

Research Article

Plant performance was greater in the soils of more distantly related plants for an herbaceous understory species

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Abstract. Growing evidence suggests that plant–soil interactions have important implications for plant community composition. However, the role of phylogenetic relatedness in governing interactions between plants and soil biota is unclear, and more case studies are needed to help build a general picture of whether and how phylogeny might influence plant–soil interactions. We performed a glasshouse experiment to test whether degree of phylogenetic relatedness between *Aquilegia canadensis* and six co-occurring heterospecifics affects *A. canadensis* biomass through soil legacy effects. We also compared performance of *A. canadensis* in soils conditioned by invasive *Alliaria petiolata* versus native heterospecifics, hypothesizing that conditioning by *A. petiolata* would suppress the performance of the focal native plant. *A. canadensis* performed significantly better in distant relatives' soils than in close relatives' soils, and this effect disappeared with soil sterilization, consistent with close relatives sharing similar pathogens. Contrary to our expectations, soils conditioned by the invasive species *A. petiolata* versus by native species had similar effects on *A. canadensis*. The greater performance of *A. canadensis* in soils of more versus less distant relatives is consistent with a hypothesis of phylogenetically constrained pathogen escape, a phenomenon expected to promote coexistence of phylogenetically distant species. However, pairwise plant–soil feedback experiments are needed to create a stronger coexistence prediction.

Keywords: Abundance; community composition; phylogenetic signal; phylogeny; plant–soil feedbacks; soil mutualists; soil pathogens.

Introduction

Recent evidence suggests that plant community diversity is influenced by plant–soil feedbacks (PSFs) and soil legacy effects, where plants alter the performance of the next plant to grow in a given patch of soil (Kulmatiski *et al.* 2008; Bever *et al.* 2010, 2015). Plant–soil interactions are likely to be influenced by many factors,

including: plant phylogeny, soil biota, and the native or introduced status of soil-conditioning plants. Here, we explore how phylogenetic relatedness influences the response of an herbaceous species, *Aquilegia canadensis*, to soil conditioning by heterospecifics. We include sterile soil controls to gain insight on the biotic drivers of plant–soil interactions (e.g. mutualists vs. pathogens), and

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compare the effects of native conditioning species with the invasive plant, *Alliaria petiolata*.

Because closely related species often share similar characteristics such as root morphology and root exudates (Comas and Eissenstat 2009; Jacquemyn *et al.* 2011; Martos *et al.* 2012; Reinhart *et al.* 2012; Valverde-Barrantes *et al.* 2014), and because close relatives might have similar soil microbial communities in their root zones (e.g. Burns *et al.* 2015), plant species might respond similarly to the soils of closely related plants. A recent meta-analysis found that phylogenetic distance was a weak predictor of relative performance in conspecific and heterospecific soils (Mehrabi and Tuck 2015). However, performance in conspecific and heterospecific soils ('net whole soil feedback') was more similar for close relatives across 57 old-field species, and the strength of the PSF correlated with abundance patterns in these species (Anacker *et al.* 2014). Case studies have also found conflicting evidence for a correlation between phylogeny and plant-soil interactions (Liu *et al.* 2012; Mehrabi *et al.* 2015; Miller and Menalled 2015; Münzbergová and Šurinová 2015).

Soil microbial communities influence plant performance through effects of both soil mutualists, like mycorrhizal fungi, and pathogens (Bever 2003; Brinkman *et al.* 2010; Diez *et al.* 2010; Kulmatiski *et al.* 2008). For example, oomycete pathogens build up in the soils of *Prunus serotina* and suppress plant performance (Packer and Clay 2000). However, the relative importance of mutualists and pathogens to plant performance is probably system specific, and has been poorly characterized for understory herbaceous plants (Kulmatiski *et al.* 2008).

Plant-soil interactions may also depend on the native or introduced status of the plants. Non-native, introduced plants often become invasive when they enter an area that lacks their natural enemies, thus allowing them to become highly abundant and reduce the success of native competitors (Callaway *et al.* 2004). Another mechanism for plant invasiveness is the production of allelochemicals that reduce native plant performance ('novel weapons') (Callaway and Ridenour 2004). In North American temperate forests, the invasive species *A. petiolata* (garlic mustard) is known to influence soil biota through allelochemicals (Roberts and Anderson 2001; Prati and Bossdorf 2004; Barto *et al.* 2011; Cantor *et al.* 2011), which inhibit the growth and germination of arbuscular mycorrhizal fungi (AMF), which many herbaceous species utilize (Wang and Qiu 2006).

Here, we ask if the phylogenetic distance between various conditioning species and subsequently grown *A. canadensis* affects *A. canadensis* performance in live and sterilized soils. This study provides the first test for an effect of phylogenetic distance on soil legacy effects in

temperate understory plants that isolates the effects of soil biota. If soil pathogens are more important to plant performance than soil mutualists, we expect a positive influence of soil sterilization on plant performance (Bever 2003; Kulmatiski *et al.* 2008; Brinkman *et al.* 2010; Diez *et al.* 2010). Alternatively, because many of these native herbaceous species are dependent on AMF mutualists (Wang and Qiu 2006), positive effects of soil biota could lead to greater performance in live than sterilized soils. Because the invasive species *A. petiolata* is known to have allelopathic effects, we also predicted that it might suppress plant performance more than native species.

Methods

This experiment took place during the summer of 2014 at Squire Valleeview Farm in Hunting Valley, OH, USA (41°29' N, 81°25' W). We chose *A. canadensis* as our focal species because it germinates readily in the lab and, like most spring flowering herbaceous understory species, it is a long-lived perennial that associates with AMF (Hale 2007). Conditioning species were selected based on their taxonomic distance from *A. canadensis*, with two confamilial species, two species in the same order, and two more distantly related species [see **Supporting Information—Table S1**]. All species were native, except the distantly related *A. petiolata*, which is introduced.

Plant collection and soil conditioning

Five replicates of each plant species were identified and collected from the field, including soil from around the root zone of each species (Fig. 1). Whole, mature plants of roughly the same size and age (based on vegetation and perennial root-growth) were collected. Plants were collected at least 10 m from one another. After collection, plants were transplanted into pots containing a mixture of equal amounts of untreated potting soil and field soil from the root zone, keeping each species and replicate separate to accurately assess the variance across soil collections (Reinhart and Rinella 2016, Fig. 1). All conditioning plants were grown in 140 mm diameter (1.65 L) pots under a randomized placement on a potting bench inside the glasshouse and were watered by hand daily or as needed. Plants conditioned their soils for ~4 weeks before their soil was collected for sterilization and inoculation.

Inoculum preparation and sterilization

After the soil was conditioned, it was removed and homogenized using a standard US 2 mm testing sieve, again fully maintaining the independence of replicates.

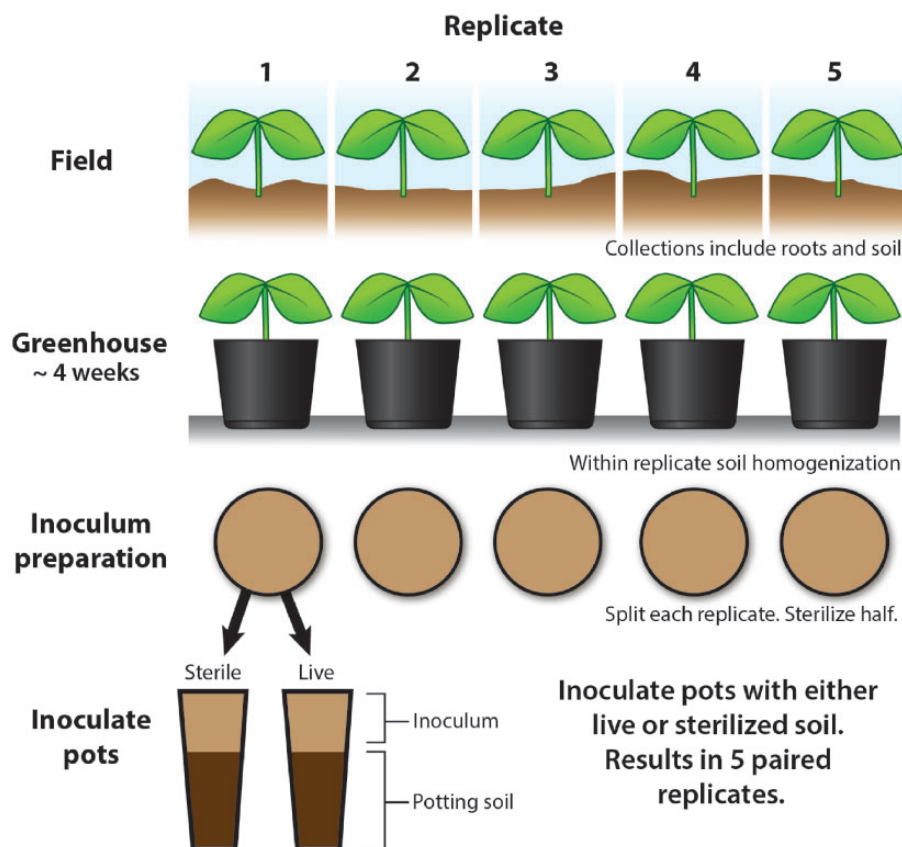


Figure 1. Experimental methods for conditioning soils. Five replicates of each of six heterospecific species [see [Supporting Information—Table S1](#)] were used to condition a mix of potting and field soils (see ‘Plant Collection and Soil Conditioning’ section), conditioned soils were either left ‘live’ or ‘sterilized’, and then *A. canadensis* was grown in each experimental treatment, resulting in paired live and sterilized soil replicates. Figure credit: Catherine Stanley, www.stanleyillustration.com, stanleyillustration@gmail.com.

All tools/equipment were sterilized between each replicate collection using a stock solution of 10 % diluted bleach. Sterilized tools were also rinsed thoroughly in water to prevent residual bleach from making contact with live soil. Half of the soil was separated for sterilization (Fig. 1) and autoclaved using a standard laboratory autoclave (Market Forge Sterilematic, model STM-E) at 121 °C for 2 h, again, fully maintaining the independence of replicate collections. The result is a paired design, with sterile and live treatments within each conditioning replicate (Fig. 1).

Focal pot preparation and inoculation

Deepots (6.4 cm diameter × 25.4 cm deep; Stuewe and Sons, Tangent, OR, USA) were prepared outside the glasshouse for planting *A. canadensis*. A meter-wide strip of weed cloth was laid along the north edge of the glasshouse and deepots were placed in blocks spaced out equally along its length. Position on the north side of the glasshouse reduced the average insolation the plants received in an attempt to mimic lower light conditions experienced in a forest understory. Pots were filled with

untreated potting soil, watered, and allowed to settle naturally with no manual compression until they were ~90 % full with roughly 500 mL of potting soil. Inoculation was achieved by adding 50 mL of conditioned soil on top of the potting soil directly prior to planting (Fig. 1). Equipment was sterilized between inoculations. Sterile and live soils were clustered within a block to avoid splash-contaminating sterilized soils during watering. Splash was minimized through spacing and careful watering techniques. Treatments were randomly assigned within blocks, and live and sterilized blocks were randomly assigned positions.

Germination, planting and harvesting

The focal species *A. canadensis* was grown in both live and sterilized soil from each of six heterospecific conditioning species [see [Supporting Information—Table S1](#)], across five-paired replicates (Fig. 1). Seeds of the focal species were ordered online through Prairie Moon Nursery (Winona, MN), cold treated for ~60 days at ~2 °C, germinated in a wet sand substrate, then placed into a growth chamber set for 12 h of light. Seedlings

were planted into treatment pots, left outside of the glasshouse from August to October, and were brought inside the glasshouse to finish growing before the first frost of the season. Plants were watered by hand daily using a mister, or as needed, depending on weather conditions and apparent soil moisture. In December plants were separated into aboveground and belowground biomass, roots were washed and dried for 7 days in a drying oven set to 30 °C. Once dried, the plants were weighed in grams using a digital scale at a resolution of 0.0001 g.

Phylogeny estimation

To estimate phylogenetic distances among species in the experiment, and to ensure that results were robust, we compared two estimated phylogenies. First, we used a molecular phylogeny, estimated *de novo* for taxa in this experiment [see [Supporting Information—Table S1](#)]. We aligned each DNA region separately in MUSCLE (Edgar 2004a, b) in the MEGA platform (version 5.2.2) and concatenated four DNA regions for analysis [see [Supporting Information—Table S1](#)]. We conducted a maximum likelihood tree search in Garli (Zwickl 2006; version 0.951) and branch lengths are in substitutions per site (Fig. 2). The result is a phylogram with fine-scale variation in phylogenetic distances among species pairs. Second, we used phyloGenerator's (Pearse and Purvis 2013) *congeneric.merge* function, which matches species in our sampled species list to genera on the global angiosperm phylogeny of Zanne *et al.* (2014). Because the genus *Anemonella* was not present in this phylogeny, we used the synonym *Anemone thalictoides*, in place of the now accepted name *Anemonella thalictoides* when conducting this merging function. The result is an ultrametric tree, with branch lengths in approximate millions of years [see [Supporting Information—Fig. S1](#)]. The phylogenetic distance between species was calculated as the summed branch lengths between them on the phylogenies. The placement of *Anemonella* in the Ranunculaceae was different for these two approaches,

and the typology of these phylogenies was otherwise congruent (Figs 2) [see [Supporting Information—Fig. S1](#)].

Data analysis

Total biomass of *A. canadensis* was log-transformed for all analyses and we used generalized linear models (GLMs) with Gaussian error structure throughout. We tested for a block effect, and finding no evidence for an effect of block ($P > 0.10$), we excluded block from all analyses. We tested for a paired replicate (Fig. 1) effect, and finding no evidence for a pair effect ($P > 0.25$), we excluded pair from all analyses. All analyses were conducted in R (version 3.0.2) (R Development Core Team 2008). Residual plots were examined, and model assumptions were well-met. Data were archived at the Dryad Digital Repository (Sweet and Burns 2017).

To test for effects of phylogenetic distance on *A. canadensis* plant performance, we modelled total biomass as a function of phylogenetic distance to the conditioning plant, sterilization treatment, and the phylogenetic distance by sterilization interaction. We compared models with phylogenetic distances based on the molecular phylogeny with those from the phyloGenerator method. Because the molecular phylogeny resulted in a more continuous range of phylogenetic distances (Figs 2, [see [Supporting Information—Table S1](#)]), we present regressions with this measure of phylogenetic distances. Because we hypothesized that phylogenetic distance effects would differ in live and sterilized treatments (Liu *et al.* 2012), we used linear models within live and sterilized treatments to describe the strength of the correlation. To account for the non-independence in the data, because branch lengths on the phylogeny may be counted more than once, we used Mantel tests on distance matrices estimated using Euclidean distances (*sensu* Weiblen *et al.* 2006; Violle *et al.* 2011; Reinhart and Anacker 2014) to test for correlations between phylogenetic distance and plant total biomass. We also

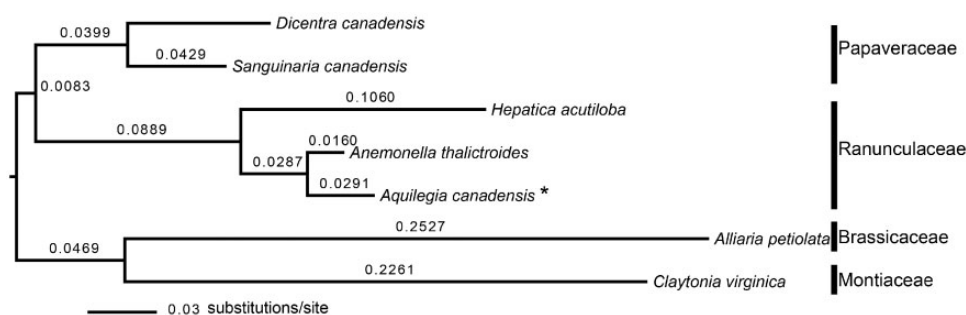


Figure 2. The molecular maximum likelihood phylogeny (phylogram), based on four DNA regions (*rbcl*, *matK*, *trnL-trnF*, ITS, [see [Supporting Information—Table S1](#)]), with branch lengths in substitutions/site above the branches. *Focal species *A. canadensis* was grown in the glasshouse-conditioned soils of six heterospecifics.

conducted Mantel tests with phylogenetic distance as a predictor with and without *A. petiolata* conditioned soils, to determine whether this invasive conditioning species influenced this relationship, compared with analyses including only the other five, native conditioning species.

To determine whether *A. canadensis* biomass depended on soil sterilization treatment or conditioning species, we used a GLM with sterilization treatment, conditioning species, and their interaction as predictors. To determine whether the introduced species, *A. petiolata*, had different effects than the native species, we contrasted native to introduced status of the conditioning species as an *a priori* contrast within this model and report the main effect and whether this contrast depended on sterilization treatment.

Results

A. canadensis plant performance was greater in soils conditioned by more distant relatives, both when

phylogenetic distances were based on a molecular phylogram ($P = 0.09$, Fig. 2, Table 1) or on a phyloGenerator ultrametric phylogeny ($P = 0.04$, Table 1). The slopes for this relationship did not depend on soil sterilization treatment (Table 1); however, phylogeny was a stronger predictor of plant biomass in live than sterilized soils, according to Mantel tests that take non-independence of branch lengths into account. Plant total biomass was greater for more phylogenetically distant heterospecific conditioning species in live soils (Fig. 3; Mantel test: Pearson correlation coefficient $r = 0.24$, $P = 0.012$). This relationship was no longer significant in sterilized soils (Fig. 3; $r = -0.03$, $P = 0.60$). When the invasive conditioning species *A. petiolata* was excluded from these Mantel tests, phylogenetic distance still correlated positively with *A. canadensis* biomass in live soils (Pearson correlation coefficient $r = 0.18$, $P = 0.047$) and again did not correlate with *A. canadensis* biomass in sterilized soils (Pearson correlation coefficient $r = 0.03$, $P = 0.36$).

Table 1. Total biomass of *A. canadensis* as a function of soil sterilization treatment, phylogenetic distance between the focal species and the conditioning species, and the sterilization by phylogenetic distance interaction.

Predictor	df	Deviance	Residual deviance	F-ratio	P-value
molecular phylogeny					
Soil sterilization treatment	1,39	1.89	21.84	3.53	0.07
Phylogenetic Distance (substitutions/site)	1,38	1.61	20.23	3.02	0.09
Sterilization × Phylogenetic Distance	1,37	0.41	19.81	0.77	0.39
phyloGenerator phylogeny					
Soil sterilization treatment	1,39	1.89	21.84	3.61	0.07
Phylogenetic Distance (MYA)	1,38	2.33	19.52	4.44	0.04
Sterilization × Phylogenetic Distance	1,37	0.15	19.37	0.28	0.60

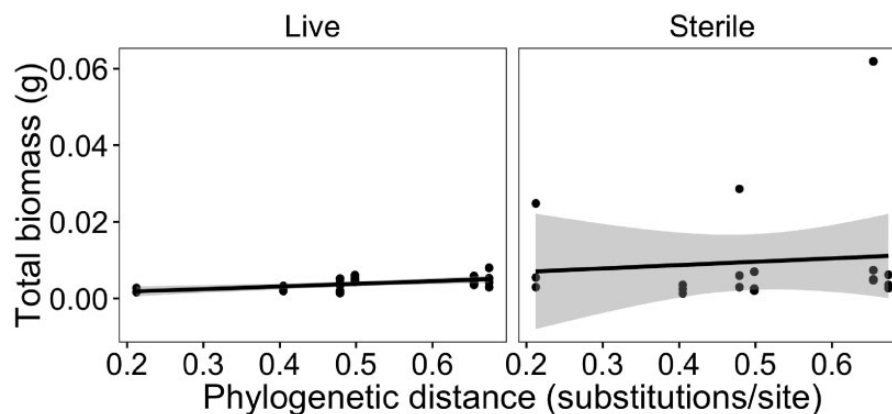


Figure 3. The biomass of *A. canadensis* was correlated with the phylogenetic distance to heterospecific conditioning species in live field soils but not in sterilized soils.

A. canadensis plant biomass was greater in sterilized than live soils (Fig. 4) and sterilization did not interact with conditioning species identity [see **Supporting Information—Table S2**] *A. petiolata* did not have a different influence on *A. canadensis* plant biomass, compared with native conditioning species ($t_{1,34} = 1.14$, $P = 0.26$), nor did the effect of native status depend on sterilization treatment ($t_{1,29} = -1.31$, $P = 0.20$).

Discussion

A. canadensis performed better in soils conditioned by more distantly related species, consistent with our hypothesis that closely related species inhibit one another through phylogenetically conserved interactions with soil microbiota, a finding consistent with results in other study systems (Liu *et al.* 2012). Second, we found that soil sterilization increased plant performance in *A. canadensis*, confirming our hypothesis that soil biota are inhibitory for this herbaceous species and suggesting that soil pathogens may play a larger role than AMF mutualists (Bever 2003; Kulmatiski *et al.* 2008; Diez *et al.* 2010). Contrary to our predictions, soil conditioned by the invasive species *A. petiolata* did not reduce performance of *A. canadensis* more than soils conditioned by native species, consistent with some evidence that *A. petiolata* may be experiencing selection for reduced allelopathy at high population densities (Lankau *et al.* 2009).

Our results are consistent with some (Liu *et al.* 2012), but not all (e.g. Mehrabi and Tuck 2015) studies of phylogenetic effects on plant–soil interactions. Many factors could explain variation in the relationship between plant phylogeny and plant–soil interactions. Experimental methods for studying PSFs vary greatly, and include field collected soils, glasshouse conditioned soils, and considerable variation in the length of time plants condition the soil, among other factors (Brinkman *et al.* 2010), and

studies that find different patterns also frequently used different methods (cf. Liu *et al.* 2012; Mehrabi and Tuck 2015). Some of these apparent discrepancies could also be influenced by variation in phylogenetic scale among studies. For example, Mehrabi and Tuck (2015) studied soil conditioning at the level of plant families, and found no correlation between phylogenetic distance and the strength of PSFs. Alternatively, Liu *et al.*'s (2012) comparison included congeners and confamilials, as have other studies finding that congeners similarly influence one another through the soil (Diez *et al.* 2010; Burns and Strauss 2011; Callaway *et al.* 2013). Because our study includes two confamilials, but no congeners, it is intermediate in phylogenetic scale, relative to other studies. Future studies should consider manipulating experimental method (e.g. length of conditioning) and phylogenetic scale to directly address these issues. The relative importance of mutualists, pathogens, and other drivers of PSFs are also likely to vary among study systems, and comparisons across ecological gradients are still needed (Smith and Reynolds 2015).

Our comparison of live with sterilized soils suggests that a role of phylogeny could be driven in part by soil biota for *A. canadensis* (Bever *et al.* 2010; Brinkman *et al.* 2010). This result is consistent with a previous study in a tropical tree, where *Castanopsis fissa* had greater survival in soils of more distant relatives in live soils and not fungicide-treated soils (Liu *et al.* 2012). Thus fungal pathogens in the soil might be shared by closely related plant species, and escape from these pathogens might increase plant performance. Closely related plants have also been shown to have similar soil fungal communities in their root zones in the field, even for congeners that occur in different habitat types (Burns *et al.* 2015), also consistent with plant relatedness influencing soil microbiota. Studies of foliar pathogens also suggest that phylogeny might influence how microbes structure plant communities (Parker *et al.* 2015), suggesting that phylogenetic conservation of pathogen effects, both above and below ground, might have broad implications for plant community structure.

Our evidence is consistent with pathogens influencing performance in heterospecific soils (Bever *et al.* 2015); however, an alternate explanation for greater performance in sterilized soils is that mycorrhizal fungi can be parasitic if the net cost of symbioses is greater than the net benefit received by the host plant (Johnson *et al.* 1997; Lapointe and Molard 1997). AMF fungi can function along a continuum ranging from mutualistic to parasitic, depending on environmental conditions and the needs of the host plant (Johnson 1993; Klironomos 2003). In the stressful conditions that plants often experience in the field, AMF mutualists can be highly beneficial, but

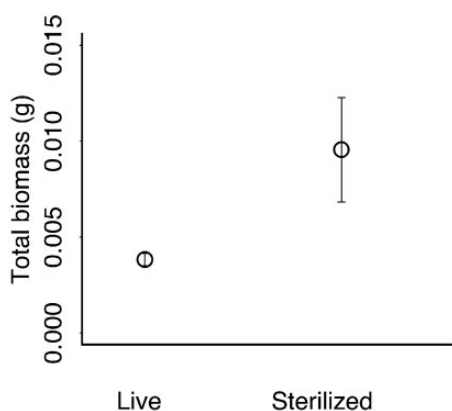


Figure 4. The biomass of *A. canadensis* across soil sterilization treatments (Table 1).

under less stressful conditions such as those experienced in a glasshouse setting, the cost of harboring AMF fungi may actually be greater than the benefits received. This could be an alternative explanation for why we observed greater *A. canadensis* biomass in sterilized compared with live heterospecific soils.

Due to the large amount of literature documenting the negative allelopathic effects of *A. petiolata* on native plant communities (e.g. Roberts and Anderson 2001; Prati and Bossdorf 2004; Barto et al. 2011; Cantor et al. 2011), we expected to find that soil conditioned by *A. petiolata* would decrease plant performance in a native plant, *A. canadensis*. However, our results showed effects of *A. petiolata* conditioned soil did not differ from effects of native species, on average. This was surprising considering *A. petiolata* limits the growth of AMF (Cantor et al. 2011), which *A. canadensis* utilizes (Wang and Qiu 2006). One explanation for this finding may be that there are differences in allelopathic concentration in above-ground and belowground structures in *A. petiolata*, suggesting that allelochemical deposition in the soil may be more significant coming from senescing leaves and stems (Cantor et al. 2011), rather than the roots which we used to condition the soil. Because *A. petiolata* is an invasive species that spreads rapidly throughout an invaded area, this species often forms large monocultures. Populations of this species that had been established for 50 years showed reduced production of allelopathic chemicals (Lankau et al. 2009), perhaps because of the inhibitory effect *A. petiolata* has on its own species at high densities (Pardini et al. 2009, 2011), which should select for reduced allelopathy at older invasion sites. The specimens collected from the field were part of a high-density patch of *A. petiolata*. Because the field site for this experiment has been invaded for a long period of time, this is a reasonable explanation for why garlic mustard was not found to inhibit the performance of *A. canadensis*.

Conclusions and Future Directions

If plants often perform better in the soils of more distant relatives, plant–soil interactions could explain patterns in community composition, such as the frequent observation of greater co-occurrence between distantly related plants at small spatial scales (Valiente-Banuet and Verdu 2007; Vamosi et al. 2009). A common explanation for this pattern is competition: if closely related plants are similar in their niche (Darwin 1859), they might compete more strongly than more distant relatives (e.g. Burns and Strauss 2011). Thus competitive exclusion by close relatives could lead to communities of more distantly related

species (Webb et al. 2002). Our results suggest that plant–soil interactions could be an alternative explanation in some systems. If plants escape from pathogens in distant relatives' soils, plant communities should be composed of more distantly related species than a random assemblage (Liu et al. 2012). This effect has been called a 'phylogenetic Janzen-Connell' effect (Liu et al. 2012), and could help explain the high diversity in systems such as tropical trees (Liu et al. 2012) and perhaps temperate herbaceous understories. Future research employing pairwise PSF experiments with con- and heterospecific plants of varying phylogenetic relatedness is needed to fully test the phylogenetic Janzen-Connell effect in temperate woodland and other systems.

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Contributions by the Authors

J.H.B. conceived the idea. J.H.B. and D.D.S. designed and performed the experiment, analysed the data, and wrote the manuscript.

Conflicts of Interest Statement

None declared.

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Data Accessibility

Data from this project are archived with the Dryad Digital Repository. (Sweet and Burns 2017) doi:10.5061/dryad.6528d

Supporting Information

The following additional information is available in the online version of this article—

Table S1. GenBank accessions used to estimate a phylogeny amongst species in this study.

Figure S1. The ultrametric phyloGenerator phylogeny, with branch lengths in approximate millions of years. Branch lengths are shown above the branches.

Table S2. Total biomass of *A. canadensis* as a function of soil sterilization treatment, the conditioning species identity, and the sterilization by conditioning species interaction.

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