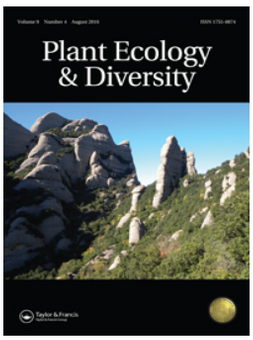

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SHORT COMMUNICATION

Inter-regional hybrids of native and non-native *Centaurea sulphurea* inherit increased competitive ability from the non-natives

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Background: Exotic species can rapidly develop adaptations to their non-native regions, such as increased size and competitive ability. Although these traits are believed to be responsible for invasive success, some non-invasive exotic species display them too. This suggests that increased size and competitive ability might be necessary but not sufficient to turn an exotic into a successful invader.
Aim: To assess size and competitive ability of the exotic non-invasive weed *Centaurea sulphurea*, and of inter-regional hybrids between native and non-native populations.
Methods: We experimentally produced a cohort of *C. sulphurea* individuals from the native range of the species in Spain, from its non-native range in California, as well as hybrids between the two regions. We grew these plants in pots in competition with the grass *Bromus hordeaceus*, or alone in control pots.
Results: Individuals from California were larger and better competitors than individuals from Spain. Furthermore, inter-regional hybrids showed competitive responses similar to that of individuals from California.
Conclusions: Our results confirm that increased competitive ability might be more frequent than previously thought among introduced species, since it can be detected in at least some exotic non-invasive species. They also illustrate the importance of maternal effects, how locally adapted traits are conserved and spread in the non-native ranges of exotic species, and suggest that plant size and competitive ability are not directly associated in this species.

Keywords: biogeography; competitive ability; exotic species; inter-regional hybrids; RII

Introduction

Native and non-native populations of exotic species are typically isolated in allopatric distributions, and geographic isolation among populations drastically reduces gene flow among them (Dobzhansky 1940; Lachmuth et al. 2011). Comparative studies of trait shifts between populations from native and non-native ranges of exotic species repeatedly find rapid evolutionary changes between them (Maron et al. 2004; Garcia et al. 2013; Hierro et al. 2013); including differences in germination, growth rates, seed production and size, and plant size and competitive ability (Graebner et al. 2012; Garcia et al. 2013). Local adaptations developed in the non-native ranges have proved to be crucial for the success of exotic species in their non-native ranges (Keller and Taylor 2010; Zenni et al. 2014). Most established exotic species naturalise in their non-native ranges but do not significantly expand from a few initial introduction points; however, some can significantly spread and dominate the local plant communities, thus causing important damage to the environment and economy (Richardson et al. 2000). An important factor that may contribute to invasive success is the development of increased competitive ability (Maron et al. 2004; Reinhart and Callaway 2006; Ridenour et al. 2008, 2008; Graebner et al. 2012; He et al. 2012; Kaur et al. 2012; Felker-Quinn et al. 2013; Shah et al. 2014).

The evolution of increased competitive ability (EICA, Blossey and Nötzold 1995) poses that the escape from specialist herbivores present in the native range, but absent from newly colonised regions, favours the reallocation of resources devoted to herbivory defence to increased competitive ability in the non-native range, typically via increases in plant sizes and growth rates. Although several studies found no clear evidence of direct growth-defence trade-offs when increased competitive ability is reported (Bossdorf et al. 2005; Joshi and Vrieling 2005), others did find reallocation of resources between defence and growth, a clear indicator of EICA (Siemann and Rogers 2001, 2003; Huang et al. 2010, 2012; Carrillo et al. 2012), while yet others found that non-native populations were both better defended and better competitors (Ridenour et al. 2008). An increased competitive ability of exotic species can result in strong impacts on native plant populations (Maddox et al. 1985; Pennings and Callaway 1992; He et al. 2003; Eriksen et al. 2012; Dlugosch et al. 2015).

The comparison of invasive and non-invasive species can be a fruitful way to predict which traits might be responsible for invasive success, particularly when congeneric species with different invasive success are studied (Gerlach and Rice 2003). A further step consists of considering such congeneric species both in their native and non-native ranges (Graebner et al. 2012; Garcia et al. 2013). Interestingly, such studies regularly report that many traits found to be advantageous for invasive species are also

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present in non-invasive congeneric exotics. Additionally, little is known about the inheritance and dominance of expression of locally adapted traits from isolated populations from the native and non-native ranges, and thus the susceptibility of traits newly developed in the non-native ranges that might be lost or reduced in frequency due to homogenising gene flow from potential new reintroductions from the native range.

Centaurea sulphurea Lag. is an annual herb with a highly restricted native range in Spain and Morocco. It has been present as an introduced species in California (USA) since at least 1923 (Muth and Pigliucci 2006), though has only managed to establish a few populations in the wild in this non-native area. It usually inhabits ruderal habitats and develops single bolting flower stems from basal rosettes. Several past studies have shown phenotypic differences between individuals from the native and non-native regions of *C. sulphurea*, and between this species and the closely related, highly invasive, *Centaurea solstitialis* L. (Graebner et al. 2012; Garcia et al. 2013; Filipe et al. Forthcoming). There has been no sign of interspecific hybridisation among these species.

We previously collected seeds from both the native and non-native ranges of this annual herb and experimentally produced a cohort of inter-regional hybrid seeds by manual cross-pollinations under common garden conditions (Montesinos et al. 2012). For the study reported here, we established a competition experiment to compare the competitive ability of individuals derived from seeds from native and non-native regions and for inter-regional hybrids. Specifically, we aimed to compare (1) the competitive ability of *C. sulphurea* individuals from its European native range, American non-native range, and their inter-regional hybrids, and (2) assess the inheritance of competitive ability of inter-regional hybrids.

Materials and methods

Experimental design

We used seeds collected in 2009 from seven different individuals from each of four different populations in Spain and three different populations in California (USA) (Table 1). The sampling covered the entire geographic distribution of the species in Spain, and, as far as we know, included all current populations in California. In early 2013 seven seeds from each population within each region were germinated in 2-L pots and watered as needed. Plants were grown in common garden conditions in the greenhouses of the Botanical Garden of the University of Coimbra, Portugal. Temperatures were kept between 15°C and 30°C. All individuals grew until bolting, when we applied several manual cross-pollination treatments among individuals within and between regions, thus obtaining an F1 cohort of pure (within population) and inter-regional hybrid seeds grown under identical environmental conditions in greenhouses, and thus expected to express reduced maternal effects (see full description in Montesinos et al. 2012). In March 2015, seeds from 10 different individuals from each of the seven populations from either Spain or California, and seeds from 70 inter-regional hybrids between the two regions were germinated and grown under similar conditions. For each of these three groups (Spain, California, and inter-regional hybrids), full sibling *C. sulphurea* plants were germinated and grown in 500-mL pots and subjected to either as control or competition groups according to the following design: one *C. sulphurea* individual (either descendant from both parents from the same region, or an inter-regional hybrid) growing alone in a control pot, and one full sibling individual (same father and mother) growing in competition with one *Bromus hordeaceus L. B. hordeaceus* is a European native annual grass native to Southern Europe that has also established and spread into California, thus sharing both ranges from where original *C. sulphurea* seeds were first collected (n = 280). Although there is little literature about *C. sulphurea, B. hordeaceus* is a highly abundant species in both ranges (www.gbif.com), which allows to infer that they should be frequent competitors in both their native and non-native ranges, even though the exact intensity of such competition in the wild is still undocumented. Since *C. sulphurea* is a self-compatible species there is a real possibility that some of our inter-regional hybrids could in fact be the result of self-pollination of the mother plant, however, this would favour accepting the null hypothesis that there are no differences among siblings of different origins, thus the potential detection of significant differences for inter-regional hybrids should indicate that most individuals would in fact be inter-regional hybrids. *B. hordeaceus* seeds were purchased from Emorsgate Seeds (UK). For *C. sulphurea*, descendants from the same father and mother were used for each paired replication (i.e. competition and control pots) in order to reduce genetic and maternal effects. Each experimental group had 10 control and 10 competition duplicates. A control group of *B. hordeaceus* was also seeded (n = 15). The plants were grown for 80 days, after which full plants including shoots and roots were harvested before bolting, and dried at 70°C for 48 h, then weighed to the nearest mg.

Table 1. Populations of origin of the *Centaurea sulphurea* seeds used for the development of the experiments.

Region	Location	Latitude	Longitude
Spain	Malaga	36.840082	−3.981880
	Malaga	36.679348	−4.832505
	Malaga	36.907818	−4.118162
	Granada	37.172880	−3.579110
California (USA)	Sacramento	38.640605	−121.156370
	Santa Clara	37.245630	−122.110390
	Sacramento	38.684210	−121.180600

Coordinates are given in WGS84.

Statistical analyses

Differences in total biomass among seed origins were tested with General Linear Mixed Models in R 3.1.2 with the procedure *lme* in the *nlme* package (R Development Core

Team 2010, Pinheiro et al. 2016) with total biomass as the response variable, and each of the four possible combinations of *C. sulphurea* seed origin (pollen donor and pollen receiver) as the fixed factor. Maternal population of origin was used as a random effect nested within each treatment. Separate tests were run for *C. sulphurea* biomass, and for *B. hordeaceus* biomass. Tukey post hoc tests were run when required by using the *glht* procedure of the *multcomp* library.

We then used biomass data to assess the strength of competitive interactions by calculating relative interaction indices (RII) (Armas et al. 2004):

$$RII = (B_w - B_0)/(B_w + B_0),$$

in which B_0 corresponds to the biomass of a control individual, and B_w corresponds to the biomass of a full sibling individual grown in competition. RII has defined limits [−1, +1], is approximately normally distributed and is symmetrical around zero, with negative values indicating stronger competition effects and positive values indicating the strength of mutualistic interactions. RII values were then statistically assessed by a similar procedure to that used with total biomass values.

Results

C. sulphurea total biomass was significantly different among groups ($F_{7,266}$ = 31.525, P < 0.001). Post hoc tests showed that descendants of Californian mothers and fathers were significantly larger (P < 0.02) than any other group in the control treatment (Figure 1). When in competition with *B. hordeaceus, C. sulphurea* descendants from Californian mother plants were significantly larger than individuals from Spanish mother plants. *B. hordeaceus* individuals competing with *C. sulphurea* also showed significant differences among groups ($F_{4,148}$ = 13.299, P < 0.001). Post hoc tests showed that grasses competing with descendants from Spanish mothers and fathers experienced lower competitive effects, and thus grew larger than any group other than control and that descendants of Californian mothers and Spanish fathers (P < 0.025; Figure 1),

RII based on total biomass showed a related pattern. We found significant differences among the effects of *B. hordeaceus* on *C. sulphurea* ($F_{3,130}$ = 22.285, P < 0.001) (Figure 2), although post hoc tests showed that only individuals with both parents from Spain were significantly different from the other groups (P < 0.001), indicating that descendants of Spanish mothers and fathers were more negatively affected by competition than individuals of any Californian descent (P > 0.05). For the effects of *C. sulphurea* on the competitor grass *B. hordeaceus*, differences among groups were only marginally significant ($F_{3,130}$ = 2.296, P = 0.081), and post hoc test did not indicate any significant difference among groups.

Discussion

Our results showed clear differences between descendants of individuals from the native and the non-native ranges of *C. sulphurea*, with consistently larger individuals from California, and consistently smaller individuals from Spain. RII also showed that descendants of Spanish fathers and mothers experienced significantly stronger

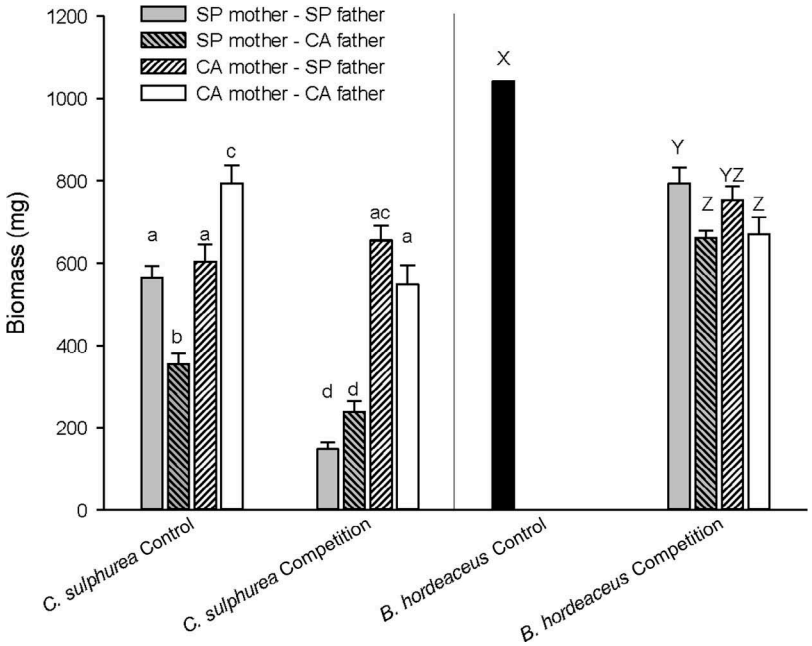

Figure 1. Total final biomass (mean ± SE; mg) for one-to-one competition experiments between *Bromus hordeaceus* and *Centaurea sulphurea* from California (CA), Spain (SP), or inter-regional hybrids. Descendants of Spanish mothers are shown in grey bars and Californian mothers in white bars. Open bars stand for descendants of fathers and mothers from the same regions, and lined bars for descendants of parents from different regions. Means with different letters are significantly different ($P \leq 0.05$).

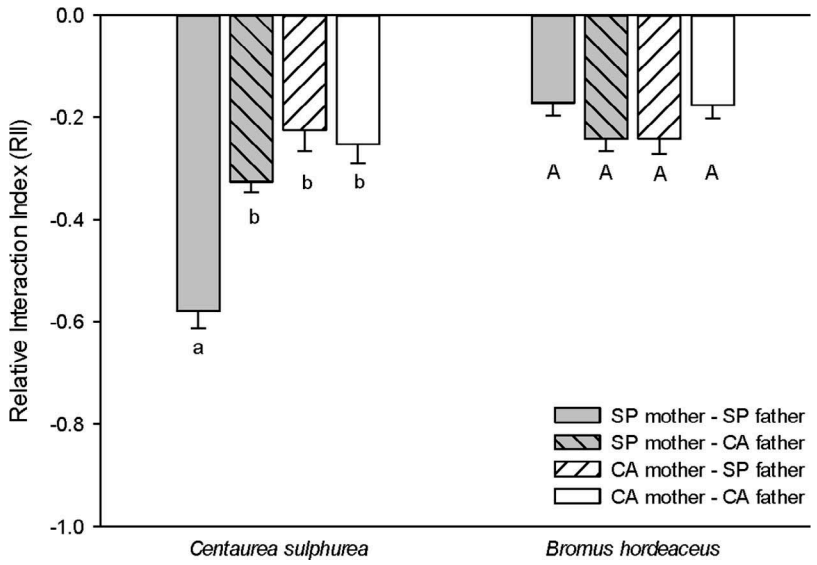

Figure 2. Relative Interaction Indexes (RII) for one-to-one competition experiments between *Bromus hordeaceus* and *Centaurea sulphurea* from California (CA), Spain (SP), or inter-regional hybrids. Descendants of Spanish mothers are shown in grey bars and Californian mothers in white bars. Open bars stand for descendants of fathers and mothers from the same regions, and lined bars for descendants of parents from different regions. Means with different letters are significantly different ($P \leq 0.05$).

competition than individuals of any Californian descent. Interestingly, inter-regional hybrid individuals not experiencing competition tended to present sizes similar to that of pure Spanish plants, thus manifesting the effect of the direction of the crosses between native and non-native regions on total biomass of control plants. However, when experiencing competition, inter-regional hybrids tended to present biomass values more similar to those of the respective region of their mothers, a pattern also showed by RII. This suggests that size and competitive ability might not be intimately bonded in this species, since inter-regional hybrids tended to be smaller in the absence of competition, like their Spanish parents, but over-performed the Spanish population when in competition, like their Californian parents. Maternal effects were apparent on growth, particularly for total biomass, even though plants were raised from seeds produced by plants grown under common garden conditions.

Our results provide the first evidence for a better competitive performance of exotic populations of *C. sulphurea* when measured in one-to-one competition with a grass species. A previous study (Graebner et al. 2012) considering competitive interactions of *C. sulphurea* individuals from Spain and California, each competing against five *B. hordeaceus* individuals reported a similar but not significant trend. One-to-one competition experiments offer a better and standardised information about competitive ability for a pair of species, but generalisations must be made with caution, since competitive interactions are likely to differ among different pairs of species. For *C. sulphurea*, previous experiments (Graebner et al. 2012) indicated that *B. hordeaceus* was a stronger competitor for *C. sulphurea* than the Californian native *Poa secunda* J. Presl., and that it was also the strongest competitor for the closely related *Centaurea* species *C. solstitialis* and *C. calcitrapa L.*

Although *C. sulphurea* is not considered an invasive species in California, it is closely related to the highly invasive *C. solstitialis* (Garcia-Jacas et al. 2006), and our results are consistent with former studies showing how exotic species have developed increased competitive ability in their non-native ranges (Ridenour et al. 2008; Zou et al. 2008; Graebner et al. 2012; Hahn et al. 2012). Although increased competitive ability is often deemed crucial for invasive success (Brown and Eckert 2005; Blossey and Nötzold 1995; Jakobs et al. 2004; Keller and Taylor 2010; Tavares 2014; Zenni et al. 2014), our results also indicate that increased competitive ability might be a necessary condition, but not the only one, that allows a species to become a successful invader, in line with previous works that indicated that non-invasive exotic species were able to develop many of the same local adaptations that invasive species exhibit (Garcia et al. 2013).

Exploring if native and introduced populations react differently to competition with the same competitor is central to evaluating whether commonly observed phenotypic differences between native and non-native ranges do actually result in greater competitive ability in the non-native regions of exotic species. Moreover, the study of experimentally produced inter-regional hybrids between native and non-native ranges might also be important in understanding biological invasions, since they illustrate the effects of potential reinforcements by new seeds from the native range on invasion dynamics. We cannot dismiss the possibility that the observed divergence between native and non-native populations observed in the present study was the result of founder events or of rapid post-

introduction evolution, as suggested by other studies (Maron et al. 2004; Hoskin et al. 2005; Montesinos et al. 2012), or a combination of both. However, our study is consistent with the EICA hypothesis (Blossey and Nötzold 1995), and recent investigations with the same study species showed that snails fed with *C. sulphurea* leaves from California exhibited higher growth rates than snails fed with leaves from Spain, suggesting that individuals in the non-native range of California might present reduced defences against generalist herbivores than in native Spain (Filipe et al. Forthcoming). A very similar combination of increased size and vulnerability to herbivory, consistent with EICA, was described in experiments conducted on *Sapium sebiferum* (L.) Small, a native plant from China in which plants from the invasive range in North America attained larger size and experienced stronger herbivory than plants from native China (Zou et al. 2008).

Three important conclusions that can be drawn from the present study are that (1) non-native populations of a non-invasive exotic species may exhibit increased competitive ability; (2) inter-regional hybrids of plants from the native and non-native regions can show increased competitive abilities similar to those of their parents in the non-native range; and (3) the direction of the crosses between native and non-native regions can determine the outcome of the competitive interactions. This experimentally illustrates the way by which newly developed traits are maintained in the non-native regions of invasive species, and how potential introductions of genotypes not yet adapted to the local non-native conditions will not substantially influence the maintenance of such traits in the non-native regions. In fact, multiple introductions are generally believed to be the key to enrich the genetic diversity available in exotic species for natural selection to act (Eriksen et al. 2014), although in some cases potential new seed introductions could result in homogenising gene flow from the native range with the potential to erode locally adapted traits important to invasive success (Montesinos and Callaway Forthcoming)

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Disclosure statement

No potential conflict of interest was reported by the authors.

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Notes on contributors

João Filipe is broadly interested in evolutionary ecology of plants, invasive plants ecology, and weeds management, working with biological invasions as a model to study functional trade-offs between the native and non-native areas of plant species.

Daniel Montesinos is a plant ecologist interested in adaptations occurring to invasive plant species across broad biogeographical ranges.

References

Armas C, Ordiales R, Pugnaire FI. 2004. Measuring plant onteractions: a new comparative index. Ecology 85:2682–2686.

Blossey B, Nötzold R. 1995. Evolution of increased competitive ability in invasive nonindigenous plants: a hypothesis. Journal of Ecology 83:887–889.

Bossdorf O, Auge H, Lafuma L, Rogers WE, Siemann E, Prati D. 2005. Phenotypic and genetic differentiation between native and introduced plant populations. Oecologia 144:1–11.

Brown JS, Eckert CG. 2005. Evolutionary increase in sexual and clonal reproductive capacity during biological invasion in an aquatic plant *Butomus umbellatus* (Butomaceae). American Journal of Botany 92:495–502.

Carrillo J, Wang Y, Ding J, Klootwyk K, Siemann E. 2012. Decreased indirect defence in the invasive tree *Triadica sebifera*. Plant Ecology 213:945–954.

Dlugosch KM, Cang FA, Barker BS, Andonian K, Swope SM, Rieseberg LH. 2015. Evolution of invasiveness through increased resource use in a vacant niche. Nature Plants 1:1–5.

Dobzhansky T. 1940. Speciation as a stage in evolutionary divergence. The American Naturalist 74:312–321. Available from: http://www.jstor.org/stable/2457524

Eriksen RL, Desronvil T, Hierro JL, Kesseli R. 2012. Morphological differentiation in a common garden experiment among native and non-native specimens of the invasive weed yellow starthistle (*Centaurea solstitialis*). Biological Invasions 1459–1467. doi:10.1007/s10530-012-0172-6

Eriksen RL, Hierro JL, Eren Ö, Andonian K, Török K, Becerra PI, Montesinos D, Khetsuriani L, Diaconu A, Kesseli R. 2014. Dispersal pathways and genetic differentiation among worldwide populations of the unvasive weed *Centaurea solstitialis* L. (Asteraceae). PLOS ONE 9:e114786.

Felker-Quinn E, Schweitzer JA, Bailey JK. 2013. Meta-analysis reveals evolution in invasive plant species but little support for Evolution of Increased Competitive Ability (EICA). Ecology and Evolution 3:739–751.

Filipe JC, Jorge A, Ö E, Sotes G, Hierro JL, Montesinos D. Forthcoming. Invasive and non-invasive congeneric *Centaurea* (Asteraceae) show contrasting patterns of herbivory by snails. Plant Ecology and Evolution 149:228–232.

Garcia Y, Callaway RM, Diaconu A, Montesinos D. 2013. Invasive and non-invasive congeners show similar trait shifts between their same native and non-native ranges. Public Library of Science ONE 8:e82281.

Garcia-Jacas N, Uysal T, Romashchenko K, Suárez-Santiago VN, Ertugrul K, Susanna A. 2006. *Centaurea* revisited: a molecular survey of the Jacea group. Annals of Botany. 98:741–753.

Gerlach JD, Rice KJ. 2003. Testing life history correlates of invasiveness using congeneric plant species. Ecological Applications 13:167–179.

Graebner RC, Callaway RM, Montesinos D. 2012. Invasive species grows faster, competes better, and shows greater evolution toward increased seed size and growth than exotic non-invasive congeners. Plant Ecology 213:545–553.

Hahn MA, Buckley YM, Müller-Schärer H. 2012. Increased population growth rate in invasive polyploid *Centaurea stoebe* in a common garden. Ecology Letters 15:947–954.

He W-M, Montesinos D, Thelen GC, Callaway RM. 2012. Growth and competitive effects of *Centaurea stoebe* populations in response to simulated nitrogen deposition. Plos One 7:e36257.

He WM, Zhang SX, Dong M. 2003. Gas exchange, leaf structure, and hydraulic features in relation to sex, shoot form and leaf form in an evergreen shrub *Sabina vulgaris* in the Semi-Arid Mu Us Sandland in China. Photosynthetica 41:105–109.

Hierro JL, Ö E, Villarreal D, Chiuffo MC. 2013. Non-native conditions favor non-native populations of invasive plant: demographic consequences of seed size variation? Oikos 122:583–590.

Hoskin CJ, Higgie M, McDonald KR, Moritz C. 2005. Reinforcement drives rapid allopatric speciation. Nature 437:1353 1356.

Huang W, Carrillo J, Ding J, Siemann E. 2012. Invader partitions ecological and evolutionary responses to above and belowground herbivory. Ecology 93:2343–2352.

Huang W, Siemann E, Wheeler GS, Zou J, Carrillo J, Ding J. 2010. Resource allocation to defence and growth are driven by different responses to generalist and specialist herbivory in an invasive plant. Journal of Ecology 98:1157–1167.

Jakobs G, Weber E, Edwards PJ. 2004. Introduced plants of the invasive *Solidago gigantea* (Asteraceae) are larger and grow denser than conspecifics in the native range. Diversity and Distributions 10:11–19.

Joshi J, Vrieling K. 2005. The enemy release and EICA hypothesis revisited: incorporating the fundamental difference between specialist and generalist herbivores. Ecology Letters 8:704–714.

Kaur R, Gonzáles WL, Llambi LD, Soriano PJ, Callaway RM, Rout ME, Gallaher TJ I. 2012. Community impacts of *Prosopis juliflora* invasion: biogeographic and congeneric comparisons. Plos One 7. doi:10.1371/journal.pone.0044966

Keller SR, Taylor DR. 2010. Genomic admixture increases fitness during a biological invasion. Journal of Evolutionary Biology 23:1720–1731.

Lachmuth S, Durka W, Schurr FM. 2011. Differentiation of reproductive and competitive ability in the invaded range of *Senecio inaequidens*: the role of genetic Allee effects, adaptive and nonadaptive evolution. The New Phytologist 192:529–541.

Maddox DM, Mayfield A, Poritz NH. 1985. Distribution of yellow starthistle (*Centaurea solstitialis*) and Russian knapweed (*Centaurea repens*). Weed Science 33:315–327. Available from: http://www.jstor.org/stable/4044265

Maron JL, Vilà M, Bommarco R, Elmendorf S, Beardsley P. 2004. Rapid evolution of an invasive plant. Ecological Monographs 74:261–280.

Montesinos D, Callaway RM. Forthcoming. Inter-regional hybrids of native and invasive Centaurea solstitialis display intermediate competitive ability. Ecography. doi:10.1111/ecog.02653

Montesinos D, Santiago G, Callaway RM. 2012. Neo-allopatry and rapid reproductive isolation. The American Naturalist 180:529–533.

Muth NZ, Pigliucci M. 2006. Traits of invasives reconsidered: phenotypic comparisons of introduced invasive and introduced non-invasive plant species within two closely related clades. American Journal of Botany 93:188–196.

Pennings SC, Callaway RM. 1992. Salt marsh plant zonation: the relative importance of competition and physical factors. Ecology 73:681–690.

Pinheiro J, Bates D, DebRoy S, Sarkar D and R Core Team. 2016. nlme: linear and nonlinear mixed effects models. R package version 3.1-128. Available from: http://CRAN.R-project.org/package=nlme.

R Development Core Team. 2008. R: A language and environment for statistical computing. Vienna: R Foundation for Statistical Computing. ISBN 3-900051-07-0. Available from: http://www.R-project.org.

Reinhart KO, Callaway RM. 2006. Soil biota and invasive plants. New Phytologist 170:445–457.

Richardson DM, Pyšek P, Rejmánek M, Barbour MG, Panetta FD, West CJ. 2000. Naturalization and invasion of alien plants: concepts and definitions. Diversity and Distributions. 6:93–107.

Ridenour WM, Vivanco JM, Feng Y, Horiuchi JI, Callaway RM. 2008. No evidence for trade-offs: *Centaurea* plants from America are better competitors and defenders. Ecological Monographs 78:369–386.

Sax DF, Gaines SD. 2003. Species diversity: from global decreases to local increases. Trends in Ecology and Evolution. 18:561–566.

Sax DF, Stachowicz JJ, Brown JH, Bruno JF, Dawson MN, Gaines SD, Grosberg RK, Hastings A, Holt RD, Mayfield MM, et al. 2007. Ecological and evolutionary insights from species invasions. Trends in Ecology and Evolution. 22:465–471.

Shah MA, Callaway RM, Shah T, Houseman GR, Pal RW, Xiao S, Luo W, Rosche C, Reshi ZA, Khasa DP, et al. 2014. *Conyza canadensis* suppresses plant diversity in its nonnative ranges but not at home: a transcontinental comparison. New Phytologist 202:1286–1296. doi10.1111/nph.12733

Siemann E, Rogers WE. 2001. Genetic differences in growth of an invasive tree species. Ecology Letters 4:514–518.

Siemann E, Rogers WE. 2003. Reduced resistance of invasive varieties of the alien tree *Sapium sebiferum* to a generalist herbivore. Oecologia 135:451–457.

Tavares D. 2014. Evolution of invasiveness: the case study of the invasive *Oxalis pes-caprae* in the Mediterranean basin. Master's thesis. Faculdade de Ciências e Tecnologia. Coimbra: Universidade de Coimbra.

Zenni RD, Bailey JK, Simberloff D. 2014. Rapid evolution and range expansion of an invasive plant are driven by provenance-environment interactions. Ecology Letters doi:10.1111/ele.12278

Zou J, Rogers WE, Siemann E. 2008. Increased competitive ability and herbivory tolerance in the invasive plant *Sapium sebiferum*. Biological Invasions 10:291–302.