



## How many, and which, plants will invade natural areas?

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### Abstract

Of established nonindigenous plant species in California, Florida, and Tennessee, 5.8%, 9.7%, and 13.4%, respectively, invade natural areas according to designations tabulated by state Exotic Pest Plant Councils. Only Florida accords strictly with the tens rule, though California and Tennessee fall within the range loosely viewed as obeying the rule. The species that invaded natural areas in each state were likely, if they invaded either of the other states at all, to have invaded natural areas there. There was a detectable but inconsistent tendency for species that invade natural areas to come from particular families. At the genus level in California and Florida, and the family level in California, there was also a tendency for natural area invaders to come from taxa that were not represented in the native flora. All three of the above patterns deserve further studies to determine management implications. Only the first (that natural area invaders of one state are likely to invade natural areas if they invade another state) seems firm enough from our data to suggest actions on the part of managers.

### Introduction

How many species, once established, will become 'pests'? Further, can we adequately predict which species these pests will be? These are the central questions faced by conservation biologists and land managers dealing with the massive influx of harmful exotic species (Simberloff 1996). The problem seems to dwarf resources available to deal with it. Gordon and Thomas (1997) report that in one year (1990) 333 million plants were brought into Florida. Between 1977 and 1980, nearly 400,000 finches and other seed-eating birds representing 67 species were imported into the United States (Nilsson 1981). How does one go about deciding where to spend limited funds given so many potentially harmful species? There is general agreement that most invaders will not become pests but much controversy about just what fraction will. Further, there are several avenues of approach to predicting which ones

these will be. One is to build decision trees that pinpoint which taxa should be blacklisted (Reichard and Hamilton 1997; Reichard 1997). Accepting that there is no magic bullet for predicting which introduced species will become invasive (Williamson 1996), can we find general principles that improve our ability to estimate how many will become problematic and to distinguish between the harmful and harmless exotic?

Williamson and Brown (1986), and later Williamson (1996) and Williamson and Fitter (1996), attempted to help answer the former question by looking at the proportion of introduced species that move from one stage of invasion to another. Williamson (1996) identifies at least three unique but nested stages of any successful invasion. These are introduction, establishment and spread. One stage precedes another, such that among all the species that spread, some larger proportion must first become established and so on. Williamson and his colleagues perceived certain regularity in these

proportions, arguing that close to 10% of introduced species will become established and 10% of these will spread to become 'pests'. Williamson (1996) then derived confidence limits or rough indices of normal variability around this percentage. This 'tens rule' is considered validated by Williamson (1996) when between 5% and 20% of species move from one stage to the next, and he felt in 1996 that enough cases supported the rule to suggest its use as a guiding principle.

A criticism of this approach is that the definition of pest is socioeconomically based and therefore has tenuous ecological meaning (Williamson 1996). This semantic problem may be an important one, especially as this is precisely the step that concerns conservationists and land managers the most. Socioeconomically defined pests typically exist in highly altered human landscapes, such as agricultural fields or tree plantations. The ecological communities that these species enter and then dominate are simplified in species number and kinds of interactions. Some authors (Elton 1958; Fox and Fox 1986) have argued that these systems may be more easily invaded, so the average of 10% of species that become pests in the studies of Williamson and his colleagues may be inflated. On the other hand, impacts of invaders into natural areas may be underestimated, because such habitats are less intensively managed and studied than agricultural and other human-generated habitats. If conservation biologists and land managers are to use the tens rule as a guiding principle, it must be shown to apply to the situations they face. In particular, does the tens rule apply to nonindigenous species that dominate natural ecosystems, that is, to ecological pests?

If 10% (or any other percentage) of established exotic species typically become invaders of natural ecosystems, is this a random 10% or is there an underlying pattern in which species become ecological pests, a pattern that might be useful in focusing efforts at interdiction and control? Simply knowing that 10% of all established exotics will become pests is not likely to be useful for land managers. Owing to funding and personnel restrictions, land managers generally prioritize their efforts to manage nonindigenous species. Probably the most important practical question that invasion research can answer is, 'Which species does one place at the top of the list?'

Below we test the tens rule using lists of ecological pest plants, then we look for patterns within these lists.

Some land managers and conservationists confronting the problem of exotic species have codified the definition of ecological pest plant. We use their lists and do not derive our own definition. Among the most widely sought patterns in invasion biology is taxonomic affiliation (Daehler and Strong 1993; Reichard 1997; Lockwood 1999). We look for three taxonomic patterns within lists of ecological pests. First, Simberloff and Boecklen (1991), Scott and Panetta (1993), and Reichard and Hamilton (1997) have suggested that an introduced species that establishes at one site will tend to establish if introduced elsewhere. By this line of reasoning, a 'good' invader possesses traits that tend to make it successful no matter where it is introduced, or at least in a wide range of sites. Thus, a plant that invades natural areas in California may be more likely to invade natural areas in Tennessee. Such a tendency would result in ecological pest plants that are commonly blacklisted across several regions.

Second, taxonomically similar species, by virtue of shared evolutionary history, may have common life history traits that make them 'good' invaders (Daehler and Strong 1993). This hypothesis is related to the above one. The evolutionary clumping of invasive traits will tend to mass invasive species within higher taxonomic groups, such as genera or families. This over-representation of higher taxa is called taxonomic selectivity following Raup (1975). In terms of conservation decisions, if a species has successfully invaded natural areas in California, a local land manager should be highly suspicious of a recent congener introduced to the state, as it may be more likely to become invasive than other exotic species in California.

Third, nonindigenous species may be more successful if they are ecologically distinct from members of the community they are invading (Lockwood et al. 1993; Williamson 1996). To some extent this prediction can be addressed by asking how taxonomically remote, or isolated, the invader is in comparison to the recipient community. If this hypothesis were true, the Florida land manager should be most suspicious of nonindigenous species that are taxonomically very different (i.e. from a family or genus new to the state) from the surrounding native biota. This taxonomically isolated species may be able to exploit a resource untapped by any native species. It may also not compete as intensely with native species and may not be eaten or parasitized as often by virtue of its locally unique ecology.

## Materials and methods

### *Exotic Pest Plant Councils*

Beginning in the late 1980s, several groups within the United States began to document and attempt to control the spread of nonindigenous species into wildlands or native ecosystems (Florida Exotic Pest Plant Council 1997). This initiative spawned the founding of several state and regional non-profit agencies devoted to stopping the spread of exotic plants, usually calling themselves Exotic Pest Plant Councils (EPPCs). These groups are composed of a variety of interested parties including land managers and researchers from local universities, state and federal agencies, and other non-profit groups (e.g. The Nature Conservancy).

One goal of these councils is to document which exotic plants pose the greatest threat to wildlands. Wildlands are typically defined as “natural areas that support native ecosystems including national, state, and local parks, ecological reserves, wildlife areas, national forests, etc.” (California Exotic Pest Plant Council 1996). EPPC lists of “the most harmful exotics”, or natural areas invaders (NAI), are developed and updated using published information as well as reports from local botanists and council review committees (California Exotic Pest Plant Council 1996). The choice of species deliberately is not based on economic harm; rather it rests entirely on the impact of a nonindigenous species on state natural areas (Florida Exotic Pest Plant Council 1997). The lists are posted for public use. We have used lists of NAI from California (California Exotic Pest Plant Council 1996), Florida (Florida Exotic Pest Plant Council 1997), and Tennessee (Killeffer 1997). The lists used here were compiled in 1996 and 1997. A slightly changed, more recent California list (California Exotic Pest Plant Council 1999) was produced after these analyses were completed.

Lists are typically divided into categories, or ranks, that reflect how harmful the invader is considered to be. To some extent these categories vary from state to state. However, the first two categories are relatively consistent. Category 1 (or A) always includes the most invasive wildland pest plants, species that are widespread and believed to be ecologically the most harmful (California Exotic Pest Plant Council 1996; Florida Exotic Pest Plant Council 1997; Killeffer 1997). Category 2 (or B) is more variable.

At a minimum, category two contains nonindigenous species that currently have a regional or limited distribution within wildlands but show several invasive characteristics and have a clear capacity to become category one pests in the future (California Exotic Pest Plant Council 1996; Florida Exotic Pest Plant Council 1997; Killeffer 1997). Beyond this level, differences between categories continue to grow; thus we limit ourselves to these two levels. If an EPPC listed plant is not listed as ‘exotic’ in that state flora (see below), it is removed from consideration. There are 61, 114, and 70 category 1 and 2 NAI in California, Florida, and Tennessee, respectively.

### *The ‘pool’ of naturalized plants*

If our goal is to identify natural area invaders from the collection of species that could invade, it is not enough simply to count the number of NAI present in each state and then compare this number to the local native flora. After all, NAI do not originate from the surrounding native flora; rather, they originate from the surrounding nonindigenous flora. If there is a pattern within the group of species that have successfully invaded natural areas, it may be found only through comparison with random (or null) expectations. These null expectations are derived from a ‘pool’ of species that could have become natural area invaders but did not (Lockwood et al. 2000); in this case, the pool includes at least all nonindigenous plants established within state borders.

We counted the number of naturalized nonindigenous plant species in the state floras to construct this pool. For California we used the Jepson Manual (Hickman 1993), for Florida we used Wunderlin (1997), and for Tennessee we used Wofford and Kral (1993). These are the same floras used for classification in the state EPPC lists. In each state flora, nonindigenous species have special designations making them easily recognizable as one moves through the species accounts. The definition of ‘exotic’ varies among floras. However, at a minimum, they designate all non-native species that have become an integral part of the state flora, live outside human cultivation, and are reproducing. This is sometimes a difficult designation to make, even for well-trained contributors (Wunderlin 1997). Further, there are clear gaps in knowledge (Hickman 1993; Wunderlin 1993). However, by using only the information contained in the state floras we are relying on ‘expert knowledge’ and do not try to

reinterpret conclusions. There are 1058, 1176, and 520 naturalized nonindigenous plant species in California, Florida, and Tennessee, respectively.

### *Statistical analyses*

We began our analyses by simply calculating the percentage of the nonindigenous state flora that constitute category 1 or 2 NAI. We asked if these percentages are statistically different from the 10% expected from Williamson's tens-rule using binomial probabilities. Within each state, the expected number of NAI is  $p*n$ , where  $p$  is 0.10 (based on the tens-rule) and  $n$  is the number of nonindigenous species in that state. We used a heterogeneity  $\chi^2$  test (Zar 1996) to determine if the different states conform to the tens rule and differ from one another.

Next we calculated the number of NAI plants shared between states and the number of NAI in one state that are present as nonindigenous (but not necessarily NAI) plants in another. We used the probability that a nonindigenous plant becomes an NAI in one state to estimate the probability that it will become an NAI in another state that it invades. For example, 15 California NAI are nonindigenous in Florida. We expect that the rate at which these 15 species will become NAI in Florida is equal to the rate at which nonindigenous species in California became NAI there ( $= 61/1058$ ). Thus,  $15*(61/1058) = 0.86$  species that are NAI in California are expected to become NAI in Florida as well. If the observed number of NAI shared between the two states is higher than the expected, then a species classed as NAI in California is a good indicator that it will also become an NAI in Florida. If the reverse is true, then perhaps the regional native flora that nonindigenous plants are attempting to invade largely determines which species become ecological pests. The binomial equation allows us to calculate the probability of obtaining a value equal to the observed ( $X$ ) given a probability of invasion  $p$ :

$$R = (n!/((X!(n - X)!))p^X q^{n-X}$$

where  $n$  is the number of nonindigenous species within a state and  $q = 1 - p$ . We calculate  $R$  as above to generate the exact probability of getting  $X$  shared NAI by chance alone. Then we sum these probabilities for all  $X$  greater than or equal to the observed value to get the tail probability for the observed shared NAI.

Our third analysis tests whether NAI constitute a random taxonomic sample from the pool of all

nonindigenous species within each state. In other words, do NAI more often come from particular families? Since nonindigenous plant species in each state can be classified into only two categories, NAI or not, we used binomial probabilities to test for deviations from randomness.  $R$  is calculated as above for  $X$ , and any possible larger value of  $X$ , and then the various  $R$ -values are summed to obtain a tail probability. In this case,  $n$  is equal to family size,  $p$  is the overall probability of being a NAI, and  $X$  is the observed number of NAI in that family. If a taxon contains more NAI than expected, then all species within this taxon may share traits that predispose them to be 'good' invaders of natural ecosystems.

In this analysis, each state flora is treated separately. Because we are making over 30 independent comparisons when considering each state nonindigenous flora, we used sequentially derived Bonferroni critical values to judge statistical significance (Rice 1989). The binomial method does not perform well at small sample sizes (Bennett and Owens 1997; Lockwood et al. 2000), thus making comparisons at the genus level unproductive.

Finally, we calculated the proportion of all NAI within a state that are taxonomically isolated. Although it is quite easy to thumb through state NAI lists and count how many NAI genera or families are composed entirely of nonindigenous species, this may be a misleading indicator of the degree of taxonomic isolation. In any such calculation, the proportion of the total flora represented by higher taxa composed entirely of nonindigenous species depends strongly on the species pool initially available for recruitment. Because we consider the group of all nonindigenous species present within a state to be the pool, we can conduct a quantitative test for the isolation pattern. We compare the proportion of NAI that represent new higher taxa (genera and families) to the proportion of non-NAI that represent new higher taxa using a Fisher's Exact Test. The comparison is made within each state. If the latter proportion is smaller than the former, species are more likely to invade natural areas if they are from higher taxa new to the state.

## **Results**

Of the 1058 nonindigenous species naturalized in California, 5.8% (61) are currently considered category 1 or 2 NAI. In Florida, of 1176 naturalized

Table 1. Heterogeneity  $\chi^2$  analysis of the applicability of the tens rule in three states.

State	Non-NAI	NAI	Total	Uncorrected $\chi^2$	df	P
California	997	61	1058	21.078	1	<0.001
Florida	1062	114	1176	0.122	1	0.75 > P > 0.5
Tennessee	450	70	520	6.923	1	0.01 > P > 0.005
Total of $\chi^2$				28.123	3	
$\chi^2$ of totals	2509	245	2754	3.729	1	
Heterogeneity $\chi^2$				24.394	2	<0.001

Table 2. NAI in common between the EPPC lists of California, Florida and Tennessee.

Natural Area Invader	States found
<i>Hedera helix</i> (English Ivy)	TN, CA
<i>Bromus tectorum</i> (cheat grass)	TN, CA
<i>Arundo donax</i> (giant reed)	TN, CA
<i>Vinca major</i> (periwinkle)	TN, CA
<i>Schinus terebinthifolius</i> (Brazilian pepper tree)	CA, FL
<i>Cirsium vulgare</i> (bull thistle)	TN, CA
<i>Cirsium arvense</i> (Canada thistle)	TN, CA
<i>Wisteria sinensis</i> (Chinese wisteria)	TN, FL
<i>Egeria densa</i> (Brazilian waterweed)	TN, CA
<i>Alternanthera philoxeroides</i> (alligator weed)	TN, FL
<i>Albizia julibrissin</i> (mimosa)	TN, FL
<i>Solanum viarum</i> (tropical soda apple)	TN, FL
<i>Pueraria montana</i> (kudzu)	TN, FL
<i>Myriophyllum aquaticum</i> (Parrot's feather)	TN, CA
<i>Myriophyllum spicatum</i> (Eurasian water-milfoil)	TN, CA, FL
<i>Ligustrum sinense</i> (Chinese privet)	TN, FL
<i>Lonicera japonica</i> (Japanese honeysuckle)	TN, FL
<i>Hydrilla verticillata</i> (Hydrilla)	TN, FL

nonindigenous species, 9.7% (114) are considered NAI. Similarly, of all naturalized Tennessee nonindigenous species (520), 13.4% (70) are considered NAI. Heterogeneity  $\chi^2$  analysis (Table 1) shows that these proportions of NAI differ among themselves ( $\chi^2 = 24.4$ ,  $df = 2$ ,  $P < 0.001$ ), and only Florida conforms to the tens rule. However, both Tennessee and California fall within the range of NAI proportions that Williamson (1996) would accept as approximating the tens rule.

If we sum the total number of NAI across states, there are 245 listings. Of these, 18 are of species found in at least two of the EPPC lists (Table 2). Thus, 7% of all NAI are species considered ecological pests in more than one state. The vast majority of species on more than one EPPC list are in Tennessee and one other state. The other state is as likely to be Florida as it is to be California (Table 2). When we compare the number of NAI between states, eight are shared between Florida and Tennessee, two between Florida and California,

and nine between California and Tennessee. If we ask how well one state's rate of natural area invasion predicts another's, in each case, the observed number of shared NAI exceeds expected (Table 3). Five of the six cases are significant at the level of  $P < 0.05$ . The NAI of Tennessee can be predicted based on their status as NAI in either California or Florida, and California NAI can be predicted based on their status in Tennessee or Florida. Florida NAI can be predicted based on their status in Tennessee. The prediction that NAI from California will invade natural areas in Florida based on their status in California is not as strong but close to statistical significance.

In our third test, we use binomial probabilities to highlight over-represented (or taxonomically selected) families. Only three families show taxonomic selectivity: one in California and two in Florida. Of the 98 families with at least one exotic plant in California, only the Tamaricaceae (tamarisk) family contains more NAI than expected by chance. Five tamarisks are naturalized in California, and the California Exotic Pest Plant Council (1996) considers four to be pests. Of the 130 families with naturalized nonindigenous species in Florida, two contain more NAI than expected. These are the Araceae (arum) and Myrtaceae (myrtle) families. Wunderlin (1997) lists 10 species as naturalized in each of these families. Of these, the Florida Exotic Pest Plant Council (1997) considers six in each family NAI. In Tennessee, 81 families have naturalized species. Though the Caprifoliaceae (honeysuckle) and Oleaceae (olive) each have over 60% of their naturalized species as NAI, no families contain more NAI than expected.

In our final test, we compare the proportion of NAI that represent new higher taxa to the proportion of established nonindigenous species (but not NAI) that represent new higher taxa. In California, NAI were much more likely to come from families  $\chi^2 = 9.55$ , Fisher's Exact  $P$ -value = 0.002) and genera  $\chi^2 = 11.05$ , Fisher's Exact  $P$ -value = 0.0009) that are new to

*Table 3.* Observed and expected numbers of shared NAI between states. Expected values are calculated by assuming state A's rate of natural area invasion rate (from Table 1) to predict state B's rate. Probabilities are tail probabilities from the binomial distribution. Statistical significance at  $P < 0.05$  is designated by an asterisk.

State A	State B	State A NAI found in state B	Expected no. state A NAI that are also state B NAI	Observed no. state A NAI that are also state B NAI	Tail probability
Tennessee	Florida	36	4.85	8	0.04*
Florida	Tennessee	9	0.87	8	$3.87 \times 10^{-10}$ *
California	Florida	15	0.86	2	0.06
Florida	California	9	0.87	2	0.04*
Tennessee	California	28	3.77	9	0.002*
California	Tennessee	10	0.58	9	$6.05 \times 10^{-13}$ *

*Table 4.* Proportions of NAI and nonindigenous species that are members of families not originally present within California, Florida and Tennessee.

	Added new family	Did not add new family
California		
NAI	5	56
Non-NAI	20	977
Florida		
NAI	6	108
Non-NAI	37	1018
Tennessee		
NAI	5	65
Non-NAI	12	438

*Table 5.* Proportions of NAI and nonindigenous species that are members of genera that were not originally present within California, Florida and Tennessee.

	Added new genus	Did not add new genus
California		
NAI	42	19
Non-NAI	468	529
Florida		
NAI	70	44
Non-NAI	519	543
Tennessee		
NAI	34	36
Non-NAI	211	239

the state flora (Tables 4 and 5). Of the five NAI species that constitute new families in the state, four are within the tamarisk family. The other is Myrtaceae (myrtle) which includes several *Eucalyptus* spp. including *E. globulus*, an NAI. Forty-two NAI represent new genera in the state; the majority of new genera are

within the Poaceae (grass) and Asteraceae (sunflower) families.

In Florida, NAI were not more likely to come from families new to the state flora (Table 4;  $\chi^2 = 0.895$ , Fisher's Exact  $P$ -value = 0.344); however, they were more likely to belong to novel genera  $\chi^2 = 6.47$ , Fisher's Exact  $P$ -value = 0.011). Seventy NAI represent new genera in Florida (Table 5). The majority of these were in the Fabaceae (peas), Araceae, and Oleaceae (olives). In Tennessee, NAI were more likely to come from families new to the state ( $\chi^2 = 3.84$ , Fisher's Exact  $P$ -value = 0.050), but not from new genera ( $\chi^2 = 0.069$ , Fisher's Exact  $P$ -value = 0.793) (Tables 4 and 5). Five NAI are in families new to Tennessee. These families are Zygophyllaceae (caltrop), Simaroubaceae (quassia), Elaeagnaceae (oleaster), and Dipsacaceae (teasel).

## Discussion

Our results indicate that Williamson's tens rule applies strictly only to the natural area invaders of Florida but is approximated by NAI of California and Tennessee. This is true despite the fact that each state shows statistically different rates of natural area invasion. Thus, most plants currently established (or that will become established) within state boundaries will not invade local natural areas. Of course, this prediction may not give much solace to the local land manager when one species of the few that do invade proceeds to devastate a locally unique flora.

Can we use what has happened in other states as a guide to what to expect in a local area? There are two ways to prioritize eradication efforts under this

conjecture. The first is to ask if an NAI is likely to be an NAI no matter where it is established. Our results indicate that there is a good chance this will be true. The species that became NAI in Tennessee, Florida and California appear largely predictable if we look at what happened with these same species in the other states. It would be useful to increase the sample of states that, unlike California and Florida, do not house huge numbers of established nonindigenous plant species.

The second approach is to 'flag' all members of families that seem to hold disproportionately many NAI. Our results lend marginal support to this approach. Of the five tamarisk species in California, four are considered NAI. Clearly, putting a moratorium on importing and planting tamarisks could have stopped the destruction of natural areas in California and may do so in the future. Instituting a ban or actively controlling the spread of tamarisk species in other states seems prudent. The same appears true for the arum and myrtle families as they contain a disproportionate number of NAI in Florida and contribute NAI to California and Tennessee. If land managers had flagged species within these families before they invaded natural areas, however, they would have been able to stop at best only 16% and 7% of the current list of NAI in Florida and California, respectively. Clearly, we need more information for effective management of invasions of natural areas in these states. However, the families identified as over-represented in NAI here also tend to be ecological pests worldwide. Daehler (1998) reports that NAI worldwide are more likely to come from seven families. This group includes the tamarisk and myrtle families.

Finally, can we flag species that come from higher taxa that are new to a state as being more likely to become natural area invaders? This approach also shows some merit. Ecological pest plants in California and Tennessee were significantly more likely to come from families not represented in the native flora, while NAI in California and Florida were significantly more likely to come from novel genera. This approach should be tested in more situations so we can grasp how widespread this pattern is and under what conditions it may be expressed.

In addition to extending the list of cases where the tens rule applies approximately, we identify three patterns that show potential in helping conservationists and land managers prevent the continued devastation of natural areas. Our results should be considered an addition to (and not a replacement for)

the growing literature on ecological correlates of invasion success such as those identified by Rejmanek and Richardson (1996). Given the probabilistic nature of invasion success, combining predictive approaches within decision trees may be the best approach to preventing invasions (e.g. Reichard and Hamilton 1997).

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