Progress in invasion biology: predicting invaders

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Predicting which species are probable invaders has been a long-standing goal of ecologists, but only recently have quantitative methods been used to achieve such a goal. Although restricted to few taxa, these studies reveal clear relationships between the characteristics of releases and the species involved, and the successful establishment and spread of invaders. For example, the probability of bird establishment increases with the number of individuals released and the number of release events. Also, the probability of plant invasiveness increases if the species has a history of invasion and reproduces vegetatively. These promising quantitative approaches should be more widely applied to allow us to predict patterns of invading species more successfully.

Many human activities, such as agriculture, aquaculture, recreation and transportation, promote both the intentional and accidental spread of species across their natural dispersal barriers. Although most organisms die in transit, or soon after release[1], those that persist can have grave effects on human health, devastating economic impacts, and can threaten native biodiversity and ecosystem function. For example, in 1991, one million people were infected with cholera and over 10 000 died, when ballast water containing the microbe *Vibrio cholerae* was released and infected drinking water in Peru[2]. Annually, NONINDIGENOUS SPECIES (Glossary: NIS, as compared with INDIGENOUS SPECIES) cause environmental damage and economic losses in excess of US$137 billion in the USA alone[3], and the introduction of the predacious Nile perch (*Lates niloticus*) in the 1950s into Lake Victoria, East Africa, led to the largest modern vertebrate extinction known (over 200 endemic fish have gone extinct over the past few decades[4]). NIS are now recognized as one of the leading global threats to native biodiversity and ecosystem function[5,6]. As the number of species being transported beyond their native range has increased with globalization, so have research efforts to understand the ecology of biological invasions.

Early interest in species invasion was sparked by Elton's 1958 *The Ecology of Invasions by Animals and Plants*[7], where he argued that biological invasions '...are so frequent nowadays in every continent and island, and even in the oceans, that we need to understand what is causing them and try to arrive at some general viewpoint about the whole business'. Much research followed[8] on case histories of single invading species, but after they were ESTABLISHED and already a nuisance and when eradication was impossible (for example, the recent literature on zebra mussels since establishment in North America[9,10]). Rising economic and ecological costs caused by NIS have encouraged more proactive research and the number of publications on predicting the identity, potential impact, or distribution of NIS has increased rapidly since 1986 (Fig. 1).

Of particular interest is whether characteristics exist that predispose a species to become a NIS. Initial efforts in 1996 to synthesize the results of such studies suggested that some generalizations about invading species could be made, but that different characteristics of species were important in different habitats[8]. Some ecologists are pessimistic, suggesting that prediction of the identity of future NIS is all but impossible and that effort should be focused elsewhere[11,12]. These suggestions are, however, premature because, before 1996, few relevant studies were rigorously quantitative. Also, earlier reviews did not separate results of different TRANSITIONS (transportation, release, establishment and spread[8]; Box 1) in the invasion process. Because several factors determine the probability that a species will complete each transition successfully, it is probable that the species characteristics important in completing different transitions will also be different. If such differences exist, previous reviews that examined all transitions together would not detect patterns in species characteristics across studies.

A review of the current literature broken down by transition in the invasion process (Box 1) is now warranted for several reasons. There is an increasing publication rate on the characteristics of invading species (Fig. 1); quantitative methods are developing rapidly; these studies contribute to understanding community assembly; and because they might be useful as building blocks for risk assessment of NIS.

We address three issues related to predicting the invasiveness of species. First, we assess what characteristics of introductions (especially aspects of propagule pressure) are related to the establishment and spread of NIS. Second, we summarize species characteristics that generally distinguish, or are common in species that invade or spread. Finally, we recommend future directions for research on predicting different aspects of species invasions. Our purpose is not to generate an all-inclusive listing of characteristics shared by NIS. Rather, we document known trends that might be taxon specific, and that highlight quantitative methods that might be applied usefully to other taxon and places.

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Glossary

Because usage of the following terms is nonuniform[a], we define our usage of them in this article below:

Established: a species with a self-sustaining population outside of its native range.

Indigenous species: a species found within its native range.

Invasive species: a nonindigenous species that spreads from the point of introduction and becomes abundant.

Nonindigenous species: a species introduced to areas beyond its native range by human activity.

Noninvasive species: a nonindigenous species that remains localized within its new environment.

Transition: one step in the invasion sequence (e.g. transportation, release and establishment).

Reference

a Richardson, D.M. *et al.* (2000) Naturalization and invasion of alien plants – concepts and definitions. *Div. Distrib.* 6, 93–108

We consider eight publications that examine the characteristics of release events or of species for plants and eight that examine these characteristics for animals. The characteristics (1) were rigorously quantitative (included statistical hypothesis testing); (2) were empirically driven (not only theoretical or modeling); (3) were field-based; (4) examined species characteristics other than taxonomic identity; (5) included at least 20 species; and (6) had analyses that included categories consisting of only NIS (Table 1). This last criterion led to the exclusion of much of the weed science literature because, although some NIS might have been included, they were not identified explicitly. Common to each of the publications was success in differentiating between subgroups of species along the invasion sequence (Box 1).

Are species more successful that are released frequently or in high numbers?

Studies addressing characteristics of release events were distributed unequally among taxa (only one study on plants[13], and eight on birds[14–21]). Characteristics of release events were usually important in determining success of NIS (Table 2).

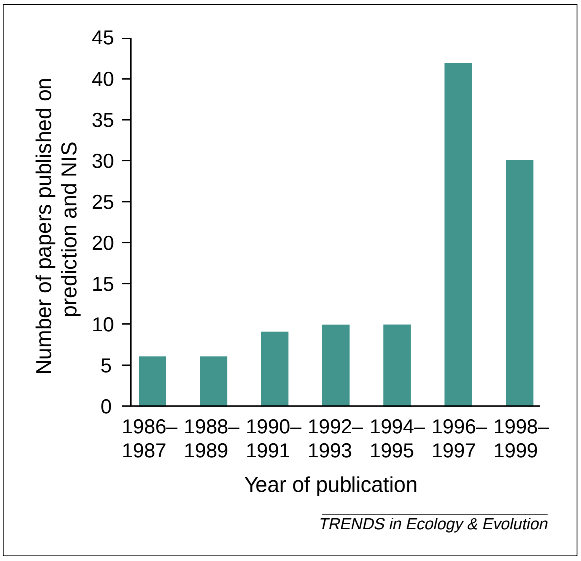


Fig. 1. The rise in the number of publications focused on predicting the occurrence and impact of nonindigenous species (NIS) in invasion biology. Data collated from *Biological Abstracts*, 1986–1999.

When results were statistically significant, the probability of a species becoming established invariably increased with the magnitude of introduction effort (including both the number of individuals released and the number of introduction attempts).

No pattern between time since introduction and successful completion of a transition has been observed across taxa or within an invasion transition (Table 2). The plant study[13] found invasiveness to be greater for longer-established species, although one bird study[14] examining this transition found no such relationship. In the three bird studies that examined the successful establishment of birds, however, one found a positive, another a negative, and a third found no relationship between year of introduction and establishment (Table 2). Whether time since introduction does actually influence the probability of a bird species becoming established outside its native range, independently from the probability that a bird species will become invasive, is unknown.

Do species characteristics distinguish invading from noninvading species?

A variety of plant species and communities have been examined from locations worldwide, although studies of animals have been limited to birds. In addition, all but one animal study (in Australia[15]) was of island ecosystems and neither have previous studies focused on a diversity of taxa or invasion transitions. Generally, successfully establishing birds have been compared with birds that have failed to establish and noninvasive plants have been compared with invasive plants (Table 3). The absence of studies that have focused on the first transition (failure or survival in transport and introduction; Box 1) is troublesome because reducing the numbers of NIS released into an ecosystem is most practical early in the invasion sequence.

Studies that compare established with failed species or invasive with NONINVASIVE SPECIES (Box 1) offer the most powerful test of characteristics that differentiate subgroups of species and directly test what makes a species a successful NIS. These tests comprise the majority of the studies reviewed here, but were infrequent in the literature because data on failures can be difficult to obtain. Two studies[22,23] correlated species characteristics with the degree of success or magnitude of invasiveness. These studies therefore examined patterns of species characteristics within one outcome of a transition. Although not distinguishing between successful and failed NIS, the potential for these studies to contribute important information towards our understanding of invasion biology is high and they are, therefore, included.

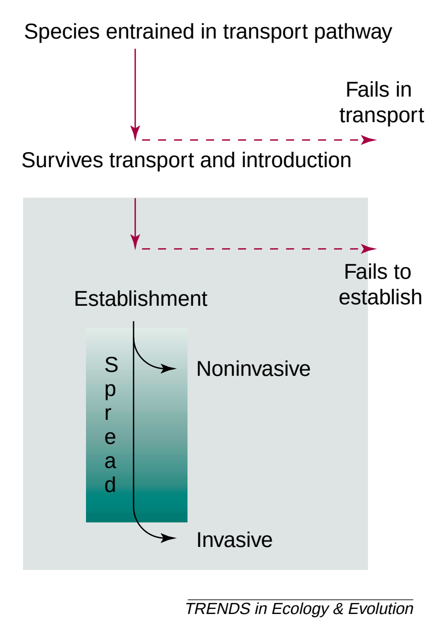
A total of 68 species characteristics were examined across all the studies; 23 appeared in two or more studies (Table 3). No more than four studies have, however, examined the same species characteristics for the same transition. Characteristics examined in

Box 1. Transitions that nonindigenous species must overcome to continue in the invasion process

Several sequential transitions must be made by a species that is overcoming a dispersal barrier and being moved outside its native range (depicted by downward arrows in Fig. I). To begin the invasion process, a species within its region of origin is entrained by a transport pathway (e.g. in the ballast water of a ship, imported intentionally for horticulture) that deposits it outside its range. Most species probably fail to become entrained by such a vector or die in transit. We found only one study partially addressing failure and success of species at this point in the invasion continuum[a].

From the time of release, the nonindigenous species (NIS) interacts with the invaded ecosystem (the green box in Fig. I), including both indigenous species and previously established NIS. These interactions, along with other factors determine whether the NIS will become established. Perhaps 10% of those released will establish a self-sustaining population in the invaded ecosystem.

Characteristics of the established NIS and interactions with species within the invaded community determine how widespread the NIS will become. Some remain relatively localized around the point of introduction (noninvasive species), whereas others spread widely (invasive species). The distinction between noninvasive and invasive is imprecise because spread is partly a function of time since establishment, which is not always known. In our analyses, we accepted the categorization of the original authors.



A progressively smaller proportion of NIS remains with each sequential transition owing to large cumulative failure rates. This schematic represents one iteration of the invasion process. The initial endpoint of a species within this framework represents the point at which the species might continue the invasion process in the future. For example, a species that fails to become entrained in the ballast water of one ship might become entrained in that of another. Also, invasive or noninvasive NIS might become entrained by another pathway in the future and continue to spread to additional ecosystems to create the 'hopping' pattern of invasion that is characteristic of many NIS.

Reference

a Goodwin, B.J. *et al.* (1999) Predicting invasiveness of plant species based on biological information. *Conserv. Biol.* 13, 422–426

Table 1. Studies using quantitative statistics to identify characteristics that distinguish groups of species more and less likely to become established or invasive[a]

Taxon	Transition examined[b]	Location	Number and types of species compared	Ref.
Plants	Within establish[c]	Global	Relative contribution of various families to NIS	23
Plants	Establish/Fail	Canada	165 successful versus 165 failed species	30
Birds	Establish/Fail	Australia	27 successful versus 39 failed species	15
Birds	Establish/Fail	Britain	30 successful versus 27 failed species	16
Birds	Establish/Fail	New Zealand	27 successful versus 52 failed species	17
Birds	Establish/Fail	New Zealand	21 successful versus 26 failed species	18
Birds	Establish/Fail	New Zealand	17 successful versus 20 failed species	19
Birds	Establish/Fail	New Zealand	15 successful versus 27 failed species	20
Birds	Establish/Fail	Global	Range of successful versus failed species	21
Plants	Invasive/Not	Australia	Predict invasiveness of 230 NIS	13
Angiosperms	Within invasive[c]	Global	Degree of invasiveness of 381 NIS (87 families)	22
Woody plants	Invasive/Not	North America	75 invasive versus 114 noninvasive species	24
Pines and *Banksia* spp.	Invasive/Not	South Africa	129 combined invasive and noninvasive species	25
Pasture plants	Invasive/Not	N. Australia	463 combined invasive and noninvasive species	31
Pine trees	Invasive/Not	Global	12 invasive versus 12 noninvasive species	32
Birds	Invasive/Not	New Zealand	34 combined invasive and noninvasive NIS	14

[a]Abbreviation: NIS, nonindigenous species.
[b]Establish/Fail: establishing birds have been compared with birds that fail to establish; Invasive/Not, invasive plants have been compared with noninvasive plants.
[c]Examines within transition and does not compare failed to successful or invasive to noninvasive species.

these studies were not selected randomly. In other words, authors selected species characteristics that were previously hypothesized to differ between successful and unsuccessful species or invasive and noninvasive species, such as a high reproductive rate, single parent or vegetative reproduction, eurytopy, polyphagy, early maturation and small body size[1] (Table 3). Although species characteristics were selected to maximize the detection of differences between subgroups of species, 39 comparisons

Table 2. Relationships between characteristics of release events and completion of an invasion transition, for species characteristics tested in at least two studies[a–c]

Characteristics	Transitions examined[d]			Refs
	Plants	Animals (birds)		
	Invasive/Not	Establish/Fail	Invasive/Not	
Number of individuals released		+, +, +, +, +, +, +, +	+	14–20
Number of introduction attempts		+, +, +, +, +, Ns, Ns	+	14,17–21
Year of introduction	–	+, –, Ns	Ns	13–15,18,20

[a]Statistically significant relationships are indicated by + (positively related to making transition) or – (negatively related to making transition).
[b]Abbreviation: Ns, not significant.
[c]Blank boxes indicate that no suitable data were available.
[d]Establish/Fail: establishing birds have been compared with birds that fail to establish; Invasive/Not, invasive plants have been compared with noninvasive plants.

produced nonsignificant associations. Fifty-five comparisons revealed characteristics that were either positively or negatively associated with transition completion (Table 3).

Where significant associations were detected within the establishment or invasiveness transition, the direction of association (positive or negative) with NIS was consistent for all but two characteristics (Table 3a,b). Thus, within a transition, study results were generally congruent. We expected, therefore, that a species characteristic enabling successful completion of one transition might be different or might even deter a species from completing another transition in the invasion sequence. For example, adaptation to feeding in darkness might aid survival of fish in ballast tanks (survival in transport, Box 1), but might hinder their establishment if water clarity is high in the new ecosystem or if the water is already inhabited by lots of nocturnal fish. Although few characteristics have been studied for more than one transition, in two cases, we did find that opposite associations existed between transitions (Table 3c,d).

Table 3. Relationships between characteristics of species and completion of an invasion transition, for species characteristics tested in at least two studies[a–d]

Characteristics	Transitions examined[e]				Refs
	Plants		Animals (birds)		
	Establish/Fail	Invasive/Not	Establish/Fail	Invasive/Not	
a. Number of seeds or eggs		+	+, –, Ns, Ns	(+/–)[f]	14–18,25
b. Fire tolerant		+, –, Ns			25,32
c. Migrating			–, –, Ns, Ns, Ns	+	14,16,17,19
d. Body mass			+, +, Ns, Ns, Ns	–	14,17–19
e. Origin[g]	*	*, *, Ns	*, *		15,18,23[h],24,31
f. Taxon[g]	*	*, *	*, Ns		17,18,22[h],23[h],31
g. History of invasion		+, +, +, +			13,24,25
h. Family or genus invasive		+, +, +, +			13,23[h],24
i. Vegetative reproduction		+, +, +			24,25
j. Variability in seed crop		–, –			25,32
k. Dispersal mechanism		Ns, Ns, Ns, +, +			24,25
l. Seed or egg mass		Ns, Ns, Ns, Ns, –, –, –		–	13,14,25,31,32
m. Length of juvenile period		Ns, Ns, –, –, –		–	14,24,25,32
n. Temp./habitat match			+	+	14,15
o. Broods per season			+, Ns	+	14,16,17
p. Flowering period length	+	Ns, Ns			24,30
q. Annual (versus perennial)		Ns, Ns			30,31
r. Range area	+	+, Ns	Ns, Ns		13,17,24[h],29,30
s. Diet breadth or type[g]			Ns, Ns		15,19
t. Inhabits diverse climates		Ns	Ns		13,20
u. Height or body length	+	+, Ns, Ns	Ns		17,25,30–32
v. Longevity		Ns		+	14,32
w. Reproductive system[g,i]	Ns	*, Ns			22[h],24

[a]Statistically significant relationships are indicated by + (positively related to transition) or – (negatively related to transition)
[b]Abbreviation: Ns, not significant.
[c]In studies that analyzed data using multiple analyses, only significant relationships are shown.
[d]Blank boxes indicate that no suitable data were available.
[e]Establish/Fail: establishing birds have been compared with birds that fail to establish; Invasive/Not, invasive plants have been compared with noninvasive plants.
[f]In the same study, one analysis with phylogenetically independent contrasts (PIC) found a + relationship, another without PIC found a – relationship.
[g]Categorical variable, significant relationship between variable and transition completion marked by an *.
[h]Examines within transition and does not compare failed to successful or invasive to noninvasive species.
[i]Reproductive system in plants (either perfect flowers, monoecious or dioecious).

Birds were more likely to become established if they were nonmigratory (three studies), whereas they were more likely to become invasive if they were migratory (one study; Table 3c). Also, birds with a higher body mass were more likely to become established (three studies), whereas birds with a lower body mass were more likely to become invasive (one study; Table 3d). Because of the small number of studies, we cannot conclude that these intuitively appealing results can be generalized.

The only species characteristic for which more than one study found only significant association (no nonsignificant results) with successful establishment was region of origin (Table 3e). This means that whether a species would become established was determined, in part, by where the species originated. On examining the invasive transition, however, five species characteristics yielded only significant relationships. Invasive plants tended to be unevenly distributed phylogenetically (Table 3f), have a history of invasion (either species, genus, or family; Table 3g, h), reproduce vegetatively (Table 3i), and have low variability in seed crops (Table 3j).

Nonsignificant associations with species characteristics for which other studies have found significant associations indicate: (1) that some sample sizes might not have been sufficient to detect differences; or (2) that the significant associations between a particular species characteristic and completing an invasion transition is contingent upon some characteristic or state of the invaded ecosystem. Expanding our consideration to species characteristics that had consistent significant relationships mixed with nonsignificant results reveals that successfully establishing birds were less likely to migrate (Table 3c) and were heavier than were those failing to become established (Table 3d). In addition, invasiveness in plants varied with region of origin (Table 3e), and differed in dispersal mechanism (Table 3k). Invasive plants tended to have small seeds (Table 3l) and short juvenile periods (Table 3m). Generally, birds tended to become established and invasive if the invaded ecosystem had similar temperature or habitats as where they were native (Table 3n), and had more broods per season (Table 3o). Some of these findings have been predicted by invasion biologists but have not been quantitatively tested until the studies reviewed here. Further quantification of these patterns could be used to screen potential NIS (Ref. 24), as is currently done in some countries[25].

Although it is important to identify characteristics significantly associated with NIS, it is equally important to identify characteristics consistently unrelated to NIS. To date, no species characteristics have been found that are consistently unrelated (i.e. at least two nonsignificant results and no significant relationships) to plant establishment or to bird invasiveness. Studies have shown that plant invasiveness is not related to the length of flowering period (Table 3p) or whether the species is an annual or a perennial (Table 3q), and that establishment in birds is not related to native range area (Table 3r), or to diet breadth (Table 3s). In addition, two studies found that plant invasiveness and bird establishment were not related to the diversity of climates inhabited in their native range (Table 3t). Some of these findings are contrary to the commonly held beliefs of invasion biologists, and ecologists and managers should not rely on the previously hypothesized traits to screen potential NIS. A few species characteristics show no pattern in significant or nonsignificant relationship to successful establishment or invasiveness (Table 3u,v,w).

Recommendations: promising avenues for ecological research

There are, therefore, consistent patterns and statistically identifiable relationships between success in invasion transitions and characteristics of release events (Table 2) and species characteristics (Table 3). The fact that patterns are emerging with respect to both species establishment and invasiveness, despite the low number of studies available, suggests that these and similar studies could lead to a broader understanding of invasions and could contribute to testing models of community assembly[26]. In addition, these studies might also help natural resource managers to predict future NIS and to reduce their occurrence and impact. Ultimately, these studies might guide the efficient allocation of management and policy efforts towards the most INVASIVE SPECIES. Two of the studies reviewed here have used species characteristics of current NIS to create statistical tools that predict the potential weed status of plants in Australia[13] and in North America[24]. One study[13] has even used the statistical model to predict the potential weed status of plants from a particular donor region. In general, however, these research approaches have been underused in the applied arena, especially in the USA. Risk assessment rating systems using other related methods are currently being developed and adopted in a few countries, such as Australia[27].

The most frequent and strong result in these studies was that successful establishment was positively related to propagule pressure. Although this result is intuitively obvious, quantifying it is not of trivial importance with respect to prevention of NIS. For example, accidental introductions of NIS via commerce-related activities, such as ballast-water release or movements of cargo containers, might be impossible to halt completely. Reducing the number of individuals released and the frequency of releases will, however, reduce the probability of establishment. Describing that relationship quantitatively for different taxa is an important challenge for population ecology, and is of immediate relevance in the development of policy and the management of NIS.

The recent successes in the predictive ecology of invasions that are highlighted here are woefully incomplete with respect to some invasion transitions (Box 1) and some taxonomic groups, and only a few studies have examined the same species characteristic at different transitions. Published research has concentrated on the later transitions, although the early transitions are the most important for management because they are the stages at which NIS can be prevented. Along the sequence of invasion transitions, management options become more constrained; once a NIS is established, eradication is often impossible, and mitigation and control are difficult and expensive, if possible at all. Thus, ecological research should be expanded to address the earlier stages of invasion, especially in the development of predictive models.

Taxonomic coverage of animal invasion studies must be expanded dramatically, especially to include animals other than birds. Studies on fish and insects would be particularly valuable because they are frequently introduced both intentionally and unintentionally, and often cause substantial ecological change and economic damages. Data on representatives of these taxa that failed in transportation (e.g. contents of ballast water) or failed to establish (e.g. stocking records) are probably more available than is commonly believed and such data could be collected. In our own ongoing work examining nonindigeous fish in the Laurentian Great Lakes (North America), we found these types of data in both the published and grey literature, and in agency records.

The quantitative methods used in the studies reviewed here are also being used in a few studies to address issues of basic community assembly by comparing NIS to IS in a given ecosystem[16,28,29]. These studies have examined fewer species characteristics than the studies reviewed here (32 compared with 68). Additional studies comparing NIS with IS are needed, however, to determine if NIS are somehow different than IS in the ecosystem being invaded.

Results summarized in this article are surprisingly consistent and reveal many useful relationships. Ecologists should recognize that the study of NIS can make valuable contributions to predictive ecology, which can be immediately relevant to our understanding of the long-standing questions about community assembly and to the management of NIS. Although ecologists have been slow to respond to Elton's 60-year-old plea for a greater understanding of NIS with quantitative studies, the recent literature reviewed here provides many promising new lines of research.

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