

Non-native conditions favor non-native populations of invasive plant: demographic consequences of seed size variation?

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Trait differences between native and non-native populations may explain the greater abundance and impact of some organisms in their non-native ranges than in their native ranges. Here, we conducted reciprocal common gardens in southwestern Turkey (home) and central Argentina (away) to explore the hypothesis that the greater success of the invasive ruderal *Centaurea solstitialis* in Argentina than Turkey is partially explained by differences between home and away populations. Unusual among common gardens, our experimental design included seed additions to explicitly evaluate population level responses, as well as disturbance and no-disturbance treatments. We documented seed mass in native and non-native populations, and during the experiment, we periodically measured density, plant size, and herbivory. After six months, we determined the establishment of plants for populations from both origins in both home and away common gardens. Seed mass was two times larger for Argentinean than Turkish populations. Density, plant size and final establishment were also greater for plants from Argentinean than from Turkish populations, but only in the common garden in Argentina. In Turkey, no differences between population origins were detected for these variables. Herbivory was similar for populations from both origins in both common gardens. As expected, disturbance generally increased plant performance in both regions. Our results suggest that increased seed size in non-native populations may have demographic consequences under non-native conditions that can contribute to the invasive success of *C. solstitialis*. This is the first reciprocal common garden that supports the idea that seed size variation contributes to demographic differences for an invasive species between native and non-native distributions, but our findings further suggest that seed size effects on demography depend on the ecological context in which population processes occur.

Anthropogenic introductions of non-native species provide prime systems to study interpopulation differentiation (Huey et al. 2000, Bossdorf et al. 2005, Zangerl and Berenbaum 2005, Hierro et al. 2009, Buswell et al. 2011), and a number of studies now indicate that trait variation between home and away populations may explain enhanced performance of some organisms in non-native relative to native ranges (Blossey and Nötzold 1995, Maron et al. 2004a, Phillips et al. 2006, Lavergne and Molofsky 2007, Ridenour et al. 2008, Feng et al. 2009, Beaton et al. 2011). For more than 70 years, reciprocal common gardens have offered the most complete experimental assessment for questions related to population differentiation (Clausen et al. 1940, Conner and Hardt 2004, Kawecki and Ebert 2004), yet only recently has this powerful approach been utilized for studying variation between home and away plant populations (Maron et al. 2004a, b, Genton et al. 2005, Maron et al. 2007, Williams et al. 2008). In a classic study, Maron et al. (2004a) found that non-native genotypes of *Hypericum perforatum* were larger and more fecund than native genotypes in only one of four experimentally

crossed common gardens conducted in two native and two non-native ranges. Their findings thus emphasize the need for designing experiments that allow assessing not only the influence of the genotype, but also that of the environment when studying differentiation.

Reciprocal common gardens and our understanding of how local differentiation contributes to the invasion process can further be enhanced by incorporating seed addition into the experimental design. This is because up to now common gardens in invasion ecology have focused on detecting variation between native and non-native individuals (Bossdorf et al. 2005, Colautti et al. 2009), and then they have assumed that differences at the individual level translate into differences at the ecological level that most defines invasions, that of the population (Grigulis et al. 2001, Sakai et al. 2001, Herrera et al. 2011). Seed addition experiments, instead, directly assess population level responses. Also, seed additions mimic initial invasion stages and allow estimation of major fitness components, such as survival, in realistic contexts and thus provide a better proxy of local adaptation (Kawecki and Ebert 2004).

Centaurea solstitialis (Asteraceae) is an annual ruderal plant that originates from the Caucasus and eastern Mediterranean regions (Prodan 1930 and Wagenitz 1955 as cited in Maddox et al. 1985). The species was later introduced into the Mediterranean region of Europe in what may be one of the first introductions linked to agriculture (N. García-Jacas, Bot. Inst. of Barcelona, pers. comm.). From there, this species was brought to Argentina, Australia, California, Chile and South Africa, probably as a contaminant of *Medicago sativa* (alfalfa) seeds in the second half of the nineteenth century (Maddox et al. 1985). The impressive success of *C. solstitialis* in some regions of its most recent range expansion has led to multiple investigations intended to reveal invasion mechanisms (Dukes 2002, Gerlach and Rice 2003, Callaway et al. 2006, Andonian et al. 2011, 2012, Andonian and Hierro 2011, Hierro et al. 2011), and recent work suggests that interpopulation differentiation could contribute to this success (Widmer et al. 2007, Hierro et al. 2009, Eriksen et al. 2012, Graebner et al. 2012).

Superior performance of *C. solstitialis* in recently introduced ranges, relative to native ranges, was shown in an experimental field study conducted in southwestern Turkey and central Argentina (Hierro et al. 2006). In the experiment, locally collected seeds (technically, achenes) were added to plots in each region, raising the possibility that differences in performance between native and non-native populations were due to variations in the ability of these populations to invade communities (i.e. invasiveness). Here we expand on these findings by studying population level establishment, growth, and herbivore impact for Turkish and Argentinean demes in reciprocal home and away common gardens.

Material and methods

We explored the possibility that Argentinean demes of *Centaurea solstitialis* are more invasive than Turkish demes by conducting a reciprocal common garden experiment, in which *C. solstitialis* seeds from non-native and native populations were added to plots located at La Mercedes Ranch (36°40'32.8"S, 64°38'37.6"W, 269 m a.s.l.) in La Pampa, Argentina, and the campus of the Adnan Menderes Univ. (37°51'06.6"N, 27°51'26.6"E, 162 m a.s.l.) in Aydin, Turkey. In both ranges, experimental sites were located in natural grasslands with deep soils (>1.00 m) and no *C. solstitialis* individuals. In Argentina, the grassland was dominated by the native perennial grasses *Piptochaetium napostense*, *Nassella tenuissima* and *N. trichotoma*, and soils were non-calcareous with 70% sand, 2% clay, and 28% silt. In Turkey, vegetation was dominated by annual and perennial grasses, such as *Avena sterilis* and *Hordeum bulbosum*, respectively, and perennial herbs, such as *Stachys cretica*, *Eryngium campestre* and *Carlina corymbosa*. Soils in Turkey were also non-calcareous with a texture of 65% sand, 8% clay, and 27% silt. Central Argentina receives rain mainly in the spring and summer (mean annual rainfall from 1911 to 2010 for Santa Rosa, 35 km W to La Mercedes Ranch, is 638 mm; G. Vergara, UNLPam, unpubl.); in contrast, southwestern Turkey has a Mediterranean climate with hot

and dry summers and cool and wet winters (mean annual rainfall from September 1971 to August 2011 for Aydin is 618 mm; Aydin Meteorological Station). Mean annual temperature is 15.4°C (1941–1990) and 17.8°C (1961–1990) for Santa Rosa and Aydin, respectively.

Seeds of *C. solstitialis* were collected from 10 populations, located 15–65 km apart, in each range (Fig. 1, Supplementary material Appendix A1) in late July 2007 in Turkey and late January–early February 2008 in Argentina. Within populations, seeds were collected from at least 30 individuals and these were mixed and used randomly within a population. In all cases, only seeds that looked healthy and filled with an embryo were used in common gardens.

Given the ruderal nature of *C. solstitialis*, the experimental design included a disturbance treatment, in which the soil of 1 × 1 m plots was turned-over with a shovel to 0.30 m deep, simulating plowing. Experimental plots were separated by 1 m from each other. Each plot received seeds from a particular population and each population was replicated in three plots. In addition, five disturbed and five undisturbed plots were not seeded, serving as controls. In total, 130 experimental plots [(2 origins × 2 disturbance treatments – soil turnover and no disturbance × 10 populations × 3 replicates per population) + 10 control plots] were established at each range in a 10 × 13 plot arrangement. To account for *C. solstitialis* seed dimorphism and differences in the number of morphs produced (Benefield et al. 2001) plots were sown with a mixture of 160 pappus and 40 non-pappus seeds, which represents a natural proportion. Pappus and non-pappus seeds were added to the 0.50 × 0.50 m center of experimental plots, to allow for a buffer zone around the edges, in fall 2008 (March in central Argentina and September in southwestern Turkey), in coincidence with the prime emergence time of the species.

To minimize risks of introducing new genotypes into native and non-native regions, a number of safety measures were followed. First, experimental sites were fenced to exclude cattle and other vertebrates. Second, upon sowing, seeds were covered with a thin layer of soil and woody frames 0.5 × 0.5 wide × 0.15 m tall were placed around the seeded area in each plot to prevent seeds from blowing out of the plots. Third, because a forecasted rain failed to occur after sowing in Argentina, we added 48 mm of water to each experimental plot the day following seed additions. In Turkey, it rained one day after sowing. This protocol is likely to have also served to reduce seed predation. Fourth, the experiment was concluded before plants flowered in October 2008 in Argentina and April 2009 in Turkey by killing all individuals with herbicide applications. After this, the top five cm of soil from experimental plots was removed and autoclaved. Finally, a second herbicide application was conducted in the winter of the following growing season, even though no *C. solstitialis* individual was observed during any periodic survey.

Several dependent variables were recorded during the study. First, seed mass from native and non-native populations of *C. solstitialis* (n = 400 seeds = 10 seeds/morph/population) was documented. Second, *C. solstitialis* density, herbivory (proportion between number of plants with signs of consumption and total number of plants present in

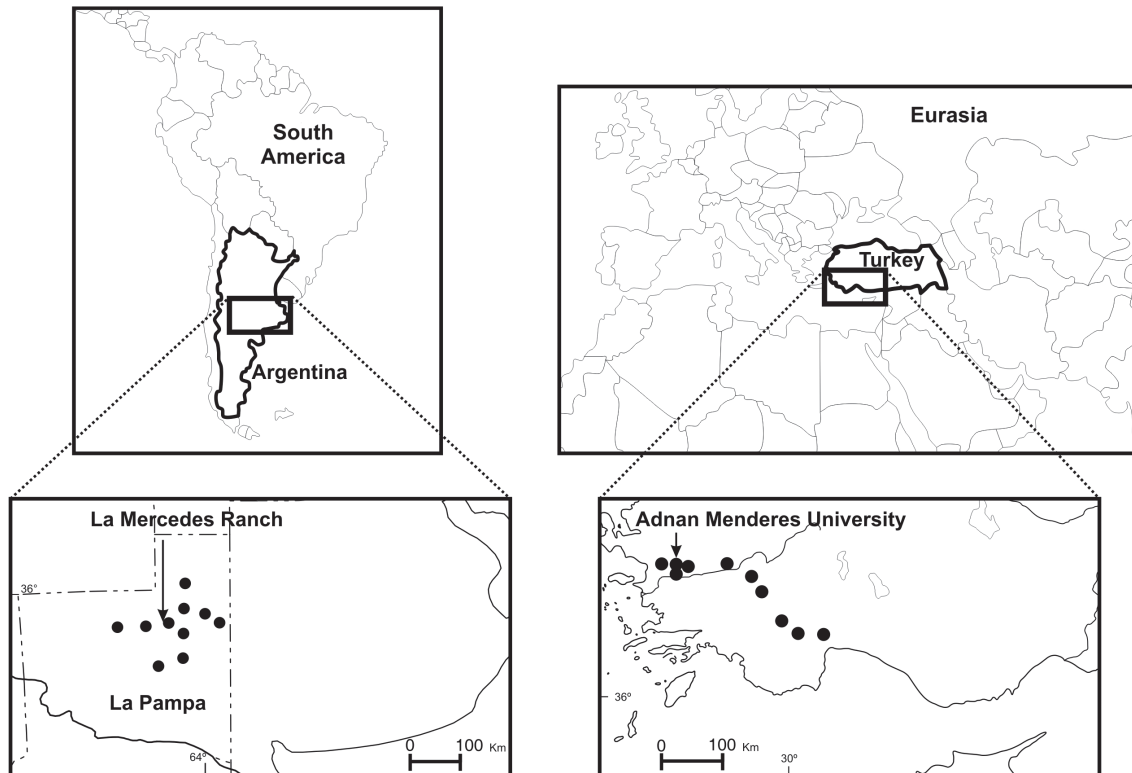


Figure 1. Distribution of Argentinean (non-native) and Turkish (native) *C. solstitialis* populations (black circles) from which seeds were collected to conduct reciprocal common gardens at La Mercedes Ranch in central Argentina and at the campus of the Adnan Menderes Univ. in southwestern Turkey.

each plot), and size (maximum width of five non-consumed individuals per plot when possible) were periodically measured throughout the duration of common gardens. Finally, the proportional establishment (number of plants present over number of seeds added) of the study plant was measured at the end of experiments.

Rainfall during the year of the study in Santa Rosa was 524 mm, lower than the historic mean, but more importantly, rainfall during the fall and winter (establishment period for *C. solstitialis*) was only 57 mm, a quarter of the historic mean for those seasons (Supplementary material Appendix A2). In Aydin, on the other hand, rainfall for the 2008–2009 growing season was 835 mm, more than 200 mm higher than the historic mean annual rainfall.

Statistical analyses

Data were analyzed using linear mixed models. For seed mass, origin, seed type, and their interaction were modeled as fixed factors and population, nested within origin, was considered as a random factor. Density, size, and herbivory through time were analyzed within each garden (Kaweki and Ebert 2004) with repeated-measures linear mixed models, where time was introduced as a repeated factor, origin, disturbance, time, and all two- and three-way interactions as fixed factors, and population(origin) as a random factor. Finally, the proportion of *C. solstitialis* individuals established at the end of experiments was also assessed for each garden separately with a linear mixed model, where origin, disturbance, and their interaction were

considered as fixed factors and population(origin) as a random factor. Data were transformed with the arcsine (seed mass, final establishment, and herbivory) and square root (density) function to meet assumptions of statistical test (Bolker et al. 2008). Analyses were performed with SPSS Statistics 20.

Results

Seeds of *C. solstitialis* from non-native Argentinean populations were nearly two times larger than seeds from native Turkish populations ($F_{\text{origin } 1,18} = 105.710$, $p < 0.001$, $F_{\text{seed type } 1,378} = 107.135$, $p < 0.001$, $F_{\text{origin} \times \text{seed type } 1,378} = 2.655$, $p = 0.104$, Fig. 2, Supplementary material Appendix A3).

In central Argentina, plant density and size through time were higher for Argentinean than Turkish populations of *C. solstitialis* ($F_{\text{origin } 1,52.097} = 88.805$, $p < 0.001$ and $F_{\text{origin } 1,98.269} = 7.742$, $p = 0.006$ for density and size, respectively, Fig. 3, Supplementary material Appendix A4 Table A4). Plants were larger and experienced higher levels of herbivory in disturbed than undisturbed plots ($F_{\text{disturbance } 1,101.605} = 83.858$, $p < 0.001$ and $F_{\text{disturbance } 1,24.977} = 44.189$, $p < 0.001$ for size and herbivory, respectively), but density through time was greater in undisturbed than disturbed plots in this region ($F_{\text{disturbance } 1,52.097} = 42.077$, $p < 0.001$). In southwestern Turkey, on the other hand, no significant differences between *C. solstitialis* origins were detected for any of

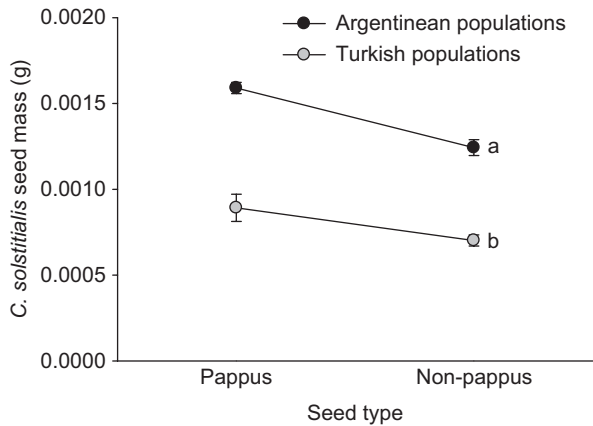


Figure 2. Mass of pappus and non-pappus seeds for non-native Argentinean and native Turkish populations of *C. solstitialis* ($n = 10$) used in reciprocal common gardens. Circles show means ± 1 SE. Different letters indicate significant differences ($p < 0.05$) between regions of origin.

these variables ($F_{\text{origin } 1,31,528} = 0.154$, $p = 0.697$, $F_{\text{origin } 1,81,133} = 0.108$, $p = 0.743$, and $F_{\text{origin } 1,156,361} = 0.165$, $p = 0.685$ for density, size, and herbivory, respectively), and disturbance promoted only plant density ($F_{\text{disturbance } 1,108,552} = 133.938$, $p < 0.001$, $F_{\text{disturbance } 1,81,133} = 0.024$, $p = 0.876$, and $F_{\text{disturbance } 1,156,361} = 0.680$, $p = 0.411$ for density, size, and herbivory, respectively, Supplementary material Appendix A4 Table A4).

Similar to plant density and size over time, the proportion of *C. solstitialis* plants established at the end of the experiment was nearly four times higher for Argentinean than Turkish populations in Argentina ($F_{\text{origin } 1,18} = 23.003$, $p < 0.001$, $F_{\text{disturbance } 1,98} = 33.145$, $p < 0.001$, $F_{\text{origin} \times \text{disturbance } 1,98} = 2.907$, $p = 0.091$), but no differences between origins were detected in Turkey ($F_{\text{origin } 1,18} = 0.276$, $p = 0.606$, $F_{\text{disturbance } 1,98} = 128.780$, $p < 0.001$, $F_{\text{origin} \times \text{disturbance } 1,98} = 1.504$, $p = 0.223$, Fig. 4, Supplementary material Appendix A3 Table A3). In both regions, final *C. solstitialis* establishment was much higher in disturbed than undisturbed plots.

Discussion

Population differentiation has been advanced as a mechanism explaining improved performance of a number of organisms in non-native ranges relative to native ranges (Lee 2002, Zangerl and Berenbaum 2005, Phillips et al. 2006, Prentis et al. 2008, Feng et al. 2009). Like other studies of invasive plants (Maron et al. 2004a, Williams et al. 2008), the current work highlights the importance of conducting reciprocal common gardens in native and non-native ranges to assess that possibility, as our conclusions would greatly differ had the experiment been performed in only one of the ranges, and in particular only the native range. Our study is, however, unique in that, by using seed additions, it measured responses at the population in addition to the individual level of organization. Our results show that non-native populations had increased seed size relative to native populations and

that, in turn, non-native populations had also greater plant size and establishment than native populations, but only where the species has been introduced by humans. Thus, increased seed size in non-native populations may have demographic consequences under non-native conditions that could contribute to the greater performance of *C. solstitialis* in central Argentina than southwestern Turkey previously reported (Hierro et al. 2006). Likely because of the drought that affected central Argentina during the study, the establishment of the invader documented here is much lower than that in previous work (Hierro et al. 2006, 2011). In Turkey, final establishment of *C. solstitialis* was also low, but comparable to earlier findings. No previous reciprocal common garden has conducted seed additions into plots with intact and disturbed natural plant communities using native and non-native populations differing in seed size, and thus our work provides the most complete assessment to date to the idea that variation in seed size can contribute to differences in plant density between native and non-native ranges (Buckley et al. 2003).

Seed attributes have been proposed to affect demographic processes (Westoby et al. 2002, Buckley et al. 2003), and increased seed size in non-native demes detected here may explain results on plant performance. Strong evidence supports the idea that larger seeds increase initial seedling reserves and size, improving survival, particularly under hazardous conditions (Leishman et al. 2000, Westoby et al. 2002, Moles and Westoby 2004, 2006). Large seeds may provide the ability to cope with the dry conditions commonly experienced by *C. solstitialis* at early developmental stages in central Argentina, where the continental rainfall regime poorly matches the emergence time of the species (Hierro et al. 2009). These conditions were especially severe during our experiment, and large Argentinean seeds, presumably having high reserve content, may have conferred increased survival to seedlings when compared to those emerging from smaller Turkish seeds. In support of this proposition, some inter-specific comparisons have shown that seedlings from large-seeded species performed better than small-seeded counterparts in dry conditions (Baker 1972, Leishman and Westoby 1994 – in the lab, but not in the field –, Caddick and Linder 2002, but see Mazer 1989). In southwestern Turkey, on the other hand, where *C. solstitialis* emergence matches the beginning of the wet season, seed size may play a less significant role in seedling performance. Similar to our work, a recent multi-species analysis of seed size responses to rainfall patterns in annual grassland revealed that plant survival was greater for large-seeded than small-seeded species in years with a dry autumn, but survival was high and independent of seed size in years with a wet autumn (Peco et al. 2009). According to Westoby et al. (2002), it is indeed expected that under favorable conditions most viable seeds, regardless of their size, will establish seedlings. Alternatively, differential seed predation between ranges, where larger seeds are preferentially consumed in native, but not in non-native ranges (Buckley et al. 2003), could have also influenced our results. Our experimental approach, however, minimized seed predation by covering seeds with soil and sowing shortly before a rain.

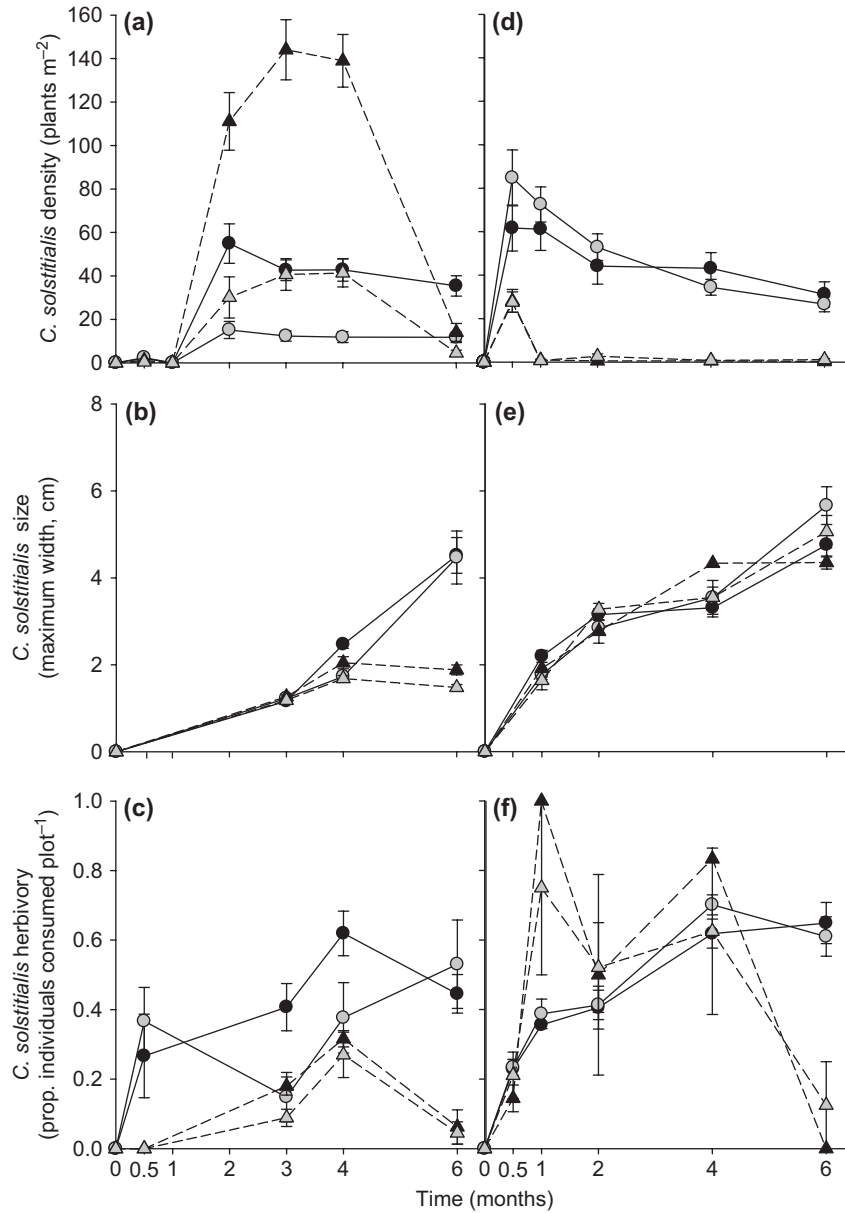


Figure 3. Density, size, and herbivory through time for Argentinean (black symbols) and Turkish (gray symbols) populations of *C. solstitialis* ($n = 10$) in disturbed (circle, solid lines) and non-disturbed (triangles, dashed lines) plots in reciprocal common gardens conducted in central Argentina (a–c) and southwestern Turkey (d–f). Symbols are means \pm 1 SE.

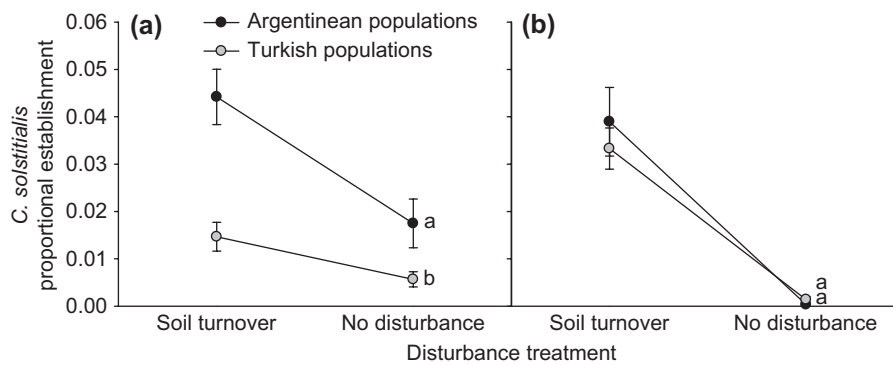


Figure 4. Proportional establishment for Argentinean and Turkish populations of *C. solstitialis* ($n = 10$) in disturbed and non-disturbed plots at the end of the reciprocal common gardens conducted in central Argentina (a) and southwestern Turkey (b). Circles show means \pm 1 SE. Different letters indicate significant differences ($p < 0.05$) between population origins.

Greater seed mass in non-native than native populations of *C. solstitialis* has already been reported for collections conducted in another non-native region where the species is highly abundant and widely distributed, western US (Pitcairn and Schoenig 2006), and Eurasia (Widmer et al. 2007, Graebner et al. 2012). Additionally, Widmer et al. (2007) determined that larger US seeds contained more starch and produced larger individuals than smaller native seeds when grown for two weeks in the lab and to maturity in common gardens in the native range, and Graebner and co-authors (2012) found that seedlings from California were larger and displayed greater competitive resistance than seedlings from Spain in greenhouse experiments. Based on this work and on that by Buckley et al. (2003), who also found differences in seed size between native and non-native populations of *Cytisus scoparius*, variation in seed size has been proposed to contribute to differences in demographic processes between native and non-native distributions and result in exotic invasion success, but importantly up to now this idea had not been tested in crossed invasion field experiments. Our findings provide support to this hypothesis, but they further suggest that, like in interspecific comparisons (Paz et al. 1999), the demographic significance of increased seed size depends on the ecological context experienced by the population.

Higher density through time in undisturbed than disturbed plots in Argentina may be related to the higher herbivory levels recorded in the latter plots. Vegetation in these plots may have provided *C. solstitialis* protection against herbivores (Graff et al. 2007). Alternatively, the drought during the study may have favored the action of another facilitative mechanism, that is, surrounding vegetation could have buffered stressful conditions and improved the survival of *C. solstitialis* seedlings (Callaway 2007, Brooker et al. 2008). Through time, however, competition seems to have prevailed over this presumed initial facilitation and resulted in lower final establishment of the invader in undisturbed relative to disturbed plots.

Several factors can contribute to differences in seed size between native and non-native populations (Buckley et al. 2003, Colautti et al. 2009). Firstly, variation may arise from maternal effects (Rossiter 1996, Agrawal 2001), and thus, to eliminate this possibility, common gardens should have been conducted with the progeny of plants grown under common conditions (Conner and Hartl 2004). Recent attempts for controlling maternal influences on seed and plant attributes (Widmer et al. 2007) and germination proportions and rates (Hierro et al. 2009) in *C. solstitialis* showed, however, that the F_1 did not alter differences between native and non-native populations detected with parental plants. Also, *C. solstitialis* is largely self-incompatible (Sun and Ritland 1998), limiting the number of seeds that can be produced through cross-pollination by hand in the greenhouse (Hierro et al. 2009) and consequently the scope of seed addition experiments, including propagule pressure on plots, sample size, number of treatments, and/or degree of reality in experimental conditions. Secondly, founder effects could have influenced changes in seed trait between studied demes, but this is unlikely because, as expected for accidental

introductions linked to agriculture (Bossdorf et al. 2005, Novak and Mack 2005), current evidence suggest that *C. solstitialis* has repeatedly been brought to Argentina from multiple sources (Hijano and Basigalup 1995, Gerlach 1997), including Turkey (R. Eriksen unpubl.). Finally, larger seeds in Argentinean than Turkish populations could have resulted from an adaptive response to local conditions. Given limited time for the appearance of beneficial mutations in Argentinean populations, adaptive changes may have resulted from enhanced survival of introduced individuals already possessing large seeds (i.e. selection of pre-adapted genotypes, Müller-Schärer et al. 2004, Leger and Rice 2007). The specific selective agent favoring large seeds in central Argentina is currently unknown, but climate and the classic selection forces proposed to shape seed mass, such as dispersal, predation, and competition (Rees and Westoby 1997, Buckley et al. 2003) could be involved. In spite of uncertainties regarding the source of seed size variation, our crossed addition gardens show that large seeds may contribute to the success of the species under the physical and biotic conditions imposed by the environment in Argentina and, together with other studies (Widmer et al. 2007, Graebner et al. 2012), suggest that similar processes could also operate for invasive populations in the US.

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Supplementary material (available online as Appendix oik-O00022 at <www.oikosoffice.lu.se/appendix>). Appendix A1–A4.