

Dissecting impact of plant invaders: Do invaders behave differently in the new range?

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Abstract. Knowledge from basic plant ecology suggests that impact of one plant species on another is driven by either competition for the same limiting resources, or by unique plant traits. These processes might be context specific, explaining a differential impact of exotic plant invaders in the native vs. introduced range. With the help of a conceptual framework, we aimed at identifying the relationship between invader biomass and impact in the invasive *Centaurea stoebe* by conducting pairwise competition experiments with 15 European (old) and 15 North American (new) neighboring species. Old neighbors grew larger and could use available soil moisture more efficiently for growth than new neighbors. Interestingly, biomass of *C. stoebe* explained a substantial amount of the variation in biomass of the coevolved neighbors, but not of the new “naïve” neighbors. Thus, impact in the home range appears to be driven by competition for the same limiting resources, but by other factors in the introduced range, possibly by exploitation of resources that are not used by the new neighbors or by interference competition. This distinction has important consequences for the management of invasive species, as in our study ecosystem recovery is less likely after simple biomass reduction.

Key words: biogeography; *Centaurea stoebe*; competition; ecological impact; exotic plants; size dependence.

INTRODUCTION

Invasions by alien plants threaten native species and communities, causing enormous economic and ecological costs (Gurevitch et al. 2011). They are also regarded as among the most important drivers of environmental change in ecosystems. Concern about the impact of exotic invaders on biodiversity and ecosystem services is fueled in part by the observation that strong invaders can reach high population densities and dominate communities in the introduced range (Ortega and Pearson 2005). This raises the question whether the impact of invaders is indeed simply a matter of numbers, or whether their impact differs between the home and the introduced ranges irrespective of their density. As it is the impact of invaders rather than their establishment per se that threatens native communities, a better understanding of the underlying factors determining impact is greatly needed (Simberloff et al. 2013).

According to Parker et al. (1999), total impact of an invader includes three fundamental dimensions: (1) range size, (2) abundance or biomass, and (3) per capita or per biomass effect. While the first dimension provides information on the geographic range where impact may

occur, the latter two describe impact in a specific area within the invaded range. However, there remains a considerable confusion over whether the local impact caused by alien invasive species is simply a consequence of the large amount of resources they use in the invaded habitats (resource competition) or whether it is primarily due to special traits of the invasive species that directly interfere with competitors (interference competition).

Insights into the type of mechanisms underlying competitive interactions of plant invaders can be gained from the analysis of the relationship between the biomass produced by the invader and that of old vs. new neighbors in competition experiments, for which we may distinguish two main patterns (Fig. 1). First, a negative correlation between the biomass produced by two plant species indicates competition for the same limiting resources. We expect such a pattern for plants that have a coevolutionary history, such as the invader and its old neighbors in the native range (Fig. 1A). If the relationship between the invader and the new neighbors in the introduced range is similar, then increased impact in the introduced range is largely related to increased abundance of the invader (Parker et al. 1999).

Second, if the relationship between the invader and the new neighbors is not based on competition for the same limiting resources, then one would expect that the biomass of the invader and that of the new neighbor are not, or only weakly, correlated with each other within the range from moderately low to moderately high

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invader biomass (Fig. 1B). Such a scenario may occur when the impact of invasive species is primarily due to their “quirks” (Simberloff 1985); e.g., the invader is able to exploit soil resources that the natives cannot, allowing them to overtop its neighbors, or the invader directly interferes with the growth of the new neighbor species (e.g., novel weapons hypothesis; Callaway and Aschehoug 2000). Including extreme invader biomass values would result in a curvilinear relationship with a threshold value for the invader biomass with no impact below it and no correlation with the neighbor biomass above it, since the line would intercept the y axis at the same point as the line in Fig. 1A.

We set out to use this conceptual framework for assessing the nature of the relationship between invader biomass and the impact underlying the competitive ability of the European *Centaurea stoebe* in the presence of old European vs. new North American plant neighbors. Introduced into North America in the late 19th century, *C. stoebe* infests, to date, more than two million hectares (five million acres) throughout the United States and Canada (Winston et al. 2010). We conducted a pairwise competition experiment to specifically explore whether (1) plant species co-occurring with *C. stoebe* in Europe and North America differ in performance and resource use, (2) European and North American *C. stoebe* differ in their impact on European vs. North American neighbors, and (3) the impact of *C. stoebe* on native plants from the two ranges is related to the biomass of *C. stoebe* or not. Using the conceptual framework developed in the previous paragraphs, we then assessed whether the type of impact imposed by *C. stoebe* differs between the native and the introduced range.

MATERIALS AND METHODS

Plant species

Centaurea stoebe L. (syn. *C. maculosa* Lam., Asteraceae), spotted knapweed, is a widespread, short-lived herb native to Europe (EU), and was introduced into North America (NA) as a seed contaminant (Roche and Roche 1991). In Europe, it exists as two cytotypes, diploids and tetraploids, but so far, only tetraploids have been recorded from its introduced North American range (Mráz et al. 2011). In our study, we only used tetraploid *C. stoebe* from both its native and introduced range (northwestern United States). Seeds of *C. stoebe* were collected from three EU and four NA populations (bulk samples of 10–20 mother plants; Appendix A: Table A1).

To assess the competitive interaction with neighbor species from the native and introduced range, seeds of 17 EU and 19 NA perennial plant species were either collected from the field (adjacent to a *C. stoebe*-infested site) or purchased from commercial suppliers in Europe and the United States for EU and NA plants, respectively. Neighbor species were chosen among plants naturally occurring at tetraploid *C. stoebe* sites

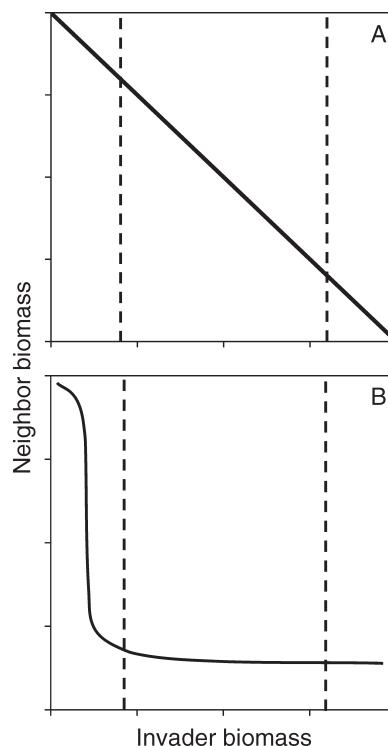


FIG. 1. Hypothetical outcomes of competition experiments between a plant invader and neighbor species from the native or introduced range. (A) The biomass of the invader explains a significant amount of variation in biomass of the neighbor species; and (B) the biomass of the invader explains a significant amount of variation in biomass of the neighbor species only at very low invader biomass levels. The two vertical dashed lines indicate the range between moderately low and moderately high levels of invader biomass; within this range, the relationship between invader biomass and neighbor biomass is close to linear in panel (A) and nonsignificant in panel (B). For a more detailed description see the *Introduction*.

to represent different functional groups and as many confamilial pairs as possible (Appendix B: Table B1). Thus, while a coevolutionary history of the EU plants with *C. stoebe* is most likely at the species level, none of the seed material used in the experiment had a direct experience with *C. stoebe*.

Experimental design

Neighbor plants from both ranges as well as tetraploid *C. stoebe* from EU and NA were grown from seeds in a greenhouse from December 2010 through April 2011. Since some neighbor species did not germinate well in the first sowing event (C1, cohort 1), we re-sowed *C. stoebe* from the two ranges and six neighbor species (C2, cohort 2). To compare the results of the two sowing events, six of the species that germinated well in the first sowing were also re-sown. Details on the setup of the two cohorts are given in Appendix B.

In total, 15 EU species and 15 NA species were included in the two cohorts (plus three species each that

were used in both cohorts). One individual of an EU or a NA neighbor species was grown alone (equaling 36 non-competition pots) or in competition with one individual of an EU or a NA *C. stoebe* plant (equaling 72 competition pots). Moreover, two pots (one each with EU and NA *C. stoebe*) per cohort were set up with *C. stoebe* grown alone (control pots). Controls and each species \times *C. stoebe* combination were replicated five times, resulting in a total of 560 pots. All populations of each *C. stoebe* origin were included in each of the five replicates. One replicate was randomly arranged on a separate bench to form a randomized complete block design.

Data collection

The length of the longest fully expanded leaf (leaves were erect at this stage) of all seedlings was assessed three days after transplanting. To assess the suitability of leaf length as a nondestructive proxy of plant size, we harvested at the same time 30 surplus individuals of all species and calculated the relationship between biomass and the length of the longest fully expanded leaf. At harvest, we measured the widest diameter of the area occupied by the plant projected to the ground surface of each individual plant to assess the relationship between this proxy of plant size and biomass at harvest of either all grass species or all forbs using noncompetition and competition individuals separately. For all species, biomass was significantly correlated with length of the longest leaf at the seedling stage ($R^2 \geq 0.446$, $P < 0.001$ for each grass species; $R^2 \geq 0.607$, $P < 0.001$ for each forb species) and with the projected widest plant diameter at harvest (overall $R^2 = 0.215$ and 0.390 , $P \leq 0.016$ for all grass species combined; overall $R^2 = 0.356$ and 0.224 , $P < 0.001$ for all forbs combined, in the absence and presence of competition, respectively).

In order to monitor water use of the various competitive assemblages, we also measured soil moisture content (SMC) in all pots one month and two months after transplanting, and at the day before harvesting (cf. Appendix B for further details). Plants of C1 were harvested on 11–13 April 2011 (days 78–80), and of C2 three weeks later, on 2 May 2011 (day 78). Plants were subsequently dried to a constant mass at 60°C for 48 h and weighed to an accuracy of ± 0.1 mg.

We assessed the relative growth rate (RGR) of each plant species by calculating $RGR_{(d)} = (\ln d_1 - \ln d_0) / \text{days}$, where d_1 is the widest projected diameter of the plant at harvest, and d_0 is the widest diameter (twice the length of the longest leaf) at the beginning of the experiment. To indicate the growth trajectories of *C. stoebe* and the neighbor plant when grown in competition, we applied the Relative Efficiency Index (REI; Connolly 1987), an indicator of mixture dynamics independent of initial plant size. REI is the difference between the relative growth rates of two competing species and was calculated here as $REI = (\ln d_{1ci} - \ln d_{0ci}) - (\ln d_{1ic} - \ln d_{0ic})$, where d_{1ci} refers to the

diameter of *C. stoebe* plants in mixture with neighbor species i at harvest, d_{0ci} to the diameter of *C. stoebe* in mixture with neighbor species i at the beginning of the experiment, d_{1ic} to the diameter of neighbor species i in mixture with *C. stoebe* at harvest and d_{0ic} to the diameter of neighbor species i in mixture with *C. stoebe* at the beginning of the experiment. Hence, the higher the REI the stronger is *C. stoebe* in dominating the neighbor species.

Statistics

Linear mixed models were fit using the lmer function obtained from the R package lme4 that uses maximum likelihood to estimate the model parameters (Bates et al. 2010). General linear mixed models were calculated to assess the effect of origin of neighbor plants and origin of *C. stoebe* on RGR, SMC, and REI, origin of *C. stoebe*, origin of native neighbors and cohort were included as fixed effects, and block and neighbor species nested within range were treated as random factors. Mixed-effects regression models were used to analyze the correlation between biomass of neighbors and *C. stoebe* under competition (cf. Appendix B for further statistical details). Eventually, model-II simple linear regression using the standard major axis (SMA) method was used to compute the relationship between biomass of neighbors and *C. stoebe* under competition. Moreover, we compared the 95% confidence interval of the slope of our model and the 45° line.

RESULTS

Neighbor species

In the absence of competition, biomass at the end of the experiment was generally higher for EU neighbors than for NA neighbors ($\chi^2 = 6.423$, $P = 0.011$; Appendix E: Fig. E1). In the competition pots, EU and NA *C. stoebe* had comparable impacts on the RGR of neighbors from the two ranges ($\chi^2 = 0.006$, $P = 0.936$; Appendix C: Fig. C1A). There was a profound reduction in RGR of both EU (56%) and NA neighbors (68%) when grown in competition with *C. stoebe* ($F_{2,344} = 112.600$, $P < 0.001$), and the reduction in RGR was not different for EU and NA neighbors ($\chi^2 = 0.342$, $P = 0.559$).

Centaurea stoebe

RGR of *C. stoebe* was slightly reduced when grown with EU neighbors ($\chi^2 = 3.200$, $P = 0.074$), but not when grown with NA neighbors ($\chi^2 = 0.158$, $P = 0.692$). Both EU and NA *C. stoebe* were similarly impacted by EU neighbors ($\chi^2 = 1.181$, $P = 0.277$; Appendix C: Fig. C1B).

Soil moisture content (SMC)

When grown alone, SMC in pots with EU neighbors was significantly lower than in pots with NA neighbors ($\chi^2 = 4.654$, $P = 0.031$; Appendix F: Fig. F1A). SMC in pots with EU neighbor species growing in competition

with *C. stoebe* was marginally significantly lower compared to that in pots with EU neighbor species growing alone ($\chi^2 = 3.162$, $P = 0.075$). However, when NA neighbors were grown in competition with *C. stoebe*, SMC was substantially reduced compared to pots with NA neighbors growing alone ($\chi^2 = 58.706$, $P < 0.001$), reaching levels as those found in pots with EU neighbor plants growing with *C. stoebe* (Appendix F: Fig. F1B).

Interactions between *C. stoebe* and its neighbor species

In the competition pots, REI of *C. stoebe* competing with EU neighbors was significantly lower (90% for mean values) than REI of *C. stoebe* competing with NA neighbors ($\chi^2 = 4.034$, $P = 0.044$; Appendix D: Figs. D1 and D2). Biomass of *C. stoebe* explained a highly significant and substantial amount of the variation in biomass of EU neighbors ($R^2 = 0.500$, $\Delta \log\text{-likelihood} = 26.264$, $P < 0.001$), but only a minor amount of the variation in biomass of NA neighbors ($R^2 = 0.036$, $\Delta \log\text{-likelihood} = 1.870$, $P = 0.174$; Fig. 2). The 45° line is just included in the 95% confidence interval of the SMA slope (Fig. 2A). Moreover, a combined analysis of the two data sets revealed a significant difference in neighbor origin ($t = -3.842$, $df = 326$, $P < 0.001$). This result is not due to the fact that large neighbors were absent in NA, as adjusting the range of EU neighbors to the one of NA neighbors (by removing all data above 2.2 g) still resulted in a highly significant negative linear correlation ($R^2 = 0.301$, $\Delta \log\text{-likelihood} = 17.843$, $P < 0.001$) between biomass of EU neighbors and biomass of *C. stoebe*.

DISCUSSION

European vs. North American neighbors

In the absence of competition, European neighbors grew significantly larger than NA neighbors. This is in line with earlier findings from biogeographic studies (He et al. 2009) and suggests that NA species growing in *C. stoebe*-invaded grasslands have an inherently lower growth rate than European species growing in grasslands in which *C. stoebe* occurs naturally. Grassland sites in Europe are generally more productive than the inter-mountain and mixed-grass prairie in the invaded region of northwestern United States, most probably due to the two- to threefold differences in precipitation between the two regions (Callaway et al. 2011). As a consequence, NA species may be adapted to more stressful environmental conditions, which should favor slower growth compared to EU plants that are adapted to greater resource levels (at least water) and have strategies to maximize their competitive ability under more favorable conditions.

SMC, measured at harvest, of pots in which plants were grown alone revealed that NA species were not able to exploit the available water to the same extent as the EU species. This result could in fact be a direct consequence of increased biomass of EU neighbors at the end of the experiment. However, as SMC of pots

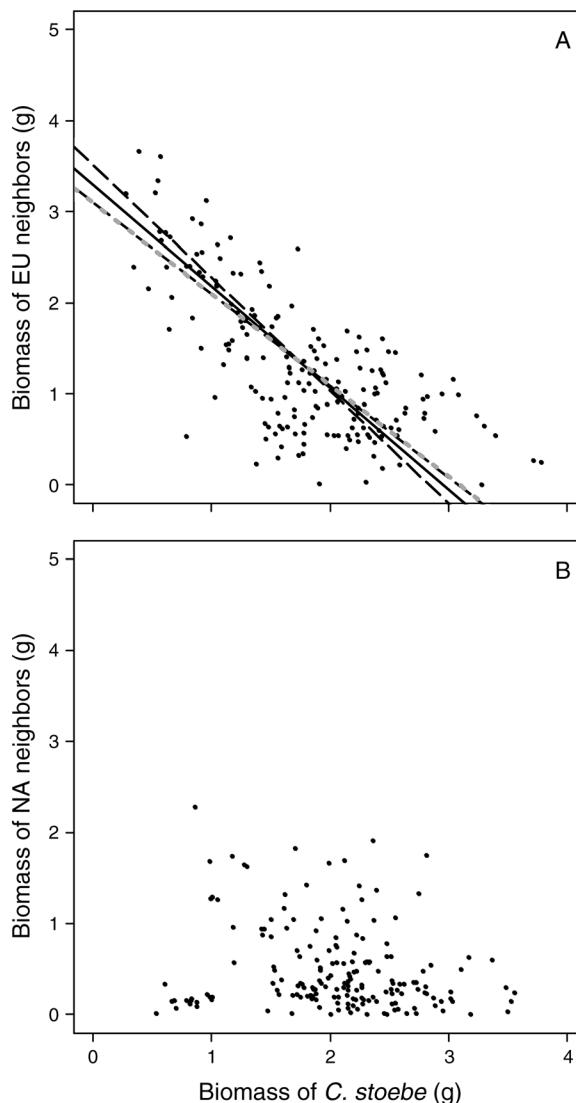


FIG. 2. Relationship between the biomass (grams dry mass) of tetraploid *Centaurea stoebe* and that of (A) European (EU) and (B) North American (NA) neighbors in a competition condition. Scatter diagram (A) shows the standard major axis (SMA) regression line (solid line) and its 95% confidence region (two black dashed lines); the 45° line is included for reference (gray dashed line). Each point represents a pot.

with EU neighbors was also significantly lower than with NA neighbors both at the end of first and second months after transplanting ($P < 0.04$), it is more likely a fundamental difference between EU and NA neighbors in their ability to exploit water resources. This supports the notion that NA neighbors have an inherently lower growth rate than European neighbors. Alternatively, NA plants might have been limited in growth by resources other than water, but this seems rather unlikely, since the standard soil we used contains a well-balanced composition of nutrients, and light was supplemented.

Interactions between *C. stoebe* and its neighbor species

In our experiment, both EU and NA neighbors were significantly suppressed when grown in competition with *C. stoebe*. However, REI as an indicator for the dynamics of mixtures of *C. stoebe* and neighbor species revealed that *C. stoebe* cannot as easily dominate in the presence of European neighbors than in the presence of NA neighbors. Although the spatial plant arrangement in our greenhouse experiment corresponds to a commonly observed neighborhood distance in both the natural EU and NA environment (Appendix B), pot size might have intensified competition in our experiment, especially with regard to interaction with NA neighbors that also occur at lower densities (John Maron, *personal communication*). Nevertheless, REI was much higher for NA as compared to EU neighbors when grown under our competitive conditions, indicating that NA neighbors are much less competitive in the presence of *C. stoebe* than EU neighbors. These findings are also consistent with the results of a field removal experiment, in which effects of EU and NA neighbors on the growth and reproduction of *C. stoebe* were compared (Callaway et al. 2011). While at EU sites *C. stoebe* biomass increased by 107%, on average, when competitors were removed, mean increase in biomass was only 18% at NA sites. Similarly to our results, Corbin and d'Antonio (2010) found that the productivity of exotic perennial grasses was not affected by the presence of native NA perennial grasses. In contrast, NA perennial grass productivity was significantly lower in plots with exotic perennial grasses, compared to plots without exotic grasses.

We found no evidence that the EU and NA populations of *C. stoebe* inherently differ in their impact on neighbors, nor that the two *C. stoebe* origins impose different impact on EU vs. NA neighbors. Ridenour et al. (2008) found that *C. stoebe* from the introduced range were larger than tetraploid plants from the home range. In our study, however, biomass of EU and NA *C. stoebe* did not significantly differ in the competition pots, nor did REI differ between pots with EU vs. NA *C. stoebe* as competitors. These findings suggest that, in our experiment, competition between *C. stoebe* and neighbor plants was largely influenced by the origin of the neighbor plants, rather than through post introduction evolutionary change for increased competitive ability in *C. stoebe*.

Impact type of *C. stoebe* at home and away

Since REI is not sensitive to variation in initial plant size (Connolly 1987), the competitive superiority of EU neighbors over NA neighbors cannot be explained by the different RGRs observed in the noncompetition pots. Rather, our results indicate that the stronger competitive ability of EU neighbors might be attributed to an inherently different mechanism underlying the competitive interactions between EU and NA neighbors when grown with *C. stoebe*. The significant negative

relationship between biomass of *C. stoebe* and biomass of its old native neighbors (Fig. 2A) follows the hypothetical relationship outlined in Fig. 1A, suggesting that competition between *C. stoebe* and its native neighbors is driven by competition for limiting resources. Moreover, the similarity to the -1 slope suggests that mainly one resource is limiting growth in our competition pots. In contrast, the biomass of *C. stoebe* explained only a very low amount of the variation in biomass of its new neighbors, which corresponds to the hypothetical relationship shown in Fig. 1B and indicates that competition is driven by mechanisms other than competition for the same limiting resource. Hence, the experimental approach taken in our study supports earlier notions that the impact of *C. stoebe* on new neighbors is primarily due to some specific “quirks” that either allow *C. stoebe* to capture resources largely unexploited by the native species, or that directly interfere with the growth of native neighbor species. The SMC values indicate that *C. stoebe* is able to exploit water resources that NA neighbors cannot. Despite our efforts to mimic low soil moisture conditions characteristic for inter-mountain grasslands in the northwestern United States, the conditions in our greenhouse experiment may still not reflect the natural conditions of the areas where spotted knapweed has become invasive. Nevertheless, it is noteworthy that declines of *C. stoebe* in Montana in early 2000s have been attributed to drought (Ortega and Pearson 2005), and that *C. stoebe* abundance appears to be rebounding in recent years of greater rainfall (Ortega et al. 2011). This suggests that soil moisture may indeed be a critical factor shaping the competitive interaction between *C. stoebe* and NA neighbors. In contrast, EU neighbors seem to be as efficient in exploiting soil moisture as *C. stoebe*.

A mechanism that may explain interference competition between *C. stoebe* and NA neighbors is allelopathy, which has been repeatedly suggested for *C. stoebe* and for other knapweed species (e.g., He et al. 2009, Callaway et al. 2011). For instance, a competition experiment with the invasive *Centaurea diffusa* Lam. (Asteraceae) and three old (Eurasian) and three relative new (North American) bunchgrasses neighbors revealed that *C. diffusa* had much stronger negative effects on its new compared to its old neighbors for both growth and phosphorus uptake (Callaway and Aschehoug 2000). When activated carbon was added, effects of *C. diffusa* on its new neighbors were greatly reduced, indicating that *C. diffusa* may use different competitive mechanisms in its home and introduced ranges. While ecological experiments have repeatedly found evidence for direct interference of various knapweed species on native NA neighbors, earlier reports that claimed to have identified the chemical substances responsible for the allelopathic effects of knapweeds have later been retracted or corrected (Bais and Kaushik 2010), and thus, the mechanisms underlying the observed ecological effects remain uncertain. Little is known about whether

the effect of allelopathy is biomass-related or not. The only study we are aware of is by Olofsson et al. (2002), who found no evidence for a genetic correlation between yield and allelopathy in rice. There is, on the other hand, growing evidence that the amount of allelopathic substances experienced by a plant competitor is significantly influenced by soil characteristics, including the binding of root exudates to soil particles (Bertin et al. 2003) and the degradation of root exudates by soil microorganisms (Lankau 2010). Such soil-driven mechanisms may lead to interference competition that is only weakly related to the biomass of the invader, but may be much more strongly related to invader density. In fact, the distinction between density and biomass may, as long as density \times biomass per plant remains constant, not be relevant in cases where plants compete for the same limiting resources (Fig. 1A), but it may become important in the context of biomass-unrelated competitive interactions such as allelopathy (Fig. 1B).

We explicitly used standard soil with no previous history with any of the plant species used in our experiment. Numerous studies provide evidence that competitive interactions between *C. stoebe* and neighbor plant species are also influenced by soil characteristics, e.g., through the lack of negative soil-plant feedback in the introduced range (Callaway et al. 2004), or through interactions with soil-born endophytes (Aschehoug et al. 2012). It is therefore likely that the use of soil from native or invaded grasslands would have influenced our results. However, we found differences in impact types of *C. stoebe* on NA and EU neighbors that are clearly in line with findings from field studies (Callaway et al. 2011), suggesting that neighbor origin is an important factor explaining the differential impact of *C. stoebe* in the native and the introduced range.

Conclusions

Comparing the ecology of plants where they are native and introduced has a great potential to further our understanding of processes that enable some plant invaders to dominate in the recipient communities. We advocate that the conceptual model outlined in Fig. 1 combined with competition experiments using the plant invader and a set of its old and new neighbors will help elucidating the pattern and potential mechanisms underlying impact of a plant invader at home and away. In the case of *C. stoebe*, our findings suggest that the impact of *C. stoebe* at home is largely driven by resource competition, while in the invaded range, impact is driven by exploitation of resources that are not utilized by native species or by interference competition. In other words, the high impact of *C. stoebe* on native plant communities in the invaded range is not simply a matter of different densities, but, in addition to different ecological settings, also due to different mechanisms operating in the two ranges. Assessing whether impact is related to biomass or not may provide important insight into the mechanism underlying impact.

This distinction also has important consequences for the management of invasive species. If the invader's impact is solely a matter of competition for the same limiting resources, then reducing the biomass of the invader will result in some degree of recovery of the neighboring vegetation. In contrast, when its impact is rather driven by interference competition, then ecosystem recovery is less likely after simple biomass reduction and may require an extended period with the invader absent or at very low densities. Further studies will hopefully reveal how the conceptual model (Fig. 1) will help elucidating the impact type of other plant invaders at home and away and the underlying mechanisms involved.

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SUPPLEMENTAL MATERIAL

Appendix A

Table of origin and description of tetraploid *Centaurea stoebe* populations ([Ecological Archives E094-197-A1](#)).

Appendix B

Details on the methods and statistics ([Ecological Archives E094-197-A2](#)).

Appendix C

Figure depicting relative growth rate ([Ecological Archives E094-197-A3](#)).

Appendix D

Figures depicting relative efficiency indices ([Ecological Archives E094-197-A4](#)).

Appendix E

Figure depicting biomass of each EU and NA neighbor in the absence of competition ([Ecological Archives E094-197-A5](#)).

Appendix F

Figure showing the relationship between soil moisture and biomass of EU or NA neighbors in the absence or presence of competition ([Ecological Archives E094-197-A6](#)).