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Plant Invasions in China: What Is to Be Expected in the Wake of Economic Development?

EWALD WEBER AND BO LI

Developing and transitional countries undergoing rapid economic development will face growing problems with biological invasions because international commerce will bring new invaders. We assessed the potential for plant invasions in China by comparing the country's current invasive flora with that of the United States, a nation of similar size and latitudinal span but with a different history of plant introductions. Invasive plant species richness in the United States is about twice as high as it is in China. The remarkably lower fraction of invasive woody plants in China suggests that more alien trees and shrubs could invade Chinese habitats. Road density correlated with invasive plant species density among geographical units, with numbers for China lower than those for the United States. The data suggest that China has been invaded less than the United States has, and that the potential for new plant invasions in China is high. Measures toward preventing biological invasions are needed and timely—steps taken now can prevent adverse impacts from future invasions.

Keywords: Asia, introduced species, invasive species, prevention, risk assessment

ost developing countries are located at low latitudes and thus share a substantial part of the world's biological diversity, because species richness increases toward the equator. However, economic pressure and habitat degradation in these countries pose serious threats to the conservation of species and habitats (Valladares-Padua 2006). Another major threat is the spread of invasive alien species, defined as "alien species whose establishment and spread threaten ecosystems, habitats or species with economic or environmental harm" (McNeely et al. 2001). Invasive alien plant species can transform species-rich native animal and plant communities into species-poor stands dominated by these alien species. One example is the North American grass Spartina alterniflora, which is invading coastal wetlands in China (figure 1; Cheng et al. 2006). Invasive species cause high costs (Pimentel et al. 2000) and thus are of concern to both ecologists and economists. The spread of invasive species is strongly linked to human activities (e.g., species introductions and habitat degradation). Species introductions, both intentional and accidental, are usually the result of trade, which delivers species to new regions where they may become established. Degradation by disturbances such as fire, grazing, or urbanization can make habitats suitable for alien weeds; such degradation often precedes an invasion (Richardson and Pysek 2006).

Economic development fosters biological invasions because growing national and international trade increases the number of species introductions and the likelihood of accidental escapes (Mack and Lonsdale 2001, Levine and D'Antonio 2003). It is therefore not surprising that alien species density is positively related to indicators of economic development (figure 2). The nonlinear nature of the relationship suggests that well-developed countries may share an above-average number of alien species, although the variation among these countries is rather large. Countries achieving a higher level of economic development will most likely face an increase in invasive species.

Only a certain fraction of the many species that humans move to new regions will be able to establish self-propagating populations ("naturalized species"), and only few of these will eventually be able to proliferate and exhibit invasive behavior. However, the greater the number of naturalized species in an area, the higher the likelihood that invasive species are among them.

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Figure 1. The grass Spartina alterniflora invades the Chongming Dongtan National Nature Reserve on Chongming Island in the Yangtze River estuary, a Ramsar Convention Wetland of International Importance. The grass converts mudflats to meadows, thereby replacing native Scirpus mariqueter and Phragmites australis and affecting birdlife by hindering wading birds in their search for food. The grass, which is native to North America, was introduced into China in 1979 for sand stabilization. Since then, it has spread rapidly along the eastern coast of China.

The above explanations suggest that the numbers of invasive species and invasion incidents are likely to increase in less-developed countries undergoing rapid economic development. Although it would be helpful in planning management strategies to be able to predict such increases, it is hard to determine which new species will become invasive. The best approach may be to compare a developing country with a developed one that is similar in size and biomes.

In this article, we present China as a case study and compare it with the contiguous United States. We focus on invasive alien plants and ask whether the differences in the two nations' current invasive alien floras allow researchers to draw conclusions about future plant invasions in China. We analyze the invasive alien floras of the two countries with regard to richness, diversity, and geographic distribution, and we explore the relationship of number of invasive alien plant species and regional socioeconomic factors. We then sketch future scenarios with regard to plant invasions in China.

China: A hotspot of threatened biodiversity

China, the third largest country in the world, is transitioning from a developing country to a highly developed nation. Its gross domestic product grew at an average annual rate of 9.4% between 1979 and 2002—the highest growth rate in the world (World Bank 2003). China also harbors a strikingly rich flora and fauna, many species of which are already threatened (SEPA 1998, Li and Wilcove 2005). Its plant diversity, with 31,000 species of vascular plants, ranks third in the world

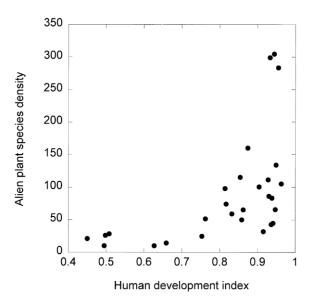


Figure 2. Relationship between the human development index (HDI) and alien plant species density for 26 countries. The HDI is a composite index measuring a country's well-being, taking into account human welfare, life expectancy, and standard of living. Invasive plant species density is the number of invasive plant species divided by the logarithm of the area. Source: Data for the HDI were obtained from UNDP (2006), and data for alien plant species numbers are from Vitousek and colleagues (1997).

(after Brazil and Colombia), which means that China is one of the world's megadiversity countries (SEPA 1998). South-central China is one of the world's 25 biodiversity hotspots identified by Myers and colleagues (2000).

China's rich biodiversity is increasingly threatened by environmental problems associated with a high population density and the rapid economic development of the last two decades (World Bank 2003, Li and Wilcove 2005). Largescale degradation of habitats and an alarming loss of biodiversity (Crooks et al. 2001) have resulted in several pleas to take measures to conserve China's unique biodiversity and the sustainable use of its natural resources (Gu 1998, Huang

et al. 2002, Liu et al. 2003, López-Pujol and Zhao 2004, Wu and Shi 2004, Yang et al. 2004).

Invasive species in China have already caused considerable economic losses (table 1), amounting to US\$14.5 billion annually (Xu et al. 2006). The impacts on native species and ecosystems have gone largely undocumented in that country (e.g., the outcompeting of native water plants by the introduced water hyacinth [Eichhornia crassipes] in Dianchi Lake, Yunnan province [Wu 1993]). Clearly, damage to natural ecosystems will occur—species that have proved to be highly invasive in other countries are now present in China.

China and the United States: Different preconditions

China and the United States are of similar size and latitudinal span (table 1) and have similar landscape features and climates, but they are fundamentally different in ways that affect the invasibility of their ecosystems. These differences are centered on the history of human impacts, the history of species introductions, the geomorphology and distribution of climates, and the specific composition of the flora.

History of human impacts. China boasts one of the world's oldest uninterrupted civilizations, dating back more than 4000 years (Lu 2006). Its advanced civilizations built infrastructures, and Chinese agriculture can be traced back 7500 years or more. Ecologically, this means that China's landscapes have been exposed to human impacts for many centuries. At the same time, China's geographical and self-imposed isolation meant that interactions with other peoples were kept to a minimum, and hence large-scale species introductions were few. Both trade volume and the number of international trade relationships have increased rapidly since the 1980s, however (Crooks et al. 2001, Normile 2004).

The most ecologically significant event in North America's history has been the country's colonization by Europeans,

Table 1. Geographic and economic data for China and the United States.

Datum	China	United States
Area (km²)	9,572,900	9,809,155
Population	1.3 billion	300 million
Population density per km ²	130	32.7
Human development index ^a	0.755	0.944
Gross national product (GNP)	US\$2,264 billion	US\$12,970 billion
Tourists per year	41.8 million	46.1 million
Railways (km)	61,015	141,961
Roads (km)	1,809,829	6,378,154
Area forested (percentage)	17.1	23.0
Deforestation rate per year (km²)	< 26,766	< 2961
Protected area (percentage)	7.8	25.9
Annual cost of invasive alien species	US\$14.5 billion	US\$137 billion ^b
Per capita annual cost of invasive alien species	US\$12.1	US\$492
Cost of invasive alien species (percentage of GNP)	0.64	1.06

Note: Unless otherwise indicated, data are from www.wikipedia.org and from standard reference works.

beginning in 1492 (Crosby 1986). Human impacts on the American landscapes were not intense until the arrival of Europeans (Cronon 2003). Native American culture was largely one of hunting and gathering, and thus did not impose strong pressures on the natural resources. European colonization resulted in large-scale ecological transformation, however, coupled with a steady influx of alien species.

The differences in the history of alien species' introductions in China and in the United States explain the differences in the current pool of invasive species in the two countries. Although plant introductions have a long history in China, the introduced species stem mostly from Eurasia, not from distant overseas regions (Xie et al. 2001). In the past, the number of introduced plant species in China was rather low: by 1970, 837 plant species had been introduced (Ding and Xie 1996). In contrast, North America received species from all over the world, notably European species that were brought to the colonies to support a European lifestyle (Crosby 1986).

Geomorphology and climate. With other Asian countries, China shares the Himalayas, the world's highest mountain range, and its terrain generally descends from west to east, forming three large steps. The highest of these is the Qinghai-Tibet plateau in the west, with an average elevation of 4000 meters above sea level. This tableland covers about 23% of China's area; no comparable landscape feature exists in the United States. In contrast to China's mountainous geography, lowland plains cover a large area in the United States. Although the climate of both nations ranges from subtropical to cold temperate, the amount of area covered by these climatic zones differs. In the United States, a subtropical climate is confined to southern Florida and some stretches of lowland Texas, whereas a large area of southeastern China experiences subtropical conditions (Hou 1983). In addition, some small regions in the south of China have a tropical climate,

b. Pimentel et al. 2000.

but China lacks the Mediterranean-type climate that is present in California.

Clearly the two nations have both similarities and dissimilarities in their natural geography, and they are correspondingly different with regard to invasion incidents. Nonetheless, the close floristic affinities between eastern Asia and North America have long fascinated botanists (Qian and Ricklefs 1999, Guo 2002)—the two areas share more than 100 genera of plants. (However, China has almost twice as many vascular plants as the United States [table 2].) Thus, although China and the United States differ in population size and living standards (table 1) as well as in some aspects of natural geography, comparing the biological invasions of these two nations might give insights into what might be expected in China in the future.

Methods and results

We gathered lists of invasive plant species for China and the United States, using a number of sources for China (see Weber et al. 2008) and the US Department of Agriculture PLANTS database (USDA NRCS 2007), complemented with regional lists of invasive plant species (e.g., Langeland and Burks 1998, Cal-IPC 2006), for the United States. Taiwan and Hong Kong were included in the data set for China. We excluded Alaska and Hawaii, and included Puerto Rico, in the data set for the United States.

Each list represents a presence/absence table for Chinese provinces and US states, respectively. We compared the specific composition of the two invasive floras with respect to life-form distribution and taxonomic diversity. Species were allocated to life-forms according to Raunkiaer (1934). Provinces and states were the spatial units used to analyze species-area relationships and to seek correlates of invasive species richness. Road density was taken as a surrogate for the degree of economic development at the regional scale. Species density was expressed as *N*/log(area), where *N* is the number of species in a province or state.

Species richness and overlap. The number of invasive plant species reported in the United States was about twice as high as that in China (table 2), and the United States has spent considerably more than China to combat invasive species (table 1). Taking provinces and states as units, mean invasive species richness differed significantly between China and the United States (t-test: F = 363.9, p < 0.0001), as did mean invasive species density (t-test: F = 280.4, p < 0.0001). In addition, the invasive flora of the United States was more diverse than that of China. In the United States, invasive plants came from more than 300 genera, whereas in China, there were only 76 genera (table 2). The species-to-family ratio was higher in the United States than in China.

The pooled species list of China and the United States yielded 731 species, a large proportion of which was invasive in only one of the two nations (30% in China and 63% in the United States [table 2]). The number of shared species was 51, or 7%.

Table 2. The native and invasive flora of mainland China and the contiguous United States.

	China	United States
Native vascular plant species	31,000	17,000
Introduced plant species	?	5,000
Invasive plant species	270	519
Families among invasive plants	57	96
Genera among invasive plants	76	330
Diversity of invasive plants	4.74	5.41
Species not invasive in the other nation	219	461

Note: Diversity of invasive plants is the ratio of species to families. Source: Native species numbers are from Flora of China (2007) and Flora of North America Editorial Committee (1993).

Ecological differences. Classifying invasive alien plants according to their life-forms gives a picture of their ecological diversity. The life-form distribution of invasive plants in the United States was remarkably different from that in China in two important aspects (figure 3). In the United States, many more woody plants and climbers were present among invasive plants, and in China, annuals were more strongly represented. When considering only terrestrial plants, the frequency of woody invasive plants was significantly higher in the United States than in China ($X^2 = 9.38$, p = 0.002). The higher proportion of succulents in China is due to invasive *Opuntia* species.

Correlates of invasive plant species richness. Our results demonstrate a clear relationship between road density and invasive alien plants density (figure 4). Road density was lower in Chinese provinces than in US states, as was the density of invasive alien plants. Linear regressions were significant for both nations (China: $r^2 = 0.46$, p < 0.001; United

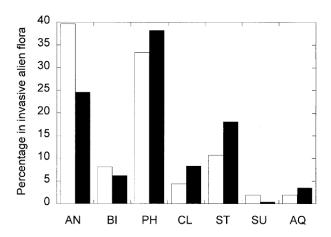


Figure 3. Life-form distribution of the invasive plants of China (white bars) and the continental United States (black bars), respectively. Abbreviations: AN, annuals; AQ, aquatic plants; BI, biennial herbs; CL, climbers; PH, perennial herbs; ST, shrubs and trees; SU, succulents.

States: $r^2 = 0.53$, p < 0.001), with the slope being steeper for China than for the United States (figure 4).

The relationships between area or population density and the number of invasive plant species were similar for the two nations, but values for invasive plant species richness were, overall, lower in Chinese provinces than in US states (figure 5).

Conclusions

The numbers and kinds of invasive plant species in a region are governed by factors such as environmental conditions and species traits, as well as by factors associated with human activities, such as planting frequency, choice of species, and ecosystem disturbance (Mack et al. 2000, Kowarik 2003).

Species richness. It is striking that the overall number of invasive plant species is lower in China than in the United States, considering that serious plant invasions have taken place in China (Xie et al. 2000), and it is unlikely that habitats in China are less invasible than comparable habitats in the United States, especially given that China's biomes have been heavily disturbed for much of the country's history, making them susceptible to colonization by alien weeds. The lower number of invasive plant species suggests that in China the potential for additional invasions is high. Moreover, the

specific composition of the two invasive floras is remarkably different. The taxonomic diversity of invasive plants is higher in the United States than in China, especially at the level of genera, reflecting a wider range of functional groups. The species overlap of only 7% between the two invasive floras may result from taxonomic differences. In addition, many species may be native to one nation but invasive in the other, and thus a compilation of common invasive species would exclude them. For example, several honeysuckles (Lonicera) of Asian origin are invasive in the United States, and many species invasive in China are native to the United States (Weber et al. 2008).

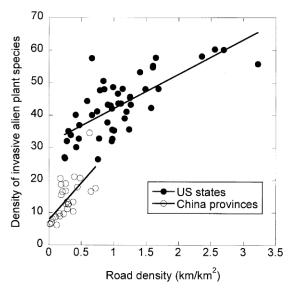


Figure 4. Relationship between road density and invasive plant species density for states of the contiguous United States and provinces of China. Road density is the total length of roads divided by the area, and invasive plant species density is the number of invasive plant species divided by the logarithm of the area. Linear regression lines are indicated for each data set.

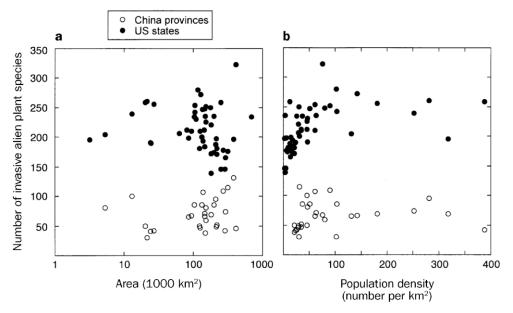


Figure 5. (a) Relationships between invasive plant species richness and area for Chinese provinces and US states, and (b) between invasive plant species richness and population density.

Life-forms. The proportion of annual plants is higher in China than in the United States, which may be attributable to geomorphology and to the numerous agricultural weeds—many of them annuals—among China's invasive plants. China's high plateaus are invaded primarily by annual and perennial forbs (Weber et al. 2008). The presence of invasive

plants in the Qinghai-Tibet plateau confirms that alien plant species can reach high elevations and adapt to these environments (Pérez 1998, Khuroo et al. 2007).

That China has a smaller fraction of woody plants than the United States does may indicate that fewer alien trees and shrubs have invaded suitable habitats in China, or that more woody invaders are present but not yet recognized as invasive. A larger number of invasive trees and shrubs may be expected in China, since these life-forms are among the most serious plant invaders in the world (Binggeli 2001, Weber 2003). In fact, tree species that became invasive in other countries are cultivated in China (e.g., *Eucalyptus globulus* and *Pinus radiata*; Chen et al. 2006). We do not know whether these species have become naturalized in China; that question remains to be answered by further surveys.

Regional patterns. China's overall lower species richness corresponds to findings at the provincial and state levels for China and the United States, respectively. The almost complete nonoverlap between Chinese provinces and US states in figures 4 and 5 demonstrates that the lesser degree of invasion is evident at the regional as well as at the national scale. The kind of distribution data we used (e.g., presence/absence in provinces and states) does not allow us to perform in-depth analyses of plant invasions among different habitat and climate types; such an approach would require fine-scale distribution data, which are currently not available for China. Nevertheless, our analyses show that the relationship between area or population size and invasive plant species density and richness is similar for China and the United States, but different in absolute numbers. Thus, the number of invasive plants overall is not lower in China because some provinces have exceptionally few invaders; rather, it is a general pattern throughout the country.

Transport corridors are dispersal vectors for invasive plants and also provide suitable habitats for population buildups of invasive plants. Roads allow alien weeds to reach remote areas, including natural, hitherto undisturbed areas. Several studies have found close relationships between alien species richness and road density (Arroyo et al. 2000, McKinney 2002). For Chinese provinces, the steeper slope of the regression line compared with US states (figure 4) implies that the invasive species spread faster as road construction advances, and that the provinces are less saturated with invasive plants than are US states.

Lacking invaders. At least 80 species invasive in the United States are not reported as invasive in China, although all of them are serious invaders of natural areas in other countries, according to Lowe and colleagues (2000) and Weber (2003). For most of these species, we do not know whether they are grown in China or have become naturalized. Australian pine (*Casuarina equisetifolia*) is widely cultivated in China (Zhong et al. 2005) and naturalized populations are likely to exist; the same applies to cultivated eucalypts and pines. Catclaw mimosa (*Mimosa pigra*) has recently spread in Vietnam, invading wetlands and national parks (Triet et al. 2004); it may be only a question of time until catclaw mimosa reaches China. Many plant species not reported to be invasive in China would very likely find suitable climatic conditions

Table 3. Twenty plant species that are serious invaders in at least three continents, including North America, and are not native to China nor reported to be invasive there.

Species	Country in which species is native	
Black wattle (Acacia mearnsii)*	Australia	
Crofton weed (Ageratina adenophora)	Mexico	
Hottentot fig (Carpobrotus edulis)	South Africa	
Australian pine (Casuarina equisetifolia)	Asia, Australia, Pacific	
Pampas grass (Cortaderia selloana)	South America	
Artichoke (Cynara cardunculus)	Africa, Eurasia	
Scotch broom (Cytisus scoparius)	Africa, Europe	
Surinam cherry (Eugenia uniflora)	South America	
Yellow ginger (Hedychium flavescens)	India, Nepal	
Velvet grass (Holcus lanatus)	Africa, Eurasia	
Paperbark tree (Melaleuca quinquenervia)*	Asia, Australia, Pacific	
Catclaw mimosa (Mimosa pigra)*	Africa, South America	
Brazilian watermilfoil (Myriophyllum aquaticum)	South America	
Kikuyu grass (Pennisetum clandestinum)	Africa	
Elephant grass (Pennisetum purpureum)	Africa	
Sweet pittosporum (Pittosporum undulatum)	Australia	
Strawberry guava (Psidium cattleianum)*	South America	
Lemon guava (Psidium guajava)	South America	
Brazilian peppertree (Schinus terebinthifolius)*	South America	
Wandering jew (Tradescantia fluminensis)	South America	

Note: Asterisks denote species belonging to the "100 worst invaders of the world" (Lowe and colleagues 2000).

and habitats there if they were introduced, making them potential invaders of natural habitats. Among those plant species not currently invasive in China are 5 that are on the list of the 100 worst invaders of the world (table 3; Lowe et al. 2000).

Implications for invasive species management in China. A comparison of the invasive flora of the United States and

China suggests that Chinese provinces are likely to become more invaded by alien plants as economic development progresses, despite some differences between the two countries in climate and elevation. Paralleling our findings for plants, the proportion of vertebrate species threatened by alien species also is much higher in the United States than in China (Li and Wilcove 2005). We believe that plant invasions will increase in China because the country's rapidly growing international trade will bring new invaders, and the disturbed riversides, secondary forests, overgrazed grasslands, and other results of widespread degradation of the land offer suitable habitats for them.

Although China has a long history of species introductions, massive plant introductions from overseas into China are a recent phenomenon (Xie et al. 2001). Many invasions undergo a time lag between the introduction of a species and its rapid range expansion; this lag can exceed 100 years (Kowarik 2003). The implication for China is that new invasion incidents may arise not only from new species introductions but

also from alien plant species already there but in a lag phase. A complete inventory of all naturalized plant species in China is indispensable for identifying such potentially invasive species.

Plant invasions may hit China's economy hard if preventive steps are not taken. Because land degradation affects mainly marginal cultivated and barren lands, plant invasions may affect the livelihood of the poorer farmers in the country, who must rely on soils of poor quality (Crooks et al. 2001). China and other Asian countries are in a position to recognize the potential danger and to take adequate measures now, before new invaders gain a foothold and existing invaders begin to spread over large areas. An efficient invasive species management program in China would do the following:

- Assemble information on the whole set of naturalized alien species
- Conduct ecological impact assessments and risk assessments for species to be introduced
- Rank invasive species by priority and compile short lists of species that need monitoring or for which prevention of establishment is feasible
- Strengthen international collaborations and research on invasive alien species

Moreover, China has been recognized as a potential source of new invasive species in the United States because trade between the two nations is increasing (NRC 2002, Callaway et al. 2006). The intentional movement of species from China to the United States (for the horticulture industry, e.g.) would involve primarily native Chinese plants, but accidental introductions may occur as well, which would bring new weedy plants to North America, plants that are not necessarily native to China. It is not unusual for invasive plant species to be introduced from their native range to a secondary range, and from there to other places. Again, close international collaboration can help protect national borders and reduce the risks of new invasions into both countries.

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