

What Traits Distinguish Invasive Plants from Non-invasive Plants?

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Non-native invasive species are one of the most pressing threats to the conservation and protection of wildlands. They impact native species and ecosystems by competing directly for resources that native species require, by altering ecosystem functions and processes such as nutrient and hydrologic cycles, and fire frequency and/or intensity. There are virtually no natural areas left that have not felt the effect of non-native invaders (Usher 1988).

Nearly all of the woody species that I have identified as invading natural areas in North America were introduced intentionally - about 85% for landscape purposes and another 14% for agricultural (Reichard 1997). Botanical gardens, nurseries, and individuals commonly import new species to meet the demands of the public for new materials. In America the horticulture industry is an important one, with gross sales of \$5.3 billion in 1992 (U.S. Department of Commerce, Economics, and Statistics 1994). The industry requires the importation of "new" species to provide the plant-buying public with interesting products.

Any restriction in plant importation laws should address the needs of those in the business of horticulture, while those in horticulture should respect the importance of protecting our native species and ecosystems. To accommodate both aims there must be an ability to distinguish species with invasive potential from those which will be beneficial and benign additions to the cultivated flora. In this paper I will discuss a number of ecological, biogeographical, and life-history traits that differ between invasive and non-invasive species, discuss statistical models based on those traits that accurately predict invasive potential, and present a decision tree which can be used to evaluate invasive potential of plants proposed for introduction and to prioritize control of new outbreaks.

Methods

Species selection

I developed a list of invasive woody species (species known to be maintaining self-sustaining populations outside of cultivation) using the United States Department of Agriculture's *National list of scientific plant names* (1982). I then verified that each species was invading one or more region of the United States using regional floras, by communicating with people in land management, and by visiting several herbaria around the country. These efforts generated a list of 235 non-native species that spread outside of cultivation in at least some part of North America. Of these, 76 species were designated as "pests" because they are particularly abundant and/or ecologically disruptive. I divided the continent up into 16 regions based mostly on climatic features and designated the species as occurring or not occurring in each region (Figure 1). Fifty-eight of the 235 species are from the central California area, Region 14.

I defined non-invasive species as those not documented as existing outside of cultivation despite being available horticulturally for at least 60 years. If the species had invasive potential it would likely have invaded in that time. These species were selected primarily from nursery and seed catalogs dated before 1930. There were 114 non-invaders continent-wide; only 14 were from Region 14. This small sample size may have affected some of the comparisons for the region.

Trait selection

A number of traits may directly or indirectly influence invasive success and therefore assist in distinguishing invasive plants from non-invasive. I analyzed a number of traits suggested by various authors including Baker (1965, 1974), Roy (1990) and others. A full list of traits and a discussion is provided in Reichard (1997). In this paper I will limit my discussion to those found to differ significantly between the two groups.

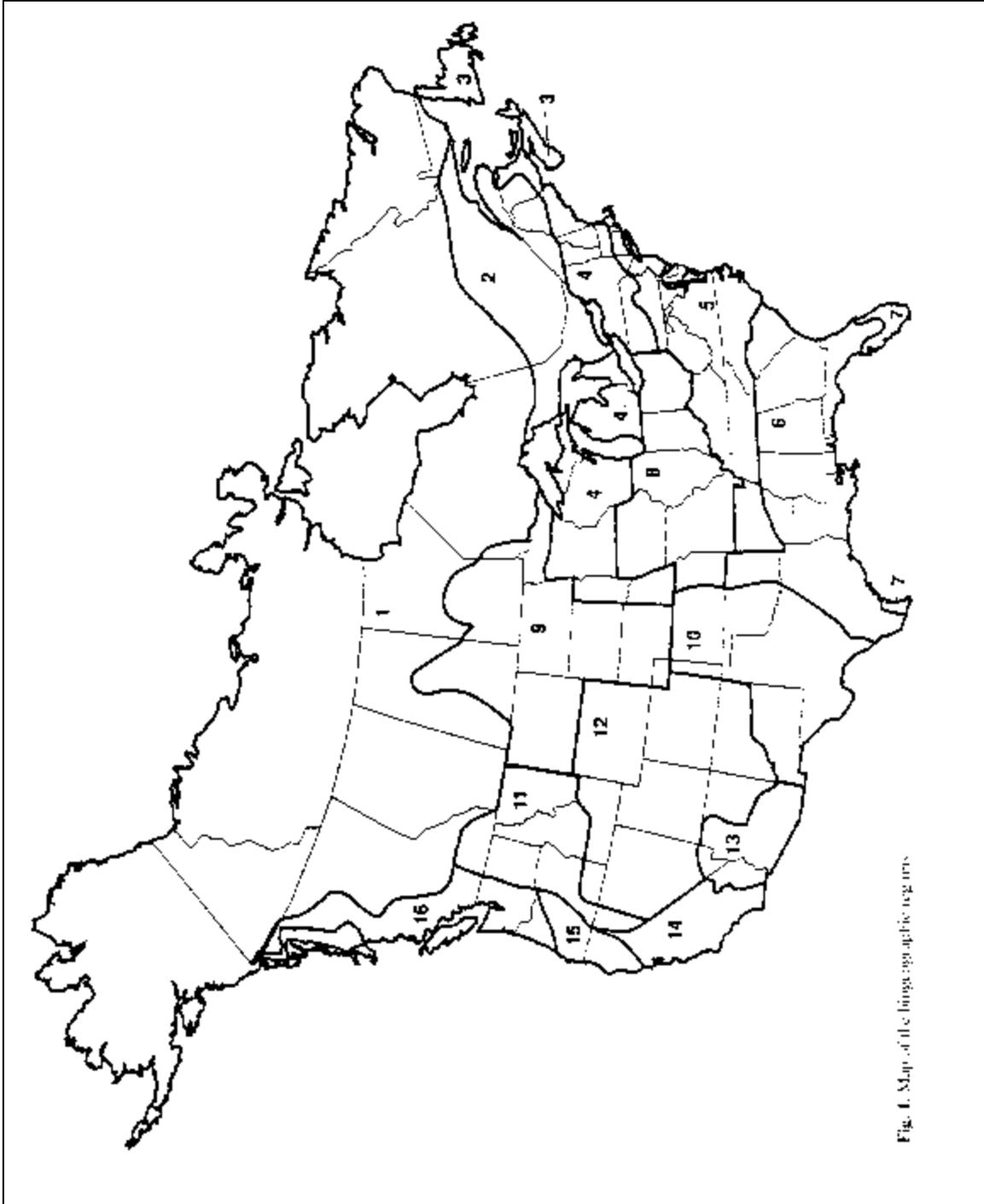


Fig. 1. Map of the biogeographic regions.

Data analysis

Analyses of the traits of invaders and non-invaders were conducted to detect whether there are any significant differences between the two groups. Independent sample t-tests were used for characters with continuous measurements (such as number of months) and log likelihood (or "g-tests") was used for those with discontinuous measurements. I used the sequential Bonferroni technique (Holm 1979) to reduce the probability of incorrectly rejecting a null hypothesis, a risk when analyzing tables of data.

To find linear combinations of characters that maximize the variation between invaders and non-invaders while minimizing the variation within each group I used stepwise discriminant analysis. This procedure selects and removes the variables with the highest discriminating power, then reevaluates the data before removing the next variable, finding combinations of traits. I fit the discriminant analysis model using a random selection of approximately 75% of the species and then tested on the remaining portion. I did this five times, selecting the model with the lowest misclassification rate in cross-validation as the most reliable.

I combined the information derived from the comparisons and discriminant analysis into a decision tree that evaluates invasive potential. This tree is designed to be used by those evaluating species for invasive potential and thus has a more practical than scientific classification - species are designated as "accept" (low probability of invasiveness), "reject" (high probability of invasiveness), and "further analysis or monitoring needed" (moderate probability of invasiveness -caution should be used). All of the invaders and non-invaders for which there were sufficient data were used to test the tree.

Results and discussion

Biogeographical traits

The performance of a species in other places where they have been introduced may be useful in predicting invasive potential. In this study the differences are clear: 54% of the invasive species (61% of the pest species) have invaded after being introduced on other continents or islands while only 15% of the species that do not invade in the U.S. have invaded elsewhere. In Region 14, 78% of the invaders and only 7% of the non-invaders are established elsewhere. Prior history of invasions is one of three characters suggested by Daehler and Strong (1993) as having utility for predicting biological invasions. It has been found to be associated with invasive plants in Australia (Scott and Panetta 1993), for birds in Hawaii (Moulton and Pimm 1986), for many vertebrates (Ehrlich 1989), and for insect species (Crawley 1987). The results of this study, in combination with these others, indicate that there are species which have traits that promote invasions and that other species lack these traits or have traits that hinder successful invasion.

Native range of a species may provide some clues to the climatic suitability of the introduced range. Some patterns that emerge from the data. Plants native to one part of North America are unlikely to have become invasive elsewhere in North America (with some notable exceptions such as *Robinia pseudoacacia* in California, Oregon, and Washington). Only 3% of the invaders are from other regions of North America whereas 25% of the non-invasive species were (Table 1). Also, several of the non-invasive species were interspecific hybrids and probably sterile, whereas only two invasive species were hybrids (Table 1). In California 21 % of the invaders and none of the non-invaders were from the Mediterranean area. Region 14 has a very similar climate to the Mediterranean, with cool moist winters and hot dry summers. The precipitation pattern might be a problem for the many species from summer rain regions (e.g., Europe and temperate Asia) but not to those from the Mediterranean.

Vegetative traits

The leaf longevity of a species can affect its ability to adapt to various conditions; all types might convey adaptations in some settings. For instance, evergreen leaves allow year-round photosynthesis in mild climates, are adaptive in low nutrient soils (Chapin 1980, Ramakrishnan 1991), and are often leathery which provides some drought tolerance and protection from herbivores (Chabot and Hicks 1982). Deciduous leaves are advantageous in periodically cold or dry climates where plants can avoid stress by dropping their leaves. Invasive and non-invasive species had similar ratios of plants with these leaf types. Semi-evergreenness.

whether from partial leaf abscission or photosynthesizing stems was the only leaf type that differed significantly, although the significance was greatly reduced when the Bonferroni technique was used. It provides the plant with the ability to continue photosynthesizing while reducing leaf surface area during stress and also may allow quicker recovery from herbivory (Bossard and Rejmárik 1992). It was rare in both groups: 14% of the invaders and 4% of the non-invaders (Table 1). In Region 14 20% of the invasive species and none of the non-invaders are semi-evergreen (Table 2), a statistically significant difference using bg likelihood tests, but not when using the Bonferroni technique.

Table 1.

Comparison of traits of invasive and non-invasive introduced woody plants in North America which differed significantly. The number to the left of the slash indicates the number of species positively identified with the trait, the number to the right is the number of species for which information was available.

* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, **** $p < 0.0001$, n.s. means not significant, \pm indicates standard deviation
+ indicates that the trait was significant at the tablewide level using the sequential Bonferroni technique

Trait	Invaders (n=235)	Non-invaders (n=114)	Log Likelihood	t-test
Invades elsewhere	126/235 (54%)	17/114 (15%)	51.902****+	
Native regions				
North America	7/235 (3%)	29/114 (25%)	39.423****+	
Eurasia	35/235 (15%)	4/114 (4%)	11.945****+	
Gr. Brit / N. Europe	34/235 (14%)	11/114 (10%)	n.s.	
Mediterranean	14/235 (6%)	7/114 (6%)	n.s.	
Aust. / New Zealand	18/235 (7%)	6/114 (5%)	n.s.	
Temp. Asia	69/235 (30%)	36/114 (32%)	n.s.	
Trop. Asia	23/235 (10%)	1/114 (1%)	12.764****+	
Trop. America	23/235 (10%)	4/114 (4%)	4.817*	
Temp. S. America	3/235 (1%)	1/114 (1%)	n.s.	
Africa	4/235 (2%)	1/114 (1%)	n.s.	
Hybrid	2/235 (1%)	13/114 (11%)	19.798****+	
Leaf longevity				
Evergreen	80/235 (34%)	48/114 (42%)	n.s.	
Deciduous	123/235 (52%)	62/114 (54%)	n.s.	
Semi-evergreen	32/235 (14%)	4/114 (4%)	10.00***	
Fixes Nitrogen	34/235 (15%)	4/113 (4%)	11.21***	
Veg. Repro.	100/228 (44%)	26/114 (23%)	15.336****+	
Mini. Juvenile period	X=4.0 \pm 4.1 yrs.	X=6.9 \pm 8.1 yrs.		-4.25***+
Fl. Period	X=3.4 \pm 4.0 mns.	X=1.7 \pm 2.1 mns.		4.09***+
Fr. Period	X=4.5 \pm 4.0 mns.	X=2.6 \pm 2.3 mns.		4.55***+
Germination req.				
None	109/212 (51%)	32/108 (30%)	14.105****+	
Cold chilling	45/212 (21%)	48/108 (44%)	18.168****+	
Scarification	26/212 (13%)	11/108 (11%)	n.s.	
Cold + Scarification	32/212 (15%)	17/108 (16%)	n.s.	

Many species have a symbiotic relationship with bacteria that convert atmospheric nitrogen to a form that may be absorbed by the plant. This relationship may increase invasive ability, especially in disturbed sites with nitrogen-poor soils (Grubb 1983). Nitrogen-fixation is commonly associated with the Fabaceae

(Leguminosae) but is found in other families with invasive species including the Casuarinaceae, Elaeagnaceae, and Myrsinaceae. The ability to fix nitrogen, although present in only 15% of the invaders across the U.S., differed significantly between the two groups when analysed without the use of the Bonferroni technique but not with it (Table 1). In California 21% of the invaders were nitrogen-fixers but there was no significant difference between invaders and non-invaders (Table 2).

Vegetative reproduction, such as root sprouting and soil layering, quickly increases populations and may contribute to recovery following disturbance. It is significantly more common in the invasive plants, with 44% of the invaders (53% of the pest species) and only 23% of the non-invaders vegetatively reproducing (Table 1). In Region 14, 45% of the invaders vegetatively reproduce but only 14% of the non-invaders do (Table 2).

Table 2.

Comparison of traits of invasive and non-invasive introduced woody plants in Region 14 (California) which differed significantly. The number to the left of the slash indicates the number of species positively identified with the trait, the number to the right is the number of species for which information was available.

* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, **** $p < 0.0001$, n.s. means not significant, \pm indicates standard deviation
+ indicates that the trait was significant at the tablewide level using the sequential Bonferroni technique

Trait	Invaders (n=235)	Non-invaders (n=114)	Log Likelihood	t-test
Invades elsewhere	45/58 (78%)	1/14 (7%)	25.256****+	
Native regions				
North America	2/59 (3%)	1/14 (7%)	n.s.	
Eurasia	4/58 (7%)	0/14	n.s.	
Gr. Brit / N. Europe	10/58 (17%)	3/14 (21%)	n.s.	
Mediterranean	12/58 (21%)	0/14	5.7*	
Aust. / New Zealand	9/58 (16%)	5/14 (36%)	n.s.	
Temp. Asia	14/58 (24%)	3/14 (21%)	n.s.	
Trop. Asia	0/58	0/14		
Trop. America	6/58 (10%)	0/14	n.s.	
Temp. S. America	1/58 (2%)	0/14	n.s.	
Africa	0/58	0/14		
Hybrid	0/58	1/14 (7%)	n.s.	
Leaf longevity				
Evergreen	23/58 (43%)	9/14 (64%)	n.s.	
Deciduous	23/58 (43%)	5/14 (36%)	n.s.	
Semi-evergreen	12/58 (20%)	0/14	5.7*	
Fixes Nitrogen	12/58 (21%)	2/14 (14%)	n.s.	
Veg. Repro.	25/56 (45%)	2/14 (14%)	4.88*	
Mini. Juvenile period	X=3.8 yrs	X=5.6 yrs.		n.s.
Fl. Period	X=3.2 mns.	X=2.4 mns.		n.s.
Fr. Period	X=4.2 mns	X=2.4 mns		n.s.
Germination req.				
None	26/52 (50%)	6/13 (46%)	n.s.	
Cold chilling	6/52 (12%)	3/13 (25%)	n.s.	
Scarification	11/52 (21%)	2/13 (15%)	n.s.	
Cold + Scarification	9/52 (17%)	2/13 (15%)	n.s.	

Reproductive traits

Many of the traits found to be positively associated with invasive ability are correlated with rapid and high reproductive output. For instance, rapid growth through the juvenile stage to reproductive adult reduces generation time and allows the next generation to be produced quickly, increasing the population growth rate and reducing the risk of extinction of the invading population (Baker 1965, 1974). I found that invasive species have a juvenile period on average three years shorter than non-invasive species in North America as a whole, a strongly significant difference (Table 1), and 1.8 years shorter in Region 14 (a weakly significant difference (Table 2). A short juvenile period was also found to be associated with invasiveness in pines (Rejmánek and Richardson 1996) and with annual weeds in Great Britain (Perrins et al. 1992).

Invasive plants in North America have flowering periods on average 1.7 months longer than non-invasive species (Table 1) though there were no significant differences for this trait in Region 14. A longer flowering period may help invasive ability by increasing the probability that flowers on a given plant will be visited and/or by increasing the number of flowers open at any one time, which in turn may enhance the overall floral display and ability to attract pollinators. In outcrossing species (typical of most woody plants) this will result in high viable seed production. Weedy annuals also typically have a longer flowering period than non-weedy ones (Perrins et al. 1992). This character is also correlated with the length of the fruiting period; it is difficult to determine from the data which character is contributing more to invasive ability. Fruit is displayed on average 1.9 months longer on invaders than on non-invaders in North America, again a significant difference (Table 1). The difference in California is 1.8 months but is not statistically significant due to differences in sample sizes (Table 2). The length of the fruiting period is positively correlated with the probability of dispersal (Stiles 1980).

Herbert Baker (1974) suggested that a weed would have germination requirements that could be fulfilled in many environments and in my study 51 % of the invaders had no special germination requirements (Table 1). A plant whose seeds are able to germinate regardless of temperature or other environmental conditions may establish in a wide variety of places and situations. Most of the non-invaders had either a physiological dormancy that required cold-chilling or a mechanical dormancy that required scarification (Table 1), perhaps limiting their flexibility in establishment. In California seeds of 50% of the invaders required no treatments to break dormancy, 21% of them needed seed coat scarification, and only 12% needed cold treatment, but these traits were not significantly different from those of non-invaders.

Predictive models

The traits discussed above are helpful in understanding something about the biology of invasive species but they do not move us much closer to being able to predict which species will harm natural areas and which species are more likely to be harmless if used horticulturally. Any given species will have some of the characters and not others; it is combinations of characters that provide predictive ability.

The discriminative analysis model (Table 3) used ten traits to predict invasive success in North America. The traits used are not necessarily those that had the most statistically significant difference in comparisons, but those that, in linear combinations, provide the greatest predictive power. Those positively associated with invaders include invading elsewhere, vegetative reproduction, perfect flowers rather than dioecious or monoecious, and a long fruiting time. Traits associated with non-invaders include evergreen leaves, flowering in winter rather than other seasons, requirement of cold chilling to break dormancy for seed germination, being native to temperate Asia (misleading because many invaders are from temperate Asia), being native to North America, and being an interspecific hybrid. Determination of group membership is based on both having the traits associated with the group and lacking those associated with the opposite group. This model accurately predicted 86% of the species in cross-validation - 97% of the invaders and 71 % of the non-invaders (Table 4). In fact, only one invasive species, *Celastrus orbiculatus*, an invader of east coast forests, was misclassified. Thus the discriminant analysis model is successful at predicting pests of natural areas but is less successful (although perhaps still adequate) in allowing harmless species in for trade purposes. The model and another created using a different statistical technique are discussed further in Reichard and Hamilton (1997).

Table 3.
Predictive model created using discriminant analysis of the North America invasive species data set. Positive values are associated with the invasive, negative with the non-invasive. Absolute value indicates the importance of the trait to the model.

Variables contributing to the model	Function coefficients
Leaves evergreen	0.41367
Invades elsewhere	-0.34944
Vegetative reproduction	-0.30118
Flowers perfect	-0.23794
Flowers in winter	0.25996
Length of time the fruit is on the plant	-0.28076
Cold chilling needed for seed germination	0.32293
Native to temperate Asia	0.34193
Native to North America (other areas)	0.69956
Interspecific hybrid	0.52100
Canonical correlation	0.667
Wilks' lambda	0.555

Table 4.
Validation of the discriminant analysis model for North American introduced plants. Model was created using 149 species (72%) selected at random and validated on remaining 58 (28%) species.

Actual group	Number of species	Predicted group membership	
		Invader	Non-invader
Invader	34	33 (97%)	1 (3%)
Non-invader	24	7 (29%)	17 (71%)
Overall percent of "grouped" species correctly classified: 86%			

Computer assisted statistical analyses are useful for detecting patterns, especially when analyzing many traits simultaneously but it is not necessary to rely on computers to evaluate invasive potential. The decision tree (Figure 2) uses some of the traits selected for discriminant analysis, some from the trait comparisons, and the taxonomic relationship of new introductions to already established invasive species. It is easy to use and, while it requires information that might call for a trip to a well-stocked library, requires no special equipment. It provides multiple paths to three possible outcomes: accept, reject, or analyze/monitor further. It was highly effective in cross-validation, admitting only three invaders (none were pest species) and denying admission to 85%. Many of the denials were on the basis of invading elsewhere (the first question in the tree) but even when that trait is omitted the tree was highly effective predicting which species would invade natural areas. The tree was less effective in predicting non-invaders, just as was the discriminant analysis model. This may indicate that there is still insufficient information to predict non-invasiveness or that there are more paths to non-invasiveness than invasiveness.

I attempted to develop special discriminant analysis models and decision trees for California, but found that those developed for North America generally were as effective as special models. The accuracy levels were very similar to those cited for North America in Tables 4 and 5.

Conclusion

The invasion of introduced plants into natural areas is likely to continue. Some changes have to be made in the way species are admitted into the country in order to restrict the entry of potentially harmful species. It is unlikely that all introductions will be restricted unless proven harmless, the so-called "clean list" approach, because it would be unfair to trade, as would holding all species until an experimental determination of invasive potential is demonstrated. The methods I present here use biogeographic, ecological, and life-history traits of past invaders to develop methods of predicting invasive potential in new introductions. While these methods will not completely prevent the introduction of new invaders into the country it will allow the elimination of some potentially invasive species. It will also allow resource managers to prioritize control of new woody species invading natural areas.

Table 5.
Validation of the decision tree for North American introduced plants (Figure 2).

Actual group	Number of species	Predicted group membership		
		Admit	Deny Admission	Further analysis/ monitoring
Invader	204	3 (2%)	173 (85%)	28 (13%)
Non-invader	87	40 (46%)	15 (18%)	31 (36%)

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