

Conyza canadensis suppresses plant diversity in its nonnative ranges but not at home: a transcontinental comparison

Manzoor A. Shah¹, Ragan M. Callaway², Tabasum Shah¹, Gregory R. Houseman³, Robert W. Pal^{2,4}, Sa Xiao^{2,5}, Wenbo Luo⁶, Christoph Rosche⁷, Zafar A. Reshi¹, Damase P. Khasa⁸ and Shuyan Chen^{2,5}

¹Department of Botany, University of Kashmir, Srinagar, 190 006 Jammu & Kashmir, India; ²Division of Biological Sciences and the Institute on Ecosystems, The University of Montana, Missoula, MT 59812, USA; ³Department of Biological Sciences, Wichita State University, Wichita, KS, USA; ⁴Faculty of Sciences, University of Pecs, Ifjúság, 6, H-7624 Pecs, Hungary;

⁵Key Laboratory of Cell Activities and Stress Adaptations (Ministry of Education), School of Life Science, Lanzhou University, Lanzhou, Gansu, People's Republic of China;

⁶Key Laboratory for Wetland Ecology and Vegetation Restoration, Northeast Normal University, Changchun 130024, China; ⁷Institute of Biology/Geobotany and Botanical Garden, Martin Luther University of Halle-Wittenberg, D-06108 Halle/Saale, Germany; ⁸Centre for Forest Research and Institute for Systems and Integrative Biology, Université Laval, Quebec City, QC G1V0A6, Canada

Summary

Author for correspondence:
Manzoor A. Shah
Tel: +11 91 9596191292
Email: mashah75@yahoo.com

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- The impact of invasive species across their native and nonnative ranges is poorly quantified and this impedes a complete understanding of biological invasions.
- We compared the impact of the native North American plant, *Conyza canadensis*, which is invasive to Eurasia, on species richness at home and in a number of introduced regions through well replicated transcontinental field studies, glasshouse experiments and individual-based models.
- Our results demonstrated mostly negative relationships between *C. canadensis* abundance and native species richness in nonnative ranges, but either positive or no relationships in its native North American range. In glasshouse experiments, the total biomass of *Conyza* was suppressed more by species from its native range than by species from regions where it is nonnative, but the effects of *Conyza* on other species did not show a consistent biogeographical pattern. Finally, individual-based models led to the exclusion of *Conyza* from North American scenarios but to high abundances in scenarios with species from the nonnative ranges of *Conyza*.
- We illustrate biogeographical differences in the impact of an invader across regional scales and suggest that inherent differences in one specific aspect of competitive ability, tolerance to the effects of other species, may play some role in these differences.

Introduction

Exotic, invasive plants can have strong negative effects on community structure in their nonnative ranges, but the magnitude of these effects varies markedly among species and the system examined (Jäger *et al.*, 2007; Brewer, 2008; Hejda *et al.*, 2009; Davies, 2011; Vilá *et al.*, 2011). The magnitude of the impacts on native diversity caused by exotic invaders can also vary substantially between their native and nonnative ranges for reasons that are poorly understood (Callaway *et al.*, 2011a; Inderjit *et al.*, 2011a, b; Kaur *et al.*, 2012). For example, a recent literature review found that in the United States six times more nonnative species have been formally classified as 'invasive' or noxious than native species, and that exotic species are 40 times more likely than a native species to be perceived as invasive (Simberloff *et al.*, 2012). However, approaches that rely on perceived effects or classification schemes both lack a strong quantitative basis and this limits our ability to directly compare the ecology of invaders among native and nonnative ranges. Therefore, direct quantitative

measurements of the community impacts of invasive species across a range of within-region and between-region scales are crucial (Hierro *et al.*, 2006; Xiao *et al.*, 2013).

Exotic invaders appear to achieve disproportional dominance in their nonnative ranges through many mechanisms (Levine *et al.*, 2003; Hierro *et al.*, 2005, 2006; Callaway *et al.*, 2008; Lankau *et al.*, 2009; Lankau, 2012), but biogeographical differences in relative competitive ability contribute at least partly to suppression of natives by invaders following invasion (Vilá & Weiner, 2004; Maron & Marler, 2008a; He *et al.*, 2009; Callaway *et al.*, 2011b; Inderjit *et al.*, 2011a). However, competitive abilities are often inferred from the outcomes of invasions rather than independent experiments that measure competition (but see Callaway *et al.*, 2012). When superior relative competitive abilities of invaders are expressed in nonnative ranges, they may be exerted through equal per-capita effects but much higher abundances (Schooler *et al.*, 2006; Vilá *et al.*, 2011), or through stronger per-capita effects in their nonnative ranges than in their native ranges (Callaway *et al.*, 2011a; Inderjit *et al.*, 2011b). For

example, Callaway *et al.* (2011a) found that the abundance of *Acroptilon repens* in North America, where it is invasive, was almost twice that in Uzbekistan, where it is native. However, this difference in abundance translated to 25–30 times lower biomass of native species in *Acroptilon* stands in North America than in Uzbekistan. This difference in impact corresponded with inherently stronger competitive and allelopathic effects of *A. repens* on North American species than on species native to Uzbekistan (Ni *et al.*, 2010). Similar comparisons between native and nonnative ranges have been reported for the allelopathic effects of other invasives, including *Ageratina adenophora* (Inderjit *et al.*, 2011b), *Centaurea stoebe* (Thorpe *et al.*, 2009), *Centaurea diffusa* (Callaway & Aschehoug, 2000), *Prosopis juliflora* (Kaur *et al.*, 2012), *Foeniculum vulgare* (Colvin & Gliessman, 2011), the red algae *Bonnemaisionia hamifera* (Svensson *et al.*, 2013), *Chromolaena odorata* (Qin *et al.*, 2013), and in a meta-analysis of invasive tree species (Lamarque *et al.*, 2011).

Here we compare the impact of the native North American plant, *Conyza canadensis* (Asteraceae, = *Erigeron canadensis*, commonly known as Canadian horseweed), which is either naturalized or is invasive in many other parts of the world, on species richness at home and in a number of regions where it has been introduced. *Conyza* provides an interesting case study, because unlike many invaders which can be relatively uncommon in their native ranges, *Conyza* could be considered to exhibit ‘invasive’ behavior in its native range. In parts of North America, *Conyza* is a persistent problem in agricultural fields and disturbed areas. However, the limited results available suggest that *Conyza* might behave as an early successional species in North America, going from a dominant immediately after disturbance to completely absent in < 10 yr (Baker & Wilson, 2004). Studies of invasive species often focus on species that undergo dramatic increases in abundance in their nonnative ranges (Inderjit *et al.*, 2011b; Kaur *et al.*, 2012). By contrast, *Conyza* appears to exhibit varying impact both in its native range and in its introduced range, offering a unique opportunity to examine biogeographical differences in ecological parameters for a species that might be considered a pest, or perhaps ‘invasive’, in its native range.

Well-replicated field studies that span native and nonnative ranges have the potential to quantify patterns that yield insight into exotic invasion; however, these correlative patterns do not provide strong evidence of whether competitive mechanisms can explain such patterns. Individual-based models, which have the capacity to sort out hypothetical priorities from complex community information (Grimm & Railsback, 2005; Xiao *et al.*, 2009, 2010; Michalet *et al.*, 2011), provide an alternative approach to dig deeper into such patterns. In our case, most importantly, these models allow exploration of the relative importance of competitive suppression (the effect of *Conyza* on other species) and competitive tolerance (the response of *Conyza* to other species). Our primary questions were as follows: does increasing *C. canadensis* abundance correlate with greater reductions in native species richness in its nonnative than in its native ranges; and do competitive interactions between *Conyza* and species from its native range differ in intensity from those between *Conyza* and

species from its nonnative ranges? We tackled these questions with transcontinental field studies, glasshouse experiments, and individual-based models that were parameterized with the results from the glasshouse experiments.

Materials and Methods

Study species

Conyza canadensis (L.) Cronquist is an annual in the Asteraceae with a wide native range in North America and an even wider nonnative range in a number of Eurasian countries where it has become invasive. In its native range, *Conyza* is a weed resistant to herbicides, such as glyphosate, that occurs along roadsides and other disturbed areas and commonly encroaches into agricultural fields, where it can reach very high densities and reduce crop yields (Bruce & Kells, 1990; Bhowmik & Bekech, 1993). This self-compatible and autogamous species (Hao *et al.*, 2011) was introduced from North America into Europe almost 300 yr ago, where it has successfully naturalized and become one of the region’s most abundant plant species (Thebaud & Abbott, 1995). *Conyza* is one of the 10 most widespread species in China (Hao *et al.*, 2011) and there, too, it is most abundant in disturbed areas (Weber *et al.*, 2008). However, *Conyza* frequently colonizes extensively into native communities in China (S. Xiao *et al.*, pers. obs.). *Conyza* appears to have invaded the Kashmir region of northern India much more recently, probably during World War II (Salisbury, 1942), and has invaded relatively intact native communities as well as disturbed areas (M. Shah, pers. obs.). The rapid global expansion of *Conyza* has been attributed to the production of massive amounts of small, wind-dispersed seeds (> 200 000 seeds per plant), high resistance to diseases and herbicides (Weaver, 2001), allelopathy (Shaukat *et al.*, 2003), and association with mycorrhizal fungi (Shah *et al.*, 2009).

Field patterns

We examined nine field sites across the native range of North America and 12 sites across the nonnative ranges of Europe, China and Kashmir, India (Supporting Information, Table S1). These ‘sites’ varied dramatically in area because *Conyza* populations can be quite concentrated at a site, allowing sampling to be completed in areas of c. 0.1–1 ha, or populations may be distributed and somewhat continuous over many square km (see Table S1). Nineteen of our 21 sites were similar in the general area sampled (0.1–1 ha), whereas two were unusual. At the Turnbull site (WA, USA), *Conyza* only occurred near the road, probably because of the pristine nature of the vegetation away from the road. Thus we sampled small patches of *Conyza* that occurred along 9 km of road. Plots were sampled over c. 100 km² of Hungary and compiled into one very large ‘site’, because no single small area was sampled with enough replication to examine it separately. In all cases, we avoided sites in which *Conyza* co-occurred with only exotic weeds, and chose sites in which *Conyza* co-occurred with at least some species native to the region. In North America this was a challenge because we found *Conyza* to

co-occur more commonly with nonnative weedy species in very disturbed areas than with other North American natives. In Hungary, where we first explored the sampling protocol, we used 2×2 m plots and sampled 133 plots regionally. After observing that similar patterns were expressed at smaller scales, we then used 1×1 m plots and sampled 15–30 plots at another 20 sites. For example, in Kashmir, even moderate *Conyza* cover corresponded with far fewer native species than in *Conyza*-free plots and therefore our sample size within a site was smaller. Across our 21 sites, the total cover of vegetation ranged from 50 to 100%, based on our visual and subjective estimates, and did not vary substantially between the ranges. Our goal was to determine if *Conyza* cover correlated with the diversity of other species, and not to estimate the relative abundances of species in general, and thus plots were not located randomly but, rather, haphazardly to maximize variation in *Conyza* cover, from zero to the highest densities we could find. At all but one site, *Conyza* cover was recorded using either quadrats gridded into 100 squares, with relative cover calculated as the number of squares containing any above-ground part of a *Conyza* plant, or visually with nongridded quadrats into 5% class groups ranging from 0 to 80% cover (see Table S1 for details on sampling). At the Quebec City site (Canada), the abundance of *Conyza* was measured by counting the number of mature plants in a plot. We then performed separate linear regressions for each site to examine the relationship between the abundance of *Conyza* and the number of native species in plots (SigmaPlot 12.0; San Jose, CA, USA).

Competition experiments

We compared the competitive interactions between *Conyza* and species native to North America with those between *Conyza* and species native to China, Europe, and Kashmir. Because we initially had problems acquiring seeds of species from Kashmir, we did this in two separate experiments. In the first experiment, we conducted competition trials using *Conyza* and six species native to North America, six native to Europe, and six native to China (Table S2). Species were chosen that commonly co-occurred with *Conyza* in the field in order to mimic natural field scenarios of species combinations and interactions in the glasshouse experiments. Species from North America occurred at a minimum of four sites, species used from China occurred in at least two of the four sites, and species from Europe occurred in 10–30% of the plots in Hungary. We used only North American *Conyza* in the glasshouse experiments (see the Discussion section). **Treatments were as follows: *Conyza* grown alone ($n = 24$); individuals of each of these 18 species grown alone (for each species $n = 8$; total $n = 144$); and eight individuals of each of these species grown with *Conyza* ($n = 144$).** Plants were grown in 500 cm^3 rocket pots in a glasshouse at the University of Montana, USA. Each pot was filled with 0.15 l pure silica sand (100–600 μm particle size) at the bottom of the pots and 0.45 l of a mixture of the same sand and potting soil (1 : 1) above the lower layer of sand. Before seeding, all seeds were surface-sterilized using 5% sodium hydrochloride in distilled water for 10–15 min, followed by rinsing with distilled water. Ten seeds of each species were sown in each pot,

and immediately after germination seedlings were thinned to a single individual in each pot where *Conyza* and other competitor species were grown alone, and two individuals (*Conyza* and the competitor species) in which they were grown together. Plants were grown in a naturally lighted glasshouse supplemented by 1000 W metal halide lights from 08:00 to 22:00 h from April to June 2012. Pots containing pairs of species were randomly placed on glasshouse benches and rotated among the benches once per week. All pots were watered daily for the first month and every other day thereafter. All plants were fertilized with 250 ml Miracle-Gro at 0.34 g l^{-1} every 4 wk. Plants were grown for 11 wk and then harvested. After harvesting, the plants were dried at 60°C for 4 d and then weighed.

In the second experiment, we conducted competition trials using *Conyza* and six species native to North America (all different species than in the first experiment) and three species (after a large number of germination failures) native to Kashmir (Table S2). Again we chose species that commonly co-occurred with *Conyza*; all three occurred at all sites. The experimental substrate, glasshouse, lighting, fertilizer, and watering conditions were the same as in the first experiment, and **we had 30 *Conyza* individuals grown alone as controls, 12 replicates of each of the 12 competitor species grown alone, and 12 replicates of each competitor species grown with *Conyza*.** Plants were grown for 17 wk and then harvested. After harvesting, the plants were dried at 60°C for 4 d and then weighed. *Conyza* used in both the glasshouse experiments was of North American origin.

We used the results for the total biomass of plants in the competition experiments to calculate relative interaction intensity (RII) values following Armas *et al.* (2004) as a measure of the competitive effects of *Conyza* on other species ('effect') and of the competitive effects of other species on *Conyza* ('response'). RIIs are centered on zero, with values between 0 and -1 indicating negative interactions (competition), and those between 0 and $+1$ indicating positive interactions (facilitation). We compared the mean competitive effects and responses for *Conyza* when interacting with North American natives with those for *Conyza* when interacting with natives to China and Europe as a group with one-way ANOVA using SPSS 20.0 for MacOSX (IBM Corp, 2011). Because we tested interactions between *Conyza* and species native to Kashmir (and again species from North America) in a separate experiment, we analyzed these results in a separate one-way ANOVA.

We also tested the potential for phylogenetic similarity to confound the results from the competition experiments. We constructed phylogenetic trees of internal transcribed spacer (ITS) and *rbcL* gene sequences from the GenBank database using three methods: neighbor-joining (NJ), maximum parsimony (MP) and maximum likelihood (ML) of the MEGA 5.2 software (Tamura *et al.*, 2011). However, we chose the ML method (Fig. S1) to rank species because of its robustness and this method seeks the tree that makes the data most likely. We then ranked the species in each of the experiments by their phylogenetic relatedness to *Conyza* and then correlated the phylogenetic rank of species with their RII value for competitive tolerance and effect in each experiment.

Individual-based models

To estimate the potential for competitive tolerance (response) and suppression (effect) of *Conyza* to affect relative abundances of other species differently in the native and nonnative ranges, we used the RIIs for competitive effects and responses for *Conyza* that were derived from the two competition experiments to build four different individual-based spatially explicit dual-lattice models of relative species abundance, one for each of the four regions from which we acquired species (Travis *et al.*, 2005, 2006; Michalet *et al.*, 2011). Most importantly, these models allowed us to explain the relative importance of the differences in competitive effects and responses we found in our competition experiments.

In our model *Conyza* occupied one two-dimensional lattice of 100×100 cells while native species occupied an overlapping two-dimensional lattice of the same size. Each individual of *Conyza* and each individual of the different native species occupied only one cell of the two lattices. Individuals produced propagules identical to the parent, and reproductive rates of *Conyza* (r_C) and all native species (r_N) were assumed to be the same. Propagules of all species were dispersed randomly to empty patches within the appropriate lattice. Propagules could only establish in empty cells and the one arriving first occupied the cell. Because we had no empirical information about intraspecific competition for any species or interspecific competition among natives, our dual-lattice model allowed competition between *Conyza* (lattice 1) and all other native species (lattice 2), but there was no RII-derived competition within a lattice. Instead, as mortality made a cell available, it was recolonized in proportion to the abundance of surviving *Conyza* or other species through 'lottery competition' (Sale, 1979; Busing & Brokaw, 2002). Thus, there was competition among individuals within the same lattice for empty cells with the presumption that they had equivalent competitive abilities for space. We used a 'wraparound' (torus) approach to avoid edge effects (Yamamura *et al.*, 2004). We assumed that the competitive effects of native species would decrease *Conyza* survival rate linearly as the RII values of native species on *Conyza* increased. Therefore, the survival rate of *Conyza* was:

$$S_C = S_{C_{\max}} - \text{RII}_{N \text{ on } C}$$

when it overlapped with native species i

$$S_C = S_{C_{\max}}$$

when it overlapped with an empty cell.

$S_{C_{\max}}$ was the maximum survival rate of *Conyza* and we assumed $S_{C_{\max}}$ was the same for *Conyza* in different biogeographical regions.

We assumed that the competitive effects of *Conyza* on native species would also decrease their survival rates linearly with the increase in RII value of *Conyza* on native species. Therefore, the survival rate of native species i was:

$$S_{Ni} = S_{N_{\max}} - \text{RII}_{C \text{ on } Ni}$$

when it overlapped with *Conyza*

$$S_{Ni} = S_{N_{\max}}$$

when it overlapped with an empty cell,

where $S_{N_{\max}}$ is the maximum survival rate of native species and we assumed $S_{N_{\max}}$ is the same for all native species in different areas.

We used asynchronous updating in the model. First, a single individual of *Conyza* or native species was selected at random and subsequently we determined whether the individual survived at a certain survival rate (with a survival probability S_C and S_{Ni} for *Conyza* and the native species, respectively). If the individual survived, it reproduced and dispersed propagules, as described earlier. Each time step was made up of $N_C + N_N$, where N_C and N_N refer to the number of all individuals of *Conyza* and all individuals of the native species, respectively.

Because the initial population size of invaders is likely to be relatively small at the beginning of invasions, all simulations were started with 100 individuals of *Conyza*. Also, to roughly mimic the process of invasion, initial conditions were started with communities saturated with native species, each having the same number of individuals. At the beginning, all individuals of *Conyza* and native species were randomly dispersed across their own lattices. Simulations were run for 10 000 time steps in order to allow the system to stabilize. All measurements were determined as the mean values of 100 independent replicate runs for each time step. Parameters used in simulations were as follows: $r_C = 1$, $r_N = 1$, $S_{C_{\max}} = 0.8$, $S_{N_{\max}} = 0.8$, and the RII values for the interactions between *Conyza* and native species. Simulations were performed in NetLogo (Wilensky, 1999), a powerful multi-agent modeling language that is particularly well suited for modeling complex systems that develop over time. The robustness of the model was tested with different combinations of parameters, such as starting abundances, survival rates, and reproductive rates, and the results were qualitatively the same as for the combinations chosen here (data not shown).

The models built for North America, Europe, and China used RIIs from the first experiment, whereas the model built for Kashmir used RIIs from the second experiment.

Results

Field patterns

In North America, the native range of *Conyza*, there was no significant negative relationship between *Conyza* cover and native species richness at any of the nine sites (Table S1; Fig. 1). At one site in the native range (Hill City, South Dakota), there was a positive relationship between *Conyza* cover and native richness. At the Quebec City site there was a significant positive relationship between the number of *Conyza* individuals and native species richness. In the nonnative region of the Himalayan Kashmir in India, all five sites showed very strong and significant negative relationships between *Conyza* cover and native species richness. The three sites in Europe also showed similar negative relationships between *Conyza* abundance and native species richness. Of

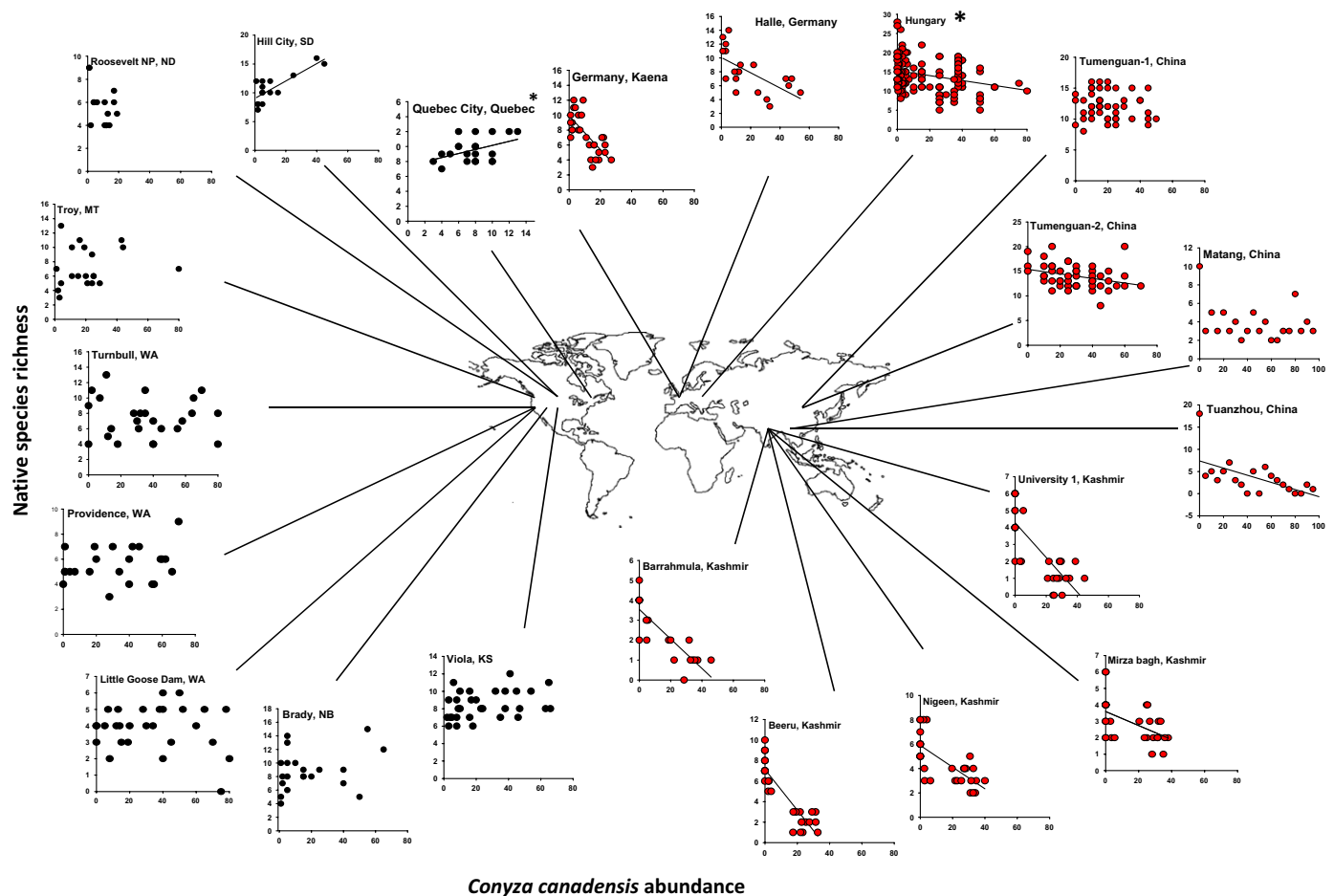


Fig. 1 Biogeographical comparison of the relationship between *Conyza canadensis* cover and native species richness in native (black symbols) and nonnative regions (red symbols). In all graphs, the x-axes show the abundance of *Conyza* measured as cover at all sites, but Quebec City, in Canada, where *Conyza* abundance was measured as density. The y-axes show native species richness. The asterisk for Hungary is to emphasize that this regression represents plots compiled over much of western Hungary, whereas all other sites were c. 1–3 ha in size. Regression lines are present when they are significant (see Table S1).

the four sites in China, two showed no relationship between *Conyza* cover and native diversity; whereas at the two other sites the relationship was significantly negative. In a comparison of slopes, whether significant or not, the mean slope for the sites in the native range was $+0.015 \pm 0.024$, which was significantly different from that for the nonnative ranges (-0.097 ± 0.019 ; t -test, $t = 3.567$; $df = -1, 20$; $P = 0.003$).

Competition experiments

In the first experiment comparing interactions between *Conyza* and species from North America or species from China and Europe, we found that *Conyza* suppressed (competitive effect) North American species more strongly than species from China or Europe (Fig. 2b). The mean RII for the competitive effect of *Conyza* on North American natives was -0.62 ± 0.07 , compared with an RII of -0.38 ± 0.07 on European natives, and an RII of -0.34 ± 0.08 on native species from China (ANOVA; $F_{\text{region}} = 16.37$; $df = 2174$; $P < 0.0001$; North America > Europe and North America > China at $P < 0.01$, using

Tukey's *post hoc* tests). By contrast, *Conyza* was more suppressed (competitive response) by North American species than by species from the nonnative ranges (Fig. 2a). The mean RII for the competitive response of *Conyza* to North American native species was -0.55 ± 0.06 , compared with an RII of $+0.02 \pm 0.16$ in response to European natives, and an RII of -0.38 ± 0.10 in response to native species from China (ANOVA; $F_{\text{region}} = 14.37$; $df = 2174$; $P < 0.001$; North America < Europe and North America < China at $P < 0.01$ in Tukey's *post hoc* tests).

In the second experiment comparing interactions between *Conyza* and species from North America or Kashmir, we found that *Conyza* suppressed species from Kashmir more strongly than species from North America and was also much more suppressed by North American species than by species from Kashmir (Fig. 3). The mean RII for the competitive effect of *Conyza* on North American natives was far lower than in the first experiment, at -0.06 ± 0.03 , compared with an RII of -0.36 ± 0.07 on natives of the Kashmir (ANOVA; $F_{\text{region}} = 23.37$; $df = 1107$; $P < 0.0001$). The mean RII for the competitive response of

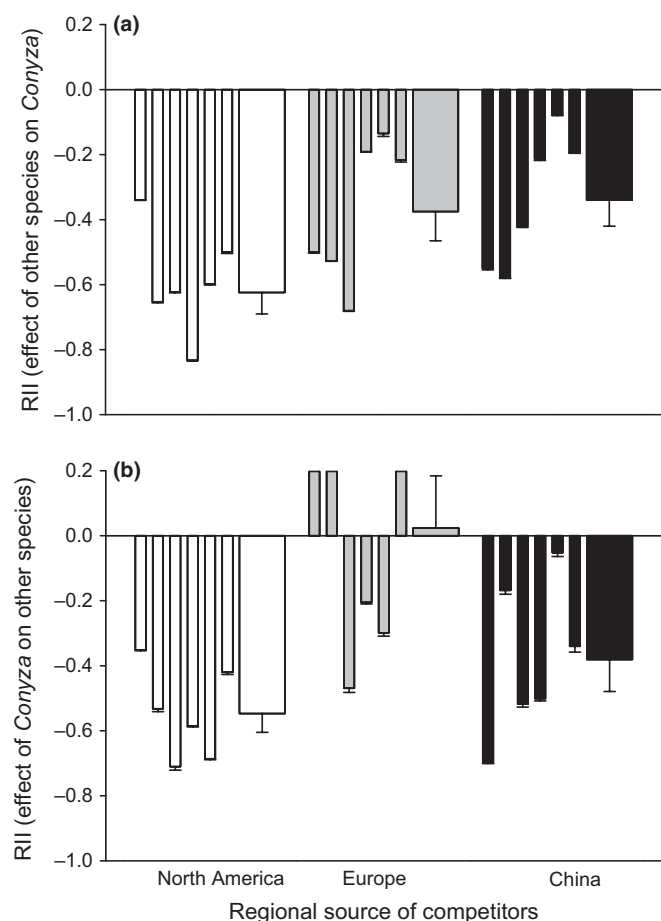


Fig. 2 Competitive effects (a) and responses (b) of *Conyza canadensis* with species from North America, Europe and China. Narrow bars show the means for individual species and wide bars show the means for a region, with error bars representing 1 SE. The species for each country are listed in Table S2, with the order from the top in the table being the order from left to right in the figure. RII, relative interaction intensity.

Conyza to North American native species was -0.54 ± 0.02 , compared with an RII of -0.19 ± 0.04 in response to native species from the Kashmir (ANOVA; $F_{\text{region}} = 69.05$; $df = 1102$; $P < 0.0001$).

When we compared RIIs for all 12 North American species used in experiments with those for all 15 species from nonnative ranges, the competitive effects of *Conyza* on other species did not differ among ranges (-0.32 ± 0.09 vs -0.36 ± 0.05 ; $P = 0.986$), whereas the competitive effects of North American species on *Conyza* were much stronger than the effects of species from nonnative ranges (-0.54 ± 0.03 vs -0.19 ± 0.09 ; $P = 0.004$).

Importantly there was no relationship in either experiment between the phylogenetic rank of species competing with *Conyza* and RII. In the first experiment, the relationship between phylogenetic rank and RIIs for the effect of *Conyza* on other species was $R^2 = 0.01$, $P = 0.774$, and that for the response of *Conyza* to other species was $R^2 = 0.05$, $P = 0.373$. In the second experiment, the relationship between phylogenetic rank and RIIs for the effect of *Conyza* on other species was $R^2 = 0.01$, $P = 0.791$, and that for the response of *Conyza* to other species was $R^2 = 0.08$, $P = 0.164$.

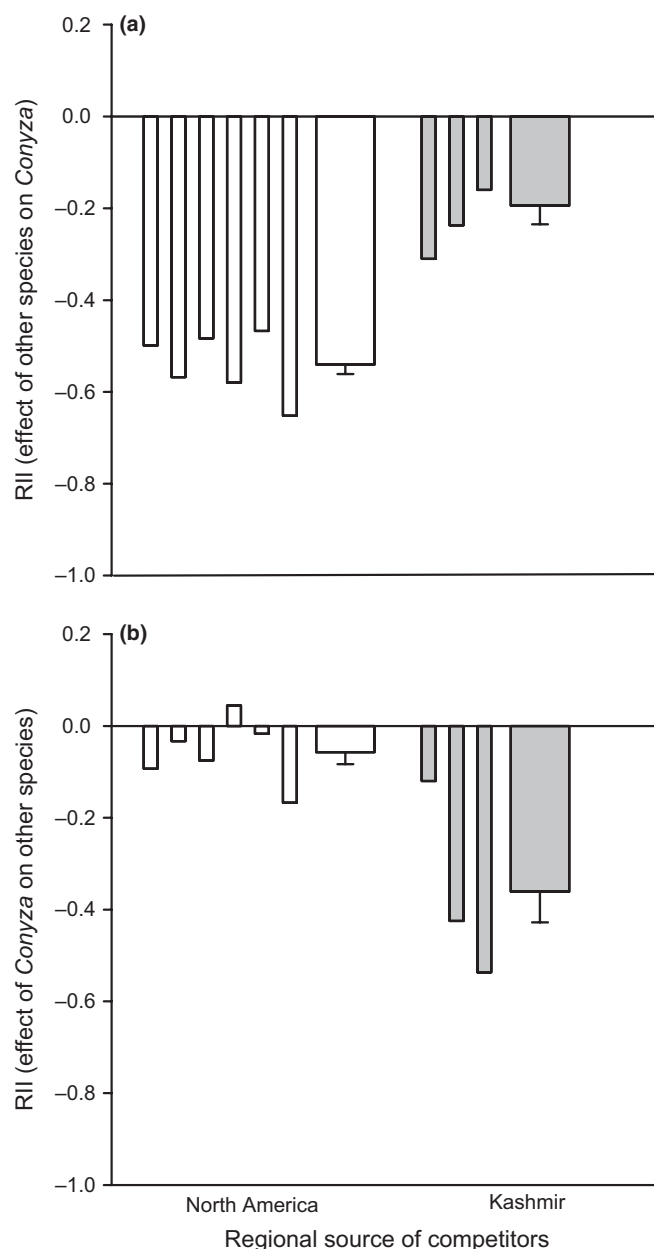


Fig. 3 Competitive effects (a) and responses (b) of *Conyza canadensis* with species from North America and the Kashmir region of the Himalaya, India. Narrow bars show the means for individual species and wide bars show the means for a region, with error bars representing 1 SE. The species for each country are listed in Table S2, with the order from the top in the table being the order from left to right in the figure. RII, relative interaction intensity.

Individual-based models

When competitive suppression (the effect of *Conyza* on other species) and competitive tolerance (the response of *Conyza* to other species) were given equal weight and all other factors kept equal in individual-based models, *Conyza* was excluded from the North American scenario but became codominant in each of the scenarios for the three nonnative ranges (Fig. 4). All native species coexisted with each other at roughly similar abundances in North

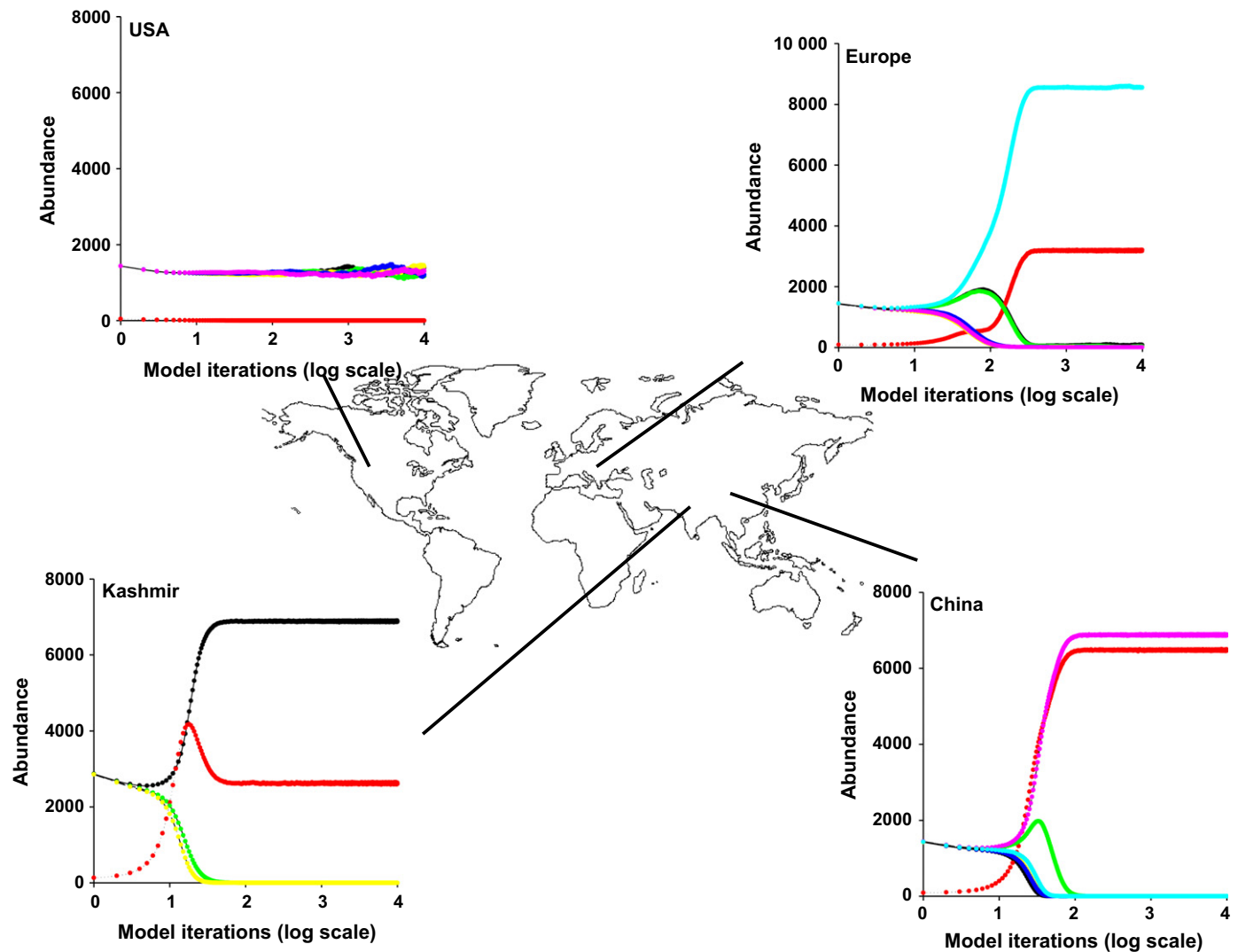


Fig. 4 Individual-based spatially explicit dual-lattice model depicting potential scenarios for the competitive effects and responses of *Conyza canadensis* with species native to North America, China, Europe, and Kashmir, India, using the relative interaction intensity (RII) values derived from the competition experiments. The red line in each graph represents *Conyza canadensis*, whereas the other lines represent the other species in the competition experiments.

America after the exclusion of *Conyza*. Importantly, the North American model was based on RIIs from the first competition experiment, and thus provided a scenario far more favorable to *Conyza* than if we used RIIs from the second experiment. In the scenario for China, only *Hemerocallis minor* remained in the models. In the European scenario *Brachypodium pinnatum*, *Dactylis glomerata* and *Molinia coerulea* survived at low abundances and *Epilobium hirsutum* remained in the scenario at a higher abundance than *Conyza*. In sum, we found that the ability of *Conyza* to tolerate (response) competition from other species was more important than its ability to suppress other species.

Discussion

Our most striking and important result was the lack of any negative correlation between *Conyza* abundance and native species richness in the native range of the weed, yet many strong negative relationships between abundance and native diversity in the

nonnative ranges of *Conyza*. In the native range of *Conyza*, we found no significant negative relationships between the cover of *Conyza* and the diversity of native species at any of the nine sites, and two positive relationships, whereas in the nonnative ranges of *Conyza* we found significant negative relationships at 10 of the 12 sites. Furthermore, the slopes of the relationship between *Conyza* abundance and local species richness were significantly more negative in the nonnative ranges than in the native range. This suggests a substantially stronger apparent impact of *Conyza* on co-occurring species in its nonnative range than in its native range. This stronger apparent impact from correlational patterns in the field corresponded with one aspect of our competition experiment, the almost three times stronger suppression of *Conyza* by North American native species than by species native to the invaded ranges of *Conyza*. It is important to note that we have not inferred competitive abilities from the outcome of invasion, but independently measured competition. However, we also note as a caveat that although North American species

consistently strongly suppressed *Conyza*, the biogeographical results from our two experiments were not the same. In the first we did not find strong suppression of species from the nonnative ranges by *Conyza*, whereas in the second experiment we did. This variation was probably a result of the very small proportion of the potential species pool used in our experiments and of differences in the growing conditions of the experiments that we could not control.

Other factors must certainly contribute to the biogeographical patterns reported here, but our results are consistent with the idea that the natural history of coevolution among plant species in communities might alter the ways in which they compete (Callaway & Aschehoug, 2000; Thorpe *et al.*, 2011). It is important to note that we used only North American *Conyza* in the glasshouse experiments, which avoided any potential effects of adaptation by *Conyza* in the nonnative ranges. If indeed *Conyza* has evolved in ways that attenuate its competitive effects in nonnative ranges, we may have measured the impact of a newly invading genotype which may not be entirely representative of the species in general. If so, we would expect weaker competitive effects and stronger responses by *Conyza* to species from the nonnative ranges if we had used *Conyza* genotypes from the nonnative ranges. A second caveat is that wide differences in sites and investigators led to some differences in the field sampling. For example, a far larger area was sampled in Hungary, which could potentially influence the patterns reported there. Nevertheless, over a wide array of sites, clear patterns emerged between the native (North America) and invaded (Eurasia).

We regressed the richness of other species against *Conyza* abundance across a very heterogeneous array of sites that varied in the number of plots sampled, the sampled area, the degree of disturbance, local species pools, and the proportion of exotics and natives present. On the one hand, the very clear biogeographical differences in the apparent impact of *Conyza* on other species despite this variation suggest that these differences are robust. On the other hand, there is a great deal of potential for this heterogeneity to confound our results. In this context, we explored how the *Conyza*–richness relationship might vary with different site characteristics and found that the slopes of the regressions for 18 of the 21 sites (three sites were excluded because the necessary characteristics were not measured) were not significantly related to the total number of species sampled in plots across all sites, an estimate of local species pool ($R^2 = 0.003$, $P = 0.984$). Nor were slopes correlated with the proportion of native species relative to exotic species at a site, with an estimate of disturbance and the history of a site ($R^2 = 0.117$, $P = 0.179$), with the total summed area of all plots at a site ($R^2 = 0.043$, $P = 0.570$), or with the estimated area of the entire site sampled ($R^2 = 0.045$, $P = 0.584$). This does not eliminate the likelihood of site conditions affecting our field results, but the basic biogeographical differences reported here appear to be robust.

Conyza potentially has greater impacts in its nonnative ranges through several different but nonmutually exclusive mechanisms. First, although our measurements of cover provided some standardization between the ranges, it is possible that cover as we measured it masked some differences in abundance between the

ranges. For example, if *Conyza* plants were taller in the nonnative ranges, we may have underestimated their biomass relative to the native range. Thus, it is possible that stronger impacts in its nonnative ranges were in part a result of greater *Conyza* biomass, which was not reflected in our measurements of cover. Secondly, there is evidence that *Conyza* is allelopathic (Shaukat *et al.*, 2003), and differences in impact and competitive outcomes might be the result of stronger allelopathic effects on nonadapted species in the nonnative ranges – the ‘novel weapons hypothesis’ (Callaway & Aschehoug, 2000; Vivanco *et al.*, 2004; Qin *et al.*, 2013; Svensson *et al.*, 2013). Thirdly, greater impact in the nonnative ranges in the field could be the result of strong indirect effects manifested through soil biota or consumers. *Conyza* is highly mycorrhizal and reduces arbuscular mycorrhizal (AM) diversity in soils in the Himalayan Kashmir (Shah, 2010; Shah *et al.*, 2010). AM diversity in soils is considered to be one of the important drivers of above-ground plant diversity and productivity (van der Heijden *et al.*, 1998), and thus invasion-induced decline in AM diversity could be linked to the impact of *Conyza* on native plant richness (see Callaway *et al.*, 2008). However, biogeographical differences in mycorrhizal interactions could not have explained our results in the competition experiments, which used soil that had been sterilized before the experiment.

Conyza at home appears to behave as an early successional weedy species and can go from a dominant immediately after disturbance to completely absent in < 10 yr in agricultural fields and disturbed areas (Baker & Wilson, 2004). Whether *Conyza* behaves in a similar way in any of its nonnative ranges is not well documented, but populations of *Conyza* in Kashmir and China appear to have been quite stable for at least a decade (W. Luo & M. Shah, pers. obs.). Nevertheless, weedy behavior coupled with efficient dispersal and a broad native range very likely predisposes *Conyza* to be abundant in both native and nonnative regions (Pyšek *et al.*, 2009; Dawson *et al.*, 2012; Shah *et al.*, 2012; Lavoie *et al.*, 2013). Also, the characteristic small seed mass, which facilitates efficient dispersal and invasiveness at continental and regional scales (Hamilton *et al.*, 2005), seems to be critical for range expansion by *Conyza*, as its seed dispersal has been reported to easily exceed 500 km in a single dispersal event (Shields *et al.*, 2006).

In Kashmir, when *Conyza* cover reached 40–50%, very few native species remained in plots. However, plots with high *Conyza* cover often had many other exotic species (data not shown). This pattern could be a result of *Conyza* and other exotics sharing positive responses to disturbance, or these exotics might function in a way that promotes ‘invasion meltdown’, a process by which a group of exotic species directly or indirectly facilitate each other and increase the overall magnitude of impact on native communities (Vitousek & Walker, 1989; Simberloff & Von Holle, 1999; Saccone *et al.*, 2010; Metlen *et al.*, 2013).

We found that North American natives suppressed *Conyza* to a greater extent than natives of Kashmir, China and Europe in glasshouse experiments. This is consistent with studies showing that in one part of its native range *Conyza* is rapidly replaced by other natives during succession (Baker & Wilson, 2004). However, we did not consistently find the opposite – that *Conyza* competitively suppressed species from the nonnative ranges to a

greater degree than those from North America. Invasive species are often assumed to be suppression (effect) specialists (Baker, 1965) and many pairwise experimental studies between invasive plant species and native species (reviewed by Vilá & Weiner, 2004) show that the effect of invasion on native species is usually stronger than the other way around. But despite this evidence and the intuitive sense that a successful invader would have exceptional competitive effects on natives, when these tolerance and suppression effects were given equal weight in individual-based models, *Conyza* was excluded from the North American scenario but was abundant in the nonnative range (Fig. 4). The disproportional importance of tolerance in community-scale outcomes would not be discernible without individual-based modeling and suggests that for invasive species we do not yet fully understand how tolerating competition from natives vs competitive suppression of natives alters community dominance. Our results contribute to a small but growing body of studies in the literature that have explored the relative importance of competitive tolerance and suppression through individual-based models parameterized with interaction strengths derived from experiments (Laird & Schamp, 2006; Allesina & Levine, 2011; Xiao *et al.*, 2013). Our results also support those of MacDougall & Turkington (2004), who reported that competitive tolerance is equally as important as, or perhaps more important than, competitive suppression in invasive success. Further efforts to tease apart competitive effects and responses (Besaw *et al.*, 2011) could help us to better understand the general role of competition in invasion. Useful insights in this regard can be obtained by comparing the competitive effects of phylogenetically related native and invasive species on each other.

Conyza canadensis is an interesting species with which to explore biogeographical differences in impact, because it is highly weedy throughout its global range, including in its native North America (<http://plants.usda.gov/java/profile?symbol=coca5>). Many invaders appear to be ruderal in their native ranges but much more abundant and competitive in their nonnative ranges, but few appear to be as weedy in their native range as *Conyza*. However, our results indicate that despite being weedy, *Conyza* does not exhibit 'invasive' behavior in its native range in terms of driving out native species as it does in some parts of the nonnative range (M. Shah, pers. obs.).

The nature of competition with *Conyza* within and among nonnative ranges may reflect differences in phylogenetic affiliations, local abiotic conditions, or the constituents of recipient communities. Perhaps the most interesting possibility is that phylogenetic differences among geographic regions may also play a role in the competitive impact of *Conyza* between native and nonnative ranges according to the phylogenetic limiting similarity hypothesis, whereby the struggle for existence is stronger between more closely related species. However, we found no relationship between RII for competitive effect or tolerance in either of our experiments.

In addition to species characteristics, the impacts of invaders may attenuate over time in the nonnative range as a result of the accumulation of new enemies, encounters with species-specific competitive suppressors, and the evolution of native organisms

(Hawkes, 2007; Lankau *et al.*, 2009; Diez *et al.*, 2010; Lankau, 2012). *Conyza* was introduced to Europe almost 350 yr ago (Thebaud & Abbott, 1995), and to China *c.* 150 yr ago (Hao *et al.*, 2011), whereas it is thought to have been introduced to the Kashmir region of India *c.* 70 yr ago; the first herbarium record in Kashmir is 1967 (M. Shah, pers. obs.). In some cases, exotic species appear to require some amount of 'lag time' to build up to invasive proportions (Castro *et al.*, 2005; Gravuer *et al.*, 2008), but if the inhibitory effects of invasive species attenuate over time as a result of the accumulation of natural enemies or adaptation by native species (Hawkes, 2007; Lankau *et al.*, 2009; Diez *et al.*, 2010; Lankau, 2012), this might explain stronger impacts of *Conyza* in the more recently invaded Kashmir. Alternatively, *Conyza* may encounter less phylogenetically similar species in Europe and China and these may provide less resistance (Strauss *et al.*, 2006). The positive relationships between *Conyza* abundance and native species richness at two sites in the native range could indicate some form of facilitation (Callaway, 2007) or a parallel response of *Conyza* to microsite conditions that favor it and larger numbers of other species.

Quantifying biogeographical differences in the impacts of invasive species is of central importance to understanding basic ecological and evolutionary processes driving invasions. Overall, our results of well-replicated, cross-continental field studies supplemented with glasshouse experiments present striking biogeographical differences in the impact of *Conyza* and suggest that inherent differences in competitive ability could play a role in these differences. The prediction of exclusion of *Conyza* from native range modeled scenarios but not in nonnative range scenarios by individual-based models further illustrates differences in the behavior of *Conyza* in and away from home. Our results also support a growing body of quantitative results that demonstrate a strong biogeographical context to exotic plant invasions. In other words, evolutionary relationships among plants species might matter a great deal in the context of community ecology (see Brooker *et al.*, 2009; Thorpe *et al.*, 2011) and can affect a number of ways in which species interact with each other.

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Supporting Information

Additional supporting information may be found in the online version of this article.

Fig. S1 Phylogenetic trees of *rbcl* gene sequences from the GenBank database using three methods: neighbor-joining (NJ), maximum parsimony (MP) and maximum likelihood (ML) of the MEGA 5.2 software.

Table S1 Description of study sites and sampling procedures for field patterns of the relationship between *Conyza canadensis* cover and native species richness in native and nonnative regions of *Conyza*

Table S2 Conspectus of species native to different biogeographical regions used in the competition experiments with *Conyza canadensis*

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