). Stable coexistence requires competitors to differ in their niches, and species that are too ecologically similar cannot coexist (limiting similarity) (2, 7, 8). Although highly similar species with nearly equal fitness may delay competitive exclusion through nearly neutral dynamics, species differences are ultimately required for stable coexistence (9, 10).

Intersecting with this discussion of ecological similarity and coexistence is the degree to which phylogenetic relatedness between species reflects their ecological similarity and thus, can be used to understand coexistence and community assembly (11). Community phylogenetics use patterns of relatedness among species in existing communities to infer the processes governing assembly (11–18). Typically, communities in the field are sampled, and the distribution of phylogenetic distances between coexisting species is compared with that of null communities that are randomly assembled from the regional species pool. Two mechanisms are commonly invoked when existing communities differ from randomly assembled ones. Limiting similarity is inferred as an important organizing process when communities are comprised of species more distantly related than expected by chance or communities are more evenly represented across the phylogenetic tree than expected (11, 12). In contrast, environmental filtering is often invoked to explain phylogenetically clustered coexisting species (13, 17, 19) (that is, closely related species that co-occur in similar environments as a result of shared traits).

A basic assumption for both of these interpretations of phylogenetic pattern is that phylogenetic relatedness is correlated with ecological similarity. Several hypotheses to explain com-

munity structure explicitly predict a link between ecological similarity and phylogenetic relatedness. Darwin's (20) naturalization hypothesis predicts that introduced species closely related to the native community are less likely to be successful colonists than are more distantly related introduced species as a result of competitive exclusion between close relatives (20). Darwin (20) argued that closely related species compete most intensely, because they have similar morphologies and niches. However, the degree to which close relatives are similar in niche is still debated (21). Some studies find evidence for phylogenetic signal in niche characteristics (22), whereas others find that important aspects of the niche are highly labile with respect to ancestry (23, 24). With few exceptions, these studies are observational (25, 26), and there has been a call for more experimental studies (13).

Owing to their sessile nature, plants can be experimentally placed into the niches of close and distant relatives in the field and then assessed for their performance. We ask whether and to what degree two important aspects of the plant niche—the germination niche and the strength of species interactions (i.e., competition and facilitation)—scale with phylogenetic relatedness. Note that, by measuring plant performance directly, we bypass the potential complications of choosing appropriate traits to measure to best characterize niche differences among species (27).

Germination has been shown to be a key process in determining plant community composition (28, 29), because a critical aspect of plant success is the ability to germinate and survive in a habitat (28, 29). We asked whether germination and early survival niches in the field are phylogenetically conserved using a field transplant experiment with native species growing at the Bodega Bay Marine Reserve. Each of the 32 focal species was planted into the microhabitats of four relatives that varied in their phylogenetic distance from the focal species. Although phylogenetic distance was calculated as a continuous metric, the planting sites were originally assigned at random from the species list of the reserve based on taxonomic rank (conspecific, congener, confamilial, and distant relatives). By planting species into the unaltered habitats of their relatives in the field, we included both biotic and abiotic components of the realized niche in our estimation of niche similarity. We then correlated focal species performance with the phylogenetic distance separating the focal species and the destination species (Fig. S1 and Table S1).

Additionally, to test whether species interact more strongly (through competition or facilitation) with close relatives than with distant relatives (11, 19, 20), we conducted a species interaction experiment in an outdoor lath house. We grew a focal species both alone and with interactors that varied in phyloge-

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netic distance from the focal species. These interaction experiments were carried out in field soils collected under species that varied in their phylogenetic distance from the focal species. If close relatives are ecologically similar, then we predict that they may experience either greater competition when grown with one another or greater facilitation if, for example, they share soil mutualists. If abiotic or biotic soil characteristics are an important part of the plant niche, we might also expect the strength or pattern of interactions to vary across soil types and with phylogenetic distance.

## Results and Discussion

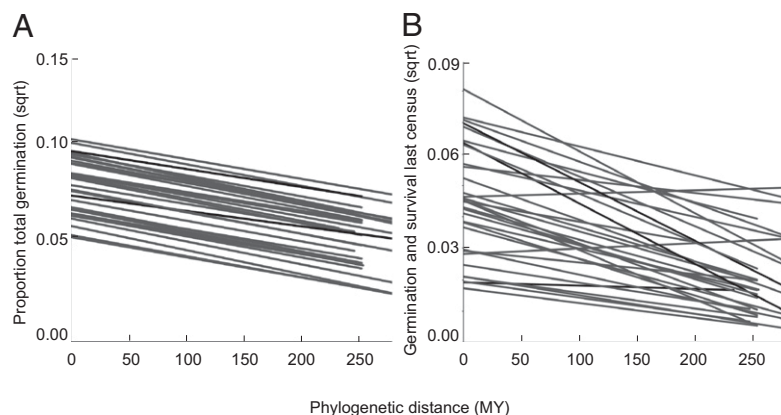
We found that phylogenetic relatedness predicted ecological similarity in both germination and early survival rates as well as in the strength of species interactions. The germination niche was strongly conserved across most species in this study, consistent with a role of habitat filtering in the assembly of these communities. We found a negative relationship between phylogenetic distance and germination rate (Fig. 1A, Table 1, and Tables S2–S4) as well as for germination plus survival over the first 3 mo (last census) (Fig. 1B, Table 1, and Tables S2 and S4). Most species performed best at conspecifics' and congeners' sites and less well at confamilials' and distant relatives' sites (Fig. S2 and Table S4). The negative relationship between germination and phylogenetic distance was robust to different methods of estimating phylogenetic distance (Fig. S2). Phylogenetic distance also scaled with taxonomic ranks as one might expect (congeners =  $30 \pm 0.62$  Mya SE; confamilials =  $81 \pm 0.75$  Mya SE; distant =  $264 \pm 1.36$  Mya SE) and was nonoverlapping among ranks (Fig. S2). Functional groups behaved similarly, with species performing less well at distant relatives' sites, even if those distant relatives were Fabaceae, which could be expected to facilitate distant relatives because of the presence of soil mutualists such as rhizobia and mycorrhizae (Table S4).

These germination and early survival patterns could be driven by multiple possible mechanisms, including shared adaptations to soil nutrient profiles, soil moisture or texture, soil biota, or herbivores, to name just a few niche axes. Although the goal of this study was to determine patterns, not mechanisms, we have some information about potential drivers of conservatism of the germination niche. First, differences in herbivory among sites could have influenced patterns with respect to early survival among sites (30), especially if herbivory is not independent of phylogenetic distance (30). We found that the amount of above-ground herbivory was low, did not differ significantly among sites,

and tended to be greater at close relatives' than distant relatives' sites (site type effect:  $\chi^2 = 5.24$ ,  $P > 0.15$ ; conspecific:  $0.004 \pm 0.002$ ; congener:  $0.005 \pm 0.003$ ; confamilial:  $0.003 \pm 0.002$ ; distant: 0% damage because of herbivory). The negative relationship between damage from herbivores and phylogenetic relatedness is consistent with other reports in the literature (30), and if it were a major driver of our patterns of niche similarity, it should result in increased survivorship with increasing phylogenetic distance, a result diametrically opposed to the pattern we found.

Second, it is possible that lower germination at phylogenetically distant relatives' sites could be the result of a greater likelihood that those sites belong to a different habitat type (e.g., coastal prairie, dune, or seep) (Fig. S1). However, most planting sites were in coastal prairie habitat and spanned the range of phylogenetic distance treatments, such that patterns in germination were not driven by gross differences in habitat type across destination sites (Table S3). Third, we explored if there was any spatial signal in the distribution of relatives at Bodega Bay Marine Reserve. Geographic distance between sites of species was positively related to phylogenetic distance between these same species (slope = 0.26;  $P < 0.001$ ), a result suggesting significant spatial autocorrelation in shared niche attributes such as biotic or abiotic soil characteristics (31). However, phylogenetic distance was a much better predictor of germination and early survival than geographic distance (Table S2). More experiments and data collections are needed to determine which mechanisms are the greatest contributors to this pattern of phylogenetic conservation of the germination niche.

We also found evidence for phylogenetic conservation of the strength of species interactions in field soils, consistent with an environment-dependent role for competition and facilitation in driving community assembly patterns at Bodega Bay Marine Reserve (Fig. 2, Figs. S3 and S4, Table 2, and Table S5). We found that most species performed better when grown with distant than with close relatives in field soils (Fig. 2, Table 2, and Fig. S4). Mortality in some soils prevented our running a full model with all interactions with soil type (Table 2). To explore interactions between soil type and the effect of phylogenetic distance, we conducted sign tests. We found that the slope relating phylogenetic distance to relative interaction intensity (RII) was positive for 10 of 12 species in conspecific soil, 9 of 12 species in congeneric soil, and 11 of 12 species in confamilial soil (sign tests significant for conspecific and confamilial soils were  $0.01 < P < 0.04$ ), but there was no consistent relationship be-



**Fig. 1.** (A) The germination niche was phylogenetically conserved. There was a negative relationship between total germination and phylogenetic distance in the mixed model with species and the interaction between species and phylogenetic distance as random effects (Table 1). (B) Germination and early survival were also phylogenetically conserved for the majority of species (last census) (Table 1). Significant slopes in black (Table S4); conditional prediction lines are from the mixed model.

**Table 1. Phylogenetic distance to species at the planting site was negatively correlated with germination proportion, germination, and survival to the last census (52)**

Source	Estimate	SE	DF denominator	t ratio	P value
Phylogenetic distance at total germination	$-8.38 \times 10^{-5}$	$1.92 \times 10^{-5}$	30	-4.36	<0.0001
Phylogenetic distance at last census	$-9.48 \times 10^{-5}$	$2.96 \times 10^{-5}$	31	3.20	<0.01

Models were selected by AICc among possible models on square root-transformed proportion germination, with species, block, geographic distance, habitat, and their interactions treated as random effects (Table S2). Results shown are for phylogenetic distance estimated using the ML phylogeny scaled to Mya using fossil calibration points (Fig. S1). Phylogenetic distance was also significant in similar analyses when estimated using a phylomatic phylogeny or the raw ML patristic distances.

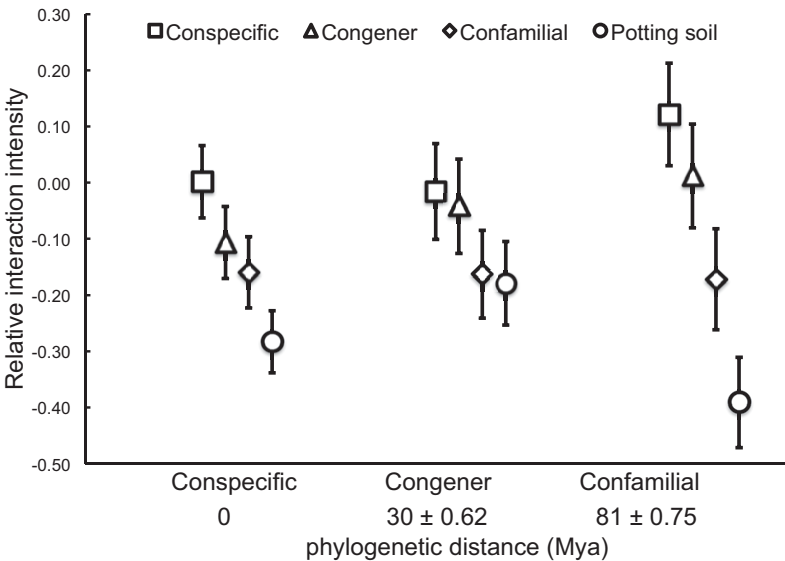
tween phylogenetic distance and RII in potting soil ( $P > 0.10$ ; 5 of 12 slopes were positive).

We also specifically compared the magnitude of RII when plants were interacting with congeners vs. when they were interacting with confamilials to ensure that the phylogenetic distance effect was not just driven by the effects of competition with conspecifics. In conspecific soils, RII was consistently more negative when plants interacted with congeners than confamilials (Wilcoxon paired signed rank test;  $W = 57$ ;  $P < 0.05$ , two-tailed test), suggesting that the effects of phylogenetic distance are still present across the scale of congener to confamilials. Consistent with the soil by phylogenetic distance effect, this result did not hold in the other soil types ( $P > 0.05$ ;  $W = 43, 33$ , and 19 in congener, confamilial, and potting soils, respectively). Thus, biotic and/or edaphic properties of field soil are essential components of the niche that contain phylogenetic signal and affect outcomes of plant interactions. The soil dependence in the outcome of species interactions could partly explain why different studies often find conflicting patterns with respect to Darwin's naturalization hypothesis (Fig. 2) (20, 32–36), and it suggests that soil properties are a key feature of plant niches (37) that cannot be well-approximated using greenhouse experiments in potting soil.

Our results have implications for conservation. The germination niche has been shown to play an important role in response to climate change (28, 29). The consistently similar performance

of species in conspecific and close relatives' sites (Fig. S2) suggests that the presence of close relatives at range edges or in areas that might be targeted as destinations in assisted dispersal efforts might increase the success of a focal species in these areas. The species interaction experiment also informs problems in biological invasions and supports Darwin's hypothesis that distant relatives of native species are more likely to invade communities than are closer relatives of natives (Fig. 2 and Fig. S4) (20, 34, 38); however, the soil dependence in that relationship suggests that the predictive ability of phylogeny for invasiveness may depend on biotic or abiotic components of the soil (Fig. 2). In general, both soil dependence and our results suggesting simultaneous action of mechanisms acting in opposition (habitat filtering and competitive exclusion) could explain some of the conflicting support for this hypothesis in the plant literature (32, 34, 36, 39).

We combined phylogenetic analyses with field and lath house experiments to rigorously test the relationships between multiple measures of ecological similarity and phylogenetic distance. We showed that for two very important aspects of plant niches—germination and plant–plant interactions—phylogenetic distance covaries with ecological similarity across a broad sample of angiosperms. Importantly, we found that the soil environment strongly influenced the outcome of species interactions. Future work will further elucidate the mechanisms that drive these patterns and determine community assembly at the Bodega Bay



**Fig. 2.** Species performed better when grown with more distant relatives than when grown with close relatives in field soils but not in potting soil. Here, for visual clarity, we present mean relative interaction intensity (RII) across interactor type (conspecific, congener, and confamilial) and by soil type; however, our analyses were all conducted on a continuous measure of phylogenetic distance to the interacting species (Table 2). Values of RII of +1 indicate obligate facilitation, values of -1 indicate competitive exclusion, and values of 0 indicate no effect of the interacting species. Squares are interactions in conspecific soil, triangles are interactions in congener soil, diamonds are interactions in confamilial soil, and circles are interactions in potting soil (means  $\pm$  SE). Plants performed best in conspecific soil (Fig. S4; SI Results and Discussion).



**Table 2. Relative interaction intensity (RII) for the lath house experiment**

Source	Count component		Zero inflation component	
	$\chi^2$	P value	$\chi^2$	P value
Species	141.84	<0.001	761.29	<0.001
Soil type	84.11	<0.01	10.56	0.10
Phylogenetic distance	30.85	<0.01	34.07	<0.01
Species $\times$ phylogenetic distance	29.01	<0.01	28.21	<0.01
Soil type $\times$ phylogenetic distance	6.43	0.09	4.27	0.23

Phylogenetic distance is distance to the interacting species in Mya on the maximum likelihood phylogeny (Fig. S1). The model uses zero inflation component models in R with effects tested by likelihood ratio tests (4).

Marine Reserve. Incorporating relatedness into community assembly experiments will help determine when phylogeny best informs the mechanisms driving patterns of species co-occurrence.

## Materials and Methods

**Germination Experiment in the Field.** To study the germination niche, we conducted field transplant experiments for 32 species from five families (Table S4) that are native to the Bodega Bay Marine Reserve. All experimental sites were located on or adjacent to the 146-ha reserve and spanned many habitat types, including coastal grassland, sand dune, and marsh (Fig. 1) but excluding salt marsh habitat. To determine whether the germination niche was phylogenetically conserved for these species, we planted seeds for each species into two conspecific microsites and two close relatives' microsites, one a relative within the same genus (congener sites) and one a relative within the same family (confamilial sites) but not the same genus, where possible. In some cases, no congeners occurred at the site; then, both close relatives' sites were confamilial. Finally, we planted each species at two distant relatives' sites (distant sites); distant was defined as belonging to a different plant family. These ranks are highly correlated with continuous measures of phylogenetic distance (see below). Species in congener, confamilial, and distant relative categories were randomly sampled from the species list at Bodega Bay Marine Reserve. Microsites were patches in which the species in question (conspecific, congener, confamilial, or distant) was locally abundant. The niche was, thus, defined in practice as microsites in the field where a species grew successfully. This approach is a direct test of niche suitability, encompassing the multidimensionality of the realized niche; it does not use species' traits to approximate the niche and is not confounded with dispersal limitation, which species range mapping might be in some cases. We also recorded habitat type for each species' conspecific sites (Fig. S1) to determine whether broad habitat classification was a driver of differential germination success in this experiment.

Seeds were collected from the field at Bodega Bay Marine Reserve from ~30 individuals per species and were stored for no more than 1 y. Field-collected seeds could differ because of genetic differences or as a result of maternal effects, and we cannot distinguish between the two here. For each species, we planted two blocks of 10 seeds each at each of the six sites, where a sufficient number of seeds were available. Blocks were smaller for some species, for which we had fewer seeds. Seeds were individually marked with blue plastic toothpicks so that the fate of each individual seed could be followed, and they were planted at a uniform depth appropriate for each species. Seeds were glued with a tiny drop of water-soluble glue (Elmer's glue; Elmer's Products) to a toothpick, such that rain would remove the glue and would not interfere with germination (40). We weeded the planting site minimally or not at all to allow natural interactions at the site to occur, which we consider to be an important component of the realized niche (41). We also disturbed the soil minimally by inserting the toothpick with the seed attached into the soil. We scarified five species (*Lupinus* sp. and *Luzula comosa*) manually with sandpaper, because they are known to require scarification (42). Although we recognize that this limits our ability to make inferences about dormancy, it was necessary to get sufficient germination. Seeds were planted between October 31, 2008 and November 7, 2008, and we began monitoring germination about every 2 wk beginning on November 14, 2009 and ending on March 14, 2009 after the end of the rainy season when germination had begun to taper off. Although we would have liked to have continued the experiment for a longer period to measure overall performance at these sites, mortality rates were too great for the

initial seed sample sizes that we planted to maintain power for detecting performance differences.

**Constructing the Phylogeny.** We estimated continuous phylogenetic distance between the focal species and the species inhabiting the growing site (e.g., conspecific, congener, confamilial, or distant relative) using a maximum likelihood phylogeny (Fig. S1) based on four DNA regions (Table S1), and we used this continuous measure of phylogenetic distance for our analyses. We took two approaches to estimate phylogenetic distance. First, we estimated a maximum likelihood (ML) phylogeny for four regions [ribulose-bisphosphate carboxylase gene (*rbcl*), maturase K (*matK*), internal transcribed spacer (ITS) flanking the 5.8S ribosomal RNA gene, and tRNA-Leu (*trnL*)] from sequence data available in GenBank (Table S1). When sequence data for a species were not available, we used a randomly chosen alternative species within the genus to estimate the relatedness to that genus (Table S1). The effect on branch length of using these substitute species is expected to be minimal given the breadth of phylogenetic sampling (43, 44). We also sampled additional species not in our experiment, both to root the tree (*Amborella* and *Magnolia*) and to increase the depth of taxon sampling, following the work of Cadotte et al. (44). Sequences were aligned for each region independently using MUSCLE (45, 46) and combined into a single supermatrix. We used Garli (version 0.951) (47) to generate ML phylogenies, allowing the general time reversible (GTR) +  $\gamma$  model to be estimated, and using the default settings; multiple runs were performed to ensure that the resulting phylogeny was not stuck on a local optimum. We present bootstrap proportions from a 100 replicate ML run (47). We then created a time-calibrated phylogeny (chronogram) using fossil calibration points derived from ref. 48 in r8s (49) using nonparametric rate smoothing (NPRS), the POWELL algorithm, cross-validation, and three starting values of the smoothing parameter (smoothing = 1, 100, and 1,000). All three smoothing parameters yielded identical branch lengths, and cross-validation indicated good convergence of the algorithm. We present chronogram results for smoothing equal to 100. We then estimated the phylogenetic distances between taxa by adding the branch length distances (in Mya) between taxa for the combined phylogeny (Fig. S1) (11, 39).

Second, to evaluate the robustness of our results to another phylogenetic approach commonly used in community phylogenetics, we used the super-tree available through phylomatic (phylomatic version 2, reference tree R20080417) (11, 50, 51). Branch lengths were estimated using a fossil calibration (48) and the *bladj* command in phylom (version 4.0.1b) (48, 50). We then added branch lengths between taxa to estimate the phylogenetic distance between them in approximate millions of years (11, 39). We compared our results using the estimates of phylogenetic distance generated by the direct estimate (ML phylogeny) and phylomatic methods. Results were generally congruent between the ML estimates of phylogenetic distance, both patristic and time-calibrated, and the phylomatic estimates, and ML and phylomatic branch lengths were strongly correlated. We present results for the time-calibrated ML phylogeny (Fig. S1).

**Species Interaction Experiment.** To test the hypothesis that phylogenetic similarity predicts ecological similarity in species interactions (competition and facilitation) (7, 8), we chose six sets of three species—two congeners (12 focal species) and a randomly selected confamilial—from five families (Rosaceae, Fabaceae, Asteraceae, Polygonaceae, and Juncaceae) (Fig. S3). Each of the focal species was grown alone, with a conspecific, a congener, and a confamilial, with eight replicates for each treatment, except for the congener treatment, which was replicated 10 times (Fig. S3).

Because both nutrients and soil biota can strongly mediate interactions between plant species in the field (37, 52), we conducted experiments in the field-collected soils taken from rhizospheres at conspecific sites and from rhizospheres of congeners and confamilials as well as in potting soil. Soil was collected in the field immediately under (within 10 cm of and to 20 cm beneath) ca. 10 individuals of each species to acquire biotic and abiotic components of the soil associated with that species (Fig. S3). Soil was then homogenized (within soil source) before planting. Thus, the soil treatment was designed to determine how the soil environment might influence the outcome of species interactions, including many abiotic and biotic elements of that soil environment. Because most plant interaction experiments are typically conducted in the greenhouse in potting soil, we were interested in the congruence of results from potting soil and field soils and whether field soils capture important aspects of plant niches. Individual seeds were planted into the experiment on November 3, 2009. Seedlings (at the cotyledon stage germinated in potting soil) were then transplanted into the experiment to fill out the design, after the majority of the germination had oc-

curred, on February 7, 2009. The experiment was harvested after 28 wk, and we measured final dry biomass.

RII was measured using a standard index (52, 53). RII ranges between  $-1$  for competitive exclusion and  $+1$  for obligate facilitation (Eq. 1):

$$\text{Relative Interaction Intensity} = \frac{B_w - B_o}{B_w + B_o}, \quad [1]$$

where  $B_w$  is the biomass when grown with an interactor and  $B_o$  is the biomass when grown alone (54).

**Statistical Analyses.** The germination experiment was analyzed using the response variables—average proportion of total germinating seeds (total germination) square root-transformed and average proportion of the seedlings surviving to the last census (last census) with standardized least squares and phylogenetic distance, species, block, geographic distance, habitat, and appropriate interactions—to determine whether phylogenetic distance predicts germination success (55) (Table 1 and Table S2). We treated species and the interaction between species and phylogenetic distance as random effects in the model. We used Akaike's information criterion, corrected for small sample sizes (AICc) to choose among models, presenting the model with the lowest AICc (Table 1 and Table S2) (53). Residuals were well-distributed; germination analyses were conducted in JMP (55). Analyses of phylogenetic signal suggest that it is not necessary to correct these analyses for phylogeny (e.g., phylogenetic-independent contrasts) (56). We found no signal of phylogeny on the effect size of the germination by phylogenetic distance slope (Bloomberg's  $K = 0.00005$ ,  $P = 0.29$ , randomizations = 1,000) (57).

For the species interaction experiment, we analyzed RII using zero inflation models, because standard distributions did not fit the data well and there were a large number of (informative) zero values because of mortality/competitive exclusion. Zero inflation models contain two components, the zero inflation component, which quantifies the effects of our experimental

treatments on survival, and the count component, which quantifies the effects of our treatments on growth given survival (58). The count component of the model was modeled with a negative binomial error distribution, and the zero inflation component was modeled with a binary model. We used a continuous estimate of phylogenetic distance estimated as the sum of the branch lengths between any two species (*Constructing the Phylogeny*), soil type, species, and interactions; residuals were well-distributed. Estimates of phylogenetic distance from the time-calibrated ML tree are shown (Fig. S1). Zero inflation analyses were conducted in R (version 2.8.1) (59). As a check to determine whether the presence of mortality in the calculation of RII influenced the statistical outcome, we also analyzed RII calculated without mortality and compared these results. We found that the same effects were significant at  $P < 0.01$  both with and without mortality in the data and thus only present the model for data including mortality. We tested the significance of individual effects in the zero inflation model by deleting effects and compared the likelihood of models with and without the effect using a likelihood ratio test with 2° of freedom (58).

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