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Species invasion alters local adaptation to soil communities in a native plant

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Abstract. Plant populations are often adapted to their local conditions, including abiotic factors as well as the biotic communities with which they interact. Soil communities, in particular, have strong effects on both the ecology and evolution of plant populations. Many invasive plant species alter the ecological relationships between native plants and soil communities; however, whether invaders also alter the evolutionary dynamics between native plants and soils is less well known. Here I show that populations of a native annual, *Pilea pumila*, shift from being maladapted to adapted to their local soil community with increasing history of invasion by *Alliaria petiolata*, an invader known to alter microbial communities. Additionally, native populations showed a signal of adaptation to soils of particular invasion stages, independent of local coevolutionary dynamics. These results suggest that invasive species affect not only the ecological, but also the evolutionary relationships of native species.

Key words: Alliaria petiolata; *invasion history; local maladaptation;* Pilea pumila.

Introduction

Local adaptation, in which local populations of a species have higher relative fitness in their home site compared to foreign populations, is commonly observed in plant species (Linhart and Grant 1996, Savolainen et al. 2007). Local adaptation requires that adaptive landscapes differ spatially, thus favoring different optimal trait combinations across sites, and restricted gene flow such that populations can respond to their local selection pressures without swamping from maladapted populations (Kawecki and Ebert 2004). The particular biotic and abiotic conditions exerting the selection pressures that lead to local adaptation can be highly variable across populations, and multidimensional even within a population (Linhart and Grant 1996). Soil conditions have particularly strong effects on plant growth and can be spatially heterogeneous, and are thus likely sources of the divergent selection necessary for local adaptation. Previous studies have found plant populations adapted to local soils in the broad sense (Macel et al. 2007, Raabova et al. 2011), as well as to particular aspects of soils such as nutrient availability (McGraw and Chapin 1989) and chemistry (Sambatti and Rice 2006, Meimberg et al. 2010, Turner et al. 2010)

Soils contain highly diverse biotic communities that can affect plant growth, due to the presence of direct plant parasites and pathogens, mutualistic species like mycorrhizal fungi, or free-living microbes that increase nutrient availability via fixation or decomposition. Soil communities exert considerable control over plant community structure and diversity through their differential effects on and responses to plant species (Klironomos 2002, Kardol et al. 2006, Kulmatiski et al. 2008). A growing body of literature suggests that soil communities may affect the evolution as well as ecology of plant populations (Johnson et al. 2010, Felker-Quinn et al. 2011, Lankau et al. 2011, Lau and Lennon 2011). Since soil microbial communities vary in their composition and function spatially, plants may be selected to adapt to their local soil community. However, the adaptive landscape created by biotic communities may not be stable if the interacting species are simultaneously adapting to the plant as well. In a coevolving system, if one of the interacting species evolves more quickly than the other, this can lead to a pattern of local maladaptation, in which genotypes perform worst in their own site because their enemies have developed particular adaptations to them. Local adaptation (or maladaptation) to soil communities (or components of the communities) has been documented (Schultz et al. 2001, Johnson et al. 2010), but whether plant populations tend to be adapted or maladapted to their local soil communities, and what controls this variation, is unclear.

Soil communities affect and respond to changes in plant community composition. In particular, exotic invasive plants can alter microbial communities by increasing the abundance of generalist pathogens (Mangla et al. 2008) or changing the composition or abundance of mutualists (Stinson et al. 2006). These changes can feed back to promote the growth of the invader or reduce the growth of competing native species (Callaway et al. 2004, van der Putten et al. 2007). However, no study to date has investigated whether invasive plants can alter the (co)evolutionary

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dynamics between native plants and soils. If native plants are adapted to local soil communities, then disruption of the soil community by an invasive plant could lead to the breakdown of local adaptation. On the other hand, if plants are locally maladapted (e.g., due to the presence of adapted pathogen strains), then disruption of soil communities by invaders may alter this pattern to the native plant population's benefit.

Here, I tested whether populations of the native *Pilea pumila* (Urticaceae) are locally adapted to their home soil community across six plant populations. These populations varied in their history with the invasive *Alliaria petiolata* (Brassicaceae), which is known to alter soil microbial communities broadly (Lankau 2011*b*), and specifically reduces the abundance and alters the composition of arbuscular mycorrhizal fungal communities (Stinson et al. 2006, Barto et al. 2011, Lankau 2011*a*, *b*). *A. petiolata* does not form mycorrhizal connections, unlike the majority of forest understory species including *P. pumila*. I hypothesized that *P. pumila* populations from an area with no history of *A. petiolata* invasion would be locally adapted to their home soil, but that the pattern of local adaptation would weaken for native populations with a longer history of *A. petiolata* invasion due to disruption of the historical microbial community structure by the invader. Additionally, I hypothesized that plant populations would be adapted specifically to the history of *A. petiolata* invasion at their site; in other words, *P. pumila* populations would show higher relative fitness when grown in soils from areas with a similar history of *A. petiolata* invasion than in soils with much shorter or longer histories of invasion.

Methods

Plant and soil sources

Seeds from up to 20 maternal families of *P. pumila* were collected from seven populations spaced from Illinois to New York, USA in September 2009 (see Appendix A for site characteristics). For the sites with *A. petiolata* invasion (all except the Vermillion River Observatory site in Illinois), seeds were collected from *P. pumila* plants growing in close proximity to *A. petiolata*. Seeds were cold stratified for three months in wet soil, and germinated in May 2010. One population (Ball State University, in Indiana) did not produce sufficient seedlings and so was not used in this experiment as a plant source, although soils from that site were included. Prior to stratification, a subsample of 20 seeds per site were weighed for use as a future covariate. Soils were collected from these seven sites in May 2010. Approximately 2 L of soil was collected from the top 10 cm of soil each site from several locations where both *P. pumila* and *A. petiolata* (excepting the uninvaded VRO site) were present, then pooled to provide one soil sample per site. Soils were kept as cool as possible in the field, and stored at 4°C until the initiation of the experiment. A sample of each soil type (both autoclaved and unmanipulated versions) was submitted to the University of Georgia Agricultural and Environmental Services Laboratory and analyzed for lime buffering capacity, pH, Ca, Mg, Mn, K, Zn, available P, NO_3, and NH_4.

The history of *A. petiolata* invasion at each site was estimated from a spatially kriged map of date of first report using ~600 dated herbarium specimens (Lankau et al. 2009). The VRO site has never been invaded by *A. petiolata* due to the vigilance of the land manager (S. Buck, *personal communication*), but is in an area with heavy *A. petiolata* invasions nearby. Thus, there is no reason to suspect that the invader could not readily invade the site were management efforts to cease.

Experimental design

Replicates of each plant population were grown in pots inoculated with live or sterilized soils from each site. Due to the lack of germination for one population, this experiment consisted of six *P. pumila* populations crossed with seven soil sources and two soil treatments (live or sterilized) for a total of 84 combinations. Each combination was replicated five times, with seed from a different maternal family for each replicate per treatment combination, for a total of 420 pots (6 plant populations × 7 soil sources × 2 soil treatments × 5 replicates). While the within population replication was low, the primary goal of this study was to test whether patterns of local adaptation varied consistently across the chronosequence of *A. petiolata* invasion; thus, the appropriate unit of replication for most analyses was the population or site.

Each plant was grown in a 650-mL Deepot (Stuewe and Sons, Tangent, Oregon, USA), which was filled with 500 mL of a sterilized background potting mixture, then 20 mL of the treatment soil, and finally topped with another 80 mL of the background mixture (leaving 50 mL of space unfilled to reduce contamination between pots). Prior to the experiment ~1.5 L of soil from each site was autoclaved twice for two hours each time (allowing the soils to cool overnight in between). Seedlings were germinated in flats filled with the same background potting mixture, and once the experimental pots had been filled, one seedling of the appropriate population was planted in each pot. I attempted to use one individual from the same five maternal families in each soil source, although this was not always possible given the number of seedlings per family. In any case, siblings were never used in the same treatment combination.

Plants grew for four months, at which point almost all individuals had flowered and were beginning to senesce. *P. pumila* plants can produce thousands of seeds in individual achenes, continuously throughout much of the growing season. As such, it was not feasible to count seeds for each individual. However, total biomass is a good predictor of seed production for this annual species in these conditions ($R^2 = 0.86$, $P = 0.0004$, $n =$

9 samples). Therefore, I collected the total above- and belowground biomass of each plant at the end of the experiment and dried the tissue for 48 hours at 60°C.

To confirm that the autoclaving treatment effectively reduced microbial interactions with plant roots, roots from 10 live and 10 sterilized pots were randomly sampled at the end of the experiment. Roots were cleared with hot KOH for 7 minutes, bleached with 3% H_2O_2 for 30 minutes, acidified with 1% HCL for 60 minutes, and then stained with Direct Blue (Acros Organics, Thermo Fisher Scientific, Morristown, New Jersey, USA). Stained roots were mounted on slides and fungal colonization scored using the grid-line intersect method (McGonigle et al. 1990). At least 50 root intersections were scored per plant, and the presence of arbuscules, vesicles, hyphae, and dark septate endophytes were recorded at each intersection. Sterilized soil had significantly lower frequency of fungal colonization (all structures, 70.8% + 0.06% [mean + SE] for live vs. 34.5% + 0.05% for sterilized pots, $F_{1,20} = 20.83$, $P = 0.0002$; AMF structures only, 63.9% + 0.06% for live vs. 17.2% + 0.05% for sterilized pots, $F_{1,20} = 36.6$, $P < 0.0001$).

Analysis

I calculated the total biomass of each individual (above- and belowground biomass), and then statistically controlled for potential maternal effects by regressing biomass against the average seed mass for that population and the initial height of the individual seedling at the start of the experiment. I used this regression to create a detrended data set in which each individual's residual value was added to the predicted biomass at the global mean values for seed mass and initial seedling height. I used this detrended dataset to answer the following questions.

Are populations genetically differentiated with respect to interactions with soil communities?—I first tested whether biomass differed between plant populations and/or soil sources, and whether the plant population effect differed across soil sources (i.e., whether there was a gene by environment interaction). Using all of the samples, I ran a linear model with plant population, soil source, and the soil sterilization treatment and all two and three way interactions as fixed effects. Plant population and soil source were treated as fixed effects because they were not sampled randomly across the range of *A. petiolata*, but rather chosen specifically to represent a chronosequence of invasion age. I also included two covariates to control for experimental variation due to greenhouse positioning: a variable (bench position) that controlled for the location of a rack of pots on the greenhouse bench, and a second variable (rack position) that controlled for location of a pot within a rack. An a priori contrast was used to test for a consistent pattern of local adaptation (or maladaptation) across all soil sources, by comparing samples local to a given soil to samples foreign to that soil across all soils. Because the soil sterilization treatment had a large and significant effect on plant biomass, separate ANOVA models were run for the live or sterilized treatments, and the local vs. foreign contrast tested within each subset.

Does the pattern of local (mal)adaptation to soils change with increasing history of invasion?—I was particularly interested in whether the pattern of local (mal)adaptation varied quantitatively across sites of increasing history of invasion. Because invasion history was confounded with soil source and plant population (each soil source and plant population had a single, unique estimate of invasion history), it was not possible to include invasion history in models with population or soil source terms. Therefore, to avoid psuedoreplication, I averaged the five replicates per treatment combination, in order to use plant population as the unit of replication for analyses. Local adaptation to soils was measured by creating a "local vs. foreign" treatment, in which plant populations growing in soil from the same source site were classified as local treatments, while plant populations growing in soil from a site different from where their seeds were collected were classified as foreign treatments. Kawecki and Ebert (2004) suggest that local vs. foreign comparisons provide stronger tests of local adaptation than "home vs. away" comparisons, which test whether a given population has higher fitness in its home site compared to other sites. The ANCOVA model included the soil sterilization treatment, the local vs. foreign treatment, and the estimated invasion history (years since first report) for the site from which the soil was collected, along with all two and three way interactions. Note that while the invasion history term is confounded with soil source, these effects are not identical: the soil source term included in the previous linear model fit seven parameters for the seven soils, to incorporate all of the variation attributable to soil sources, while the invasion history term used here fits a single parameter, accounting for only that variation among soil sources that can be attributed to a linear pattern across the chronosequence. A significant local vs. foreign effect would be evidence for local adaptation (or maladaptation depending on the direction of the effect) to soils, while significant interactions of this treatment with invasion history would be evidence that the pattern of local adaptation to soils changes with increasing history with the invasive *A. petiolata*. Finally, interactions between these terms and the soil sterilization treatment suggest that the patterns depend on a living soil community. To further test whether these patterns could be explained by differences in soil chemistry, I first used PCA to reduce the variation among the 10 soil chemical measures to three orthogonal axes that retained ~92% of the original variation (see Appendix C). Including these three PCs as additional covariates in the ANCOVA model did not qualitatively change the results of any other model terms (see Appendix C for full results).

If the mean performance of all plant populations varies across soil sources, independent of whether the plant population is local or foreign to that soil, this could complicate interpretations of local adaptation. Thus, I also performed the same analysis using residual values of biomass from an ANOVA that only included the seven soil sources as a categorical variable. This had the effect of statistically removing any mean differences in plant biomass across soils, while maintaining the relative differences between plant populations grown in a given soil. Thus, in this analysis a significant local vs. foreign effect tests whether plant populations in their home soil have greater biomass *relative to the other plant populations growing in that soil,* independent of the overall quality of that soil for *P. pumila* growth. Because the mean differences between soil sources have been removed, this eliminated any main effect of soil invasion history. However, the soil invasion history term could still interact with other terms. For instance, a local vs. foreign by invasion history interaction tests whether the relative advantage of local vs. foreign populations increases or decreases in soils with greater invasion history, independent of any overall differences in soil quality for *P. pumila* growth.

Variation across soils in the sterilized soil treatment should primarily reflect abiotic differences among soils, while variation in the live soil treatment reflects both biotic and abiotic differences. Therefore, to isolate plant responses to soil biota, I used the relative interaction intensity (Weigelt and Jolliffe 2003), calculated as

$$\text{RII} = \frac{\text{biomass in live soil} - \text{biomass in sterilized soil}}{\text{biomass in live soil} + \text{biomass in sterilized soil}}.$$

RII was calculated for each population in each soil source, using the average of the five replicates per population in each soil source and treatment. RII is bounded between −1 and 1, and in this situation measures whether the net effect of the soil community was negative (RII $<$ 1), neutral (RII $=$ 0), or positive (RII $>$ 1) for the plant population. I chose to use RII, rather than the percent change in biomass in live vs. sterilized soil because RII is less sensitive to inflation by the very small biomass measures in sterilized soil that occurred for some populations in some soils. RII was then used as the dependent variable in an ANCOVA model that included the local vs. foreign classification, the estimated invasion history of the soil source, and their interaction as predictors. Again, I repeated this analysis using residual values of RII after removing the mean differences between the seven soil sources.

Are native populations adapted to soil invasion history, independent of local factors?—I was additionally interested in whether plant populations harbored adaptations to the invasion history of soils, independent of their degree of adaptation to their specific local soil. To test this, I calculated the difference in invasion history between the plant population source and soil source for each population × soil combination. I then regressed the RII of plants in each combination against the difference in invasion history for that combination. A linear trend would suggest that plants perform better with soil communities with longer (or shorter) invasion histories, independent of the invasion history of that plant population. On the other hand, a significant quadratic relationship (convex down or hump-shaped) would imply that plant biomass is optimized when plants grow in soils with a similar invasion history as the plant population. Plant populations in their local soil would have a difference in invasion history of zero; thus, a strong pattern of local adaptation could create a significant quadratic relationship. Therefore, I also performed this analyses with the local comparisons removed: if the relationship remains significantly hump-shaped, this would suggest that plants have developed adaptations to the general structure of soil communities present at a given stage of invasion, independent of direct coevolution between plants and soil microbes at a given site. Again, these analyses were performed with raw RII and with residual RII after removing mean effects of soil sources. All of the above analyses were performed in JMP Pro 9 (SAS Institute, Cary, North Carolina, USA).

Results

Are populations genetically differentiated with respect to interactions with soil communities?

Plant biomass differed substantially both among source populations and among soil inocula from different sites (plant population effect, $F_{6,315} = 2.78$, $P = 0.01$; soil source effect, $F_{6,315} = 3.43$, $P = 0.003$; Appendix B: Table B1). Additionally, biomass was significantly lower in the live vs. sterilized soil treatment, but this effect varied among plant populations and soil sources (soil treatment effect, $F_{1,315} = 69.1$, $P < 0.0001$; soil treatment × plant population, $F_{5,315} = 2.77$, $P = 0.02$; soil treatment × soil source, $F_{5,315} = 7.80$, $P < 0.0001$; Table B1). Plant population responses to soil sterilization differed marginally across soil sources (soil treatment × plant population × soil source, $F_{30,315} = 1.41$, $P = 0.08$; Appendix B).

When grown with live soil inocula, the performance of plant populations differed significantly among soil sources, indicating a gene-by-environment interaction (plant population × soil source, $F_{30,155} = 1.76$, $P = 0.02$). There was no indication of a gene-by-environment interaction for plants grown in sterilized soil (plant population × soil source, $F_{30,157} = 1.08$, $P = 0.37$). However, the gene-by-environment interaction in live soil was not structured in a way suggestive of local adaptation, since the plant population local to a given soil source did not perform better (or worse) on average than populations foreign to that soil, averaged across all soil sources (local vs. foreign contrast, $F_{1,155} < 0.18$, $P > 0.066$ for both live and sterilized soils, Appendix B).

TABLE 1. ANCOVA models of *Pilea pumila* biomass or residual biomass after removing mean differences between soil sources.

Effect	Biomass		Residual biomass	
	F	*P*	*F*	*P*
Soil treatment	**19.83**	**<0.0001**	**22.62**	**<0.0001**
Local vs. foreign	0.33	0.57	0.27	0.61
Soil trt × lvf	0.01	0.92	0.01	0.91
Soil invasion history	0.82	0.37	0.02	0.90
Soil trt × soil hist	**5.45**	**0.02**	**6.21**	**0.01**
Lvf × soil hist	0.04	0.83	0.03	0.87
Soil trt × soil hist × lvf	*3.68*	*0.06*	**4.20**	**0.04**

Notes: Soil treatment (Soil trt) levels are live vs. sterilized soils. Local vs. foreign (Lvf) refers to whether the *P. pumila* population grew in soil from its own source site (local) or not (foreign). Soil invasion history (Soil hist) is the estimated years since first report of *Alliaria petiolata* at the site from which the soil inoculum was sampled. Boldface text highlights model terms significant at $P < 0.05$; italics denote marginally significant model terms ($P < 0.10$). Degrees of freedom are 1, 81 for all effects.

Does the pattern of local (mal)adaptation to soils change with increasing history of invasion?

While there was no consistent pattern of local adaptation across all sites, this masked significant variation in the local vs. foreign comparison across soils of different invasion history. In order to test whether local (mal)adaptation varied quantitatively across the invasion chronosequence, I averaged the five replicates per plant population × soil source × soil treatment combination, in order to use plant population as the unit of replication. When including the invasion history of the soil source and its interactions with the local vs. foreign contrast and the soil sterilization treatment into the ANCOVA model, there was a significant interaction between soil invasion history and the soil sterilization treatment, and a marginally significant three way interaction between soil invasion history, soil sterilization treatment, and the local vs. foreign contrast (Table 1). Using the relative interaction intensity (RII) to isolate the response of plant populations to different soil communities, I again found a significant interaction between invasion history of the soil source and the local vs. foreign comparison (Table 2). Interestingly, there was no indication that soil quality increased or decreased consistently with invasion history when considering only the foreign comparisons, either in the live or sterilized soil or in their RII (Fig. 1 A, C, E). Similarly, there was no trend for plant populations with a longer or shorter history of interaction with *A. petiolata* to have higher or lower biomass across all soils ($P > 0.17$ for biomass in live or sterilized soil or RII). However, when considering only the local comparisons, total biomass increased strongly in the live soil, while decreasing in the sterilized soil, with increasing invasion history (Fig. 1A and C). Together this led to a very strong increase in RII with increasing invasion history (Fig. 1E). None of these patterns changed when including the three principle components to control for variation in soil chemistry (Appendix C).

Testing for local adaptation across multiple sites requires one to compare the relative, rather than absolute fitness, of local vs. foreign populations across sites. Since the seven soil sources differed in their average quality for *P. pumila* growth, comparisons of raw biomass may be misleading. Therefore, I also analyzed residual biomass and RII, in which the mean differences between soil sources were removed in order to focus on the relative biomass of populations within a given soil source. Using residual biomass, the three-way interaction between the soil sterilization treatment, invasion history of the soil source, and the local vs. foreign comparison was significant (Fig. 1B, D; Table 1). Similarly, when analyzing residual RII, the local vs. foreign comparison interacted significantly with the invasion history of the soil source (Table 2). These interactions arose because in soils with no or only a short history of invasion by *A. petiolata*, the local *P. pumila* population tended to perform poorly relative to foreign populations, while this pattern reversed in soils with a long history of invasion, where the local population performed better than any foreign populations (Fig. 1F). Again, none of these patterns changed when including the three principle components to control for variation in soil chemistry (Appendix C).

Are native populations adapted to soil invasion history, independent of local factors?

To test whether *P. pumila* populations developed adaptations to the soil community present at particular stages of invasion, I regressed the RII (and residual RII after removing site effects) against the difference between the invasion history of the plant population and the invasion history of the soil community in which it was grown. When including all plant–soil combinations, there was a marginally significant quadratic relationship for raw RII ($R^2 = 0.12$, $P = 0.051$), and significant relationship with residual RII ($R^2 = 0.12$, $P = 0.046$), with RII optimized when the invasion history of the plant population and soil community were similar (Fig. 2A and B). This relationship was obscured to some

TABLE 2. ANCOVA models of the relative interaction intensity (RII) for *P. pumila* populations in live vs. sterilized soil.

Effect	RII		Residual RII	
	F	*P*	*F*	*P*
Soil invasion history	**8.09**	**0.007**	2.87	0.098
Local vs. foreign	0.27	0.609	0.01	0.912
Lvf × soil hist	**5.17**	**0.029**	**6.17**	**0.018**

Notes: RII is the ratio of the difference in biomass between the treatments to the sum of biomass in the two treatments. Residual RII is the residual RII score after removing mean differences between soil sources. Boldface text highlights model terms significant at $P < 0.05$. Degrees of freedom are 1, 41 for all effects.

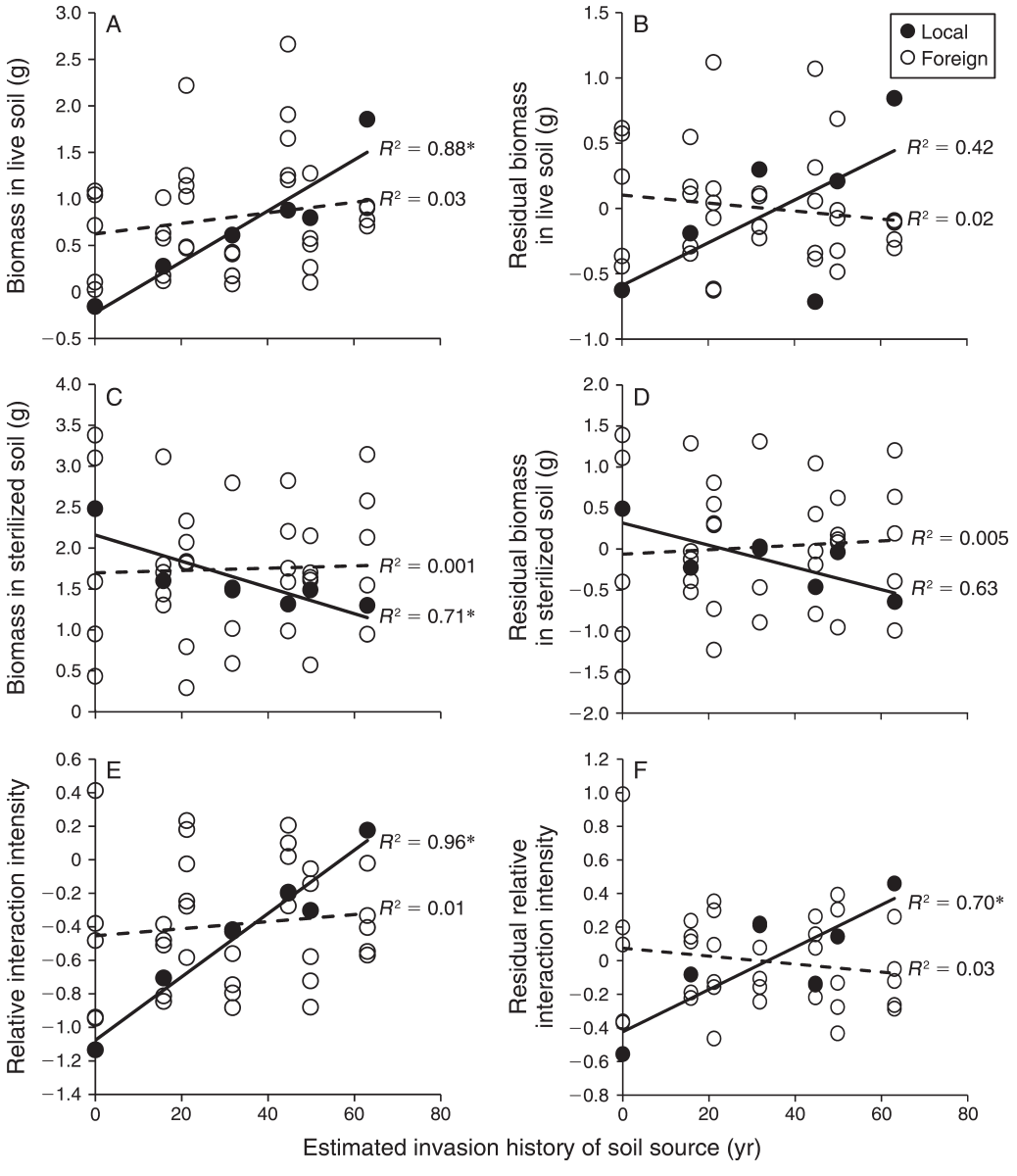

FIG. 1. *Pilea pumila* (A, C) biomass, (B, D) residual biomass after removing mean differences between soil sources, (E) relative interaction intensity (RII) of live vs. sterilized soil, and (F) residual RII after removing mean differences between soil sources vs. the estimated invasion history of the site from which soil inocula were sampled (estimated years since first report, see *Methods* for details). Each point represents one *P. pumila* population in one soil source (mean of five replicates per population per soil source). Solid symbols denote "local" combinations, *P. pumila* populations growing in soil sampled from the same source site. Open symbols denote "foreign" combinations, *P. pumila* populations growing in soil sampled from a different source site. Asterisks denotes R^2 values from linear regressions with slopes significantly different from 0 at $P < 0.05$.

degree by the wide variation in RII among local comparisons (difference in invasion histories = 0), discussed above. When local comparisons were removed from the analysis, the hump-shaped relationship tightened for both raw ($R^2 = 0.17$, $P = 0.027$) and residual RII ($R^2 = 0.14$, $P = 0.046$, Fig. 2A and B), primarily due to the reduction in variability in the center of the graph (difference in invasion history = 0) rather than a change in the shape of the curve (Fig. 2A and B, solid vs. dotted lines).

DISCUSSION

Soil communities exert considerable control over plant community structure and diversity through their differential effects on and responses to plant species (Klironomos 2002, Reynolds et al. 2003, Kardol et al. 2006). A growing body of literature suggests that soil communities may affect the evolution as well as ecology of plant populations (Johnson et al. 2010, Felker-Quinn et al. 2011, Lankau et al. 2011, Lau and Lennon 2011).

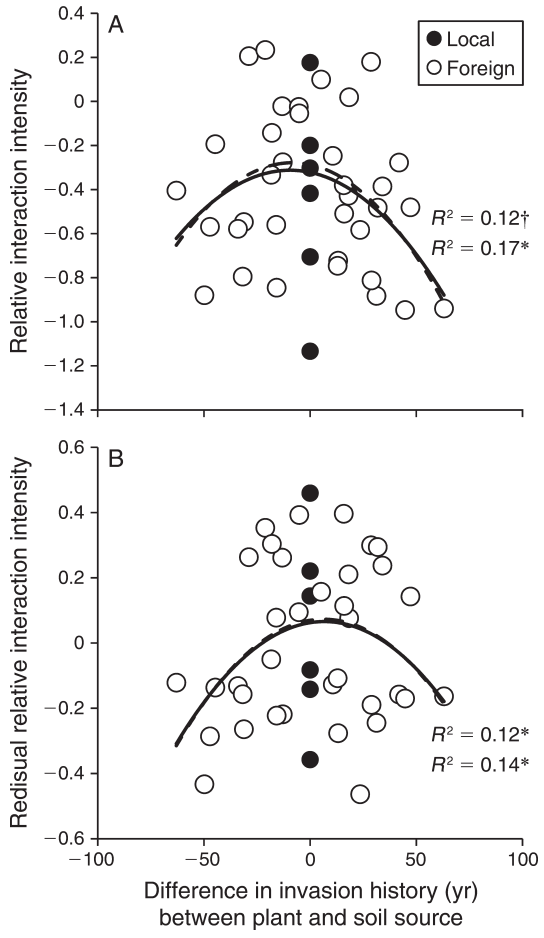

FIG. 2. (A) Relative interaction intensity and (B) residual RII after removing mean differences among soil sources graphed against the difference in invasion history between the plant population and soil source. Each point represents one *P. pumila* population in one soil source. Solid symbols denote "local" combinations, *P. pumila* populations growing in soil sampled from the same source site. All "local" combinations have a difference in invasion history equal to 0. Open symbols denote "foreign" combinations, *P. pumila* populations growing in soil sampled from a different source site. Trend lines represent quadratic regressions for all points (solid line) or only "foreign" combinations (dashed line). In both cases the higher R^2 value refers to the dashed line. Asterisks denotes R^2 values from regressions where the quadratic term was significantly different from 0 at $P < 0.05$; daggers denote regressions where the quadratic value was marginally significantly different from 0 ($P < 0.10$).

Here, I show that populations of a native annual varied in how adapted they were to their local soil communities, and this variation was explained in part by the history of invasion by an exotic plant known to alter soil communities. Furthermore, even when excluding local adaptation, native plant populations tended to have the highest growth in soil communities with a similar history of invasion, suggesting that populations of this native plant develop adaptations to consistent changes in soil community structure or diversity caused by the invader, in addition to the unique coevolutionary dynamics that occur in each local community.

I originally hypothesized that native plant populations would be locally adapted to their soil communities, especially in areas with no or only a short history of invasion by *A. petiolata*. Additionally, I hypothesized that, since *A. petiolata* alters soil microbial communities, local adaptation would decrease with increasing history of invasion, since the invader would push soil communities away from the original composition to which native plants were presumably adapted. However, the data showed the opposite pattern: in the uninvaded soil, the local population had the most negative response to its own soil community compared to the other plant populations. This pattern shifted to one of local adaptation as the history of *A. petiolata* invasion at a site increased. It is important to note that the overall quality of the soil communities across the seven sites did not vary with invasion history when averaging across all of the "foreign" populations planted in them. So, it was not the case that a longer history of *A. petiolata* increased or decreased soil quality in any general sense; what changed was the relative fitness of the local population vs. the five foreign populations in a given soil.

Local maladaptation, as observed in the uninvaded soil, can occur in coevolving systems if the target species is behind in a coevolutionary arms race with one or more other species. Since soil communities are phylogenetically and functionally diverse (containing plant pathogens, plant mutualists, saprophobes, etc.), and composed of microbial species with high population sizes and short generation times, plants may frequently interact with microbial species that are better able to adapt to the plant population than the other way around. For specialized microbial species (e.g., pathogens), the selection to adapt to the local host genotypes is likely to be strong and consistent (Springer 2007). Plants, on the other hand, interact simultaneously with a wide variety of species, including competitors, herbivores, pathogens, and mutualists, and the diversity of selection pressures imposed by the different interactors may inhibit a consistent response to the selection imposed by any particular species due to conflicting selection on the same trait or genetic correlations between traits (Iwao and Rausher 1997). For example, Lau and Lennon (2011) found that selection differentials on biomass for *B. rapa* plants were stronger when grown with simplified vs. complex soil microbial communities.

The complexity of the coevolutionary adaptive landscape may provide a possible explanation for the unexpected finding that a longer history of invasion by *A. petiolata* led to a greater signal of local adaptation to soil communities. *A. petiolata* alters soil communities through the production of toxic secondary compounds (Callaway et al. 2008, Cantor et al. 2011). One result of this is likely to be a reduction in community diversity and complexity over time as the invader extirpates all

but the most resistant microbial taxa. This is consistent with the reduction in taxa richness in bacterial, fungal, and arbuscular mycorrhizal fungal communities in soils across most of the chronosequence of *A. petiolata* invasion (Lankau 2011*b*). In complex, uninvaded soil communities, plant populations may be locally maladapted as numerous pathogenic species adapt to the local plant genotypes while the plant population is constrained by the diversity of interactions from adapting efficiently to any one interacting species. Plant populations interacting with a less complex soil community may be better able to respond to the selection pressures imposed by particular microbial taxa (or groups), leading to the switch from local maladaptation to adaptation across the chronosequence of *A. petiolata* invasion. Further research will be necessary to conclusively determine which aspects of soil communities best explain the observed patterns.

The particular coevolutionary processes at play in local populations may mask more general patterns of adaptation to environmental gradients. Previous studies of soil microbial community composition in 15 soils across a chronosequence of *A. petiolata* invasion found that the compositions of bacterial, fungal, and AMF communities were more similar in soils with similar lengths of invasion, independent of geographical proximity or the similarity of soil abiotic conditions (Lankau 2011*b*). This suggests that *A. petiolata* invasion leads to general changes to soil community structure, to which native plant populations might adapt. However, testing whether *P. pumila* plants are adapting to the changes in soil microbial communities caused by *A. petiolata* is complicated by the specific interactions between local plant populations and coevolving microbial strains. Thus, I performed an additional analysis in which I removed all local comparisons, and tested whether foreign plant populations tended to have more positive interactions with soil communities in soils with a similar history of invasion. Since invasion history was not correlated with geography in this set of seven sites, each plant population should be equally naïve to the particular soil communities. Despite this equal naivety, in a given soil community, plant interactions with soil communities tended to be most positive in the population with the most similar invasion history as the soil. For instance, in uninvaded soil (0 years of invasion), the plant populations with the least history with *A. petiolata* tended to have the most positive RII. Alternatively, in the soil with the longest history with *A. petiolata* (~63 years of invasion) the plant populations with the longest history with the invader tended to have the highest RII. The result was a significant hump-shaped relationship between a plant population's response to a given soil community and the difference in the invasion history of the plant population and the soil community (RII was maximized when this difference approached zero, and declined as this difference increased in either direction). This pattern suggests that in addition to specific coevolutionary dynamics between local populations and microbial strains, native *P. pumila* populations have also evolved traits in response to the general structure of microbial communities created at different stages of *A. petiolata* invasion.

Local adaptation is common phenomenon among plant species, and can be mediated by a number of biotic and abiotic selective pressures. Soil microbial communities can strongly affect plant fitness, playing an important role in structuring plant communities. Despite these strong ecological effects, relatively little is known about the evolutionary consequences of plant–soil community interactions for plant populations. Here I found that invasion by the exotic *A. petiolata*, which changes soil microbial communities via allelochemical production, alters the pattern of local adaptation of native plants to their home soil microbial communities. In addition to their specific interactions with their local soil community, native populations also showed evidence of adaptation to the general structure of soil communities present during different stages of invasion. Together these results suggest that invader-driven alteration of soil communities may affect evolutionary, as well as ecological, processes in native populations. Moreover, evolutionary responses in native plants may partially mitigate the ecological effects of plant invasions, potentially increasing the likelihood of native species persistence in the face of exotic invasions.

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Literature Cited

Barto, E. K., P. M. Antunes, K. Stinson, A. M. Koch, J. N. Klironomos, and D. Cipollini. 2011. Differences in arbuscular mycorrhizal fungal communities associated with sugar maple seedlings in and outside of invaded garlic mustard forest patches. Biological Invasions 13:2755–2762.

Callaway, R. M., D. Cipollini, K. Barto, G. C. Thelen, S. G. Hallett, D. Prati, K. Stinson, and J. Klironomos. 2008. Novel weapons: Invasive plant suppresses fungal mutualists in America but not in its native Europe. Ecology 89:1043–1055.

Callaway, R. M., G. C. Thelen, A. Rodriguez, and W. E. Holben. 2004. Soil biota and exotic plant invasion. Nature 427:731–733.

Cantor, A., A. Hale, J. Aaron, M. B. Traw, and S. Kalisz. 2011. Low allelochemical concentrations detected in garlic mustard-invaded forest soils inhibit fungal growth and AMF spore germination. Biological Invasions 13:3015–3025.

Felker-Quinn, E., J. K. Bailey, and J. A. Schweitzer. 2011. Soil biota drive expression of genetic variation and development of population-specific feedbacks in an invasive plant. Ecology 92:1208–1214.

Iwao, K., and M. D. Rausher. 1997. Evolution of plant resistance to multiple herbivores: Quantifying diffuse coevolution. American Naturalist 149:316–335.
Johnson, N. C., G. W. T. Wilson, M. A. Bowker, J. A. Wilson, and R. M. Miller. 2010. Resource limitation is a driver of local adaptation in mycorrhizal symbioses. Proceedings of the National Academy of Sciences USA 107:2093–2098.
Kardol, P., T. M. Bezemer, and W. H. van der Putten. 2006. Temporal variation in plant–soil feedback controls succession. Ecology Letters 9:1080–1088.
Kawecki, T. J., and D. Ebert. 2004. Conceptual issues in local adaptation. Ecology Letters 7:1225–1241.
Klironomos, J. N. 2002. Feedback with soil biota contributes to plant rarity and invasiveness in communities. Nature 417:67–70.
Kulmatiski, A., K. H. Beard, J. R. Stevens, and S. M. Cobbold. 2008. Plant-soil feedbacks: a meta-analytical review. Ecology Letters 11:980–992.
Lankau, R. A. 2011*a*. Intraspecific variation in allelochemistry determines an invasive species' impact on soil microbial communities. Oecologia 165:453–463.
Lankau, R. A. 2011*b*. Resistance and recovery of soil microbial communities in the face of *Alliaria petiolata* invasions. New Phytologist 189:536–548.
Lankau, R. A., V. Nuzzo, G. Spyreas, and A. S. Davis. 2009. Evolutionary limits ameliorate the negative impact of an invasive plant. Proceedings of the National Academy of Sciences USA 106:15362–15367.
Lankau, R. A., E. Wheeler, A. E. Bennett, and S. Y. Strauss. 2011. Plant–soil feedbacks contribute to an intransitive competitive network that promotes both genetic and species diversity. Journal of Ecology 99:176–185.
Lau, J. A., and J. T. Lennon. 2011. Evolutionary ecology of plant–microbe interactions: soil microbial structure alters selection on plant traits. New Phytologist 192:215–224.
Linhart, Y. B., and M. C. Grant. 1996. Evolutionary significance of local genetic differentiation in plants. Annual Review of Ecology and Systematics 27:237–277.
Macel, M., et al. 2007. Climate vs. soil factors in local adaptation of two common plant species. Ecology 88:424–433.
Mangla, S., Inderjit, and R. M. Callaway. 2008. Exotic invasive plant accumulates native soil pathogens which inhibit native plants. Journal of Ecology 96:58–67.
McGonigle, T. P., M. H. Miller, D. G. Evans, G. L. Fairchild, and J. A. Swan. 1990. A new method which gives an objective measure of colonization of roots by vesicular arbuscular mycorrhizal Fungi. New Phytologist 115:495–501.
McGraw, J. B., and F. S. Chapin. 1989. Competitive ability and adaptation to fertile and infertile soils in two Eriophorum species. Ecology 70:736–749.
Meimberg, H., N. F. Milan, M. Karatassiou, E. K. Espeland, J. K. McKay, and K. J. Rice. 2010. Patterns of introduction and adaptation during the invasion of *Aegilops triuncialis* (Poaceae) into Californian serpentine soils. Molecular Ecology 19:5308–5319.
Raabova, J., Z. Munzbergova, and M. Fischer. 2011. The role of spatial scale and soil for local adaptation in *Inula hirta*. Basic and Applied Ecology 12:152–160.
Reynolds, H. L., A. Packer, J. D. Bever, and K. Clay. 2003. Grassroots ecology: Plant-microbe-soil interactions as drivers of plant community structure and dynamics. Ecology 84:2281–2291.
Sambatti, J. B. M., and K. J. Rice. 2006. Local adaptation, patterns of selection, and gene flow in the Californian serpentine sunflower (*Helianthus exilis*). Evolution 60:696–710.
Savolainen, O., T. Pyhajarvi, and T. Knurr. 2007. Gene flow and local adaptation in trees. Annual Review of Ecology, Evolution, and Systematics 38:595–619.
Schultz, P. A., R. M. Miller, J. D. Jastrow, C. V. Rivetta, and J. D. Bever. 2001. Evidence of a mycorrhizal mechanism for the adaptation of *Andropogon gerardii* (Poaceae) to high- and low-nutrient prairies. American Journal of Botany 88:1650–1656.
Springer, Y. P. 2007. Clinal resistance structure and pathogen local adaptation in a serpentine flax–flax rust interaction. Evolution 61:1812–1822.
Stinson, K. A., S. A. Campbell, J. R. Powell, B. E. Wolfe, R. M. Callaway, G. C. Thelen, S. G. Hallett, D. Prati, and J. N. Klironomos. 2006. Invasive plant suppresses the growth of native tree seedlings by disrupting belowground mutualisms. PLoS Biology 4:727–731.
Turner, T. L., E. C. Bourne, E. J. Von Wettberg, T. T. Hu, and S. V. Nuzhdin. 2010. Population resequencing reveals local adaptation of *Arabidopsis lyrata* to serpentine soils. Nature Genetics 42:260–U242.
van der Putten, W. H., J. N. Klironomos, and D. A. Wardle. 2007. Microbial ecology of biological invasions. ISME Journal 1:28–37.
Weigelt, A., and P. Jolliffe. 2003. Indices of plant competition. Journal of Ecology 91:707–720.

Supplemental Material

Appendix A

Location and estimated invasion history of the seven study sites from which soil communities and *Pilea pumila* seeds were collected (*Ecological Archives* E094-005-A1).

Appendix B

Tests of gene × environment interactions for *Pilea pumila* population responses to soil communities (*Ecological Archives* E094-005-A2).

Appendix C

PCA loadings for 10 soil chemical variables and statistical analyses of *Pilea pumila* biomass controlling for soil chemistry (*Ecological Archives* E094-005-A3).