

Propagule pressure: a null model for biological invasions

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Abstract

Invasion ecology has been criticised for its lack of general principles. To explore this criticism, we conducted a meta-analysis that examined characteristics of invasiveness (i.e. the ability of species to establish in, spread to, or become abundant in novel communities) and invasibility (i.e. the susceptibility of habitats to the establishment or proliferation of invaders). There were few consistencies among invasiveness characteristics (3 of 13): established and abundant invaders generally occupy similar habitats as native species, while abundant species tend to be less affected by enemies; germination success and reproductive output were significantly positively associated with invasiveness when results from both stages (establishment/spread and abundance/impact) were combined. Two of six invasibility characteristics were also significant: communities experiencing more disturbance and with higher resource availability sustained greater establishment and proliferation of invaders. We also found that even though ‘propagule pressure’ was considered in only ~29% of studies, it was a significant predictor of both invasiveness and invasibility (55 of 64 total cases). Given that nonindigenous species are likely introduced non-randomly, we contend that ‘propagule biases’ may confound current paradigms in invasion ecology. Examples of patterns that could be confounded by propagule biases include characteristics of good invaders and susceptible habitats, release from enemies, evolution of ‘invasiveness’, and invasional meltdown. We conclude that propagule pressure should serve as the basis of a null model for studies of biological invasions when inferring process from patterns of invasion.

Introduction

Charles Darwin (1859) was among the first to identify apparent patterns in the establishment of nonindigenous species (NIS), noting that habitats containing ‘naturalised’ NIS seemed to have few native congeners and that habitats varied in their number of established NIS. Elton (1958) later emphasised biotic resistance and niche theory as processes underlying these patterns. More recently, theoretical arguments have been invoked to identify ‘invasiveness’ characteristics – features associated with species that establish or proliferate in

novel habitats (e.g. Baker 1965, 1974; Gray 1986; Ehrlich 1989; Lodge 1993; Mack 1996; Williamson and Fitter 1996; Rejmánek 2000).

Similar attempts have been made to identify ‘invasibility’ characteristics – attributes associated with the susceptibility of particular habitats to the establishment and proliferation of NIS (e.g. Grover 1994; Moyle and Light 1996; Shea and Chesson 2002; Van Ruijven et al. 2003). Many of these models are rooted in the biotic resistance paradigm and emphasise competition for limited resources among native and nonindigenous species. However, this view has recently been

challenged by studies of facilitative interactions involving NIS (Simberloff and Von Holle 1999). Few predictive efforts have examined empirical relationships between 'propagule pressure' (i.e. the number of individuals introduced and the number of introduction attempts) and invasion success, which we define broadly as the successful establishment, spread, or proliferation of NIS in novel regions (e.g. Lonsdale and Lane 1994; Veltman et al. 1996; Wonham et al. 2000; Forsyth and Duncan 2001; Rouget and Richardson 2003). Contrary to Baker, Ehrlich, and others, Williamson (1996) stressed the importance of propagule pressure to patterns of successful establishment by NIS, and suggested that invasions were otherwise largely unpredictable. Although Williamson used several case studies to support his assertions, the recent surge in studies of invasiveness and invasibility allows for a more comprehensive test for the generality of his assertions.

Here, we present a review of recent literature reporting characteristics correlated with the ability of NIS to invade, spread, and increase in abundance (i.e. invasiveness characteristics) and the susceptibility of habitats to the establishment and proliferation of NIS (i.e. invasibility characteristics). We also assess the importance of propagule pressure to the establishment and proliferation of NIS. In an attempt to identify generalities, these studies are addressed in a systematic fashion, employing a simple meta-analysis approach that is broad in taxonomic scope and combines studies with differing methods. Our intention is not to present a comprehensive review of the current invasion literature, but to look for general characteristics associated with invasiveness and invasibility, and to assess the role of propagule pressure.

Methods

We reviewed the modern invasion literature by searching the titles, abstracts, and keywords of articles characterising invasive species or invaded habitats using the Institute for Scientific Information (ISI) Web of Science search engine. We included only articles that were listed on the Science Citation Index as of May 2004. Since we

were only interested in characteristics of good invaders and susceptible habitats, we chose only papers that included an objective contrast of two or more species (e.g. nonindigenous vs. native; abundant vs. rare) or habitats (e.g. invaded vs. pristine; infested vs. lightly invaded). Thus, we excluded theoretical papers, *post hoc* examinations of specific invaders without the use of a contrast group for comparison (e.g. native or failed invaders), comparisons of the same species in their native and introduced ranges (i.e. biogeographical studies), and reviews or syntheses lacking original, empirical data.

We scanned the abstracts of about 1000 articles dating from 1968, focusing on 13 invasiveness characteristics: invasion history or widespread distribution elsewhere, physiological tolerance, resource consumption efficiency, body size or biomass, individual growth rate, lifespan or generation time, germination success or rate, seed size, reproductive output, length of growing or breeding season, hermaphroditic or asexual reproduction, niche habitat separation or other measures of competitive interactions (scored only as yes or no), and the effects of herbivores or predators on each species or contrast group. We also categorised invasibility characteristics into one of seven categories: intensity of anthropogenic activity (i.e. where no distinction is made between propagule pressure and human disturbance), disturbance intensity, availability or quality of food or chemical resources, light availability, richness or diversity of species already present in the community, abundance of resident species, and effects of herbivores or predators. We also recorded whether abstracts noted an explicit consideration of propagule pressure or some correlate thereof. For each characteristic, we recorded whether its association with invasiveness or invasibility was reported as positive, negative, or not different. We organised the results into five taxonomic groups: plants, invertebrates (including micro-organisms), fishes, birds, and mammals.

All papers were also categorised in terms of theme (i.e. invasiveness or invasibility) and taxon studied, as well as by the invasion 'stage' examined (establishment/spread or abundance/impact). If results from a single study were relevant to more than one category, we included results from the same study in each one. For example, Kolar

and Lodge (2002) examined characteristics of both established fishes, and those that had an impact. We grouped studies of local spread with those examining establishment because few abstracts differentiated between these stages, and because the difference between these two stages is primarily a matter of spatial scale. For example, virtually all experimental studies of establishment examined NIS that were obtained locally, thus they are really testing local spread rather than establishment from a distant native source region.

Owing to the large number of studies included in our analysis, we included only results that were mentioned in the abstract of each paper. This approach will likely result in an under-reporting of non-significant results, but has the advantage of only including the characteristics deemed most important by each researcher and is more likely to exclude characteristics for which power was too low to detect important differences. Low sample size for many characteristics required us to pool samples across taxa and contrast types, potentially limiting our ability to identify significant characteristics. The different analysis techniques (e.g. phylogenetically controlled, multi-species contrasts vs. uncontrolled pairwise contrasts), spatial scales, and contrast types (i.e. a few congeners to complete floras) in the studies themselves may also restrict our ability to identify important characteristics. However, our approach is sufficient to identify any broad-scale, taxa-independent patterns in the characteristics associated with invasibility or invasiveness.

To test for generalities in characteristics of invasiveness and invasibility across a broad range of taxa, we used a G-test (following Sokal and Rohlf 1995) to test for an evenness of studies reporting positive, negative or no difference for each trait at each invasion stage, and when both stages (establishment/spread and abundance/impact) were combined. Rejection of the null hypothesis meant that studies were not evenly distributed between the three outcomes. However, this could result from an under-reporting of non-significant results, so we then conducted a second G-test on each significant result to see if the characteristic was significantly positively or negatively over-represented. Following Sokal and

Rohlf (1995), we excluded any comparisons where the expected number of cases in each category was <3 . All significant findings reported are $P \leq 0.05$. All studies used in our meta-analysis are available from the lead author upon request, or online (see acknowledgements).

Invasiveness traits

We found 91 contrasts from 79 studies of characteristics associated with successful invaders. Analyses of invasiveness characteristics were primarily *post hoc* observational comparisons that contrasted established NIS with one of five different contrast groups in tests of invasion success: (i) species native to the invaded region; (ii) introduced species that failed to establish self-reproducing populations; (iii) species found in the same source region(s) as the NIS; (iv) a list of global congeners; or (v) other established NIS that varied in their rates of spread or their abundance.

Consistent with Williamson's (1996) assertion, most invasiveness characteristics were not significantly associated with the establishment/spread or abundance/impact of NIS. Only niche/habitat separation was significantly associated with the establishment or spread of NIS (Table 1), suggesting that NIS tend to occupy similar habitats or compete with species in the contrast groups, usually native species. Additionally, propagule pressure was significantly positively associated with the establishment stage, suggesting that established species are introduced more often and/or in greater numbers than their contrast group, usually introduced species that failed to establish. Body size/biomass was not significantly different between established NIS and the contrast groups used; all other characteristics contained too few studies to conduct a G-test. At the abundance/impact stage, only the effects of herbivores and predators were significant, as abundant species appear to be less affected, in terms of damage or number of enemy species, than the contrast groups, which were usually less abundant NIS or native species. Physiological tolerance was not significantly associated with the abundance or impact of species, while all other characteristics contained too few contrasts.

Table 1. Summary of species-specific observations (usually separate studies) implicating positive/negative/no significant difference between contrast groups used to identify characteristics of 'successful' invaders (i.e. 'invasiveness' characteristics). Symbols <5 or ≥5 refer to the number of species or groups examined.

Taxon	Characteristics associated with 'Invasiveness' (+/-/nd)													
	0	1	2	3	4	5	6	7	8	9	10	11	12	13
<i>Establishment/Spread</i>														
Birds	4/0/1	3/0/0			1/2/0		0/1/0			2/0/0	0/1/0		1/0	
Fishes (>5)	3/0/0	1/0/0	3/0/0		0/0/1	1/0/0	1/0/0			0/0/1			0/2	
Invertebrates (<5)	1/0/0												1/3	0/2/0
Invertebrates (≥5)														
Mammals	2/0/0	1/0/0					0/1/0							
Plants (<5)					1/0/0	0/0/1		1/0/1		1/0/1			1/5	1/1/0
Plants (≥5)	1/0/0		0/0/1	0/0/1	1/1/1	1/0/0	0/2/0		2/1/1	1/0/0	1/0/0	2/0/0	0/1	
Total	11/0/1*	5/0/0	3/0/1	0/0/1	3/3/2	2/0/1	1/4/0	1/0/1	2/1/1	4/0/2	1/1/0	2/0/0	3/11*	1/3/0
<i>Abundance/Impact</i>														
Fishes (<5)			1/0/0										1/0	
Fishes (≥5)	1/0/0	1/0/0	2/0/0		1/0/0	0/1/0								
Invertebrates (<5)			2/2/1	1/0/0	0/1/0	1/0/0	0/1/0			2/0/0			0/3	5/1/1
Invertebrates (≥5)		1/0/0			0/1/0									
Mammals	1/0/0	1/0/0			0/1/0		0/1/0			1/0/0				
Plants (<5)			5/5/1	6/4/4	2/0/1	3/1/1	1/0/0	4/0/1		2/1/0	1/0/0		0/5	0/0/1
Plants (≥5)	0/0/1		1/0/0	2/0/0	2/0/0	1/0/0	0/1/0	1/0/0					0/2	0/0/1
Reptiles				1/0/0									0/1	1/0/0
Total	2/0/1	1/0/0	11/7/2	10/4/4	5/3/1	5/2/1	1/3/0	5/0/1		5/1/0	1/0/0		1/11*	6/1/3*
Combined total	13/0/2*	6/0/0	14/7/3	10/4/5	8/6/3	7/2/2	2/7/0	6/0/2*	2/1/1	9/1/2*	2/1/0	2/0/0	4/22*	7/4/3

Niche separation (characteristic 12) contains only two categories – yes and no. Characteristics that are significantly ($P < 0.05$) associated positively or negatively with invasiveness are denoted by '*'. Characteristics examined are: 0 – Propagule pressure effect; 1 – Invasion history/widespread; 2 – Physiological tolerance; 3 – Consumption efficiency; 4 – Body size/biomass; 5 – Individual growth rate; 6 – Lifespan/generation time; 7 – Germination success/rate; 8 – Seed size; 9 – Reproductive output; 10 – Length of growing/ breeding season; 11 – Hermaphroditic/asexual reproduction; 12 – Niche/habitat separation; 13 – Effects of herbivores/predators.

When results from both stages were combined, propagule pressure and niche/habitat separation were still positively and negatively associated with invasiveness, respectively. Physiological tolerance, body size/biomass, growth rate, lifespan/generation time, consumption efficiency and the effect of herbivores or predators were not significantly associated with invasiveness; seed size, invasion history, and length of growing/breeding season and hermaphroditic/asexual reproduction still did not contain enough studies to draw any conclusions (Table 1).

Invasibility traits

Our review of invasibility traits resulted in 188 contrasts from 163 studies. To identify differences in habitat invasibility, studies characterised susceptible habitats based on one or more of the

following measurements: (i) abundance of NIS, including biomass or area of cover; (ii) diversity or richness of NIS; (iii) survivorship and/or reproduction of particular NIS in different habitats; (iv) presence/absence of particular species among habitats; or (v) some combination of these.

Similar to invasiveness characteristics, propagule pressure was significantly positively associated with the establishment/spread of NIS in invaded habitats, as was anthropogenic activity. Only two of six other characteristics – disturbance and resource availability – were associated with habitats in which species established, while species richness was not generally associated with invasibility. Light availability, species abundance or density and the effects of herbivores or predators did not contain enough studies to conduct a G-test. Results were similar at the abundance/impact stage, but anthropogenic activity dropped

Table 2. Summary of habitat-specific observations (usually separate studies) implicating positive/negative/no significant difference in the relationships of characteristics (0–6) of habitats susceptible to invasion (i.e. invasibility characteristics), based on four parameters (abundance, diversity, presence/absence, and survivorship of the nonindigenous species).

Taxon	Characteristics associated with 'invasibility' (+/–/nd)							
	0	0/1	1	2	3	4	5	6
<i>Establishment/Spread</i>								
Birds	5/0/0	2/0/0	1/0/0			1/5/2		0/0/1
Fish	0/0/1		1/0/0			0/1/0		
Mammals		1/0/0				0/1/0		
Invertebrates (< 5)	4/0/0	3/0/0	1/1/0	1/1/2	1/0/0	0/1/2		0/1/1
Invertebrates (> 5)	4/0/0		1/0/0	1/0/0		2/2/0	1/0/0	1/0/1
Plants (< 5)	7/0/0	1/1/0	7/2/2	2/0/2	2/2/1	4/7/1	0/2/0	1/6/2
Plants (> 5)	14/0/3	12/0/2	18/2/4	9/0/2	1/0/0	18/15/8	2/4/4	1/0/0
Total	34/0/4*	19/1/2*	29/5/6*	13/1/6*	4/2/1	25/32/13	3/6/4	3/7/5
<i>Abundance/Impact</i>								
Invertebrates (< 5)			3/0/0	2/0/1		0/0/1	0/1/0	0/1/1
Invertebrates (> 5)			1/0/0	1/0/0		0/2/0		1/0/1
Plants (< 5)	5/0/1	1/0/0	7/0/1	5/2/0	6/2/0	0/3/1	0/1/0	0/3/2
Plants (> 5)	3/0/2	2/0/1	6/3/2	4/1/1		2/2/1	1/2/1	3/0/0
Total	8/0/3*	3/0/1	17/3/3*	12/3/2*	6/2/0	2/7/3	1/4/1	4/4/4
Combined total	42/0/7*	22/1/3*	46/8/9*	25/4/8*	10/4/1	27/39/16	4/10/5	7/11/9

Characteristics that are significantly ($P < 0.05$) associated positively or negatively with invasiveness are denoted by '*'. Characteristics examined in the invaded community are: 0 – Propagule pressure effect; 0/1 – Anthropogenic activity; 1 – Disturbance; 2 – Resource/food availability or quality; 3 – Light availability; 4 – Species richness or diversity; 5 – Species abundance or density; 6 – Effects of herbivores/predators.

out because it contained only four comparisons and could not be tested. When results from both stages were combined, propagule pressure, anthropogenic activity, disturbance, and resource or food availability were all significantly positively associated with invasibility, while light availability, species richness/diversity, species abundance, and the effects of herbivores or predators were all non-significant.

The role of propagule pressure

We identified 13 of 79 invasiveness studies and 57 of 163 invasibility studies that explicitly considered the effects of propagule pressure on establishment success. Additionally, 28 invasibility studies used experimental designs that would reduce any potentially confounding effects of propagule pressure but did not necessarily consider it (Figure 1). Studies that did explicitly consider propagule pressure measured it in one of three ways: (i) deliberate introduction of a known number of propagules into replicated plots

(e.g. Mesleard et al. 1993; Miller et al. 2002); (ii) replicated plots colonised naturally by both native and nonindigenous species (e.g. Shurin 2000); (iii) historical records of the number of individuals introduced, or some proxy of it; these included records of introduction by regional governments or 'acclimatisation societies' (e.g. Veltman et al. 1996; Duncan et al. 2001) and the use of transport vector activity as a surrogate (e.g. Buchan and Padilla 2000).

Where propagule pressure was explicitly examined, 13 of 15 invasiveness contrasts and 42 of 49 invasibility contrasts identified positive associations with the success of invaders at both the establishment/spread and the abundance/impact stages, with no studies finding a negative association (Tables 1 and 2). Additionally, 22 of 26 studies that examined anthropogenic activity, representing both human disturbance and propagule pressure, found positive associations, while one study found a negative association (Table 2). It is important to note, however, that some studies of propagule pressure were from the same region, and therefore do not represent indepen-

dent samples (e.g. bird introductions to New Zealand). Nevertheless, propagule pressure and anthropogenic activity were highly significantly associated with invasiveness and invasibility, and this pattern was generally consistent across taxa and invasion stages (Tables 1 and 2). Despite this strong association, studies that identified other invasiveness and invasibility characteristics often did not consider propagule pressure hypotheses (Figure 1).

Predicting invasions

In support of Williamson's (1996) assertions, we found that (i) propagule pressure was frequently associated with the success of invaders and the susceptibility of habitats to invasion, (ii) only 3 of 13 other invasiveness characteristics were significantly positively or negatively associated with invasiveness, and (iii) only 2 of 6 other invasibility characteristics were likewise significant. Additionally, we found that the majority of studies were taxonomically biased toward plants. This may bias the results of combining taxa, but the results among most taxa are consistent even though there were too few studies for formal testing in most cases (Tables 1 and 2).

The importance of propagule pressure raises an analytical dilemma in that there is a reciprocal possibility for cause-and-effect. In other words, introduced species may be more successful because more propagules are introduced, or invaders may be introduced more because they are better at establishing. However, two lines of reasoning suggest to us that propagule pressure is likely an important factor. First, biases that affect unintentionally introduced NIS are not part of this dilemma, yet these introductions are often strongly correlated with measurements of propagule pressure. For example, Lonsdale (1999) found that invasibility of nature reserves was strongly correlated with the number of visitors, and Vilà and Pujadas (2001) and Levine and D'Antonio (2003) found strong correlations between the intensity of commodity import and the number of established NIS. Invasions in the Laurentian Great Lakes and many navigable waterways are likewise biased toward biota linked by dominant shipping vectors (e.g. MacIsaac et al.

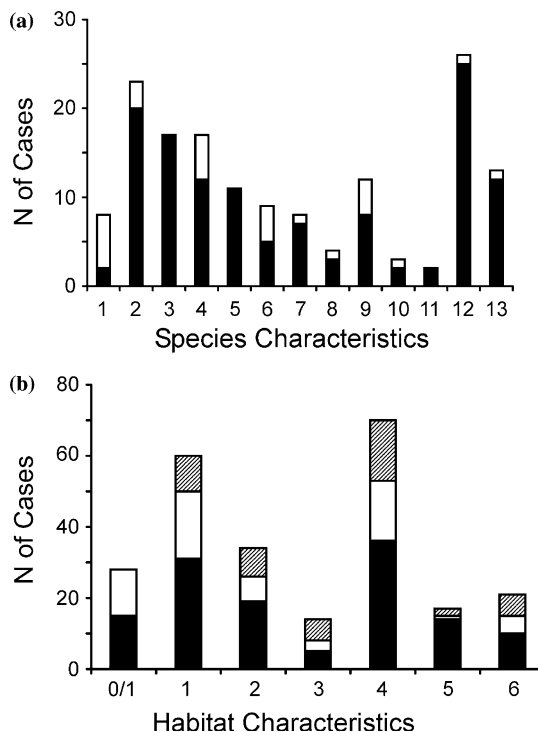


Figure 1. The total number of contrasts identifying characteristics of successful invaders or habitats susceptible to invasion. Most contrasts did not consider the potentially confounding effects of propagule pressure (black bars). However, some contrasts did measure (white bars), or control for (diagonal stripes), variation in propagule pressure. (a) Characteristics of successful invaders (invasiveness): 1 – Invasion history/widespread; 2 – Physiological tolerance; 3 – Consumption efficiency; 4 – Body size/biomass; 5 – Individual growth rate; 6 – Lifespan/generation time; 7 – Germination success/rate; 8 – Seed size; 9 – Reproductive output; 10 – Length of growing/breeding season; 11 – Hermaphroditic/asexual reproduction; 12 – Niche/habitat separation; 13 – Effects of herbivores/predators. (b) Characteristics of habitats susceptible to invasion (invasibility): 0/1 – Anthropogenic activity; 1 – Disturbance; 2 – Resource/food availability or quality; 3 – Light intensity; 4 – Species richness or diversity; 5 – Species abundance or density; 6 – Effects of herbivores/predators.

2001; Grigorovich et al. 2003; see also Carlton 1996; Ruiz et al. 2000). Second, experimental studies that have explicitly tested propagule pressure for individual species, as in biological control experiments, have consistently found a positive effect on establishment success (e.g. Hopper and Roush 1993; Memmot et al. 1998; Grevstad 1999).

Excluding propagule pressure and anthropogenic activity, the majority of invasiveness and

invasibility characteristics do not show evidence of consistency among successful invaders or susceptible habitats. Kolar and Lodge (2001, 2002) advocated that NIS characteristics be assessed at each stage of the invasion process. Our results support this view only for the ‘effects of herbivores/predators’ category, which was significant at the abundance/impact stage but not when both stages were combined. Other characteristics were not significant at either stage but were significant when both stages were combined (Table 1). Although this stage-specific approach has been validated for particular systems (e.g. Kolar and Lodge 2002; Forsyth et al. 2004) our results suggest that this alone cannot account for the lack of predictable characteristics at the broad taxonomic scale of our analyses.

The lack of generality may also reflect a difference in analytic procedures among the studies reviewed here. For example, Cassey (2001) noted that smaller birds tended to be more successful at establishing than larger ones, but after controlling for taxonomic similarity the pattern was reversed. Another possible explanation is the inherent complexity of biological invasions, such that predicting invasions might necessarily be confined to particular species-by-habitat interactions (Simberloff 1986, 1989; Tucker and Richardson 1995; Kolar and Lodge 2002). A lack of clear, operational definitions in invasion ecology may also be a source of confounding of invasion patterns because inexact definitions have likely led to the splitting of common phenomena and the lumping of unique ones (see Richardson et al. 2000; Colautti and MacIsaac 2004).

Additionally, the importance of propagule pressure identified in our meta-analysis raises the possibility that studies of invasiveness and invasibility might be confounded by variation in propagule pressure. Below we explore this possibility in more detail.

Propagule biases

Species that are deliberately introduced represent nonrandom samples of all possible invaders because they are chosen according to human preference (Lockwood and McKinney 2001). Consequently, when processes underlying invasion success are inferred from *post hoc* analyses

of ‘natural’ invasions, there is an inherent risk for spurious correlations between species-specific characteristics and invasion success. Studies that examine characteristics of deliberately introduced NIS are therefore prone to ‘propagule biases’. We define ‘propagule biases’ as nonrandom variation in the delivery of propagules, resulting in spurious correlations between invasion success and some characteristic or pattern of interest such as habitat diversity, flower size, or introduced range.

Owing to the likelihood of nonrandom variation in propagule pressure of deliberately introduced organisms, propagule biases may confound studies of numerous taxa. For example, globally invasive birds tend to belong to just seven families (of ~204 worldwide; Clements 2000), including Anatidae (ducks and geese), Phasianidae (pheasants) and taxa commensal with humans (Lockwood 1999; Duncan et al. 2003). Perhaps the best examples derive from studies of introduced birds reviewed by Duncan et al. (2003). These studies suggest that birds chosen for introduction are non-random with respect to taxonomy, native range, and a host of life history and ecological characteristics (Duncan et al. 2003). Similarly, Mack and Erneberg (2002) estimated that well over 50% of nonindigenous plants were intentionally introduced to the United States for anthropogenic use, while Richardson (1998) suggested that globally ‘invasive’ *Pinus* species tend to be those planted the most widely and for the longest time. It is therefore apparent that a large number of introductions have been nonrandom, and are thus prone to propagule biases.

Accidental introductions also may be prone to propagule biases. In the Great Lakes, for example, approximately 85% of established NIS result from unintentional introductions, primarily through discharge of contaminated ballast water (Mills et al. 1993; Ricciardi 2001; Grigorovich et al. 2003). The majority of these introductions originate from relatively few regions of the world (MacIsaac et al. 2001; Colautti et al. 2004a), and are thus nonrandom samples of the global species pool. Additional propagule biases may arise because species characteristics likely reflect their propensity for uptake and survival in the (ballast) transport vector, rather than inherent

ecological or evolutionary advantages over congeners native to the Great Lakes (Carlton 1985; Ricciardi and MacIsaac 2000). Because transport vectors including shipping, railroads, and air transport, generally operate along regular routes, NIS are likely transported nonrandomly throughout the world. This, along with nonrandom variation in transport survival and introduction, means that the majority of accidentally introduced NIS likely represent non-random samples before they are even introduced to new habitats where community and environmental interactions may become important for establishment. Yet it is on the latter factors that interpretations of invasiveness and invasibility characteristics have primarily focused.

Although a dearth of data for most species makes it difficult to test for propagule biases, several recent studies of birds and ungulates have identified potentially important confounding effects of propagule pressure (Duncan 1997; Forsyth and Duncan 2001; Duncan and Blackburn 2002; Cassey et al. 2004 Colautti 2005). For

example, Cassey et al. (2004) found that the significance of characteristics associated with established NIS changed with the choice of the contrast group because species chosen for transport and introduction were nonrandom selections of the source pool of potential invaders.

To help conceptualise the potential for propagule biases like those identified by Cassey et al. (2004), Figure 2 (after Colautti and MacIsaac 2004) combines invasion models from Carlton's (1985) ballast water transport model, Williamson's (1996) 'tens rule', barriers to invasion in Richardson et al. (2000), and Kolar and Lodge's (2001) 'transitions' model. The invasion process is broken into stages where sequential filters may preclude species from reaching subsequent stages. Factors affecting transition between each stage (i.e. 'determinants') can be categorised as propagule pressure (A; Figure 2), physico-chemical conditions (B), or community interactions (C). Particular invasion determinants act to promote or impede the transition of species to each stage (Figure 2). Propagule biases can be conceptua-

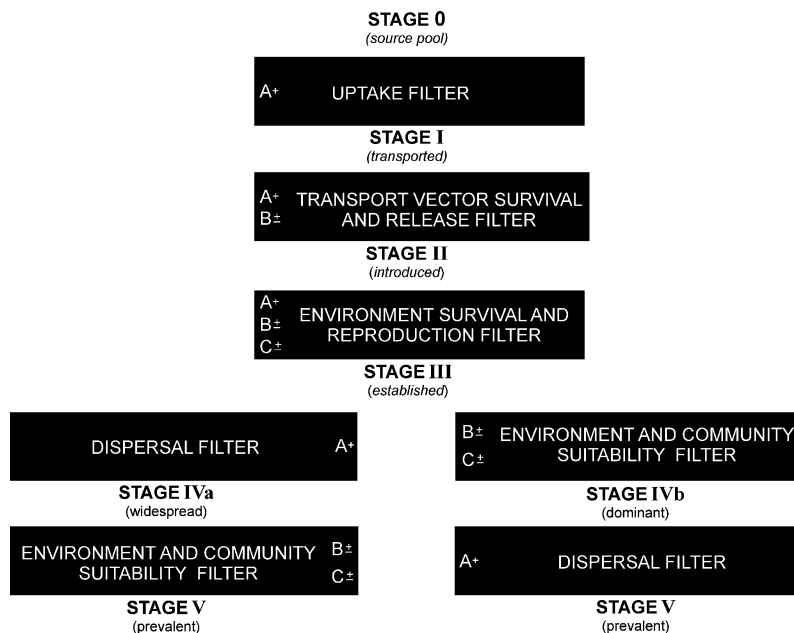


Figure 2. Invasions are modelled as a series of successive stages (0–V) after Colautti and MacIsaac (2004). Beginning with a pool of species in a source region, subsampling of species occur at early stages of the invasion process. Three classes of determinants may act to aid (+) or impede (–) the transition of species to each subsequent stage: propagule pressure (A), physico-chemical factors (B) and community interactions (C). Filters (e.g. survival and reproduction) act at each stage to preclude transition between stages and can lead to propagule biases. Note that species may be widespread but rare (stage IVa), localised but dominant (stage IVb) or widespread and dominant (i.e. stage V).

lised in this framework as nonrandom variation in A-class determinants that result in spurious patterns at later stages.

To demonstrate how propagule pressure can bias invasion patterns, Figure 3a shows a propagule bias arising from four A-class determinants influencing which species establish, based upon commercial value and popularity in the case of deliberate introduction; or conversely, pelagic life stage and survival of transport in the case of accidental introduction. In the simplest case, we ignore any species–ecosystem interactions by assuming a 15% flat rate of establishment success, and find that established species represent a non-random sample of their source pool. To demonstrate how this can bias patterns of ‘invasiveness’, Figure 3b illustrates how the choice of contrast groups can lead to spurious patterns of NIS characteristics, independent of any ecological interac-

tions such as competition or facilitation. Confounding effects emerge because contrast groups are not exposed to the same filters (Figure 3a) and are, therefore, not subject to the same A-class determinants at similar intensities.

Logically, determinants may only confound patterns at the same or subsequent stages of the invasion process. As a result, identifying the important determinants based on *post hoc* analyses (i.e. observational studies) could be difficult. For example, several determinants can result in significant differences in flower size between Stage III (established) plants and native species within the same community. One possible explanation is that larger flowers confer a competitive advantage by attracting more pollinators. However, a trend toward larger flowers could also emerge if there was a strong commercial market, and thus strong A-class determinants, for plants with larger

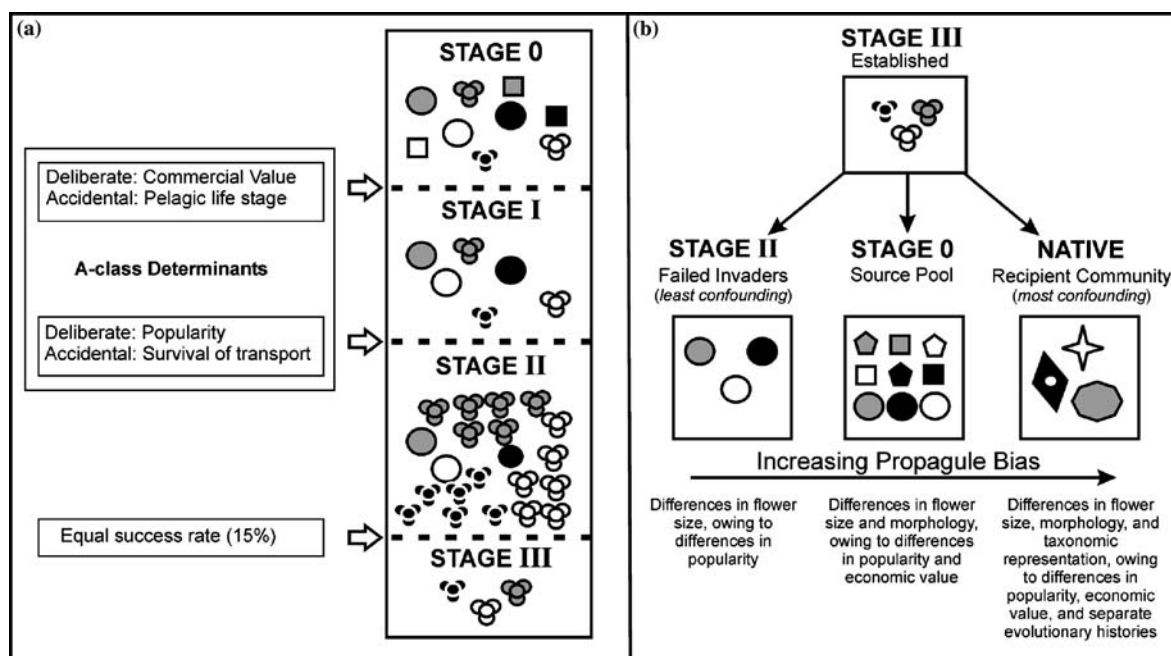


Figure 3. Propagule pressure may confound reported characteristics of established, nonindigenous species (NIS). Each symbol represents a different species, with similar symbols representing species with similar characteristics. (a) Non-random variation in propagule pressure (i.e. propagule biases), such as commercial value or survival of transport, may act at early stages of the invasion process resulting in non-random transport and introduction of NIS with similar characteristics. For simplicity, establishment is modelled as a flat-rate of all introduced species (15%). (b) Examples of contrast groups used to identify characteristics of invasiveness. One of three groups of species are typically contrasted to identify characteristics of established nonindigenous species: ‘native’ – native to the invaded region; ‘stage 0’ – species from the same source region; and ‘stage II’ – introduced but not established. Differences between contrast groups are expected to increase with the number of potential propagule biases, as exemplified by flower size, morphology, and taxonomic representation.

flowers. Thus, a widespread distribution could result from an ecologically significant interaction or simply due to a propagule bias. This characteristic may imply an advantage over native congeners, leading researchers to conclude that long flower duration is an important characteristic of 'invasiveness'. Yet this would be a logical fallacy if the prevalence of this trait owed to its preferential importation rather than to any advantage it confers. Another way to think of this is to ask, 'Would this characteristic be significant absent propagule bias?' In this case, the null hypothesis should be 'no', because other species with shorter flowering periods may have been just as successful but were never introduced. Indeed, this seems to be the case for forms of *Butomus umbellatus* in the Great Lakes region: widespread, triploid individuals have larger flowers than the more geographically restricted diploid ones. However, flower size is not likely responsible for the success of the triploids since they produce very few viable seeds compared to the diploids (Lui et al. 2004). Instead, it appears that flower size is spuriously correlated with introduction effort (Lui et al. 2004). Table 3 lists a number of oft-cited invasiveness characteristics that may be directly confounded by propagule biases in a similar manner.

In addition to these *direct* biases, some characteristics correlated with invasion success may be *indirectly* confounded by propagule biases. Such a case might exist, for example, if a smaller biomass was correlated with larger flower size, a common life-history trade-off. Disproportionate importation of larger flowers could thus result in an *indirect* propagule bias toward smaller biomass, or *vice versa*. Characteristics that are prone to a *direct* propagule bias are likely to reflect human influence or transport uptake and survival (Table 3), whereas any characteristic conceivably could be confounded by an *indirect* propagule bias. Like invasiveness characteristics, invasibility characteristics are equally prone to propagule biases where individuals are introduced nonrandomly to different habitats.

Propagule bias and invasion modelling

Given an historic lack of predictability among invasion studies, recent attempts have been made to predict high-risk species using statistical

Table 3. Some commonly cited invasiveness characteristics that may be confounded by a *direct* 'propagule bias' (i.e. non-random variation in propagule pressure).

Stage I (transport) biases

Ease of cultivation, desirability, or covariates thereof

Competitive ability
Growth rate
Reproductive rate
Time to maturity
Vegetative/asexual reproduction
Presence of dormant stage
Size of propagules
Presence of predators/parasites
Phenology compared to native species.
Taxonomic over/under-representation
Physiological tolerances
Body size
Ability to utilise local pollinators
Root density

Attainability and factors affecting accidental transport

Reproductive rate
Vegetative/asexual reproduction
Presence of dormant stage
Size of propagules
Dispersal mode/efficiency
Invasive elsewhere

Stage II (introduction) bias

Survival of transport

Competitive ability ('hardiness')
Reproductive rate
Vegetative/asexual reproduction
Presence of a dormant stage
Size of propagules
Dispersal mode/efficiency
Physiological tolerances
Pre-germination treatment

Stage IVa (spread) bias

Human-mediated dispersal

Growth rate
Reproductive rate
Time to maturity
Vegetative/asexual reproduction
Presence of dormant stage
Size of propagules
Dispersal mode/efficiency
Invasive elsewhere

Characteristics are separated by 'stages' of the invasion process from Figure 2 (bold), and some possible propagule biases (italics) driving nonrandom variation in propagule pressure at each stage.

models based on characteristics of NIS (Tucker and Richardson 1995; Reichard and Hamilton 1997; Kolar and Lodge 2002). Such studies may be system-specific, but represent significant advances in invasion ecology. However, we feel it

important to consider the potential danger in developing management strategies when causation is certain. This is particularly important in the case of invasions, where innocuous species may be blacklisted simply because they share traits with species that are introduced often (i.e. type I error). Alternatively, species that are rarely introduced could still have a potential to become widespread or abundant, yet may be allowed entry because they do not share traits common among historically introduced species (i.e. type II error). This might occur if models were inadvertently built on characteristics reflecting the common geographic origins of NIS found in a particular region. If import origins then change, as might be the case of increasing trade with a developing country, or changes in global availability, then predictive models could fail. More importantly, if the ability of imported species to establish and proliferate is at least partially dependent upon propagule pressure, as suggested by our meta-analysis, then classifying a species as harmless could potentially serve to increase its rate of importation, thereby facilitating its invasion.

Propagule biases may also confound theoretical expectations. For example, some ecosystems have experienced a series of successful invasions by species native to one particular geographic area, as has happened in the Great Lakes (Ricciardi and MacIsaac 2000). While this pattern is consistent with an 'invasional meltdown' scenario in which early invaders facilitate later ones (Simberloff and Von Holle 1999; Ricciardi 2001), it could also result from a propagule bias in which species from a particular donor area are differentially transported to the recipient ecosystem. These processes needn't be mutually exclusive; propagule pressure might be more important in determining which species invade and spread (i.e. stages 0–IVa), while facilitative interactions determine which species become dominant or prevalent (stage IVb or V). The two processes may also act synergistically, if for example, a higher inoculum size also increases the chance of introducing facilitators. Nevertheless, we argue that the potential for propagule biases necessitates that great care be taken when inferring process from pattern.

Propagule pressure: a null model

We propose that propagule pressure should form the basis of a null model for invasion studies because it has consistently been associated with invasion success, because it has potential to confound interpretations of invasion patterns, and because it models invasions simply as a probabilistic process. Furthermore, we contend that future attempts to interpret characteristics of invaders should first attempt to dismiss potential confounding effects of propagule biases before other processes are implicated. Although this seems obvious, our review suggests that this approach has not been widely used (Figure 1). Perhaps it is because such a protocol seems daunting. However, compared to the myriad possibilities underlying biological interactions it may prove useful in harmonising discordant characteristics of successful invaders or susceptible habitats. For example, our review revealed that invasibility is similarly associated with species-rich and species-poor communities; this pattern is analogous to the highly controversial diversity-stability debate (e.g. McGrady-Steed et al. 1997; Hector et al. 1999; Stachowicz et al. 1999; Huston et al. 2000). Levine and D'Antonio (1999) reviewed studies relating species diversity to invasibility and noted that experimental studies tended to find diverse communities more resistant to invasion, while observational studies often found the opposite. Levine (2000, 2001) later demonstrated that spatial scale was likely important, owing to the importance of propagule pressure at larger scales.

Eliminating propagule biases

Simply by considering propagule pressure, one can formulate testable hypotheses to help tease out the possibility of propagule bias as a confounding variable. Returning to the example of larger flower size, a null hypothesis might be: given the same level of propagule pressure, large- and small-flowered species should have equal likelihood of establishing. This might be falsified using microcosm or field experiments on different species, or on different phenotypes of the same species that vary in flower size. In fact, progress is

already being made toward eliminating propagule biases. Several experimental studies have correlated species characteristics to different aspects of invasion success even after considering propagule pressure. This has been accomplished either by controlling the number of propagules (e.g. Grotkopp et al. 2002), or through a multi-step regression analysis in which introduction effort is accounted for (e.g. Sol and Lefebvre 2000; Duncan et al. 2001). Similarly, experimental studies of invasibility have found significant relationships between habitat characteristics and the successful establishment of NIS, even when plots received equal numbers of propagules. Using experimental plots with equal numbers of seed propagules, for example, Burke and Grime (1996) and Davis and Pelsor (2001) found strong support for the importance of disturbance and resource availability to invasibility. These types of studies will continue to increase our understanding of factors affecting invasiveness and invasibility. However, it is important to extend these studies to natural ecosystems, and to better explore the factors that influence success at each invasion stage (from Figure 2). Moreover, there still remains a large gap in experimental tests of the relative importance of propagule pressure and other biotic and environmental factors to the success of NIS at each of the invasion stages.

Additionally, propagule biases may be better addressed by understanding biological invasions as biogeographical phenomena, rather than something inherent to the taxonomy of NIS (Richardson et al. 2000). Biogeographic studies are those that examine different populations of the same species, and are therefore less likely to be confounded by propagule biases. For example, some studies have attempted to relate the impact of NIS to the number of enemies present (i.e., the 'enemy release hypothesis'; (e.g. Keane and Crawley 2002; Mitchell and Power 2003; Torchin et al. 2003), or to identify 'evolutionary' changes in the mean phenotypic traits of introduced populations that may account for their success (e.g. Lee 2002; Leger and Rice 2003). However, even these biogeographical studies are prone to propagule biases if contrast groups are not chosen judiciously, and if biases in transport and introduction are not considered. This may indeed be the case for studies of enemy release, where analyses often in-

clude data from areas that probably did not act as invasion sources (Colautti et al. 2004b, 2005).

Our intention is not to repudiate the importance of biological processes as determinants of invasion success; rather we propose that hypotheses based on the concept of propagule pressure represent the appropriate starting point to predict successful transition of the invasion stages (Figure 2). Instead of focusing on complex, system-specific biotic interactions, management efforts may be better spent reducing opportunities for unintentional introductions and escapes, while activities that deliberately introduce NIS should be re-examined. Given the implications of propagule pressure for invasions, eradication programs should weigh heavily the importance of propagule pressure on the spread of established NIS. For example, prescribed burnings designed to open space for native species may prove futile if propagules from nearby populations of NIS are not precluded from subsequent colonization (e.g. Simberloff et al. 2003).

The consideration of propagule biases and acknowledgement of their potentially confounding effects can greatly assist the quest for generalities in invasion ecology. We anticipate that our suggestions will not be universally accepted, but hope that at the very least they will provide a framework to guide invasion biologists to a better understanding of patterns and processes underlying the ecology of invasions.

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