



Variation in plant–soil interactions among temperate forest herbs

Jared J. Beck 

Received: 3 November 2020 / Accepted: 12 August 2021 / Published online: 23 August 2021
© The Author(s), under exclusive licence to Springer Nature B.V. 2021

Abstract Antagonistic interactions between plants and soil biota promote species diversity in many plant communities but little is known about how these plant–soil interactions influence herbaceous species in temperate forests. To assess the potential for soil biota to affect the growth of forest herbs, I conducted a greenhouse experiment in which seedlings of nine focal herb species common in Wisconsin (USA) forests were grown in soil derived from conspecific and heterospecific plants. This soil origin treatment was crossed with a subsequent treatment in which half of the soils were pasteurized to eliminate soil biota. The presence and origin of soil biota had variable effects on plant growth among the nine focal species. *Thalictrum dioicum*, *Elymus hystrix*, and *Solidago flexicaulis* growth were inhibited by the presence of soil biota in unpasteurized soils. *Thalictrum dioicum*

seedlings grown in conspecific, unpasteurized soil accumulated 30% less biomass than seedlings grown in heterospecific, unpasteurized soil indicating that host-specific effects of microbial pathogens restrict seedling growth. Similarly, *E. hystrix* seedlings were 11% smaller in conspecific-trained soils. The remaining herb species showed no significant response to experimental treatments manipulating soil biota. These variable growth responses highlight the potential for differences in plant–soil interactions among plant species to influence local plant distributions and community dynamics. Janzen–Connell effects, like those observed in *T. dioicum* and *E. hystrix*, could promote coexistence among certain species and contribute to high local plant diversity in temperate forest understories.

Keywords Plant–soil feedbacks · Janzen–Connell effects · Temperate forest herbs · *Thalictrum dioicum* · *Elymus hystrix*

Communicated by Timothy Bell.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s11258-021-01173-x>.

J. J. Beck (✉)
Department of Botany, University of Wisconsin-Madison,
430 Lincoln Drive, Madison, WI 53706, USA
e-mail: jared.j.beck@gmail.com

J. J. Beck
Negaunee Institute for Plant Conservation Science,
Chicago Botanic Garden, 1000 Lake Cook Road,
Glencoe, IL 60022, USA

Introduction

Plant–soil interactions play a fundamental role in shaping the composition and diversity of plant communities (Ehrenfeld et al. 2005; Bever et al. 2010). Apart from responding to variation in soil texture, soil fertility, and the community of microorganisms

present in soil, plants modify both abiotic and biotic soil properties in ways that influence subsequent plant growth or survival (Reynolds et al. 2003; Bennett and Klironomos 2019). Positive plant–soil feedbacks occur when plants alter biotic and abiotic soil properties in ways that promote the growth and survival of other, often conspecific, neighboring plants (Bever et al. 1997; Van der Putten et al. 2013). These positive feedbacks may result from mutualistic relationships with microorganisms or the creation of favorable environmental conditions that promotes the survival and growth of conspecific individuals (Bennett and Klironomos 2019). While positive feedbacks have been observed in some plant communities, negative plant–soil feedbacks appear to be far more common (Kulmatiski et al. 2008). Negative plant–soil feedbacks are the product of plant–soil interactions that are detrimental to plant growth and survival, often impairing the growth of conspecific individuals (Bever et al. 1997; Van der Putten et al. 2013). These negative feedbacks may result from the depletion of soil nutrients that limit the growth of conspecific plants or from the accumulation of greater densities of pathogens or herbivores that inhibit conspecific growth or survival (Ehrendfeld et al. 2005; Mordecai 2011; Bever et al. 2015; Liu et al. 2015; Bennett and Klironomos 2019).

Density-dependent growth and mortality caused by pathogens has been implicated as a potentially important mechanism facilitating coexistence and maintaining species diversity in many plant communities (Janzen 1970; Connell 1971; Wright 2002; Mordecai 2011; Terborgh 2012; Bever et al. 2015; Crawford et al. 2019; Ke and Wan 2019). The accumulation of pathogens with host-specific effects at high population densities or near conspecific adults can cause increased mortality among conspecific individuals or alter competitive dynamics in ways that stabilize multi-species coexistence (Janzen 1970; Connell 1971; Bonanomi et al. 2005; Bever et al. 2015; Ke and Wan 2019; Spear and Broders 2021). Natural enemies may play a particularly important role in tropical forests (Givnish 1999; Wright 2002; Terborgh 2012; Comita et al. 2014; LaManna et al. 2017) where pathogenic fungi and other soil pathogens cause density-dependent growth and mortality in many species (Bell et al. 2006; Bagchi et al. 2010, 2014; Maron et al. 2016; Johnson et al. 2017). Negative plant–soil feedbacks are also prevalent

among herbaceous plants in temperate grasslands (Klironomos 2002; Petermann et al. 2008; Fitzsimons and Miller 2010; Reinhart 2012) and temperate forest trees (Packer and Clay 2000; Johnson et al. 2014; Bennett et al. 2017; Lankau and Keymer 2018). Despite growing recognition that interactions with soil biota influence the composition and diversity of many plant communities, relatively little is known about the prevalence of plant–soil feedbacks among herbaceous understory species in temperate forests (Whigham 2004; Comita et al. 2014; but see Shannon et al. 2012; Smith and Reynolds 2015; Sweet and Burns 2017).

Herbaceous taxa represent more than 80 percent of plant species in temperate forests with high densities and diversities of these herbs co-occurring within small areas (Gilliam 2007; Peet et al. 2014). Spatial resource partitioning and environmental heterogeneity are the most widely cited mechanisms facilitating coexistence among forest herbs (Bell et al. 2000; Bartels and Chen 2010; Beatty 2014; Catella et al. 2019; Beck and Givnish 2021). Forest herb distributions vary in response to environmental variation at a variety of spatial scales (Curtis 1959; Struik and Curtis 1962; Beatty 2014; Peet et al. 2014). At local scales, differential plant responses to fine-scale variation in soil depth (Bratton 1976; Beck and Givnish 2021), soil fertility and soil moisture (Collins et al. 1984; Crozier and Boerner 1984; Vellend et al. 2000), microtopography (Beatty 1984; Peterson et al. 1990), light availability (Anderson et al. 1969; Thompson 1980), and other abiotic factors can promote coexistence via spatial resource partitioning. Yet, spatial resource partitioning cannot account for coexistence among many functionally similar species at small spatial scales (Gilliam 2007; Beatty 2014; Peet et al. 2014; Beck 2020). Potential interactions among herbaceous plants and soil biota could shape many understory community dynamics and potentially promote local coexistence, but these require further study in temperate forest understories (Whigham 2004; Comita et al. 2014). I hypothesize that such interactions, especially antagonistic interactions with soil pathogens, play an important but previously unappreciated role in shaping local plant distributions and maintaining herbaceous plant diversity in temperate forests.

Apart from the prevalence of negative plant–soil feedbacks in other temperate ecosystems (Klironomos 2002; Bell et al. 2006; Kulmatiski et al. 2008; Petermann et al. 2008; Fitzsimons and Miller 2010),

negative host-specific impacts appear to be common among the temperate forest herbs. Empirical studies have documented evidence of negative plant–soil feedbacks among a handful understory plant species (Shannon et al. 2012; Smith and Reynolds 2015; Sweet and Burns 2017; Ma et al. 2019). Moreover, apparently host-specific pathogens, typically fungal pathogens, have been described for numerous temperate herbs (Tiffany et al. 1984). In some cases, different strains of the same fungal pathogen differentially infect cryptic variations of the same species (Parker 1985; Kartzinel et al. 2016). These infections, in turn, can affect the growth and survival of forest herbs (Wennstrom and Ericson 1994). Plant–soil interactions also mediate the success of species’ invasions in temperate forest understories (Shannon et al. 2012, 2014; Smith and Reynolds 2012). For example, *Alliaria petiolata*’s capacity to disrupt mycorrhizal associations contributes to its ability to successfully invade temperate forest understories and displace native herbs and tree seedlings (Prati and Bossdorf 2004; Burke 2008; Wolfe et al. 2008; Lankau 2011; Hale et al. 2016). Nevertheless, assessing how plant–soil interactions shape local herb distributions and diversity in temperate forests requires further examination.

To explore how plant–soil interactions influence the growth of temperate forest herbs, I conducted a greenhouse experiment designed to assess plant–soil interactions among nine herbaceous plant species common to North American temperate deciduous forests. Seedlings of each focal species were grown in soils trained by conspecific and heterospecific plants. These soils were then either pasteurized to remove soil biota or left untreated (unpasteurized). If antagonistic interactions between plants and soil microbes promote herbaceous plant diversity, I expected to observe reduced seedling growth and increased mortality when exposed to soil microbial communities trained by conspecific plants. In contrast, if mutualistic interactions are more important, I expected greater seedling growth in unpasteurized soils or conspecific, unpasteurized soils if host-specific mutualists are responsible for the improved seedling performance.

Materials and methods

Focal species

This study focuses on nine native herbaceous plant species common to woodlands and forests of eastern and central North America. To select focal species, I first identified a suite of ~ 20 candidate species representative of the evolutionary lineages, life histories, and physiological characteristics of many forest herbs (Bierzzychudek 1982; Whigham 2004). From the list of candidate species, I selected the nine focal species for this experiment because they were common within the study area where I planned to collect field soil and germinated in sufficient numbers to perform the experiment (Table 1). In fall 2018 and early 2019, I conducted a two-phase greenhouse experiment to characterize the strength and prevalence of plant–soil feedbacks among these nine focal species (Fig. 1). In the first phase of the experiment, I conditioned field-collected soil by allowing microbial communities to acclimate to host plant species. In the second phase of the experiment, I treated these soils to eliminate or retain soil microbial communities and then used these conditioned soils as substrates to examine plant–soil feedbacks. This two-phase experimental approach was chosen to assess plant responses to soil biota independent of associations between plant density and microbial abundance in natural communities that would be unavoidable without first conditioning the soil (see Brinkman et al. 2010).

Conditioning phase

I obtained seeds from Prairie Moon Nursery (Winona, Minnesota, USA) and followed their directions for germinating seeds. Seeds of seven species received a 60-day cold-moist stratification treatment in sterile sand before being sown in germination media. The germination media comprised peat moss mixed with fine vermiculite, perlite, and dolomite particles. One other species required 15-days of cold-moist stratification (*H. glutinosum*). The last species required no germination treatment (*E. hystrix*). When true leaves began to emerge (approximately one week after germination), I transplanted seedlings into autoclaved 0.5 L pots filled with field-collected soil to begin the soil conditioning phase of the experiment. I collected field soil from two ~ 4 ha forest sites within the

Table 1 List of focal species included in the plant–soil feedback experiment and summary of ecological characteristics including flowering phenology, photosynthetic phenology (season during which the species is most photosynthetically active), and mode of seed dispersal

Species	Family	Flowering phenology	Leaf phenology	Dispersal mode
<i>Ageratina altissima</i> (L.) R. M. King and H. Rob	Asteraceae	July–October	Late summer	Wind-dispersed
<i>Aquilegia canadensis</i> L.	Ranunculaceae	May–July	Early summer	Ballistic
<i>Elymus hystrix</i> L.	Poaceae	July–September	Late summer	Gravity
<i>Geranium maculatum</i> L.	Geraniaceae	May–June	Early summer	Ballistic
<i>Hylodesmum glutinosum</i> (Muhl. ex Willd.) H. Ohashi and R. R. Mill	Fabaceae	June–August	Late summer	Epizoochorous
<i>Polemonium reptans</i> L.	Polemoniaceae	May–July	Early summer	Gravity
<i>Polygonum virginianum</i> L.	Polygonaceae	July–September	Late summer	Ballistic
<i>Solidago flexicaulis</i> L.	Asteraceae	August–October	Late summer	Wind-dispersed
<i>Thalictrum dioicum</i> L.	Ranunculaceae	April–June	Early summer	Gravity

Baraboo Hills, the largest contiguous complex of forested habitats in southern Wisconsin and a regional biodiversity hotspot supporting > 1300 vascular plant species (Lange 1998). Forest stands where the soil was collected were dominated by oaks (*Quercus rubra* and *Quercus alba*) and maples (*Acer rubrum* and *Acer saccharum*) with *Prunus serotina*, *Carya cordiformis*, *Carya ovata*, *Fraxinus americana*, *Tilia americana*, *Populus grandidentata*, and *Ostrya virginiana* also present in the canopy. Soils within these stands were classified as silt loams. I collected bulk soil samples (~ 2 L) from 20 locations spaced evenly across the two forest sites. I also collected targeted soil samples immediately adjacent to each focal species using a 2.5 cm soil corer (10–15 cores per species). Field-collected soils were homogenized in a large plastic tub and stored at 4 °C for 4–6 weeks before beginning the soil conditioning phase. Refrigeration reduces microbial activity, preventing shifts in the composition of soil biota between the time of field collection and when seedlings are transplanted (Lankau and Keymer 2018). The homogenized, field-collected soil was then equally distributed into the 0.5 L pots before seedlings were transplanted. I aimed for 30 training pots per focal species, but limited germination led to smaller sample sizes for *A. canadensis* ($N = 22$ training pots),

G. maculatum ($N = 18$), and *T. dioicum* ($N = 25$). Seedlings were watered daily and allowed to grow for 2–3 months (70–96 days depending on timing of germination).

Experiment phase

After the soil conditioning period, I removed all aboveground plant material and substantial belowground material (e.g., large roots and rhizomes) but did not remove fine roots from the training pots. I then divided the trained soil from each conditioning pot in half and randomly selected one subset to be pasteurized using an autoclave. Soil samples from different training pots were kept separate throughout the experiment phase. Soil subsets assigned to the pasteurization treatment were autoclaved for 45 min at 121 °C. I monitored temperature in a subset of autoclaved soil samples. Soil temperatures in all monitored samples reached at least 100 °C for at least 30 min. This combination of temperature and duration is sufficient to kill nearly all soil microorganisms, although some of the most hardy soil organisms may survive (Baker and Roistacher 1957). Pasteurized and unpasteurized soil pairs from the conditioning pots were used as inoculum in the plant–soil feedback

experiment. Tracking the identity of conditioning pots facilitates a “split-pot” design that allows me to account for variation in soil characteristics among training pots unrelated to the sterilization treatment (e.g., soil fertility, texture, and moisture).

For the plant–soil feedback experiment, I stratified seeds of our focal species following the protocols outlined for the conditioning phase. I then sowed seeds in a germination media before transplanting seedlings into sterilized 0.5 L pots filled with 95% pasteurized fill soil and 5% experimental inoculum (pasteurized and unpasteurized soil pairs from the conditioning phase). The fill soil contained little organic matter (mostly sand and clay particles) and serves as a common background medium for the experiment and reduces the potential influence of differences in soil characteristics other than microbial composition such as differences in nutrient availability, soil texture, or the release of chemical compounds during soil pasteurization that could confound experimental manipulation of soil biota. Fill soil was autoclaved for 90 min at 121 °C. While autoclaving soils can alter nutrient availability, the use of a common soil medium that has been autoclaved reduces such potential confounding effects when evaluating experimental treatments (Brinkman et al. 2010).

I transplanted seedlings of each focal species into pots with inoculum derived from conspecific- and heterospecific-trained soils that had been pasteurized or left unpasteurized. For each focal species, I randomly selected three heterospecific species to serve as training hosts (Table S1). Throughout the experiment, I kept track of the inoculum origin and paired experimental pots using pasteurized and unpasteurized inoculum from the same conditioning pot. This allows me to statistically account for non-independence among soil inoculum originating from the same conditioning pots due to differences in soil fertility, texture, or chemistry (Brinkman et al. 2010). For each focal species, I aimed for 60 conspecific-trained soils (30 pasteurized, 30 unpasteurized) and 90 heterospecific-trained soils (15 pasteurized, 15 unpasteurized for each of three heterospecific training hosts; Table S1). However, realized sample sizes were constrained by the number of seeds that germinated (Table S2). The transplant order and position of experimental pots within the greenhouse were randomized within focal species.

At the end of the experiment, I clipped and harvested aboveground biomass for all plants approximately two months after seeds were transplanted (47–77 days depending on the timing of germination). For a random subset of experimental plants representing each focal species, I harvested both aboveground and belowground biomasses. Roots were washed using a fine sieve (2 mm). All harvested plant material was dried in a drying oven at 75 °C for 72 h before being weighed.

Data analysis

I analyzed plant performance (aboveground biomass production) for each species separately using linear mixed effects models. Fixed effects included exposure to soil microorganisms (pasteurized versus unpasteurized), training host (conspecific versus heterospecific), and the interaction between these factors. I accounted for the split-pot design by including a random effect for training pot. This approach accounts for the non-independence among experimental pots with soil inoculum from the same training pot. I also included the number of days between transplanting and biomass harvest as a random effect for species that were harvested over multiple days. This random effect accounts for how differences in growth time or transplant date affect biomass production independent of experimental treatments. To illustrate variation in plant–soil feedbacks among focal species, I extracted estimated marginal means and confidence intervals of differences in biomass between experimental soil treatments. Using these model-based contrasts, I calculated the log response ratio comparing biomass production in unpasteurized soil versus pasteurized soil: $\ln(\text{unpasteurized}/\text{pasteurized})$. This metric quantifies the generalized effect of soil microorganisms on plant growth. Negative values reflect a net reduction in plant growth in the presence of soil microorganisms while positive values suggest soil microbes benefit plant growth. Log response ratios facilitate comparisons among species that differ in biomass production (Brinkman et al. 2010). I also compared the difference in plant biomass produced in conspecific, unpasteurized soil versus heterospecific, unpasteurized soil: $\ln(\text{conspecific}_{\text{unpasteurized}}/\text{heterospecific}_{\text{unpasteurized}})$. This metric reflects how specialized any plant–soil interactions are with negative values (pathogens reducing seedling growth in conspecific-trained soils)

suggesting host-specific effects while positive values reflect presumed host-specific mutualisms that promote seedling growth. I performed all analyses using R 4.0.2 (R Core Team 2020). I fit mixed models using the ‘lme4’ package (Bates et al. 2015) and generated figures using ‘ggplot2’ (Wickham 2009).

Results

Aboveground biomass was strongly correlated with total plant biomass across all focal species (Pearson correlation: $r > 0.71$ and $P < 0.001$ for all species; Table S3; Fig. S1), confirming that aboveground biomass provides a suitable proxy for total plant growth and fitness. Above- and belowground plant

biomasses were also strongly correlated across the focal species (all $r > 0.63$ and $P < 0.002$; Table S3; Fig. S2).

The effects of manipulating soil biota on plant growth varied among species (Fig. 2). In four of the nine focal species, plants grown in unpasteurized soil performed worse than plants grown in pasteurized soils (Table 2; Fig. 3a). Seedling biomass in unpasteurized soils declined relative to biomass in pasteurized soils by 20.2% in *T. dioicum* (ANOVA: $F_{1136.5} = 8.300$, $P = 0.005$), 8.6% in *E. hystrix* ($F_{1126.7} = 7.35$, $P = 0.008$), 12.3% in *S. flexicaulis* ($F_{1136.2} = 4.739$, $P = 0.031$), and tended to decline (9.7%) in *P. reptans* ($F_{1108.4} = 2.892$, $P = 0.092$). Differences in plant growth between pasteurized and unpasteurized soils were negligible for *P. virginianum* (− 14.9%), *A. altissima* (+ 0.0%), *A. canadensis* (+ 4.6%), *H. glutinosum* (+ 15.2%), and *G. maculatum* (+ 17.1%; see Fig. 3a and Table 2).

The origin of soil biota affected plant growth in certain species (Fig. 3b). In *Thalictrum dioicum*, conspecific, unpasteurized soils depressed seedling biomass by 30.0% relative to heterospecific, unpasteurized soils. Similarly, *E. hystrix* seedlings were 11.0% smaller in conspecific, unpasteurized soil relative to heterospecific, unpasteurized soil. There was no significant effect of soil origin on the growth of *Polygonum virginianum* (− 16.8%), *Polemonium reptans* (− 5.0%), *S. flexicaulis* (+ 0.01%), *A. canadensis* (+ 4.2%), *H. glutinosum* (+ 7.3%), *Ageratina altissima* (+ 9.2%), or *Geranium maculatum* (+ 24.4%).

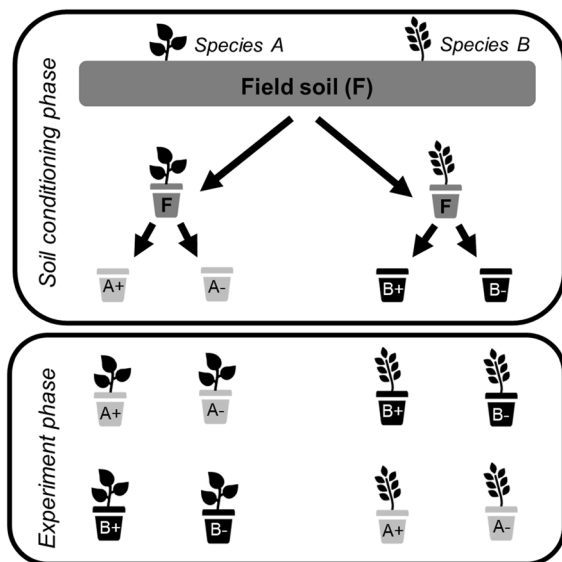


Fig. 1 Diagram illustrating simplified experimental design for two hypothetical focal species (species A and B). Field soil (F) was collected from forest stands in which focal species were present. During the soil conditioning phase of the experiment (top panel), each focal species was grown in field soil within training pots for two months (20–30 training pots for each focal species). Soil from each training pot was then divided equally. Half of the soil from each training pot was pasteurized using an autoclave (microbes absent, −) and the other half left unpasteurized (microbes present, +). Soil from different training pots was kept separate throughout the experiment. During the experiment phase (bottom panel), I grew each focal species in a common soil medium inoculated with soil from the conditioning phase. Experimental treatments included soil inoculum from different training hosts (conspecific- versus heterospecific-trained soils) and with different exposure to soil microbes (pasteurized versus unpasteurized)

Discussion

Plant–soil interactions, especially negative plant–soil feedbacks that can facilitate coexistence and promote species diversity, have received relatively little attention in the herbaceous plant communities of temperate forests (Whigham 2004; Comita et al. 2014; but see Shannon et al. 2012; Smith and Reynolds 2015; Sweet and Burns 2017). Here I examined how plant–soil interactions influence the growth of nine herbaceous plant species common in North American temperate forests. The effect of soil biota and their origin on seedling growth varied among focal herb species. Three of the nine exhibited reduced growth in unpasteurized soils and another tended to accumulate

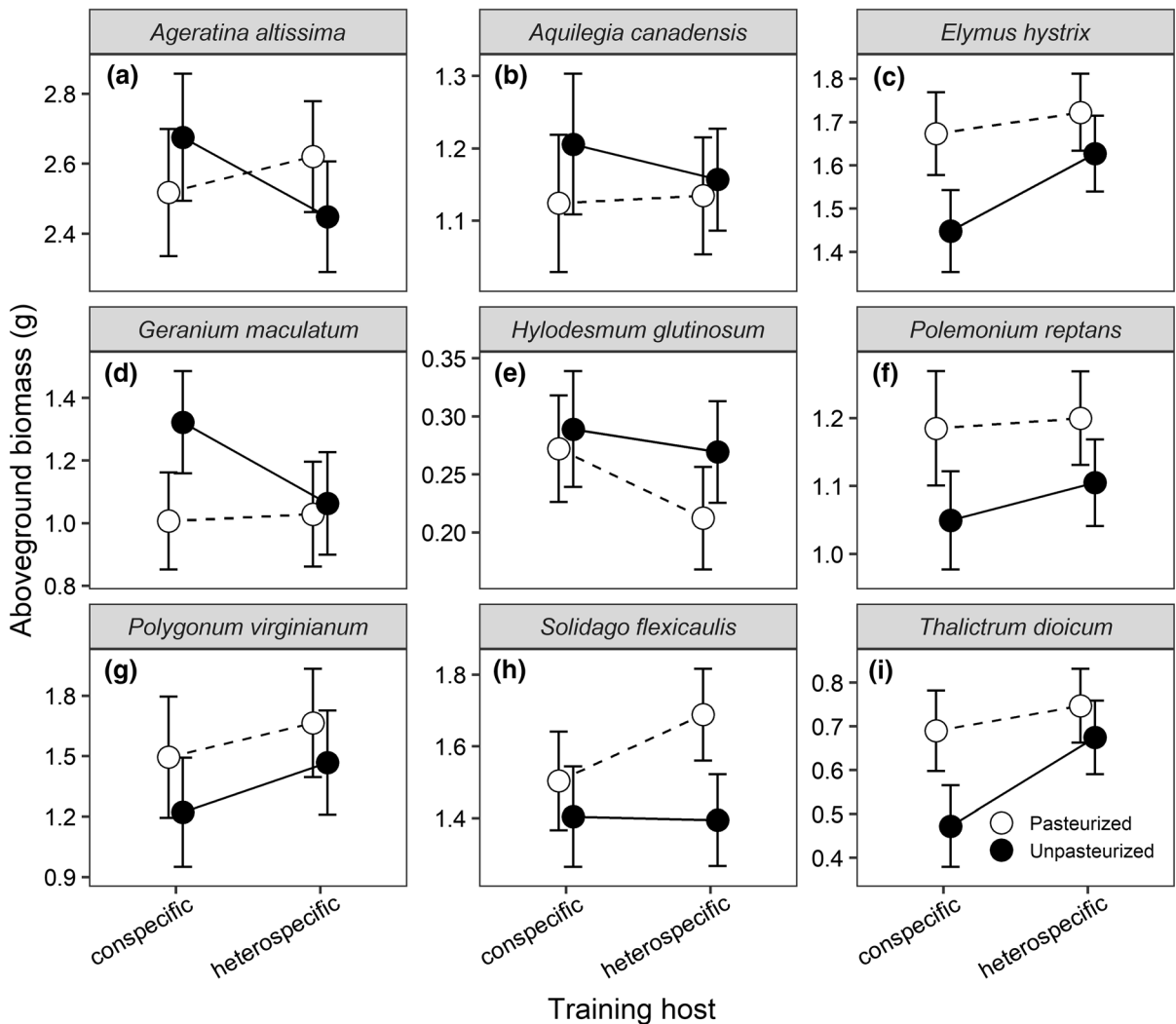


Fig. 2 Estimated marginal means of aboveground biomass (in grams) for each focal species across the four experimental treatments. Pasteurized soils are represented by open circles and dashed lines while unpasteurized soils are represented by closed circles and solid lines. Error bars represent one standard error of the marginal means. Range of sample sizes (seedlings per experimental treatment) for each species: (a) *A. altissima*,

(N = 31–44), (b) *A. canadensis* (N = 17–31), (c) *E. hystrix* (N = 29–45), (d) *G. maculatum* (N = 13–19), (e) *H. glutinosum* (N = 15–33), (f) *P. reptans* (N = 23–35), (g) *P. virginianum* (N = 14–21), (h) *S. flexicaulis* (N = 29–43), (i) and *T. dioicum* (N = 28–45). See Table S2 for realized sample sizes within each treatment

less biomass in unpasteurized soils suggesting generalized, antagonistic interactions with soil biota affect several herb species (Figs. 2 and 3a). More specialized plant–soil feedbacks were also present. In both *T. dioicum* and *E. hystrix*, seedling performance declined in conspecific, unpasteurized soils relative to heterospecific, unpasteurized soils suggesting host-specific pathogens or pathogens with host-specific effects may depress seedling growth near maternal

plants or at high local population densities. The Janzen–Connell hypothesis predicts that the accumulation of host-specific pathogens should inhibit the growth of individuals near conspecific adults, causing negative distance- or density-dependence that can promote species coexistence (Janzen 1970; Connell 1971; Packer and Clay 2000; Reinhart and Clay 2009; Comita et al. 2014; Bever et al. 2015). Observed patterns of seedling growth in *T. dioicum* and *E.*

Table 2 Summary of statistical models examining the effects of experimental treatments on aboveground biomass production

Focal species	Soil treatment		Host treatment		Soil × Host treatment	
	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
<i>Ageratina altissima</i>	0.003	0.954	0.168	0.686	1.658	0.200
<i>Aquilegia canadensis</i>	0.497	0.483	0.039	0.844	0.156	0.695
<i>Elymus hystrix</i>	8.949	0.003	3.265	<i>0.087</i>	1.496	0.224
<i>Geranium maculatum</i>	<i>3.004</i>	<i>0.091</i>	0.567	0.460	1.971	0.168
<i>Hylodesmum glutinosum</i>	2.094	0.152	2.303	0.141	0.597	0.442
<i>Polemonium reptans</i>	2.892	<i>0.092</i>	0.209	0.651	0.089	0.766
<i>Polygonum virginianum</i>	1.525	0.222	1.280	0.271	0.045	0.833
<i>Solidago flexicaulis</i>	4.739	0.031	0.895	0.350	1.145	0.287
<i>Thalictrum dioicum</i>	8.300	0.005	4.584	0.039	2.083	0.151

For each species, I report *F* statistics and *P*-values for the effect of soil treatment (pasteurized versus unpasteurized soil inoculant), host treatment (conspecific versus heterospecific training host), and their interactions. Significant effects are bolded, marginally significant effects are italicized

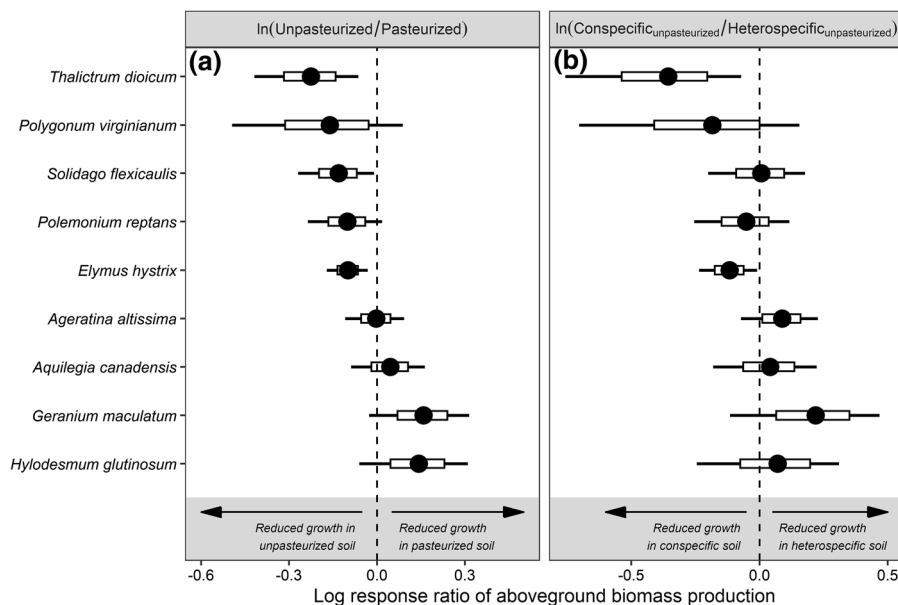


Fig. 3 Variation in plant–soil interactions among species illustrated for **a** differences in aboveground biomass production between pasteurized and unpasteurized soil treatments and **b** differences in biomass production between conspecific- and heterospecific-trained soil inocula that were not pasteurized. In **(a)**, negative values indicate reduced growth in unpasteurized soil compared to pasteurized soil. In **(b)**, negative values indicate reduced growth in unpasteurized, conspecific-trained

soil relative to unpasteurized, heterospecific-trained soil. Points represent the estimated log response ratio of aboveground biomass production in pasteurized versus unpasteurized soils **(a)** or conspecific_{unpasteurized} versus heterospecific_{unpasteurized} soils **(b)**, white bars indicate \pm one standard error, and black lines represent a 95 percent confidence interval for this log response ratio

hystrix were consistent with these predictions (Fig. 3b), although I did not attempt to identify the pathogenic microbes responsible or their host specificity. Smith and Reynolds (2015) also documented

evidence of conspecific inhibition for *E. hystrix* and two other understory forest species. Although I found little effect of soil treatments on *A. canadensis* performance in this study, Sweet and Burns (2017)

reported that this species was more strongly inhibited by close relatives than distantly related but co-occurring forest herbs. These results highlight the potential role host-specific pathogens and negative plant–soil feedbacks play in facilitating local coexistence among at least some herbaceous plant species in temperate forests. Janzen–Connell effects may be especially important within guilds of functionally similar species that share responses to environmental variation and frequently co-occur but do not exhibit conspicuous differences in resource use (Beck 2020).

Despite evidence for negative plant–soil feedbacks and Janzen–Connell effects in *T. dioicum* and *E. hystrix*, most focal species in this experiment were apparently unaffected by the biotic soil community. The lack of treatment effects for these species could reflect several factors and does not necessarily demonstrate that plant–soil interactions are unimportant. My approach for evaluating plant–soil interactions quantifies only the net effect of soil biota (Ehrenfeld et al. 2005; Kulmatiski et al. 2008; Brinkman et al. 2010; Van der Putten et al. 2013). Because pasteurizing soil eliminates both pathogens and mutualists, it may obscure complex plant–soil interactions that could affect plant growth and survival. For example, most forest herbs associate with mycorrhizal fungi and exchange carbon-rich compounds for mineral nutrients (Whigham 2004). These associations can benefit plant growth and may offset the negative effect of pathogens (Whigham 2004; Burke 2012; Burke et al. 2018). Moreover, this study was conducted under ideal growing conditions over a relatively short period of time. The influence of plant–soil interactions may be more pronounced over longer time periods in natural conditions where limited light, less consistent water supply, competition, herbivory, and greater microbial density may increase stress and exacerbate the influence of antagonistic interactions with soil microbes. Thus, caution is warranted when extrapolating results from a greenhouse experiment to natural settings. Comparisons of paired greenhouse and field experiments reveal that plant–soil feedbacks measured in controlled greenhouse settings are not necessarily good predictors of how soil biota influence plant growth and survival in natural conditions (Heinze et al. 2016; Beals et al. 2020). Nevertheless, many results from controlled greenhouse experiments faithfully replicate the realized effects of plant–soil interactions in field conditions (e.g., Packer and Clay

2000; Mangan et al. 2010). More generally, the experimental design of this study has limitations for quantifying effects of heterospecific plant species. Each focal species was grown in soil conditioned by a subset of the other study species. While such studies still offer valuable insights into plant–soil feedbacks (Petermann et al. 2008; Burns and Strauss 2011), fully factorial experiments that include all pairwise species combinations capture a fuller range of possible heterospecific effects and can facilitate examination of the potential for pairwise coexistence (sensu Fitzsimons and Miller 2010).

Several other factors may mediate the effects of soil biota on plant growth in both experimental studies and natural settings. Plant–soil interactions can vary among life stages or different environmental contexts (Smith-Ramesh and Reynolds 2017). Although seedlings are generally expected to respond more sensitively to soil microbes than adult plants, little is known about the effects of soil microbes on seeds or seed germination (Nelson 2018). Seeds are exposed to a diverse assortment of microorganisms while dormant in the soil. Although rarely quantified, these interactions could generate positive or negative plant–soil feedbacks distinct from those exhibited by seedlings (Kirkpatrick and Bazzaz 1979; Burns and Strauss 2011; Nelson 2018; Miller et al. 2019). Soil fertility, light availability, and soil moisture may also mediate the effects of soil microbes on plant growth and mortality (Givnish 1999; Shannon et al. 2012; Larios and Suding 2015; Smith and Reynolds 2015). Fungal communities vary seasonally and among years in response to environmental variation, especially soil moisture (Gilliam et al. 2014; Burke 2015). A handful of empirical studies demonstrate that the strength and net effect of plant–soil interactions on plant growth may depend on environmental conditions such as light, water, or nutrient availability (Smith and Reynolds 2015). Consequently, soil biota, plant–soil feedbacks, and the influence of plant–soil interactions on plant fitness could vary both spatially and temporally in plant communities (Brandt et al. 2013). Soil communities and the nature of plant–soil interactions may be especially heterogeneous in temperate forest understories. In contrast to trees, which possess extensive root systems and greater biomass, the rhizosphere of forest herbs is comparatively small. Forest herbs also typically occur at low densities. As a result, forest herbs likely influence soil communities at

much finer scales than do trees potentially leading to heterogeneity in soil biota and plant–soil interactions at finer spatial scales within forest stands. Likewise, plant–soil interactions may be heterogeneous at larger spatial scales due to geographic variation in microbial communities and localized co-evolution between plants and microbes (Lankau and Keymer 2018).

The observed variation in plant–soil interactions among forest herbs in this study parallels previous research documenting variation in plant–soil feedbacks among temperate forest trees (Bennett et al. 2017), grassland plant species (Klironomos 2002; Fitzsimons and Miller 2010; Reinhart 2012; Maron et al. 2016), and plant species in other communities (Kulmatiski et al. 2008; Mangan et al. 2010; Teste et al. 2017). This variation has potentially important implications for the distribution, abundance, and diversity of plants in all these ecosystems. In both temperate grasslands (Klironomos 2002) and tropical forests (Mangan et al. 2010), the strength of plant–soil feedbacks is associated with the relative abundance of plant species in the community (but see Reinhart et al. 2021). The stronger negative plant–soil feedbacks observed in many rare species suggest that their susceptibility to pathogens may contribute to their rarity. All nine of the focal species studied here are relatively common. It is noteworthy, however, that *A. altissima*, *G. maculatum*, and *H. glutinosum* – all species exhibiting neutral plant–soil feedbacks – tend to form dense, monospecific patches and all but *H. glutinosum* will spread aggressively via vegetative reproduction (J. Beck, *personal observation*). Smith and Reynolds (2015) similarly noted that two monoculture-forming understory plants (*Asarum canadense* and the invasive *Euonymus fortunei*) exhibited neutral plant–soil feedbacks. In contrast, the species with strongly negative plant–soil feedbacks in our study (e.g., *T. dioicum* and *E. hystrix*) often exhibit patchy, rather sparse local distributions and rarely form dense, monospecific clusters (J. Beck, *personal observation*; also see Smith and Reynolds 2015). There have been very few investigations of distance- or density-dependence among temperate forest herbs, so it is unclear whether the local spatial distribution of forest herbs reflects Janzen–Connell effects and elevated mortality near adult conspecifics (Bever et al. 1997; Comita et al. 2014). However, temperate forest tree species that exhibit negative plant–soil feedbacks, such as *Prunus serotina*, rarely cluster and tend to

occur more regularly than expected if distributed spatially at random (Packer and Clay, 2000; Johnson et al. 2017; J. Beck, *unpublished data*). Future investigation into fine-scale spatial distributions of forest herbs as well as spatial patterns of recruitment and mortality, especially in relation to plant–soil feedbacks, may provide valuable insights into how plant–soil interactions shape the local distributions of forest herbs.

Herbaceous plant species in temperate forest occur at high local densities, with a dozen or more species occupying one square meter of substrate (Rogers et al. 2008; Peet et al. 2014). Plant–soil interactions could play an important but previously underappreciated role in structuring the local distribution, abundance, and diversity of these herbs. In this study, I demonstrate that negative plant–soil feedbacks influence at least some herbaceous plant species in ways that could promote species coexistence at small spatial scales. Moreover, the observed variation in how soil biota affect herb species is consistent with findings from other plant communities and suggests differences in plant–soil interactions among species may be key to understanding local herb distributions and abundance in temperate forests. While future research is clearly needed to extrapolate these findings to natural settings, examine a broader suite of species, and more fully understand how plant–soil interactions influence the understory plant community of temperate forests, this study adds to a growing body of knowledge about how plant–soil interactions may shape the composition and diversity of different plant communities (Ehrenfeld et al. 2005; Kulmatiski et al. 2008; Mordecai 2011; Bever et al. 2015).

Acknowledgements The author thanks D. Waller, T. Givnish, R. Lankau, A. Ives, M. Turner, and B. Larget for providing advice and encouragement. Four anonymous reviews offered constructive feedback that improved the manuscript. C. Kestel and B. Bowser assisted with experiment preparation and data collection. C. Streeker, I. Jordan-Thalen, and UW-Botany greenhouse staff offered logistical support for the experiment. This research was funded by a 2018 Graduate Student Research Award from the Botanical Society of America and a Davis Research Grant from the UW–Madison Department of Botany. J. Beck was also supported as an NSF Graduate Research Fellow (DGE-1747503). Opinions, findings, and conclusions expressed here are those of the authors and do not reflect the views of the NSF. Support was also provided by the Graduate School and the Office of the Vice Chancellor for Research and Graduate Education at the University of Wisconsin–Madison with funding from the Wisconsin Alumni Research Foundation.

Author contributions JB designed the study, collected and analyzed the data, and wrote the manuscript.

Funding This research was funded by a 2018 Graduate Student Research Award from the Botanical Society of America and a Davis Research Grant from the UW–Madison Department of Botany. J. Beck was also supported as an NSF Graduate Research Fellow (DGE-1747503).

Data availability All data presented in manuscript are included in the supplemental material.

Code availability R code used to analyze data and produce graphs is included in the supplemental material.

Declarations

Conflict of interest The author declares no conflict of interest.

References

- Anderson ARC, Loucks OL, Swain AM (1969) Herbaceous response to canopy cover, light intensity, and throughfall precipitation in coniferous forests. *Ecology* 50:255–263
- Bagchi R, Swinfield T, Gallery RE, Lewis OT, Gripenberg S, Narayan L, Freckleton RP (2010) Testing the Janzen–Connell mechanism: pathogens cause overcompensating density dependence in a tropical tree. *Ecol Lett* 13:1262–1269. <https://doi.org/10.1111/j.1461-0248.2010.01520.x>
- Bagchi R, Gallery RE, Gripenberg S, Gurr SJ, Narayan L, Addis CE, Freckleton RP, Lewis OT (2014) Pathogens and insect herbivores drive rainforest plant diversity and composition. *Nature* 506:85–88. <https://doi.org/10.1038/nature12911>
- Baker KF, Roistacher CN (1957) Principles of heat treatment of soil. In: Baker KF (ed) *The U.C. system for producing healthy container grown plants, manual 23*. University of California, Division of Agricultural Sciences, Agricultural Experiment Station, Extension Service, Berkeley, CA, pp 138–161
- Bartels SF, Chen HYH (2010) Is understory plant diversity driven by resource quantity or resource heterogeneity? *Ecology* 91:1931–1938. <https://doi.org/10.1002/ecy.1730>
- Bates D, Maechler M, Bolker B, Walker S (2015) Fitting linear mixed-effects models using lme4. *J Stat Softw* 67:1–48
- Beals KK, Moore JAM, Kivlin SN, Bayliss SLJ, Lumibao CY, Moorhead LC, Patel M, Summers JL, Ware IM, Bailey JK, Schweitzer JA (2020) Predicting plant–soil feedback in the field: meta-analysis reveals that competition and environmental stress differentially influence PSF. *Front Ecol Evol* 8:1–14. <https://doi.org/10.3389/fevo.2020.00191>
- Beatty SW (1984) Influence of microtopography and canopy species on spatial patterns of forest understory plants. *Ecology* 65:1406–1419
- Beatty SW (2014) Habitat heterogeneity and the maintenance of species in understory communities. In: Gilliam FS (ed) *The herbaceous layer in forests of Eastern North America*. Oxford University Press, New York, NY, USA, pp 215–232
- Beck JJ (2020) Factors shaping the distribution, abundance, and diversity of temperate forest plants. Dissertation, University of Wisconsin–Madison
- Beck JJ, Givnish TJ (2021) Fine-scale environmental heterogeneity and spatial niche partitioning among spring-flowering forest herbs. *Am J Bot* 108:1–11. <https://doi.org/10.1002/ajb2.1593>
- Bell G, Lechowicz MJ, Waterway MJ (2000) Environmental heterogeneity and species diversity of forest sedges. *J Ecol* 88:67–87. <https://doi.org/10.1046/j.1365-2745.2000.00427.x>
- Bell T, Freckleton RP, Lewis OT (2006) Plant pathogens drive density-dependent seedling mortality in a tropical tree. *Ecol Lett* 9:569–574. <https://doi.org/10.1111/j.1461-0248.2006.00905.x>
- Bennett JA, Klironomos J (2019) Mechanisms of plant–soil feedback: interactions among biotic and abiotic drivers. *New Phytol* 222:91–96. <https://doi.org/10.1111/nph.15603>
- Bennett JA, Maherali H, Reinhart KO, Lekberg Y, Hart MM, Klironomos J (2017) Plant–soil feedbacks and mycorrhizal type influence temperate forest population dynamics. *Science* 355:181–184
- Bever J, Westover K, Antonovics J (1997) Incorporating the soil community into plant population dynamics: the utility of the feedback approach. *J Ecol* 85:561–573
- Bever JD, Dickie IA, Facelli E, Facelli JM, Klironomos J, Moora M, Rillig MC, Stock WD, Tibbett M, Zobel M (2010) Rooting theories of plant community ecology in microbial interactions. *Trends Ecol Evol* 25:468–478. <https://doi.org/10.1016/j.tree.2010.05.004>
- Bever JD, Mangan SA, Alexander HM (2015) Maintenance of plant species diversity by pathogens. *Annu Rev Ecol Evol Syst* 46:305–325. <https://doi.org/10.1146/annurev-ecolsys-112414-054306>
- Bierzychudek P (1982) Life histories and demography of shade-tolerant temperate forest herbs: a review. *New Phytol* 90:757–776
- Bonanomi G, Giannino F, Mazzoleni S (2005) Negative plant–soil feedback and species coexistence. *Oikos* 111:311–321. <https://doi.org/10.1111/j.0030-1299.2005.13975.x>
- Brandt AJ, De Kroon H, Reynolds HL, Burns JH (2013) Soil heterogeneity generated by plant–soil feedbacks has implications for species recruitment and coexistence. *J Ecol* 101:277–286. <https://doi.org/10.1111/1365-2745.12042>
- Bratton SP (1976) Resource division in an understory herb community: responses to temporal and microtopographic gradients. *Am Nat* 110:679–693
- Brinkman EP, Van der Putten WH, Bakker EJ, Verhoeven KJF (2010) Plant–soil feedback: experimental approaches, statistical analyses and ecological interpretations. *J Ecol* 98:1063–1073. <https://doi.org/10.1111/j.1365-2745.2010.01695.x>
- Burke DJ (2008) Effects of *Alliaria petiolata* (garlic mustard; Brassicaceae) on mycorrhizal colonization and community structure in three herbaceous plants in a mixed deciduous forest. *Am J Bot* 95:1416–1425. <https://doi.org/10.3732/ajb.0800184>

- Burke DJ (2012) Shared mycorrhizal networks of forest herbs: does the presence of conspecific and heterospecific adult plants affect seedling growth and nutrient acquisition? *Botany* 90:1048–1057. <https://doi.org/10.1139/b2012-065>
- Burke DJ (2015) Effects of annual and interannual environmental variability on soil fungi associated with an old-growth, temperate hardwood forest. *FEMS Microbiol Ecol* 91:1–13. <https://doi.org/10.1093/femsec/fiv053>
- Burke DJ, Klenkar MK, Medeiros JS (2018) Mycorrhizal network connections, water reduction, and neighboring plant species differentially impact seedling performance of two forest wildflowers. *Int J Plant Sci* 179:314–324. <https://doi.org/10.1086/696686>
- Burns JH, Strauss SY (2011) More closely related species are more ecologically similar in an experimental test. *Proc Natl Acad Sci* 108:5302–5307. <https://doi.org/10.1073/pnas.1116085108>
- Catella SA, Eysenbach SR, Abbott KC (2019) Novel insights into how the mean and heterogeneity of abiotic conditions together shape forb species richness patterns in the Allegheny plateau ecoregion. *Ecol Evol*. <https://doi.org/10.1002/ece3.5508>
- Collins BS, Ferrara LS, Motto HL (1984) Coincidence of spring herb distribution and flowering with tree bases in a New Jersey Piedmont forest. *Bull Torrey Bot Club* 111:301. <https://doi.org/10.2307/2995911>
- Comita LS, Queenborough SA, Murphy SJ, Eck JL, Xu K, Krishnadas M, Beckman N, Zhu Y (2014) Testing predictions of the Janzen–Connell hypothesis: a meta-analysis of experimental evidence for distance- and density-dependent seed and seedling survival. *J Ecol* 102:845–856. <https://doi.org/10.1111/1365-2745.12232>
- Connell JH (1971) On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. In: PJ den B, GR G (eds) *Dynamics of populations*. The Netherlands: Centre for Agricultural Publishing and Documentation, pp. 298–312
- Crawford KM, Bauer JT, Comita LS, Eppinga MB, Johnson DJ, Mangan SA, Queenborough SA, Strand AE, Suding KN, Umbanhowar J, Bever JD (2019) When and where plant–soil feedback may promote plant coexistence: a meta-analysis. *Ecol Lett*. <https://doi.org/10.1111/ele.13278>
- Crozier CR, Boerner REJ (1984) Correlation of understory herb distribution patterns with microhabitats under different tree species in a mixed mesophytic forest. *Oecologia* 62:337–343
- Curtis JT (1959) *The vegetation of Wisconsin: an ordination of plant communities*. The University of Wisconsin Press, Madison, WI
- Ehrenfeld JG, Ravit B, Elgersma K (2005) Feedback in the plant–soil system. *Annu Rev Environ Resour* 30:75–115. <https://doi.org/10.1146/annurev.energy.30.050504.144212>
- Fitzsimons MS, Miller RM (2010) The importance of soil microorganisms for maintaining diverse plant communities in tallgrass prairie. *Am J Bot* 97:1937–1943. <https://doi.org/10.3732/ajb.0900237>
- Gilliam FS (2007) The ecological significance of the herbaceous layer in temperate forest ecosystems. *Bioscience* 57:845. <https://doi.org/10.1641/B571007>
- Gilliam FS, Hedl R, Chudomelova M, McCulley RL, Nelson JA (2014) Variation in vegetation and microbial linkages with slope aspect in a montane temperate hardwood forest. *Ecosphere* 5:1–17. <https://doi.org/10.1890/ES13-00379.1>
- Givnish TJ (1999) On the causes of gradients in tropical tree species diversity. *J Ecol* 87:193–210. <https://doi.org/10.1046/j.1365-2745.1999.00333.x>
- Hale AN, Lapointe L, Kalisz S (2016) Invader disruption of belowground plant mutualisms reduces carbon acquisition and alters allocation patterns in a native forest herb. *New Phytol* 209:542–549. <https://doi.org/10.1111/nph.13709>
- Heinze J, Sitte M, Schindhelm A, Wright J, Joshi J (2016) Plant–soil feedbacks: a comparative study on the relative importance of soil feedbacks in the greenhouse versus the field. *Oecologia* 181:559–569. <https://doi.org/10.1007/s00442-016-3591-8>
- Janzen DH (1970) Herbivores and the number of tree species in tropical forests. *Am Nat* 104:501–528. <https://doi.org/10.1086/282687>
- Johnson DJ, Bourq NA, Howe R, Mcshea WJ, Johnson DJ, Bourq NA, Howe R, Mcshea WJ, Wolf A, Clay K (2014) Conspecific negative density-dependent mortality and the structure of temperate forests. *Ecology* 95:2493–2503
- Johnson DJ, Condit R, Hubbell SP, Comita LS (2017) Abiotic niche partitioning and negative density dependence drive tree seedling survival in a tropical forest. *Proc Royal Soc B* 284:1–8
- Kartzinel RY, Spalink D, Waller DM, Givnish TJ (2016) Divergence and isolation of cryptic sympatric taxa within the annual legume *Amphicarpaea bracteata*. *Ecol Evol* 6:3367–3379. <https://doi.org/10.1002/ece3.2134>
- Ke PJ, Wan J (2019) Effects of soil microbes on plant competition: a perspective from modern coexistence theory. *Ecol Monogr*. <https://doi.org/10.1002/ecm.1391>
- Kirkpatrick BL, Bazzaz FA (1979) Influence of certain fungi on seed germination and seedling survival of four colonizing annuals. *J Appl Ecol* 16:515. <https://doi.org/10.2307/2402526>
- Klironomos JN (2002) Feedback with soil biota contributes to plants rarity and invasiveness in communities. *Nature* 417:67–69
- Kulmatiski A, Beard KH, Stevens JR, Cobbold SM (2008) Plant–soil feedbacks: a meta-analytical review. *Ecol Lett* 11:980–992. <https://doi.org/10.1111/j.1461-0248.2008.01209.x>
- LaManna JA, Mangan SA, Alonso A, Bourq NA, Brockelman WY, Bunyavejchewin S, Chang L, Chiang J, Chuyong GB, Clay K, Condit R, Cordell S, Davies SJ, Furniss TJ, Giardina CP, Gunatilleke IAUN, Gunatilleke CVS, He F, Howe RW, Hubbell SP, Hsieh C-F, Inman-Narahari FM, Janík D, Johnson DJ, Kenfack D, Korte L, Král K, Larson AJ, Lutz JA, McMahon SM, McShea WJ, Memiaghe HR, Nathalang A, Novotny V, Ong PS, Orwig DA, Ostertag R, Parker GG, Phillips RP, Sack L, Sun I-F, Tello JS, Thomas DW, Turner BL, Vela Díaz DM, Vrška T, Weiblen GD, Wolf A, Yap S, Myers JA (2017) Plant diversity increases with the strength of negative density dependence at the global scale. *Science* 356:1389–1392. <https://doi.org/10.1126/science.aam5678>
- Lange KI (1998) *Flora of Sauk County and Caledonia Township, Columbia County, south central Wisconsin*. Madison, WI
- Lankau RA (2011) Resistance and recovery of soil microbial communities in the face of *Alliaria petiolata* invasions.

- New Phytol 189:536–548. <https://doi.org/10.1111/j.1469-8137.2010.03481.x>
- Lankau RA, Keymer DP (2018) Simultaneous adaptation and maladaptation of tree populations to local rhizosphere microbial communities at different taxonomic scales. *New Phytol* 217:1267–1278. <https://doi.org/10.1111/nph.14911>
- Larios L, Suding KN (2015) Competition and soil resource environment alter plant–soil feedbacks for native and exotic grasses. *AoB Plants* 7:1–9. <https://doi.org/10.1093/aobpla/plu077>
- Liu Y, Fang S, Chesson P, He F (2015) The effect of soil-borne pathogens depends on the abundance of host tree species. *Nat Commun* 6:4–10. <https://doi.org/10.1038/ncomms10017>
- Ma S, De Frenne P, Wasof S, Brunet J, Cousins SAO, Decocq G, Kolb A, Lemke I, Liira J, Naaf T, Orczewska A, Plue J, Wulf M, Verheyen K (2019) Plant–soil feedbacks of forest understorey plants transplanted in nonlocal soils along a latitudinal gradient. *Plant Biol* 21:677–687. <https://doi.org/10.1111/plb.12960>
- Mangan SA, Schnitzer SA, Herre EA, MacK KML, Valencia MC, Sanchez EI, Bever JD (2010) Negative plant–soil feedback predicts tree-species relative abundance in a tropical forest. *Nature* 466:752–755. <https://doi.org/10.1038/nature09273>
- Maron JL, Smith AL, Ortega YK, Pearson DE, Callaway RM (2016) Negative plant–soil feedbacks increase with plant abundance, and are unchanged by competition. *Ecology* 97:2055–2063. <https://doi.org/10.1002/ecy.1431>
- Miller EC, Perron GG, Collins CD (2019) Plant-driven changes in soil microbial communities influence seed germination through negative feedbacks. *Ecol Evol* 9:9298–9311. <https://doi.org/10.1002/ece3.5476>
- Mordecai E (2011) Pathogen impacts on plant communities: unifying theory, concepts, and empirical work. *Ecol Monogr* 81:429–441. <https://doi.org/10.1890/10-2241.1>
- Nelson EB (2018) The seed microbiome: origins, interactions, and impacts. *Plant Soil* 422:7–34. <https://doi.org/10.1007/s11104-017-3289-7>
- Packer A, Clay K (2000) Soil pathogens and spatial patterns of seedling mortality in a temperate tree. *Nature* 404:278–281. <https://doi.org/10.1038/35005072>
- Parker MA (1985) Local population differentiation for compatibility in an annual legume and its host-specific fungal pathogen. *Evolution* 39:713–723
- Peet RK, Palmquist KA, Tessel SM (2014) Herbaceous layer species richness of southeastern forests and woodlands: patterns and causes. In: Gilliam FS (ed) *The herbaceous layer in forests of Eastern North America*. Oxford University Press, New York, NY, USA, pp 255–276
- Petermann JS, Fergus AJF, Turnbull LA, Petermann JS, Fergus AJF, Turnbull LA, Schmid B (2008) Janzen–Connell effects are widespread and strong enough to maintain diversity in grasslands. *Ecology* 89:2399–2406
- Peterson CJ, Carson WP, Mccarthy BC, Pickett STA, Peterson CJ, Carson WP, Mccarthy BC, Pickett STA, Microsite STA (1990) Microsite variation and soil dynamics within newly created treefall pits and mounds. *Oikos* 58:39–46
- Prati D, Bossdorf O (2004) Allelopathic inhibition of germination by *Alliaria petiolata* (Brassicaceae). *Am J Bot* 91:285–288. <https://doi.org/10.3732/ajb.91.2.285>
- R Core Team (2020) A language and environment for statistical computing
- Reinhart KO (2012) The organization of plant communities: negative plant–soil feedbacks and semiarid grasslands. *Ecology* 93:2377–2385
- Reinhart KO, Clay K (2009) Spatial variation in soil-borne disease dynamics of a temperate tree, *Prunus serotina*. *Ecology* 90:2984–2993
- Reinhart KO, Bauer JT, McCarthy-Neumann S, MacDougall AS, Hierro JL, Chiufo MC, Mangan SA, Heinze J, Bergmann J, Joshi J, Duncan RP, Diez JM, Kardol P, Rutten G, Fischer M, van der Putten WH, Bezemer TM, Klironomos J (2021) Globally, plant–soil feedbacks are weak predictors of plant abundance. *Ecol Evol* 11:1756–1768. <https://doi.org/10.1002/ece3.7167>
- Reynolds HL, Packer A, Bever JD, Clay K (2003) Grassroots ecology: plant–microbe–soil interactions as drivers of plant community structure and dynamics. *Ecology* 84:2281–2291. <https://doi.org/10.1890/02-0298>
- Rogers DA, Rooney TP, Olson D, Waller DM (2008) Shifts in southern Wisconsin forest canopy and understorey richness, composition, and heterogeneity. *Ecology* 89:2482–2492. <https://doi.org/10.1890/07-1129.1>
- Shannon S, Flory SL, Reynolds HL (2012) Competitive context alters plant–soil feedback in an experimental woodland community. *Oecologia* 169:235–243. <https://doi.org/10.1007/S00442-011-1129-1>
- Shannon SM, Bauer JT, Anderson WE, Reynolds HL (2014) Plant–soil feedbacks between invasive shrubs and native forest understorey species lead to shifts in the abundance of mycorrhizal fungi. *Plant Soil* 382:317–328. <https://doi.org/10.1007/s11104-014-2158-x>
- Smith LM, Reynolds HL (2012) Positive plant–soil feedback may drive dominance of a woodland invader, *Euonymus fortunei*. *Plant Ecol* 213:853–860. <https://doi.org/10.1007/s11258-012-0047-z>
- Smith LM, Reynolds HL (2015) Plant–soil feedbacks shift from negative to positive with decreasing light in forest understorey species. *Ecology* 96:2523–2532
- Smith-Ramesh LM, Reynolds HL (2017) The next frontier of plant–soil feedback research: unraveling context dependence across biotic and abiotic gradients. *J Veg Sci* 28:484–494. <https://doi.org/10.1111/jvs.12519>
- Spear ER, Borders KD (2021) Host-generalist fungal pathogens of seedlings may maintain forest diversity via host-specific impacts and differential susceptibility among tree species. *New Phytol* 231:460–474. <https://doi.org/10.1111/nph.17379>
- Struik GJ, Curtis JT (1962) Herb distributions in an *Acer saccharum* forest. *Am Midl Nat* 68:285–296
- Sweet DD, Burns JH (2017) Plant performance was greater in the soils of more distantly related plants for an herbaceous understorey species. *AoB Plants* 9:1–9. <https://doi.org/10.1093/aobpla/plx005>
- Terborgh J (2012) Enemies maintain hyperdiverse tropical forests. *Am Nat* 179:303–314. <https://doi.org/10.1086/664183>
- Teste FP, Kardol P, Turner BL, Wardle DA, Zemunik G, Renton M, Laliberté E (2017) Plant–soil feedback and the maintenance of diversity in Mediterranean-climate shrublands.

- Science 355:173–176. <https://doi.org/10.1126/science.aai8291>
- Thompson JN (1980) Treefalls and colonization patterns of temperate forest herbs. *Am Midl Nat* 104:176. <https://doi.org/10.2307/2424969>
- Tiffany LH, Knaphus G, Tiffany LH, Knaphus G (1984) The plant rusts (Uredinales) of the driftless area of northeastern Iowa. *Proc Iowa Acad Sci* 91:28–31
- Van der Putten WH, Bardgett RD, Bever JD, Bezemer TM, Casper BB, Fukami T, Kardol P, Klironomos JN, Kulmatiski A, Schweitzer JA, Suding KN, Van de Voorde TFJ, Wardle DA (2013) Plant–soil feedbacks: the past, the present and future challenges. *J Ecol* 101:265–276. <https://doi.org/10.1111/1365-2745.12054>
- Vellend M, Lechowicz MJ, Waterway MJ (2000) Environmental distribution of four *Carex* species (Cyperaceae) in an old-growth forest. *Am J Bot* 87:1507–1516. <https://doi.org/10.2307/2656877>
- Wennstrom A, Ericson L (1994) The effect of the systemic smut *Urocystis carcinodes* on the long-lived herb *Actaea spicata*. *Oikos* 71:111–118. <https://doi.org/10.2307/3546178>
- Whigham DE (2004) Ecology of woodland herbs in temperate deciduous forests. *Annu Rev Ecol Syst* 35:583–621. <https://doi.org/10.2307/annurev.ecolsys.35.021103.30000022>
- Wickham H (2009) *ggplot2: Elegant graphics for data analysis*. Springer-Verlag New York
- Wolfe BE, Rodgers VL, Stinson KA, Pringle A (2008) The invasive plant *Alliaria petiolata* (garlic mustard) inhibits ectomycorrhizal fungi in its introduced range. *J Ecol* 96:777–783. <https://doi.org/10.1111/j.1365-2745.2008.0>
- Wright JS (2002) Plant diversity in tropical forests: a review of mechanisms of species coexistence. *Oecologia* 130:1–14. <https://doi.org/10.1007/s004420100809>

Publisher's Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.