

BIOGEOGRAPHIC EFFECTS ON EARLY ESTABLISHMENT OF AN INVASIVE ALIEN PLANT¹

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- *Premise of the study:* Biotic resistance is often studied in the context of how interactions between native biota and invading species influence the success of those invaders. Seldom, however, is the strength of “resistance” compared biogeographically, where the ability of a species to impede invader establishment is contrasted between an invader’s native and introduced recipient community.
- *Methods:* We conducted an experiment to examine how community diversity influences seedling recruitment of a plant invader where it is native and contrasted with results previously published from introduced ranges. In Switzerland, we created recipient communities that varied in species and functional richness and invaded them, or not, with seeds of *Centaurea stoebe*, a native European plant that has been previously used in an identical experiment in North America, where it is a prominent invader.
- *Key results:* The biogeographic comparison revealed that the recipient community largely prevented *C. stoebe* seedling establishment at home (Switzerland), but not away (Montana, USA), and that diversity of the resident vegetation did not contribute to the effects observed in the introduced range.
- *Conclusions:* Our results provide evidence that differences in the biogeographic conditions and/or overall level of competition of resident community between the native and introduced range considerably suppresses seedling recruitment of the invasive plant, rather than resident diversity itself. In the case of *C. stoebe*, the surprisingly low establishment success in the experiments conducted in the native compared with the introduced range is likely to be influenced by the higher level of competition with resident community, by abiotic environmental conditions or interactions between these two factors in the native range. Release from factors suppressing seedling recruitment at home may contribute to the successful invasion of *C. stoebe* in North America.

Key words: Asteraceae; biological invasions; biotic resistance; *Centaurea stoebe*; community diversity; establishment; neighbor origin.

During biological invasions, species are moved from their native range, where their populations are controlled by a specific set of factors, to regions beyond natural dispersal barriers, where their abundance may be influenced by a different set of factors (Hierro et al., 2005). Altered biotic interactions (e.g., interactions of invaders with enemies, mutualists, or competitors) may prevent the invasion of alien species into recipient communities, as stated by the biotic resistance hypothesis

(Elton, 1958), or, alternatively, they may contribute to invasion success (Mitchell et al., 2006). To be successful, an alien plant species must establish, survive, and attain a positive rate of population increase while living on the resources left unconsumed by the resident species (Seabloom et al., 2003). Examining the early stages of plant establishment is an important component of understanding invasion success, since plants at this stage in particular suffer from both environmental constraints and competition (Harper, 1977; Levine et al., 2004; Holle and Simberloff, 2005; Norden et al., 2007).

One component of biotic resistance that has received considerable attention concerns the role of native plant diversity in resisting invasion. In experiments where local diversity has been manipulated, it is often found that more diverse assemblages are more difficult to invade than are less diverse assemblages (Levine and D’Antonio, 1999). The mechanism driving this pattern is often believed to be resource-use complementarity, where fewer “free” resources are available for an invading species in high diversity than low diversity assemblages (Spehn et al., 2000; Maron and Marler, 2007). Levine et al. (2004) proposed that high richness of resident plant species primarily constrains the performance of alien plant species once they have established, rather than seedling establishment itself.

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Typically, experiments addressing the diversity–invasibility relationship are conducted using native assemblages and an exotic “invader”, but the diversity–invasibility relationship might vary depending on whether the “invader” attempts to colonize its native or its invaded community. Recent studies suggest that competitive interactions between resident species with a shared evolutionary history may well differ from those between resident and invasive alien plant species, with old neighbors more strongly suppressing an “invader” than novel neighbors (Callaway et al., 2011; Sun et al., 2013). Hence, a biogeographic approach would not only allow a determination of how diversity affects community resistance but also whether this relationship varies depending on whether the community is evolutionarily “naive” or shares a coevolutionary history with the invader. Comparing the community resistance at home vs. away will hence further our understanding of the role of evolutionary history in shaping community assemblages and the factors contributing to the invasion success of invasive alien species (Davis et al., 2011). Here, we report results of an experiment carried out in Switzerland and compare our findings with the results of a previous study conducted by Maron and Marler (2007) in the United States to examine whether experimental assemblages that vary in native plant diversity at neighborhood-scale differently affect the establishment of *Centaurea stoebe* L. in its native European compared with its introduced North American range.

MATERIALS AND METHODS

Model species—*Centaurea stoebe* L. (syn. *C. maculosa* Lam., Asteraceae), spotted knapweed, is a widespread, short-lived, perennial herb native to Europe and was introduced into North America 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 found across the introduced range in North America (Mráz et al., 2011). At the European site, we used tetraploid *C. stoebe* from its native range in Europe, while the experimental plots in northwestern United States were invaded with tetraploid *C. stoebe* from its introduced range. We chose *C. stoebe* as our model species for the biogeographic study as this species showed higher invasion success in the experiment carried out by Maron and Marler (2007, 2008) than two other exotics they used (*Linaria dalmatica* and *Potentilla recta*). Seeds of *C. stoebe* were collected from six populations in Switzerland and Germany (Appendix S1, see Supplemental Data with the online version of this article).

Design of the experimental plots—In March–April 2010, we created 42 unique native perennial plant assemblages in a grassland near Delémont, Switzerland (47°37′30.01″N, 7°32′63.89″E), which is situated within the western part of the native range of *C. stoebe* (Hahn and Müller-Schärer, 2013), where *C. stoebe* primarily occurs in open grasslands (e.g., in well-drained habitats or on steep slopes), where it can reach high densities (Treier et al., 2009). The study site is characterized by shallow soil on limestone, and the experiment was conducted in a southwest-exposed grassland that has not been fertilized for at least 20 yr. To facilitate comparison of our experimental results with those reported by Maron and Marler (2007), we used the same criteria for selecting native plant species and an identical design for setting up the native perennial plant assemblages. Our experimental native communities were composed of plants that commonly co-occur with *C. stoebe* in its home range. Plant assemblages varied in both species richness (2–16 species) and richness of functional groups (1–6 functional groups; Table 1). Since the functional diversity of resident plant communities is likely to affect the amount of resources remaining for invaders (Fargione and Tilman, 2005), we chose native species that varied in the timing and depth of resource uptake. The 16 species we used belong to the following six functional groups: grasses, early-flowering forbs that branch with short rhizomes or stolons or at the root crown, midseason forbs with spreading rhizomes, midseason forbs with woody root crowns, early-flowering ephemeral forbs with a shallow taproot, and late-season forbs with deep taproots (see Table 1 for species names). If mixtures contained a subset of species from a particular functional group, species from that functional group were randomly

TABLE 1. Native species, functional type, and code used in experimental assemblages.

Species	Functional group	Species code
<i>Bromus erectus</i> Hudson ^{2,3}	Grasses	G _{1a}
<i>Festuca valesiaca</i> Schleich. ^{3,4}	Grasses	G _{1b}
<i>Koeleria pyramidata</i> (Lam.) Beauv. ^{2–4}	Grasses	G _{1c}
<i>Primula veris</i> (L.) Huds. ¹	Early season, rhizomatous	F _{1a}
<i>Sanguisorba minor</i> Scop. ^{1,3}	Early season, rhizomatous	F _{1b}
<i>Veronica teucrium</i> L. ^{3,4}	Early season, rhizomatous	F _{1c}
<i>Achillea millefolium</i> L. ^{1,3}	Midseason, spreading rhizomes	F _{2a}
<i>Dianthus carthusianorum</i> L. ^{1,3}	Midseason, spreading rhizomes	F _{2b}
<i>Galium verum</i> L. ^{2–4}	Midseason, spreading rhizomes	F _{2c}
<i>Artemisia campestris</i> L. ^{2–4}	Midseason, woody root crowns	F _{3a}
<i>Leontodon hispidus</i> L. ^{3,4}	Midseason, woody root crowns	F _{3b}
<i>Scabiosa columbaria</i> L. ^{1,3}	Midseason, woody root crowns	F _{3c}
<i>Plantago media</i> L. ^{2–4}	Spring ephemerals, shallow taproot	F _{4a}
<i>Ranunculus bulbosus</i> L. ^{3,4}	Spring ephemerals, shallow taproot	F _{4b}
<i>Cichorium intybus</i> L. ^{3,4}	Late season, deep taproot	F _{5a}
<i>Echium vulgare</i> L. ^{2–4}	Late season, deep taproot	F _{5b}

Notes: The superscript numbers after each species represent the source of seeds: (1) collected from field where *Centaurea stoebe* occurred; (2) B-and-T World Seeds, Pagnignan, France; (3) UFA-Samen, Winterthur, Switzerland; and (4) Jelitto, Schwarmstedt, Germany. Species codes were used in the experimental community composition design in online Appendix S2, see Supplemental Data with the online version of this article.

assigned. In cases where different diversity treatments had identical functional richness (i.e., treatments 5 and 6; Appendix S2, see online Supplemental Data), the treatments varied in the functional groups from which species were drawn. Each diversity treatment was replicated six times, with species drawn at random from a particular functional group.

Experimental procedure—Seeds of 16 European perennial plant species were either collected in the field (bulk samples of 10–20 mother plants per population adjacent to sites with *C. stoebe* populations) or purchased from commercial suppliers (B-and-T World Seeds, Pagnignan, France; UFA-Samen, Winterthur, Switzerland and Jelitto, Schwarmstedt, Germany). In January 2010, all species were germinated from seeds and individual plants were grown in “conetainers” (2.5 cm × 16.5 cm; Stuewe and Sons, Corvallis, Oregon, USA) filled with a mixture of commercial soil (Selmaterra, Eric Schweizer AG, Thun, Switzerland), sand and vermiculite (Vermisol, granular form, VTT AG, Muttenz, Switzerland) in the ratio 4 : 2 : 1 in a greenhouse at the CABI Centre in Delémont, Switzerland. In March–April 2010, we transplanted the plants into the experimental plots. To remove vegetation before setting up the experiment, we treated the plots with herbicide (Roundup Star, Monsanto Europe N.V., Stähler Suisse SA, Zofingen, Switzerland) twice up to 2 wk before transplanting. We established 42 mixed-species plots 3 × 3 m (7 diversity treatments × 6 replicates = 42), with each plot divided into four spatially separate 1.3 m × 1.3 m subplots (separated by 0.2 m buffer strips; Appendix S3, see online Supplemental Data). Subplots within plots were planted with identical mixtures of native species at identical initial densities of 48 individuals per subplot. Planted individuals that died were replaced in each spring of 2010–2012. The ultimate density of most species in subplots, however, was considerably higher than the planted density due to natural recruitment following abundant seed set in 2010–2012. Assemblages were watered from April to August 2010 to help transplanted seedlings survive and were weeded continuously to maintain predetermined levels of species and functional richness during the whole experiment. Continuous weeding enabled us to remove plants when they were tiny, thereby minimizing disturbance.

In March 2011, we also set up plots without vegetation (empty plots) by randomly selecting 11 plots interspersed with the diversity plots, treating them with Roundup Star and dividing the plots into four spatially separate 1.3 m × 1.3 m subplots.

For the biogeographic comparison with the experiment conducted by Maron and Marler (2007), in April 2011, we randomly selected two of the four subplots within each diversity plot, invaded one subplot with seeds of *C. stoebe* and used the other as the control; and also randomly sowed seeds in empty subplots. All seedlings except those of the sown *C. stoebe* were continuously removed

from the empty plots. The remaining subplots within each diversity plot and within the empty plots were invaded by either an alien invasive or a native species; the results of the latter study will be reported elsewhere.

To compare with the experiment conducted in Montana, we added the same number of seeds as Maron and Marler (2007), i.e., 10 g *C. stoebe* seeds (ca. 5000 seeds) to the central 1 m² of the subplots assigned to the “*C. stoebe* invasion experiment”. In total, six subplots were invaded at each diversity level as well as five empty subplots. In April 2012, the same numbers of seeds were again added to all subplots assigned to the *C. stoebe* invasion experiment.

We calculated the average number of *C. stoebe* seedlings across all treatments and average biomass of *C. stoebe* in the control subplots, and their standard error of the mean. The experimental design did not allow us to statistically examine the effects of biogeographic region, since only one experiment was set up in each region. We therefore only qualitatively compared the patterns of the results obtained in the two experiments. All analyses and figures were performed using R statistical software, version 3.0.3 (R Development Core Team, 2014).

RESULTS AND DISCUSSION

We found no seedlings of *C. stoebe* from seed additions at the end of the second year, and only two of 42 recipient subplots had seedlings at the end of the third year, with each less than 10 individuals of *C. stoebe* (Fig. 1). In the experiment in Montana, United States, Maron and Marler (2007) found on average 129 ± 14 recruitments per subplot 1 year after seeds were added in September 2005 and 215 ± 20.2 seedlings per subplot in April 2006 (Fig. 1). In Montana, there was no significant effect of species richness on initial seedling recruitment of *C. stoebe* in 2005 ($F_{1,67} = 2.4, P = 0.12$) and 2006 ($F_{1,67} = 2.1, P = 0.16$), although there was ultimately a very strong and significant effect of native diversity on the number of adult knapweed that established in plots (Maron and Marler, 2008). In empty subplots in Switzerland, *C. stoebe* recruited in high numbers (84 ± 14.5 in 2011); by the end of the second (2011) and third season (2012) of the experiment, the total *C. stoebe* biomass in empty subplots averaged $365 \text{ g} \pm 110 \text{ g}$ and $1195 \text{ g} \pm 178 \text{ g}$, respectively. By comparison, *C. stoebe* biomass found by Maron and Marler (2007) in bare plots in Montana invaded with *C. stoebe* averaged $641 \text{ g} \pm 200 \text{ g}$ in 2006.

Even though the two experiments cannot be compared statistically due to lack of replication across both ranges, these results suggest that fundamental differences between the neighboring

communities or other environmental conditions at home and away account for the high resistance to establishment by *C. stoebe* in the native range. In Switzerland, *C. stoebe* recruitment was strongly inhibited across all levels of native diversity, whereas in North America, *C. stoebe* abundantly invaded plots regardless of their underlying native diversity. It should be noted, though, that a strong negative diversity–invasibility relationship was found in North America with regard to abundance and biomass of *C. stoebe* at the end of the experiment (Maron and Marler, 2008); however, the least invaded high-diversity assemblages contained more *C. stoebe* than what established in any levels of native diversity plots in Switzerland.

Biotic resistance prevented establishment at home, but initial recruitment was relatively high across plots in the introduced range. Different interspecific interactions between *C. stoebe* and the resident community may at least partly account for the different results in the experiments conducted in the native and the introduced range. Previous studies showed a stronger competitive effect of coevolved European plants on *C. stoebe* than of naïve North American plants (Callaway et al., 2011; Sun et al., 2013). In a biogeographic field study, biomass of *C. stoebe* significantly increased when neighbors were removed in its native range but not in its nonnative range, suggesting strong negative competitive effects of neighboring vegetation on *C. stoebe* in native European grasslands (Callaway et al., 2011). In addition, productivity, widely considered to affect community invasibility in grasslands (Davis and Pelsor, 2001; Sperfeld et al., 2010), may also allow *C. stoebe* to more easily establish in North American than in European grasslands. On average, dry mass of the aboveground biomass in our uninjured subplots was approximately 1000 g/m², which is considerably higher than in the Montana experiment (approximately 200 g/m²; Maron and Marler, 2008) and in other studies assessing the diversity–invasibility relationship in North America (e.g., approximately 250 g/m² in Fargione et al., 2003). Grassland sites in western Europe are generally more productive than the intermountain and mixed-grass prairie in the invaded region of northwestern United States, most probably due to the 2- to 3-fold differences in precipitation between the two regions (Broennimann et al., 2007; Smit et al., 2008; Callaway et al., 2011). Plant species often require an opening in neighboring vegetation for successful establishment of new seedlings (Goldberg and Werner, 1983).

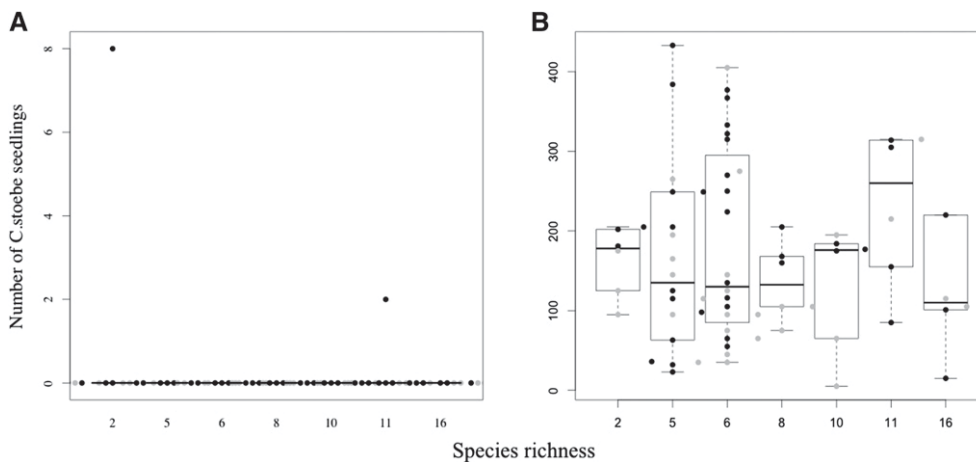


Fig. 1. Effect of species richness on *Centaurea stoebe* seedling abundance at the end of the second experimental year 2011 (gray) and at the end of the third year 2012 (black) in Switzerland (A), and in fall of the second experimental year 2005 (gray) and in spring of the third year 2006 (black) in Montana (B).

Thus, the climatic conditions at the experimental site in Switzerland may interact with the presence of coevolved competitors in suppressing recruitment of *C. stoebe*.

The successful invasion by *C. stoebe* in the introduced range may further be modified by genetic factors of the invader. Postintroduction evolutionary changes in North American *C. stoebe* were found to contribute to their invasion. In monocultures, Hahn et al. (2012) found increased seedling recruitment of North American *C. stoebe*, which was explained by increased seed size in introduced populations associated with increased seed viability and seedling emergence rates as compared with European *C. stoebe* (Hahn et al., 2013).

Another possibility is that the lack of natural enemies that attack *C. stoebe* seeds in the soil or at the seedling stage in the invaded North American grasslands may explain its increased recruitment there (Keane and Crawley, 2002; Colautti et al., 2004). Several studies (Callaway et al., 2004; Maron et al., 2014) have found different plant–soil feedback processes between *C. stoebe* and soil biota at home compared with its introduced North American range, suggesting that in the introduced range *C. stoebe* escapes at least partially from soil pathogens. However, we found good establishment of *C. stoebe* in the empty subplots, indicating that the presence of natural enemies, different soil pathogens, postintroduction evolution or seed quality are not the main factors contributing to the failure of establishment of *C. stoebe* in the mixed species assemblages at home, unless these factors differ fundamentally between the empty subplots and those with experimental plant assemblages.

Biogeographic studies can elucidate how the different ecological interactions between the home and introduced ranges affect biotic resistance during the establishment phase of biological invasions. Our results provide evidence that native plant diversity does not play a major role in suppressing *C. stoebe* during the establishment phase. However, the biogeographic pattern of differential establishment success of *C. stoebe* likely reflects greater competitive resistance to *C. stoebe* in Switzerland than Montana. Although the design of this comparative study does not allow us to disentangle the relative importance of the various potential drivers, we propose that the more intense competitive environment in Switzerland may be due to both characteristics of the resident community and how it interacts with local abiotic conditions to influence aboveground productivity and hence competition for light. This study therefore provides additional evidence that the biogeographic origin of species does indeed matter for understanding biological invasions.

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