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# Distributions of Exotic Plants in Eastern Asia and North America

Qinfeng Guo
*U.S. Geological Survey*

Hong Qian
*Illinois State Museum*

Robert E. Ricklefs
*University of Missouri-St Louis*, ricklefs@umsl.edu

Weimin Xi
*University of North Carolina, Chapel Hill*

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**LETTER**

# Distributions of exotic plants in eastern Asia and North America

**Qinfeng Guo,[1]*† Hong Qian,[2]† Robert E. Ricklefs[3]† and Weimin Xi[4]‡**

[1]*U.S. Geological Survey, Northern Prairie WRC, 8711 37th St. SE, Jamestown, ND 58401, USA*

[2]*Research and Collections Center, Illinois State Museum, 1011 East Ash Street, Springfield, IL 62703, USA*

[3]*Department of Biology, University of Missouri-St Louis, 8001 Natural Bridge Road, St Louis, MO 63121-4499, USA*

[4]*Department of Biology, University of North Carolina, Chapel Hill, NC 27599-3280, USA*

**Correspondence: E-mail: qguo@usgs.gov*

*†These authors contributed equally*

*‡Present address: 406 Heep Center, The Knowledge Engineering Laboratory, Entomology Department, Texas A&M University, College Station TX 77840, USA*

## Abstract

Although some plant traits have been linked to invasion success, the possible effects of regional factors, such as diversity, habitat suitability, and human activity are not well understood. Each of these mechanisms predicts a different pattern of distribution at the regional scale. Thus, where climate and soils are similar, predictions based on regional hypotheses for invasion success can be tested by comparisons of distributions in the source and receiving regions. Here, we analyse the native and alien geographic ranges of all 1567 plant species that have been introduced between eastern Asia and North America or have been introduced to both regions from elsewhere. The results reveal correlations between the spread of exotics and both the native species richness and transportation networks of recipient regions. This suggests that both species interactions and human-aided dispersal influence exotic distributions, although further work on the relative importance of these processes is needed.

## Keywords

Competition, distribution, ecological release, enemy release, habitat suitability, human activity, invasive species, plant introductions, range area.

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## INTRODUCTION

Intercontinental biotic invasion is currently a major threat to global ecology and economy (Mack *et al.* 2000). Many recent studies address the causes of species invasiveness (Rejmánek & Richardson 1996; Grotkopp *et al.* 2002; Daehler 2003; Cox 2004) and habitat invasibility (Elton 1958; Crawly 1987; Stachowicz & Tilman 2005). Factors influencing the spread of alien species include competitive exclusion by native species, disturbance, enemy release and habitat suitability (Levine & D'Antonio 1999; Keane & Crawley 2002; Mitchell & Power 2003; Lafferty *et al.* 2005), but their relative effects in most cases remain unclear (Lonsdale 1999; Larson *et al.* 2001; Levine *et al.* 2004).

Most studies of invasion success have included small-scale experiments or field observations, or have focused on individual species (Tilman 1997; Naeem *et al.* 2000; Hector *et al.* 2001). However, several hypotheses concerning the spread of exotics also predict unique relationships between the distributions of species in their native and non-native regions. For example, under a competitive exclusion model embodied in the biotic resistance hypothesis, aliens should spread less in spatial extent and more slowly over time where native plant species richness is higher, provided that environments are otherwise similar. The enemy release hypothesis predicts that when exotics escape their enemies, they become more abundant locally and are likely to spread more widely in non-native than in native regions. In addition, if human land use and migration promoted the spread of non-native species after introduction, the distribution patterns of exotics would reflect the effects of human activities in the introduced region. Thus, comparisons of entire exotic floras in native and non-native regions would reveal patterns that must be explained by any general hypothesis for the spread of exotic species.

To date, efforts to quantify invasion success on regional and continental scales have been hampered by inadequate quantitative information on species distributions, especially on large scales (Kitayama & Mueller-Dombois 1995). A meaningful measure of invasion success is the area occupied in the non-native region because geographic range of a species is generally positively correlated with its abundance (Brown 1984; Blackburn & Gaston 2001; Gaston 2003). To control for the potentially confounding effects of status (native vs. introduced) and region, the introduced range of a species can be compared with the distributional area in its native region and to that of a similar native species in the region of introduction (Guo 2006). Although such analyses might suffer from uncertain comparability of species, regional analyses of entire non-native floras or faunas minimize this difficulty. Comprehensive reciprocal comparisons of distributions in native and non-native ranges between regions with similar environments provide controls on variation in regional ecology and individual traits of species (Rejmánek & Richardson 1996; Guo 2002).

Hundreds of species of plants have been transported, both intentionally and accidentally, between temperate regions of eastern Asia (EAS) and North America (NAM). These two regions have similar ranges of ecological conditions (Ricklefs & Latham 1992; Qian & Ricklefs 2000) and share many genera and species of native plants (Qian 1999), reflecting long-standing biogeographic connections. However, the regions differ in native vascular plant diversity (EAS > NAM), even when area and climate conditions are accounted for (Qian & Ricklefs 2000; Qian 2002), and NAM has experienced more extended within-region human migration during the period of most intense plant introductions.

Here, we compare the geographic range sizes of all transpacific introduced vascular plants between EAS and NAM in both their native and introduced regions. We additionally examine the effects of time since introduction when known. Specifically, we determine whether (a) EAS, with higher regional and local diversity of native plants, has a lower richness and narrower distributions of introduced species (predicted by the biotic resistance hypothesis); (b) introduced species tend to occupy larger distributions than native source populations (predicted by the enemy release hypothesis); and (c) a relatively longer history of human migration is associated with the spread of non-native species (predicted by the human activity hypothesis).

Our analyses take advantage of the global 'natural' experiment resulting from intercontinental introductions. All the species included in this analysis have been established as exotics within the two temperate regions. Therefore, each comparison of ranges between the two regions involves the same species distributed in similar environments, providing internal controls on both species traits (Daehler 2003) and environmental characteristics (Blackburn & Gaston 2001).

## MATERIALS AND METHODS

The regions compared in EAS and NAM occupy 22.0 and $19.1 \times 10^6$ km$^2$, respectively. The extents of each of the 14 world biomes (World Wildlife Fund Biomes http://www.worldwildlife.org/science/data/attributes.cfm) had a correlation of $r = 0.80$ between the regions. The mismatch is largely due to 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 (see http://www.grid.unep.ch/data/index.php: GRID-Geneva Data Sets, Biosphere, GNV5) had a correlation of 0.90 between the regions. Thus, in spite of differences in

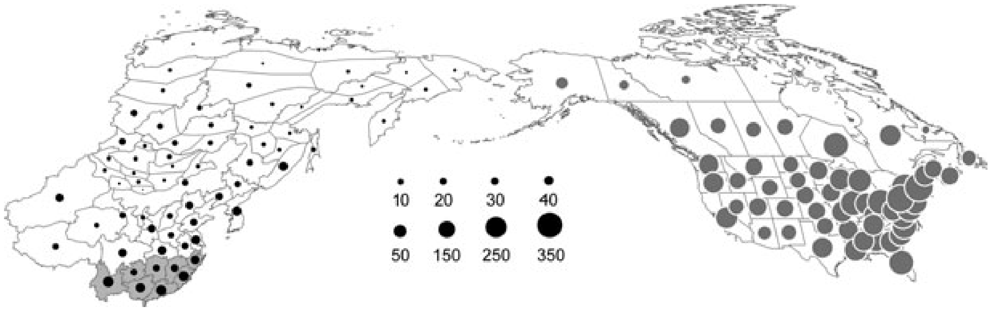

**Figure 1** The number of trans-Pacific introduced plant species in each geographic unit in EAS (black symbols) and NAM (grey symbols). The eight symbols in the middle of the map provide scale references for the number of species in each geographic unit. Most introduced species occur at lower latitudes and are distributed in the south-eastern regions of both continents, which have similar warm-temperate climates and broadly overlapping native floras at the level of plant genera. The pattern of the trans-Pacific introduced species richness is similar to the general trend of native species diversity along the latitudinal gradient. The shaded area in EAS represents the eight southern Chinese provinces excluded in certain analyses.

climate seasonality related to the strong monsoon of EAS, the two regions are broadly similar ecologically.

Each region was divided into geographic units (mostly provinces in EAS, $n = 67$; states and provinces in NAM, $n = 58$), corresponding to consistently available data on plant distributions (see Fig. 1). We combined some small units (e.g. Connecticut, Massachusetts, New Hampshire, Rhode Island and Vermont in the USA) and split some large units (e.g. the former Northwest Territories in Canada) 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). We excluded islands (e.g. Japan, Taiwan and Hainan in EAS) in order to minimize the island effect on introduced species richness.

We compiled a comprehensive checklist summarizing the distribution and status as native or non-native of all species of plants ($n = 1567$) shared by EAS and NAM and present as introduced species in at least one of the regions. Botanical nomenclature was standardized according to Kartesz (1999) except for a few species whose nomenclature followed other recent literature. Presence or absence, and status as native or non-native, of each species in each geographic unit within each region were determined from a large body of literature. The distributional range for each species within each region was calculated as the number of geographic units from which the species has been reported, divided by the total number of geographic units in the region. Thus, the proportion of geographic units (i.e. the geographic range for each species within each region) varies between 0 and 1. Because the same methods of dividing regions into units and quantifying distributional ranges were used in both continental regions, there should be no systematic bias with regard to region.

We were concerned that the following factors might influence the results of this study: (a) the presence in EAS of several provinces in China largely south of 30°N, which contain extensive tropical and subtropical environments not represented in NAM; (b) large areas towards the west of the EAS region dominated by dry environments and high elevations that are unsuitable for most exotic species; and (c) differences in the relative time spans of introduced species in each region. Accordingly, we conducted parallel analyses with and without the eight southern Chinese provinces (see Fig. 1); we estimated the relative number of 'equally suitable' geographic units in each region by calculating a Simpson index of diversity (i.e. $1/\Sigma p_i^2$) based on the proportions ($p_i$) of native species occurrences in each unit ($i$); and we determined the year of introduction of as many exotic species in EAS and NAM as were available and fit the relationship between age and extent by logistic and Michaelis–Menton equations to describe the average spread of exotic species within each region.

Averages of proportional area (units) for native and non-native species in each region were compared with $t$-tests assuming unequal sample sizes and variances. Nonlinear curve fitting was done with the SAS procedure NLIN (SAS Institute, Inc. 1990).

## RESULTS

Recent exchanges of plant species between EAS and NAM have been asymmetrical. For example, there are 781 EAS native species established in NAM but only 148 NAM natives in EAS. The range extents of native species average about twice as large in NAM as in EAS (Table 1). The ranges of exotic species also are about twice as large in NAM as in EAS, whether they are reciprocal introductions or from outside of both regions. Within each region, the ranges of exotics are about half the size of those of natives. These relationships have the interesting consequence that the ranges of EAS native plants are almost identical on average in NAM as they are in EAS ($P > 0.05$), but NAM natives occupy only one-quarter the area in EAS as they do in NAM. The proportional ranges occupied by the same species on the two continents are significantly correlated (Fig. 2), with coefficients ($r$) of 0.407 (EAS natives, $n = 781$ in NAM, $P < 0.0001$), and 0.268 (NAM natives, $n = 148$ in EAS, $P = 0.001$), and 0.488 (natives from elsewhere, $n = 638$, $P < 0.0001$).

**Table 1** Distributions of the introduced species in EAS and NAM measured as proportion of geographic units occupied in both native and non-native ranges

| Region of origin | Number of species | Region of occupation* | | Relative area† | | % NAM > EAS |
|---|---|---|---|---|---|---|
| | | EAS | NAM | NAM > EAS | EAS > NAM | |
| Eastern Asia | 781 | **0.221** ± 0.172 | 0.221 ± 0.254 | 329 | 452 | 42.1 |
| North America | 148 | 0.111 ± 0.131 | **0.443** ± 0.296 | 131 | 17 | 88.5 |
| Elsewhere | 638 | 0.139 ± 0.150 | 0.315 ± 0.312 | 442 | 196 | 69.3 |

*Values are the mean ± SD. Boldface type indicates species in their native regions.

†Relative area indicates the number of species for which ranges are larger in either NAM or EAS, which is highly heterogeneous among the samples. The last column indicates the percentage of species for which the distribution in NAM exceeds that in EAS. $G_{adj} = 180$, d.f. = 2, $P < 10^{-6}$.

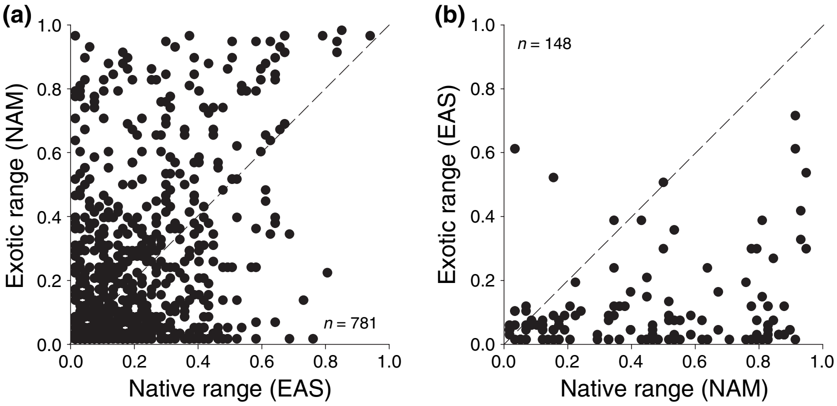

**Figure 2** Distributional relationships of trans-Pacific introduced plants. (a) Species native to eastern Asia (EAS) and exotic to North America (NAM); (b) species native to NAM and exotic to EAS. Distribution is measured as the proportion of geographic units each species occupies in each continent. Each symbol represents a single species and the dashed diagonal line in each diagram is the line of equity.

We were concerned that these results might be influenced by phylogenetic inertia and unbalanced sampling of phylogenetic groups, on one hand, and by non-normal distribution of range extents, on the other. Accordingly, we assigned each species to orders, families, and genera (according to the Angiosperm Phylogeny Group II 2003 for flowering plants), conducted a nested analysis of variance, and calculated variance component correlations with the SAS proc NESTED (SAS Institute, Inc. 1990) for the groups of species native to EAS, NAM, and elsewhere. We also $\log_{10}$-transformed and arcsin-square root-transformed the proportional areas. Most of the variance in range area resided at the genus and, especially, species levels, as has been found in studies of other groups of organisms (Gaston 1998; Scheuerlein & Ricklefs 2004). Thus, phylogenetic inertia is not a concern with our data on plant distributions. Where suitable variance existed, correlations between ranges in EAS and NAM at species and genus levels did not differ significantly from correlations within the whole data set, and transformations had little effect on the analyses (results not shown).

Times since introduction differed little between the two regions (EAS: 147 years ± 128 SD, range 26–599, $n = 55$; NAM: 159 years ± 79 SD, range 17–405, $n = 187$; $F_{1,240} = 0.73$, $P = 0.39$), although a non-parametric rank-order test found a significant difference between the two samples (Kruskal–Wallis $\chi^2 = 9.1$, d.f. = 1, $P = 0.0025$). The relationship between proportional areas occupied and time (Fig. 3) clearly shows an increase in geographic range, as one would expect. We fit this relationship within each region with a logistic equation: range = asymptote/{1+exp[−$k$(time-inflection)]}, where the asymptote is the plateau for range area within a region, the inflection point is the time at which half the asymptotic value is achieved, and $k$ is the rate at which the asymptote is achieved (year$^{-1}$). Compared with exotics in NAM, the fitted curve for EAS had a younger inflection point (63 years ± 14 vs. 116 ± 21), a lower asymptote (0.16 ± 0.02 vs. 0.87 ± 0.10), and more rapid approach to the asymptote (0.046 ± 0.035 vs. 0.012 ± 0.003). We also fit a Michaelis–Menton function to the data: range = asymptote × time/($b$ + time), where $b$ is the time to half the asymptotic value. The results were similar, with exotics in EAS taking less time to half of the asymptote ($b$ = 79 ± 54 vs. 132 ± 10) and reaching a lower asymptote (0.22 ± 0.06 vs. 0.98 ± 0.44). Thus, neither age nor rate of spread can explain the smaller areas occupied by exotic species in EAS compared with NAM. Moreover, the average distribution for EAS natives in NAM (0.22) appears to be further below the asymptotic range (0.87) than NAM natives exotic to EAS (0.11 vs. 0.16). Thus, the observed difference between the proportional ranges occupied by exotics in NAM and EAS will likely increase with time.

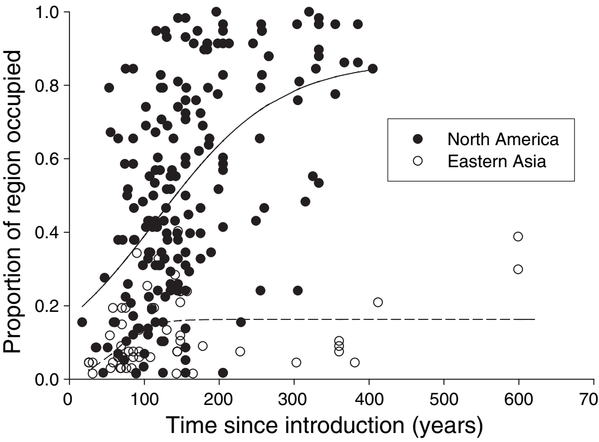

**Figure 3** Comparison of the proportional range area of introduced plants as a function of time since introduction in EAS and NAM using all introduced plant species for which the year of introduction has been identified. The lines are fitted logistic equations (see text).

To examine whether the presence in EAS of extensive tropical and subtropical environments not represented in NAM influences the results, we repeated the analyses in Table 1 for EAS and NAM excluding the eight provinces in China that lie primarily south of 30°N (Fig. 1). This had a negligible effect on the proportional ranges of both natives and exotics in EAS, but slightly increased the proportional ranges of both types of species in NAM (results not shown). The latter effect reflects the fact that native and exotic species limited to the eight southern provinces of China have smaller than average distributions in NAM.

We determined the number of equally suitable geographic units in EAS and NAM taking into consideration the relative proportions of all native species in each of the units within each region. The Simpson index for EAS was 44.8 equivalent units (66.9% of 67 units total) or 38.5 (65.3% of 59 units) when the units below 30°N were removed. In NAM, there were 51.7 equivalent units, which is 89.1% of the 58 units. Once again, removing the eight EAS units below 30°N had a negligible effect. It is also clear, however, that NAM is more hospitable for native species (and presumably also for exotics) than EAS. The relative areas suitable for plant species (NAM/EAS = 0.891/0.653 = 1.36) suggest that the values for EAS distributions in Table 1 should be increased by about one-third to place the comparisons on an equal basis. Thus, the observed distributions of native plants in EAS (0.221 × 1.36 = 0.301) are larger on average than in NAM (0.221). However, the difference in relative suitable area does not account for the striking decrease in ranges of exotics introduced to EAS compared with their native regions (NAM, 0.443 > 0.111 × 1.36 = 0.151).

Introduced NAM species in EAS occupy only 25% – or 25 × 1.36 = 34% when the relative suitable area is taken into consideration – of the proportional range filled by the same species in their native regions. By comparison, EAS native plants have spread almost as broadly in NAM as in their home region. Considering only the trans-Pacific disjunct species resulting from colonization between EAS and NAM, the asymmetry of invasion applies to areas of lower diversity in the north of each region as well as areas of higher diversity in the south (Fig. 1). That is, within each region, areas having many native source species also harbour many established introduced species, with the higher numbers of transplanted species occurring at lower latitudes (Fig. 4).

## DISCUSSION

The comparisons presented here are the most comprehensive to date relating distributional areas of introduced species in native and non-native regions. Clearly, most of the introduced species included in our analysis would not be considered invasive because they have small distribution ranges (Williamson & Fitter 1996). Nonetheless, many species have restricted distributions within their native regions, and geographic extents in both native and introduced areas were correlated (Fig. 2). This suggests that variation in range reflects species-specific characteristics and that species with larger distributions in their native regions would fill their potential distributions in non-native regions more fully and quickly (Peterson 2003; Pyšek *et al.* 2004; Svenning & Skov 2004). Although it is also possible that some exotic regions lack the range of environments occupied by species in their native regions, the distributions of habitat types are roughly comparable in EAS and NAM and the numbers of introduced and native plants are highly correlated over geographic units (Fig. 4) suggesting overall comparability between native and non-native environments.

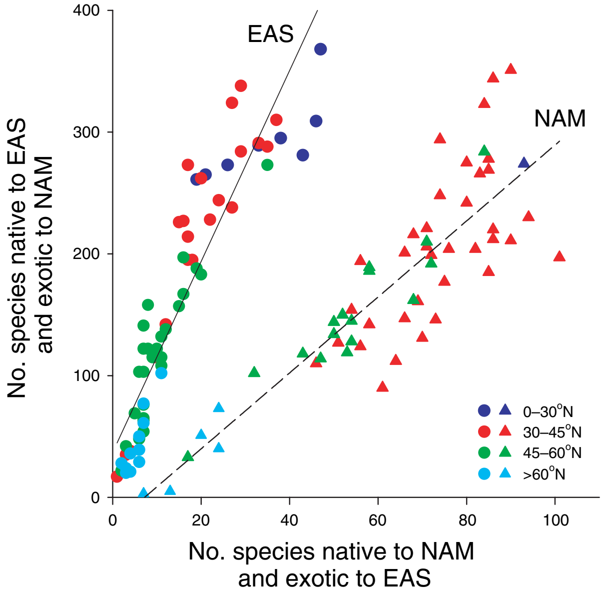

**Figure 4** Relationships between the number of species native to NAM and exotic to EAS and the number of species native to EAS and exotic to NAM on each continent. Each dot represents a geographic unit; colour is keyed to the latitude of the mid-point of each unit. Although geographic units tend to increase in area towards higher latitudes, and diversity generally increases with area, the size of a geographic unit was statistically not a significant effect on the relationship between number of native and introduced species.

Native vs. non-native region and EAS vs. NAM exerted strong statistical effects on the geographic ranges of north temperate native and exotic plant species. Average proportional range of native species is much smaller in EAS than in NAM, notwithstanding that the regions contain similar diversity of ecological zones. Indeed, the product of total species richness and the average proportional range occupied per species varies little between EAS [28 200 species (H. Qian, unpublished data) × 0.221 = 6232] and NAM (15 300 × 0.443 = 6778) indicating nearly complete compensation between species richness and geographic range. Within each region, areas having many native species also have more introduced species, with the higher numbers of transplanted species occurring at lower latitudes (Fig. 1). This observation seems to be consistent with the habitat suitability hypothesis (Blackburn & Duncan 2001) that invasion success (establishment and spread) depends on the abiotic conditions at the introduction locations.

Region of origin appears to have little influence on spread in non-native regions. The spread of exotics from outside EAS and NAM (primarily from Europe) shows a similar pattern of nearly twofold greater area in NAM (Table 1). Time since introduction also cannot explain differences in geographic extent between regions because plant introductions from around the world started even earlier in EAS than in NAM and times since introduction across the Pacific differed little between the two regions.

## Regional diversity and biotic resistance

The smaller proportional ranges of non-native species in the region with more native species could be caused either by interspecific competition or by different ecological heterogeneity within regions. Higher richness and greater ranges of EAS natives in NAM than of NAM natives in EAS support the hypothesis that regional diversity resists invasion. First, native species appear to be self-inhibiting in the sense that average native range area is inversely related to the size of the regional flora. Second, the spread of introduced species from NAM is constrained to a greater degree in EAS than vice versa. Indeed, EAS exotics occupy almost as much suitable area, on average, in NAM as they do in their native region. Thus, the tendency of non-native species to have restricted ranges is partly lifted for EAS natives in NAM. The relatively small numbers of NAM natives in EAS might also reflect, in part, a low establishment rate following introduction; unfortunately, no reliable data exist for either region on the proportion of introduced species that become established. Overall, the influence of regional diversity on the spread of introduced species may operate through more numerous native competitors and enemies, reducing opportunities for introduced species to establish themselves and spread. This may be the case for NAM natives in EAS. Species introduced from diverse to depauperate regions, as in the case of EAS natives in NAM, would avoid the abundant competitors and enemies in their native ranges and experience ecological release, allowing them to spread widely.

Although the poor performance of non-native species in EAS may be associated with a diverse native flora (and, perhaps, fauna), at least at the regional level, the extent to which invasion resistance is caused locally by competitive exclusion or unusually high pest pressure in EAS remains an open question. Although relevant data are largely lacking for EAS, higher regional diversity (Qian 2002), typically translating into higher local diversity and species turnover (Srivastava 1999; Ricklefs 2004), might also signal a more specialized flora whose individual species are highly competitive. Besides higher diversity, natural plant communities in EAS also include a larger proportion of species with tropical affinities than NAM. These plants could further restrict the spread of species introduced from other north temperate regions, either because they uniquely fill ecological niche space or because they support a broader range of herbivores and plant pathogens.

## Enemy escape

Many exotic species can spread widely and rapidly in non-native regions because they have left behind predators, herbivores and pathogens in their native regions, and failed to gain new ones in their adopted homelands (Keane & Crawley 2002). However, we found that non-native species are, on average, more narrowly distributed in non-native ranges than in their native ranges. This pattern applies to EAS native species in NAM when the relative ecological suitability of the regions is taken into account. These results contradict the enemy escape hypothesis in general, but the test is weakened by potential confounding factors. One of these is that introduced species have not had enough time to reach the full extent of their distributions in exotic areas. Logistic curves fitted to the relationship between proportional area and years since introduction indicate plateaus of 0.87 in NAM and 0.16 in EAS. The value for NAM is considerably higher than that for native species (0.448), and the value for EAS is not markedly lower than that for native species (0.195). It is clear, however, that the average range area in the sample of EAS species in NAM for which year of introduction is available (0.52 ± 0.29 SD, $n = 187$) is not representative of the whole sample of exotics (0.221). In contrast, NAM natives with known dates of introduction to EAS have similar ranges (0.13 ± 0.10 SD, $n = 55$) as the whole sample (0.111). On balance, it would appear that the eventual plateau ranges for exotics are similar to those for native species. The fitted logistic functions also suggest that exotics in EAS approach the regional plateau in geographic range as rapidly, if not more so, as in NAM (see Fig. 3 and fitted values of $k$). Thus, it is unlikely that different times of colonization in the two regions are responsible for the differences in realized range areas. Although the enemy release hypothesis is not supported for most species by the distributional range data of this study, it is possible that the effect of enemy release may occur at smaller spatial scales or may be observed when local abundance data are examined.

## Human influence

The relatively larger ranges of EAS species in NAM and smaller ranges of NAM species in EAS could also be caused at least in part by human movement and transport patterns within each region. Most exotics have been introduced in the last 400 years (Fig. 3). Thus, although the prior land use practices might have selected for weedy qualities in exotic species from EAS, extensive human migration during the period of introductions in NAM, facilitated by mechanized transportation, likely promoted the rapid spread of non-native species (di Castri 1989; Rejmánek 2003). EAS is more densely populated than NAM, but movement within the region has occurred extensively only in the last two decades, after China opened its doors to the world and initiated economic reforms (Fan 2005). Thus, the distribution patterns of exotics in the introduced regions support the hypothesis that human migration promotes their spread. Different agricultural practices might also be important. Federal agencies, such as the U.S. Natural Resources Conservation Service (NRCS), selected and widely planted numerous exotic grasses, shrubs, trees, and flowering plants. However, the level to which such activities differed between regions and contributed to observed patterns requires further investigation.

## CONCLUSION

Distributions of introduced plants highlight the influence of regional factors on the spread of introduced species in non-native regions and suggest that, to some extent, regional native plant diversity constrains spread. Comparisons of the distributions of complete samples of introduced species with ranges in native regions provide no general support for the enemy release hypothesis, which predicts larger ranges in the region of introduction. The extensive spread of exotics in NAM is consistent with the biotic resistance hypothesis, although transportation networks in both regions undoubtedly facilitated spread. Geographic extent often differs widely among close relatives (Gaston 1998) or among populations of the same species in different regions, emphasizing the influence of idiosyncratic factors. However, the large samples of introduced species used in this study allow one to identify regional differences in their relative geographic spread. Although it is difficult to attribute these differences to particular factors that vary between regions, consistency or inconsistency with predictions concerning controls on the spread of exotics does strengthen some hypotheses (biotic resistance, human-assisted spread) and weaken others (enemy release, selection of weedy properties). The analysis of large samples also cautions against drawing general conclusions from studies of a smaller number of introduced species, which would be a biased sample if their choice was based on their relative success.

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