Tree range expansion may be enhanced by escape from negative plant–soil feedbacks

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Abstract. Many plant species are expected to shift their distributional ranges in response to global warming. As they arrive at new sites, migrant plant species may be released from their natural soil pathogens and/or deprived of key symbiotic organisms. Under such scenarios plant–soil feedbacks (PSF) will likely have an impact on plant species' ability to establish in new areas. In this study we evaluated the role that PSF may play on the migratory potential of dominant temperate tree species at the northern limit of their distributional range in the Great Lakes region of North America. To test their ability to expand their current range, we assessed seedling establishment, i.e., survival, of local and potential migrant tree species in a field transplant experiment. To test for the presence and strength of PSF, we also assessed seedling survival during establishment in a greenhouse experiment, where the potential migrant species were grown in soils collected within and beyond their distributional ranges. The combination of experiments provided us with a comprehensive understanding of the role of PSF in seedling establishment in new areas. In the field, we found that survival for most migrant species was similar to those of the local community, ensuring that these species could establish in areas beyond their current range. In the greenhouse, we found that the majority of species experienced strong negative conspecific feedbacks mediated by soil biota, but these responses occurred for most species only in low light conditions. Lastly, our combined results indicate that migrant tree species can colonize and may even have enhanced short-term recruitment beyond their ranges due to a lack of conspecific adults (and the resulting negative PSF from these adults).

Key words: Acer rubrum; Acer saccharum; Carya glabra; *climate change; hierarchical Bayes; light availability;* Liriodendron tulipifera; *Lower Peninsula, Michigan, USA;* Prunus serotina; Quercus rubra; Quercus velutina; Robinia pseudoacacia.

Introduction

Many species are predicted to shift their distributions in response to current trends in climate (e.g., Parmesan et al. 1999, Walker et al. 2002). A suitable regeneration niche will be required to ensure range expansion by species tracking global warming (Ibáñez et al. 2006). A niche determined not only by climate, but also by all the abiotic and biotic conditions (e.g., soil nutrients, photoperiod, interactions with competitors, herbivores, predators, symbionts, and pathogens) that affect recruitment of new individuals and characterize a particular site (Ibáñez et al. 2008, 2009). In order to determine future distributions, we will need species-specific information on species' performance not only with respect to the changing climate, but also with respect to the new environment as a whole (i.e., the suite of biotic and abiotic factors that characterize a site).

In particular, interactions between trophic levels such as plant–soil feedbacks (PSF) may have a large effect on seedling establishment of migrant plant species and

ultimately on their new distributions. These feedbacks occur through interactions between plants and the soil in which they grow, and can cause changes to soil conditions (biotic, physical, and/or chemical) that affect plant performance (Bever 1994, Ehrenfeld et al. 2005). Plant–soil feedbacks may result in a wide range of effects, including changing population abundance (Bever et al. 1997), restricting establishment for species into certain habitats (Augspurger and Kelly 1984, O'Hanlon-Manners and Kotanen 2004), altering successional trajectories (Kardol et al. 2007), maintaining species diversity (Mangan et al. 2010, McCarthy-Neumann and Kobe 2010*a*, Kulmatiski et al. 2011), shifting species distributions (Reinhart and Callaway 2006, van Grunsven et al. 2010), and altering ecosystem services (Schnitzer et al. 2011). The direction of the feedback depends on the balance between positive effects of mycorrhizal fungi, N-fixing bacteria, and other beneficial bacteria, and negative effects of pathogens, parasites, and herbivores (Klironomos 2002, Callaway et al. 2011). Adding to this complexity is the presence of abiotic mediated PSF created by the production of allelochemicals (Stinson et al. 2006), alterations to soil physical properties (Rillig et al. 2002), and changes in nutrient availability (Finzi et al. 1998*a, b*).

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As seedling establishment constitutes a major demographic bottleneck for plant populations (Gurevitch et al. 2002), a species' ability to colonize a new site will depend not only on seed dispersal, but also on other factors during this vulnerable stage of recruitment. In particular, plant–soil feedbacks are likely to be one of the "important filters" (i.e., the multitude of factors influencing performance; Harper 1977) that determine recruitment patterns. Thus, focusing on PSF at the seedling stage will be critical for assessing forest dynamics in general and short-term tree species range expansion in particular.

Specifically, PSF's potential effects on species distribution patterns and abundances in a warmer world have not been thoroughly studied (but see Engelkes et al. 2008, van Grunsven et al. 2010). The impact of biotic PSF on migrant plant species ability to expand their range might be influenced by the migration ability of microorganisms comprising the soil community in their local range (e.g., most fungal soil pathogens disperse primarily through spore hydrochory and hyphal growth; Agrios 1997), and the host specificity of these organisms (Konno et al. 2011). If migrant species respond to release from enemies (Reinhart et al. 2003), but continue to interact with mycorrhizae (Callaway et al. 2011) as has shown to be the case with invasive species, we may expect a greater dominance of migrant relative to local species in the new habitat. However, establishment of migrant species may be impeded if both migrant and local species are responding to generalist pathogens, as these species may face both continued disease pressure and stress of establishing in these new habitats (which may have different resource levels and species assemblages than migrant species experienced in their old habitats).

To investigate the role of PSF in determining tree range expansion, we followed an approach in which a large-scale transplant field experiment in the Great Lakes region of North America and a greenhouse experiment were carried out simultaneously. The Great Lakes region is an area of particular interest in climate change research because it is where many temperate deciduous tree species reach their northern distributional limit due to short growing seasons (Barnes and Wagner 2004; Table 1, Fig. 1), and is therefore an area where we expect to first observe the expansion of their distributional ranges. The field transplant experiment tested the effects of the new range on recruitment of migrant tree species with respect to the local community and provided us with realistic survival rates among the species. We also conducted a greenhouse experiment to test actual mechanisms underpinning survival patterns in the field, specifically: (1) whether PSF mediated by soil biota and/or soil abiotic factors are important in survival for our study species, and (2) whether PSF facilitate or impede successful establishment of migrant species in regions beyond their ranges. Answers to these questions allowed us to evaluate the role that PSF, both biotic and abiotic, may play on tree species range expansion.

METHODS

Field transplant experimental design

To test seedling survival beyond their distributional range and across a wide range of resources (moisture, soil fertility, and light), we conducted a seedling transplant experiment with local and potential migrant tree species at two latitudes, within and beyond the migrants' northern range, in Michigan Lower Peninsula (Table 1, Fig. 1). Our primary goal with this experiment was to estimate in situ rates of seedling survival at these two latitudes that could then be compared among local and potential migrant species (Table 2).

Sites.—The field experiment took place during the summers of 2009 and 2010. The northernmost sites were located at the University of Michigan Biological Station. These sites, referred to from now on as northern sites or soils, represented a region into which all the selected migrant species have been predicted to move into under most climate scenarios (Prasad et al. 2007). The southernmost sites were located at the University of Michigan Edwin S. George Reserve and Radrick Forest. These forests are located in southeastern Michigan and currently contain all the selected species (Table 1, Fig. 1), and in the remainder of the study will be referred to as southern sites or soils. To sample the environmental gradients and soil communities in the area, we selected stands within the major vegetation types of the area (Table 1, Fig. 1), and in each stand we set up plots in different habitats (canopy gap vs. forest understory), which are a proxy for different light conditions.

Species.—Eighteen temperate tree species were used in the field experiment (Table 2). Species were selected based on their distributional ranges and their predicted distributional shifts (Prasad et al. 2007). We classified all species as "local," currently growing in the area, or "migrant," species predicted to move into the area. These species represent a broad range in seed sizes, shade tolerance classifications, and mycorrhizal associations (Table 2). Whereas local seed sources were used for local species, seeds were collected from locations in the northern limit of their ranges for migrants (Appendix A). Additionally, seeds were collected from southern and northern populations for some species with distributional ranges extending throughout the Great Lakes region, and were analyzed independently as if they were different species (Appendix A). Seeds that could not be collected from local forests were purchased from Sheffields Seed (Locke, New York, USA). All seeds were surface sterilized (0.6% NaOCl solution) prior to stratification and again prior to germinating in greenhouse potting soil (Metro-Mix 380; Sun Gro Horticulture Canada, Vancouver, British Columbia, Canada).

Experimental design.—At each latitudinal site, we selected four vegetation stands. In each stand, we set up four replicate plots measuring 4 × 5 m; two plots under forest canopy and two plots under natural canopy gaps.

TABLE 1. Locations and site description for the field transplant experiment and soil collection sites for the greenhouse experiment in Michigan's Lower Peninsula, USA.

Site description	North 45°36′ N–84°41′ W	South 42°28′ N–84°00′ W
Average extreme minimum temperature	−28°C	−22°C
Geology	moraine ridges and poorly drained outwash	end-moraine ridges and ground moraine
Growing season	108 days	158 days
Soil textures	gravelly sandy, loamy	loamy and clayey
Major soil orders	Spodosols, Entisols	Alfisols
Dominant canopy species		
Stand 1	*Fagus grandifolia* and *Acer saccharum*	*Quercus alba* and *Quercus velutina*
Stand 2	*Pinus strobus* and *Populus grandidentata*	*Quercus velutina* and *Carya glabra*
Stand 3	*Abies balsamea* and *Thuja occidentalis*	*Acer saccharum* and *Quercus rubra*
Stand 4	*Populus grandidentata*	

Notes: North and south refer to the location of the transplant sites and also to where soils were collected for the greenhouse experiment. Elevation along the sites ranges from 180 to 525 m. In each of the stands four plots (two in canopy and two in gap habitats) were established (except for stands 2 and 3 in the south, with six plots each) for the transplant experiment. Stand 1 in the north and an additional stand not used in the field experiment (located at University of Michigan's Horner Woods in Ann Arbor, Michigan) were used to collect soil for the greenhouse experiment.

We had a total of 16 plots (2 latitudes × 3–4 stands × 2 canopy levels × 2–4 plots), and in each of the experimental plots, we transplanted 5–20 seedlings of each species (number of seedlings varied among species depending on germination success) that were ~4 weeks in age. Seedlings were planted 25 cm apart. Additionally, seedlings in one of the replicated plots were treated immediately after planting with a mixture of fungicides (Subdue Maxx and Medallion; Syngenta, Basel, Switzerland); seedlings in the control plots were watered with the same volume of water (100 mL). However, there was no evidence that fungicide treatment had any effect on seedling survival (data not shown), and the fungicide factor was excluded from any further comparisons in the model. A total of 7683 seedlings in 2009 and 6672 seedlings in 2010 were planted (Table 2).

Environmental measurements.—We combined temporally extensive (hourly) environmental data taken at one point for each stand with spatially extensive environmental data taken at each of the four plots per stand to estimate cumulative light (PAR, phototosynthetically active radiation) and average soil moisture at each plot for every two-week period during the 2009 and 2010 growing seasons (see Appendix B for more detailed methods). Soil resources (inorganic N, NH_4^+, NO_3^-, total soil C and N, Mg^{2+}, Ca^{2+}, K^+ and PO_4^-, and soil pH) were also measured for each plot (see Appendix C for methods and results).

Seedling measurements.—Height was measured before planting to account for any differences in survival due to initial seedling size. Survivorship was recorded every two weeks after transplant into the field for 10 weeks. The first census was used to identify seedlings that died due to transplant shock during the first two weeks and their data were not used in the analyses.

Greenhouse experimental design

To investigate the role of plant–soil feedbacks in determining seedling establishment in new areas, we conducted a greenhouse experiment with eight tree species common to the region (all southern seed sources; Table 2). We collected soils near adults of each species in a southern site, and for three species soils were also collected in a northern site (Table 1, Fig. 1). We grew seedlings in either non-sterile or sterilized field soils across a range of irradiance levels and assessed survival. Seed collection and preparation followed the same protocol as described for the field experiment.

Soil sources.—We did not follow the common approach of setting up multistage feedback experiments (e.g., Bever et al. 2010). Instead we used soil cultured in situ by mature trees for several reasons: (1) to minimize changes in soil biota composition and diversity that our experimental seedlings initially experience (Sykorova et al. 2007); (2) because individual mature trees (unlike grasses which are the focal species in most PSF experiments) have an easily discernible area where soil
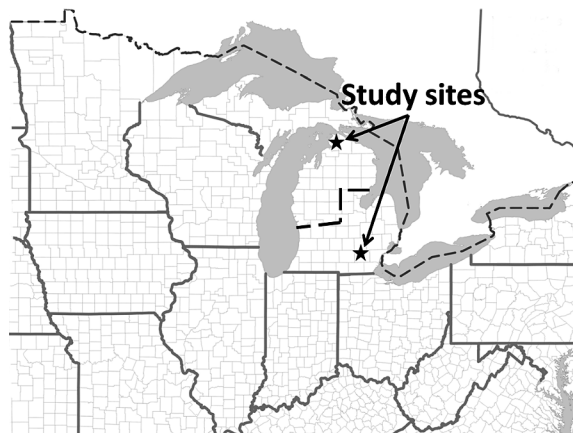

FIG. 1. Locations for the field transplant experiment and soil collection sites for the greenhouse experiment in Michigan's Lower Peninsula, USA. The black dashed line indicates the northern distributional limit for the studied potential migrant tree species in Michigan (Little 1971).

TABLE 2.   Study species, local and potential migrants, their geographical source, summer planted, shade tolerance status, symbiotic associations, and average seed mass.

| Species name (code) | Field transplant sites, northern (N) and southern (S) | | | | Shade tolerance | Mycorrhizal association | Seed mass (mg) |
| | Geographic source | | Summer planted | | | | |
	2009	2010	2009	2010			
Local species							
Acer rubrum (**Acru**)	N	N and S	N	S	tolerant	AMF	19.6
Acer saccharum (**Acsa**)	N and S	S	S	S	very tolerant	AMF	64.9
Betula papyrifera (Bepa)	N and S		N and S		intolerant	AMF and EMF	0.3
Pinus banksiana (Piba)	N		N		intolerant	AMF and EMF	3.4
Pinus strobus (Pist)	N		N		intermediate	AMF and EMF	17.1
Prunus serotina (**Prse**)				N and S	intolerant	AMF	94.3
Quercus rubra (**Quru**)	N and S	N and S	N and S	N and S	intermediate	AMF and EMF	4127.0
Tsuga canadensis (Tsca)				N and S	very tolerant	AMF and EMF	10.0
Migrant species							
Carya glabra (**Cagl**)	S	S	S	S	intermediate	AMF and EMF	2272.0
Carya ovata (Caov)	S	S	S	S	intermediate	AMF and EMF	4545.0
†*Celastrus orbiculatus* (Ceor)				S	tolerant	AMF	17.5
†*Elaeagnus umbellata* (Elum)				S	intolerant	AMF, EMF, and NFB	16.1
Liquidambar styraciflua (List)		S		S	intolerant	AMF	6.1
Liriodendron tulipifera (**Litu**)		S		S	intolerant	AMF	40.0
Nyssa sylvatica (Nysy)	S	S		S	intolerant	AMF	153.8
Quercus alba (Qual)		S		S	intolerant	AMF and EMF	6676.0
‡*Quercus velutina* (**Quve**)	S_U	S_U and S_L	S_U	S_U and S_L	intolerant	AMF and EMF	1570.0
†*Robinia pseudoacacia* (**Rops**)		S			intolerant	AMF, EMF, and NFB	18.9

Notes: Species in bold were also used in the greenhouse experiment. Abbreviations are: N, northern sources; S, southern sources; AMF, arbuscular mycorrhizal fungi; EMF, ectomycorrhizal fungi; and NFB, nitrogen-fixing bacteria. Northern and southern sites refer to the location of the transplant sites. Shade tolerance status and seed mass data are from Burns and Honkala (1990).
 † Species considered invasive in Michigan.
 ‡ Seeds for *Q. velutina* were collected from two latitudes within the southern region: S_U from the upper and S_L from the lower location.

interaction could be occurring and attributable to that one individual (i.e., under its crown); and (3) since trees are long-lived species, specific changes to the soil are already in place, which means that further culturing in the greenhouse does not necessarily change the feedback created in the field (McCarthy-Neumann and Kobe 2010*b*).

We collected soil from southern and northern forest communities for three of the species (*A. rubrum*, *A. saccharum*, and *Q. rubra*). In addition, we collected soils at the southern location from under the canopy of the four southern species (*C. glabra*, *L. tulipifera*, *Q. velutina*, and *R. pseudoacacia*) and of *Prunus serotina*. Although considered local at our northern latitude, this last species was not present as an adult in the northern area. We removed soil samples (30 cm diameter × 15 cm depth) from four points within 1 m from the bole of four mature adults. To minimize potential for multispecies culturing of soil, we took soil under trees that were at least two crown diameters away from adults of other study species. Soil was collected in late October through early November 2009 when microorganisms were likely

to be present as spores, enabling higher microbe survival during transport and cold storage (Reinhart et al. 2005).

Each soil source (species of adult tree culturing the soil) at a particular site was aggregated into one bulk sample and prepared for use in the experiment by dicing roots and sifting soil through a 1-cm mesh sieve. Each soil source was split into two fractions with three-fourths of the soil sterilized by gamma irradiation (~30 KGray; Sterigenics International, Schaumburg, Illinois, USA). Non-sterilized field soil was stored at 4°C for two months; soil destined for irradiation was stored for one month at 4°C and then an additional month at ambient greenhouse temperatures (~21°C) after irradiation. To avoid cross-contamination and transfer of soil biota, all tools and surfaces coming in contact with non-sterilized soil were soaked in 10% bleach solution or surface sprayed with 70% ETOH solution. To test for chemical differences among soils, we measured a variety of nutrients in two replicates for each soil source and treatment as well as the sterile commercial peat soil at the onset of the experiment (Appendix C).

Planting methods and data collection.—Seeds with newly emerged radicles were weighed and then planted

into 6.4 cm diameter × 25 cm depth pots. Seedlings were grown in: (1) the "non-sterile treatment," a 1:1:2 mixture of non-sterile field soil, sterile field soil, and sterile peat soil (Fafard Mix number 2; Conrad Fafard, Agawam, Massachusetts, USA); (2) a "sterile treatment," a 1:1 mixture of sterile field soil and sterile peat soil; and (3) a control with seedlings planted in 100% sterile peat soil. Individual pots were set up on 12 benches where all combinations were represented.

To mimic the variability of the light environment in the field, seedlings were grown at three light levels (comparable to 1.3%, 3.8%, and 29% full sun, respectively; see Appendix B). Seedlings were watered (~50 mL of deionized water, DI) by hand every three days for 10 weeks. To determine if irradiance influenced water availability, we measured percentage soil moisture at each bench (see Appendix B). Due to low seed germination, some species were not grown in all soil sources from the southern range (see Appendix D). Emergence and survival were recorded once a week. We assigned date of death as the first census with total leaf and/or stem tissue necrosis.

Analytical approach

We used a counting process in a Cox survival model (Andersen and Gill 1982) to include as many factors as possible that could have influenced seedling survival. This model allows for ample flexibility in the estimation of the hazard and the frailty (Fleming and Harrington 1991, Andersen et al. 1993). Here the data for each seedling i and each time t, N_{it}, are coded as 0 until the seedling is found dead, then $N_{it} = 1$, which would be the last time period accounted for. A count process models the number of events (failures, N_{it}) that have occurred up to continuous time. We model the likelihood as

$$N_{it} \sim \text{Poisson}(\lambda_{it})$$

where λ is the intensity function, that is then estimated as a function of the intrinsic rate of mortality, or hazard h, and the extrinsic risk of mortality, or risk μ:

$$\lambda_{it} = h_t e^{(\mu_{it})}.$$

Parameters in the model were estimated at the species level following a Bayesian approach that allowed us to consider the different sources of uncertainty associated with the data and gave us flexibility when including fixed and random effects (Clark 2005, Gelman and Hill 2007). The hazard was estimated for each time step, h_t, from a gamma distribution with noninformative parameter values, $h_t \sim \text{gamma}(0.01, 0.01)$. This intrinsic mortality rate reflects the temporal variability in mortality that is not accounted for by the risk function, μ_{it}. The risk, μ_{it}, was estimated as a function of the covariates included in the analysis, $\mu_{it} = \mathbf{X}_{it}\mathbf{B}$. $\mathbf{X}_{it}$ is the matrix of covariates associated with each seedling i at each time t. $\mathbf{B}$ is the vector of fixed effect coefficients associated with each covariate. These coefficients were estimated from

normal distributions with noninformative parameter values, $\mathbf{B}_k \sim \text{normal}(0, 10\,000)$. We tried several combinations of covariates (seed or seedling size, soil moisture, light level, soil nutrients for both field and greenhouse experiment; habitat, region, and fungicide treatment for the field experiment; and soil source, region, and soil sterilization treatment for the greenhouse experiment). Random effects (e.g., year, stand, and plot for the field experiment, and bench for the greenhouse) were also included in the different models we tried. We then selected the model that best predicted the data across species based on the DIC (deviance information criterion; Spiegelhalter et al. 2000). For the final model, the covariates included in the analysis of the field data were: seedling size, soil moisture, light, habitat type (open vs. canopy), and region × fungicide treatment (north–south and fungicide-control combinations; for this covariate, we only report results for the control group as the fungicide treatment did not have an effect). For the greenhouse experiment, the covariates included were: seed mass, soil moisture, light, soil source (species), and treatment (non-sterile vs. sterile). To test the difference between habitats and regions for the field experiment and treatments and soil sources for the greenhouse experiment, we estimated the difference between associated parameters (e.g., open-canopy or sterile–non-sterile); a significant result would then have a 95% credible interval around the posterior mean of the difference that does not include zero.

As differences in survival are ecologically more meaningful than model parameter comparisons, we obtained predicted survival from the parameter values in our field- and greenhouse-based models. Predicted survival to time t, $\hat{S}_t$, was estimated as part of the Markov chain Monte Carlo simulation once the parameters had converged:

$$\hat{S}_t = \exp\left(-\int_1^t h\right)^{\exp(\mu_t)}.$$

This procedure allowed us not only to consider the variability inherent in each parameter (their variances), but also the correlations between parameters (their covariances). Predicted survival values were used to assess whether there were differences in how species responded to habitat (canopy vs. open) and region (north vs. south) for the field experiment, and to soil source groupings (conspecific vs. pooled heterospecific groupings) and light levels (low vs. high) for the greenhouse experiment.

Models were run for each species separately in OpenBUGS 1.4 (Thomas et al. 2006); simulations (three chains) were run until convergence of the parameters was ensured (~50 000 iterations) and then run for another 25 000 iterations from which posterior parameter values and predicted survival were estimated. The Cox survival model analyzes risk of mortality, so we report the posterior values for the fixed effect coeffi-

cients (B_k) multiplied by −1 to reflect their effect on survival instead.

Determination of plant–soil feedbacks in the greenhouse experiment.——In order to test for the effect of plant–soil feedbacks, we assessed seedling survival between soil sources in non-sterile soil. Plant–soil feedbacks were deemed negative when conspecific soil was detrimental relative to heterospecific soils (individual and pooled soils) and were deemed positive when conspecific soil was beneficial relative to heterospecific soils. In order to test whether the mechanism causing the PSF was biotic or abiotic, we determined whether the PSF occurred only when comparing non-sterile soil sources (biotic agent) or in both non-sterile and sterile soils sources (abiotic agents). If the mechanisms causing the PSF were determined to be biotic, we compared survival between non-sterilized and sterilized soils to determine if the biotic agents were occurring in conspecific and/or heterospecific soil.

RESULTS

Field survival

Seedling hazard varied among species, but the general pattern showed peak mortality a few weeks after planting, and a decline as the season progressed (Appendix E). The effect of initial seedling size, soil moisture, and light availability also varied among species (see Appendix F for the full table of parameter values). Of 18 species planted in the field experiment, 15 species had greater survival with larger initial size, and most species experienced enhanced survival under higher soil moisture. In addition, most species had higher survival in lower light plots (PAR in understory plots = 13.9 ± 3.7, and in gap plots, PAR = 47.3 ± 3.7 μmol photons·m²·s; mean ± SD).

After accounting for light and soil moisture, seven species had significantly higher survival under canopy relative to open habitats at the northern site (Fig. 2a). Overall survival of migrant species was similar to or higher than survival of all local species (Fig. 2b). For instance, in canopy plots at the northern stands seven of the southern species/populations (*A. rubrum*, *A. saccharum*, *C. glabra*, *C. ovata*, *L. tulipifera*, *Q. alba*, and *R. pseudoacacia*) had survival rates significantly higher than those of three of the local species/populations (*A. rubrum*, *B. papyrifera*, and *P. banksiana*; 95% predicted survival intervals do not overlap). Southern *B. papyrifera*, *N. sylvatica*, and *Q. rubra* also had significantly higher survival in northern plots than northern *A. rubrum* and *B. papyrifera*. In addition, southern *C. glabra* had higher survival in the north than northern *A. saccharum*, and southern *A. saccharum* had higher survival in the north than northern *A. saccharum* and *P. strobus*. Lastly, there were no southern species whose survival was significantly lower in the northern canopy plots than any of the local species (Fig. 2b).

When just comparing canopy habitats, two of the local tree species (*P. banksiana* and *P. strobus*) had

significantly greater survival in the north than the south (Fig. 2b). Among the group of potential migrants, *L. tulipifera* and the southern populations of *A. rubrum* and *B. papyrifera* had greater survival in northern plots, whereas *Q. velutina* upper and lower ranges and *C. ovata* had greater survival in southern plots (Fig. 2b).

PSF in the greenhouse experiment

For small-seeded species, hazard curves show a peak in mortality around week 3–4 and in some species there were also multiple peaks of relatively higher mortality over the course of the experiment (Appendix E). Large-seeded species (*C. glabra*, *Q. rubra*, and *Q. velutina*) tended to have nearly no change until the end of the experiment, which was around the time these seedlings began to lose their cotyledon support (S. McCarthy-Neumann, *personal observation*).

Covariates also had a varying effect on the study species (see Appendix F for the full table of parameter values). Seed mass significantly affected survival for only two species (*L. tulipifera* and *R. pseudoacacia*). Survival was not significantly influenced by differences in soil moisture for any species. Survival increased with light in four of the smaller seeded species (*A. rubrum*, *A. saccharum*, *P. serotina*, and *R. pseudoacacia*), whereas light did not affect survival of the large-seeded species (*C. glabra*, *Q. rubra*, and *Q. velutina*), or *L. tulipifera*.

Plant–soil feedbacks.——Sterilization of soil biota through gamma irradiation and efforts to minimize cross contamination appeared to have been effective. We assessed mycorrhizal fungal colonization for all harvested seedlings and found zero colonization in the sterilized field or peat soil treatments (S. McCarthy-Neumann and I. Ibáñez, *unpublished manuscript*). Additionally, dying seedlings in the non-sterile field soil often experienced classic damping-off symptoms.

Soil source and sterilization treatments had varying effects on seedling survival (see Appendix F for the full table of parameter values). Soil source affected survivorship in seven species when comparing non-sterile soil sources. The incidence of PSF varied depending on the region or origin and on the light treatment. When comparing southern soils, three species (*P. serotina*, *Q. rubra*, and *R. pseudoacacia*) experienced negative PSF, meaning that conspecific soil was detrimental relative to pooled heterospecific soils, but only in low light (Fig. 3a). Only one species experienced negative PSF at both high and low light (*L. tulipifera*), and one species (*Q. velutina*) experienced positive PSF, manifesting higher survival in its own soil in comparison with pooled heterospecific soils at low light. Comparisons between regions, southern conspecific soil, and northern heterospecific soils (Fig. 3b), show the same pattern except for two species: *Q. velutina*, for which southern conspecific soils did not seem to enhance survival over northern heterospecific soils, and *A. rubrum*, which experienced negative PSF. For the three species that we have northern soil sources, negative PSF only occurred for
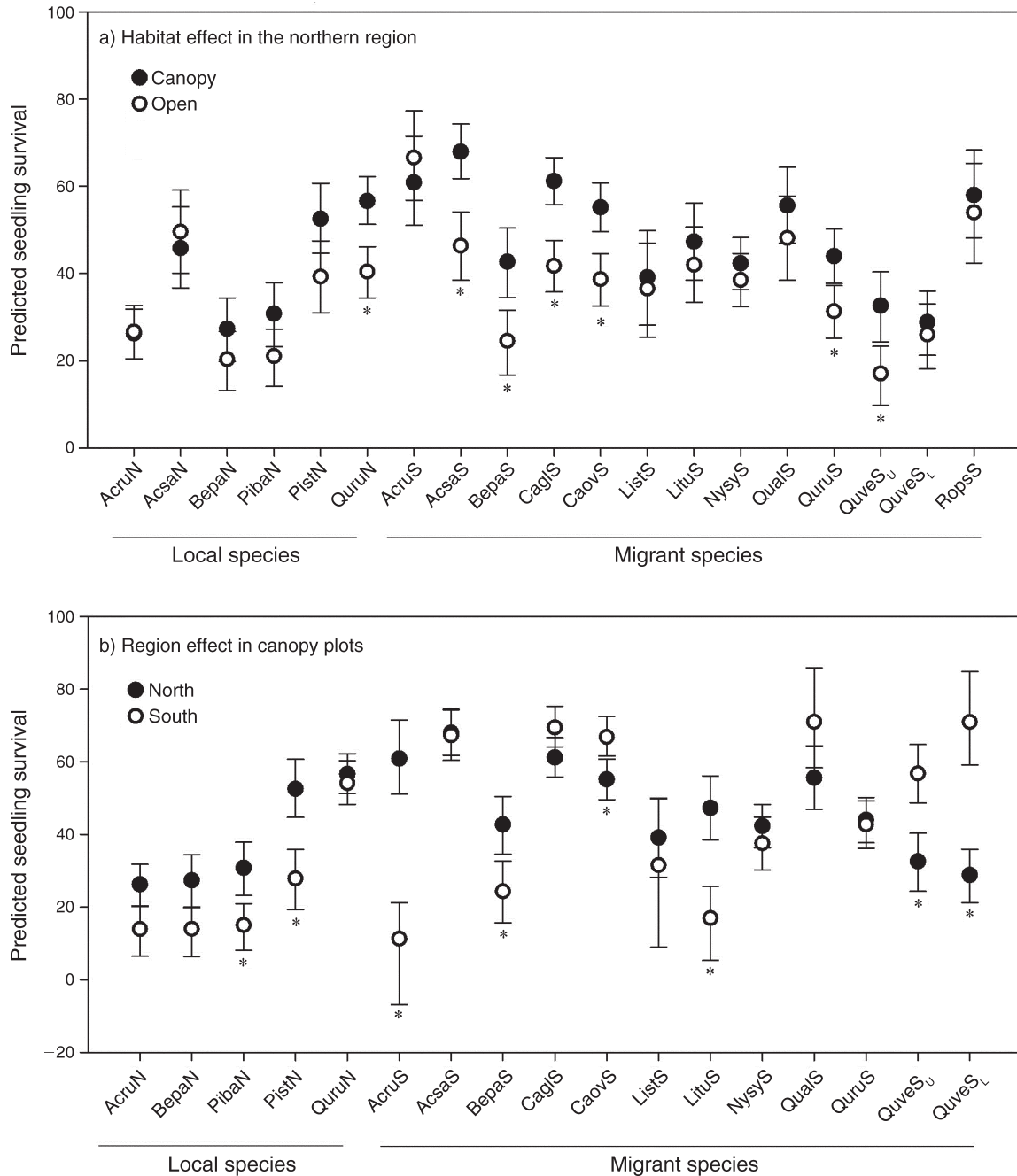
FIG. 2. Predicted seedling survival (mean and 95% prediction intervals) for each field study species after 10 weeks based on model parameters: (a) in canopy vs. open habits in northern sites, and (b) in north vs. south regions in canopy habitats. Intervals that do not overlap indicate statistically significant differences between habits or regions and are indicated by an asterisk. For species code key see Table 2; seed source abbreviations are N, northern, and S, southern.
* $P > 0.05$.

A. saccharum seedlings at low light (Fig. 3c). These PSF interactions were species-specific (e.g., the heterospecific species culturing the soil mattered) because all species (except *Q. rubra*) that had an overall PSF between conspecific and pooled heterospecific soils did not have significant differences with each individual heterospecific soil (Table 3, Fig. 4).

Besides the strong influence that conspecific soils had on survival, there were two other important soil source trends. Survival was greatest for five out of eight species in *A. saccharum* soil (Appendix F: Fig. F1); for most species this was due to favorable abiotic effects and occurred regardless of sterilization treatments (Table 3; Appendix F: Fig. F1). In general, seedlings also had
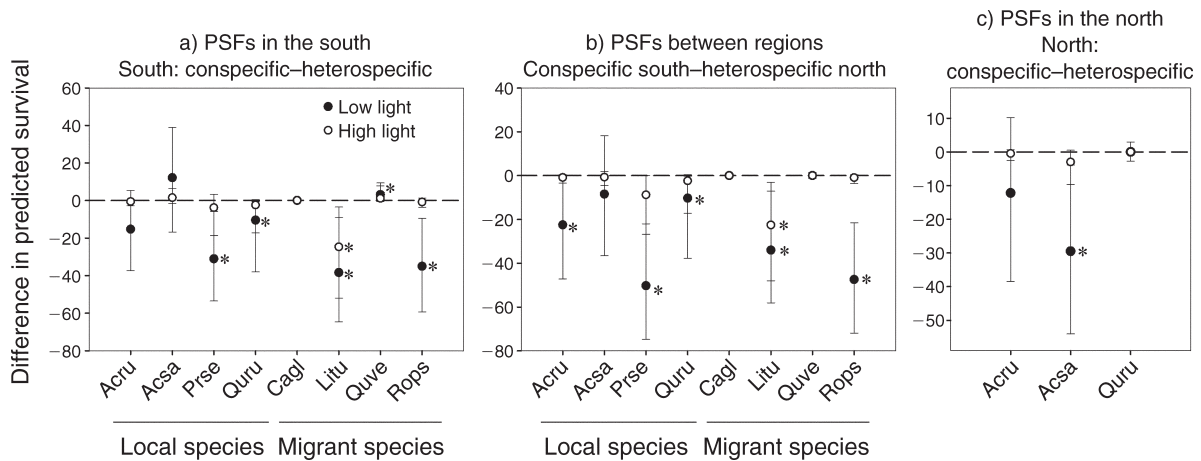
FIG. 3. Plant–soil feedback (PSF) effect at both low and high light (predicted survival in conspecific–pooled heterospecific non-sterile soil sources; mean and 95% CI): (a) in the southern range, (b) during range expansion, and (c) in the northern range. Confidence intervals that do not overlap indicate statistically significant differences in predicted survival between soil source treatments, as indicated by asterisks. For species code key see Table 2.
  * $P > 0.05$.

better survival in northern than southern *Q. rubra* soil, which may have been primarily driven by a release from soil pathogens associated with the southern-collected *Q. rubra* soil (Table 3; Appendix F: Fig. F1).

Biotic and abiotic effects of PSF.—When comparing sterile vs. non-sterile soils to discriminate between the biotic vs. abiotic nature of the PSF, we found that most PSF were caused by the negative effects of soil biota in conspecific soil (Table 3). *Q. velutina*, however, experienced positive PSF between conspecific and some heterospecific soils, which was due to the negative effects of soil biota in the heterospecific soils. There were also three instances (with *A. rubrum* and *Q. rubra* seedlings) in which a negative PSF between a conspecific

and heterospecific soil was due to both the negative effects of soil biota in the conspecific soil and the positive effects of soil biota in the heterospecific soil. In addition, for *R. pseudoacacia*, we could only determine that the negative PSF between conspecific and northern *A. saccharum* soils was mediated by soil organisms, but we could not isolate whether the effects were in the conspecific or heterospecific soils. There were very few instances where the PSF was mediated by soil abiotic properties (Table 3). Among the southern soils, only *R. pseudoacacia* experienced negative abiotic PSF in comparison with *A. rubrum* and *A. saccharum* soils. Negative abiotic PSF also occurred when comparing southern conspecific soil with northern *A. saccharum*

TABLE 3. Summary of the results indicating the occurrence of PSF (plant–soil feedbacks, positive or negative) and the mechanisms causing them, biotic or abiotic.

Species†	Southern soils								Northern soils		
	Acru	Acsa	Cagl	Litu	Prse	Quru	Quve	Rops	Acru	Acsa	Quru
Acru	own soil	PSF− Biotic−		NA				PSF− Biotic +, −			
Acsa		own soil	NA	NA	NA	NA	NA	NA			
Cagl			own soil	NA	NA		NA	NA			
Litu		PSF− Biotic−	NA	own soil	NA		NA	NA			PSF− Biotic−
Prse		PSF− Biotic−	NA	NA	own soil		PSF− Biotic−			PSF− Abiotic	PSF− Biotic−
Quru	PSF− Biotic−	PSF− Biotic−	PSF− Biotic+, −	NA	PSF− Biotic−	own soil	PSF− Biotic+, −	PSF− Biotic−	PSF− Biotic−	PSF− Biotic−	PSF− Biotic−
Quve		PSF+ Biotic−		NA	PSF+ Biotic−	PSF+ Biotic−	own soil				
Rops	PSF− Abiotic	PSF− Abiotic	NA	NA	NA			own soil	PSF− Abiotic	PSF− Biotic‡	PSF− Abiotic

Notes: Following Appendix F: Table F2 and Fig. F1, only statistically significant results indicated by nonoverlapping 95% CI are presented. Empty cells indicate that no significant PSF occurred for seedlings of this species that were planted in that soil. NA, not applicable; seedlings of this species were not planted in that soil.
  † For species code key, see Table 2.
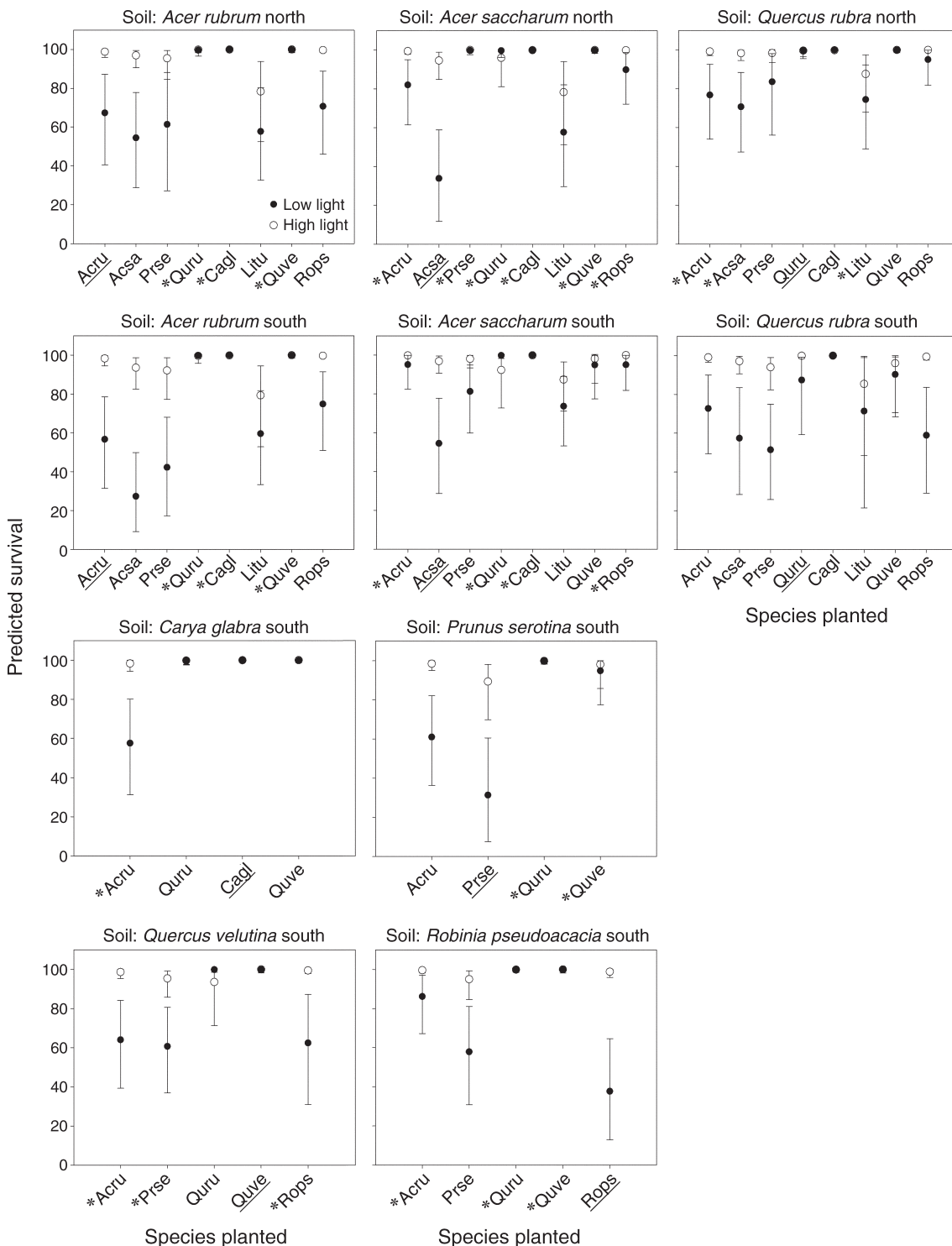 ‡ We were not able to determine the type of biotic effect.

Fig. 4.   Predicted seedling survival (mean and 95% PI) after 10 weeks in each soil source for each greenhouse study species based on model parameters from non-sterile soil. Conspecific seedling species codes are underlined. Asterisks indicate statistically different survival between heterospecific and conspecific seedlings in a given soil source based on nonoverlapping 95% PI. For each species, the predicted intervals that do not overlap indicate statistically significant differences in survival between low and high light treatments.

soils (*P. serotina* seedlings), and northern *A. rubrum* and *Q. rubra* soils (*R. pseudoacacia* seedlings).

DISCUSSION

In this study, we investigated the role that plant–soil feedbacks (PSF) may play in determining tree range expansion in response to global warming. We found that field survival for most of the potential migrant tree species was similar or even higher than those of the local community. This finding suggests that these species may be able to establish in areas beyond their current distributional ranges. In the greenhouse experiment, we were able to assess the ubiquitous soil mediated interactions between tree adults and seedlings that may underlie patterns of survival. The majority of species grown in canopy-specific soils experienced strongly negative conspecific feedbacks mediated by soil biota. The effects of soil biota and plant–soil feedbacks on survival were restricted to low-light conditions for the majority of our study species (Figs. 3 and 4). For many species, soil biota in northern soils had less of an effect on survival, regardless of whether a species was local or migrant. Thus, southern populations of both local and migrant tree species may experience a release from soil biota effects during their migration northwards that may contribute to their successful establishment in new regions.

The role of plant–soil feedbacks in tree range expansion

Although other factors besides PSF (e.g., propagule availability) will also affect the success and rate of tree range expansion, our results provide additional support to previous work indicating that plant species may have better performance in an expanded range (e.g., Engelkes et al. 2008, van Grunsven et al. 2010, Callaway et al. 2011). This finding is similar to the often-reported results for exotic species invading a new area (Reinhart and Callaway 2006, Inderjit and van der Putten 2010). The greenhouse experiment allowed us to specifically evaluate the role of PSF in post-dispersal establishment potential of tree species into northern regions. For two out of four potential migrant species in the study (*L. tulipifera* and *R. pseudoacacia*), we recorded higher survival in northern soils. Better survival in northern soils also occurred for *A. rubrum*, *P. serotina*, and *Q. rubra* (species whose range already extends throughout the region), as they were also released from what seems to be a more virulent pathogen community in the south. Range expansion may occur at a faster rate for *R. pseudoacacia* and the southern populations of *P. serotina* because of the relatively large release from negative PSF in northern heterospecific soils (>50%; Fig. 3b). For *Q. rubra*, even though survival is better in all tested northern soils than in the southern conspecific soil, the overall effect on survival is much smaller (~10%; Fig. 3b) and thus in relative terms may result in slower range expansion. Out of our study species, *C. glabra*, *Q. velutina*, and the southern populations of *A. saccharum*

may all experience slower relative range expansion for different reasons. *C. glabra* may have slow range expansion because soil biota and PSF do not appear to influence survival in the seedling establishment phase. However, *Q. velutina* and southern populations of *A. saccharum* may have even slower or impeded range expansion due to PSF processes because seedling survival is lower in northern soils for these species.

The role of plant–soil feedbacks on tree seedling establishment

We were able to determine both the spatial ("home-south" vs. "away-north") and specificity ("conspecific" vs. "heterospecific") effect of PSF by testing PSF for multiple species in each others' cultured soils. In our greenhouse study, PSF appear to be widespread and primarily driven by negative biota from soil near conspecific adult trees (Table 3), suggesting that dispersal away from conspecific adults is advantageous for most species. In addition, when comparing recruitment in soils collected under different tree species (the specificity of feedbacks), we found that in some soils (*A. saccharum*, *P. serotina*, and *R. pseudoacacia* soils), conspecific seedlings were at a disadvantage relative to heterospecifics (Fig. 4). This result is likely due in some cases (e.g., *P. serotina*) to intrinsic differences in survival among species (e.g., statistically higher heterospecific survival relative to conspecific seedlings only occurred for large-seeded species). However, the higher survival by small-seeded heterospecific species in *A. saccharum* and *R. pseudoacacia* cultured soils indicate that these soil mediated feedbacks between tree adults and seedlings are somewhat species-specific. This result is similar to findings by Konno et al. (2011), in which a ubiquitous seedling pathogen can attack a wide range of host species, but virulence is stronger for conspecific than heterospecific individuals.

We were able to focus on both biotic and abiotic PSF because we took the unconventional approach of not trying to eliminate abiotic differences among soil sources (but see Bezemer et al. 2006). The majority of the negative conspecific feedbacks were due to soil biota, whereas the positive heterospecific feedbacks were primarily due to abiotic factors. We do not believe that the negative biotic feedbacks in our study were actually due to an increase in the concentration of nutrients in sterile soil (Powlsen and Jenkinson 1976) because we did not find any soil chemistry differences between sterile and non-sterile soils.

Heterospecific seedlings often survived best in *A. saccharum* soils, whereas *A. saccharum* seedlings had low survival in all soils (both their own and heterospecific soils; Appendix F: Fig. F1). The decline of *A. saccharum* in eastern North America is well-documented (Siccama et al. 2007) and thought to be due to a reduction in soil calcium status (Juice et al. 2006). However, our results suggest that the sensitivity of *A. saccharum* to soil source (the most negatively affected species by rank in five of

six soils) may also contribute to its declining abundance, and there is evidence that *A. saccharum* seedlings are sensitive to mortality from a fungus in the genus *Rhizoctonia* (Cleavitt et al. 2011).

Lastly, we found *R. pseudoacacia* had reduced performance in conspecific soils taken from their expanded range (Figs. 3 and 4). Effects of conspecific soil on survival were due to abiotic factors, whereas effects of growth were due to soil biota (S. McCarthy-Neumann and I. Ibáñez, *unpublished data*). These results suggest that for *R. pseudoacacia*, any release from enemies found in their native range and subsequent enhanced performance in their expanded and invaded ranges (e.g., Callaway et al. 2011) may be temporary and last only until *R. pseudoacacia* adults are present. Furthermore, heterospecific seedlings benefit from growing in soils cultured by *R. pseudoacacia*.

Plant–soil feedbacks and the light environment

Seedling survival is often thought to be higher in high light areas due to better carbon balance (Canham et al. 1999) and decreased disease (Augspurger 1990). However, our field results suggest that for many species, regardless of their shade tolerance, these sites may be hostile environments because they have lower levels of inorganic nitrogen (Appendix C) and higher levels of desiccation and possibly predation and herbivory.

The greenhouse experiment allowed us to explicitly investigate the complex interaction between light and the effect of PSF on seedling survival, as other factors such as soil moisture and nutrients and the lack of predation or herbivory remained the same. In general survival was higher at high light levels (Fig. 4). Results also indicate that PSF may be restricted to low light environments for most species and may provide an additional mechanism for explaining recruitment dynamics in temperate forests other than the classic shade-tolerance niche partitioning model (Kobe et al. 1995, Kobe 1999; Fig. 3). For instance, tree species classified as shade intolerant often have establishment restricted to high light areas. Reduced establishment in some species may not be due to physiological carbon balance requirements, but rather due to their susceptibility to soil pathogens in low light conditions. Consequentially, potential migrant species with strong negative conspecific feedbacks may be able to establish, at least in the short term, in shadier conditions in their expanded range, as they may be released from soil biota associated with conspecific adults.

The difference in seedling response to low light between the field (where survival was reduced in gap plots) and greenhouse experiments (where soil biota and plant–soil feedbacks were restricted to low light environments with corresponding reductions in survival) may be due to a variety of reasons. First, although the majority of species in the field had better survival in plots with lower light, the benefit derived from these canopy plots occurred for most species even when light

and soil moisture were accounted for in the analysis. Thus, other factors associated with these habitats such as soil nutrient levels or herbivory and predation may have been more important than irradiance. Additionally, canopy plots experienced relatively moderate to high light levels ($\sim$13.9 $\pm$ 3.7 µmol photons·m^2·s PAR) relative to the low light treatment in the greenhouse ($\sim$0.5 $\pm$ 0.2 µmol photons·m^2·s PAR). Thus, seedlings in the field canopy plots may not have experienced low mortality due to soil biota and PSF because these effects were found to be restricted to lower light levels in the greenhouse.

Conclusions

The complementarities of the field and greenhouse experiments provided us with a comprehensive understanding of the role of plant–soil feedbacks (PSF) in seedling establishment and tree range expansion. The field experiment produced realistic establishment rates that we can use to compare species and inform vegetation models and management practices, while the greenhouse experiment allowed us to explore the mechanisms behind tree seedlings responses to PSF in the context of tree range expansion. This study reveals that migrant tree species can colonize and may even have better short-term survival as they migrate northwards due to a lack of conspecific adults (and the resulting negative PSF) in these northern communities. The current findings also suggest biotic mediated plant–soil feedbacks may enhance light gradient partitioning among tree species ultimately influencing succession and species coexistence in forest communities. Our results illustrate the complexity of the establishment process and the different environmental filters individuals experience (Harper 1977, Gurevitch et al. 2002), as well as give us a better understanding of the potential role of PSF in tree seedling establishment in response to climate change. The ultimate outcome for whether a seedling successfully establishes will depend on the complex interaction of all of those filters, and only by investigating and quantifying their effects will we be able to reliably predict shifts in species distributional ranges.

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SUPPLEMENTAL MATERIAL

Appendix A

Seed origins for field transplant and greenhouse experiments (*Ecological Archives* E093-245-A1).

Appendix B

Light and soil moisture measurements for field transplant and greenhouse experiments (*Ecological Archives* E093-245-A2).

Appendix C

Soil resource measurements for field transplant and greenhouse experiments (*Ecological Archives* E093-245-A3).

Appendix D

Greenhouse experimental design: soil sources each study species was grown in and number of seedlings allocated to these soil source treatments (*Ecological Archives* E093-245-A4).

Appendix E

Hazard curves over 10-week periods for field transplant and greenhouse species (*Ecological Archives* E093-245-A5).

Appendix F

Parameter estimates (mean posterior values and 95% CI) for fixed-effects coefficients: β parameters in the field transplant, and greenhouse studies (*Ecological Archives* E093-245-A6).