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ORIGINAL ARTICLE

Geographic mosaics of plant–soil microbe interactions in a global plant invasion

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ABSTRACT

Aim Our aim in this study was to document the global biogeographic variation in the effects of soil microbes on the growth of *Centaurea solstitialis* (yellow starthistle; Asteraceae), a species that has been introduced throughout the world, but has become highly invasive only in some introduced regions.

Location To assess biogeographic variation in plant–soil microbe interactions, we collected seeds and soils from native Eurasian *C. solstitialis* populations and introduced populations in California, Argentina and Chile.

Methods To test whether escape from soil-borne natural enemies may contribute to the success of *C. solstitialis*, we compared the performance of plants using seeds and soils collected from each of the biogeographic regions in greenhouse inoculation/sterilization experiments.

Results We found that soil microbes had pervasive negative effects on plants from all regions, but these negative effects were significantly weaker in soils from non-native ranges in Chile and California than in those from the non-native range in Argentina and the native range in Eurasia.

Main conclusions The biogeographic differences in negative effects of microbes in this study conformed to the enemy-release hypothesis (ERH) overall, but the strong negative effect of soil biota in Argentina, where *C. solstitialis* is invasive, and weaker effects in Chile where it is not, indicated that different factors influencing invasion are likely to occur in large scale biogeographic mosaics of interaction strengths.

Keywords

Asteraceae, biogeography, biological invasion, *Centaurea solstitialis*, enemy-release hypothesis, geographic mosaics, invasive species, plant–soil interactions, soil microbes, yellow starthistle.

INTRODUCTION

Exotic invasions pose serious threats to local biodiversity, cause massive economic losses, and are among the most pressing topics in ecology and evolutionary biology (Wilcove *et al.*, 1998; Pimentel *et al.*, 2005; Callaway & Maron, 2006). While biological invasions have received much attention (reviewed by Mack *et al.*, 2000; Sakai *et al.*, 2001; Hierro *et al.*, 2005; Dietz & Edwards, 2006), most research is directed at identifying locally occurring mechanisms that might drive invasions (Blossey & Nötzold, 1995; Colautti *et al.*, 2004; Levine *et al.*, 2004; but see Agrawal *et al.*, 2006). However, because invasions involve dramatic differences in ecological or evolutionary processes in native and non-native ranges, understanding invasions requires a biogeographic approach (Hierro *et al.*, 2005). Furthermore, because invasions often occur across multiple continents, it is possible to study them in the context of a biogeographic mosaic of interaction strengths (Callaway *et al.*, 2005; Thompson, 2005).

In their non-native ranges, invasive species interact with novel suites of natural enemies, mutualists and competitors that can influence establishment, spread, abundance and impact (Parker & Gilbert, 2004; Mitchell *et al.*, 2006; Vavra *et al.*, 2007). The most widely accepted ecological mechanism for plant invasions is the enemy-release hypothesis (ERH), which suggests that invasive species succeed in non-native

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regions because they have left behind the specialist natural enemies that keep them in check in native regions (Elton, 1958; Keane & Crawley, 2002). Alternatively, invasive species may encounter mutualists in introduced regions that are more beneficial than those in native regions, a pattern often observed in plant–soil microbe interactions (Richardson *et al.*, 2000; Reinhart & Callaway, 2006). Thus the newly acquired natural enemies, mutualists and competitors of the introduced species can determine whether the latter become invasive or remain simply exotic. In this context, the microbial pathogens and mutualists that plants encounter below-ground can have a significant impact on plant communities (van der Heijden *et al.*, 1998; Petermann *et al.*, 2008) and can play an important role in plant invasion (Klironomos, 2002; Callaway *et al.*, 2004; Reinhart & Callaway, 2004).

Some species have been introduced throughout the world, yet have become successful invaders in only some of their non-native ranges (Lambrinos, 2002; Shea *et al.*, 2005). The reasons why invasions are conditional are often unknown, but they provide opportunities for exploring the basic mechanisms that drive invasions, and how mechanisms responsible for successful invasions vary geographically (Hierro *et al.*, 2005). For example, Zangerl *et al.* (2008) detected geographic mosaics in defence chemical production and herbivore attack among introduced populations of *Pastinaca sativa* that were associated with invasion success. Thus escape from natural enemies may drive invasion in some parts of a species' non-native range but not others. There are very few studies that have examined biogeographic variation in invasive processes across the non-native and native ranges of invasive species (but see Hierro *et al.*, 2009).

Centaurea solstitialis L. (yellow starthistle; Asteraceae) is an annual forb that has been introduced in many places throughout the world. In its native range, it generally occurs at low densities (Uygur *et al.*, 2004; Hierro *et al.*, 2006), but it is highly invasive and spreading rapidly in some introduced regions, such as California and Argentina (Hierro *et al.*, 2006; Pitcairn *et al.*, 2006). However, *C. solstitialis* is not an aggressive invader and appears to spread slowly and with minimal impact, at least for the time being, in other areas where it has been introduced, such as Chile (L. Cavieres, pers. obs.; Andonian *et al.*, 2011). Other highly invasive congeners have strong interactions with soil biota that contribute to their spread in North America (Callaway *et al.*, 2004; Kulmatiski & Beard, 2006; Meiman *et al.*, 2006). Although *C. solstitialis* can alter soil microbial communities and utilize soil microbes to enhance its competitiveness (Batten *et al.*, 2006; Callaway *et al.*, 2006; Hierro *et al.*, 2006), we know little about variation in how soil microbes interact with *C. solstitialis* throughout its global non-native range (but see Andonian *et al.*, 2011). With this aim, we conducted greenhouse experiments using seeds and soils from four regions to test: (1) whether *C. solstitialis* is released from soil-borne natural enemy pressure in introduced regions, and (2) how the effects of soil microbes vary throughout regions where *C. solstitialis* has been introduced.

MATERIALS AND METHODS

Study system and biogeographic regions

Centaurea solstitialis is native to the eastern Mediterranean and the Caucasus region in Eurasia, but now occurs on every continent except Antarctica (Maddox, 1981; Maddox *et al.*, 1985). We sampled populations from three regions where *C. solstitialis* has been introduced that show different degrees of invasiveness (highly invasive: Argentina and California; non-invasive: Chile), and from its native region in Eurasia spanning populations in the Republics of Armenia and Georgia. We categorized Argentina and Chile as two separate regions because they are separated by a major biogeographic barrier – the Andes – and thus have very different climates and plant communities. The populations we sampled in Chile have a mediterranean climate characterized by summer droughts with plant communities dominated by annual grasses, much like California, while Argentinean sites receive summer rains with plant communities dominated by perennial grasses. However, Eurasian populations from the Republics of Georgia and Armenia are both in a similar ecoregion to the south of the Caucasus Mountains, with similar climate and plant communities, and thus represent a single region in this study. According to current estimates of introduction history, *C. solstitialis* is believed to have first been introduced to the Americas in Chile; from Chile into California *c.* 1850 (Gerlach, 1997); and into Argentina *c.* 1870 (Hijano & Basigalup, 1995).

We collected soil samples from six representative established *C. solstitialis* populations per region, at least 10 km apart, in order to capture a broad sample of the soil microbes with which *C. solstitialis* interacts in each region (see Appendix S1 in Supporting Information). From each population, we collected 4 L soil from the top 15 cm using a shovel sterilized in bleach (6% NaOCl solution). All soils were collected during summer months during peak flowering and were subjected to slow air-drying to mimic natural drought conditions. In total, we sampled soils from 24 populations spanning four regions. The parent materials of California soils originating from the Sierra Nevada foothills are primarily Quaternary alluvium from the Mesozoic, Holocene and Pleistocene, which include a mixture of alfisols, entisols, inceptisols and mollisols (Graham & O'Geen, 2010). Eurasian soils originating from the Caucasus region are meadow-steppe soils composed primarily of alluvial and fluvial soils (Urushadze, 1997; Molchanov, 2009). Parent materials of Chilean soils collected from sites east of 70°30′ W longitude are volcanic, with andesite and diorite substrates composed of pre-Andean entisols and fluvetic haploxerolls; while the parent materials of Chilean soils in areas with longitude west of 70°30′ W are alluvial, with a substrate composed of coarse sand and gravels composed of entisols and ultic haploxeroll (Luzio *et al.*, 2009). The parent materials of Argentinean soils correspond to a loess of brown to dark brown colour, classified as molisols and entisols (Menéndez & La Rocca, 2007).

Argentina has a continental climate while the other three regions have a mediterranean-type climate, although Eurasian populations encounter more regular summer rains (Hierro *et al.*, 2009). The plant communities in Eurasia, California and Chile were dominated by annual grasses such as *Avena* and *Bromus* (Stromberg *et al.*, 2007; Gabrielyan & Fragman-Sapir, 2008), but despite these ecological similarities, *C. solstitialis* grew to much greater densities in California than did Eurasian or Chilean populations (Hierro *et al.*, 2006; Andonian *et al.*, 2011).

We tested the effects of soil microbes against seeds collected from one *C. solstitialis* population per region that was not included in the soil collections, to avoid potential local bias that may confound comparisons (Appendix S1). The goals of this study were to examine the variation in the effects of soil microbes throughout the distribution of *C. solstitialis*, so we stressed replication at the soil population level while using seeds from one population per region. In a related study, we tested for plant genotypic variation among populations and replicated seed populations within each region (Andonian & Hierro, 2011).

Soil inoculation experiment

We tested the effects of soil microbes from multiple sites in each of the four regions on *C. solstitialis* performance in a greenhouse at the University of California, Santa Cruz. We used only regionally sympatric seed–soil combinations in this study to provide ecologically accurate snapshots of the plant–soil microbe interactions in the different regions. Thus we have not parsed the effects of soil source from genotype source, but our focus was on comparing complete plant–soil microbe interactions among regions. However, in a previous common garden study, we found no difference in the biomass of *C. solstitialis* grown from seeds collected from the various populations used in this study (Andonian *et al.*, 2011). We grew plants in 600-mL 'conetainers' (Stuewe & Sons, Inc., Tangent, OR, USA) inoculated with 150 mL field soil in each pot. To reduce potential nutrient differences among soil samples, we fertilized plants every 2 weeks with 1/8 strength Hoagland's solution (PhytoTechnology Labs®, Shawnee Mission, KS, USA). We also diluted the field soil in a 20:80 soil : sand mixture using 20-grit blasting-grade sand. To reduce the probability of cross-contamination by soil microbes via watering splash, we topped off all pots with a 1-cm layer of 30-grit sand. We autoclaved half the soils on three successive days to sterilize soils. Then we planted four seeds from one locally occurring *C. solstitialis* population into all pots, and thinned to one individual upon germination.

In total, treatments were: 4 soil regions × 6 soil populations per region × 2 sterilization treatments × 5–6 replicates per treatment = 248 plants. We monitored germination time, harvested plants 110 days after germination, and separated above- and below-ground tissues. All plants were dried for 72 h at 60 °C and weighed.

Statistical analysis

We tested the effects of soil treatments (region, population[region], sterilization, and region × sterilization) 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's honestly significant difference (HSD) *post-hoc* analyses at $\alpha = 0.05$. We also calculated net effects of soil microbes using log response ratios with the following equation:

$$R_m = \log[\text{biomass (field soil)}/\text{biomass (sterile soil)}]$$

where R_m = response to soil microbes; biomass (field soil) = mean biomass of plants grown in unsterilized field soil; biomass (sterile soil) = mean biomass of plants grown in sterilized soil. The log response ratios are zero when there is no difference between the means of sterile and field soils; negative when microbes have negative effects (denominator is greater than numerator); and positive when microbes have positive effects (greater biomass in field than sterile soil).

We used SYSTAT 12 (SYSTAT Software Inc., Richmond, CA, USA) for the specific contrasts and JMP 7.0 (SAS Institute Inc., Cary, NC, USA) for all other statistical analyses.

RESULTS

Centaurea solstitialis in Argentinean and Eurasian soils had the highest root biomass, although these differences were not statistically significant (Fig. 1; Table 1). *Centaurea solstitialis* in Californian and Chilean soil treatments had the highest shoot

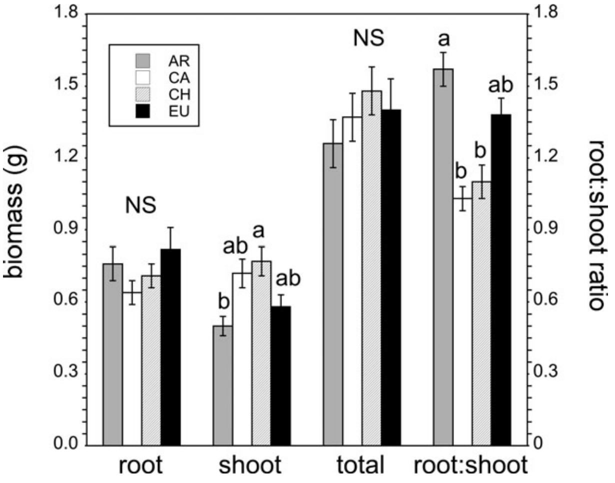

Figure 1 Summary of measured response variables from *Centaurea solstitialis* grown in soils from four regions (AR = Argentina, CA = California, CH = Chile, EU = Eurasia). Data represent means ± 1 SE. Different letters represent significant differences after Tukey's honestly significant difference (HSD) *post-hoc* tests on log-transformed data.

Table 1 ANOVA statistics for the effects of region and sterilization on *Centaurea solstitialis* root biomass (g), shoot biomass (g), total biomass (g), and root : shoot ratio. Regions include Argentina, California, Chile and Eurasia. All variables were log transformed to meet ANOVA assumptions of normality and homoscedasticity. Asterisks indicate significant treatment effects (*$P < 0.05$; **$P < 0.001$; ***$P < 0.0001$).

Effect	d.f.	*F*
Root biomass		
Region	3, 18	1.06
Sterilization	1, 211	953.69***
Region × sterilization	3, 211	12.17***
Shoot biomass		
Region	3, 18	4.27*
Sterilization	1, 211	1266.13***
Region × sterilization	3, 211	3.26*
Total biomass		
Region	3, 18	1.82
Sterilization	1, 211	2193.48***
Region × sterilization	3, 211	15.22***
Root : shoot		
Region	3, 18	6.00**
Sterilization	1, 211	0.05
Region × sterilization	3, 211	2.58*

biomass (Fig. 1), but there was no significant effect of source region on total biomass (Table 1). The lack of regional differences in the effects of soils on most biomass metrics was likely to be due to the high variance among populations within regions; population[region] explained 23%, 42% and 43% of the total variation in root, shoot and total biomass, respectively. There was a significant interaction effect of soil region on RSR, where plants in Argentinean soils had the greatest RSR, followed by Eurasian treatments, with the lowest RSR in Californian and Chilean soil treatments ($F_{1,3} = 6.00$, $P = 0.005$; Table 1; Fig. 1).

Soil microbes had strong negative effects on *C. solstitialis* from all four regions (Fig. 2) as shown by the fact that sterilization consistently increased above- and below-ground biomass (Table 1; Fig. 2). However, the effects of microbes varied across regions, with significant region × sterilization interactions for all biomass response variables (Table 1). Overall, soil microbes from native populations had more negative effects on plants than soils from introduced populations (Fig. 3). Eurasian soil microbes had the most negative effects on *C. solstitialis* total biomass, which were significantly different from the effects of Californian and Chilean microbes on *C. solstitialis*, but not different from Argentinean soil microbes (Fig. 3; Tukey HSD at $\alpha = 0.05$). This general pattern held for root and shoot biomass (Table 2). Significant effects of soil region on total biomass occurred only in field soil treatments ($F_{3,19} = 4.42$, $P = 0.02$), but this effect of region disappeared in sterile soil treatments ($F_{3,20} = 0.53$, $P = 0.66$), suggesting that soil microbes were responsible for driving the patterns in total biomass.

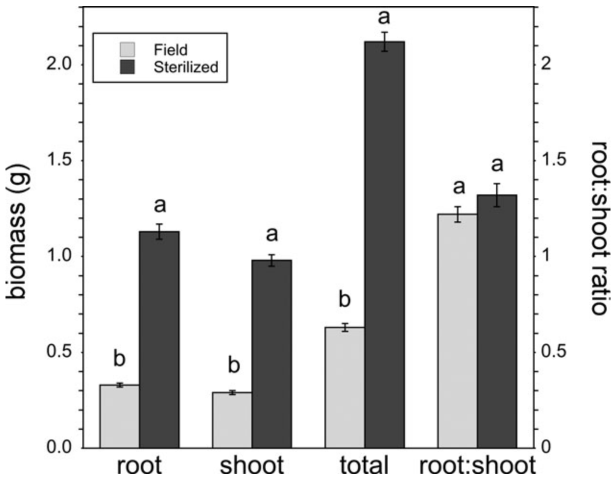

Figure 2 Summary of measured response variables of *Centaurea solstitialis* grown in field (light bars) and sterilized (dark bars) soils. Data represent means ± 1 SE. Different letters represent significant differences after Tukey's honestly significant difference (HSD) *post-hoc* tests on log transformed data.

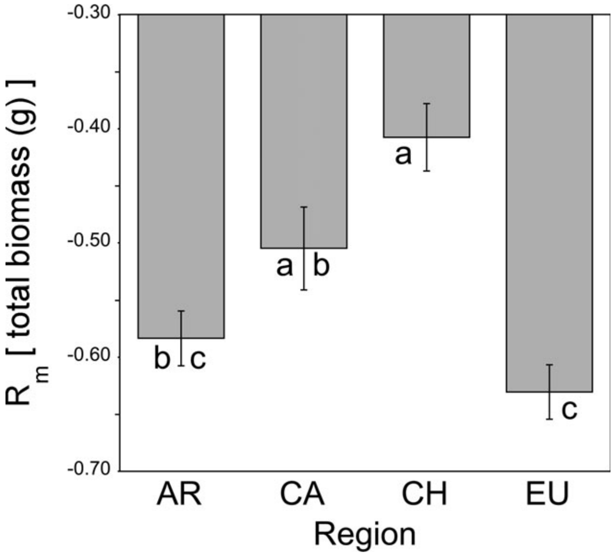

Figure 3 Log response ratios demonstrating the net effects of soil microbes (R_m) on the total biomass (g) of *Centaurea solstitialis* from different regions (AR = Argentina, CA = California, CH = Chile, EU = Eurasia). Negative bars represent negative effects of soil microbes (e.g. positive effects of sterilization) on total biomass. Bars represent means ± 1 SE. Different letters represent significant differences after Tukey's honestly significant difference (HSD) *post-hoc* tests. All R_m values were significantly < 0 after *t*-tests.

The effects of soil region and soil microbes demonstrated a very different pattern for RSR, with significant regional differences and region × sterilization interactions, and no overall effect of sterilization (Table 1). Soil microbes decreased RSR in Argentinean and Eurasian samples, but had neutral effects on Californian and Chilean samples of *C. solstitialis*

Table 2 Means and standard errors (SEM) of the four response variables for the main effects of region (AR = Argentina, CA = California, CH = Chile, EU = Eurasia) and soil sterilization (Field, Sterilized) on *Centaurea solstitialis*. Superscripts indicate significant differences among regions within sterilization treatments after Tukey's honestly significant difference (HSD) *post-hoc* contrasts.

	Field soil				Sterilized soil			
Response variable	AR	CA	CH	EU	AR	CA	CH	EU
N	30	36	30	30	30	36	24	29
Root biomass (g)	0.31^{A}	0.31^{A}	0.40^{A}	0.30^{A}	1.21^{AB}	0.96^{C}	1.00^{BC}	1.36^{A}
± SEM	0.02	0.02	0.02	0.02	0.06	0.06	0.06	0.10
Shoot biomass (g)	0.22^{B}	0.33^{A}	0.38^{A}	0.25^{B}	0.78^{B}	1.11^{A}	1.13^{A}	0.92^{AB}
± SEM	0.01	0.02	0.03	0.01	0.04	0.07	0.07	0.04
Total biomass (g)	0.53^{B}	0.64^{B}	0.78^{A}	0.54^{B}	2.00	2.08	2.13	2.28
± SEM	0.02	0.03	0.05	0.03	0.07	0.09	0.08	0.11
Root : shoot	1.45^{A}	1.05^{B}	1.19^{AB}	1.21^{AB}	1.69^{A}	1.01^{B}	1.01^{B}	1.55^{A}
± SEM	0.09	0.07	0.09	0.06	0.13	0.09	0.11	0.12

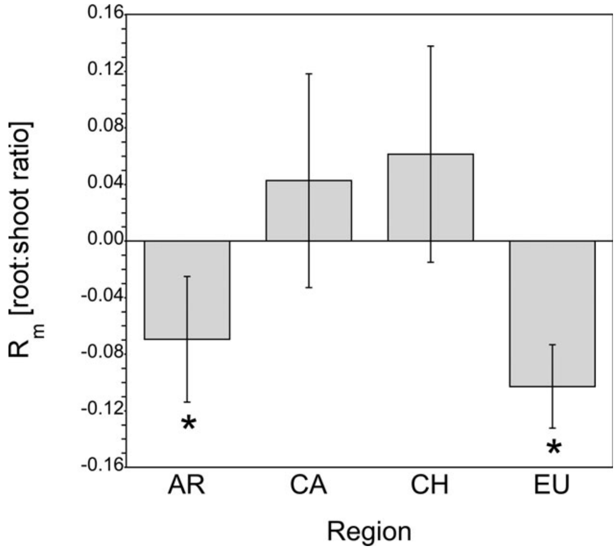

Figure 4 Log response ratios demonstrating the net effects of soil microbes (R_m) on root : shoot ratio (RSR) of *Centaurea solstitialis* from different regions (AR = Argentina, CA = California, CH = Chile, EU = Eurasia). Soil microbes decreased the RSR of *C. solstitialis* from AR and EU, but the small positive effects of soil microbes on RSR in CA and CH were not significantly different from 0 after *t*-tests. Bars represent means ± 1 SE. Asterisks represent significant differences in RSR when grown in field versus sterile soils after *t*-tests.

(Table 2; Fig. 4). Finally, even though soil microbes increased allocation to root biomass in soils from introduced populations, soil microbes did not increase the relative root mass of *C. solstitialis* in native Eurasian soils.

DISCUSSION

Natural enemy release and biogeographic variation in soil pathogen pressure

Soil microbes from all regions had strong negative effects on the growth of *C. solstitialis*, but *C. solstitialis* experienced less enemy pressure in most soils from non-native ranges than in those from its native range. If we draw comparisons between 'native' and 'introduced' regions by considering all three introduced regions together, the effects of soil microbes conform to the basic predictions of the ERH. However, the effects of native Eurasian soil microbes did not differ statistically from those in Argentinean soils, despite highly successful invasion by *C. solstitialis* in Argentina. *Centaurea solstitialis* in California and Chile appears to have been released from soil-borne natural enemies, which is consistent with results from greenhouse experiments with plant–soil feedbacks (Andonian *et al.*, 2011) and generally consistent with other soil sterilization experiments with *C. solstitialis* (Hierro *et al.*, 2006), its congeners *C. maculosa* and *C. diffusa* (Callaway *et al.*, 2004; Kulmatiski, 2006), and soil feedback experiments with invasive species in general (Kulmatiski *et al.*, 2008). However, the region where release from soil-based enemies appeared to be strongest was Chile, where *C. solstitialis* grows at low densities, similar to densities in its native range (Andonian *et al.*, 2011). Thus, although soil microbes had strong effects on the growth of *C. solstitialis*, which varied throughout its distribution, the geographic patterns in intensity of release were not fully consistent with general patterns of the degree of invasion, except for the Eurasia–California comparison. For example, soil microbes may be keeping *C. solstitialis* populations in check in its native range, but the species is spreading rapidly in Argentina, where we found strong negative effects of soil biota. It is possible that *C. solstitialis* experiences enemy release from soil pathogens in some parts of its introduced range, such as California, while other factors (such as empty niche, evolution of invasiveness or escape from herbivory) may contribute proportionally more to its success in other parts of its introduced range. If so, this suggests a fascinating biogeographic mosaic of interaction strengths among soil biota and *C. solstitialis* and perhaps other organisms involved in its invasive success (Thompson, 2005; McNeely & Power, 2007; Springer, 2009). It is important to note that, unlike the species-specific pairs of interactions used to develop theory about geographic mosaics (Thompson &

Cunningham, 2002), soil biota comprise a 'black box' with respect to the identity of the soil microbes. Although our results contribute to an understanding of 'regional evolutionary trajectories' (see Callaway & Ridenour, 2004) and exotic plant invasions, to extend our results into the co-evolutionary theory of Thompson's geographic mosaic of co-evolution would require the identification and study of specific microbial taxa that interact with *C. solstitialis* in its different ranges. Other analyses, however, have shown that soils from the native range of *C. solstitialis* contain higher densities of at least one genus of fungal pathogen, *Pythium* sp., than is found in soils from introduced populations (K. Reinhart, USDA-ARS, pers. comm.), thus providing additional support for the role of pathogens in limiting growth in native populations.

Those regions where soil microbes had the most negative effects (in Argentina and Eurasia) were also regions where plants allocated a greater proportion of their biomass to root tissue. Increased RSR has been associated with plant responses to stress (Chapin, 1980; van Noordwijk *et al.*, 1998; Grantz *et al.*, 2006), so geographic variation in RSR could be an indicator of the variation in pathogen pressure. Interestingly, there was no net effect of soil microbes on RSR, owing to the interaction between soil region and sterilization.

Alternative explanations

Soil microbes had strong effects on the growth of *C. solstitialis*, but these effects do not correlate completely with provenance or regional patterns of invasion success. This may be due to the difficulty of sampling the key microbial taxa in an entire region accurately if they vary substantially in space and time. In other words, the spatial distributions of soil biota are likely to be highly heterogeneous, and sampling collects a minuscule representation of all possible sites and microsites. Thus the particular taxa exerting the strongest effects within a region are easy to miss. Collecting and storing regional representative samples of soil microbes also poses logistical challenges, and the amount of soil we sampled in each region may have missed certain influential soil microbial taxa. Also, it is possible that we may have altered soils in some regionally specific way by storing or transporting them. To address these challenges, we collected samples from as many replicate populations as we could from each region; nonetheless, sampling at the appropriate scale is very difficult to determine correctly.

An alternative explanation for our results lies in the constraints of extrapolating data from greenhouse experiments to ecological interactions in the field. Although our methods minimized potential physical and chemical differences among soil populations, it is still difficult to conclude whether the negative effects of microbes were due to direct effects on *C. solstitialis* or a consequence of different degrees of microbial immobilization of nutrients in different soils. Thus we have an incomplete understanding of the direct and indirect effects of the entire microbial community, potentially as root pathogens and in mediating plant available nutrients. Although greenhouse experiments can introduce such problems of artefactual effects of pot environments, our results provide informative insights to the global variation of the effects of soil microbes on *C. solstitialis* invasions.

Our results also suggest that mechanisms for invasion, even for the invasion of a single species, are not mutually exclusive. In other words, different abiotic and biotic factors affect the invasion success of *C. solstitialis* in different parts of the world. Natural enemy release may contribute to the invasion success of *C. solstitialis* in some regions, such as California, but in other regions *C. solstitialis* may invade successfully due to other factors. A primary hypothesis for invasive success is escape from specialist insect herbivores, and this may play an important role in some regions. However, *C. solstitialis* endures greater attack by natural enemies via biocontrol agents in its introduced range in California than it does in its native range (K. Andonian, pers. obs.). In California, biocontrol weevils can be found in over 50% of *C. solstitialis* inflorescences and in over 90% of plants (Gutierrez *et al.*, 2005; Swope & Parker, 2010), but in native regions in Eurasia no more than 18% of plants in a population have been found to be infested (Uygur *et al.*, 2004). However, escape from other specialist herbivores may contribute importantly to the spread of *C. solstitialis* in Argentina.

CONCLUSIONS

Our results indicate that *C. solstitialis* experiences biogeographic mosaics of plant–soil interactions that vary in their interaction strengths and influence its world-wide performance. Such regional variability in interaction strengths may translate into geographic variation in selective pressures that can push introduced plants into divergent evolutionary trajectories with potential community-level consequences (Callaway *et al.*, 2005; Brooker *et al.*, 2009). Results such as these may begin to become more common as researchers begin sampling more sites throughout the distributions of invasive species. Our results highlight the difficulty in making generalizations about the mechanisms behind biological invasions, yet highlight the potential for using invasive species to explore the biogeographic mosaics of species interactions.

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REFERENCES

Agrawal, A.A., Lau, J.A. & Hamback, P.A. (2006) Community heterogeneity and the evolution of interactions between plants and insect herbivores. *Quarterly Review of Biology*, **81,** 349–376.

Andonian, K. & Hierro, J.L. (2011) Species interactions contribute to the success of a global plant invader. *Biological Invasions*, **13,** 2957–2965.

Andonian, K., Hierro, J.L., Khetsuriani, L., Becerra, P., Janoyan, G., Villarreal, D., Cavieres, L., Fox, L.R. & Callaway, R.M. (2011) Range-expanding populations of a globally introduced weed experience negative plant–soil feedbacks. *PLoS ONE*, **6,** e20117. doi:10.1371/journal.pone.0020117

Batten, K.M., Scow, K.M., Davies, K.F. & Harrison, S.P. (2006) Two invasive plants alter soil microbial community composition in serpentine grasslands. *Biological Invasions*, **8,** 217–230.

Blossey, B. & Nötzold, R. (1995) Evolution of increased competitive ability in invasive non-indigenous plants: a hypothesis. *Journal of Ecology*, **83,** 887–889.

Brooker, R.W., Callaway, R.M., Cavieres, L., Kikvidze, Z., Lortie, C., Michalet, R., Pugnaire, F.I., Valiente-Banuet, A. & Whitham, T.G. (2009) Don't diss integration: a comment on Ricklefs' disintegrating communities. *The American Naturalist*, **174,** 919–927.

Callaway, R.M. & Maron, J.L. (2006) What have exotic plant invasions taught us over the past 20 years? *Trends in Ecology and Evolution*, **21,** 369–374.

Callaway, R.M. & Ridenour, W.M. (2004) Novel weapons: invasive success and the evolution of increased competitive ability. *Frontiers in Ecology and the Environment*, **2,** 436–443.

Callaway, R.M., Thelen, G.C., Rodriguez, A. & Holben, W.E. (2004) Soil biota and exotic plant invasions. *Nature*, **427,** 731–733.

Callaway, R.M., Hierro, J.L. & Thorpe, A.S. (2005) Evolutionary trajectories in plant and soil microbial communities: *Centaurea* invasions and the geographic mosaic of coevolution. *Species invasions: insights into ecology, evolution and biogeography* (ed. by D.F. Sax, J.J. Stachowicz and S.D. Gaines), pp. 341–364. Sinauer Associates, Sunderland, MA.

Callaway, R.M., Kim, J. & Mahall, B.E. (2006) Defoliation of *Centaurea solstitialis* stimulates compensatory growth and intensifies negative effects on neighbors. *Biological Invasions*, **8,** 1389–1397.

Chapin, F.S., III (1980) The mineral nutrition of wild plants. *Annual Review of Ecology and Systematics*, **11,** 233–260.

Colautti, R.I., Ricciardi, A., Girgorovich, I.A. & MacIsaac, H.J. (2004) Is invasion success explained by the enemy release hypothesis? *Ecology Letters*, **7,** 721–733.

Dietz, H. & Edwards, P.J. (2006) Recognition that causal processes change during plant invasion helps explain conflicts in evidence. *Ecology*, **87,** 1359–1367.

Elton, C.S. (1958) *The ecology of invasions by animals and plants*. Methuen, London.

Gabrielyan, E. & Fragman-Sapir, O. (2008) *Flowers of the Transcaucasus and adjacent areas*. A.R.G. Gantner Verlag Kommanditgesellschaft, Würselen, Germany.

Gerlach, J.D., Jr (1997) The introduction, dynamics of geographic range expansion, and ecosystem effects of yellow starthistle (*Centaurea solstitialis*). *Proceedings of the California Weed Science Society*, **49,** 136–141.

Graham, R.C. & O'Geen, A.T. (2010) Soil mineralogy trends in California landscapes. *Goederma*, **154,** 418–437.

Grantz, D.A., Gunn, S. & Vu, H.B. (2006) O_3 impacts on plant development: a meta-analysis of root/shoot allocation and growth. *Plant, Cell & Environment*, **29,** 1193–1209.

Gutierrez, A.P., Pitcairn, M.J., Ellis, C.K., Carruthers, N. & Ghezelbash, R. (2005) Evaluating biological control of yellow starthistle (*Centaurea solstitialis*) in California: a GIS based supply–demand demographic model. *Biological Control*, **34,** 115–131.

van der Heijden, M., Klironomos, J.N., Ursic, M., Moutoglis, P., Streitwolf-Engel, R., Boller, T., Wiemken, A. & Sanders, I.A. (1998) Mycorrhizal fungal diversity determines plant biodiversity, ecosystem variability and productivity. *Nature*, **396,** 69–72.

Hierro, J.L., Maron, J.L. & Callaway, R.M. (2005) A biogeographic approach to plant invasions: the importance of studying exotics in their introduced and native range. *Journal of Ecology*, **93,** 5–15.

Hierro, J.L., Villareal, D., Eren, O., Graham, J.M. & Callaway, R.M. (2006) Disturbance facilitates invasion: the effects are stronger abroad than at home. *The American Naturalist*, **168,** 144–156.

Hierro, J.L., Eren, O., Khetsuriani, L., Diaconu, A., Torok, K., Montesinos, D., Andonian, K., Kikodze, D., Janoian, L., Villarreal, D., Estanga-Mollica, M. & Callaway, R.M. (2009) Germination responses of an invasive species in native and non-native ranges. *Oikos*, **118,** 529–538.

Hijano, E. & Basigalup, D. (1995) El cultivo de la alfalfa en la República Argentina. *La alfalfa en la Argentina* (ed. by E. Hijano and A. Navarro), pp. 13–18. Instituto Nacional Tecnológico Agropecuaria, Buenos Aires, Argentina.

Keane, R.M. & Crawley, M.J. (2002) Exotic plant invasions and the enemy release hypothesis. *Trends in Ecology and Evolution*, **17,** 164–170.

Klironomos, J.N. (2002) Feedback with soil biota contributes to plant rarity and invasiveness in communities. *Nature*, **417,** 67–70.

Kulmatiski, A. (2006) Exotic plants establish persistent communities. *Plant Ecology*, **187,** 261–275.

Kulmatiski, A. & Beard, K.H. (2006) Activated carbon as a restoration tool: potential for control of invasive plants in abandoned agricultural fields. *Restoration Ecology*, **14,** 251–257.

Kulmatiski, A., Beard, K.H., Stevens, J. & Cobbold, S.M. (2008) Plant–soil feedbacks: a meta-analytical review. *Ecology Letters*, **11,** 980–992.

Lambrinos, J.G. (2002) The variable invasive success of *Cortaderia* species in a complex landscape. *Ecology*, **83,** 518–529.

Levine, J.M., Adler, P.B. & Yelenik, S.G. (2004) A meta-analysis of biotic resistance to exotic plant invasions. *Ecology Letters*, **7,** 975–998.

Luzio, W., Seguel, O. & Casanova, M. (2009) Suelos de la zona Mediterránea árida (desde 32°00′ LS hasta 37°45′). *Suelos de Chile* (ed. by W. Luzio), pp. 125–194. Universidad de Chile Press, Santiago, Chile.

Mack, R.N., Simberloff, D., Lonsdale, W.M., Evans, H., Clout, M. & Bazzaz, F.A. (2000) Biotic invasions: causes, epidemiology, global consequences, and control. *Ecological Applications*, **10,** 689–710.

Maddox, D.M. (1981) *Introduction, phenology, and density of yellow starthistle in coastal, intercoastal, and central valley situations in California, ARR-W-20US*. Department of Agriculture, Agricultural Research Service, Washington, DC.

Maddox, D.M., Mayfield, A. & Poritz, N.H. (1985) Distribution of yellow starthistle (*Centaurea solstitialis*) and Russian knapweed (*Centaurea repens*). *Weed Science*, **33,** 315–327.

McNeely, C. & Power, M.E. (2007) Spatial variation in caddisfly grazing regimes within a northern California watershed. *Ecology*, **88,** 2609–2619.

Meiman, P.J., Redente, E.F. & Paschke, M.W. (2006) The role of the native soil community in the invasion ecology of spotted (*Centaurea maculosa* auct. non Lam.) and diffuse (*Centaurea diffusa* Lam.) knapweed. *Applied Soil Ecology*, **32,** 77–88.

Menéndez, J.L. & La Rocca, S.M. (2007) *Estado de conservación del distrito del caldén*. Secretaría de Ambiente y Desarrollo Sustentable de la Nación, Buenos Aires, Argentina.

Mitchell, C.E., Agrawal, A.A., Bever, J.D., Gilbert, G.S., Hufbauer, R.A., Klironomos, J.N., Maron, J.L., Morris, W.F., Parker, I.M., Power, A.G., Seabloom, E.W., Torcin, M.E. & Vazquez, D.P. (2006) Biotic interactions and plant invasions. *Ecology Letters*, **9,** 726–740.

Molchanov, E.N. (2009) Mountainous meadow-steppe soils in high mountains of the Eastern Caucasus region. *Eurasian Soil Science*, **42,** 591–599.

van Noordwijk, M., Martikainen, P., Bottner, P., Cuevas, E., Rouland, C. & Dhillion, S.S. (1998) Global change and root function. *Global Change Biology*, **4,** 759–772.

Parker, I.M. & Gilbert, G.S. (2004) Evolutionary ecology of novel plant–pathogen interactions. *Annual Review of Ecology, Evolution, and Systematics*, **35,** 675–700.

Petermann, J.S., Fergus, A.J.F., Turnbull, L.A. & Schmid, B. (2008) Janzen–Connell effects are widespread and strong enough to maintain diversity in grasslands. *Ecology*, **89,** 2399–2406.

Pimentel, D., Zuniga, R. & Monison, D. (2005) Update on the environmental and economic costs associated with alien-invasive species in the United States. *Ecological Economics*, **52,** 273.

Pitcairn, M.J., Schoenig, S., Yacoub, R. & Gendron, J. (2006) Yellow starthistle continues its spread in California. *California Agriculture*, **60,** 83–90.

Reinhart, K.O. & Callaway, R.M. (2004) Soil biota facilitate exotic *Acer* invasions in Europe and North America. *Ecological Applications*, **14,** 1737–1745.

Reinhart, K.O. & Callaway, R.M. (2006) Soil biota and invasive plants. *New Phytologist*, **170,** 445–457.

Richardson, D.M., Allsopp, N., D'Antonio, C.M., Milton, S.J. & Rejmánek, M. (2000) Plant invasions: the role of mutualisms. *Biological Review*, **75,** 65–93.

Sakai, A.K., Allendorf, F.W., Holt, J.S., Lodge, D.M., Molofsky, J., With, K.A., Baughman, S., Cabin, R.J., Cohen, J.E., Ellstrand, N.C., McCauley, D.E., O'Neil, P., Parker, I.M., Thompson, J.N. & Weller, S.G. (2001) The population biology of invasive species. *Annual Review of Ecology and Systematics*, **32,** 305–332.

Shea, K., Kelly, D., Sheppard, A.W. & Woodburn, T.L. (2005) Context-dependent biological control of an invasive thistle. *Ecology*, **86,** 3174–3181.

Springer, Y.P. (2009) Edaphic quality and plant–pathogen interactions: effects of soil calcium on fungal infection of a serpentine flax. *Ecology*, **90,** 1852–1862.

Stromberg, M.R., Corbin, J.D. & D'Antonio, C.M. (2007) *California grasslands: ecology and management*. University of California Press, Berkeley, CA.

Swope, S. & Parker, I.M. (2010) Trait-mediated interactions and lifetime fitness of the invasive plant *Centaurea solstitialis*. *Ecology*, **91,** 2284–2293.

Thompson, J.N. (2005) *The geographic mosaic of coevolution*. University of Chicago Press, Chicago, IL.

Thompson, J.N. & Cunningham, B.M. (2002) Geographic structure and dynamics of coevolutionary selection. *Nature*, **417,** 735–738.

Urushadze, T.F. (1997) *The main soils of Georgia*. Metzniereba, Tbilisi.

Uygur, S., Smith, L., Uygur, F.N., Cristofaro, M. & Balciunas, J. (2004) Population densities of yellow starthistle (*Centaurea solstitialis*) in Turkey. *Weed Science*, **52,** 746–753.

Vavra, M., Parks, C. & Wisdom, M. (2007) Biodiversity, exotic plant species, and herbivory: the good, the bad, and the ungulate. *Forest Ecology and Management*, **246,** 66–72.

Wilcove, D.S., Rothstein, D., Dubow, J., Phillips, A. & Losos, E. (1998) Quantifying threats to imperiled species in the United States. *BioScience*, **48,** 607–615.

Zangerl, A.R., Stanley, M.C. & Berenbaum, M.R. (2008) Selection for chemical trait remixing in an invasive weed after reassociation with a coevolved specialist. *Proceedings of the National Academy of Sciences USA*, **105,** 4547–4552.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Location and elevation of *Centaurea solstitialis* populations used for seed and soil collections for greenhouse experiments.

BIOSKETCH

Krikor Andonian earned his PhD from the Department of Ecology and Evolutionary Biology at the University of California, Santa Cruz. His research interests include plant ecology, invasion biology, plant–soil microbe interactions and biogeography. The research outlined here was part of an international collaboration of ecologists that comprised part of Dr Andonian's dissertation research. In addition to being an ecologist and educator, Krikor is also an artist and musician performing in the band audiafauna.

Author contributions: K.A., J.L.H. and R.M.C. conceived the ideas and experimental design and, along with L.R.F., designed the experiments; K.A., J.L.H., L.K., P.B., G.J., D.V. and L.C. conducted field surveys and collected soil and seed samples; K.A. performed the experiments and, along with L.R.F., analysed the data and wrote the manuscript.

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