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Species interactions contribute to the success of a global plant invader

Krikor Andonian · José L. Hierro

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Abstract Biological invasions are ubiquitous ecological phenomena that often impact native ecosystems. Some introduced species have evolved traits that enhance their ability to compete and dominate in recipient communities. However, it is still unknown if introduced species can evolve traits that may enhance their species interactions to fuel invasion success. We tested whether *Centaurea solstitialis* (yellow star-thistle) from introduced populations have greater performance than native counterparts, and whether they generate more beneficial plant-soil interactions. We used common garden and plant-soil feedback experiments with soils and seeds from native Eurasian and introduced Californian populations. We found that performance of *Centaurea* did not differ among source genotypes, implying that the success of this invasive species is not due to evolutionary changes. However, *Centaurea* grew significantly larger in soils from introduced regions than from native regions, indicating a reduction in natural

enemy pressure from native populations. We conclude that species interactions, not evolution, may contribute to *Centaurea*'s invasion success in introduced populations.

Keywords *Centaurea solstitialis* · Plant-soil microbe feedbacks · Biological invasions · Soil microbes · Enemy release hypothesis (ERH) · EICA

Introduction

Biological invasions have become ubiquitous ecological phenomena that have the potential to cause great economic and ecological impacts on recipient communities (Wilcove et al. 1998; Parker et al. 1999). The novel species interactions invasive plants encounter in their introduced range can determine whether or not introduced plants become invasive (Parker and Gilbert 2004; Verhoeven et al. 2008). For example, the Enemy Release Hypothesis (ERH) predicts that introduced species succeed because they leave behind the natural enemies from their native distribution (Elton 1958; Keane and Crawley 2002). Although much attention is placed on interactions that take place above ground, the diverse community of pathogens and mutualists that inhabit soils has been shown to influence the success of introduced plants (Klironomos 2002; Wolfe and Klironomos

K. Andonian (✉)
Department of Ecology and Evolutionary Biology,
University of California, Santa Cruz, CA 95064, USA
e-mail: andonian@biology.ucsc.edu

J. L. Hierro
Facultad de Ciencias Exactas y Naturales, Universidad
Nacional de La Pampa, 6300 Santa Rosa, Argentina

J. L. Hierro
CONICET AR, 6300 Santa Rosa, Argentina

2005; Reinhart and Callaway 2006; Pringle et al. 2009). Recent studies have demonstrated that introduced species encounter less inhibitory effects of soil biota where they are introduced than in their home range (Callaway et al. 2004; Hierro et al. 2005; van Grunsven et al. 2010). Thus, soil microbes can promote invasion in recipient communities while inhibiting plants at home.

Specific mechanisms by which soil microbes may affect plants include plant-soil feedbacks (Bever 2002). In this process plant roots ‘train’ soils by accumulating host-specific assemblages of microbes, stimulated by the release of root exudates creating conditions suitable for microbial growth in the rhizosphere (Eom et al. 2000). The resulting host-specific microbial community generated by plant-soil feedbacks (PSFs) can have either positive or negative effects on plant hosts (Bever 2002). Plant-soil feedbacks are often calculated as relative metrics by comparing performance of plants in soils with a history of conspecifics versus other species (Kulmatiski et al. 2008). There is tremendous variation in PSFs generated by plants; some species generate positive feedbacks by accumulating soil communities that are highly beneficial, while other species generate negative feedbacks with strong net negative effects on hosts (Levine et al. 2006; Kulmatiski et al. 2008). In a study examining PSFs of 61 species in a Canadian old field, Klironomos (2002) found that invasive plants generated positive feedbacks while rare natives generated negative feedbacks, and that PSFs accounted for 60% of the variance in plant abundance in the field. Although empirical examples demonstrating strong effects of PSFs on invasive plants are increasing, there are still very few biogeographic comparisons of these interactions in soils from native and introduced regions (but see Reinhart and Callaway 2004; te Beest et al. 2009).

In addition to strong ecological interactions, the novel environments and species interactions plants encounter upon introduction often impose strong selective pressures and can result in evolutionary change. The evolution of increased competitive ability (EICA) hypothesis states that plants that have escaped their natural enemies undergo selection to reduce allocation to defense in favor of increased growth and competitiveness (Blossey and Notzold 1995). There are many examples that illustrate how introduced species can undergo evolutionary change

enabling them to establish and spread in their introduced range (Leger and Rice 2003; Blair and Wolfe 2004; Bossdorf et al. 2005; Barney et al. 2009; O’Donnell and Armbruster 2009; Orians and Ward 2010), but there are few studies testing whether invasive species can evolve traits that modify the way they interact with other species (but see Seifert et al. 2009).

Genotype-specific variation in plant–microbe interactions has been documented in plants (Timonin 1940; Harley 1950; Gilbert et al. 1994; Siddiqui and Shaikat 2003; Burdon and Thrall 2008), but it is still unclear if this variation can manifest in the evolution of traits that enhance introduced plants’ invasiveness in their new range. In a recent study, Hawkes et al. (2010) found that the degree of enemy release (from insects and pathogens) became more variable as residence time of introduced *Senecio* species in the UK increased, and Seifert et al. (2009) discovered that introduced North American populations of *Hypericum* have evolved reduced dependence on their mycorrhizal symbionts. Thus, invading plants may evolve traits that not only modify their competitiveness, but also their interactions with other species.

Populations of introduced plants experiencing different selection pressures across broad ranges may result in differentiated genotypes that cultivate unique PSFs (Gilbert et al. 1994; Seifert et al. 2009). Thus, introduced plants have the potential to undergo evolutionary change that influences the outcome of their species interactions. Although genotype-specific species interactions have been considered by agronomists and ecologists (Ahlholm et al. 2002; Bailey et al. 2005; Petrisko and Windes 2009; Piubelli et al. 2009; Saunders and Kohn 2009), they have rarely been considered in the field of invasion biology. If plants evolve traits that enhance the benefit of their species interactions in introduced regions, we may observe a scenario where plants undergo ‘evolution of enhanced species interactions’ that fuel their establishment and spread in new regions, yet this still remains untested.

Documenting population level variation in species traits is a critical first step in testing the EICA hypothesis. In this study, we aimed to test for genetically based differences in performance among native and introduced populations, and the potential for the ‘evolution of enhanced species interactions’ in

Centaurea solstitialis (yellow starthistle, Asteraceae; hereafter referred to as *Centaurea*), an annual forb native to Eurasia that has been introduced throughout the world and now occurs in every continent except Antarctica (Maddox 1981; Maddox et al. 1985). *Centaurea* has been growing in much greater densities and spreading much more rapidly where it has been introduced in California than in its native Eurasia (Hierro et al. 2006; Pitcairn et al. 2006, Andonian et al. unpublished data). Widmer et al. (2007) observed differences in seed starch content among *Centaurea* from native and introduced populations in common garden experiments, providing some preliminary evidence for potential evolutionary shifts in introduced *Centaurea* genotypes. Specifically, we tested whether *Centaurea* from introduced populations grow more vigorously than native *Centaurea*, and whether they interact with soil microbes to positively influence growth. We addressed the following questions: (1) Do *Centaurea* genotypes from introduced populations grow more vigorously than from native populations? (2) Do *Centaurea* from introduced populations generate more positive plant-soil feedbacks? In other words, do plants in introduced populations cultivate a more self-beneficial soil community than plants from native populations? And lastly, (3) How do the effects of soil-borne natural enemies vary between native and introduced *Centaurea* populations?

In this study, we conducted a series of greenhouse experiments using seeds and soil collected from *Centaurea*'s native and introduced range to test for effects of soil environment and source genotype on *Centaurea*'s growth and interactions with soil microbes. We utilized a novel approach to address these questions by incorporating established plant-soil feedback experimental techniques to train soils using different genotypes of a single plant species, to determine if plants from introduced populations engage in novel interactions with soil biota. Although there have been many studies testing PSF responses of invasive plants (Klironomos 2002; Petermann et al. 2008; Brandt et al. 2009; van Grunsven et al. 2010), very few have tested how PSFs vary among native and introduced regions (Callaway et al. 2004, Reinhart and Callaway 2004, te Beest et al. 2009), and no studies to date have tested potential variation in PSFs among populations within a species.

Methods

Soil and seed collections

We collected soil and seed samples from six native (Eurasian) and six introduced (Californian) *Centaurea* populations in order to capture a broad sample of the soil biota and genetic variation *Centaurea* exhibits within each region (Table 1). Sampling sites in Eurasia spanned populations in the Republics of Armenia and Georgia. Some populations were used for both seed and soil samples ($N = 1$ and 3 for California and Eurasia, respectively), whereas others were used for either only seeds ($N = 5$ and 4 for California and Eurasia, respectively) or soil ($N = 5$ and 3 for California and Eurasia, respectively). We collected seeds haphazardly from each population and pooled seeds from different mothers within populations. For soil samples, we collected 4L of soil from the top 15 cm using a shovel sterilized in bleach (6% NaOCl solution) from each population. All soils were collected during the summer months and subjected to slow air-drying to mimic natural drought conditions. California soils originated in the Sierra Nevada foothills and were primarily quaternary alluvium from the Mesozoic, Holocene, and Pleistocene that include a mixture of alfisols, entisols, inceptisols, and mollisols (Graham and O'Geen 2010). The parent materials of these soils consisted of hornblende, plagioclase (andesine and albite), cristobalite, tridymite, and quartz. These soils had a loamy texture with 36 g kg^{-1} of organic material and were composed of 43% sand, 40% silt, and 17% clay (Graham and O'Geen 2010). Eurasian soils originated from the Caucasus region and are meadow-steppe soils composed primarily of alluvial and fluvial soils (Molchanov 2009). These soils had a clay-loamy texture with 9% organic material, 44% sand, 27% silt, and 20% clay. The mineralogical composition of the clay in these soils is represented by hydromica, kaolinite, and montmorillonite (Molchanov 2009). Both regions have a Mediterranean type climate but Eurasian populations encounter more regular summer rains (Hierro et al. 2009). The plant communities in both regions were dominated by annual grasses such as *Avena* and *Bromus* (Stromberg et al. 2007; Gabrielyan and Fragman-Sapir 2008), but despite this *Centaurea* grew to much greater densities in

Table 1 Location and elevation of seed and soil collection sites used in greenhouse experiments

Region and location	Collection	Latitude	Longitude	Elevation (m)
California				
Howard Hill	soil	N 39°14'41"	W 121°19'16"	130
Browns Valley	soil	N 39°14'53"	W 121°19'03"	173
Sicard Flat	soil	N 39°13'22"	W 121°20'28"	77
Spencer Field Wildlife Area	soil	N 39°07'02"	W 121°18'29"	89
Saddleback Ranch	soil, seeds	N 39°16'16"	W 121°27'30"	47
Putah Creek	seeds	N 38°31'05"	W 121°45'39"	5
Sierra Foothill R.E.C.	seeds	N 39°15'50"	W 121°19'19"	245
Jasper Ridge	seeds	N 37°24'25"	W 122°13'30"	122
Mt. Diablo	seeds	N 37°52'54"	W 121°54'50"	151
Grass Valley	seeds	N 39°12'14"	W 121°06'03"	210
Maxwell	seeds	N 39°18'40"	W 122°11'30"	27
Eurasia				
Ujan (A)	soil	N 40°16'57"	E 44°11'41"	1,084
Kashmi (G)	soil	N 41°44'32"	E 45°12'08"	775
Kachreti (G)	soil	N 41°38'33"	E 45°38'19"	485
Garni (A)	soil, seeds	N 40°07'54"	E 44°45'45"	1,557
Tskarostavi (G)	soil, seeds	N 41°43'51"	E 45°16'21"	815
Marktopi (G)	soil, seeds	N 41°41'33"	E 45°01'13"	583
Armavir (A)	seeds	N 40°06'36"	E 44°05'05"	860
Aparan (A)	seeds	N 40°16'58"	E 44°11'45"	1,161
Kakheti (G)	seeds	N 41°45'00"	E 45°43'00"	1,390
Etchmiadsin (A)*	seeds	N 40°09'45"	E 44°28'27"	897

Asterisk (*) represents the population from which seeds were used in phase ii of the plant-soil feedback experiment. Letters in parentheses next to Eurasian collection sites indicate if sites were located in the Republic of Armenia (A) or Georgia (G)

California than Eurasian populations (Hierro et al. 2006; Andonian et al. unpublished data).

Our main focus in this study was to test for evolutionary and ecological differences among *Centaurea* genotypes, so we pooled soils from all six soil populations within regions, resulting in one bulk soil sample per region. However, we kept all seeds from different populations separate and were thus able to test for differences among populations within regions, between regions, and for potential genotype * environment interactions between plant genotype and the soil environment.

Reciprocal common garden experiment

To test whether *Centaurea* from introduced populations grew more vigorously than plants from native populations, we established a reciprocal common garden experiment in a rooftop greenhouse at the University of California, Santa Cruz. We grew Eurasian and Californian *Centaurea* seeds from each of the 6 populations per region and replicated this

common garden in both Eurasian and Californian soils. We grew plants in 600 ml 'conetainers' (Stuewe & Sons, Inc.) with 150 ml of pure field soil in each pot. To reduce the potential chemical and physical differences among soil samples we diluted field soil in a 20:80 soil:sand mixture using 20/30-grit blasting grade sand and fertilized plants every 2 weeks with 1/8 strength Hoagland's solution. We layered pure field soils above 350 ml 20-grit sand, then planted 4 *Centaurea* seeds per pot and covered seeds with a 100 ml (~ 1 cm) layer of 30-grit sand to prevent cross contamination via water splash. We thinned all pots to one individual upon germination.

In total, the treatments were: 2 soil regions * 2 seed regions * 6 seed populations nested within region * 10 replicates = 240 plants. We monitored germination dates and harvested above-ground tissues 110 days after germination. We did not harvest below-ground tissues in this experiment because we used these soils to inoculate plants in the subsequent soil feedback experiment (see below). All plants were dried for 72 h at 60°C and weighed.

Statistical analysis

We tested the effects of treatments (soil region, seed region, seed population [seed region], and seed region * soil region) on germination time and above-ground biomass using a mixed model analysis of variance (ANOVA) with population[region] as a random effect. Response variables were log transformed to meet the assumptions of normality and homoscedasticity. We tested for potential genotype by environment (G*E) interactions by using the interaction term of seed region (genotype) by soil origin (environment). We used JMP 7.0 for all statistical analyses.

Plant-soil feedback experiment

We used a plant-soil feedback experiment (Bever 2002) to test whether different *Centaurea* genotypes generate unique interactions with soil biota. This is a unique approach to test for local genetic differentiation because we are not only testing for morphological differences among genotypes, but also whether introduced genotypes generate unique species interactions, in this case, with the soil community. We used the same growing conditions as in the Reciprocal Common Garden Experiment outlined above.

In the first phase of the feedback experiment, we ‘trained’ soils from each region by growing *Centaurea* from all seed populations in them for 110 days. During this soil-training period, we expect that soil microbial communities will begin to differentiate among soil training treatments. After this initial soil-training period, we harvested above ground tissues and then grew *Centaurea* from one Eurasian population (Table 1) as a bioassay to test the effects of soil training. These seeds were not used during the training phase of the experiment. We planted 4 seeds in each pot and thinned to one individual upon germination. In total, treatments were: 2 soil regions * 2 seed regions (for training) * 6 seed populations nested within region (for soil training) * 10 replicates = 240 plants. We monitored germination time and harvested plants 110 days after germination, separating above- and below-ground tissues. All shoots and a subsample of the roots were harvested and dried for 72 h at 60°C and weighed. We subsampled roots (N = 3 out of 10 potential replicates) due to constraints during harvest in the

greenhouse. We used biomass as our focal response variable because *Centaurea* biomass was strongly correlated with flower production, and thus fitness, in microcosm experiments (Zavaleta and Hulvey 2004).

Statistical analysis

We tested the effects of treatments (soil region, seed region, seed population [region], and seed region * soil region) on root biomass, shoot biomass, total biomass, and root:shoot ratio (RSR) using a mixed model analysis of variance (ANOVA), with population [region] as a random effect. All response variables were log transformed to meet the assumptions of normality and homoscedasticity. Specific contrasts were made using Tukey HSD post-hoc analyses at $\alpha = 0.05$. We used Systat 12 for the specific contrasts and JMP 7.0 for all other statistical analyses.

Results

Reciprocal common garden experiment

There was no effect of soil or seed origin on germination time ($F_{1,229} = 0.72$; $P = 0.40$ and $F_{1,10} = 0.79$; $P = 0.39$, respectively). There was no significant difference in the above ground biomass of *Centaurea* from native vs. introduced regions ($F_{1,11} = 0.14$; $P = 0.71$; mean shoot biomass = 0.302 and 0.312 from California and Eurasia, respectively). However, Eurasian *Centaurea* had more than double the variance in biomass among populations (CV = 17.8) than Californian *Centaurea* (CV = 7.64). Overall, seed population [seed region] explained 18% of the variation in above ground biomass. In contrast, *Centaurea* performed 27% better in California soils than in Eurasian soils (all genotypes combined), resulting in a significant effect of soil region on *Centaurea* above ground biomass ($F_{1,221} = 44.5$; $P < 0.0001$). Thus, soil origin had a much greater effect on *Centaurea* biomass than seed origin (Fig. 1).

Plant-soil feedback experiment

Soil training by *Centaurea* from different populations did not have significant effects on any of the response

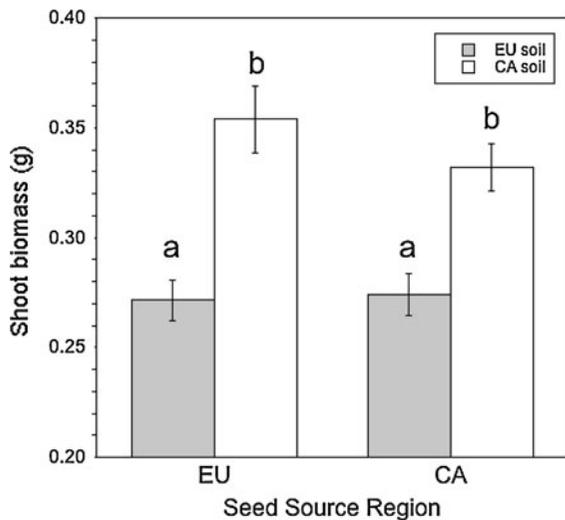


Fig. 1 Above ground biomass (g) of *Centaurea* from California and Eurasia ($N = 6$ populations per region) grown in soils from California (white bars) and Eurasia (shaded bars) in the Reciprocal Common Garden Experiment. Abbreviations for California and Eurasia are CA and EU, respectively

variables we measured (Table 2). There was no effect of soil origin or soil training on germination time (Table 2). Seed population [seed region] explained 25, 1, 27, and 6% of the total variance in root biomass, shoot biomass, total biomass, and RSR, respectively. *Centaurea* had significantly greater shoot biomass in Californian than in Eurasian soils, but there were no significant effects of soil region on root or total biomass (Table 2). Sample sizes for shoot and root biomass were 10 and 3, respectively, and these low sample sizes for root biomass (and thus total biomass) resulted in statistical power that was too low ($\alpha = 0.09$) to detect any differences among treatments. Lastly, *Centaurea* in Eurasian soil had significantly greater RSR than in Californian soil (Table 2).

Discussion

Have introduced *Centaurea* populations undergone evolutionary change that enhance invasiveness?

We found no evidence for evolutionary differences among native and introduced *Centaurea* populations. Although *Centaurea* demonstrated differences in

Table 2 ANOVA statistics for the effects of soil region and seed region on *Centaurea* germination, root biomass, shoot biomass, and root:shoot ratio from the plant-soil feedback experiment

Effect	df	F
Germination time (days)		
Soil region	1, 220	0.01
Seed region	1, 8	0.14
Soil region * seed region	1, 220	1.10
Root biomass (g)		
Soil region	1, 40	0.02
Seed region	1, 8	1.00
Soil region * seed region	1, 40	0.28
Shoot biomass (g)		
Soil region	1, 220	22.75***
Seed region	1, 10	0.007
Soil region * seed region	1, 220	1.316
Total biomass (g)		
Soil region	1, 220	1.029
Seed region	1, 8	0.867
Soil region * seed region	1, 220	0.03
Root:shoot		
Soil region	1, 220	4.101*
Seed region	1, 8	0.399
Soil region * seed region	1, 220	0.841

All variables were log transformed to meet ANOVA assumptions of normality and homoscedasticity. Asterisks indicate significant overall treatment effects (* $P < 0.05$, ** $P < 0.001$, *** $P < 0.0001$)

seed starch content among native versus introduced populations in another common garden study (Widmer et al. 2007), there were no differences in terms of biomass, consistent with our results (see also Hierro et al. 2006). *Centaurea* exhibits greater levels of genetic diversity within than among populations in California and has likely undergone multiple introductions (Sun 1997). Recent molecular studies on *Centaurea* revealed that there was no difference in allelic diversity among native and introduced regions, although California had much lower genetic variance among populations than any other region (Eriksen et al. unpublished manuscript). This high within population diversity and lack of population genetic structure may have translated into our observed lack of differences among native and introduced *Centaurea* populations. We also observed less variation in plant biomass among populations in California than

in Eurasia, consistent with patterns of allelic richness from molecular analyses by Eriksen et al. (unpublished manuscript). Our experimental set-up also allowed us to test whether plants were locally adapted (regionally) to their respective soil communities and to test for potential genotype \times environment interactions, but we did not detect either of these patterns. Although we found no support for the ‘evolution of enhanced species interactions’, this was the first study to explicitly test this hypothesis and it is possible that this mechanism may underpin the success of spread of other invasive species. Future studies may test the potential for the ‘evolution of enhanced species interactions’ for species that are known to differ morphologically or genetically among native and introduced populations (Blossey and Notzold 1995; Siemann and Rogers 2001, 2003; Jakobs et al. 2004).

Have introduced *Centaurea* populations escaped from soil-borne natural enemies?

Centaurea performed better in California than Eurasian soils, suggesting there are differences between soils that make them more favorable for *Centaurea* in California. Although these effects were only significant in above-ground biomass, this is the most commonly used metric in plant-soil feedback experiments (Kulmatiski et al. 2008). These differences may be due to the soil microbes, but can also be caused by physical or chemical differences in structure and composition of the soils themselves. We anticipated these potentially confounding variables and diluted all pots with 80% sand, drastically reducing the potential for chemical or physical differences among soils. The 20% of field soil we used to inoculate the pots would provide abundant microbial fauna, while minimizing physical or chemical differences. We also fertilized all plants with dilute fertilizer to reduce any potential nutrient differences among soils. Therefore, soil microbes are likely to have had the greatest influence on the differences in biomass we observed in greenhouse experiments.

Although we took a ‘black box’ approach to the identity of the soil community, our main goals were to examine broad biogeographic patterns rather than identity of the specific microbes responsible for the pattern. Nonetheless, researchers have found higher concentrations of at least one fungal pathogen (*Pythium* sp.) in *Centaurea* rhizospheres from native

European populations than in North America (K. Reinhart, *personal communication*). Other studies have also reported biogeographic variation in soil enemy pressure consistent with our findings (Hierro et al. 2006, Andonian et al. unpublished data). Thus, these results provide preliminary evidence for *Centaurea*’s escape from soil-borne natural enemies from native Eurasian populations.

Conclusions

We conclude that species interactions with soil microbes have a greater influence on the global invasion success of *Centaurea* than potential evolutionary mechanisms. Our results suggest that EICA is an unlikely mechanism driving *Centaurea* invasions, and that plants from different populations do not generate different PSFs. In our experiments, *Centaurea* grew to a greater biomass in California soils, irrespective of seed origin. Although soil samples from replicate populations were pooled, these results provide preliminary evidence for the influence of soil microbes on the success *Centaurea* in introduced regions.

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