

Plant–soil feedback links negative distance dependence and light gradient partitioning during seedling establishment

SARAH MCCARTHY-NEUMANN¹ AND INÉS IBÁÑEZ

School of Natural Resources and Environment, University of Michigan, Ann Arbor, Michigan 48109 USA

Abstract. Tree species coexistence has often been explained through either negative distance-dependent/density-dependent (NDD) mortality or resource-based niche partitioning. However, these two influential mechanisms for structuring community dynamics have rarely been investigated simultaneously. Negative conspecific effects, like those caused by plant–soil feedbacks (PSF), could link these two mechanisms by being restricted to low-light environments and determined by seedling shade intolerance. We conducted a 10 week long greenhouse experiment where we assessed survivorship of eight temperate tree species that varied in local adult abundance and seedling shade tolerance, to non-sterile vs. sterile soils collected under the canopy of conspecific vs. heterospecific adult trees grown at low and high light. We found that half of our species experienced strong negative conspecific feedbacks. For three out of four species, the PSF were biotic mediated. However, their effects on survival were often restricted to low-light conditions. Species sensitivity to negative PSF also increased with local adult rarity and with seedling shade intolerance. Our findings taken together indicate that biotic-mediated PSF may enhance the variety of recruitment niches among coexisting species via NDD processes as well as through intensifying light gradient partitioning among tree species.

Key words: *Horner-McLaughlin Woods, Ann Arbor, Michigan, USA; irradiance; Janzen-Connell hypothesis; plant abundance; plant–soil feedbacks; resource partitioning; seedling survival; shade tolerance; soil pathogens.*

INTRODUCTION

According to classical ecological theories, competitively dominant species are expected to exclude less competitive species (Gause 1934); however, natural biodiversity patterns tell us otherwise. In the case of plant communities, the seedling-establishment phase is a major demographic bottleneck for populations, and thus a critical stage for the maintenance of future community-wide species diversity (Gurevitch et al. 2006). There has been a vast array of hypotheses proposed for how dominance by the most competitive species can be precluded during the seedling establishment phase (Palmer 1994). Two of the most influential mechanisms proposed for plant species coexistence have been negative distance- and density-dependent mortality (NDD; Janzen 1970, Connell 1971), and resource-based niche partitioning (Denslow 1980). In our present study we demonstrate that these two mechanisms are interconnected and do not act independently while determining tree species seedling-recruitment dynamics.

Tree seedling performance is highly influenced by biotic agents, such as natural enemies (Gilbert 2002).

Janzen (1970) and Connell (1971) proposed that host-specific natural enemies could maintain high tree diversity by reducing seed and/or seedling survivorship near conspecific adults and/or at high conspecific densities. Such NDD seedling mortality would favor establishment of heterospecific individuals under an adult tree, and thus promote species coexistence (Mangan et al. 2010, Alvarez-Loayza and Terborgh 2011). There is accumulating empirical evidence for NDD in forests (e.g., Hille Ris Lambers et al. 2002, Kobe and Vriesendorp 2011; although the mechanisms creating these patterns were not investigated). There is also evidence that NDD processes might affect species unevenly; conspecific NDD may be correlated with local tree abundance (i.e., rarer species are more negatively affected by conspecifics) in both tropical (Comita et al. 2010) and temperate (Johnson et al. 2012) forests.

Tree-seedling performance is also greatly dependent on the availability of light in forests (Pacala et al. 1996). Thus, for tree species an influential mechanism for reducing competitive exclusion and maintaining tree species richness occurs when a forest is heterogeneous with respect to light, and when species differ in their seedling performance at different light levels (Kobe 1999, Montgomery and Chazdon 2002). This variation in performance with respect to light is often due to trade-offs among species between low-light survival and high-light growth that correspond to shade-tolerance classifications (e.g., Kitajima 1994, Pacala et al. 1996).

Manuscript received 1 August 2012; revised 12 December 2012; accepted 3 January 2013. Corresponding Editor: B. B. Casper.

¹ Present address: Department of Forestry, Michigan State University, East Lansing, Michigan 48824 USA.
E-mail: sneumann@msu.edu

This is a specialized form of resource-based niche partitioning (Denslow 1980), which results in no species being competitively dominant across all resource conditions, but rather each species dominates at a given level within the light gradient of the forest (Kobe 1999, Clark et al. 2003).

NDD and resource-based niche partitioning have rarely been investigated simultaneously (but see Augspurger 1984), and are often viewed as competing alternatives for structuring community dynamics. However, plant–soil feedbacks (PSF, a type of conspecific effect) may connect both mechanisms if feedbacks are primarily negative (i.e., seedlings do worse in soils near conspecific vs. heterospecific adults, a sign of NDD), as well as being restricted to low-light environments (a sign of resource-based niche partitioning). The result would be a large variety of outcomes in the recruitment niche of tree species, dependent on the combined effects of light availability and PSF associated with conspecific canopies.

Plant–soil feedbacks (PSF) are created when a plant's presence alters soil conditions (biotic, physical and/or chemical), which in turn affects its own and other plants' performance (Bever 2003). Negative plant–soil feedbacks have been shown to decrease performance of conspecific individuals for many species (e.g., Mangan et al. 2010, McCarthy-Neumann and Kobe 2010a, b, McCarthy-Neumann and Ibáñez 2012). This particular mechanism for conspecific NDD would then prevent plant species from spreading and dominating the community (e.g., Bever 2003). Uneven effects of negative PSF have also been linked to local tree abundance, and simulation models have shown how the strength of PSF can explain the observed natural patterns of tree species abundance (Mangan et al. 2010).

The occurrence of PSF could also be determined by environmental factors. For instance, there is evidence that under low-light conditions tree seedlings are more susceptible to disease-related mortality (Augspurger and Kelly 1984, Hood et al. 2004, but see Alvarez-Loayza et al. 2011). Since soil pathogens are often the causal agent creating PSF (e.g., Packer and Clay 2000, McCarthy-Neumann and Ibáñez 2012), recruitment patterns may be influenced by increased risk of diseases in low-light conditions.

Also, shade-intolerant species may be more likely to experience biotic-mediated negative PSF. Kobe and Vriensdorp (2011) found that conspecific NDD was closely correlated with seedling shade tolerance, and speculated that the mechanism creating these patterns was due to biotic-mediated negative PSF. Shade-tolerant species tend to invest more in functions that enhance survival, such as defense against natural enemies (Coley et al. 1985, Coley and Barone 1996) and carbohydrate storage (Kobe 1997, Myers and Kitajima 2007), while shade-intolerant species tend to invest in traits that maximize growth (Herms and Mattson 1992, Reich et al. 1998). These differences in life-history strategies likely

contribute to why seedlings of shade intolerant species tend to be more susceptible and/or respond more negatively to disease (Augspurger and Kelly 1984, McCarthy-Neumann and Kobe 2008), which in turn may contribute to the trade-off between low-light survival and high-light growth among tree species.

To assess whether the light environment (resource-based niche partitioning) alters the presence or magnitude of conspecific negative distance effects (NDD), we conducted a greenhouse experiment with eight temperate tree species grown under different light and soil treatments. We then related these results with adult tree abundance and seedling shade tolerance, and investigated some of the potential mechanisms (involving NDD and resource partitioning) by which tree species coexistence could be enhanced. In particular, we tested three hypotheses:

1) All or most tree species experience PSF (negative conspecific effects that would enhance heterospecific seedling recruitment under tree canopies). Thus, PSF would maintain species coexistence independently of the light environment.

2) Only a subset of tree species experience PSF (differential NDD), and if there is a positive relationship between the strength of negative PSF and local adult density (promoting plant rarity) then PSF would partially maintain species coexistence independently of the light environment.

3) Only a subset of tree species experience PSF, and if there is a negative relationship between the strength of negative PSF and shade intolerance then PSF would partially maintain species coexistence through heightening light-gradient partitioning which would then exacerbate shade-tolerance differences among species.

Testing these particular hypotheses would allow us to address the following questions: (1) How prevalent are negative PSF on seedling survival, and when occurring does the light environment alter the occurrence of these PSFs? (2) If present, what was the nature of the PSF, biotic or abiotic? (3) Are rare species more affected by PSF than common ones? And (4) Are shade-intolerant species more affected by PSF than shade-tolerant ones?

METHODS

To link the existence and strength of PSF (plant–soil feedbacks) with the light environment and test their combined effects during tree seedling recruitment, we conducted a 10-week long greenhouse experiment from January through April 2010 where we assessed survivorship of eight temperate tree species (Table 1) to non-sterile vs. sterile soils collected under the canopy of conspecific vs. heterospecific adult trees and grown at low and high light.

Soil sources and adult tree density measures

We collected soil (top 15 cm) within 1 m from the bole of four mature adults for each of our study species in the

TABLE 1. The study's eight tree species, heterospecific soil source origins, estimated shade intolerance, and local adult-tree density. Data are means with SD in parentheses.

Species name (code)	Heterospecific soil sources†	Shade intolerance‡	Adult (≥ 10 cm dbh) density (no./ha)§
<i>Acer rubrum</i> (Acru)	Acsa, Cagl, Prse, Quru, Quve, and Rops	8.6 (5.3)	34.0 (33.1)
<i>Acer saccharum</i> (Acsa)	Acru and Quru	–	133.0 (82.2)
<i>Carya glabra</i> (Cagl)	Acru, Acsa, and Quru	0.0 (1.6)	37.0 (24.1)
<i>Liriodendron tulipifera</i> (Litu)	Acru, Acsa, and Quru	17.5 (11.7)	1.0 (3.2)
<i>Prunus serotina</i> (Prse)	Acru, Acsa, Quru, Quve, and Rops	20.1 (10.6)	9.0 (16.6)
<i>Quercus rubra</i> (Quru)	Acru, Acsa, Cagl, Prse, Quve, and Rops	0.2 (1.6)	19.0 (31.8)
<i>Quercus velutina</i> (Quve)	Acru, Acsa, Cagl, Prse, Quru, and Rops	0.0 (0.8)	7.0 (13.4)
<i>Robinia pseudoacacia</i> (Rops)	Acru, Acsa, Cagl, Quru, and Quve	50.5 (13.2)	1.0 (3.2)

Notes: *Robinia pseudoacacia* is considered invasive in Michigan. *A. saccharum* had very low seed viability, so there were not enough controls to allow us to estimate shade intolerance.

† Species of adults culturing soil used for each species (see *Methods: Soil sources* . . .).

‡ Shade intolerance was measured as the difference in percentage survival between seedlings of each species grown in sterile potting soil in high vs. low light.

§ Adult trees at Horner McLaughlin Woods (Ann Arbor, Michigan, USA) where soil for the greenhouse experiment was collected.

fall of 2009 at Horner McLaughlin Woods, a 36-ha plant preserve in Ann Arbor, Michigan, USA. To minimize the potential for multi-tree species influencing the soil, we took soil under trees that were at least two crown diameters away from adults of other study species (Table 1). Soils from the same species were aggregated into one bulk sample and prepared for use by dicing roots and sifting soil through a 1-cm-mesh sieve. Each soil source (species specific) was kept separate throughout the course of the experiment. The biotic and abiotic characteristics of each soil were maintained at the species level, but not at the parent-tree level; thus, our results only constitute a measure of the population's overall PSF effect on the community. Soil nutrient content was relatively similar among the different soil sources (McCarthy-Neumann and Ibáñez 2012). Half of the field and all of the potting soil (Fafard Mix #2, Conrad Fafard, Agawam, Massachusetts, USA) were sterilized by gamma irradiation prior to the start of the experiment (~30 KGray; Sterigenics International, Schaumburg Oak Brook, Illinois, USA). At the same site, adult local density was determined in June 2012 by taking an inventory of presence and diameter at breast height (dbh) for all living individuals of our study species in ten 20 × 50 m plots randomly located throughout our soil collection site.

Planting methods

All seeds were collected from southeastern Michigan forests, or purchased from Sheffield's Seed Company (Locke, New York, USA) when local seeds were not available. To minimize diseases from non-experimental soil sources (e.g., from the collection sites), seeds were surface sterilized (0.6% NaOCl solution) prior to stratification and again prior to germinating in perlite. Seeds with newly emerged radicles were weighed and then planted into 6.4 cm diameter × 25 cm depth pots and grown at greenhouse facilities on Michigan State University's campus. Soil treatments consisted of: (1) "non-sterile treatment," a 1:1:2 mixture of non-sterile

field soil, sterile field soil, and sterile potting soil; (2) "sterile treatment," a 1:1 mixture of sterile field soil and sterile potting soil; and (3) "control," 100% sterile potting soil.

Seedlings were grown at two light levels comparable to 1.3% and 29% full sun, respectively mimicking conditions from understory and tree-fall gaps encountered in Michigan forests (Schreeg et al. 2001). The low-light treatment was created by covering benches with an inner layer of black shade cloth and an outer layer of reflective knitted poly-aluminum shade cloth. We had a total of 10 replicate seedling pots per experimental treatment (i.e., soil source [conspecific vs. each of the heterospecific soils] × soil treatment [sterile vs. non-sterile] × light availability [low vs. high]). Due to low seed germination some species were not grown in all heterospecific soil sources (Table 1). Individual pots were set up on 12 different benches where all combinations of soils and soil treatments were represented, and were watered (~50 mL of deionized water) by hand every three days for 10 weeks. Emergence and survival were recorded weekly, and date of death was assigned as the first census with total leaf and/or stem tissue necrosis.

Analytical approaches

To obtain a robust indication of the overall importance of conspecific feedbacks, specifically whether seedlings were more likely to have worse survival in their own soil relative to soils cultured by other tree species, for the analysis we pooled all heterospecific soil sources into one category and compared it with conspecific survival.

We used an individual-based Cox survival model (Andersen and Gil 1982) to include as many factors as possible that could have influenced seedling survival, e.g., soil source (conspecific vs. heterospecific), soil treatment (non-sterile vs. sterile), standardized seed size, light, and soil moisture. Model parameters were estimated at the species level following a Bayesian

approach that allowed us to consider the different sources of uncertainty associated with the data (see Appendix A for a thorough description of the analysis and Appendix B for model parameters). Using the parameter estimates (means, standard deviations, and covariances) we calculated predicted survival for all combinations of conspecific vs. heterospecific soils (NDD mechanisms via occurrence of PSF), sterile vs. non-sterile treatments (biotic or abiotic nature of PSF), and low vs. high light levels (differential strength of PSF) (Appendix C). We then used these predicted survival values and their associated uncertainty to explicitly assess whether there were differences in how species responded to soil source and treatment at low vs. high light levels (testing the three proposed hypothesis of tree species coexistence). Differences that did not include zero in their 95% credible intervals were considered statistically significant.

We then used multiple step-wise regressions (SPSS version 18.0; SPSS 2009) to determine if local plant adult abundance and seedling shade tolerance were correlated with the effect of PSF in non-sterile soil. We calculated the strength of PSF at each light level as $\ln(X_C/X_H)$, where X_C is mean survival in conspecific soil and X_H is mean survival in heterospecific soil. Since species shade tolerance can vary based on ontogeny and local site conditions (Valladares and Niinemets 2008), instead of using published rankings we characterized species shade tolerance as sensitivity to light within our experiment. Thus, shade intolerance was measured as the difference in survival between seedlings of each species grown in sterile potting soil, our control, at high vs. low light. For one species, *Acer saccharum*, we had very low seed viability so we were not able to plant enough seedlings in the peat moss control soils to reliably estimate shade intolerance. Thus, we excluded it from the shade-tolerance comparisons, although this species is considered very shade tolerant as a seedling (e.g., Burns and Honkala 1990, Barnes and Wagner 2004). Both adult abundance and seedling shade-tolerance data was log-transformed prior to analysis to help homogenize the random-error variance; a value of 1 was added to all shade-intolerance values prior to log transformation.

RESULTS

Testing hypothesis 1

How prevalent are negative plant–soil feedbacks (PSF) on seedling survival, and when occurring does the light environment alter the occurrence of these PSFs?—Half of the study species (*Liriodendron tulipifera*, *Prunus serotina*, *Quercus rubra*, and *Robinia pseudoacacia*) experienced negative PSF, meaning that conspecific soil was detrimental relative to pooled heterospecific soils (Fig. 1a; Appendix C). Light availability influenced whether three of the four species experienced PSF. Only in low light did seedlings of *Prunus serotina*, *Quercus rubra*, and *Robinia pseudoacacia* experience negative PSF, whereas

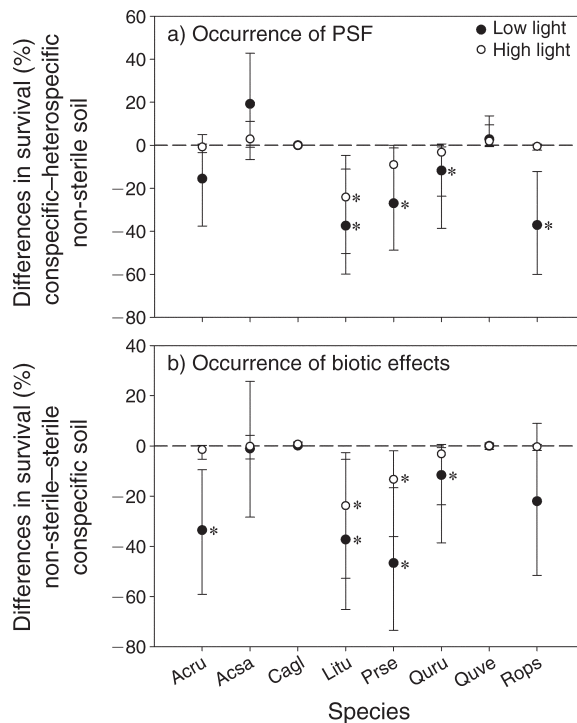


FIG. 1. Differences in predicted seedling survival of eight deciduous trees (see Table 1 for full scientific names) in a greenhouse experiment conducted under low light and high light that (a) tested for the occurrence of plant–soil feedbacks (PSFs) and (b) tested for biotic effects. Data are means with 95% credible intervals; credible intervals that do not overlap with the zero line are statistically significant.

* $P < 0.05$.

Liriodendron tulipifera seedlings experienced negative PSF at both high and low light (Fig. 1a; Appendix C).

What was the nature of the PSF?—Soil biota in conspecific soil, not abiotic factors, reduced survival for two out of eight species (*Acer rubrum* and *Q. rubra*) under only low light, and for two species (*L. tulipifera* and *P. serotina*) under both low and high light (Fig. 1b; Appendix C). Reduced survival in non-sterile conspecific cultured soil was significantly less for *P. serotina* in high vs. low light, whereas *L. tulipifera* reductions in survival were statistically similar at both light levels (Fig. 1b). In addition, biota from soils collected near heterospecific adults reduced survival for *A. saccharum* and *P. serotina* seedlings in both low and high light (Appendix D). The negative biotic effect from heterospecific-collected soils was more severe for *A. saccharum* and less severe for *P. serotina* seedlings than from conspecific soils (Fig. D-1 in Appendix D vs. Fig. 1b) resulting in the absence of a significant feedback for *A. saccharum*, and a significant negative conspecific feedback for *P. serotina* seedlings (Fig. 1a).

Testing hypothesis 2

Are rare species more affected by PSF than common ones?—In low light, species that were locally rare as

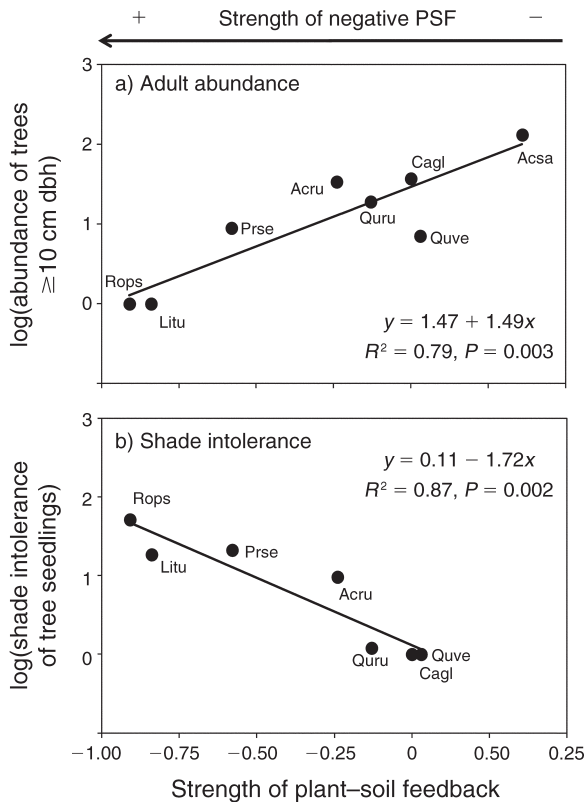


FIG. 2. Strength of plant-soil feedback [$\ln(\text{survival in conspecific soil})/(\text{survival in heterospecific soil})$] in non-sterile treatment at low light in relation to (a) local adult abundance at the site where soil was collected for the greenhouse experiment, and (b) seedling shade intolerance.

adults in the forest were the ones most affected by negative PSF ($F = 23.0$, $df = 1, 6$, $P = 0.003$, $R^2 = 0.79$; Fig. 2a), but this pattern did not hold at high light ($F = 3.5$, $df = 1, 6$, $P = 0.11$, $R^2 = 0.37$; data not shown).

Testing hypothesis 3

Are shade intolerant species more affected by PSF than shade-tolerant ones?—For the seven species for which we had an experimental metric of shade intolerance, shade intolerance co-varied with species sensitivity to mostly negative PSF in low light ($F = 32.3$, $df = 1, 5$, $P = 0.002$, $R^2 = 0.87$; Fig. 2a), but not high light ($F = 1.1$, $df = 1, 5$, $P = 0.34$, $R^2 = 0.18$; data not shown).

DISCUSSION

We investigated if plant-soil feedbacks (PSF) could act as a link between negative distance-dependent and resource-based niche partitioning mechanisms in a temperate forest, and further enhance the variety of recruitment niches among coexisting species. Although the heterospecific species culturing the soil mattered (McCarthy-Neumann and Ibáñez 2012), to address the role of conspecific soil vs. the soils associated with other species common in the natural community we compared

seedling response to conspecific vs. pooled heterospecific soils (i.e., the community effect). We found that four out of eight species experienced strong negative conspecific feedbacks (i.e., differential strength of PSF, discarding hypothesis 1). For three of these species, the feedback was biotic mediated. Additionally, the effect of PSF and soil biota on survival was often restricted to low-light conditions. Lastly, we found that tree species that showed stronger negative feedbacks were rare as adults in the forest community (supporting hypothesis 2), and their seedlings were shade intolerant (also supporting hypothesis 3). These findings suggest that PSF may facilitate species coexistence via both differential negative distance-dependent processes as well as through intensifying light- gradient partitioning among tree species, that is, by enhancing the multidimensionality of the recruitment niche.

Previous studies report a general increase in soil diseases at low light (e.g., Augspurger and Kelly 1984, Hood et al. 2004, O'Hanlon-Manners and Kotanen 2004), but these studies did not take PSF into consideration (but see Hood et al. [2004] where PSF were investigated but the interaction between disease and light occurred regardless of soil source). Thus, our results are the first direct evidence that light conditions influence whether negative PSF are experienced by tree species (Fig. 1a). For most of our species, the negative effect of soil biota in conspecific cultured soil was the mechanism creating these feedbacks, and was also restricted for some species to low-light conditions (Fig. 1b). Density of fungal populations and expression of disease symptoms have been positively associated with soil moisture (e.g., Augspurger 1990, Martin and Loper 1999). In our experiment there were minimal soil moisture differences between our low- and high-light treatments (soil moisture in low irradiance = $21.3\% \pm 4.8\%$ (mean \pm SD), and in high irradiance = $18.1\% \pm 3.8\%$). Thus, our results—that PSF and negative effects of soil biota are often restricted to low light conditions—are rather conservative.

The strength of negative PSF on seedling survival was also positively correlated with field-based adult abundance, bolstering the proposal that rarity may be promoted by differential PSF (Fig. 2a), which may in turn enhance species coexistence (e.g., Yenni et al. 2012). Our result is consistent with previous work in temperate grassland (Klironomos 2002) and tropical forest (Mangan et al. 2010) systems, where rarity seems to be reinforced by strong negative PSF. However, rarity could still be an advantage at the community level, even if rare species experience stronger negative PSF, simply because progeny of rare species are less likely to encounter areas “cultured” by conspecifics than common species. As a note of caution, we want to reiterate our result is associational and does not necessarily imply causation between the process operating at the seedling level and adult plant abundance. Also, this is a species effect (we bulked all the soils from the same species), but

the strengths of PSF could also vary from tree to tree. In a recent review, strength of PSF was shown to be an infrequent predictor of plant abundance in the field (K. O. Reinhart et al., *unpublished manuscript*).

We found an equally strong pattern between seedlings' shade intolerance and their susceptibility to negative PSF (Fig. 2b). Thus, a seedling's shade tolerance may not be solely due to physiological carbon balance requirements (e.g., the carbon-gain hypothesis; Givnish 1988), but also due to the plant's resistance to biotic stresses (e.g., the stress-tolerance hypothesis; Kitajima 1994). A major consequence of this dynamic is that when PSF are present light gradient partitioning among species is intensified (through amplifying species differences in survival along the light gradient), enhancing the multidimensionality of recruitment niches, and thus contributing to species coexistence (e.g., Kobe 1999).

Our results illustrate how PSF, soil biota, and irradiance may interact. The overall effect of these environmental filters on seedlings is likely quite complex, and as illustrated here may also be influenced by a species' shade tolerance. For instance, successful seedling recruitment for shade-intolerant species that experience PSF only in low-light conditions will likely be dependent on dispersing into high-light areas or away from conspecific adults under closed-canopy conditions (where survival may be low in comparison with high-light sites, but not as low as establishing under a conspecific adult). Whereas our results suggest that recruitment for shade-tolerant species will likely not be dictated by light conditions or conspecific canopy presence, but rather by other factors. These various seedling-recruitment-niche scenarios would then influence local adult abundance in closed-canopy forests. We do acknowledge that these results are based on associational patterns, and do not necessarily indicate causation. However, our results are the first direct, experimental evidence that tree seedlings' survival response to PSF are mainly restricted to low light, covary with adult abundance, and that species considered shade intolerant are more likely to be susceptible to this process. This is an important discovery since it shows that NDD (negative distance-dependent and density-dependent mortality) and light-based niche partitioning are not mutually exclusive mechanisms, but rather can operate together to structure community dynamics and maintain tree species coexistence via PSF processes.

ACKNOWLEDGMENTS

We are grateful to two anonymous reviewers, GCEL at the University of Michigan, and Rich Kobe's group at Michigan State University for helpful comments on the manuscript. We thank the numerous assistants who helped during the experiment. This research was funded by NSF grant DEB-EAGER 0947783.

LITERATURE CITED

- Alvarez-Loayza, P., and J. Terborgh. 2011. Fates of seedling carpets in an Amazonian floodplain forest: intra-cohort competition or attack by enemies? *Journal of Ecology* 99: 1045–1054.
- Alvarez-Loayza, P., J. F. White, Jr., M. S. Torres, H. Balslev, T. Kristiansen, J. Svenning, and N. Gil. 2011. Light converts endosymbiotic fungus to pathogen, influencing seedling survival and niche-space filling of a common tropical tree, *Iriartea deltoidea*. *PLoS ONE* 6:e16386.
- Andersen, P. K., and R. D. Gil. 1982. Cox's regression model for counting processes: A large sample study. *Annals of Statistics* 10:1100–1120.
- Augsburger, C. K. 1984. Seedling survival of tropical tree species: interactions of dispersal distance, light-gaps, and pathogens. *Ecology* 65:1705–1712.
- Augsburger, C. K. 1990. Spatial patterns of damping-off disease during seedling recruitment in tropical forests. Pages 131–144 in J. Burdon, and S. Leather, editors. *Pests, pathogens, and plant communities*. Blackwell Scientific Publications, Oxford, UK.
- Augsburger, C. K., and C. K. Kelly. 1984. Pathogen mortality of tropical seedlings: experimental studies of the effects of dispersal distances, seedling density, and light conditions. *Oecologia* 61:211–217.
- Barnes, B. V., and W. H. Wagner. 2004. *Michigan trees*. The University of Michigan Press, Ann Arbor, Michigan, USA.
- Bever, J. D. 2003. Soil community feedback and the coexistence of competitors: conceptual frameworks and empirical tests. *New Phytologist* 157:465–473.
- Burns, R. M., and B. H. Honkala. 1990. *Silvics of North America: 1. Conifers; 2. Hardwoods*. Agriculture Handbook 654, USDA Forest Service, Washington, D.C., USA.
- Clark, J. S., J. Mohan, M. Dietze, and I. Ibáñez. 2003. Coexistence: how to identify trophic trade-offs. *Ecology* 84: 17–31.
- Coley, P. D., and J. A. Barone. 1996. Herbivory and plant defenses in tropical forests. *Annual Review of Ecology and Systematics* 27:305–335.
- Coley, P. D., J. P. Bryant, and F. S. Chapin, III. 1985. Resource availability and plant antiherbivore defense. *Science* 230:895–899.
- Comita, L. S., H. C. Muller-Landau, S. Aguilar, and S. P. Hubbell. 2010. Asymmetric density dependence shapes species abundances in a tropical tree community. *Science* 329:330–332.
- Connell, J. H. 1971. On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. Pages 298–312 in P. J. Den Boer and G. R. Gradwell, editors. *Dynamics of populations*. Centre for Agricultural Publishing and Documentation, Wageningen, The Netherlands.
- Denslow, J. S. 1980. Gap partitioning among tropical rainforest trees. *Biotropica* 12:47–55.
- Gause, G. F. 1934. *The struggle for existence*. Lippincott, Williams & Wilkins, Baltimore, Maryland, USA.
- Gilbert, G. S. 2002. Evolutionary ecology of plant diseases in natural ecosystems. *Annual Review of Phytopathology* 40: 13–43.
- Givnish, T. J. 1988. Adaptation to sun and shade: a whole-plant perspective. *Australian Journal of Plant Physiology* 15:63–92.
- Gurevitch, J. S., M. Scheiner, and G. A. Fox. 2006. *The ecology of plants*. Second edition. Sinauer Associates, Sunderland, Massachusetts, USA.
- Herns, D. A., and W. J. Mattson. 1992. The dilemma of plants: to grow or defend. *Quarterly Review of Biology* 67:283–335.
- Hille Ris Lambers, J., J. S. Clark, and B. Beckage. 2002. Density-dependent mortality and the latitudinal gradient in species diversity. *Nature* 417:732–735.
- Hood, L. A., M. D. Swaine, and P. A. Mason. 2004. The influence of spatial patterns of damping-off disease and arbuscular mycorrhizal colonization on tree seedling estab-

- ishment in Ghanaian tropical forest soils. *Journal of Ecology* 92:816–823.
- Janzen, D. H. 1970. Herbivores and the number of tree species in tropical forests. *American Naturalist* 104:501–528.
- Johnson, D. J., W. T. Beaulieu, J. D. Bever, and K. Clay. 2012. Conspecific negative density dependence and forest diversity. *Science* 336:904–907.
- Kitajima, K. 1994. Relative importance of photosynthetic traits and allocation patterns as correlates of seedling shade tolerance of 13 tropical trees. *Oecologia* 98:419–428.
- Klironomos, J. 2002. Feedback with soil biota contributes to plant rarity and invasiveness in communities. *Nature* 417:67–70.
- Kobe, R. K. 1997. Carbohydrate allocation to storage as a basis of interspecific variation in sapling survivorship and growth. *Oikos* 80:226–233.
- Kobe, R. K. 1999. Light gradient partitioning among tropical tree species through differential seedling mortality and growth. *Ecology* 80:187–201.
- Kobe, R. K., and C. F. Vriesendorp. 2011. Conspecific density dependence in seedlings varies with species shade tolerance in a wet tropical forest. *Ecology Letters* 14:503–510.
- Mangan, S. A., S. A. Schnitzer, E. A. Herre, K. Mack, M. Valencia, E. Sanchez, and J. D. Bever. 2010. Negative plant–soil feedback predicts tree-species relative species abundance in a tropical forest. *Nature* 466:752–755.
- Martin, F. N., and J. E. Loper. 1999. Soilborne plant diseases caused by *Pythium* spp.: ecology, epidemiology, and prospects for biological control. *Critical Reviews in Plant Science* 18:111–181.
- McCarthy-Neumann, S., and I. Ibáñez. 2012. Tree range expansion may be enhanced by escape from negative plant–soil feedbacks. *Ecology* 93:2637–2649.
- McCarthy-Neumann, S., and R. K. Kobe. 2008. Tolerance of soil pathogens co-varies with shade tolerance across species of tropical tree seedlings. *Ecology* 89:1883–1892.
- McCarthy-Neumann, S., and R. K. Kobe. 2010a. Conspecific plant–soil feedbacks reduce survivorship and growth of tropical tree seedlings. *Journal of Ecology* 98:396–407.
- McCarthy-Neumann, S., and R. K. Kobe. 2010b. Conspecific and heterospecific plant–soil feedbacks influence survivorship and growth of temperate tree seedlings. *Journal of Ecology* 98:408–418.
- Montgomery, R. A., and R. L. Chazdon. 2002. Light gradient partitioning tropical tree seedlings in the absence of canopy gaps. *Oecologia* 131:165–174.
- Myers, J. A., and K. Kitajima. 2007. Carbohydrate storage enhances seedling shade tolerance in a neotropical forest. *Journal of Ecology* 95:383–395.
- O'Hanlon-Manners, D. L., and P. M. Kotanen. 2004. Evidence that fungal pathogens inhibit recruitment of a shade-intolerant tree, white birch (*Betula papyrifera*), in understory habitats. *Oecologia* 140:650–653.
- Pacala, S. W., C. D. Canham, J. Saponara, J. A. Silander, Jr., R. K. Kobe, and E. Ribbens. 1996. Forest models defined by field measurements: estimation, error analysis and dynamics. *Ecological Monograph* 66:1–43.
- Packer, A., and K. Clay. 2000. Soil pathogens and spatial patterns of seedling mortality in a temperate tree. *Nature* 404:278–281.
- Palmer, M. W. 1994. Variation in species richness: towards a unification of hypotheses. *Folia Geobotanica et Phytotaxonomica* 29:511–530.
- Reich, P. B., M. G. Tjoelker, M. B. Walters, D. W. Vanerklein, and C. Bushena. 1998. Close association of RGR, leaf and root morphology, seed mass and shade tolerance in seedlings of nine boreal tree species grown in high and low light. *Functional Ecology* 12:327–338.
- Schreeg, L. A., R. K. Kobe, and M. B. Walters. 2001. Tree seedling growth, survival, and morphology in response to landscape-level variation in soil resource availability in northern Michigan. *Canadian Journal of Forest Research* 35:263–273.
- SPSS. 2009. SPSS, version 18. SPSS, Chicago, Illinois, USA.
- Valladares, F., and U. Niinemets. 2008. Shade tolerance, a key plant feature of complex nature and consequences. *Annual Review of Ecological Systems* 39:237–257.
- Yenni, G., P. B. Adler, and S. K. M. Enest. 2012. Strong self-limitation promotes the persistence of rare species. *Ecology* 93:456–461.

SUPPLEMENTAL MATERIAL

Appendix A

Analytical approach ([Ecological Archives E094-066-A1](#)).

Appendix B

A table presenting parameter estimates (mean posterior values and 95% credible interval) for fixed-effects coefficients, β parameters, for each study species ([Ecological Archives E094-066-A2](#)).

Appendix C

A table presenting predicted survival values (mean and 95% credible interval based on parameter values from Appendix B) by soil source, treatment, and light level for each species ([Ecological Archives E094-066-A3](#)).

Appendix D

A figure presenting differences in predicted survival in testing for biotic effects in conspecific soil ([Ecological Archives E094-066-A4](#)).