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BIODIVERSITY
RESEARCH

Growth form and distribution of introduced plants in their native and non-native ranges in Eastern Asia and North America

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ABSTRACT

There is a growing interest in understanding the influence of plant traits on their ability to spread in non-native regions. Many studies addressing this issue have been based on relatively small areas or restricted taxonomic groups. Here, we analyse a large data base involving 1567 plant species introduced between Eastern Asia and North America or from elsewhere to both regions. We related the extent of species distributions in each region to growth form and the distinction between upland and wetland habitats. We identified significant relationships between geographical distribution and plant traits in both native and exotic ranges as well as regional differences in the relationships. Range size was larger for herbaceous graminoids and forbs, especially annuals compared to perennials, than for woody species, and range size also was larger for plants of wetland compared to upland habitats. Distributions were more extensive in North America than in Eastern Asia, although native plants from both regions had broader distributions than non-natives, with exotics from elsewhere intermediate. Growth form and environment explained more of the variance in distribution of plants in North America than in Eastern Asia. The influence of growth form and habitat on distribution suggests that these traits might be related to tolerance of ecological conditions. In addition, the smaller extents of species in non-native compared to native areas suggest roles for dispersal limitation and adaptation to region-specific ecological conditions in determining distribution.

Keywords

Biological invasions, Eastern Asia, invasibility, invasion resistance, native vs. exotic ranges, North America, wetland vs. upland habitat.

INTRODUCTION

Factors that determine the geographical distributions of populations, whether native or exotic, are not yet fully understood (Gaston, 2003). With respect to exotic species, ecologists have focused on release from predators and pathogens in promoting spread (Maron & Vila, 2001; Keene & Crawley, 2002; Wolfe, 2002; Mitchell & Power, 2003; Torchin *et al.*, 2003) and competitive exclusion by native species in preventing spread (Naeem *et al.*, 2000; Hector *et al.*, 2001; Richardson & Pyšek, 2006), although the local numbers of exotic and native species also covary to a considerable extent (Stohlgren *et al.*, 1999; Qian & Ricklefs, 2006). The invasion success of exotic plants varies widely (Elton, 1958; Blackburn & Duncan, 2001), but appears to be influenced by a number of plant traits related to growth rate, nutrient use efficiency, stress tolerance, herbivore resistance and seed production and dispersal (Rejmánek & Richardson, 1996; Daehler, 2003; Lloret *et al.*, 2005; Pyšek & Richardson, 2007). If interactions with pathogens and herbivores have determined the distribution of exotic species, one would not expect to find strong associations of geographical extent with most plant traits. A continental-scale comparison of exotic plants in temperate Eastern Asia and North America showed that areas occupied by exotic species in their native and non-native regions are correlated (Guo *et al.*, 2006), suggesting the influence of species-specific traits is unrelated to release from pathogens and herbivores, or to ability to invade local non-native plant assemblages.

Plant traits have been associated with geographical extent in several studies with a narrow geographical or taxonomic focus (Pyšek & Richardson, 2007). For example, small seed mass, rapid maturity, and large and frequent seed crops predict invasiveness in pines (*Pinus*) and other plants (Salisbury, 1942; Rejmánek & Richardson, 1996; Richardson & Rejmánek, 2004). Efficient resource use, rapid relative growth rates and reproductive

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self-compatibility have also been associated with invasiveness (Burns, 2004; Rambuda & Johnson, 2004). Here, we examine the relationship between the continental distributions of both native and exotic plants in temperate Eastern Asia and North America and attributes of growth form and habitat. The two regions have similar ranges of ecological conditions (Qian & Ricklefs, 2004) and share many genera and some species of native plants (Qian & Ricklefs, 2004), reflecting long-standing biogeographical connections. In addition, hundreds of species of plants have been transported, both intentionally and accidentally, between Eastern Asia and North America, providing an opportunity to compare distributions in native and introduced areas (Guo *et al.*, 2006).

All the species compared in this analysis have been established as exotics within north temperate environments of either Eastern Asia (EAS) or North America (NAM). Because our data set was compiled from a variety of sources, we were not able to adopt standardized criteria for 'established' or 'naturalized' (see Pyšek *et al.*, 2004). However, each comparison of ranges in different regions involves the same species distributed in similar environments, providing internal controls both for species traits (Daehler, 2003) and for environmental characteristics (Blackburn & Duncan, 2001). In this study, we ask whether geographical distribution can be related to growth form or habitat distribution, and whether the relative success of alien species, measured by distribution, depends to any degree on these traits. We use growth form and habitat type because such information is currently available for all the species included in this study, although clearly it would be desirable to have information on other plant traits (Pyšek & Richardson, 2007).

METHODS

This analysis includes all species of vascular plants introduced from Eastern Asia to North America (781 species), from North America to Eastern Asia (148 species), or from elsewhere to both areas (638 species). We scored distribution as a qualitative, three-state variable.

Each region was divided into geographical units (mostly provinces in EAS, $n = 67$; states and provinces in NAM, $n = 58$; Fig. 1), corresponding to consistently available data on plant distributions. Some of the smaller units were grouped, and some larger ones divided, to minimize differences in area of units within and between continents (mean area = 328,996 km^2 in EAS and 329,690 km^2 in NAM). The distributional range for each species within each region was calculated as the number of geographical units from which the species has been reported, divided by the total number of units in the region. Thus, the proportion of area (i.e. the geographical range for each species within each region) varies between 0 and 1. Although these values overestimate geographical distribution to the extent that plant populations do not occupy the entire area of any given political unit, they provide a useful comparative index to invasion extent on a regional scale (see details in Guo *et al.*, 2006; also Appendix S1 in the Supplementary Materials). Because the same approach was used in both regions, there appears no systematic bias to estimated distributional extent with regard to region.

The regions compared in EAS and NAM occupy a total of 22.0 and 19.1×10^6 km^2, respectively, and include a similar distribution of ecological biomes. Guo *et al.* (2006) determined that the extents of each of the 14 global biomes (World Wildlife Fund Biomes, http://www.worldwildlife.org/science/ecoregions/biomes.cfm) had a correlation of $r = 0.80$ between the regions. The mismatch was resulting primarily from the larger representation of tropical and subtropical moist broadleaf forests in the south of EAS, and of Montane grasslands and shrublands in the west of EAS. The extents of each of 14 categories of Holdridge Life Zones (http://www-cger.nies.go.jp/grid-e/griddoc/holdride.html) had a correlation of 0.90 between the regions. Thus, the ecological settings of the two regions are reasonably comparable.

Each species was characterized with respect to (1) annual or biennial vs. perennial (2) herbaceous vs. woody (3) graminoid, forb, subshrub-shrub-liana, and tree growth form and (4) upland vs. aquatic-wetland habitat. Plants included in the category of aquatic-wetland habitat are those classified as aquatic, floating, submerged or wetland plants in Kartesz (1999); all other plants were included in the category of upland habitat. Traits 1–3 were reduced to the following categories: annual or biennial forb (483 species), annual graminoid (90), perennial forb (439), perennial graminoid (110), perennial subshrub-shrub-liana (241), and perennial tree (204). These categories were scored as a qualitative, six-state variable. Wetland vs. upland was scored as a qualitative, two-state variable.

The statistical contribution of each independent variable to variation in geographical range was determined by analysis of

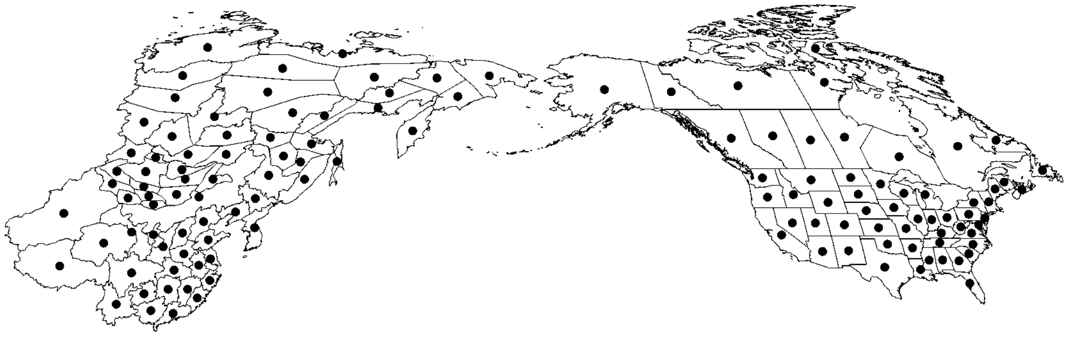

Figure 1 Geopolitical units used to document exotic plant species distributions in Eastern Asia (EAS) and North America (NAM).

Table 1 Least squares means for each of the main effects in analyses of variance of distributions in Eastern Asia and North America with respect to habitat type, growth form, and native distribution.

		In Eastern Asia		In North America	
Trait	d.f.	Type III SS	F	Type III SS	F
Habitat type	1	0.73	30.3	7.49	112.5
Growth form	5	1.32	11.0	11.03	33.1
Distribution	2	3.93	81.6	3.14	23.6
	Category	LSMean	$P < 0.05$	LSMean	$P < 0.05$
Habitat type	Wetland	0.169	a	0.391	a
	Upland	0.121	b	0.239	b
Growth form	Annual forb	0.192	a	0.434	a
	Annual graminoid	0.131	cd	0.395	a
	Perennial forb	0.168	bc	0.321	b
	Perennial graminoid	0.138	bcd	0.310	b
	Shrub	0.118	d	0.229	c
	Tree	0.123	d	0.202	c
Distribution	EAS native	0.221	a	0.246	c
	Non-native	0.132	b	0.319	b
	NAM native	0.081	c	0.381	a
		Mean	SD	Mean	SD
Overall		0.177	0.165	0.280	0.291

Note: All interaction terms were $P > 0.05$, except for growth form distribution for NAM proportion, for which $F_{10,1548} = 3.63$, $P < 0.0001$, and the sum of squares (SS = 2.38) accounted for less than 10% of the model SS (31.6). The interaction term was dropped for subsequent analysis. The error degrees of freedom were 1558. All P-values for main effects < 0.0001. $R^2 = 0.125$ in EAS and 0.220 in NAM.

variance (SAS GLM procedure) on the categorical variables as main effects. We calculated least squares means, which account for unbalanced statistical designs, for each state of each of the categorical variables. Statistical significance of differences between groups was determined by pairwise t-tests (PDIFF option of the LSMEANS statement in the GLM procedure) or with the Scheffé multiple comparison procedure on main effects in the MEANS statement.

RESULTS

Statistical associations of plant characteristics and geographical distribution are summarized in Table 1 and shown graphically in Fig. 2. Habitat, growth form and distribution explained 12.5% of the variance in range area in EAS and 22.0% of the variance in NAM. Range sizes of species were generally larger in North America (0.280 ± 0.291) than in Eastern Asia (0.177 ± 0.165). However, natives to EAS had similar range sizes in EAS and NAM, whereas NAM natives and exotics to both regions were much more widely distributed in NAM than in EAS. Traits associated with variation in range size were consistent among regions. Wetland plants had significantly broader distributions than upland species. Annual and biennial plants, especially forbs, had broader distributions than perennial species. Herbaceous species (forbs and graminoids) were more widely distributed than woody species (shrubs and trees). Across all plant species, ranges in EAS and NAM were correlated ($r = 0.337$), but this correlation accounted for only about 10% of the total variance in area occupied in each region.

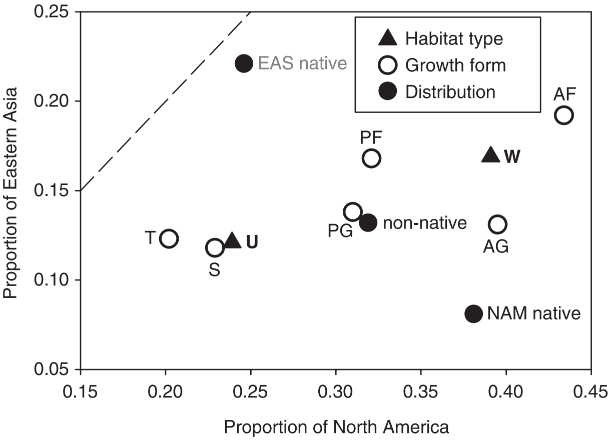

Figure 2 Distributions of plants in Eastern Asia and North America grouped by habitat type (U = upland, W = wetland), growth form (T = tree, S = shrub, PG = perennial graminoid, PF = perennial forb, AG = annual graminoid, AF = annual forb), and native distribution. The diagonal dashed line represents equal proportional areas in both regions.

As we have noted before (Guo *et al.*, 2006), Eastern Asian native species are distributed as widely in their native region as in North America, but North American native species are narrowly distributed, on average, in Eastern Asia. This discrepancy depends primarily on woody plants, among which distributions of Eastern Asian upland species in native and exotic regions are more similar.

Because five times as many species have been introduced from EAS to NAM as in the reverse direction, the results of our analyses might be biased with respect to region. Therefore, we conducted a similar analysis to that reported in Table 1 including only the 638 species exotic to both EAS and NAM. The analysis was conducted separately for upland and wetland habitats (Table 2). The results for the distributional areas are similar to those for the entire sample, in that NAM > EAS regardless of habitat type and growth form. We also found that for woody plants (shrubs and trees), EAS ≅ NAM for upland species but EAS < NAM for wetland species. Thus, much of the discrepancy between the magnitude of the difference between EAS and NAM for upland and wetland species is a function of differences among woody elements of the vegetation.

DISCUSSION

We have found that geographical extents of vascular plants in Eastern Asia and North America are statistically related to the distinction between wetland and upland habitat and to differences among growth forms. Many attributes of plants that have

Table 2 Mean and standard deviation of distributions of the 638 vascular plant species exotic to both Eastern Asia and North America with respect to habitat type and growth form.

	Upland				Aquatic and wetland			
	N	EAS	NAM	*P*	*N*	EAS	NAM	*P*
Annual forb	158	0.142 ± 0.142	0.373 ± 0.277	< 0.0001	80	0.224 ± 0.178	0.521 ± 0.329	< 0.0001
Annual graminoid	21	0.120 ± 0.144	0.462 ± 0.359	0.0006	17	0.189 ± 0.189	0.499 ± 0.354	0.006
Perennial forb	101	0.125 ± 0.147	0.231 ± 0.263	0.0006	54	0.197 ± 0.163	0.407 ± 0.348	0.0002
Perennial graminoid	17	0.104 ± 0.153	0.218 ± 0.280	0.16	26	0.170 ± 0.168	0.572 ± 0.338	< 0.0001
Shrub	58	0.081 ± 0.105	0.095 ± 0.156	0.57	9	0.050 ± 0.028	0.176 ± 0.239	0.15
Tree	79	0.087 ± 0.100	0.097 ± 0.146	0.62	18	0.080 ± 0.091	0.204 ± 0.253	0.07
Overall	434	0.117 ± 0.134	0.251 ± 0.274	< 0.0001	204	0.186 ± 0.170	0.452 ± 0.344	< 0.0001

Note: *P*-values represent *t*-tests of differences between Eastern Asia and North America.

been used in similar analyses, including seed size and number of propagules, were not included in the study because we lacked suitable comparative data. Nonetheless, we can infer that individual plant traits determine distribution to some extent from the correlation between the ranges of the same species of plants in different regions (Guo *et al.*, 2006). In the present analysis, the correlation coefficient (r) between range sizes in the two regions was 0.34, accounting for only about 10% of the variance and indicating considerable heterogeneity or estimation error.

Several aspects of the data might spuriously influence the results of our analyses. Our sample included only species of plants that occur in both Eastern Asia and North America, which are species that have been introduced from Asia (781 species), North America (148), or elsewhere (638). The 1567 species included in our analysis comprised only 5.6% of the vascular flora of Eastern Asia (Qian, 2002) and 10% of that of North America (Guo *et al.*, 2006). Thus, our sample might have been selected for certain traits that favour naturalization in exotic regions. However, this presumably would affect the mix of species traits as a whole and not explain the association of variation in distribution with particular plant traits.

Distributions might be better characterized in North America than in Eastern Asia; however, we have not examined this potential discrepancy and have taken the data at face value. Eastern Asian distributions were based on a large body of literature and original data from collections. We found that more variation in distribution was explained by habitat, growth form, and native distribution in North America (22%) than in Eastern Asia (12.5%). Species included in our sample native to North America or regions other than Asia tend to be more widely distributed in North America than in Eastern Asia by a substantial margin; Asian natives have similar ranges in both regions (Guo *et al.*, 2006). The larger ranges of many species in North America might indicate more complete filling of potential environmental space, hence more determinism in their distributions, whereas correlations between distribution and plant traits in Eastern Asia could be constrained by dispersal limitation, particularly among exotic species. Although many exotics, especially weedy species, have had longer history of association with people and agriculture in eastern Asia, extensive industrialization, transportation and human migration were relatively recent (i.e. past 200–400 years), and much more dramatic in North America than in eastern Asia. In addition, higher native species diversity associated with more complex landforms in eastern Asia might to some extent have limited the spread of introduced species (Guo *et al.*, 2006).

Several influences of plant traits on distribution area stand out in this analysis: annual/biennial > perennial, herbaceous > woody, wetland habitat > upland habitat. The effect of these traits on distribution might not be related to the ability of alien plant populations to spread through non-native regions because their statistical influences are similar in native and alien areas. In addition, Guo *et al.* (2006) found little relationship in exotic species between distributional extent and time since introduction, following an initial rapid expansion in range. Woody plants tend to have larger fruits and seeds than perennial herbaceous plants, which in turn have larger fruits and seeds than annual/biennial herbaceous plants (Salisbury, 1942; Leishman *et al.*, 1995; Lord *et al.*, 1995; Moles *et al.*, 2007). Reduced dispersal distance related to large propagule size could contribute to the pattern of range size among the three groups of plants.

Woody taxa do not appear to have more narrowly defined environmental conditions than herbaceous plants (Qian & Ricklefs, 2004). The greater spread of herbaceous exotics might reflect relationships between life histories and genetics. For example, herbs typically have high population densities and short generation times, which could facilitate genetic adaptability in new environments (Cox, 2004), and large numbers of small seeds, which enhance dispersal ability. Wetland plants might occupy uniformly broader ranges because their primary habitats are broadly distributed in low-lying areas and are more strongly determined by local distribution of surface water than by prevailing climate. Many long-distance migrating birds frequently stop at moist and wetland sites and they disperse seeds of wetland plants either through droppings or shedding of small seeds adhering to plumage and feet. Many wetland invasive plants have a free-floating growth form that is easily dispersed by water movement and may be advantaged by having both sexual and asexual modes of reproduction (e.g. *Butomus umbellatus*, *Eichhornia crassipes*).

Unexplained variation in distributional extent is undoubtedly related to plant traits not considered in this analysis, differences in the ecological geography of North America and Eastern Asia, variation in the time and location of introductions of exotic species (e.g. Castro *et al.*, 2005), potential for spread by humans either intentionally or not (Wilson *et al.*, 2007), and variation introduced by our estimation of distributional extent (see Guo *et al.*, 2006). Additional factors such as land use patterns (disturbance) and escape from natural enemies would also influence the distributions of both native and exotic species.

Although growth form is strongly associated with distribution in native and exotic regions (Pyšek & Richardson, 2007), the individualistic nature of species, the history of introductions, and the variable landscape context in non-native regions (Wilson *et al.*, 2007) might limit our ability to use plant traits as a predictive tool for invasion success in particular cases. However, a deeper understanding of the general relationship between plant traits and the establishment and spread of exotic species will likely come with further studies relating plant traits to ecological and geographical ranges.

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SUPPLEMENTARY MATERIAL

The following supplementary material is available for this article:

Appendix S1 Plot showing frequency distribution of exotic species among geographical units in Eastern Asia (EAS) and North America (NAM).

This material is available as part of the online article from:
http://www.blackwell-synergy.com/doi/abs/10.1111/j.1472-4642.2007.00457.x
(This link will take you to the article abstract).