A Geographic Assessment of the Risk of Naturalization of Non-native Woody Plants in Iowa[1]

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Abstract

The objective of this study was to determine whether patterns of native distributions of naturalized woody plants and their relationships to climatic analogs can serve as a sound basis to help identify high- and low-risk regions from which to introduce new woody plants to Iowa. We compared the native ranges of 28 non-native species naturalized in Iowa with those of 72 different, non-native species widely cultivated in Iowa, but with no record of naturalization. From this comparison, we tested two related hypotheses: (1) regions with the highest number of native species that have naturalized in Iowa have a significantly higher proportion of naturalizing species than predicted by the overall ratio of the number of naturalizing species to the total number of non-native species studied; and (2) regions identified as climatic analogs to Iowa conditions, based on important determinants of woody plant adaptation, have a significantly higher proportion of naturalizing species than predicted by the overall ratio of naturalizing species to the total number of non-native species studied. We discovered that the two regions with the highest number of naturalizing species (in southeastern Europe and northeastern China) have a significantly higher proportion of naturalizing species than would be predicted by chance alone. Two of the five regions identified as climatic analogs to Iowa conditions (in northeastern and central Asia) also displayed significantly higher proportions of naturalizing species, while a third (in southeastern Europe) was statistically significant only at the 10% level.

Index words: climatic analog, distribution, native range, tree, shrub, exotic plant, naturalize, invasive.

Significance to the Nursery Industry

The North American nursery and landscape industry has long advocated the introduction of non-native woody plants to lend diversity and interest to managed landscapes. Unfortunately, a small proportion of non-native species (*Rhamnus cathartica* and *Rosa multiflora*, for example) have become serious pests. This has caused some green-industry professionals and government agencies to adopt policies that strongly favor or exclusively use native plants. Ideally, a balance should be struck between prohibiting all non-native species and the uninformed introduction of potentially invasive, non-native woody plants. In this research, we found that a geographic analysis including climatic analogs and native ranges of both naturalizing and non-naturalizing species was a valuable predictive tool for identifying high-risk regions in Europe and Asia that may serve as future sources for naturalizing woody plants in Iowa. Geographic risk analysis is no substitute, however, for field monitoring and early identification of plants escaping cultivation. A vigilant and conscientious team of land managers, botanists, horticulturists, and nursery professionals is still the best safeguard against the introduction and spread of invasive landscape plants.

Introduction

North Americans rely upon a wide range of introduced trees, shrubs, and vines as important sources of food and forest products, as well as for urban horticulture, amenity and wildlife plantings, and windbreaks. Unfortunately, a small proportion of these species have become serious invasive pests, disrupting well-established native plant communities or functioning as range and agricultural weeds (36). Notable examples in Iowa include *Rhamnus cathartica* and *Rosa multiflora*. These and other invasive plants in the United States, along with information about the threats these plants cause, are well documented in databases maintained by the U.S. Department of Agriculture — Natural Resources Conservation Service and the Plant Conservation Alliance — Alien Plant Working Group (24, 33). Other introduced woody plants are not yet serious pests, but have escaped cultivation and may become invasive, a pattern consistent with data assembled for plants in many parts of the world (15, 17, 31, 50).

There are two other important sources of potentially invasive woody plants worth noting. The first group consists of those species that are not (or are only rarely) cultivated, for which we may know little about their range of adaptation and reproductive biology. The second includes new populations of commonly cultivated plants, which may prove more invasive than populations already present in a region.

Nursery and landscape professionals and their clients have great interest in expanding the range of plants that are functional, aesthetically pleasing and well adapted to managed landscapes. To accomplish this goal, plant explorers, horticulturists, and other interested parties have routinely introduced new plant species and populations into the market-

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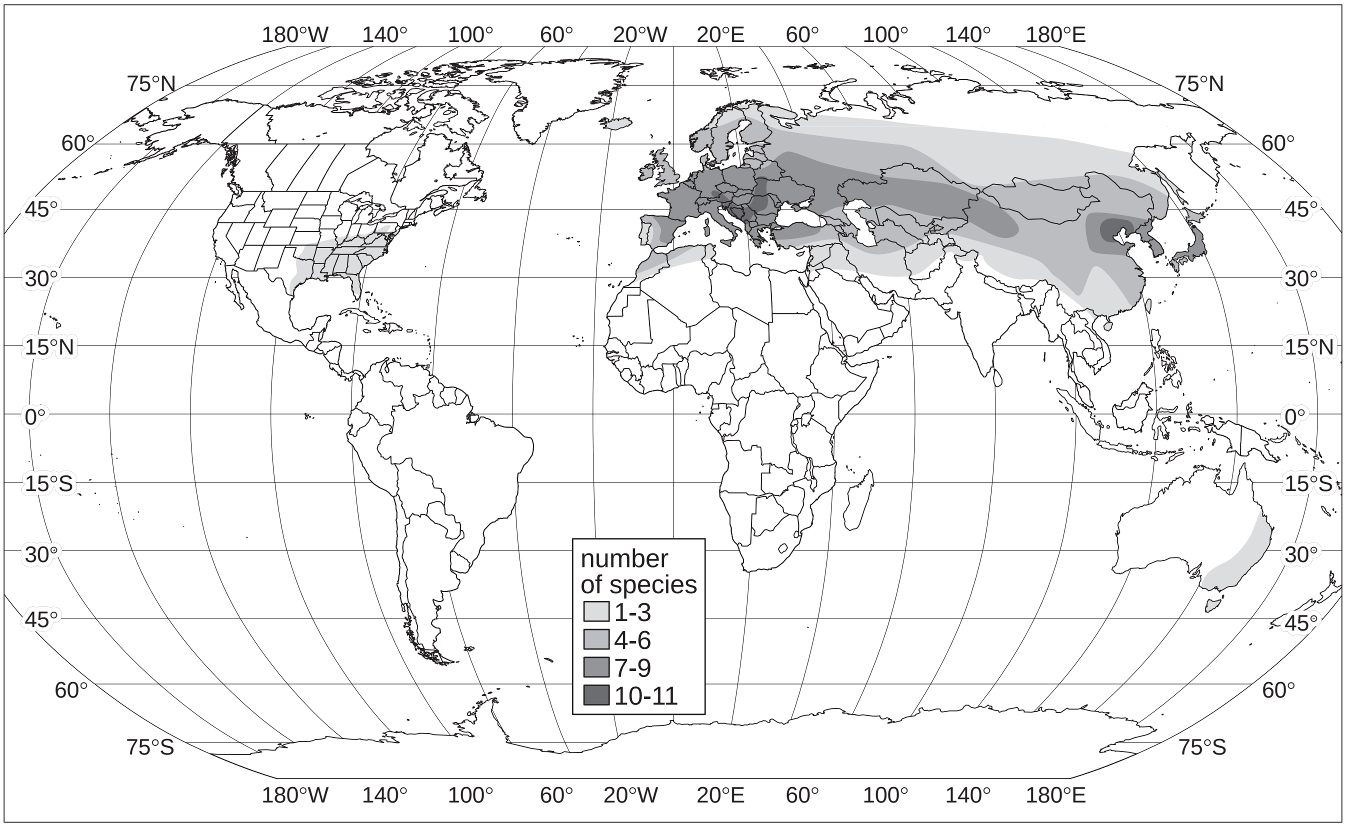

Fig. 1. Composite distribution of 28 non-native, woody species known to be naturalized in Iowa.

place. Appropriate safeguards are needed to minimize the risk that these new introductions may one day invade natural plant communities or otherwise become pests.

Reichard and Hamilton (35) developed criteria for evaluating the invasive potential of woody plants in North America. Their criteria were based upon detailed analyses of life-history characteristics, biosystematics, phytogeography, and known histories of invasions from other parts of the world. This approach may prove extremely useful, but by attempting to develop criteria that apply continent-wide, they were unable to incorporate important characteristics about relationships between woody plants and the environments in which they evolved and noted that analysis of geographic origin 'may be most useful in regional models' (35).

Thus, more robust, predictive models of invasiveness suitable for specific regions might be developed by accounting for environmental conditions where the plants evolved. Such approaches proved useful in assessing potential weeds in Australia and New Zealand (28–30, 37).

Recently, Widrlechner (47) mapped and analyzed the native ranges of 28 species of non-native, woody plants known to have naturalized in Iowa. He examined the composite ranges of those 28 species and compared them to measures of climatic similarity to Iowa conditions. He identified two regions with particularly high concentrations of those species: one region in northeastern China and another in southeastern Europe (Fig. 1). Those two areas overlapped with regions that experience climates analogous to Iowa conditions, based upon three important determinants of woody plant adaptation in the north central United States: January mean temperature, moisture balance, and photoperiod regimen (44, 48).

The observed correspondence between climatic analogs and native distributions of non-native, naturalized woody plants in Iowa suggested that climatic analogs might be useful to identify foreign regions with native woody floras that could be pre-adapted to Iowa conditions and, thus, qualify as high-risk regions harboring potentially invasive plants.

But before such a generalization can safely be made, it is crucial to question whether the composite distribution of a group of naturalized species is an artifact of some larger phenomenon that might interfere with the utility of climatic analogs in risk assessment. For example, is it possible that a high proportion of **all** non-native, woody plants widely grown in Iowa originate from northeastern China and southeastern Europe?

The objective of our study was to determine whether patterns of native distributions of naturalized woody plants and their relationships to climatic analogs can serve as a sound basis for geographic risk analysis. To this end, we compared the composite ranges of the 28 non-native species naturalized in Iowa with the native ranges of a larger set of non-native species widely cultivated in Iowa, but with no record of naturalization. From this comparison, we tested two related hypotheses:

(1) Regions with the highest number of native species that have naturalized in Iowa have a significantly higher proportion of naturalizing species than predicted by the overall ratio of the number of naturalizing species to the total number of non-native species studied; and

Table 1. Core list of non-native woody plants naturalized in Iowa[z].

Amur Maple (*Acer tataricum* L. subsp. *ginnala* (Maxim.) Wesm.)
Tree of heaven Ailanthus (*Ailanthus altissima* (Mill.) Swingle)
Japanese Barberry (*Berberis thunbergii* DC)
Common Trumpetcreeper (*Campsis radicans* (L.) Seem ex Bureau)
Northern Catalpa (*Catalpa speciosa* (Warder ex Barney) Warder ex Engelm.)
Russianolive (*Elaeagnus angustifolia* L.)
Autumn Elaeagnus (*Elaeagnus umbellata* Thunb.)
Winged Euonymus (*Euonymus alatus* (Thunb.) Siebold)
Amur Honeysuckle (*Lonicera maackii* (Rupr.) Maxim.)
Tatarian Honeysuckle (*Lonicera tatarica* L.)
Barbary Wolfberry (*Lycium barbarum* L.)
Osageorange (*Maclura pomifera* (Raf.) C.K. Schneid.)
Crabapple (*Malus sylvestris* Mill.)
White Mulberry (*Morus alba* L.)
White Poplar (*Populus alba* L.)
Manchu Cherry (*Prunus tomentosa* Thunb.)
Common Buckthorn (*Rhamnus cathartica* L.)
Black Locust (*Robinia pseudoacacia* L.)
Japanese Rose (*Rosa multiflora* Thunb.)
Sweetbrier Rose (*Rosa rubinigosa* L.)
Japanese Raspberry (*Rubus parvifolius* L.)
White Willow (*Salix alba* L.)
Brittle Willow (*Salix fragilis* L.)
Whitecrack Willow (*Salix* x *rubens* Schrank)
European Mountainash (*Sorbus aucuparia* L.)
Siberian Elm (*Ulmus pumila* L.)
European Cranberrybush Viburnum (*Viburnum opulus* L. var. *opulus)*
Wayfaringtree Viburnum (*Viburnum lantana* L.)

[z] Taxonomy follows the Germplasm Resources Information Network database for the National Plant Germplasm System (23, 49) <http://www.ars-grin.gov/npgs> and common names follow Kelsey and Dayton (14).

Table 2. List of 72 non-native, woody plants cultivated in Iowa, but not known to naturalize[z].

White Fir (*Abies concolor* (Gordon & Glend.) Lindl. ex F. H. Hildebr.)
Hedge Maple (*Acer campestre* L.)
Red Chokeberry (*Aronia arbutifolia* (L.) Pers.)
Korean Barberry (*Berberis koreana* Palibin)
Asian White Birch (*Betula platyphylla* Sukaczev)
Gray Birch (*Betula populifolia* Marshall)
Littleleaf Box (*Buxus microphylla* Siebold & Zucc.)
Russian Peashrub (*Caragana frutex* (L.) K. Koch)
European Hornbeam (*Carpinus betulus* L.)
Chinese Chestnut (*Castanea mollissima* Blume)
Katsuratree (*Cercidiphyllum japonicum* Siebold & Zucc.)
Common Floweringquince (*Chaenomeles speciosa* (Sweet) Nakai)
American Yellowwood (*Cladrastis lutea* (F. Michx.) K. Koch)
Italian Clematis (*Clematis viticella* L.)
Summersweet Clethra (*Clethra alnifolia* L.)
Flowering Dogwood (*Cornus florida* L.)
Corneliancherry Dogwood (*Cornus mas* L.)
Turkish Filbert (*Corylus colurna* L.)
Common Smoketree (*Cotinus coggygria* Scop.)
Cranberry Cotoneaster (*Cotoneaster apiculatus* Rehder & E. H. Wilson)
Bearberry Cotoneaster (*Cotoneaster dammeri* C. K. Schneid.)
Hedge Cotoneaster (*Cotoneaster lucidus* Schltdl.)
Washington Hawthorn (*Crataegus phaenopyrum* (L. f.) Medik.)
Fuzzy Deutzia (*Deutzia crenata* Siebold & Zucc.)
Slender Deutzia (*Deutzia gracilis* Siebold & Zucc.)
Winterberry Euonymus (*Euonymus bungeanus* Maxim.)
European Beech (*Fagus sylvatica* L.)
Vernal Witchhazel (*Hamamelis vernalis* Sarg.)
Shrubalthea (*Hibiscus syriacus* L.)
Smooth Hydrangea (*Hydrangea arborescens* L.)
Panicle Hydrangea (*Hydrangea paniculata* Siebold)
Pyramid Chinese Juniper (*Juniperus chinensis* L.)
Savin Juniper (*Juniperus sabina* L.)
Rocky Mountain Juniper (*Juniperus scopulorum* Sarg.)
Panicled Goldenraintree (*Koelreuteria paniculata* Laxm.)
Beautybush (*Kolkwitzia amabilis* Graebn.)
European Larch (*Larix decidua* Mill.)
American Sweetgum (*Liquidambar styraciflua* L.)
Star Magnolia (*Magnolia stellata* (Siebold & Zucc.) Maxim.)
Russian Arborvitae (*Microbiota decussata* Kom.)
Northern Bayberry (*Myrica pensylvanica* Mirb.)
Black Tupelo (*Nyssa sylvatica* Marshall)
Sweet Mockorange (*Philadelphus coronarius* L.)
White Spruce (*Picea glauca* (Moench) Voss)
Colorado Spruce (*Picea pungens* Engelm.)
Swiss Mountain Pine (*Pinus mugo* Turra)
Austrian Pine (*Pinus nigra* J. F. Arnold)
Ponderosa Pine (*Pinus ponderosa* P. Lawson & C. Lawson)
Mazzard Cherry (*Prunus avium* (L.) L.)
Almond Cherry (*Prunus glandulosa* Thunb.)
Amur Chokecherry (*Prunus maackii* Rupr.)
Common Douglasfir (*Pseudotsuga menziesii* (Mirb.) Franco)
Callery Pear (*Pyrus calleryana* Decne.)
English Oak (*Quercus robur* L.)
Black Jetbead (*Rhodotypos scandens* (Thunb.) Makino)
Alpine Currant (*Ribes alpinum* L.)
Japanese Spirea (*Spiraea japonica* L. f.)
Japanese Pagodatree (*Styphnolobium japonicum* (L.) Schott)
Meyer Lilac (*Syringa meyeri* C. K. Schneid.)
Japanese Tree Lilac (*Syringa reticulata* (Blume) H. Hara)
Late Lilac (*Syringa villosa* Vahl)
Fivestamen Tamarisk (*Tamarix ramosissima* Ledeb.)
Japanese Yew (*Taxus cuspidata* Siebold & Zucc.)
Littleleaf Linden (*Tilia cordata* Mill.)
Silver Linden (*Tilia tomentosa* Moench)
Canada Hemlock (*Tsuga canadensis* (L.) Carriere)
Koreanspice Viburnum (*Viburnum carlesii* Hemsl.)
Witherod Viburnum (*Viburnum cassinoides* L.)
Rusty Blackhaw Viburnum (*Viburnum rufidulum* Raf.)
Siebold Viburnum (*Viburnum sieboldii* Miq.)
Fox Grape (*Vitis labrusca* L.)
Oldfashioned Weigela (*Weigela florida* (Bunge) A. DC.)

[z] Taxonomy and common names follow sources used in Table 1 (14, 23, 49).

(2) regions identified as climatic analogs to Iowa conditions, based on important determinants of woody plant adaptation, have a significantly higher proportion of naturalizing species than predicted by the overall ratio of naturalizing species to the total number of non-native species studied.

Materials and Methods

We employed two lists of non-native, woody plants cultivated in Iowa. The first list of 28 species (Table 1), with a known history of naturalization in Iowa, was recently described and published by Widrlechner (47). We then compiled a second list of 72 species (Table 2), with no record of naturalization in Iowa. These lists yielded a combined set of 100 non-native species. And, if native distributions were randomly distributed, approximately 28% of the species native to a region should be members of the naturalizing list.

We compiled the list of 72, non-naturalizing species as follows. First, we created an extensive list of woody plants cultivated in Iowa, targeting species with a relatively long history of cultivation to reduce the possibility of including those that are still in a lag period prior to naturalization (15). We compared this list to the published checklist of Iowa's flora (5) and recent additions to it (16, 26), eliminating any species noted as possibly escaping from cultivation. Further refinement was accomplished by reviewing herbarium specimens collected in Iowa held in Iowa's two largest herbaria, the Ada Hayden Herbarium at Iowa State University, Ames, and the University of Iowa Herbarium, Iowa City. Species were eliminated from further consideration when herbarium specimens documenting naturalization were discovered. During the course of mapping native ranges for the remain-

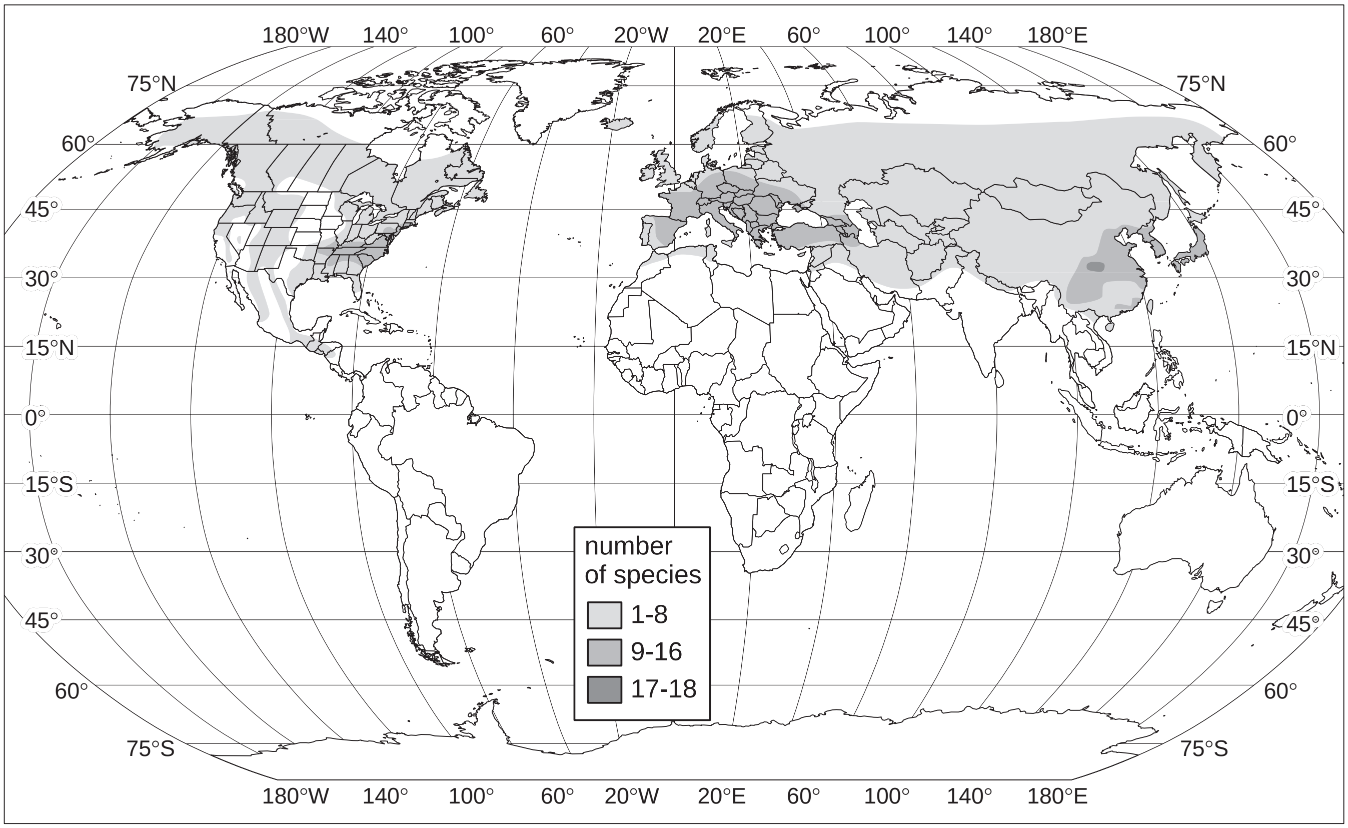

Fig. 2. **Composite distribution of 72 non-native, woody species cultivated but not known to be naturalized in Iowa.**

ing 74, non-naturalizing species, two more species were deleted, *Ginkgo biloba* and *Malus sargentii*, because they are known only from cultivation and lack defined, native ranges.

Distributional data were obtained from the Germplasm Resources Information Network database for the National Plant Germplasm System (23) <http://www.ars-grin.gov/npgs> and supplemented with range information from numerous taxonomic and floristic publications (4, 7–9, 11–13, 19, 21, 22, 25, 27, 32, 34, 39, 41, 43). A composite map of the native distributions of the 72 non-naturalizing species was then prepared (Fig. 2).

We then mapped the ratio between the number of naturalizing species and the total number of naturalizing and non-naturalizing species native to each region to help visualize spatial patterns of risk (Fig. 3). Only regions with at least a minimum combined sample size of 10 species were mapped, because of sampling errors and potentially misleading results that can result from excessively small samples. The risk categories delimited in Fig. 3 were chosen in relation to differences in ratios that could be explained solely by chance, given a minimum sample size of 10 and a mean sample size of 16. Statistical significance of deviations in the proportions of naturalizing species was determined with the Chi-square goodness of fit test (10) for individual locations. The 'Combined Probabilities from Independent Tests' procedure of Sokal and Rohlf (38) was used to test deviations within larger regions.

The maps of world climatic analogs to Iowa conditions (Fig. 4) used in our study were developed by Widrlechner (47).

Results and Discussion

The composite distribution of the 28 non-native, woody plants known to naturalize in Iowa (Fig. 1) displays several notable geographic patterns. Of these 28 species, 4 are native to the southeastern United States, and the other 24 are primarily native to Eurasia, with outlying populations in North Africa and Australia. The highest numbers of these species are found in two regions: the larger with 10 species, includes parts of Belarus, Ukraine, Romania, the former Yugoslavia, Albania, Austria, and Germany, and a smaller region with 10–11 species located in Hebei and Liaoning Provinces in northeastern China.

The composite distribution of our set of 72, non-native, non-naturalizing woody plants (Fig. 2) has both interesting similarities and differences when compared to that of naturalizing species (Fig. 1). In Eurasia and North Africa, the broad area represented by at least one species in Fig. 1 closely resembles that for Fig. 2. In North America, the area represented by non-naturalizing species (Fig. 2) is much more extensive than shown for naturalizing species (Fig. 1), but the southeastern United States holds the highest numbers of both naturalizing and non-naturalizing species in the New World.

The largest number of non-naturalizing species in the southeastern United States, 14 species, occurs native in northwestern South Carolina in the southern Appalachian Mountains, a region widely recognized for its diversity of woody plants (18, 40). But, world-wide, the highest number of non-naturalizing species, 17–18 species, is native to an-

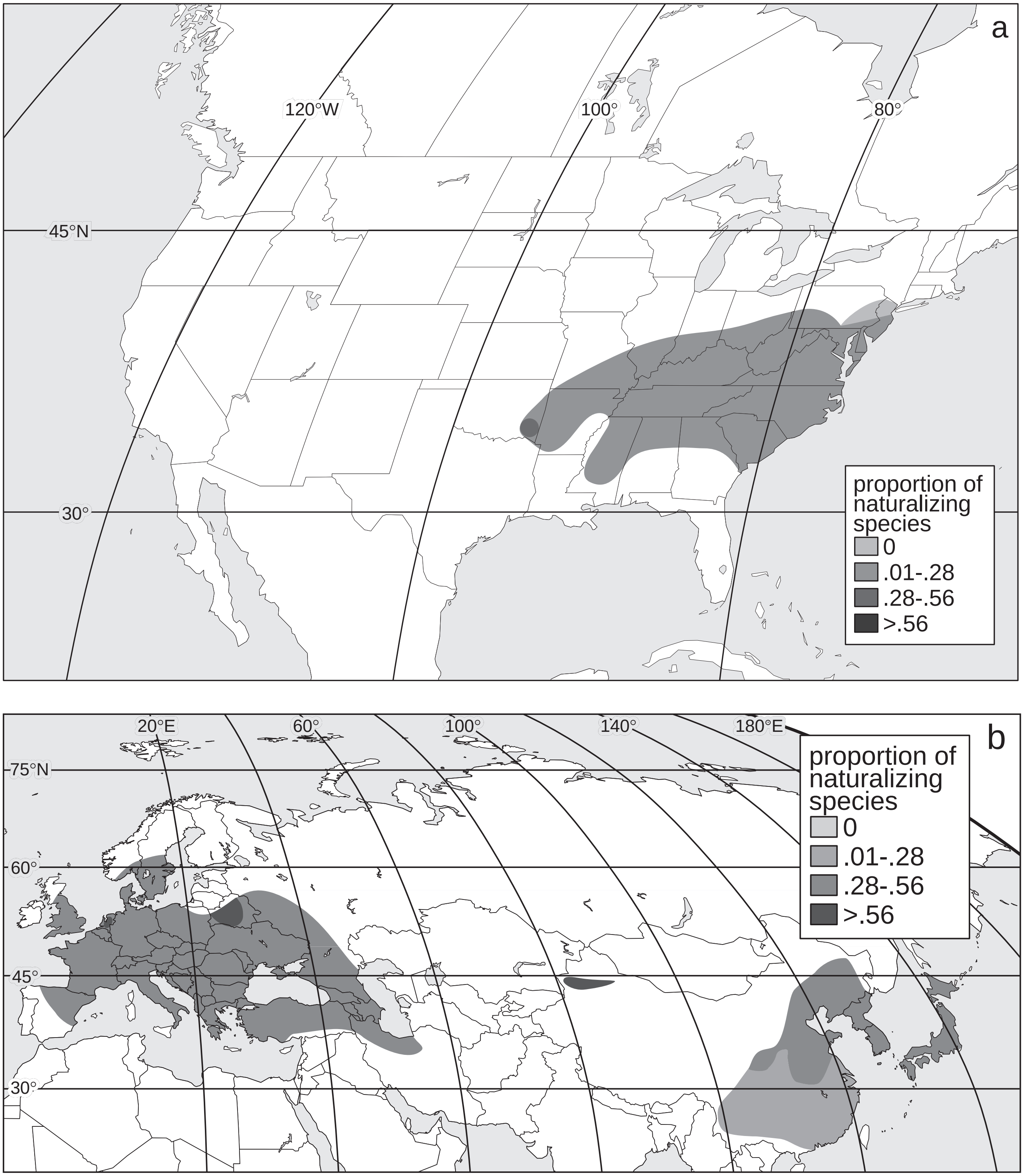

Fig. 3. Maps of the ratio of the number of non-native, woody species known to be naturalized in Iowa versus the total number of non-native woody species examined in this study. Fig. 3a maps North America, and Fig. 3b maps Eurasia.

other region of great botanical diversity, Gansu and Shaanxi Provinces in central China (40). Notably, the Qinling Mountains in Shaanxi Province stand at the transition between the warm temperate and north subtropical climatic zones in central China and hold an extremely diverse flora with 150 endemic (localized, native) plant species (3).

A notable difference between these two composite distributions is reflected in their relative degree of geographic concentration. Approximately the same relative proportions of naturalizing and non-naturalizing plants are represented by each type of shading in Figs. 1 and 2. Evidently, the ranges of naturalizing species (Fig. 1) are much more similar to each

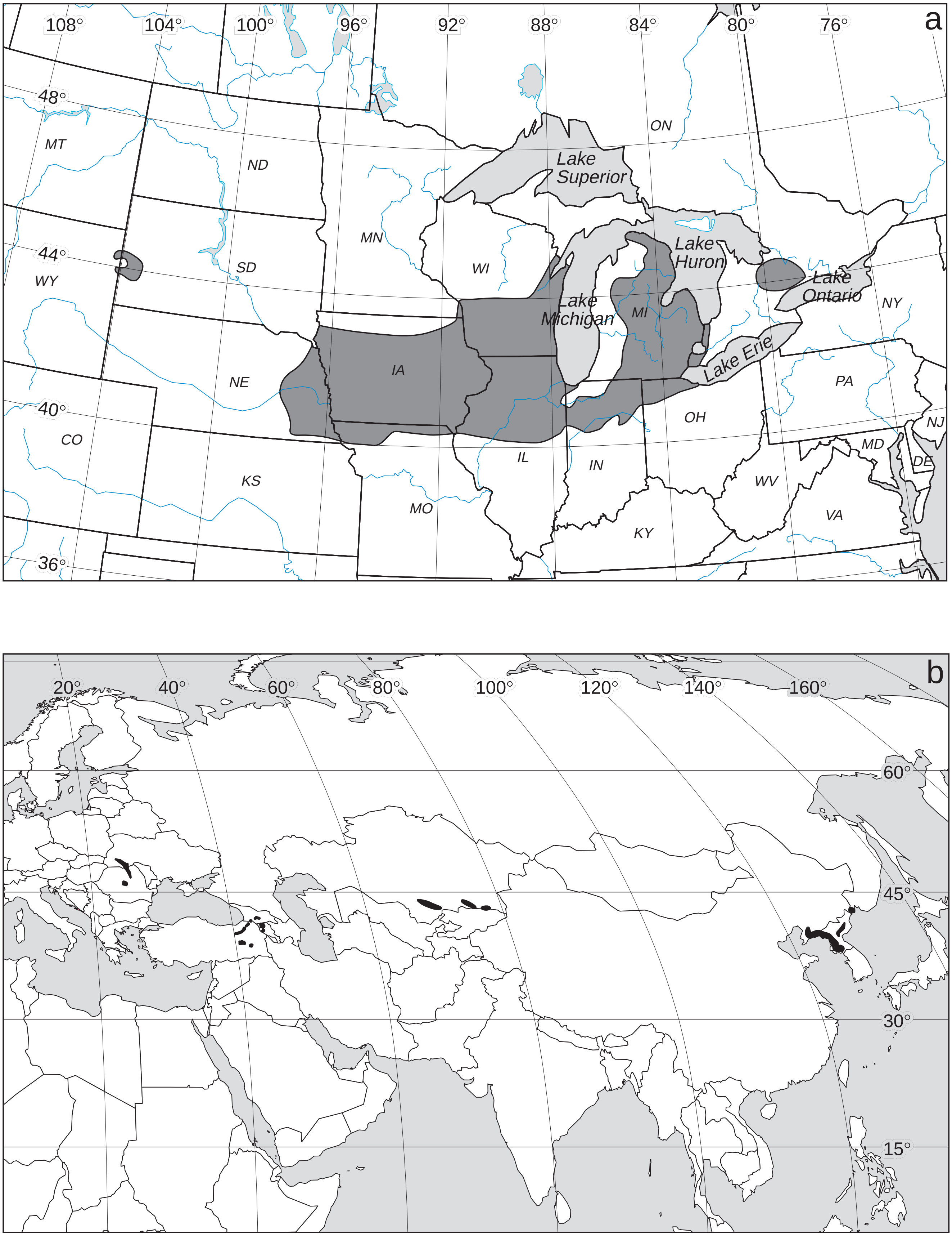

Fig. 4. Maps of climatic analogs to Iowa conditions, based on January mean temperature, moisture balance, and photoperiod regimen following Widrlechner (47). Fig. 4a maps North America, and Fig. 4b maps Eurasia.

Table 3. Proportion of species naturalizing in Iowa among all species analyzed that are native to the regions of highest concentration.

Region of highest concentration	Proportion	Sample size
southeastern Europe (10 naturalizing species)		
southern Belarus	.625**	16
western Ukraine	.435 to .5*	20-23
Romania	.417	24
Yugoslavia	.4	25
northern Albania	.417	24
Austria	.417	24
southern Germany	.476*	21
northeastern China (10-11 naturalizing species)		
Liaoning (10 species)	.526*	19
Hebei (11 species)	.524*	21

*, **, values significantly higher than the expected value of .28 at the .05 and .01 levels, respectively, as tested by Chi-square goodness of fit (10).

other than are those of their non-naturalizing counterparts (Fig. 2). At least 35% (10–11) of 28 naturalizing species occur together either in southeastern Europe or in northeastern China (Fig. 1). In contrast, the highest proportion of non-naturalizing species, found in central China, includes only about 24% (17–18) from our set of 72 species (Fig. 2).

Figure 3 maps the proportion of the composite native ranges of all the woody species examined in our study that are known to be naturalized in Iowa. Only regions with a sample size of at least 10 native species are mapped. The map is divided into four categories (0, 0.01–0.28, 0.28–0.56, and >0.56), each reflecting the relative risk that a woody plant native to the mapped region may naturalize in Iowa. The categories are numbered in order of increasing risk:

Category 1 includes the areas of least risk, found where the proportion of naturalizing species is zero. It is the smallest of the four categories and is only found in northeastern Pennsylvania and northern New Jersey (Fig. 3a).

Category 2 includes areas of below-average risk where the proportion of naturalizing species is greater than zero but less than 28%, the value predicted under an assumption of random distribution of naturalizing species for our sample of 100 species. It encompasses much of the southeastern United States (Fig. 3a) and south-central China (Fig. 3b).

Category 3 includes areas of above-average risk where the proportion of naturalizing species is greater than or equal to 28% but less than 56%, between one and two times the predicted proportion based on an assumption of randomness. It encompasses much of Europe and western Asia, northern China, Korea, and Japan (Fig. 3b) as well as a small region in southeastern Oklahoma (Fig. 3a).

Category 4 includes the areas of highest risk where the proportion of naturalizing species is greater than or equal to 56%, at least twice the predicted proportion based on an assumption of randomness. It is found in three isolated locations: the Netherlands, Belarus, and Xinjiang Province in western China (Fig. 3b).

We also noted regions with particularly low or high proportions of naturalizing species beyond the borders mapped in Figs. 3a and 3b. However, the regions outside the borders contain fewer than 10 of the 100 species studied. With such small sample sizes, we approach them cautiously and use them only to suggest general trends. Beyond the mapped borders of Fig. 3a, the regions of least risk would also include most of the rest of North and Central America, except for Oklahoma, Texas, the southernmost parts of the southeastern United States, and small areas adjacent to those mapped as Category 2. Beyond the mapped borders of Fig. 3b, the regions of greatest risk would also include Finland and the Baltic States, adjacent to and north of Belarus, along with much of central Asia, stretching from Mongolia to the Caspian Sea, including Xinjiang Province in China.

We then tested our first hypothesis that regions with the highest number of native species that have naturalized in Iowa have a higher proportion of naturalizing species than predicted by the overall ratio of naturalizing species to the total set of species studied (28%). Table 3 indicates that the proportion of naturalizing species in the region with the highest concentration of naturalizing species in southeastern Europe (Fig. 1) ranges between 40 and 62.5%. In southern Germany, southern Belarus, and parts of western Ukraine, individual ratios are significantly higher than our expected value of 28% at the 5% level. The overall, regional p-value for comparisons of the reported ratios with the expected value, as determined by the 'Combined Probabilities from Independent Tests' procedure of Sokal and Rohlf (38), is highly significant at the 0.01% level. For northeastern China, the two, calculated ratios of naturalizing species were just above 52%, values significantly higher than our expected value of 28% at the 5% level. The combined significance level for these

Table 4. Proportion of species naturalizing in Iowa among all species analyzed that are native to the climatic analogs (47).

Climatic analog	Proportion	Sample size
North America		
southern Ontario	0	6
southern Michigan	0	5
northwestern Ohio	0	6
northern Indiana	0	6
northern Illinois	0	0-4
southern Wisconsin	0	0-2
western South Dakota	0	3
eastern Wyoming	0	3
southeastern Europe		
southwestern Ukraine	.435	23
Romania	.417	24
western Asia		
Georgia	.353	17
Armenia	.4	15
northeastern Turkey	.381	21
central Asia		
Kazakhstan	.778***	9
northeastern Asia		
Liaoning Prov., China	.526*	19
North Korea	.4	20
Primorye Prov., Russia	.5	8

*, ***, values significantly higher than the expected value of .28 at the .05 and .001 levels, respectively, as tested by Chi-square goodness of fit (10).

two values representing Hubei and Liaoning Provinces in northeastern China lies between 0.1 and 1%.

In turn, we tested our second hypothesis that five regions identified as having climatic conditions analogous to those in Iowa (Fig. 4), based on factors known to be important determinants of woody plant adaptation (47), have a higher proportion of naturalizing species than would be predicted by chance (Table 4).

No species from the list of non-native woody plants naturalized in Iowa (Table 1) were native to the climatic analogs found in the north central United States and southern Canada (Fig. 4a). However, sample sizes were insufficient to observe statistically significant differences, when compared to an expected value of 28%. In southeastern Europe (Fig. 4b), where the climatic analogs are a subset of the region of highest concentration discussed previously in reference to Table 3, the proportion of naturalizing species within the climatic analogs varied between 40 and 43.5%. The combined p-value for these two areas in southeastern Europe was not significant at the 5% level ($0.05 < p < 0.10$). The proportion of naturalizing species found in climatic analogs in western Asia (Fig. 4b) varied between 35 and 40%. The combined p-value for the areas in western Asia was not significant ($0.3 < p < 0.5$). The proportion of naturalizing species found in the climatic analog in central Asia (Kazakhstan) (Fig. 4b), at 77.8%, was among the highest observed in this study. It was significantly higher, at the 0.1% level, than the expected value of 28%. Southern Kazakhstan may be a region of especially high risk for the introduction of woody plants that could naturalize in Iowa. Finally, the proportion of naturalizing species in the northeastern Asian climatic analogs (Fig. 4b) varied between 40 and 52.6%. The combined p-value for these areas in northeastern Asia was significant at the 5% level ($0.02 < p < 0.05$).

In general, the two regions (in southeastern Europe and northeastern Asia) having the highest numbers of species that have naturalized in Iowa are also regions with an above-average risk of naturalization. Two of five climatic analogs, based on low winter temperature, moisture balance, and photoperiod regimen (47), in northeastern Asia and Kazakhstan (Fig. 4b) were regions with significantly above-average risk of naturalization. A third analog, which includes a part of the region with the highest number of naturalizing species in southeastern Europe, was significant only at the 10% level. The remaining analogs in western Asia and North America were not associated with significantly above-average risks. Based on these results, we believe that Widrlechner's (47) initial determination of climatic analogs should be refined to include seasonality of precipitation, because seasonal patterns of precipitation in Turkey and the Caucasus (western Asia) differ substantially from conditions in Iowa. Notably, the situation for climatic analogs in the states surrounding Iowa is a special case, as most woody species found there are also native to Iowa and thus not candidates for the list of non-native, naturalizing species.

By evaluating the geographic distribution of the ratios of the number of non-native, woody species known to be naturalized in Iowa to the total number of non-native woody species studied, as mapped in Fig. 3, certain trends are evident. Areas of below-average risk are associated with two phenomena: high woody-plant diversity and climates that are considerably milder than conditions in Iowa. Two of the world's most diverse regions for temperate woody flora, the southern Appalachian Mountains (18, 40) and the mountains of central and southern China (3, 40), contain below-average proportions of woody plants that have naturalized in Iowa. It is possible that habitats with high species diversity have narrower ecological niches and proportionally fewer species that are colonizers or otherwise invasive.

In addition, these areas of below-average risk experience winter conditions equivalent to USDA Hardiness Zones 5b to 8a in the United States (1) and USDA Hardiness Zones 7 to 10 in China (45), less severe than Iowa's USDA Hardiness Zones 4b to 5a (1). They also experience positive moisture balances greater than those typically found in Iowa (2, 20, 46). And, from a latitudinal perspective, the photoperiod regimens experienced at these locations (ranging south to 22° North in China) are generally poor matches for conditions in Iowa.

In contrast to areas with below-average risk, areas of highest risk are associated with the depauperate, post-glacial woody flora of northern Europe (42) and the islands of montane forest above the deserts of northwestern China. We suspect, given the recent nature of the northern European woody flora, that it has a higher than typical proportion of colonizing or potentially invasive species. In the case of mountains of northwestern China (and perhaps also for those nearby in Kazakhstan, Kirghizia, and Tajikistan), the local woody floras may have evolved stress tolerances that pre-adapt them to stresses also present in Iowa. This could result in higher risk.

In this research, we have attempted to validate the use of climatic analogs and native ranges as predictive tools to identify regions of high risk as sources of naturalizing woody plants for Iowa. Although the validation was imperfect, more importantly, these two lines of evidence (climatic comparisons and analyses of native ranges of both naturalizing and non-naturalizing species) taken together are of greater value as a predictive tool than either is alone. We feel that the next step in refining our risk analysis is to include one more important factor, comparative analysis of life-history characteristics. This is important in light of Reichard and Hamilton's (35) findings that life-history characteristics, such as modes of reproduction and seed dispersal, were important factors in developing their risk criteria and Farrar's (6) report that 75% of the most invasive, non-native woody plant species in Iowa have bird-dispersed seeds.

The methods we employed in the present study could not confidently assess risk for regions where too few of the evaluated plant species are native. This limitation could be overcome, in part, by using more extensive lists of species cultivated in the region of interest (in our case, Iowa). Other types of floristic and climatic analyses may also be necessary in such cases.

For climatic analysis to be most useful, it is crucial to develop criteria that produce biologically significant analogs, from the perspective of woody plant performance in each region of interest. Thus, we are also interested in determining whether risk assessments based on similar geographic and climatic analyses are applicable to other parts of the United States, especially given the wide range of environmental factors that limit woody plant survival throughout the nation.

More comprehensive geographic and life-history analyses focusing on all species of certain horticulturally important, woody genera, such as *Acer*, *Ligustrum*, *Lonicera*, etc., may also shed light on specific factors related to invasiveness for each genus, predict where individual species might naturalize, and identify those species of low risk for escape into natural ecosystems.

Given the ecological damage that invasive plants can cause and the past history of horticultural introductions as sources of invasive plants, geographic risk analysis should be most valuable in relation to new plant introduction and exploration. However, it cannot replace efforts in the field to document what is already occurring. We believe the present efforts of botanists and herbaria to document plants as they escape from cultivation and naturalize should be strengthened, with the overall goal of developing an early warning system to identify new invasions while they are still controllable. Horticulturists and nursery industry professionals can play an important role in the development of such systems, and we would encourage such developments.

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