



Evidence of within-species specialization by soil microbes and the implications for plant community diversity

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Microbes are thought to maintain diversity in plant communities by specializing on particular species, but it is not known whether microbes that specialize within species (i.e., on genotypes) affect diversity or dynamics in plant communities. Here we show that soil microbes can specialize at the within-population level in a wild plant species, and that such specialization could promote species diversity and seed dispersal in plant communities. In a shadehouse experiment in Panama, we found that seedlings of the native tree species, *Virola surinamensis* (Myristicaceae), had reduced performance in the soil microbial community of their maternal tree compared with in the soil microbial community of a nonmaternal tree from the same population. Performance differences were unrelated to soil nutrients or to colonization by mycorrhizal fungi, suggesting that highly specialized pathogens were the mechanism reducing seedling performance in maternal soils. We then constructed a simulation model to explore the ecological and evolutionary consequences of genotype-specific pathogens in multispecies plant communities. Model results indicated that genotype-specific pathogens promote plant species coexistence—albeit less strongly than species-specific pathogens—and are most effective at maintaining species richness when genetic diversity is relatively low. Simulations also revealed that genotype-specific pathogens select for increased seed dispersal relative to species-specific pathogens, potentially helping to create seed dispersal landscapes that allow pathogens to more effectively promote diversity. Combined, our results reveal that soil microbes can specialize within wild plant populations, affecting seedling performance near conspecific adults and influencing plant community dynamics on ecological and evolutionary time scales.

plant–soil feedback | Janzen–Connell hypothesis | species coexistence | community simulation | seed dispersal

The specialist natural enemies of plants (e.g., pathogens or herbivores) are thought to maintain plant species diversity by limiting the survival of seedlings of their host species when the species is common, allowing rare species to persist (1, 2). Demographic patterns consistent with species-specific natural enemies have been documented in numerous plant communities worldwide (3), with accumulating evidence suggesting that these patterns are often caused by pathogens in the soil (4–11). Pathogen specialization at higher taxonomic levels (i.e., on genera or families) is also thought to maintain plant species diversity (12, 13). In agricultural and model plant systems, it is well known that pathogen effects can also vary within species (e.g., due to variation in resistance among host genotypes) (14–17). Though variation in host resistance also occurs in wild plant species (18), it is not known how within-species specialization by pathogens might affect diversity and drive ecological dynamics in plant communities.

There have been a wealth of studies showing that species-specific pathogens tend to build up in the soil near their host plants (4–11), resulting in plant–soil feedbacks that drive plant

community dynamics (19). In a similar manner, “genotype-specific” pathogens in the soil could help maintain diversity in wild plant systems. By accumulating in the soil near plants with genotypes they can infect, genotype-specific pathogens could limit the growth or survival of each plant’s progeny (or that of closely related individuals) relative to other seedlings in the population (19). Therefore, in addition to limiting the recruitment of seedlings of common species via known plant–soil feedback processes, the accumulation of pathogens around adult plants could maintain genetic diversity within plant populations by limiting the recruitment of seedlings with locally common genotypes (20). It has been shown that soil microbes can specialize among populations within species and favor the survival of seedlings from genetically distant host populations (21). Soil microbes can also differentially affect the performance of seedlings within host populations (19). However, it is not known whether soil microbes can maintain diversity by specializing within wild plant populations.

The abundance of specialist pathogens near adult plants has also been hypothesized to play a role in the evolution of seed dispersal. Howe and Smallwood (22) proposed that seed dispersal may have evolved because it allows offspring to escape the specialist enemies accumulated near their parent. Evidence in support of this hypothesis is provided by studies showing that

Significance

It is widely known from agriculture that pathogens can specialize on genotypes within plant species, but such highly specialized pathogens have rarely been studied in natural plant communities. Although empirical evidence in natural plant communities demonstrates that pathogens can specialize at the level of species, our experiment in Panama demonstrates specialization of soil microbes within a wild plant population. Our complementary computer simulations suggest that genotype-level specialization by microbes may help maintain plant species diversity and promote the evolution of increased seed dispersal. Together, our results improve understanding of the role of microbes in natural plant communities by showing that microbes that specialize within species could influence diversity and dynamics in plant communities.

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seed and/or seedling survival tends to increase with distance away from a conspecific adult (3, 23). However, such studies typically do not consider the level of relatedness between conspecific seeds/seedlings and adults, or the possibility for genotype-specific pathogen effects. Whether pathogens (and other enemies) specialize on genotypes within species (in addition to specializing at the species level) could determine the effectiveness of seed dispersal as an enemy escape strategy. If pathogens are only species specific, seeds that disperse away from their parent tree could still encounter their enemies if they disperse near another adult of their species. In contrast, if pathogens are also genotype specific, seeds are likely to escape some of their enemies even if they disperse near a conspecific adult (provided the adult does not share their genotype). Thus, because the fitness benefits of seed dispersal should be greater if pathogens are genotype specific as well as species specific, the host specificity of pathogens could play an important role in the evolution of seed dispersal.

In this study, we employed a combined experimental and theoretical approach to test for impacts of genotype-specific microbes on plant performance in a natural plant population, and then explore the long-term ecological and evolutionary consequences of such impacts for plant communities. First, we conducted a shadehouse experiment to test the hypothesis that soil microbes specialize on nearby adults and disproportionately reduce performance of their own progeny in natural plant populations. To test this, we studied the impact of maternal vs. nonmaternal soil microbial communities on seedling performance in a population of the native tree, *Virola surinamensis* (Rol. ex Rottb.) Warb. (Myristicaceae), in a diverse forest in central Panama. We experimentally isolated the net effect of soil-borne microbes on offspring performance, explicitly testing whether *V. surinamensis* seedlings had reduced growth in the microbial community associated with their maternal tree relative to a nonmaternal *V. surinamensis* adult. We further explored whether soil nutrients and colonization by arbuscular mycorrhizal fungi (AMF) (important soil-borne mutualists of tropical tree seedlings; refs. 24 and 25) might have contributed to any measured differences in seedling performance across the maternal and nonmaternal microbial

sources. To examine the ecological and evolutionary effects of genotype-specific microbes, we then developed a theoretical model (informed by our experimental data) to determine how genotype-specific pathogens might affect species coexistence and the evolution of seed dispersal in plant communities.

Results

Experimental Evidence of Within-Population Specialization of Soil Microbes. We found that *V. surinamensis* seedlings grown in the soil microbial community associated with their maternal tree had lower biomass than seedlings grown in the soil microbial community associated with a different reproductive female in the population at the end of the 8-mo shadehouse experiment (Fig. 1A and *SI Appendix, Table S1*). This pattern was consistent across nearly all 11 maternal trees in the experiment (Fig. 1B). We did not find a relationship between seedling biomass and AMF colonization (*SI Appendix, Fig. S2 and Table S2*), although overall colonization by AMF was lower in seedlings grown in the soil microbial community associated with their maternal tree versus a nonmaternal conspecific (*SI Appendix, Fig. S3 and Table S3*). We found that soil nutrient conditions were similar for seedlings in maternal and nonmaternal conspecific treatment groups (*SI Appendix, Table S4*), and there was no relationship between soil nutrient conditions and final biomass of seedlings (*SI Appendix, Table S5*). Thus, our experimental results suggest that highly specialized soil pathogens, rather than mutualists or soil nutrients, drove the negative plant-soil feedbacks between seedlings and their maternal trees.

For comparison, we also grew *V. surinamensis* seedlings in the soil microbial communities associated with five other species at the site (i.e., heterospecifics). Overall, final biomass of these seedlings was not significantly different from that of seedlings grown in the two conspecific soil treatments (*SI Appendix, Fig. S1A and Table S1*). However, there was significant variation among the soils of the heterospecific species in their effect on *V. surinamensis* seedling biomass (*SI Appendix, Fig. S1B and Table S6*), indicating that impacts of heterospecific soil communities are highly species dependent. Neither soil nutrients nor AMF colonization

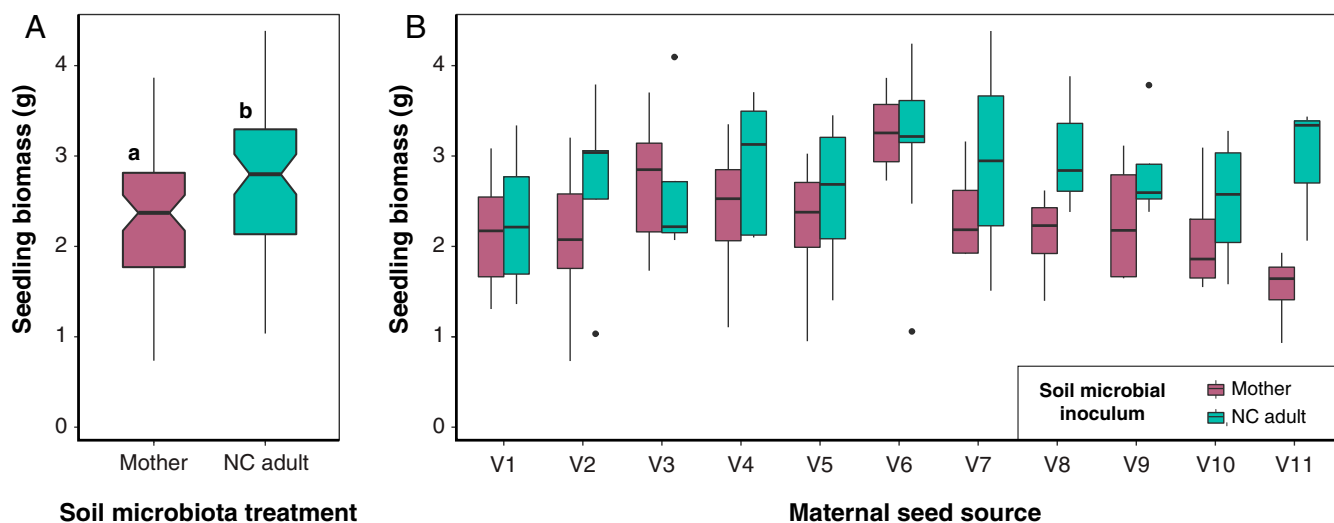


Fig. 1. Offspring seedlings grew less than nonoffspring seedlings in the soil microbial communities of conspecific adults, suggesting highly specialized pathogen effects. (A) In an experiment with the tropical tree *V. surinamensis*, the total above- and below-ground biomass of seedlings grown in the soil microbial community from beneath their mother tree was significantly lower at the end of the experiment than the biomass of seedlings grown in the soil microbial community from beneath a nonmaternal conspecific tree from the same population (NC adult). Differing letters indicate a significant difference ($P < 0.05$) in the estimated biomass of the two seedling groups for all soil microbial sources combined as predicted by a linear mixed-effects model ($n = 138$ seedlings; *SI Appendix, Table S1*). (B) A similar pattern can be seen in the estimates of seedling biomass for each seed source separately. In both panels, box belts show the median predicted biomass. In A, box notches represent a roughly 95% confidence interval for comparing predicted medians. In both panels, box hinges correspond to the first and third quartiles, while box whiskers extend to the largest and smallest value no further than 1.5 \times the interquartile range from hinges.

explained patterns of seedling biomass in heterospecific and conspecific soils (*SI Appendix*, Fig. S2 and Tables S2 and S5).

Theoretical Implications for Plant Community Dynamics. In our simulations, genotype-specific pathogens allowed competing plant species to coexist but were less efficient at maintaining species diversity than species-specific pathogens (Fig. 2). Communities became less stable as the proportion of pathogens that were genotype specific (rather than species specific) increased, with declines in stability more pronounced in communities with higher versus lower levels of genetic diversity (Fig. 2). This is because when most pathogens in the community were species specific, seeds of common species had few pathogen-free sites when dispersing (1) and were attacked more often than seeds of rare species (Fig. 3), thus stabilizing coexistence. In contrast, when most pathogens in the community were genotype specific, seeds that dispersed away from their parent were more likely to avoid their pathogens, even for common species (Fig. 3). Thus, when pathogens were genotype specific, rare and common plant species had more similar mortality risks than when pathogens were species specific, resulting in weaker negative density dependence (Fig. 4).

We found that whether genotype-specific pathogens promote species coexistence depends on the relative performance of seedlings in nonparent conspecific vs. heterospecific sites. If heterospecific sites were more suitable for seedlings than nonparent conspecific sites, this resulted in stable communities (as per expectations from the literature, ref. 26) (*SI Appendix*, Fig. S44). If nonparent conspecific sites were more suitable than

heterospecific sites, this created a priority effect that led to the monodominance of one species in the community (*SI Appendix*, Fig. S4C). If nonparent conspecific sites and heterospecific sites were equally suitable, then species neutrally co-occurred (*SI Appendix*, Fig. S4B). Thus, genetic diversity weakens the stabilizing impact of genotype-specific pathogens because it makes nonparent conspecific sites more suitable (*SI Appendix*, Fig. S5).

In our simulations exploring the evolution of seed dispersal, we found that genotype-specific pathogens selected for higher seed dispersal compared with species-specific pathogens (Fig. 5). This occurred because dispersed seeds escaped genotype-specific pathogens more easily than species-specific pathogens (Fig. 3).

Discussion

Our findings show that within-species specialization by soil microbes can occur in tropical tree communities, and that this level of specialization influences plant community dynamics differently than species-specific pathogens. Our experimental results support the hypothesis that soil pathogens specialize within wild plant populations, limiting the performance of closely related seedlings near conspecific adults. We found no evidence that soil mutualists or nutrients caused this response. Our simulation model expands upon these findings to show that genotype-level specialization by soil microbes can help competing plant species to coexist. Though genotype-specific microbes promoted plant species coexistence in our simulation, ours and previous theoretical studies (12, 13) suggest that microbes such as pathogens are most effective at maintaining species diversity when they specialize at the species level. In addition, we found that the extent to which genotype-specific microbes can maintain species diversity varies depending on the genetic diversity of the community: genotype-specific microbes were more important in maintaining species diversity in communities where genetic diversity was relatively low. Our simulations also showed that genotype-specific microbes select for higher seed dispersal rates than species-specific microbes. Previous theoretical studies have shown that species-specific natural enemies are most able to promote plant species diversity if seeds are widely dispersed (26–28). Therefore, by helping to create the seed dispersal landscape that best enables species-specific natural enemies to promote species diversity, genotype-specific effects may have additional positive impacts on species diversity over evolutionary time.

Our model suggests that the effect of genotype-specific pathogens on plant species coexistence depends on the relative performance of seedlings in nonparent conspecific sites relative to heterospecific sites. Specifically, our simulations show that genotype-specific pathogens allow plant species to coexist when seedlings perform better in heterospecific sites than nonparent conspecific sites. In contrast, if nonparent conspecific sites are more suitable for seedlings than heterospecific sites, then genotype-specific pathogens undermine coexistence via a priority effect. Finally, if seedlings perform similarly in nonparent conspecific sites and heterospecific sites, then genotype-specific pathogens cause species to neutrally co-occur. Though seedling performance is often shown to be reduced in conspecific environments relative to heterospecific environments (3, 8–11), in our experiment, *V. surinamensis* seedling growth varied in the soils of individual heterospecific species. Because we do not have data on the impact of the heterospecific species on their own seedlings, we cannot fully assess species coexistence in the community (19). Thus, it is not clear which of the above model scenarios best predicts coexistence (or lack thereof) in our study system. Nonetheless, our simulations show the range of possible impacts that genotype-specific pathogens can have on species coexistence and illustrate gaps in our knowledge that need to be filled to determine whether long-term coexistence is predicted to occur in natural communities.

If genotype-specific pathogens are common in natural systems, then we may need to reconsider the species-level approach commonly used in studies of pathogen impacts on plant species

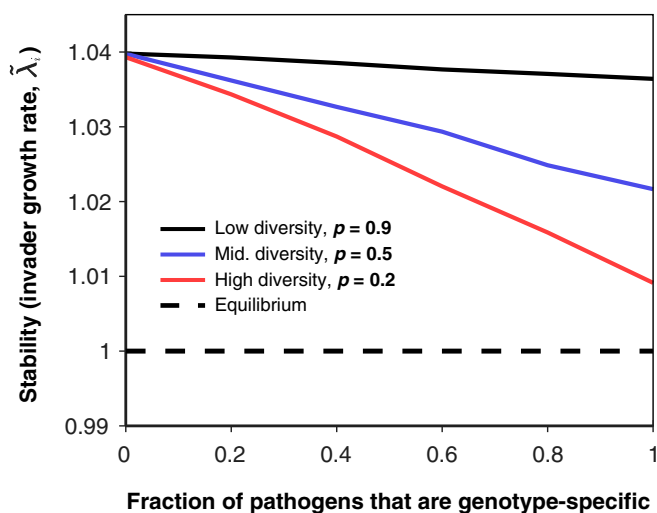


Fig. 2. Genotype-specific pathogens maintain less plant species diversity than species-specific pathogens, especially when genetic diversity is high. We calculated community stability (i.e., the growth rate of an invading plant species at zero density when its competitors are at equilibrium; the community is neutral when this value is $\lambda_i = 1$ and more stable the higher λ_i is) in a simulated four-species plant community. In the simulation, we kept the mean effect of pathogens (i.e., the chance a seed was killed if it did not disperse) constant but varied the fraction of genotype-specific pathogens vs. species-specific pathogens in the community. Species-specific pathogens killed any seed (invader or otherwise) that grew in a site previously held by its parent or a nonparent conspecific with probability α_S ; genotype-specific pathogens killed seeds that grew in a site held by their parent or by a nonparent conspecific with the same genotype, with probability α_G . The genetic diversity parameter p is the probability that two conspecifics share genotype-specific pathogens. Thus, a seed under its parent died with probability $\alpha_S + \alpha_G$, and a seed under a nonparent conspecific died with probability $\alpha_S + p\alpha_G$. The community became less stable as the fraction of genotype-specific pathogens in the community increased, especially when genetic diversity was high. Parameters: $\alpha_S + \alpha_G = 0.6$, $d = 0.65$, $\delta = 0.4$.

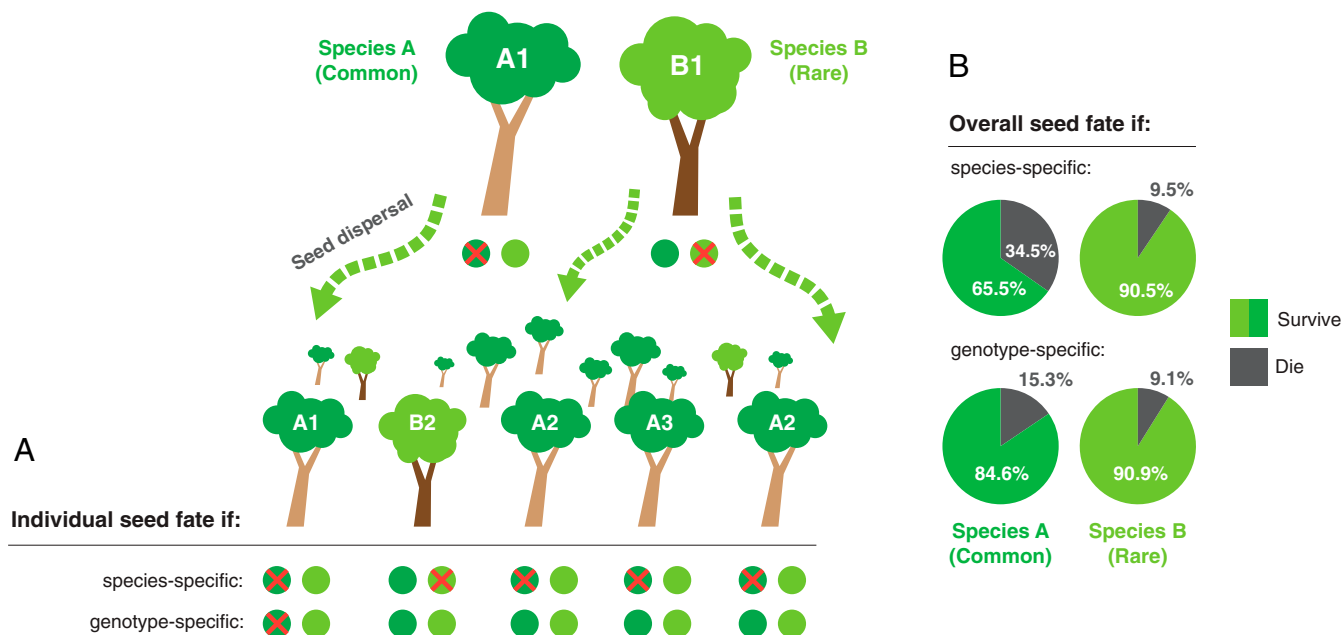


Fig. 3. Negative density dependence is stronger when pathogens are species specific rather than genotype specific. (A) Seeds of a common plant species, A, are likely to encounter conspecific adults when they disperse, whereas seeds of a rare plant species, B, are not. Thus, when pathogens are species specific (i.e., when they affect all genotypes within the species, with different genotypes indicated by different numbers, e.g., A1, A2, and A3), common species are much more likely to encounter their pathogens than rare species, giving rare species a survival advantage. However, if pathogens are genotype specific, then seeds are less likely to encounter their pathogens when they disperse near a conspecific, especially in common species. In this case, most seeds only encounter pathogens if they do not disperse—an effect that is independent of density. (B) Therefore, genotype-specific pathogens do not give rare species as much of an advantage as species-specific pathogens. Seed fate was calculated using $\alpha_S + \alpha_G = 0.6$, $d = 0.85$, $P = 0.25$, $N_A = 0.5$, and $N_B = 0.01$.

diversity. For instance, in observational studies, if seeds frequently fall near their maternal tree, the negative impact of being close to a conspecific adult tree on seedling survival would be overestimated if the tree's offspring grow worse than other conspecific seedlings (and the benefit of dispersing away from the parent tree would be underestimated). Additionally, the common experimental practice of combining soil from multiple conspecific individuals to study pathogen effects (e.g., refs. 8, 10–11, 21) could increase the chance of introducing genotype-specific microbes, and lead to overestimations of the strength of distance-dependent mortality (by attributing maternal soil effects to general conspecific soil effects). These complexities warrant further examination and highlight the importance of accounting for genotype-specific pathogens when examining pathogen effects. Future studies that explicitly examine levels of host specificity in the pathogens of wild plant species are needed to determine how often genotype-specific pathogens occur in natural plant systems.

In addition to influencing species diversity, soil microbes that specialize within species could also help maintain genetic diversity in plant populations by favoring the recruitment of more distantly related seedlings near established plants. A recent observational study showed that seedlings near close relatives have reduced performance (29). Other studies show that the seedlings that establish near conspecific adults are not necessarily offspring, but instead represent a diversity of genotypes (30, 31). In addition, recent experimental work with a tropical palm species has shown that seedlings with rare genotypes are more likely to survive than seedlings with common genotypes (20), and related theoretical work suggested that this can promote population-level genetic diversity (32). Our experimental results suggest that the patterns found in those previous studies could have been driven by highly specialized soil microbes, but additional studies are needed to confirm whether soil microbes produce these patterns of seedling recruitment under natural environmental conditions. At the same time, our simulations suggest that levels of genetic diversity within

plant populations can influence plant–pathogen interactions and species coexistence. Consistent with this, a recent empirical study of genetic diversity of tropical tree species at our field site showed that tree species with a higher diversity of pathogen resistance genes suffered less from soil pathogens and negative density-dependent mortality than species with lower resistance gene diversity and were more abundant in the community (33). The effect of genotype-specific pathogens on plant diversity and abundance could also vary depending on the strength of conspecific negative density dependence (CNDD) experienced by the community, as well as on variation among species in CNDD strength and seed dispersal rates (34). Our simulation, though simplifying the relationship between dispersal and distance-dependent mortality in the community, shows that selection for higher seed dispersal should be even stronger for conspecific negative density dependence that comes from genotype-specific pathogens, relative to CNDD that comes from species-specific pathogens (Fig. 5).

Soil microbes that specialize within species are an overlooked but potentially important component of plant communities. Widespread variation in host resistance (35), pathogenicity (36), and microbial community composition (37) in natural plant systems suggests the potential for genotype-specific pathogens to influence eco-evolutionary dynamics in a variety of plant communities. Our results suggest that genotype-specific microbes could play a significant role in influencing patterns of diversity, abundance, and seed dispersal in wild plant populations and communities. By limiting the performance of seedlings that are close relatives of nearby plants, soil microbes could help maintain species diversity in plant communities, along with genetic diversity within species, over ecological and evolutionary time scales.

Materials and Methods

Shadehouse Experiment.

Study species and site. We conducted a plant–soil feedback experiment with *V. surinamensis* on Barro Colorado Island (BCI), Republic of Panama (9°09' N,

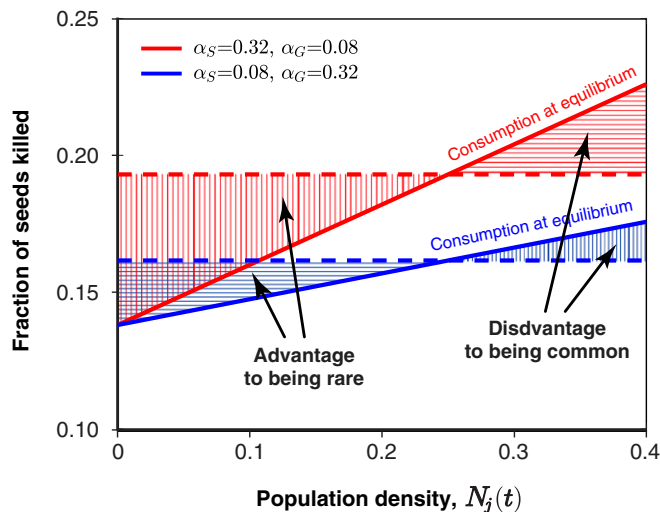


Fig. 4. Rare-species advantages are greater when pathogens are species specific rather than genotype specific. Here, α_S represents the proportion of seeds that are killed if they are exposed to species-specific pathogens, and α_G represents the proportion that are killed if they are exposed to genotype-specific pathogens. Here we vary the relative values of α_S and α_G but hold $(\alpha_S + \alpha_G)$ constant. We find that if most pathogens in a plant community are species specific (high α_S , shown in red), seeds of rare species (i.e., species at low population density) are consumed much less, and common species (i.e., species at high population density) are consumed far more, than if most pathogens are genotype specific (high α_G , shown in blue). For example, seeds of this species are 40% more likely to be consumed if the species is at equilibrium (i.e., when it occurs at equal abundance as the other species in the community) than if it is very rare. If 80% of pathogens in a plant community are genotype specific (high α_G , depicted in blue), then seeds of rare species are consumed around the same amount as seeds of common species. For example, seeds of this species are only 17% more likely to be consumed when they are at equilibrium than when they are very rare. Parameters: $(\alpha_S + \alpha_G) = 0.4$, $d = 0.65$, $P = 0.2$, $\delta = 0.4$, and the communities contained four species.

79°51' W). BCI is a diverse, 15.6 km² moist tropical lowland forest (~2,600 mm rainfall per year) (38, 39). *V. surinamensis* is a relatively common canopy tree species on BCI and is native to tropical and subtropical wet lowland forests across Central America and Amazonia (38). *V. surinamensis* is dioecious (40), fly pollinated (41), and produces large seeds (~2 cm) that are borne singly and surrounded by a nutritious aril that attracts several species of birds and monkeys as primary seed dispersers (42). On BCI, *V. surinamensis* flowering peaks in the dry season (~January) and seed production peaks in the following wet season (~July) (43).

Experimental design. We collected seeds from the ground beneath the canopy of fruiting *V. surinamensis* on BCI during the peak of its fruiting (in June and July) in 2014. We assigned the tree that a seed was collected beneath as the seed's putative maternal parent. After collection, seeds were surface sterilized, air dried, planted in autoclaved BCI soil in the shadehouse, and kept well watered and shaded. The maternal trees yielding ≥ 10 seedlings were included in the experiment, for a total of 11 maternal trees and 196 experimental seedlings. The trees were located within a ~3.5 km² area of BCI (SI Appendix, Fig. S6).

We then collected soil from beneath the canopy of each of the 11 maternal trees to use as microbial inocula for the experimental seedlings (SI Appendix). To create one soil microbial inoculum for each of the trees, we collected soil at a depth of 10 cm from three random points within 3 m of the tree's base, then coarsely sieved, combined, and homogenized the soil from the three points. We also created soil microbial inocula from beneath the canopy of five reproductive-size heterospecific trees within the study area. Thus, we created a total of 16 soil microbial inocula from 16 adult trees (11 conspecific and five heterospecific trees). The five heterospecific trees represent a range of species: *Anacardium excelsum* (Bertero & Balb. ex Kunth) Skeels (Anacardiaceae), *Ormosia macrocalyx* Ducke (Fabaceae), *Platyopodium elegans* Vogel (Fabaceae), *Protium tenuifolium* (Engl.) Engl. (Burseraceae), and *Spondias mombin* L. (Anacardiaceae). Approximately one-third of the seedlings from each maternal seed source were assigned at random to each of three soil inoculum treatments: maternal soil inoculum ($n = 70$ seedlings),

nonparent conspecific soil inoculum ($n = 68$ seedlings), and heterospecific soil inoculum ($n = 54$ seedlings). Each seedling was assigned to the soil inoculum of only one of the 16 adult trees in the study. All inocula were used in the experiment within 2 d after field collection.

In a shadehouse on BCI, each seedling was transplanted at ~1 mo of age into its own 2-L pot containing 20% by volume of soil microbial inoculum from its assigned tree and 80% by volume of a common planting medium (a steam-sterilized 1:1 mixture of BCI soil and sand). Relatively small volumes of soil microbial inoculum were used to minimize the effect of any potential variation in nutrients among soil inocula on seedling performance. Seedlings were randomly assigned to one of four benches in the shadehouse (SI Appendix, Fig. S7). Each shadehouse bench was covered with two layers of 80% shade cloth (to mimic a shady understory) and shielded from rainfall with a roof of clear plastic lining. Stem height was measured for each seedling immediately after transplant. Seedlings remained in their experimental treatments for ~8 mo and were given ample water three times per week. After 8 mo, the 192 surviving seedlings were harvested to obtain measurements of final oven-dried biomass and to collect fine root samples. Fine root samples were stored in 70% ethanol and refrigerated until being shipped to Yale University for AMF quantification (SI Appendix). A sample of the soil surrounding the roots of each harvested seedling was also collected and refrigerated until being taken to the Soils Lab at the Smithsonian Tropical Research Institute (Panama) for nutrient quantification (SI Appendix). To more fully investigate differences in growth among experimental soil microbial communities, we then analyzed whether (i) colonization by AMF or (ii) soil nutrients differed among treatments or affected seedling total dry biomass at harvest (SI Appendix).

Statistical analysis. We analyzed the effect of the experimental soil microbial treatment group (i.e., maternal soil, nonparent conspecific soil, or heterospecific soil) on seedling total dry biomass at harvest using a linear mixed-effects model. We focused on growth because survival was high in the shadehouse (98%, 192 of 196 seedlings). Dead seedlings were not included in the growth analysis. Maternal seed source, soil microbial inoculum source, and shadehouse bench were included as random effects in the model. To account for the potential impact of variation in the size of the seedlings at the beginning of the experiment, we also included an estimate of initial seedling dry biomass as a covariate in the model (SI Appendix). All mixed-effects analyses were performed with the lme4 package (44) in the R environment (45). *P* values for mixed-model predictors were obtained with the lmerTest package (46).

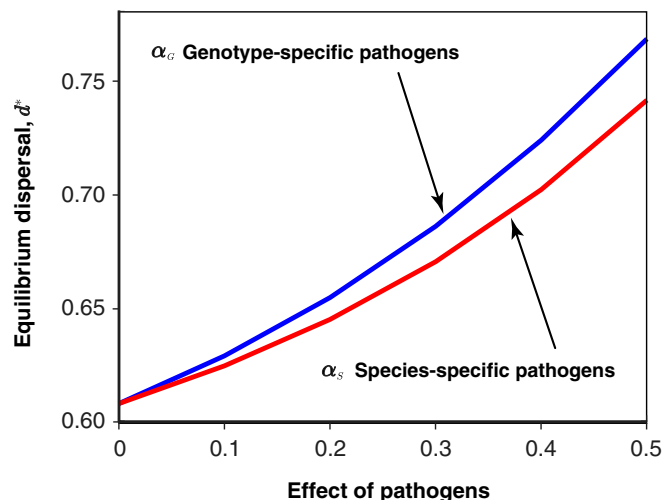


Fig. 5. Genotype-specific pathogens increase selection for seed dispersal. We simulated plant community dynamics assuming there was a cost to seed dispersal (SI Appendix). The effect of pathogens represents the chance that a seed that is exposed to pathogens is killed (α_G or α_S for genotype- or species-specific pathogens, respectively), and the equilibrium seed dispersal fraction (d^*) represents the proportion of seeds dispersed in the community when the community arrives at the evolutionary stable strategy. We found that equilibrium seed dispersal fraction evolved to higher levels when pathogens were genotype specific rather than species specific. This is because a dispersed seed is more likely to escape genotype-specific pathogens. Here, $P = 0.2$, $\delta = 0.4$, $Y = 3 - d^2$, and the communities contained four species.

Simulation of Plant Community Dynamics. To explore the implications of genotype-specific pathogens at the community level, we conducted a simulation of a plant community based on the model described in Stump and Chesson (26). In brief, the model simulated a multispecies plant community containing a finite number of adults, including seed dispersal, adult mortality, and seedling mortality due to both competition and pathogens (full model details can be found in *SI Appendix*). In the model, pathogen effects were dependent on the type of site a seed occupies. A seed that stays in the site held by its parent is exposed to species- and genotype-specific pathogens. A seed that disperses to a site held by a conspecific other than its parent is exposed to species-specific pathogens and is exposed to genotype-specific pathogens only if the seed and adult are the same genotype. Consistent with studies showing increased survival of seeds and/or seedlings near heterospecific vs. conspecific adults (3, 8–11), seeds that dispersed to a site held by a heterospecific avoided pathogens. After pathogen-related mortality, a surviving seed was randomly chosen to become the new adult by the next time step. We assessed how genotype-specific and species-specific pathogens affected species coexistence in communities that varied in genetic diversity using invasion analysis (*SI Appendix* and refs. 47 and 48). We then created several variations of the model to explore how variation in the suitability of parent, nonparent conspecific, and heterospecific sites for seedlings might affect species coexistence (*SI Appendix*).

To study the evolution of seed dispersal, we modified our original model to include an inherent cost to dispersing seeds (which offset the benefit of escaping pathogens). We then calculated the selection coefficient on dispersal and determined its evolutionarily stable strategy, i.e., the point at which increasing or decreasing dispersal reduced fitness (*SI Appendix* and refs. 49 and 50).

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