The importance of factors controlling species abundance and distribution varies in native and non-native ranges

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How variation in factors controlling species abundance and distribution between native and non-native ranges compares to that within ranges remains poorly understood. We used a globally distributed ruderal, *Centaurea solstitialis* (*Centaurea*), to explore the possibility that the importance of those factors exhibits great variation between and within ranges. To test our hypothesis, we established seed addition experiments with soil disturbance (turnover and control) and biocide (fungicides, insecticide, and control) treatments in two regions within native (the Caucasus and south-western Turkey) and non-native (the western United States – US – and central Argentina) distributions. Also, we estimated the rate of vegetation recovery after disturbance (resilience) and related it to *Centaurea* density in experimental plots. Disturbance strongly increased *Centaurea* density in all regions. Density was similar between the native Caucasus and non-native Argentina and much greater in those regions than in the native Turkey and non-native US in biocide-free plots. Fungicides had positive effects on density in the US and negative ones in the Caucasus and Argentina, resulting in no differences between those three regions and greater density in the US than Turkey. Insecticide applications promoted *Centaurea* density in Turkey and Argentina, but inter-regional comparisons of density in treated plots were comparable to those in biocide-free plots. Overall, plants were smaller and less fecund in Turkey than the other regions, except the US. The greatest fungal attack was documented in Turkey, and herbivory was stronger there and in Argentina than in the Caucasus and US. The resilience of the local community explained a large proportion of variation in *Centaurea* density. These results support our hypothesis, and reveal that the speed at which competition is re-gained after disturbance may influence global variation in *Centaurea* abundance. Because many ruderals exhibit native and non-native distributions, our results are likely to be generalized to other systems.

Studying species in native and non-native ranges has provided considerable insight into the ecological and evolutionary mechanisms underlying invasions (Maron et al. 2004, Firn et al. 2011, Parker et al. 2013, Sun et al. 2015, Taylor et al. 2015), expanding our understanding of the processes that control species abundance and distribution (Hierro et al. 2005, Callaway and Maron 2006, Sax et al. 2007, Capinha et al. 2015). For example, field experiments conducted in the native and non-native range of *Clidemia hirta* have shown that herbivores and fungal pathogens decrease its survival in understory habitats at home, limiting the distribution of the species to open habitats in the native range; however, the absence of enemies abroad apparently allows the species to invade forest understory in the non-native range (DeWalt et al. 2004). Also, greenhouse studies have demonstrated that *Alliaria petiolata*, one of the most aggressive plant invaders in North America, indirectly suppresses competitors more strongly in non-native than native ranges (Callaway et al. 2008). Recently, the success of non-native populations of *Centaurea solstitialis* in California annual grasslands has been linked to the evolution of a higher-fitness life history in response to high water availability deep in the soil of that non-native region (Dlugosch et al. 2015). Taken together, these examples show that species invasions provide exceptional opportunities to explore how geographic variation in ecological and evolutionary responses influence species abundance at a global scale (Thompson 2005, Hierro et al. 2009, Andonian et al. 2012, Cronin et al. 2015).

Despite the knowledge gained from comparing species in native and non-native ranges, at least three issues are hindering progress in this realm of ecological biogeography. First, field experiments assessing factors that

may influence species abundance in native vs non-native ranges are still rare (DeWalt et al. 2004, Hierro et al. 2006, 2013, Williams et al. 2010, Callaway et al. 2011, Maron et al. 2013). Second, these experiments have usually been conducted within a single region with relatively uniform growing conditions in the respective ranges (but see DeWalt et al. 2004). This approach can be problematic because species often exhibit large variation in abundance throughout their distribution, reflecting spatial and temporal changes in the conditions that influence the growth of their populations (Andrewartha and Birch 1954, Brown et al. 1995, Kawecki 2008). Lastly, biogeographical field experiments have largely been designed to test the effects of single factors on species performance (but see Hierro et al. 2013, Maron et al. 2013), despite our understanding that the abundance, size, and fecundity of organisms are controlled by the combined action of many factors (Connell 1961, Holmgren et al. 1997, Maron et al. 2012). As a result of these limitations, how variation in factors controlling species abundance and distribution between native and non-native ranges compares to that within ranges is poorly understood, and establishing multi-factorial field experiments in regions encompassing diverse environmental conditions within both ranges is greatly needed.

Centaurea solstitialis (Asteraceae) is a widespread annual species that is adapted to disturbed environments (i.e. ruderal; Grime 1974). The species originated in the Anatolian and Caucasus regions (ancestral range; Maddox et al. 1985, Eriksen et al. 2014), and latter migrated to central and southern Europe (expanded range) in a range expansion likely aided by humans (N. García-Jactas, Botanical Inst. of Barcelona, pers. comm.). Both ancestral and expanded ranges are commonly considered as the native range of the species (Hierro et al. 2009). Starting in the mid 1800s, *C. solstitialis* was introduced as an agricultural seed contaminant in many regions around the world, including the western United States (US), southern South America, southern Africa, and southern Australia (non-native range). In field samplings and experiments, the species has consistently shown increased size, fecundity, and density in the western US and central Argentina relative to south-western Turkey (Uygur et al. 2004, Hierro et al. 2006, 2013). In a descriptive study in the Caucasus, however, the abundance, size and fecundity of *C. solstitialis* in disturbed natural grasslands have been documented to be as high as those in the US and Argentina (Khetsuriani and Lachashvili 2008, but see Andonian et al. 2011 for a different scenario described along roadsides), suggesting that the performance of the species varies within its ancestral range. In addition, greenhouse experiments exploring plant–soil feedbacks in *C. solstitialis* and soil from the Caucasus and several non-native regions detected a geographic mosaic of biotic interactions (Andonian et al. 2012), in which *C. solstitialis* generated neutral feedbacks in Caucasian and Chilean soils and strong negative feedbacks in soils from California and Argentina (Andonian et al. 2011). This information fits expected variation in performance over the distribution of a species (Andrewartha and Birch 1954, Brown et al. 1995, Kawecki 2008); however, to our knowledge, this variation has not been assessed in multi-factorial field experiments located in different regions within both native and non-native ranges.

Here, we used *C. solstitialis* as a model system to test the hypothesis that the importance of factors controlling species abundance and distribution varies not only between native and non-native ranges, but also between regions in each of the distributional ranges.

To explore this possibility, we performed a multi-factorial field experiment in two regions within the native range of *C. solstitialis*, the Caucasus and south-western Turkey, and two regions within the non-native range, the western United States (US) and central Argentina, in which we added seeds of the target species and manipulated three factors commonly thought to influence species abundance and distribution in general and non-native plant invasions in particular, soil disturbance (Grime 2001, Hierro et al. 2006, Williams et al. 2010), interactions with fungi (Callaway et al. 2004, Bell et al. 2006, Maron et al. 2013), and insect herbivory (Wolfe 2002, DeWalt et al. 2004, Müller-Schärer et al. 2004), by applying soil turnover and biocide treatments. In addition, we conducted frequent samplings throughout the duration of the experiment to closely follow the recovery of the plant community after applying the soil disturbance treatment (community resilience, sensu Begon et al. 2006) in all four study regions.

Material and methods

Study area

Within the native range of *C. solstitialis*, field experiments were conducted at three sites in the Caucasus region (Martkopi and Sakadagiano in Georgia, and Yerevan Botanical Garden in Armenia) and two sites in south-western Anatolia, on the campus of the Adnan Menderes Univ. (ADÜ) in Aydin, Turkey (Supplementary material Appendix 1, Table A1). Sites encompassed the entire elevational gradient covered by the species in the native range (0 to 1400 m, Eren and Hierro unpubl.), and were separated by 40 to 180 km in the Caucasus, and 1 km in Turkey. Similarly, within the non-native range, three sites were established in western US (California) and three sites in central Argentina. Sites in California were located within the Sierra Foothill Research and Extension Center (SFREC) of the Univ. of California at Davis. In central Argentina, sites were located on a private ranch (La Mercedes) in La Pampa province. Distance between sites ranged from 2 to 5 km in the US, and 2 to 3 km in Argentina. In all cases, experimental sites were natural grasslands with deep soils (>1 m) and typical of the region (Supplementary material Appendix 2, Table A2). *Centaurea solstitialis* was not present in these grasslands at the onset of the experiment, but based on site characteristics and pre-experimental conditions, they were ideal for the establishment and growth of the species if dispersed there. Sites in Georgia receive precipitation throughout the year, but most occurs in the spring and summer (Table 1). Precipitation in Yerevan also peaks in the spring, and summers are drier than the fall and winter. South-western Turkey experiences a Mediterranean climate with hot and dry summers and cool and wet winters. Similarly, climate in the western US is Mediterranean. Finally, central Argentina receives most of the rain in the spring and summer.

Table 1. Climatic information of experimental sites in the four regions explored in this study.

Region	Meteorological station	Mean annual precipitation (mm)	Mean annual temperature (°C)	Precipitation during the study (mm)
Caucasus	T'bilisi	496	13.3	495
	Yerevan	299	11.3	447
South-western Turkey	Aydin	618	17.8	659
Western US	Sierra Foothill Research and Extension Center	728	16.7	460
Central Argentina	Santa Rosa	638	15.4	630

Experimental design and seed addition

The experimental design included a soil disturbance treatment (with and without disturbance), a seed addition treatment (with and without *C. solstitialis* seeds), and a biocide treatment (with fungicides, insecticide, and a control with water only). Treatments were replicated five times, for a total of 60 plots per site (2 levels of disturbance × 2 levels of the seed addition × 3 levels of biocide × 5 replicates). All sites were fenced at the beginning of the experiment to exclude domestic animals. Experimental plots were 1×1 m in size, and they were separated by 1 m. The cover of all plant species was measured in 15 non-disturbed plots to record pre-experimental conditions in all sites (Supplementary material Appendix 2, Table A2). *Centaurea solstitialis* seeds (technically, achenes) were collected from field populations located near experimental sites in the summer previous to the beginning of the experiment. In all cases, seeds added to plots were local to the experimental site. Seed additions were conducted by seeding plots with 600 seeds. To account for *C. solstitialis* seed dimorphism and differences in the number of morphs produced (Benefield et al. 2001), added seeds consisted of a mixture of 480 pappus and 120 non-pappus seeds, which represents the natural proportion. Pappus and non-pappus seeds were added in fall 2006 (Caucasus and the US) and 2007 (Turkey and Argentina), in coincidence with the prime emergence time of the species. Seeds were added shortly before a rain, which in regions with a Mediterranean climate corresponded with the first seasonal rain event. Only seeds that looked healthy and filled with an embryo were used in the experiment. Seeds were added to the 0.50×0.50 m centre of plots to allow for a buffer zone around the edges, covered with a thin layer of soil, and prevented from blowing away with wood frames 0.5×0.5 m wide $\times 0.15$ m tall placed around the seeded area. Frames were removed after the first rains. In combination, this protocol is likely to have reduced seed predation (Hierro et al. 2013). At the end of the experiment, *C. solstitialis* plants were removed from sites located in the non-native range. In addition, these sites were re-visited to assure they have not been invaded by the non-native plant.

Treatment application

For the disturbance treatment, the soil within plots was turned over as in Hierro et al. (2006). For the biocide treatment, plots received applications of fungicide (i.e. fungicide and oomyceticide), insecticide, or water (no biocide). Based on consultation with specialists (W. Koeller and G. Abawi, Cornell Agricultural Station, pers. comm.) and product application instructions, fungicide applications were a combination of the soil oomyceticide Ridomil Gold® (active ingredient, mefenoxam, a synthetic isomer of metalaxyl; chemical formula, $C_{15}H_{21}NO_4$), soil fungicide Terraclor® (pentachloronitrobenzene; $C_6Cl_5NO_2$), and foliar fungicide Compass® (trifloxystrobin; $C_{20}H_{19}F_3N_2O_4$). Based also on recommendations (T. Busbice, Bayer representative, pers. comm.), insecticide applications were conducted with Merit 75 WP® (Imidacloprid; $C_9H_{10}ClN_5O_2$), a systemic and broad-spectrum insecticide. See Supplementary material Appendix 3 for further information on biocides and their applications.

The efficacy of biocide applications was validated by quantifying the density of a soil-borne pathogenic oomycete, *Pythium* (see Supplementary material Appendix 4 for methods and results), and assessing aboveground *C. solstitialis* plants for signs of fungal (e.g. colored and necrotic tissue) and herbivore attack (e.g. holes and bites) in treated and non-treated plots. In addition, potential effects of biocides on nutrient inputs were evaluated by analyzing NH_4^+ and NO_3^- concentrations in mixed-bed resin capsules (Supplementary material Appendix 4). No biocide contained phosphorus.

Sampling

Experimental plots were sampled at half, one, two, four, six, and nine months after the first rain that initiated the emergence of *C. solstitialis*. At each sampling, the percent cover of each plant species was estimated. In Armenia, this schedule was interrupted during the winter months (two and four months after the significant rain) because the site was covered with snow. Once the identification of *C. solstitialis* was possible, individuals of the species with and without signs of both fungal and herbivore attack were counted inside plots at the above time intervals, and *C. solstitialis* damage was estimated as the proportion between the number of plants with signs of attack and the total number of plants present in each plot. A large number of Asteraceae species, looking similar to *C. solstitialis* seedlings, delayed the first counting of individuals until one and four months after the rain in California and Turkey, respectively. Similarly, the first counting of *C. solstitialis* individuals in non-disturbed plots in the Caucasus was only possible at the one-month sampling. At the peak of *C. solstitialis* flowering, during the nine-month sampling, the height and number of capitula of a maximum of five randomly selected individuals per plot were measured.

In our study, resilience is used as the rate of vegetation recovery up to six months after applying the soil disturbance treatment. Six months is the time at which the cover of alive vegetation peaked in the Mediterranean regions of southwestern Turkey and the US. Resilience was measured in no biocide and no seed addition plots, and it was calculated as Σn, where n is the percent cover of the vegetation at each sampling time. This simple formula was borrowed from germination studies, where it is known as the Timson's index (Timson 1965) and used to calculate germination rates (Baskin and Baskin 2001).

Statistical analyses

Region, treatment, and their interactive effects on dependent variables were assessed with generalized linear mixed models (GLMMs) that assumed a Poisson distribution and log link function for count variables (density and fecundity of *C. solstitialis* and plant richness), binomial distribution and logit link function for proportions (*C. solstitialis* damage and plant cover), and normal distribution and identity link function for linear response variables (*C. solstitialis* height). In addition, analyses over time were conducted with repeated-measures GLMMs. Pair-wise comparisons in GLMMs allowed evaluating treatment effects both within and between regions. In the model used to assess effects on *C. solstitialis* density and damage over time, experimental plots were introduced as subjects, time as repeated measures, region, disturbance, biocide, and all two- and three-way interactions as fixed factors, and site, nested within region, as a random factor. In the model used to compare effects on *C. solstitialis* density at the end of the experiment (i.e. final density or density of adult established plants) region, disturbance, biocide and all their two- and three-way interactions were considered as fixed factors, and site(region), as a random factor. Due to low *C. solstitialis* recruitment in nondisturbed plots, only data from soil turnover plots were used in analyses of treatment effects on the height and number of capitula of *C. solstitialis* at the end of the experiment. The statistical model included, region, biocide, and their interaction as fixed factors, and site(region) and plot(site(region)) as random ones. Comparisons of community resilience between regions were performed with a model that included region as a fixed factor and site(region) as a random one. In addition, this rate was linearly regressed against the density of *C. solstitialis* at the six months sampling also in disturbed plots that did not receive biocide applications. The average of both rate of vegetation recovery and *C. solstitialis* density at each site were used in the analysis (n = 11). Density data were transformed with the square root function to meet linear regression assumptions (Zar 2003). Also, the presence of influential data were assessed using the recommended threshold value of $4/(n - k - 1)$ of the Cook's distance, where n is the number of observations and k the number of explanatory variables (Cook 1977). Changes through time in the percent cover of alive plants in disturbed plots were also evaluated (Supplementary material Appendix 5). Finally, plant richness in disturbed plots at the six-month-sampling, period of maximum plant richness (spring) in all four regions, was compared between regions with a model in which region, biocide, and their interaction were considered as fixed factors, and site(region) as a random factor. Analyses were performed with IBM® SPSS® Statistics 22 (GLMMs) and Systat software® SigmaPlot 11.0 (regressions).

Data available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.d08fb> (Hierro et al. 2016).

Results

As expected for a ruderal species, soil disturbance had strong positive effects on *C. solstitialis* density over the extent of the experiment in all four study regions (p < 0.050 for all pairwise comparisons, Fig. 1). The effects of biocides, instead, varied according to the region and, in some instances, they depended on disturbed conditions. When compared to plots free of biocides, fungicides decreased *C. solstitialis* density throughout the experiment in the native Caucasus and non-native central Argentina in plots with soil disturbance (p < 0.050). In sharp contrast, fungicides consistently increased the density of our target species in the non-native US in both disturbed and non-disturbed plots (p < 0.050). Insecticide applications promoted final density in the native Turkey (p = 0.042) and the non-native Argentina (p = 0.017) in plots with soil disturbance.

Treatment effects on *C. solstitialis* density also varied when they were compared between regions, and the variation was largely independent of the native/non-native nature of the region (Fig. 1). In plots with no biocide applications, the final density of *C. solstitialis* was similar between the native Caucasus and non-native Argentina (p = 0.183), and density in these regions was at least six times greater than that in both the native Turkey (vs the Caucasus, p = 0.014; vs Argentina, p = 0.017) and the non-native US (vs the Caucasus, p = 0.022; vs Argentina, p = 0.045). Plant density was, in turn, marginally similar between Turkey and the US (p = 0.065) in non-treated plots. As a result of the strong positive effects of fungicides on *C. solstitialis* in the US and negative ones in the Caucasus and Argentina, density in the US was similar to that in the Caucasus (p = 0.117) and Argentina (p = 0.528), and marginally greater than that in Turkey (p = 0.042) in plots treated with fungicides. In plots treated with the insecticide, inter-regional comparisons were comparable to those in plots without biocides.

Fungicides increased the number of *C. solstitialis* capitula only in the US, where plants growing in treated plots were twice as fecund as those growing in plots with no biocides (p = 0.025; Fig. 2). The insecticide promoted plant size only in central Argentina, where individuals in treated plots were 15% larger than those in biocide-free plots (p = 0.001). In addition, plants were smaller and less fecund in the native Turkey than the rest of the regions (p < 0.050; Fig. 2), except the US (p > 0.050), and exhibited similar size and fecundity between the Caucasus, the US, and Argentina (p > 0.050) in plots with no biocides and in those with the insecticide. In plots treated with fungicides, *C. solstitialis* plants were smaller and less fecund in Turkey than in any other region (p < 0.05), highlighting again the positive effects of fungicides on the species in the US.
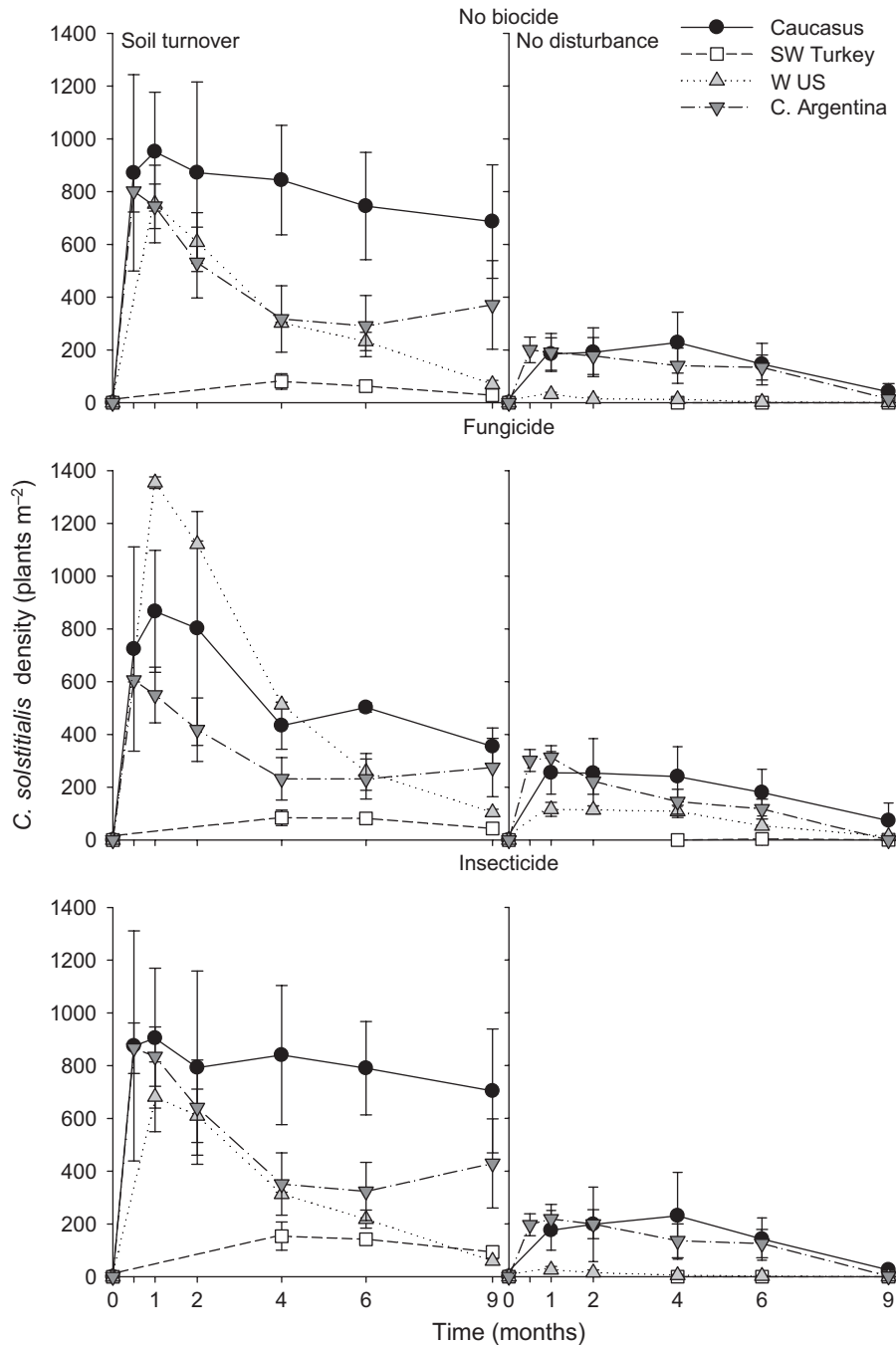
Figure 1. Density over time of *C. solstitialis* under experimental treatments in all four study regions (native, Caucasus and south-western Turkey; non-native, western US and central Argentina). Symbols show means for three study sites ($\pm$ SE) in each region, except for Turkey, where two sites were established (n = 5 plots per site in all regions). Density over time: $F_{Region\ 3,\ 1536} = 8.913$, $p < 0.001$; $F_{Disturbance\ 1,\ 1536} = 17.007$, $p < 0.001$; $F_{Biocide\ 2,\ 1536} = 0.108$, $p = 0.897$; $F_{Region*Disturbance\ 3,\ 1536} = 17.224$, $p < 0.001$; $F_{Region*Biocide\ 6,\ 1536} = 8.762$, $p < 0.001$; $F_{Disturbance*Biocide\ 2,\ 1536} = 0.037$, $p = 0.963$; $F_{Region*Disturbance*Biocide\ 6,\ 1536} = 2.412$, $p = 0.025$. Final density: $F_{Region\ 3,\ 305} = 9.523$, $p < 0.001$; $F_{Disturbance\ 1,\ 305} = 1926.876$, $p < 0.001$; $F_{Biocide\ 2,\ 305} = 34.070$, $p < 0.001$; $F_{Region*Disturbance\ 3,\ 305} = 141.113$, $p < 0.001$; $F_{Region*Biocide\ 6,\ 305} = 82.450$, $p < 0.001$; $F_{Disturbance*Biocide\ 2,\ 305} = 61.217$, $p < 0.001$; $F_{Region*Disturbance*Biocide\ 6,\ 305} = 46.324$, $p < 0.001$.

In south-western Turkey, fungicides reduced by around half the proportion of *C. solstitialis* individuals damaged by fungi ($p < 0.001$; Fig. 3). In contrast, in the other native region, the Caucasus, fungicide-treated and untreated individuals showed similar levels of fungi attack over the course of the experiment ($p > 0.05$). No fungal attack was observed in the non-native regions. Comparisons between regions also showed that *C. solstitialis* plants suffered considerably higher fungal attack over time in Turkey than in any other region ($p < 0.001$ for all pair-wise comparisons; Fig. 3), and it was similar for plants growing in the Caucasus, US, and Argentina ($p > 0.05$).

The proportion of *C. solstitialis* individuals damaged by herbivores was lower in treated than non-treated plots only
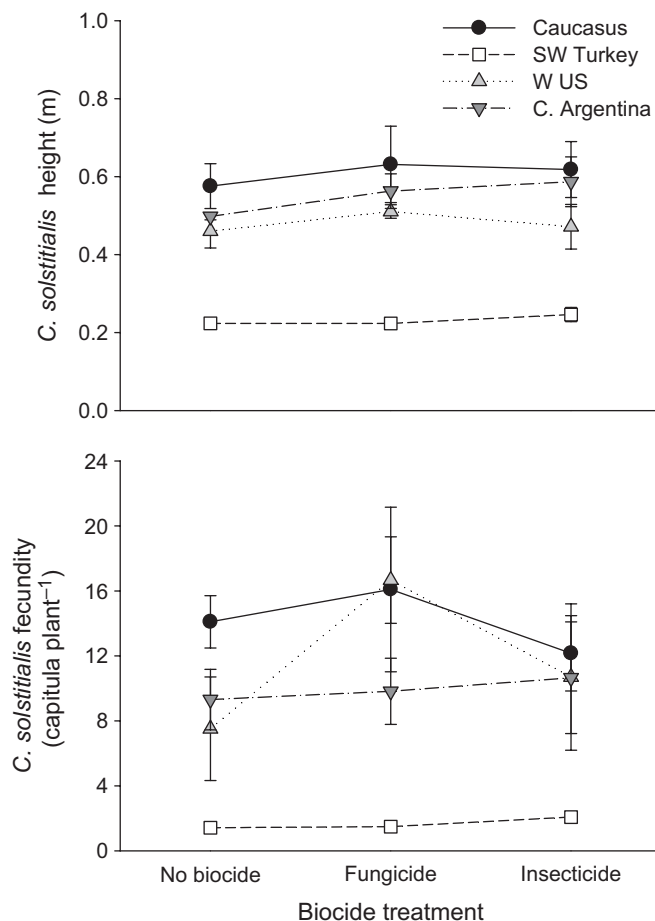
Figure 2. Size and fecundity of *C. solstitialis* at the end of the experiment under biocide treatments in disturbed plots in the four study regions (native, Caucasus and south-western Turkey; non-native, western US and central Argentina). Symbols show means for three study sites ($\pm$ SE) in each region, except for Turkey, where two sites were established (n = 5 plots per site in all regions). Size, $F_{Region\ 3,\ 734} = 5.221$, p = 0.001; $F_{Biocide\ 2,\ 734} = 4.689$, p = 0.009; $F_{Region*Biocide\ 6,\ 734} = 1.882$, p = 0.081. Fecundity, $F_{Region\ 3,\ 734} = 6.083$, p < 0.001; $F_{Biocide\ 2,\ 734} = 1.667$, p = 0.190; $F_{Region*Biocide\ 6,\ 734} = 1.533$, p = 0.164.

in the non-native region of central Argentina (p = 0.042; Fig. 4). Also, herbivory on our target plant was an order of magnitude higher in both Turkey and Argentina than in the Caucasus and the US (p < 0.010 for all pair-wise comparisons; Fig. 4), and it did not differ between Turkey and Argentina (p = 0.079) and between the Caucasus and the US (p = 0.749). Disturbance had no effect on the degree of fungal or herbivore damage (see legends in Fig. 3 and 4).

Vegetation in disturbed plots recovered faster in Mediterranean (Turkey, Timson's index: 349.900 $\pm$ 2.687; the US, 264.560 $\pm$ 23.623; mean $\pm$ SD) than temperate regions (Caucasus, 22.000 $\pm$ 30.204; Argentina, 10.686 $\pm$ 1.950; $F_{Region3,\ 51} = 21.605$, p < 0.001; pair-wise comparisons, p < 0.001), and recovery was similar within each of these climatic groups (Turkey vs US, p = 0.695; Caucasus vs Argentina, p = 0.999). Interestingly, the rate of vegetation recovery explained a large proportion of the variation in *C. solstitialis* density ($r^2 = 0.413$, $F_{1,\ 9} = 6.338$, p = 0.033; Fig. 5), and the relationship became even stronger ($r^2 = 0.721$, $F_{1,\ 8} = 20.648$, p = 0.002) after removing one of the sites in Argentina, which was singled out as an influential datum by the analysis. Finally, plant richness in disturbed plots was statistically similar between all study

regions (Turkey, 10.733 $\pm$ 4.311; Caucasus, 3.556 $\pm$ 2.932; US, 5.111 $\pm$ 0.991; central Argentina, 3.000 $\pm$ 1.049; $F_{Region\ 3,\ 150} = 1.676$, p = 0.175; $F_{Biocide\ 2,\ 150} = 3.898$, p = 0.022; $F_{Region*Biocide\ 6,\ 150} = 0.940$, p = 0.468; Supplementary material Appendix 6, Table A6).

Discussion

Establishing field experiments in species' native and non-native ranges is an important development in ecological biogeography that has helped to understand factors that contribute to the establishment and spread of non-native species (DeWalt et al. 2004, Hierro et al. 2006, 2013, Williams et al. 2010, Callaway et al. 2011, Maron et al. 2013). Most of these experiments were conducted within one general region in each distributional range, encompassing similar climatic and biotic conditions (but see DeWalt et al. 2004), and designed to assess the importance of single factors on species performance (but see Maron et al. 2013). This approach has overlooked expected environmental variation and related changes in species abundance within ranges (Kawecki 2008). Here, we conducted parallel field
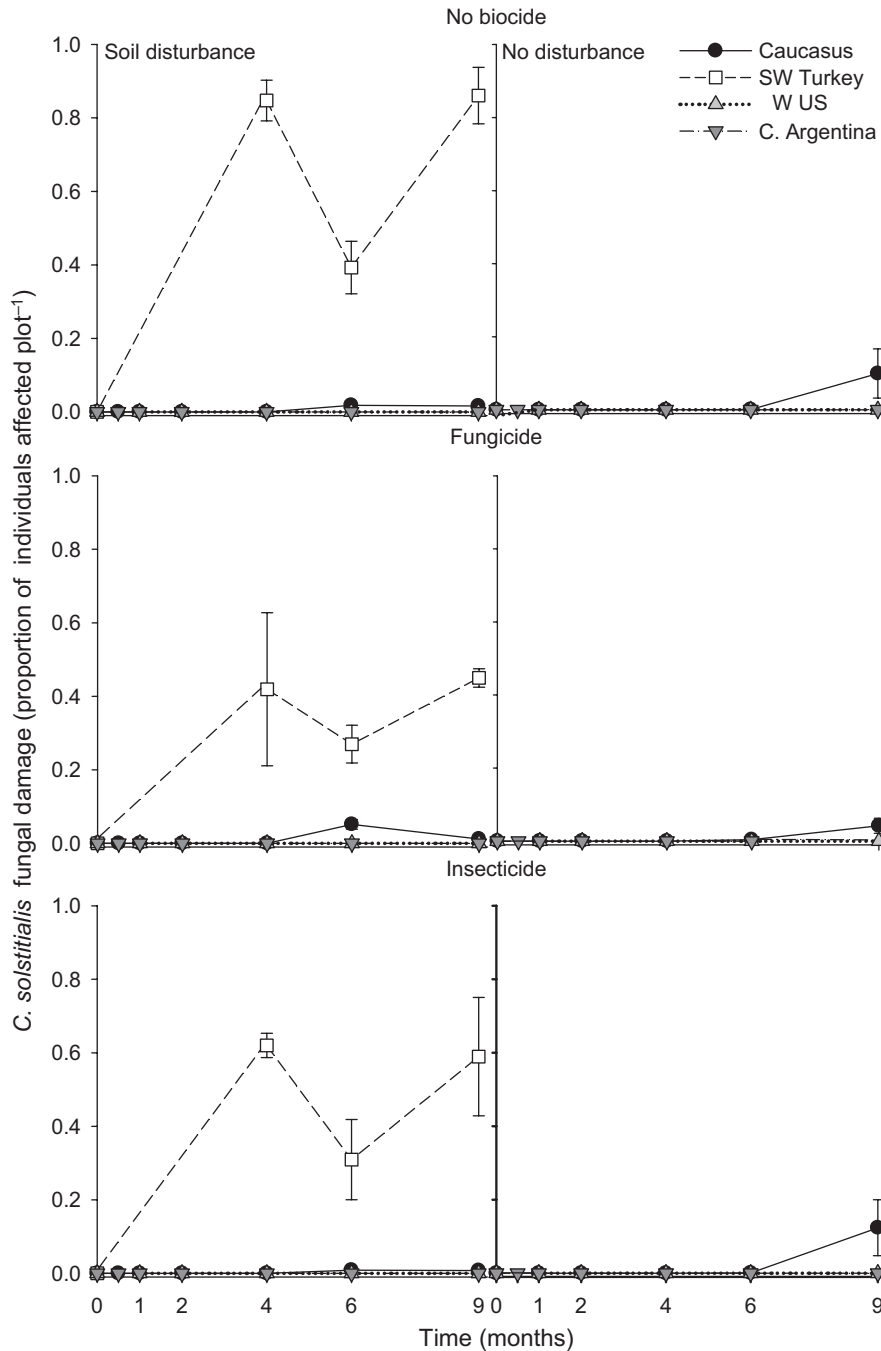
Figure 3. Fungal damage of *C. solstitialis* throughout its lifespan under experimental treatments in the four study regions (native, Caucasus and south-western Turkey; non-native, western US and central Argentina). Symbols show means for three study sites ($\pm$ SE) in each region, except for Turkey, where two sites were established (n = 5 plots per site in all regions). $F_{Region\ 3,\ 1290} = 169.337$, $p < 0.001$; $F_{Disturbance\ 1,\ 1290} = 0.935$, $p = 0.334$; $F_{Biocide\ 2,\ 1290} = 98.941$, $p < 0.001$; $F_{Region*Disturbance\ 2,\ 1290} = 0.312$, $p = 0.817$; $F_{Region*Biocide\ 6,\ 1290} = 32.981$, $p < 0.001$; $F_{Disturbance*Biocide\ 2,\ 1290} < 0.001$, $p = 1.000$; $F_{Region*Disturbance*Biocide\ 4,\ 1290} < 0.001$, $p = 1.000$.

experiments in two regions with contrasting conditions within both the native and non-native range of a globally distributed ruderal, *C. solstitialis*, and explored population- and individual-level responses of the species to three factors thought to influence its abundance and distribution, soil disturbance, interactions with fungi, and insect herbivory. We found that the importance of explored factors exhibited large variation between study regions, and that this variation was in general not related to the native or non-native nature of the region, providing general support to our working hypothesis. Also, we detected a strong negative relationship between the resilience of the local plant community and *C. solstitialis* density, which raises the possibility that the speed at which competition is re-gained after disturbance explain global variation in *C. solstitialis* abundance. Because many ruderals are globally distributed (<www.darwin.edu.ar>, <www.plants.usda.gov>), our results are likely to be gener- alized to other systems.
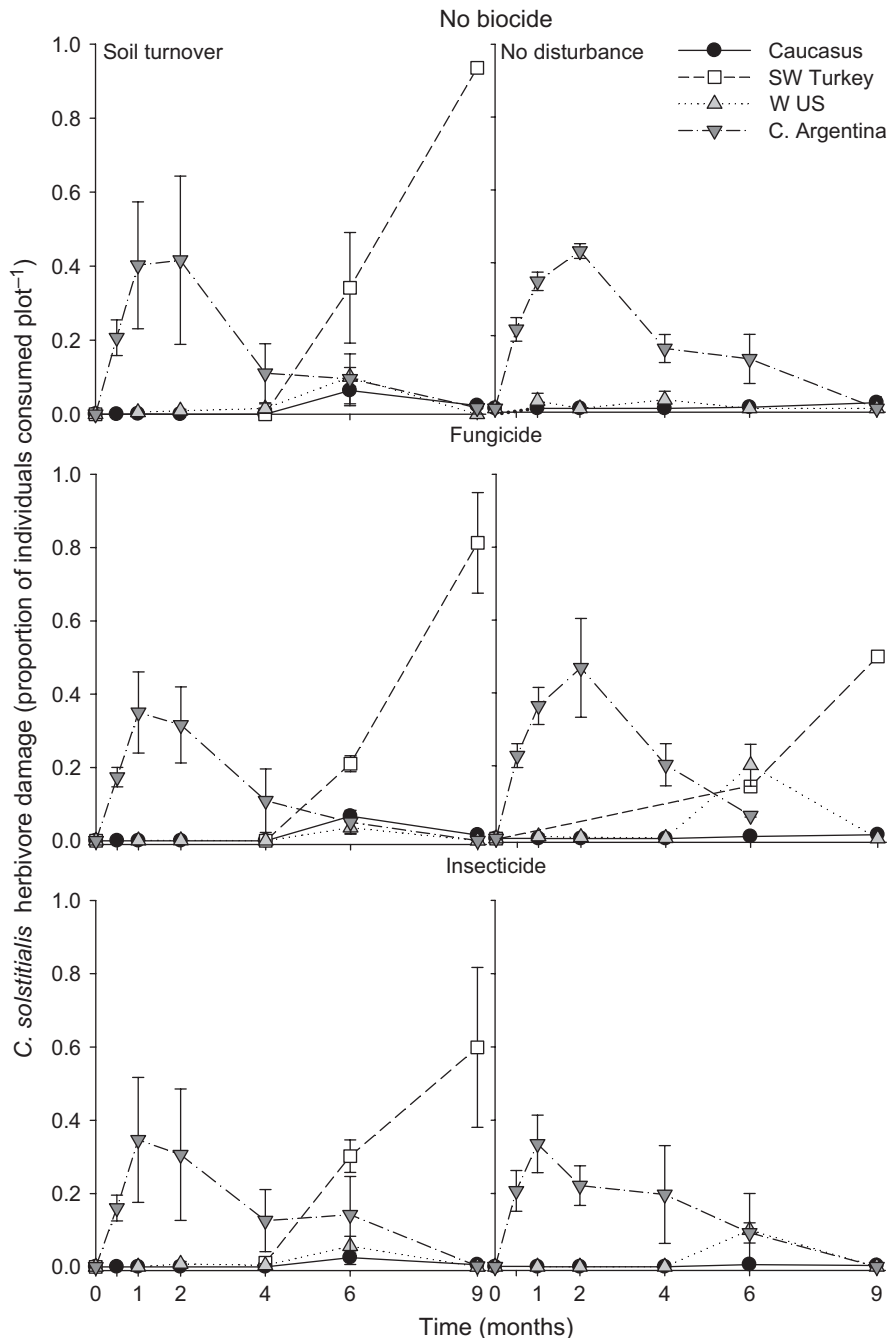
Figure 4. Herbivore damage of *C. solstitialis* throughout its lifespan under experimental treatments in the four study regions (native, Caucasus and south-western Turkey; non-native, western US and central Argentina). Symbols show means for three study sites ($\pm$ SE) in each region, except for Turkey, where two sites were established (n = 5 plots per site in all regions). $F_{Region\ 3,\ 1304} = 22.539$, $p < 0.001$; $F_{Disturbance\ 1,\ 1304} = 0.360$, $p = 0.549$; $F_{Biocide\ 2,\ 1304} = 1.392$, $p = 0.249$; $F_{Region*Disturbance\ 3,\ 1304} = 2.545$, $p = 0.055$; $F_{Region*Biocide\ 6,\ 1304} = 0.365$, $p = 0.901$; $F_{Disturbance*Biocide\ 2,\ 1304} = 2.338$, $p = 0.097$; $F_{Region*Disturbance*Biocide\ 4,\ 1304} = 1.017$, $p = 0.397$.

Previous observational and experimental studies conducted in the native south-western Turkey, non-native western US, and non-native central Argentina, showed that the abundance, size, and fecundity of *C. solstitialis* were much greater in non-native than native ranges (Uygur et al. 2004, Hierro et al. 2006, 2013), which is consistent with our current results. Here, however, we enlarged our geographical scope within the native range to include the Caucasus and found that *C. solstitialis* performance in parts of the range

where it originated can be comparable to its performance in parts of the range where it has been introduced. In a descriptive study conducted in several grasslands near our study sites in the Republic of Georgia (Caucasus), Khetsuriani and Lachashvili (2008) also found that in sites disturbed by humans, *C. solstitialis* dominated plant communities (42 to 70% plant cover and 100% frequency presence in sampling plots) and exhibited individuals with relatively large sizes (0.25 to 0.50 m tall on average per site). In our work, we
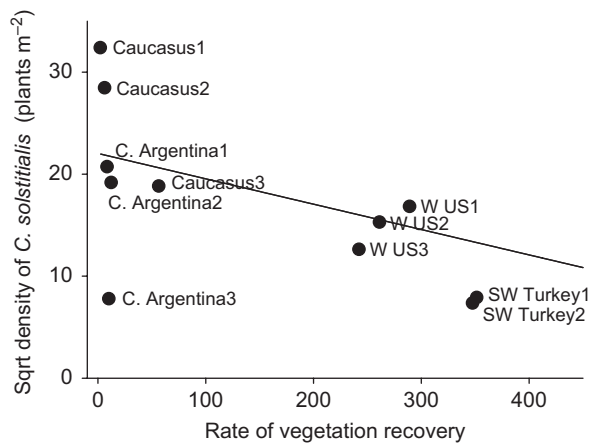
Figure 5. The relationship between the rate of vegetation recovery after disturbance and density of *C. solstitialis* for the 11 study sites distributed in four regions (native, Caucasus and south-western Turkey; non-native, western US and central Argentina). Data points are means of five experimental plots in each site. Site 3 in central Argentina is an influential point, according to Cook's distance.

additionally observed that *C. solstitialis* suffered one of the lowest levels of damage from aboveground fungi and herbivores in this native region relative to the others. Similarly, community resilience in the Caucasus was one of the slowest of the study regions, which could translate into weak competitive effects from recovering neighbors. These results suggest that factors limiting *C. solstitialis* do not occur uniformly across its native distribution (Andrewartha and Birch 1954, Brown et al. 1995, Reinhart et al. 2005), and favorable conditions encountered abroad can also be present at home (Firn et al. 2011). The native Caucasus could, in fact, be considered as a 'core habitat' for *C. solstitialis* (Kawecki 2008). Our study questions then the common assumption in invasion biology that successful non-native species exhibit greater density and performance in non-native than native ranges, and highlights the importance of exploring variation in growing conditions and species responses within both ranges in order to properly establish patterns and formulate derived hypotheses for invasion success (Hierro et al. 2005, Firn et al. 2011).

In contrast to generally favorable growing conditions, the density of soil-borne pathogens (*Pythium* spp.) was relatively high in the Caucasus. Fungicides effectively reduced *Pythium* concentrations in the soil; however, fungicides also decreased the density of *C. solstitialis*, suggesting that fungi as a whole may exert net positive effects on the species in the Caucasus, also contributing to its high performance in the region. Importantly, this conclusion is generally supported by earlier greenhouse studies designed to evaluate the importance of the soil biota on *C. solstitialis* growth, as *C. solstitialis* was found to generate neutral plant–soil feedbacks when growing in soils from the Caucasus (Andonian et al. 2011). Comparisons between our results and those from the greenhouse studies are not, however, straightforward because our work intended to control the effects of only a portion of the soil biota, whereas plant–soil feedback essays evaluated those of the whole soil microbial community. Also, although our

selection of fungicides was guided by the advice of experts and results from previous ecological studies showing both target (Bell et al. 2006) and no non-target effects (Maron et al. 2013), our conclusions need to be taken with caution because applying broad-spectrum fungicides is not free of shortcomings (Maron et al. 2013). For example, because we limited our efficacy assessments to only measure *Pythium* density, we cannot know how fungicides affected the density of other pathogens, as well as the interplay of microbial interactions and their consequences for plant growth and establishment. Further work is warranted to understand the net positive effects of fungi on *C. solstitialis* density detected here for the Caucasus.

In sharp contrast to the Caucasus, the species performed poorly in south-western Turkey. Coincidently, limiting conditions for *C. solstitialis* establishment, growth, and reproduction were strong in that native region, as enemy attack and plant community resilience were both high in Turkey. Fungicide applications effectively reduced aboveground infections, but the damage was still substantial in treated plots, and the performance of the species was similar in plots with and without fungicides. These results suggest three possibilities; stronger doses are needed to detect effects on plant performance, fungi do not alter *C. solstitialis* performance (and aboveground assessments of fungi attack do not accurately reflect fungi effects), and/or other factors are more important at controlling the species in Turkey. Currently, we cannot rule out any of these possibilities, and additional work is needed to substantiate interpretations. The proportion of plants damaged by herbivores, on the other hand, was similar between insecticide-treated and non-treated plots, which could suggest that herbivores other than insects are also consuming *C. solstitialis* individuals. One of these herbivores could be *Helix lucorum*, a snail common in our study sites in Turkey. Insecticide applications increased, however, plant numbers as compared to those in the controls in disturbed plots, but these positive effects were not strong enough to increase the density of our target species to levels comparable to those observed in regions where *C. solstitialis* exhibited high abundance, such as the Caucasus and central Argentina. These results suggest that while herbivores can contribute to limit *C. solstitialis* abundance in south-western Turkey, additional controlling factors are operating, among which, the rapid establishment of competitive effects from the neighboring vegetation as a result of the high resilience of the local plant community could be of primary importance.

Given the known success of *C. solstitialis* in the western US (Dukes 2002, Gerlach and Rice 2003, Uygur et al. 2004, Andonian et al. 2011), detecting strong net negative effects of fungi on population-level responses of *C. solstitialis* is counterintuitive. The response of *C. solstitialis* to fungicides in the US offers, however, field support to previous plant–soil feedback experiments conducted with the species under greenhouse conditions by Andonian and colleagues (2011), who found that *C. solstitialis* generated strong negative plant–soil feedbacks in soils from our study sites in the US, and proposed that negative plant–soil interactions may provide a mechanism for invasive spread by encouraging expanding growth at population edges. More generally, other studies have also found relatively high rates of pathogen attack on non-native populations in recipient communities

(Nijjer et al. 2007, Parker and Gilbert 2007, Flory and Clay 2013). The low incidence of aboveground fungal damage in the western US suggests that soil fungi may be the main contributors to the general negative effects, and although US soils were free of *Pythium*, other non-assessed pathogens could be responsible. In addition to the inhibitory effects of fungi, we found evidence for intense competitive effects from the recovering resident plant community in this region. We also observed a decline in the density of *C. solstitialis* at the end of the experiment, which was likely due to spring drought conditions. Drought conditions probably also affected plant size and fecundity in that non-native region. Thus, our study may have underestimated the performance of *C. solstitialis* at the end of the experiment in the US.

The high density, size, and fecundity of *C. solstitialis* in central Argentina, as compared to the other regions, confirm results from previous field experiments (Hierro et al. 2006, 2013). The observed performance corresponds with the virtual absence of *Pythium* in soil samples, positive effects of fungi (i.e. negative effects of fungicides) on *C. solstitialis* density, and relatively slow community resilience in Argentina. In general agreement with the positive effects of fungi detected here, *C. solstitialis* plants were found to exhibit similar size in field and sterilized Argentinean soils (Hierro et al. 2006) and generate neutral feedbacks when growing in those soils (Chiuffo et al. 2015). In contrast, Andonian et al. (2011) detected negative plant–soil feedbacks for our target species in soils from Argentina. Differences in methodological protocols, such as the identity of the trainer of heterospecific soils (native grasses in Andonian et al. 2011 vs native herbs in Chiuffo et al. 2015) may help to explain the contrasting results. As also found in other studies (Hierro et al. 2013), plants suffered substantial herbivory in Argentina. Correspondingly, insecticide applications reduced plant damage and increased plant density and size. Because no enemy has been introduced from the native range of *C. solstitialis* to Argentina, plant damage in this region was likely caused by herbivores native to Argentina. In fact, the native caterpillar *Paracles deserticola* was commonly observed in our experimental plots. These results show that *C. solstitialis* is not free of biotic control in this non-native region (Keane and Crawley 2002), where it is highly successful.

Competition is thought to play a central role in non-native plant invasion (Gioria and Osborne 2014), and based on plant strategy theory the importance of the interaction can be expected to be particularly high for ruderals (Grime 1974). In our study, differences in plant community resilience between regions are likely driven by variation in emergence and growth rates between the plant functional groups that dominate their respective grasslands; that is, annual versus perennial grasses and herbs. Differences in those rates could, in turn, translate into variation in the speed at which competitive effects from recovering annuals and perennials on *C. solstitialis* develop after disturbance, thus explaining the strong negative relationship between community resilience and *C. solstitialis* density. Studies on a congeneric species, *C. stoebe*, detected stronger competitive effects from the surrounding vegetation at home than abroad, which could explain the greater abundance of the species in non-native

relative to native ranges (Callaway et al. 2011, Maron et al. 2013). Our results indicate that competitive effects can also vary substantially within ranges.

Because we added locally collected seeds of *C. solstitialis* in all four study regions, chances are that our results are influenced by genetic factors (Ellstrand and Schierenbeck 2000, Lai et al. 2008, Eriksen et al. 2014). Widmer et al. (2007) determined that seeds from non-native US populations were larger, contained more starch, and produced larger individuals than seeds from native Eurasian populations when grown for two weeks in the lab and to maturity in common gardens in the native range. Similarly, Graebner and co-authors (2012) found that seedlings from California were larger and displayed greater competitive resistance than seedlings from Spain in greenhouse experiments. In a common garden with populations from the same regions studied here, Eriksen et al. (2012) found that plants from the US grew larger than plants from any other region. In addition, Dlugosch et al. (2015) reported that non-native US populations have evolved a higher-fitness life history at the expense of an increased dependency on water in response to the presence of an 'empty niche' created by the widespread replacement of native perennial by Eurasian annual grasses and concomitant increases in deep soil water availability (Holmes and Rice 1996, Dyer and Rice 1999). Interestingly, these results could help to explain why the 'empty niche' idea applies to the US, but not to large portions of the native range of the species, where grasslands are also dominated by annuals. Evolutionary mechanisms can thus contribute to the success of *C. solstitialis* in the US. The highest performance of the species in our study, however, was not measured in the US, but in the Caucasus and central Argentina, suggesting that genetic factors cannot fully explain the geographic variation in *C. solstitialis* abundance reported here.

Another uncontrolled factor in our experiment was soil properties; however, *C. solstitialis* was highly successful in both sandy soils (e.g. central Argentina) and those with a high proportion of clay (e.g. the Caucasus). Thus, soil properties do not seem to be a factor explaining variation in *C. solstitialis* abundance.

In conclusion, our study shows a geographic mosaic of signs and intensities of species interactions (Thompson 2005, Andonian et al. 2012) that is not entirely congruent with the assumption that invasive species encounter better conditions in non-native relative to native ranges. Our work thus contributes to the general understanding of geographic variation in the importance of factors that control species abundance and distribution at a global scale.

References

Andonian, K. et al. 2011. Range-expanding populations of a globally introduced weed experience negative plant–soil feedbacks. – PLoS One 6: e20117.

Andonian, K. et al. 2012. Geographic mosaics of plant–soil microbe interactions in a global plant invasion. – J. Biogeogr. 39: 600–608.

Andrewartha, H. G. and Birch, L. C. 1954. The distribution and abundance of animals. – Univ. of Chicago Press.

Baskin, C. C. and Baskin, J. M. 2001. Seeds: ecology, biogeography and evolution of dormancy and germination. – Academic Press.

Begon, M. et al. 2006. Ecology: from individuals to ecosystems, 4th ed. – Blackwell.

Bell, T. et al. 2006. Plant pathogens drive density dependent seedling mortality in a tropical tree. – Ecol. Lett. 9: 569–574.

Benefield, C. B. et al. 2001. Reproductive biology of yellow starthistle: maximizing late-season control. – Weed Sci. 49: 83–90.

Brown, J. H. et al. 1995. Spatial variation in abundance. – Ecology 76: 2028–2043.

Callaway, R. M. and Maron, J. L. 2006. What have exotic plant invasions taught us over the past 20 years? – Trends Ecol. Evol. 21: 369–374.

Callaway, R. M. et al. 2004. Soil fungi alter interactions between the invader *Centaurea maculosa* and North American natives. – Ecology 85: 1062–1071.

Callaway, R. M. et al. 2008. Novel weapons: invasive plant suppresses fungal mutualists in America but not in its native Europe. – Ecology 85: 1043–1055.

Callaway, R. M. et al. 2011. Escape from competition: neighbors reduce *C. stoebe* performance at home but not away. – Ecology 92: 2208–2213.

Capinha, C. et al. 2015. The dispersal of alien species redefines biogeography in the Anthropocene. – Science 348: 1248–1251.

Chiuffo, M. C. et al. 2015. Native and non-native ruderals experience similar plant–soil feedbacks and neighbor effects in a system where they coexist. – Oecologia 179: 843–852.

Connell, J. H. 1961. The influence of interspecific competition and other factors on the distribution of the barnacle *Chthalamus stellatus*. – Ecology 42: 710–723.

Cook, R. D. 1977. Detection of influential observations in linear regression. – Technometrics 19: 15–18.

Cronin, J. T. et al. 2015. Biogeography of a plant invasion: plant–herbivore interactions. – Ecology 96: 1115–1127.

DeWalt, S. J. et al. 2004. Natural enemy release facilitates habitat expansion of the invasive tropical shrub *Clidemia hirta*. – Ecology 85: 471–483.

Dlugosch, K. M. et al. 2015. Evolution of invasiveness through increased resource use in a vacant niche. – Nat. Plants 1: 1–5.

Dukes, J. S. 2002. Species composition and diversity affect grassland susceptibility and response to invasion. – Ecol. Appl. 12: 602–617.

Dyer, A. R. and Rice, K. J. 1999. Effect of competition on resource availability and growth of a California bunchgrass. – Ecology 80: 2697–2710.

Ellstrand, N. C. and Schierenbeck, K. A. 2000. Hybridization as a stimulus for the evolution of invasiveness in plants? – Proc. Natl Acad. Sci. USA 97: 7043–7050.

Eriksen, R. L. et al. 2012. Morphological differentiation in a common garden experiment among native and non-native specimens of the invasive weed yellow starthistle (*Centaurea solstitialis*). – Biol. Invasions 14: 1459–1467.

Eriksen, R. L. et al. 2014. Dispersal pathways and genetic differentiation among worldwide populations of the invasive weed *Centaurea solstitialis* L. (Asteraceae). – PLoS One 9: e114786.

Firn, J. et al. 2011. Abundance of introduced species at home predicts abundance away in herbaceous communities. – Ecol. Lett. 14: 274–281.

Flory, S. L. and Clay, K. 2013. Pathogen accumulation and long-term dynamics of plant invasions. – J. Ecol. 101: 607–613.

Gerlach, J. D. and Rice, K. J. 2003. Testing life history correlates of invasiveness using congeneric plant species. – Ecol. Appl. 13: 167–179.

Gioria, M. and Osborne, B. A. 2014. Resource competition in plant invasions: emerging patterns and research needs. – Front. Plant Sci. 5: 1–21.

Graebner, R. et al. 2012. Invasive species grows faster, competes better, and shows greater evolution toward increased seed size and growth than exotic non-invasive congeners. – Plant Ecol. 213: 545–553.

Grime, J. P. 1974. Vegetation classification by reference to strategies. – Nature 250: 26–31.

Grime, J. P. 2001. Plant strategies, vegetation processes, and ecosystem properties, 2nd ed. – John Wiley and Sons.

Hierro, J. L. et al. 2005. A biogeographical approach to plant invasion biology: the importance of studying exotics in their introduced and native range. – J. Ecol. 93: 5–15.

Hierro, J. L. et al. 2006. Disturbance facilitates invasion: the effects are stronger abroad than at home. – Am. Nat. 168: 144–156.

Hierro, J. L. et al. 2009. Germination responses of an invasive species in native and non-native ranges. – Oikos 118: 529–538.

Hierro, J. L. et al. 2013. Non-native conditions favor non-native populations of invasive plant: demographic consequences of seed size variation? – Oikos 122: 583–590.

Hierro, J. L. et al. 2016. Data from: The importance of factors controlling species abundance and distribution varies in native and non-native ranges. – Dryad Digital Repository, <http://dx.doi.org/10.5061/dryad.d08fb>.

Holmes, T. H. and Rice, K. J. 1996. Patterns and growth and soil–water utilization in some exotic annuals and native perennial bunchgrasses of California. – Ann. Bot. 78: 233–243.

Holmgren, M. et al. 1997. The interplay of facilitation and competition in plant communities. – Ecology 78: 1966–1975.

Kawecki, T. J. 2008. Adaptation to marginal habitats. – Annu. Rev. Ecol. Evol. Syst. 39: 321–342.

Keane, R. M. and Crawley, M. J. 2002. Exotic plant invasions and the enemy release hypothesis. – Trends Ecol. Evol. 17: 164–170.

Khetsuriani, L. and Lachashvili, N. 2008. Invasion of *Centaurea solstitialis* L. in steppe vegetation of T'bilisi surroundings. – Proc. Georgian Acad. Sci. Biol. Ser. B 6: 16–24.

Lai, Z. et al. 2008. Natural variation in gene expression between wild and weedy populations of *Helianthus annuus*. – Genetics 179: 1881–1890.

Maddox, D. M. et al. 1985. Distribution of yellow starthistle (*Centaurea solstitialis*) and Russian knapweed (*Centaurea repens*). – Weed Sci. 33: 315–327.

Maron, J. L. et al. 2004. Rapid evolution of an invasive plant. – Ecol. Monogr. 74: 261–280.

Maron, J. L. et al. 2012. Seed size and provenance mediate the joint effects of disturbance and seed predation on community assembly. – J. Ecol. 100: 1492–1500.

Maron, J. L. et al. 2013. Effects of soil fungi, disturbance and propagule pressure on exotic plant recruitment and establishment at home and abroad. – J. Ecol. 101: 924–932.

Müller-Schärer, H. et al. 2004. Evolution in invasive plants: implications for biological control. – Trends Ecol. Evol. 19: 417–422.

Nijjer, S. et al. 2007. Negative plant–soil feedbacks may limit persistence of an invasive tree due to rapid accumulation of soil pathogens. – Proc. R. Soc. B 274: 2621–2627.

Parker, I. M. and Gilbert, G. S. 2007. When there is no escape: the effects of natural enemies on native, invasive and non-invasive plants. – Ecology 88: 1210–1224.

Parker, J. D. et al. 2013. Do invasive species perform better in their new ranges? – Ecology 94: 985–994.

Reinhart, K. O. et al. 2005. Soil feedback and pathogen activity in *Prunus serotina* throughout its native range. – J. Ecol. 93: 890–898.

Sax, D. F. et al. 2007. Ecological and evolutionary insights from species invasions. – Trends Ecol. Evol. 22: 465–471.

Sun, Y. et al. 2015. Biogeographic effects on early establishment of an invasive alien plant. – Am. J. Bot. 102: 1–5.

Taylor, K. T. et al. 2015. Drivers and impacts of plant invasion vary globally: evidence from pine invasions within six ecoregions. – Global Ecol. Biogeogr. 25: 96–106.

Thompson, J. N. 2005. The geographic mosaic of coevolution. – Univ. of Chicago Press.

Timson, J. 1965. New method of recording germination data. – Nature 207: 216–217.

Uygur, S. et al. 2004. Population densities of yellow starthistle (*Centaurea solstitialis*) in Turkey. – Weed Sci. 52: 746–753.

Widmer, T. L. et al. 2007. Enhanced growth and seed properties in introduced vs. native populations of yellow starthistle (*Centaurea solstitialis*). – Weed Sci. 55: 465–473.

Williams, J. L. et al. 2010. Effects of disturbance and herbivory on invasive plant abundance at home and abroad. – Ecology 91: 1355–1366.

Wolfe, L. M. 2002. Why alien invaders succeed: support for the escape-from-enemy hypothesis. – Am. Nat. 160: 705–711.

Zar, J. H. 2003. Biostatistical analysis, 4th ed. – Pearson Education.