

The changing nature of plant–microbe interactions during a biological invasion

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Received: 18 November 2015 / Accepted: 2 August 2016 / Published online: 17 August 2016
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Abstract Invasive plant species can alter belowground microbial communities. Simultaneously, the composition of soil microbial communities and the abundance of key microbes can influence invasive plant success. Such reciprocal effects may cause plant–microbe interactions to change rapidly during the course of biological invasions in ways that either inhibit or promote invasive species growth. Here we use a space-for-time substitution to illustrate how effects of soil microbial communities on the exotic legume *Vicia villosa* vary across uninvaded sites, recently invaded sites, and sites invaded by *V. villosa* for over a decade. We find that soil microorganisms from invaded areas increase *V. villosa* growth compared to sterilized soil or live soils collected from uninvaded sites, likely because mutualistic nitrogen-fixing rhizobia are not abundant in uninvaded areas. Notably, the benefits resulting from inoculation with live soils were higher for soils from recently invaded sites compared to older invasions, potentially indicating that over longer time scales, soil microbial communities change in ways that may reduce the

success of exotic species. These findings suggest that short-term changes to soil microbial communities following invasion may facilitate exotic legume growth likely because of increases in the abundance of mutualistic rhizobia, but also indicate that longer term changes to soil microbial communities may reduce the growth benefits belowground microbial communities provide to exotic species. Our results highlight the changing nature of plant–microbe interactions during biological invasions and illustrate how altered biotic interactions could contribute to both the initial success and subsequent naturalization of invasive legume species.

Keywords Biotic interaction · Facilitation · Plant-soil feedback · Resource mutualism · Rhizobia · *Vicia villosa*

Introduction

Invading plant species engage in many novel interactions during the invasion process. These altered biotic interactions have the potential to limit (e.g., biotic resistance) or promote invasive species success (e.g., enemy release and/or mutualist accumulation) (Elton 1958). One unique feature of biotic interactions, however, is their potential to change over time in ways that influence invasion outcomes. For example, many exotic species may escape from herbivores early

Electronic supplementary material The online version of this article (doi:10.1007/s10530-016-1245-8) contains supplementary material, which is available to authorized users.

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in the invasion process only to experience high levels of attack as native herbivores evolve or learn to consume them, or as new herbivores are introduced to the region (Hawkes 2007; Schultheis et al. 2015). If such patterns are common, then changing biotic interactions may alter the success and effects of invaders over time.

The belowground microbial communities interacting with invasive plants are especially dynamic and likely to change over the time course of invasion because of plant-soil feedbacks, resulting from the accumulation of enemies or mutualists (Wolfe and Klironomos 2005). Plant-soil feedbacks occur when the invasive plant species cultivates microbial communities that either inhibit or facilitate the invasive plant's growth (Bever et al. 1997, 2010; Klironomos 2002). In the case of leguminous plants engaged in mutualism with rhizobia, for example, soil rhizobium populations may increase over time as a direct result of the dramatic fitness gains associated with nodulation (reviewed in Denison 2000; Denison and Kiers 2011). Although few studies have investigated changes in mutualist abundance during biological invasions, the spatial distribution of soil mutualists suggests that mutualist accumulation can occur—for example, in invaded ranges, *Acacia* spp. near conspecifics were not limited by rhizobium mutualists, but *Acacia* spp. growth in areas where conspecifics were absent was significantly limited by a lack of rhizobium partners (Wandrag et al. 2013). Similarly, rhizobia addition to invasive *Cytisus scoparius* plants more than doubled plant biomass, and uninoculated *C. scoparius* seedlings planted near native legumes harboring compatible rhizobia experienced increased nodulation and growth (Parker et al. 2006). In short, a lack of rhizobium mutualists may sometimes constrain the growth and invasion success of legume hosts, potentially explaining reduced colonization success of legumes compared to non-legumes (Rejmanek et al. 1991; see also Scott and Panetta 1993); however, rapid increases in rhizobium abundance to a critical density should theoretically increase legume colonization success (Parker 2001). Other studies, however, find little evidence for a lack of rhizobia limiting invasion success (e.g., Birnbaum et al. 2012), likely because some species co-invade with compatible rhizobia from the native range or successfully form new mutualistic associations with novel rhizobium communities in the introduced range (e.g., Birnbaum et al. 2012; Ndlovu et al. 2013).

Invasive species also may accumulate enemies. Although little data exists for belowground pathogens, increasingly negative plant-soil feedbacks during invasion have been attributed to pathogen increases in invasive *Sapium* populations (Nijjer et al. 2007). Similarly, increasingly negative plant soil feedbacks were observed with increasing time since invasion in twelve New Zealand exotic plant species (Diez et al. 2010). Both above- and belowground enemy abundance and diversity are often positively associated with the spatial extent of a species (Strong and Levin 1975; Clay 1995; Mitchell et al. 2010) and time since introduction (Hawkes 2007; Mitchell et al. 2010), suggesting that invasives commonly accumulate enemies over the course of invasion (reviewed in Flory and Clay 2013). How accumulation of enemies or mutualists influences long-term outcomes of invasion remains unknown, however (Flory and Clay 2013).

Here we use a space-for-time substitution to test how soil microorganisms and changes in soil microbial communities during the course of an invasion influence invasive plant performance. We capitalize on a dataset showing changes in plant species local distributions over a decade and compare growth of the invasive leguminous plant *Vicia villosa* (Roth) inoculated with soils from uninvaded areas versus nearby areas that have been invaded by *V. villosa* for at least 10 years (old invasions) or more recently invaded areas (invaded for 1–7 years). We hypothesize that a lack of soil rhizobium mutualists (*Rhizobium leguminosarum* bv. viciae) may limit the invasive success of *V. villosa* and predict that plants inoculated with uninvaded soils will produce fewer nodules and less biomass than plants inoculated with invaded soils. We also hypothesize that the effects of belowground microbial communities on invasive species performance may change over the course of the invasion, potentially having increasingly negative (or reduced positive) effects as enemies or less effective mutualists accumulate or having increasingly positive effects as the abundance of mutualists increases.

Materials and methods

Study system

We used a dataset mapping changes in the local distribution of the exotic plant *Vicia villosa* over a

10 years time span combined with experimental soil inoculations in the greenhouse to test for effects of soil microorganisms and changes to soil microbial communities during invasion on *V. villosa* growth. *V. villosa* is a rapidly growing, weedy, vine or forb that invaded California from Eurasia in the early 1900s. In our study site, *V. villosa* forms dense stands of up to 320 individuals per m² and appears to displace native vegetation (Suwa and Lau, *personal observation*). *Vicia villosa* forms symbiotic associations with *Rhizobium leguminosarum* bv. *viciae*. This classic mutualism involves the trade of nitrogen fixed by the rhizobium symbionts in exchange for carbon fixed through photosynthesis. *Rhizobium leguminosarum* bv. *viciae* allegedly forms associations with all species in the tribe Viciae, consisting of the genera *Vicia*, *Lathyrus*, *Pisum* and *Lens* (Mutch and Young 2004); however, *V. villosa* was the only member of this tribe, and, therefore, the only putative host plant observed in our study site.

The 550 × 350 m field census area covers a patchy distribution of serpentine and nonserpentine grasslands at the University of California McLaughlin Natural Reserve (38° 51'N, 123° 30'W). These grasslands were never farmed, but had been grazed by cattle until 2005. The area was first surveyed in 2001, 2002, and 2003 by assessing presence/absence of each plant species in four 1-m² quadrats located around each of 132 gridpoints (spaced 50 m apart) within the census area (see Davies et al. 2005). In 2010, we re-censused 118 of the original gridpoints for *V. villosa* presence/absence and abundance (number of individuals per m²). *V. villosa* was present in only 6 of the 132 gridpoints surveyed in the 2001, 2002, 2003 dataset. By 2010, 25 of 118 re-censused gridpoints had been invaded by *V. villosa*. Based on our census and results from prior censuses, we selected 15 gridpoints for inclusion in the experiment, with three gridpoints selected within each of five spatial blocks: one gridpoint had been invaded for at least 10 years (i.e., *V. villosa* detected in 2001, 2002, 2003 censuses and also present in 2010), one gridpoint had been invaded for 1–7 years (i.e., *V. villosa* absent during 2001, 2002, and 2003 censuses, but present in 2010), and a third gridpoint was uninvaded (*V. villosa* absent in all censuses). Uninvaded gridpoints were selected based on proximity and edaphic and plant community similarity; neither soil elemental composition nor plant species richness or community composition

differed significantly among uninvaded, recently invaded sites, and older invasions (Table 1). Although we do not know when *V. villosa* first invaded our survey area, the earliest herbarium records for California are from 1913 and the earliest in the vicinity of our study site date to 1928 (Data provided by the participants of the Consortium of California Herbaria; ucjeps.berkeley.edu/consortium/). We also acknowledge the possibility that *V. villosa* may have repeatedly invaded and gone extinct from some of our sampling sites; for example, our old invasion sites may not have been continuously invaded from 2001 to 2010, and it is possible that even uninvaded sites have been invaded at some point in the past. This potential variability, however, should reduce the likelihood of detecting significant differences between uninvaded, recently invaded, and older invasion sites, making our results conservative.

Soil inoculation experiment

On 07 April 2010, we planted *V. villosa* seedlings into 656 mL DeepotsTM (Stuewe & Sons Inc., Corvallis, OR, USA) filled with low nutrient potting media (Sunshine Mix #5; Sun Gro Horticulture Canada Ltd., Alberta, Canada). *Vicia villosa* genotypes used in this experiment were obtained from the USDA Germplasm Resources Information Network (GRIN). On 15 April 2010, we collected four soil samples from each identified gridpoint using a 5 cm soil corer. The four soil samples from each gridpoint were homogenized and plant material was removed from each soil sample by hand, yielding a total of 15 soil samples (3 invasion treatments × 5 blocks). We used these soil samples to create inocula by combining 10 g of field-collected soil with 50 mL dI water. Half of each inoculum was sterilized by autoclaving (121 °C, 31psi, 60 min). We inoculated 5 randomly assigned plants with each microbial community by applying 5 mL of live soil inoculum to the base of each *V. villosa* seedling on 19 April 2010. To control for variation in nutrient content among inocula, we inoculated 2 additional randomly assigned plants with each sterilized inoculum, yielding a total of 105 experimental plants (15 live soil inocula representing three invasion treatments inoculated onto 5 plants each and 15 sterilized inocula inoculated onto 2 plants each).

Plants were top-watered as needed, but did not receive any supplemental fertilizer. After 8 weeks of

Table 1 Soil characteristics (in ppm) and plant species richness (Mean \pm 1SE) of uninvaded, recently invaded, and older invaded plots

	Uninvaded	Recent invasion	Old invasion
Potassium	262 \pm 46	272 \pm 15	237 \pm 23
Sodium	39.7 \pm 17.1	35.2 \pm 8.0	68.1 \pm 42.3
Nickel	13.08 \pm 4.65	7.53 \pm 2.95	9.05 \pm 3.78
Nitrate	6.28 \pm 1.22	6.46 \pm 0.75	4.78 \pm 1.00
Sulfur	1.46 \pm 0.46	0.42 \pm 0.28	1.34 \pm 1.13
Calcium	1336 \pm 293	1314 \pm 261	1985 \pm 415
Magnesium	1581 \pm 476	1836 \pm 338	1930 \pm 89
Phosphorus	17.42 \pm 5.90	7.10 \pm 1.39	7.70 \pm 2.19
Plant species richness	22.6 \pm 2.73	23.6 \pm 2.52	22.0 \pm 0.63

Soil data was collected from the sampling area in 2001 and plant occurrence data was collected in 2003 (see main text and Davies et al. 2005 for detailed methods). We found no difference between uninvaded, recently invaded, and older invasions in soil chemistry composition (perMANOVA based on Bray-Curtis distances of soil chemical components, $P = 0.37$), plant species richness (ANOVA on number of plant species m^{-2} , $P = 0.87$), or plant community composition (perMANOVA based on Jaccard distances calculated from presence/absence data of each species at each gridpoint in 2003, $P = 0.40$). Analyses were performed in R with the *car* and *vegan* packages (3.0.2, R core development team)

growth, we harvested each plant and counted and collected all nodules produced. We estimated above-ground biomass and mean nodule mass (calculated as total nodule mass divided by nodule number) by weighing all plant and nodule material after drying for >2 days at 65 °C. We used mixed model ANOVA (Proc MIXED, SAS Institute 2001) to test for effects of soil microbes and changes in soil microbial communities on plant aboveground biomass. The model included invasion status (uninvaded, recent invasion, or old invasion), inoculum type (live or sterilized) and invasion status \times inoculum type as fixed predictor variables. Block (referring to the spatial structure of field soil samples) and soil sample (nested within invasion status) were included as random factors. To test for effects of changes in soil microbes on nodule number and mean nodule mass we used mixed model ANOVA with invasion status included as a fixed predictor variable and block and soil sample (nested within invasion status) as random factors. Only plants inoculated with live soils were included in analyses of nodule traits. In all models, Tukey-adjusted post hoc contrasts were used to assess the statistical significance of pairwise differences between treatments. Response variables were not transformed because residuals did not deviate substantially from normal distributions. We also used ANCOVA to test for changes in the mutualistic quality

of rhizobium communities. These ANCOVA test for differences in per nodule fitness benefits provided to plants by including plant biomass as a response variable, nodule number as a continuous predictor variable, and invasion status as a fixed predictor variable. Soil sample (nested within invasion status) and block were included as random factors. Interactions between invasion status and nodule number suggest that per nodule fitness benefits change during the invasion process. Only plants inoculated with live microbial communities were included in this analysis. Additionally, because only eight plants inoculated with uninvaded soils produced nodules (see results), per nodule fitness benefits of uninvaded sites should be interpreted cautiously.

Results

Inoculation with live soils from old and recently invaded sites increased *V. villosa* biomass compared to control plants treated with sterilized inocula. In contrast, live soils from uninvaded sites did not significantly affect *V. villosa* biomass compared to control plants treated with sterilized inocula (significant invasion status \times inoculum type interaction $F_{2,90} = 6.36$, $P = 0.0026$; Fig. 1). *Vicia villosa* plants inoculated with live soils from recently invaded sites

produced significantly more biomass than plants inoculated with live soils from older invasions, which in turn produced more biomass than plants inoculated with live soils from uninvaded sites (Fig. 1). No significant differences in plant biomass were detected between invasion statuses when plants were treated with sterilized inocula (Fig. 1).

Plants inoculated with live soils from uninvaded sites produced very few nodules (only 8 of 25 plants produced nodules), suggesting that these plants are rhizobium limited at uninvaded sites. In contrast, plants inoculated with soils from both older and more recent invasions produced numerous nodules (significant invasion status effect: nodule number $F_{2,8} = 8.20$, $P = 0.011$; Fig. 2). Inoculation with soils from uninvaded, recently invaded, and older invaded sites did not result in significant differences in mean nodule mass ($F_{2,49} = 1.63$, $P = 0.21$). Notably, per nodule fitness benefits to plants tended to be greater for soils from uninvaded sites and more recently invaded sites than soils from older invasions (nodule number \times invasion status interaction on plant biomass $F_{2,44} = 3.62$, $P = 0.035$; Fig. 3); however, this result should be interpreted cautiously as removing one outlier (see Fig. 3) caused this trend to become nonsignificant ($P = 0.16$).

Differences in soil inoculation effects on plant growth and per nodule fitness benefits between older

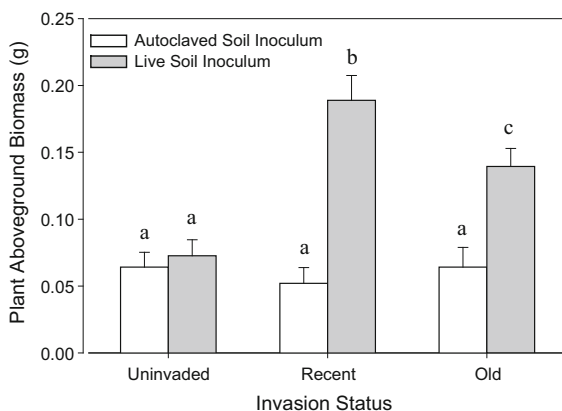


Fig. 1 Aboveground biomasses (Mean + 1SE) of *Vicia villosa* seedlings inoculated with autoclaved (white bars) or live field soils (gray bars) collected from sites that have not been invaded by *V. villosa* (“Uninvaded”), sites that have been invaded by *V. villosa* for 1–7 years (“Recent”), and sites that have been invaded by *V. villosa* for a decade or more (“Old”). Treatments with different letters differ significantly ($P < 0.05$) based on Tukey-adjusted post hoc contrasts

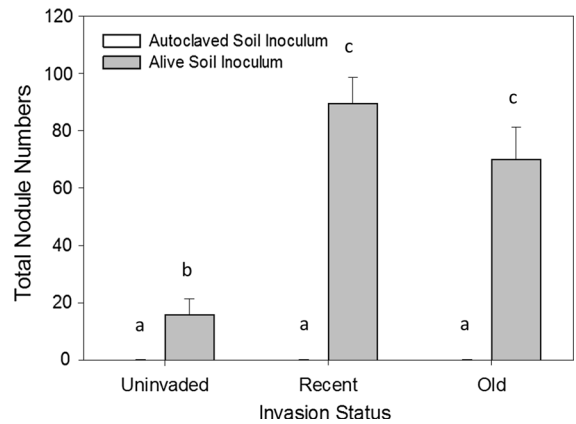


Fig. 2 Mean (+1SE) number of nodules produced by *Vicia villosa* seedlings inoculated with autoclaved (white bars) or live field soils (gray bars) collected from sites that have not been invaded by *V. villosa* (“Uninvaded”), sites that have been invaded by *V. villosa* for 1–6 years (“Recent”), and sites that have been invaded by *V. villosa* for a decade or more (“Old”). Treatments with different letters differ significantly ($P < 0.05$) based on Tukey-adjusted post hoc contrasts

and more recently invaded sites could result from higher *Vicia* abundances in recently invaded locations (Mean number of *Vicia* individuals m^{-2} : recent invasions = 78.25 ± 18.41 ; older invasions = 16.80 ± 16.47). However, *Vicia* abundance was never a significant predictor of nodule number, plant biomass, or per nodule fitness benefits (all $P > 0.42$), and

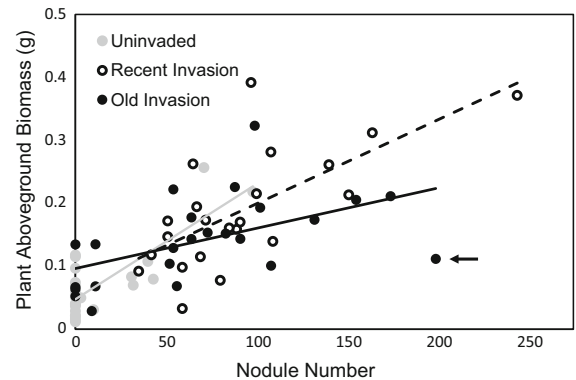


Fig. 3 The relationship between nodule number and plant biomass for *Vicia villosa* seedlings inoculated with soils from uninvaded sites (gray symbols, gray regression line), sites that have been invaded by *V. villosa* for 1–7 years (white symbols and dashed regression line), and sites that have been invaded by *V. villosa* for more than 10 years (black symbols, black regression line). The black arrow indicates the outlier whose removal eliminated the statistical significance of the nodule number \times invasion status interaction

including *Vicia* abundance as a covariate in the analyses described above reduced the statistical significance of differences in biomass production and nodule number between plants inoculated with soils from recently invaded versus older invaded sites, but did not qualitatively change observed patterns and had minimal effect on the magnitude of observed differences (Online Resource 1).

Discussion

Soil microbial communities strongly affect the growth of the invasive plant *V. villosa*. Inoculation with a live soil microbial community collected from areas already invaded by *V. villosa* more than doubled *V. villosa* growth compared to plants inoculated with live soil inocula collected from uninvaded sites or sterilized soil inocula. This result suggests that soil microbial communities change following invasions in ways that facilitate *V. villosa* growth (i.e., positive plant soil feedbacks). Such invasion-induced changes to microbial communities may be common (reviewed in Wolfe and Klironomos 2005; Reinhart and Callaway 2006) and may occur rapidly. For example, changes to microbial communities were evident less than three months after exotic understory plant species were planted into uninvaded soils (Kourtev et al. 2003), and invading cheatgrass changed microbial community composition in less than 2 years (Belnap and Phillips 2001). Although it is also possible that variation in microbial communities predates the invasion and contributes to invasion, we think this alternative hypothesis is unlikely for two reasons: First, because uninvaded and invaded sites are similar in terms of both edaphic properties and plant community composition (Table 1), we expect variation in invasive presence to be driven more by patterns of dispersal than soil or plant community properties likely to influence microbial community structure. Second, the observed effects of soil microbial communities on plant growth are likely driven by changes in the abundance of nitrogen-fixing rhizobia; plants inoculated with soils from invaded sites produced approximately fivefold more nodules than plants inoculated with soils from uninvaded sites. The increase in rhizobia in invaded sites is likely a direct result of positive fitness feedbacks between legumes and their rhizobium symbionts. Nodulation of a legume host can increase rhizobium

fitness dramatically (Denison 2000; Denison and Kiers 2011), leading to rapid increases in rhizobium abundance where host populations persist. Regardless of whether microbial communities are a pre-condition to invasion or change in response to invasion, however, our results suggest that soil microbial communities are important determinants of invasive species growth. Our plant growth assays were conducted in low nutrient potting media, which may increase the importance of microbial communities, especially resource mutualists like rhizobia, to plant growth relative to higher nutrient field soils (Heath and Tiffin 2007; Lau et al. 2012). However, the field soils at our study site are relatively low nutrient (Table 1), likely increasing the potential for important microbe-mediated effects on plant growth. Furthermore, our findings are consistent with other theoretical and empirical studies indicating that soil mutualists may promote exotic plant growth and in some cases invasion success (e.g., Parker 2001; Parker et al. 2006; Rodriguez-Echeverria et al. 2009), suggesting that such microbe-mediated effects may be common.

We also find that the positive benefits of soil microbial communities to invasive species decline over the time course of invasion. This decline could be driven by accumulation of pathogens as documented in other systems (e.g., *Sapium* trees, Nijjer et al. 2007), but may also be caused by ecological or evolutionary shifts in the composition of rhizobium or other mutualist (e.g., AMF) communities. For example, Rodriguez-Echeverria et al. (2007) documented increased rhizobium diversity in a site that had been invaded by *Acacia longifolia* for a longer time period. Our data suggest that per nodule fitness benefits might tend to be lower in sites that had been invaded for more than a decade compared to more recently invaded areas, potentially indicating that the rhizobia populations or communities decrease in cooperativeness, providing fewer benefits to the plants or extracting higher costs (i.e., providing less nitrogen for a given amount of carbon received), with increasing invasion age (Fig. 3). These findings should be interpreted cautiously, however, as many other components of the microbial community (both mutualists and pathogens) also may change over time and contribute to the variation in plant growth effects observed here. More manipulative experiments isolating different components of the microbial community are needed to disentangle these potential mechanisms.

Because invasive plants influence soil microbial communities by changing soil inputs or plant community composition, the effects of belowground microbial communities on invasive plants may vary over the course of invasion. While repeatedly measuring the effects of microbes on plants during the course of an invasion would convincingly demonstrate the temporal dynamics of plant–microbe interactions by accounting for any pre-existing differences in microbial communities or soil properties that may contribute to the patterns observed here, our study using a space-for-time substitution depicts how the effects of microbial communities on biological invasions may change over time. Initially, *V. villosa* appears to be mutualist limited, with the absence of N-fixing rhizobia minimizing growth and potentially limiting invasive species spread and impacts. The presence of rhizobia then either allows *V. villosa* to colonize new areas or rhizobium abundances rapidly increase post-colonization, allowing for dramatic (>125 %) increases in plant growth. Finally, these microbial benefits may decline following colonization, leading to reduced legume growth. This final stage of invasion may be common, but remains understudied. We know very little about the long-term effects of biological invasions and whether invasive species continue to be perpetually problematic or whether the negative effects of invasion decline as invasives assimilate into natural communities (reviewed in Strayer et al. 2006). Two recent studies suggest that effects of invasive species on co-occurring natives may decline over time, however, and in some cases reduced effects of invasive species may be due to shifts in microbial communities. In one study, Yelenik and D’Antonio (2013) show that the strong effects of exotic grasses on nitrogen-mineralization rates were reduced over a 20 year time period minimizing the positive feedbacks that initially threatened to accelerate the invasion. In this case, the reduced abundance of exotic grasses and associated changes to soil nutrients did not favor native species, but instead led to increased abundances of other exotics (Yelenik and D’Antonio 2013). In another study, Dostal et al. (2013) showed how the abundance of invasive *Heracleum mantegazzianum* and effects on native community members declined over a four decade time period in association with increasingly negative plant soil feedbacks at older invasion sites, presumably because of increasing pathogen

accumulation with increasing invasion age. Our results and the results of other recent studies (e.g., Nijjer et al. 2007; Dostal et al. 2013) suggest that microbes may be part of this assimilation process, potentially helping to shape invasive species into more benign community members.

Acknowledgments We thank T. Bassett, K. Keller, M. Hammond, S. Magnoli, E. Schultheis, and two anonymous reviewers for providing comments that substantially improved this manuscript and S. Harrison for providing 2001, 2002, and 2003 plant census and soil data. All field work was conducted at the McLaughlin Reserve. This work was funded by a National Science Foundation award (DEB-0918963) to J. A. L. This is KBS publication #1797.

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