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RESEARCH ARTICLE

Biotic Homogenization Caused by the Invasion of *Solidago canadensis* in China

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Abstract

Although studies argue that invasive species can cause biotic differentiation, some cases show that biological invasions actually decrease biodiversity through biotic homogenization. The concept of biotic homogenization through the invasion of a certain serious invasive plant species merit more studies. Hence, we used field surveys to quantitatively compare invasive populations of *Solidago canadensis* (SC) in China with the control sites (adjacent sites to SC present sites yet without the species) and SC native populations in the USA. We found that plant communities in SC invaded habitats shared similarities with those in SC native ranges. Bray-Curtis similarity clearly showed that the composition of plant communities in SC invaded habitats were similar to those in SC native ranges. Both in the native and introduced range, plant communities with SC present were characterized by SC being dominant, significantly lower species richness, α-diversity and β-diversity, as well as a decrease in the correlation coefficient between geographic distance and floristic similarities. SC favors fertile and moist loam habitat, while it dominated in various habitats in China, where more than 20 different dominants should have occurred. In conclusion, serious invasive species can quickly remodel and homogenize diverse communities by dominating them.

Key words: biodiversity, control site, field survey, geographic distance, invasive population, native population, similarity

INTRODUCTION

Globalization and international trade are major contributors to the spread of invasive species around the world, which in turn contributes to global biotic homogenization (Olden 2006; Romagosa *et al*. 2009). Biotic homogenization is a process by which the genetic, taxonomic or functional similarities of regional biotas increase over time (Olden *et al*. 2006; Pino *et al*. 2009). The process by which biological invasions lead to biotic homogenization remains complex and poorly understood (Olden and Rooney 2006; Cassey *et al*. 2007; Olden *et al*. 2008).

Biological invasions cause serious threats to global biodiversity, and many studies clearly show that invasive species can decrease local biodiversity (Li *et al*. 2002, 2012; Levine *et al*. 2003), as well as lead directly to biological homogenization (Oliveras *et al*. 2005; Hansen *et al*. 2009). Examples include the invasion of *Anthriscus caucalis* in Chile (Castro *et al*. 2010) and *Eichhornia crassipes* in lakes worldwide (Masifwa *et al*. 2001). Piazzi and Balata (2008) reported that the invasions of *Caulerpa racemosa* var. *cylindracea* in the Mediterranean Sea caused the significant decrease of α-diversity and variability in taxa composition. In contrast, Murria *et al*. (2008) reported that invasions of *Potamopyrgus antipodarum* in a small Mediterranean

stream showed little influence on local community biodiversity; and Castro and Jaksic (2008) reported that alien plant species do not seem to cause obvious biological homogenization in Chile. Moreover, Qian and Ricklefs (2006) concluded that exotic plants produce differentiation of floras among neighboring areas but homogenization at a greater distance, and introduced species tend to have a more homogenizing (or less differentiating) effect with increasing distances (Qian *et al*. 2008), in particular in large scales (Winter *et al*. 2008). However, Lambdon *et al*. (2008) argued that species invasions could lead to biotic homogenization at small spatial scales. McKinney (2005) demonstrated that species introduced from ecologically similar adjacent regions would have a greater homogenizing effect on community composition than those from more distant regions. These complicated conclusions on the effects that biological invasions may have on biotic homogenization may be attributed to the differences in species groups studied, for example contrasting all alien species in a region *vs*. only those that are serious invaders. Alien species that differ in invasiveness may have quite different influences on biotic homogenization (Qian *et al*. 2010). More serious invaders may directly and quickly cause biotic homogenization (Spyreas *et al*. 2010), while those with lower invasiveness may not (Hickerson *et al*. 2005; Qian and Ricklefs 2006; Qian *et al*. 2008; Winter *et al*. 2008). Therefore, it is of great importance to understand the pattern and mechanism by which invasive species may cause biotic homogenization.

The biotic homogenization caused by *Solidago canadensis* invasions in China may provide one important example of this process. *S. canadensis*, native to North America, was first introduced into eastern China in the 1930s as an ornament plant (Li and Xie 2002). This plant invader exhibits high competiveness over local species and high reproductive output and is locally adapted to a broad range of environmental conditions (Huang *et al*. 2007). Now, it has been characterized as one of the most notorious invasive species in China (Guo *et al*. 2009), creating homogenized landscapes over large areas. However, to date there is no comprehensive research relating *S. canadensis* to biotic homogenization in China, nor on its quantitative distribution and spread across the whole country.

To understand the relationship between *S. canadensis* invasion in China and biotic homogenization, we surveyed the communities in the field invaded by *S. canadensis* in China and compared these with two types of controls: 1) with native, natural communities in the USA with *S. canadensis* present, and 2) exotic, natural communities in China, adjacent to but without *S. canadensis* present.

RESULTS

## Comparisons on species composition and α-diversity

The Chinese sites surveyed were located from 0 to 375 m in elevation, 25.6169°N to 34.7898°N latitude and 106.3701°E to 122.0549°E longitude (Fig. 1). In the 53 China-SC sites, we observed 111 vascular plant species in 89 genera and 30 families. In the 53 control (CK) sites, we found 181 vascular species from 127 genera and 41 families. The 34 sites with *Solidago* species surveyed in the USA were with the elevations ranged from 35 to 564 m, latitude from 39.0133°N to 46.9108°N and longitude from 71.5372°W to 97.6575°W (Fig. 1). Among these 34 sites, we observed 93 vascular species from 69 genera and 29 families. Among the 34 sites surveyed, 26 had *S. canadensis* individuals present.

Species richness among sample quadrats in both China-SC sites (averagely 3.77 species in one quadrat) and US-SC sites (4.12) was significantly lower than those in CK sites (7.26). There is no significant difference between invasive (China-SC) sites and native (US-SC) sites in species richness (Fig. 2).

S. canadensis had the highest ecological important value (EIV) across all China-SC sites which averaged 0.563 *vs*. 0.300 in US-SC sites (Fig. 2). There was only one exception in Yichang, where *S. canadensis* EIV in the site was 0.166, lower than that of *Arthraxon hispidus* (0.250). Nevertheless, in CK sites, the maximum EIV of the dominant on average was 0.196, by far the lowest among the three survey sites. The species with the highest EIV across the CK sites were diversified comprising 23 different species including *Alternanthera philoxeroides*, *Artemisia lavandulaefolia*,
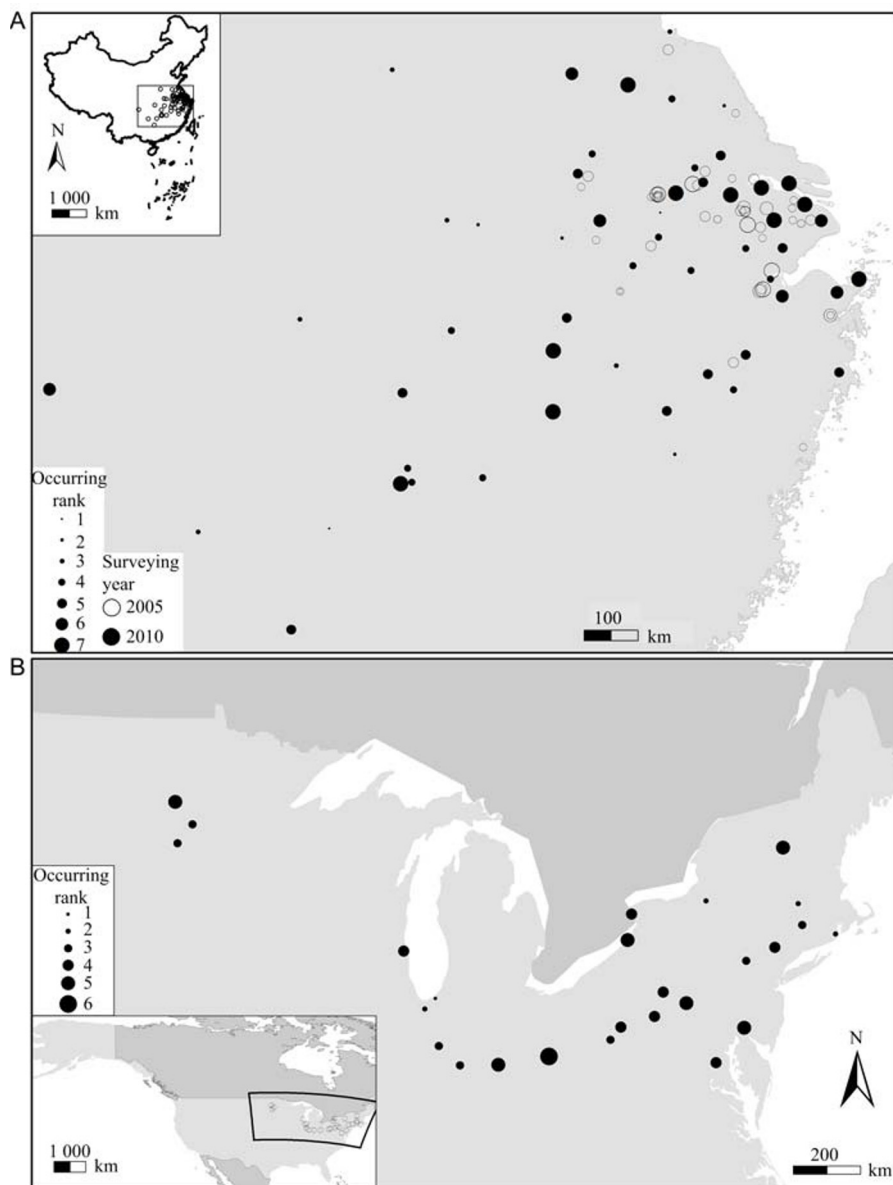
Fig. 1 The wild populations of *Solidago canadensis* investigated in China (A) and the USA (B). The population locations and the relative occurring ranks (which are recorded by the estimation of flowering stem number in one kilometer around the site-center as: 1 (<20), 2 (20-60), 3 (61-300), 4 (301-1 200), 5 (1 200-6 000), 6 (6 001-60 000) and 7 (>60 000)) are also showed.
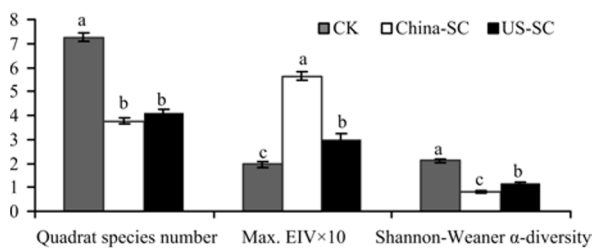

Fig. 2 Comparison among *S. canadensis* native populations (US-SC), invasive populations (China-SC) and the control sites (CK, in China) surveyed in 2009. Max. EIV, species maximum ecological important value in the sites surveyed. Bars with the same letters are not significantly different (*P*<0.05).

Arthraxon hispidus, *Aster subulatus*, *Digitaria sanguinalis*, *Humulus scandens*, *Imperata cylindrical*, *Microstegium vimineum*, etc.

The CK sites had significantly higher (*P*<0.001) α-diversity than the other two site groups (Fig. 2). And α-diversity across China-SC sites was significantly lower (*P*<0.005) than that of US-SC sites.

Comparisons on β-diversity

The mean pairwise Bray-Curtis similarity (Fig. 3) among
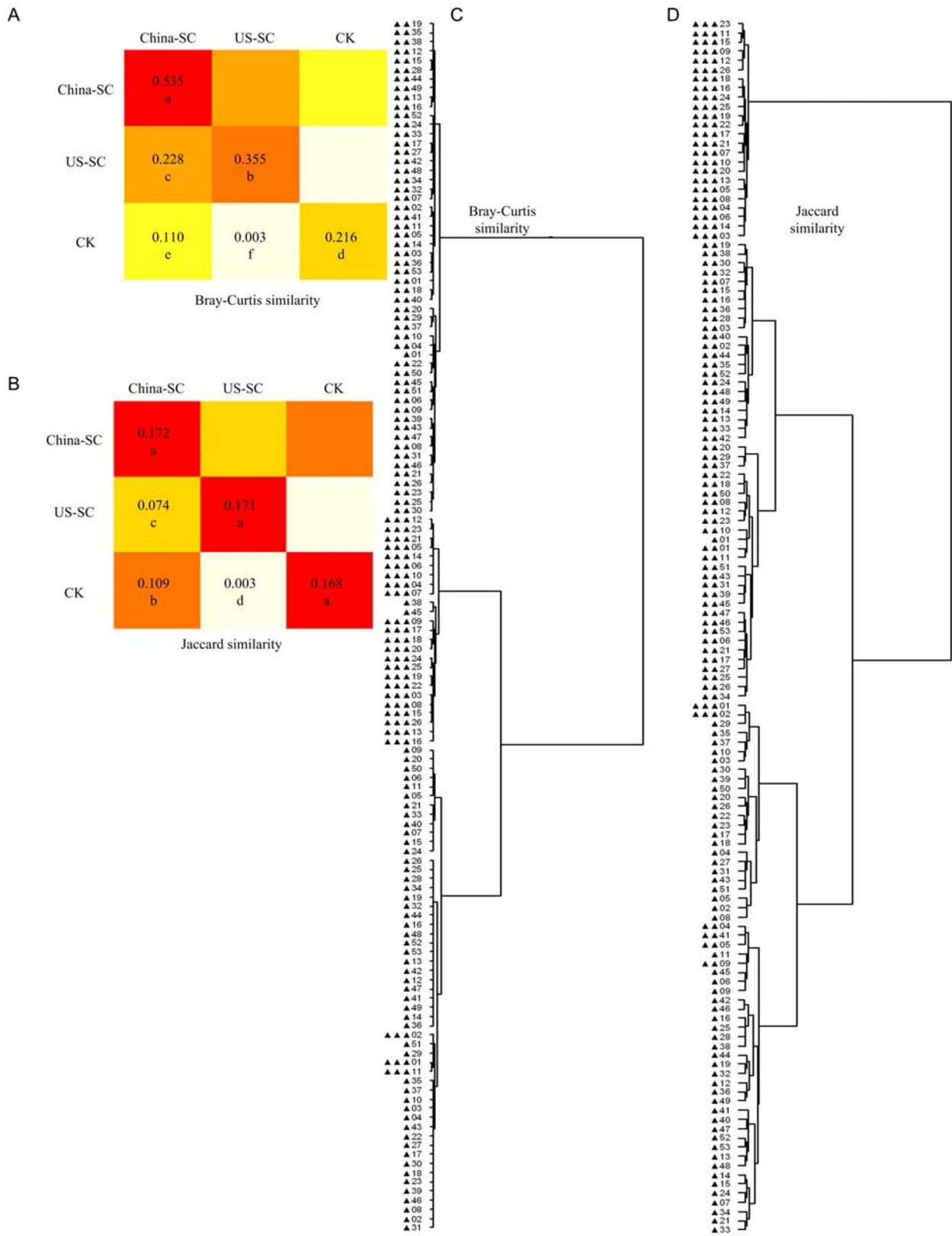
Fig. 3 Pairwise similarities (A and B) and cluster analyses (C and D) of the total 132 sites surveyed in 2009, including 26 *Solidago canadensis* native populations (▲▲▲), 53 invasive populations (▲) and 53 control sites (▲▲) which were adjacent to the invasive populations but without *S. canadensis*. Cells with the same letters are not significantly different (*P*<0.001).

China-SC sites was statistically significant as well as the highest (0.535), followed by significantly lower values of those among US-SC sites (0.355), that between China-SC and US-SC sites (0.288), and those among CK sites (0.216). Moreover, Bray-Curtis similarities of the pairs between China-SC and CK, and the value of the pairs between CK and US-SC sites were significantly the lowest. Additionally, cluster analyses (Fig. 3) with these Bray-Curtis similarities clearly showed two major groups: 1) a cluster of 52 out of 53 China-SC sites plus the 26 US-SC sites; and 2) the total 53 CK sites plus one China-SC site. Furthermore, the group with SC present sites could be divided into two subgroups: one with 50 out of 53 China-SC sites, and the other with remanent sites.

The mean Jaccard similarities (Fig. 3) between the site pairs in the same site group were all approximately 0.17, with no significant difference among China-SC, CK and US-SC sites. While the mean values of the pairs between China-SC sites and CK sites (0.109) was significantly lower. Moreover, the Jaccard similarities between China-SC sites and US-SC sites (0.074) as well as those between CK sites and US-SC sites (0.003) were significantly low. Cluster analyses with the above Jaccard similarities (Fig. 3) also showed two major groups: 24 out of the 26 US-SC sites formed the first group, and the others (including the total China-SC and CK sites) in the other group. Also, 50 out of 53 CK sites plus one China-SC site formed a subgroup with the remnant sites formed another subgroup, including 52 China-SC sites, two US-SC sites and three CK sites.

For China-SC sites and CK sites, both the two similarity indices significantly correlated with geographic distance (Fig. 4), while in US-SC sites, only Jaccard similarity significantly correlated with geographic distance. Moreover, the correlation coefficient (R^2) of the linear regressions in CK sites were much higher than both of the coefficients the relative regressions in China-SC sites and US-SC sites.

Correlation analyses

Correlation analyses (Table 1) showed that the three occurring indices significantly correlated with each other. The environmental factors, including latitude, sandy loam, clay soils, proximity to water and soil moist

rank, were not correlated significantly with any of the three *S. canadensis* occurring indices. Quadrat biomass significantly and negatively correlated with canopy cover ($P<0.001$) and positively correlated with soil fertility rank ($P<0.001$). Abundance rank significantly and negatively correlated with canopy cover ($P<0.001$) and elevation ($P=0.003$), while positively correlated with longitude ($P=0.046$), soil type loam ($P=0.028$) and soil fertility rank ($P=0.007$). Ecological important value (EIV) significantly and negatively correlated with canopy cover ($P=0.007$).

DISCUSSION

Years of field observations have convinced us that the invasion and dissemination rates of *S. canadensis* are speeding up across China. *S. canadensis* is leading to a pervasive biotic homogenization across China.

Solidago canadensis homogenizes communities and landscapes across diverse habitats in China

Firstly, our results show that *S. canadensis* invasions across China share similarities of plant communities with native ranges in the USA (Fig. 3). Specifically, *S. canadensis* tends to be the dominant species (Fig. 2), with lower species richness (Fig. 2) and α-diversity and β-diversity than adjacent, intact native communities (Figs. 2 and 3). These similarities among *Solidago* communities are striking in spite of originally different community structures due to obvious geographic barriers (Fig. 3).

Secondly, *S. canadensis* invasions in China have resulted in community homogenization across diverse habitats and landscapes formerly dominated by different species. Results on floristic similarities (Fig. 3) clearly suggest that the community patterns in the sites with invasive *S. canadensis* populations are highly similar to each other, and dissimilar to the control sites. Also, the communities invaded by *S. canadensis* share similar structures, in particular, the mean pairwise Bray-Curtis similarity value in China-SC sites is as high as 0.535. And nearly all the China-SC sites grouped together. Whereas, in the control, the floristic similarities between the 53 CK sites are significantly much
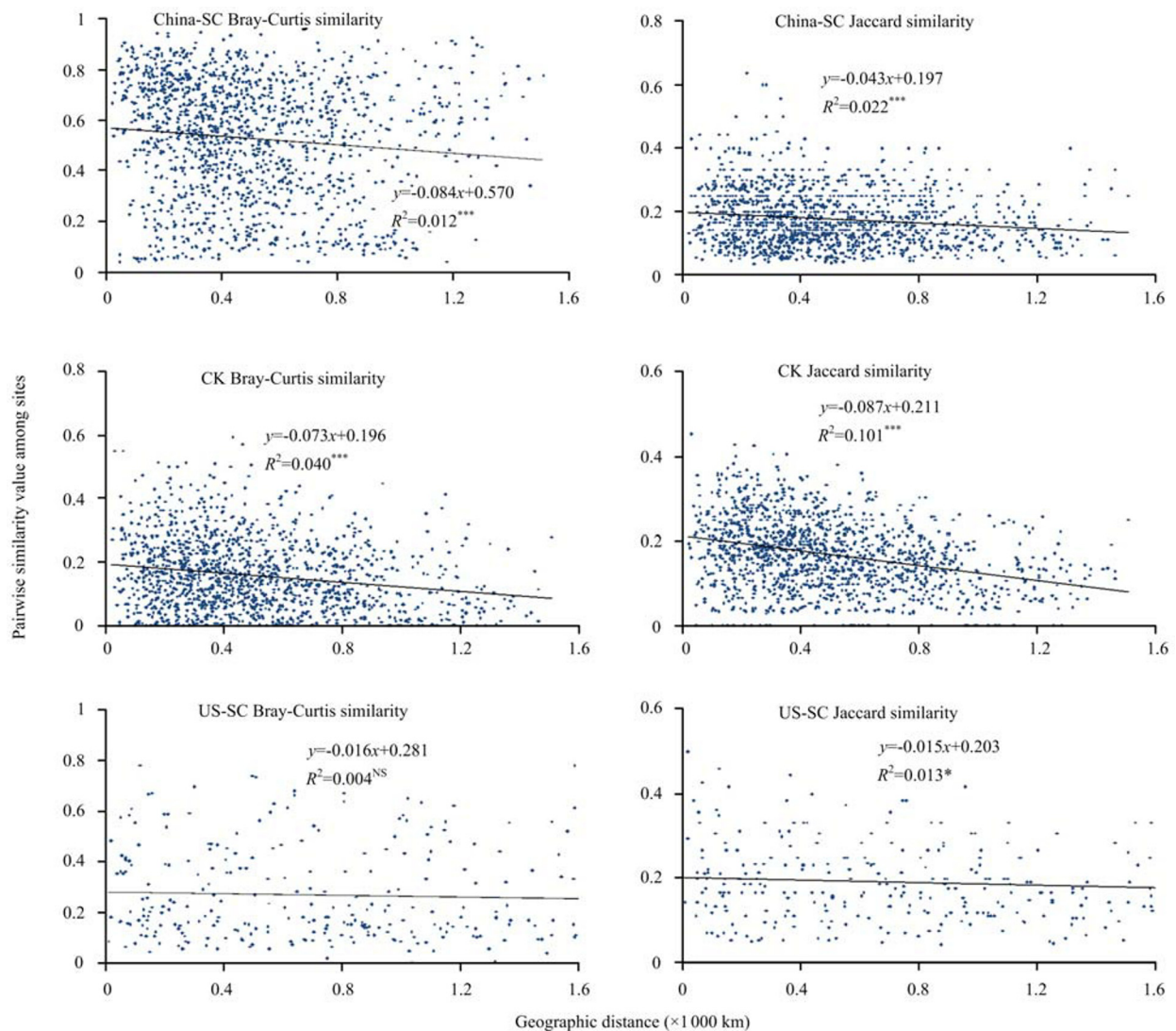
Fig. 4 The relationships between geographic distance and floristic similarities innative *Solidago canadensis* populations (US-SC), invasive populations (China-SC) and the control sites in China (CK). *, $P<0.05$; ***, $P<0.001$; NS, no significant difference. Regressions are drawn and the relative formulations and R^2 values are shown.

Table 1 Pearson correlation coefficients among the three *S. canadensis* occurring indices and ten environmental factors[1]

	Quadrat mass	Occurring rank	Important value
Occurring rank	0.543**		
Important value	0.434**	0.187	
Altitude	-0.113	-0.350*	-0.013
Elevation	0.032	0.028	-0.088
Longitude	0.019	0.289*	0.025
Loam	0.368**	0.366**	0.059
Sandy loam	-0.266	-0.181	-0.189
Clay	-0.143	-0.207	0.219
Near water source	0.147	0.121	0.204
Canopy	-0.390**	-0.490**	-0.300*
Soil moisture rank	-0.285*	-0.164	-0.214
Soil fertility rank	0.368**	0.268	0.101

[1] Quadrat mass was calculated by mean height×stem number in the quadrat; occurring rank was recorded the same as in Fig. 1. Environmental factors were corded as in Table 1. *, $P<0.05$; **, $P<0.01$.

lower (averagely 0.355), in which 23 different species held the highest ecological important value in different sites. After established, *S. canadensis* commonly dominates these communities and eliminate the intrinsic species (Huang *et al*. 2007), which greatly changed the community assemblages as both the pairwise similarities of Bray-Curtis and Jaccard indices of the site pairs between China-SC and CK sites are very low (Fig. 3). Due to the significantly lower species richness in the sites invaded by *S. canadensis*, pairwise Jaccard similarities in China-SC sites are low but still hold a relative high level compared with those in CK sites (Fig. 3). In addition, the invasions of *S. canadensis* lessen the

strength of correlation between geographic distance and floristic similarity of communities (Fig. 4).

Moreover, *S. canadensis* is able to invade and dominate diverse habitats with broad environmental conditions. Correlation analyses (Table 1) suggest that the optimal habitat for *S. canadensis* is fertile loamy soil. But infestations are also frequent in low fertility xeric wasteland soil as well as sandy soil and clay soil. In addition, *S. canadensis* can also invade habitats with high canopy, although at lower occurrence levels. These results reflect the findings by many other researchers, which show the powerful adaptation of *S. canadensis* to many contrasting environmental conditions (Jin *et al.* 2004; Huang *et al.* 2007; Banta *et al.* 2008). Besides, several studies report that *S. canadensis* invasive populations are able to alter rhizosphere soil physico-chemical properties and microbial communities (Zhang C B *et al.* 2009; Zhang S S *et al.* 2009; Zhang *et al.* 2010; Sun *et al.* 2010), which benefit its invasions. As well, *S. canadensis* was reported to have allelopathic effects to other plants (Pisula *et al.* 2010; Xie *et al.* 2010). Therefore, *S. canadensis* dominates the vegetation in invaded habitats replacing more than 20 different locally dominant species that would have occurred across the landscape, creating new phenological patterns distinct from other dominant invaders. For example, communities dominated by *Erigeron annus* or *Daucus carrota* form white colored patches in the landscape in early summer, and those dominated by *Artemisia* sp. or *Conyza* sp. produce grey patches in the autumn. In contrast, the mono-dominance of *S. canadensis* yields communities that are green colored in spring-summer, yellow in autumn and brown in winter. *Solidago canadensis* invasion leads to homogenized landscape.

Furthermore, *S. canadensis* spreads rather quickly and broadly in subtropical to warm temperate climate zones in China (Fig. 1). *S. canadensis* quadrat biomass shows no significant correlations with either longitude, latitude or elevation (Table 1). This suggests that the invasion of *S. canadensis* here is far from equilibrium.

Nevertheless, analyses on floristic similarities (Fig. 3) with species list (Jaccard index) suggested that the species lists of the sites with invasive populations were dissimilar to those with native ones but much more similar to the control sites. Hence, although *S. canadensis* usually remodels and homogenizes the invaded communities by dominating them and supplanting native species in short time, it even gets the invaded communities to have a more similar landscape to those in native ranges. However, the invasions of *S. canadensis* do not completely change the species composition of the local communities. Also, the Bray-Curtis similarities between the control sites and the sites with invasive populations were significantly higher than the similarities between the control sites and the sites with native populations (Fig. 3). Considering that the presence of *S. canadensis* greatly decreases community α-diversity and β-diversity, we conclude that *S. canadensis* invasions in China do in fact create a homogenized landscape replacing more diverse assemblage of local communities.

Why *S. canadensis* may cause such a widespread biotic homogenization in China?

The relationship between biological invasions and biotic homogenization is not well understood yet at present. Biological invasions typically cause biotic homogenization by decreasing biodiversity (Oliveras *et al.* 2005; Piazzi and Balata 2008; Hansen *et al.* 2009). For example, the consequences of diversity decline and landscape change caused by invasions of *Eupatorium adenophorum* in southern areas (Sang *et al.* 2010) and *Eichhornia crassipes* in aquatic areas (Ren *et al.* 2005) in China. In contrast, some studies suggest that invasive species may increase biodiversity and thus cause biotic differentiation at least at small scales (Sala *et al.* 2006). The reasons why *S. canadensis* cause such a widespread biotic homogenization in China may compose of three aspects: 1) the high invasiveness of *S. canadensis*; 2) the invasibility of habitats in China; and 3) the problems on management.

There are many studies which show that *S. canadensis* is highly competitive in its invasive range, reproducing and being adapted to a broad range of environmental conditions (Jin *et al.* 2004; Huang *et al.* 2007; Banta *et al.* 2008). These attributes enable *S. canadensis* to establish populations in a diversity of habitats and spread quickly. *S. canadensis* plant grows robustly; the flowering stems average 170.72 cm in

height with 43.56 flowering stems per m² across the 99 sites surveyed in China. Thus most local plant species would be shaded and then excluded in short time. The exceptions would be those with high invasiveness such as *Aster subulatus* or lianas such as *Humulus scandens*. As a robust perennial with well-developed rhizome system, *S. canadensis* generally occupies space continuously all year round. In the present areas invaded by *S. canadensis* in China, this species has double phenological advantages. During autumn-winter season when other plants with spring or summer flowering tend to germinate and grow, *S. canadensis* generally sprouts from perennial rhizomes two or three weeks before other species sprout or germinate. This competitive advantage tends to seriously inhibit the occurrence of other plant species. During the spring-summer season when other plants with autumn flowering tend to germinate, *S. canadensis* seedlings and rhizomes densely cover invaded habitats (Huang *et al.* 2007), depriving the opportunity for the most plants to germinate and become established. Thus, as long as *S. canadensis* becomes naturalized, few other species are capable of competing locally for space. In the 53 China-SC sites, 111 vascular plant species were observed with an average of 3.77 per m². Among the 111 species, 23.42% species (26) had frequencies exceeding 10% of which 38.46% were lianas and 38.46% were other alien invasive species. For example, the five companion species with the highest frequencies in *S. canadensis* plots were *Alternanthera philoxeroides* (49.49%, a liana), *Humulus scandens* (46.46%, a liana), *Setaria viridis* (38.38%), *Artemisia lavandulaefolia* (38.38%), and *Cynodon dactylon* (34.34%) which are all serious weedy species in China, except for *Artemisia lavandulaefolia* (a native common weed). However, in the 53 control sites in China, 182 vascular plant species were observed with an average of 7.26 species per m². And the rank of most common species in China-CK sites are quite different with frequencies clearly higher, as *Setaria viridis* (71.70%), *Cynodon dactylon* (64.15%), *Conyza bonariensis* (60.38%), *Alternanthera philoxeroides* (58.49%, a liana), *Conyza sumatrensis* (58.49%) and *Artemisia lavandulaefolia* (58.49%).

The invisibility of habitats in China is another important reason for the infestation of *S. canadensis* in China. Among the 99 invasive *S. canadensis* populations we

surveyed in China, 18 were located in urban areas, 77 were in suburban areas and only four are in rural areas. Large development zones with road networks, which cause large areas of temporary wastelands, usually characterize urbanization in China. The road networks in and around an urban area provide optimal corridors for the diffusion of *S. canadensis* seeds, and the wastelands become the most common springboard habitats for *S. canadensis*. The wind dispersion mechanism employed by *S. canadensis* seeds also contributes to wide dispersion that may speed up its spread and invasion.

MATERIALS AND METHODS

Wild *S. canadensis* populations surveyed

We have extensively gathered the distributional data of *S. canadensis* since 2002. During October and November of 2005, we surveyed 46 field sites (which represent most wild *S. canadensis* populations in Jiangsu, Anhui, Shanghai and Zhejiang provinces of China) and 53 additional sites (which represent most wild *S. canadensis* populations in China) in October and November of 2009 (Fig. 1). In addition, in August and September of 2009 we surveyed 34 US sites (native range of *S. canadensis*) with *Solidago* species present, including 26 sites with *S. canadensis* populations present (Fig. 1).

Site setting and environmental factors recorded

For each *S. canadensis* wild population, a 200 m×200 m sample site was set in the region with the greatest abundance of *S. canadensis* individuals. Ten environmental factors (Table 2) referring to location, soil characters and tree canopy were recorded for each site. The landscape-level abundance rank of *S. canadensis* was recorded by visually observing the number of flowering stems in 1 km area around the site-center: 1 (<20), 2 (20-60), 3 (61-300), 4 (301-1 200), 5 (1 200-6 000), 6 (6 001-60 000) and 7 (>60 000).

Quadrat setting for *S. canadensis* populations and control sites

For each site, three (2005) or five (2009) 1 m×1 m quadrats were set in the patches with the most *S. canadensis* stems; the intervals between each quadrat were no less than 5 m. For each *S. canadensis* quadrat surveyed in 2009 in China,

Table 2 The ten environmental factors recorded in each site

Environmental factor	Environmental factor
F1: Elevation of site-center	F7: Soil fertility rank: 1=very low fertility (e.g.comprised of coarse waste soils); 2=low fertility;
F2: Latitude of site-center	3=intermediate; 4=semi-fertile (e.g. surrounding by arable land); 5=fertile arable land
F3: Longitude of site-center	F8: Soil moisture rank: 0=submerged; 1=very wet; 2=wet; 3=moderate; 4=slightly; 5=xeric; 6=very xeric
F4: Loam soil type: 1=yes, 0=no	F9: Near water source: 1=within 100 m; 0=otherwise
F5: Sandy loam soil type: 1=yes, 0=no	F10: Canopy (%)
F6: Clay soil type: 1=yes, 0=no	

a control quadrat without *S. canadensis* was selected which within 2 m from the edge of the highest density of *S. canadensis* with the highest vegetation coverage.

Vegetation survey

In each quadrat, all the vascular plant species were recorded except tall trees, as well as the number of stems or plant individual, mean height and coverage rank (according to the Braun-Blanquet scale (Mueller-Dombois *et al*. 1974) of each species. Relative abundance, coverage, frequency and height for each species were then calculated as: (total value of the species)/(total values of all the species in the site). And the ecological important value (EIV) for each species was determined by the mean values of relative frequency, coverage, abundance and height (Fang *et al*. 2009). Species richness and the Shannon-Weiner index (based on the number of each species) at each site were also calculated (Fang *et al*. 2009). Three stems of *S. canadensis* for each site were collected for specimens.

Data analyses

In total 132 sites were surveyed in 2009: 53 sites with *S. canadensis* invasions in China (China-SC site), 53 adjacent control sites in China (CK site) and 26 native range sites with *S. canadensis* occurrences in the US (US-SC site). The data presented are the means±SE. And the analyses were conducted with R2.12.1 by The R Development Core Team (2011).

Ecological important value (EIV), abundance rank and quadrat biomass (estimated as height×stem number) were used as *S. canadensis* occurrence indices for each site. The potential relationships among *S. canadensis* occurring indices and environmental factors were tested using Pearson correlation analyses.

Shannon-Weaner α-diversity at each site was calculated. Significant differences among China-SC sites, CK sites and US-SC sites were tested with a one-way ANOVA. Variances that were not homogeneous were square root transformed.

To date, β-diversity and its relationship with geographic distance were usually analyzed in the study of biotic homogenization. Thus, β-diversities were determined with pairwise Jaccard (based on species lists) and Bray-Curtis (based on species abundances) similarity indices for the total 132 sites surveyed in 2009 (Oksanen *et al*. 2011). Hence, a lower pairwise similarity between sites means a higher β-diversity. Also, the pairwise similarities were regressed with geographic distances with linear model (Qian and Ricklefs 2006). Moreover, the above pairwise Bray-Curtis and Jaccard similarities among the 132 sites were classified with a cluster analysis with a Ward's method.

Acknowledgements

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