Opinion TRENDS in Ecology and Evolution Vol.20 No.5 May 2005

The role of propagule pressure in explaining species invasions

Julie L. Lockwood[1], Phillip Cassey[2] and Tim Blackburn[2]

[1]Ecology, Evolution and Natural Resources, Rutgers University, 14 College Farm Road, New Brunswick, NJ 08901, USA
[2]School of Biosciences, University of Birmingham, Edgbaston, Birmingham, UK, B15 2TT

Human-mediated species invasions are a significant component of current global environmental change. There is every indication that the rate at which locations are accumulating non-native species is accelerating as free trade and globalization advance. Thus, the need to incorporate predictive models in the assessment of invasion risk has become acute. However, finding elements of the invasion process that provide consistent explanatory power has proved elusive. Here, we propose propagule pressure as a key element to understanding why some introduced populations fail to establish whereas others succeed. In the process, we illustrate how the study of propagule pressure can provide an opportunity to tie together disparate research agendas within invasion ecology.

Introduction

Propagule pressure (also termed 'introduction effort' [1]) is a composite measure of the number of individuals released into a region to which they are not native [2]. It incorporates estimates of the absolute number of individuals involved in any one release event (propagule size) and the number of discrete release events (propagule number). As the number of releases and/or the number of individuals released increases, propagule pressure also increases. Here, we concentrate on the role of propagule pressure in determining the establishment success or failure of non-native populations (Figure 1). However, increasing propagule pressure might be equally important in understanding the rate of geographical spread of non-native populations (e.g. [3]) (Box 1). Determining the role of propagule pressure within these different invasion contexts should lead to broader ecological and management insights into invasive species biology.

Variation in invasion success

Propagule pressure is an 'event-level' characteristic [1,4]: that is, it can differ for each introduced population. This is in contrast to location- and species-level traits, which are constant across repeated introductions (e.g. [5]). For example, rainbow trout *Oncorhynchus mykiss* have been purposefully introduced into Africa, Australia, New Zealand, Europe and many other locations worldwide [6]. We can explain the success of rainbow trout using its life history or ecological traits (e.g. dietary generalism), which are species-level characters that do not differ across the locations to which the rainbow trout was introduced or across independent release events carried out in any one location. Alternatively, we can explain the success of rainbow trout using characteristics of each location into which the trout were released and subsequently established. A site will have a standard set of ecological and environmental conditions that will not differ between release events separated by some relatively small timeframe. However, the number of individual rainbow trout released during any one event will vary through time and across locations. Thus, exploring the role of propagule pressure on establishment success requires us to shift the focus away from comparisons of the fate of different species to comparisons of the fate of incipient non-native populations [7]. The fact that some of these populations experience long-lasting success whereas others do not has

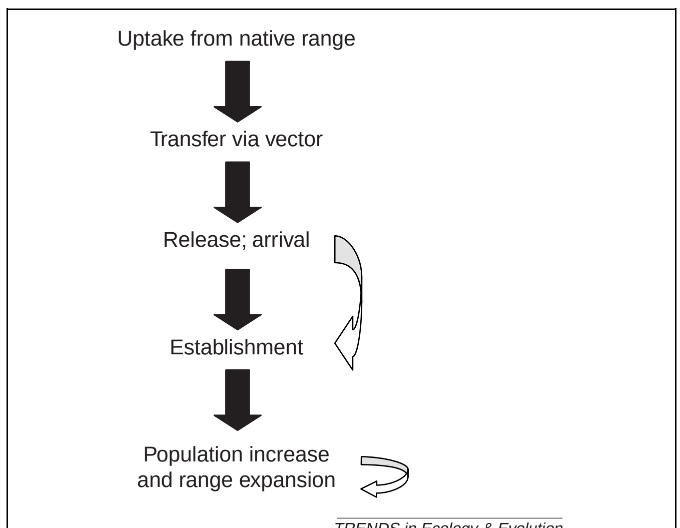

Figure 1. The multi-step process of non-native species invasion. For non-native species to cause economic or ecological harm, they must first be transported out of their native range and released within a novel locality, establish a self-sustaining population in this new location, and expand their geographical range beyond the point of initial establishment. Each of these successful transitions is represented by a solid black arrow [3,10]. Propagule pressure will increase the likelihood of establishing a non-native population and of this population expanding its geographical range (white arrows). Our primary aim is to consider evidence for the role of propagule pressure in determining initial establishment success. In this context, propagule pressure is a product of patterns in the transport vector(s) and modes of release and arrival. Thus, propagule pressure provides a crucial conceptual link between the early and later invasion stages, and might also account for differences between species in their invasion success rates across regions.

Corresponding author: Lockwood, J.L. (lockwood@aesop.rutgers.edu).
Available online 23 February 2005

www.sciencedirect.com 0169-5347/$ - see front matter doi:10.1016/j.tree.2005.02.004

Box 1. Propagule pressure, establishment success and the rate of geographical range expansion

There is considerable empirical and modeling evidence that, once a non-native population has established, proximity to a source of dispersing individuals will increase the likelihood that the invasive species will expand its geographical range [3,52]. For example, the distribution and percentage cover of three widespread invasive plants in South Africa were predicted well by the distance of each newly invaded location to the original invasion foci [3]. Sites close by received many more seeds than did those further away because the seeds were wind dispersed. Similarly, the distribution of zebra mussels in the Great Lakes region of North America was well predicted by the proximity of each newly invaded lake to one that was already infested as these lakes were more likely to have been visited by infested small recreational boats [52].

The number of dispersing individuals is often termed 'propagule pressure' in relation to the source of dispersing individuals; however, the spatial scale and mechanisms determining propagule pressure are distinct from those that we review here. In the above examples, the invasive populations of zebra mussels and plant species had already established self-sustaining populations in North America and South Africa, respectively. The sites surrounding the original invasion foci were likely to receive large numbers of colonizing individuals because of the spatial dynamics of local individual dispersal movements, and because of the localized physical or social forces constraining that movement (i.e. boat and wind traffic, respectively). Establishment success reflects very large-scale movements of non-native individuals that, by definition, achieve this movement with the purposeful or inadvertent help of humans. The social forces driving these large-scale movements reflect patterns in global trade and economy. Propagule pressure in this context reflects human preferences for particular non-native species, extent of commercial trade between two (or more) countries, and the effort that humans expended in importing and releasing large numbers of non-native individuals.

Although our critics may claim that we are cutting this distinction too finely, we suggest that the differences in how spatial scale and 'dispersal' mechanism correlate to propagule pressure are large enough to consider the role of propagule pressure independently within each invasion stage. We do recognize that the theory and models used when explaining the role of propagule pressure in geographical spread might be readily adapted for use in predicting the role of propagule pressure in ensuring establishment success (and vice versa), and we encourage such cross-fertilization of ideas.

been one of the more frustrating elements of attempts to find predictive features of the invasion process [8]. We suggest that differences in propagule pressure between releases of non-native individuals are a major component of that variation in invasion success [9,10].

Two decades of modeling and field observation have shown that small populations are more likely than larger ones to become extinct [11]. Small populations succumb more often to stochastic (e.g. environmental variation) or inverse density-dependent (e.g. Allee) effects. When population models include a spatial element, two further principles emerge. First, declining populations can often be sustained over the long term through constant immigration (i.e. sources and sinks [12]). Second, populations are less likely to go extinct if individuals are spread across space such that adverse conditions in one location (a 'subpopulation') will not also negatively affect individuals in another [13]. From this theory, conservation biologists argue for intervention on behalf of a declining population before it passes a size below which extinction is almost assured. It also implies that we should maintain as many subpopulations as possible, and ensure that individuals can successfully disperse between them.

The same arguments can be invoked in the context of biological invasions, making it immediately clear why propagule size and number are likely to be so relevant to invasion success. Releases of large numbers of individuals should enable the incipient exotic population to weather the inevitable decreases in survival or reproduction caused by the environment or demographic accidents. The repeated release of individuals into one location essentially functions as a source pool of immigrants, thus sustaining an incipient population even if the initial release was of insufficient size (or badly timed) to facilitate long-term establishment. Large or consistent releases of individuals into one location should enable the incipient population to overcome behavioral limitations or other problems associated with small population sizes. Propagule pressure can also be positively related to the amount of genetic variation in the introduced population, improving the chances that the population will be able to adapt successfully to novel selection pressures in the recipient location [14]. Finally, spatially disjunct releases help ensure that at least some of the non-native individuals find a location where environmental conditions are favorable for establishment.

Given the focus of conservation biologists on problems associated with declining and small populations, we might expect these principles to have been fully explored within the context of biological invasions. However, early workers failed to recognize the importance of the relationship between propagule pressure and invasion success, especially as it relates to differences in non-native species richness across locations [15]. One possible reason for this failure is the limited amount of information readily available about propagule pressure for historical invasions. Although the probable importance of propagule pressure is now recognized [10], the lack of information about it is rarely mentioned as a hindrance to explaining past patterns in invasion, or to our ability to predict future invasions (but see [16]).

Nevertheless, those researchers that have been able to locate such information consistently find that propagule pressure explains significant variation in establishment success (Table 1). Evidence from analyses of historical introductions is matched in its consistency with experimental analyses (Table 1). In addition, many of the studies show that the influence of propagule pressure swamps the effects of other postulated influences on establishment, such as body size, native range size, or introduction timing. It is unusual to find such a consistent result within invasion ecology, and even more unusual to find one factor that reliably explains large amounts of variation in the outcome of biological invasions across taxa, locations and modes of inquiry.

The idiosyncrasy of the invasion process

The importance of propagule pressure to establishment success can also explain why the invasion process often appears so idiosyncratic. In a recent exploration of the role of propagule pressure in the establishment of non-native bird populations, Cassey and colleagues [16] identify two

Table 1. Published evidence for the positive effect of propagule pressure on non-native population establishment[a]

Taxonomic group[b]	Geographical location	Mode of inquiry (observation or experimental)	Propagule pressure analyzed (size or number)[c]	Refs
Waterstriders	Finland	Experimental	Size	[14]
Biocontrol insects	Canada	Observational	Size and number	[35]
	USA	Observational	Size	[36]
Chrysomelid beetles	New York, USA	Experimental	Size	[37]
Freshwater fishes	California	Observational	Size	[38]
Birds	New Zealand	Observational	Size	[39]
	New Zealand	Observational	Size	[40]
	New Zealand	Observational	Size and number	[41]
	New Zealand	Observational	Size	[42]
	New Zealand	Observational	Size and number	[43]
	Australia	Observational	Number	[44]
	Australia	Observational	Size	[45]
	Worldwide	Observational	Size and number	[16]
Galliform birds	New Zealand	Observational	Size	[46]
Game birds	USA	Observational	Size	[24]
Mammals	Australia	Observational	Number	[47]
Mice	Maine Islands, USA	Experimental	Size	[48]
Bank vole	Stockholm Archipelago, Sweden	Experimental	Size	[49]
Ungulates	New Zealand	Observational	Size	[50]
Birds and mammals, reintroductions	Worldwide	Observational	Size	[23]
	Worldwide	Observational	Size	[51]

[a]Publications listed are those that we could find that explicitly tested for a relationship between propagule pressure and establishment success. We did not include studies that explored the relationship between propagule pressure and rate of geographical spread of invasive populations (Box 1).
[b]The preponderance of bird studies reflects the greater availability of propagule pressure data for species in this taxon.
[c]Size, number of individuals released in any one event; number, the number of independent release events.

reasons for this importance. First, this research showed that most variation in propagule size was clustered among release events [16]. Thus, a single species that has been introduced to several islands or continents (e.g. the house sparrow *Passer domesticus*) is likely to have been released in widely varying propagule sizes or numbers across those locations. It follows that the influence of forces such as environmental stochasticity and Allee effects will manifest at the event level on the invasion process, making invasion outcomes at the species or location level unpredictable. Because propagule pressure consistently explains much about establishment outcome, we should expect establishment success to appear idiosyncratic in the absence of such information. Some researchers have suggested that such 'unexplainable' differences in establishment outcome for one species introduced across several locations is sufficient reason to doubt the utility of predictive efforts [17,18].

Second, Cassey and colleagues found that propagule size was also correlated to several species-level traits that are commonly considered relevant predictors of establishment success [16]. Thus, the inclusion of propagule size within multivariate statistical models profoundly influenced the conclusions drawn. When propagule size was included, it and an increased propensity for dietary generalism were the only variables independently associated with the establishment success of non-native birds. However, when propagule size was excluded, greater dietary generalism, larger native geographical range, being introduced to an island rather than a mainland, less tendency to migrate, and less difference between donor and recipient latitudes were all independently associated with greater establishment success. This set of variables has been found to be important in several analyses of historical bird introductions (reviewed in [4]), and are commonly mentioned as traits that might provide some explanatory power for the invasion success of other taxa [19]. That these variables are confounded with propagule size in this case raises considerable doubts about their direct influence on establishment success. If these results generalize, the commonly observed disparities in the ability of species- and/or location-level traits to account for variation in invasion success will, to a greater or lesser degree, be due to their hidden relationship with propagule pressure. Although such correlations could in theory provide us with surrogates for propagule pressure, we do not yet know the consistency of these relationships. Nevertheless, the inconsistency of correlations between introduction success and most variables other than propagule pressure suggests that their potential as surrogates would be poor.

Understanding the role of propagule pressure

The strength of the relationship between propagule pressure and establishment success does not, however, negate roles for location and species [20,21], although it is the interaction of these factors with propagule pressure that might be the more important element to furthering our understanding of invasions. In that regard, we highlight four research agendas that can promote our understanding of the role of propagule pressure within invasions beyond recognizing the importance of large numbers.

Propagule size and number

First, we echo the call of Ruiz and Carlton [22] for more nuanced analyses of the relationship between propagule pressure and establishment success. These authors reframe this relationship within a biophysical context and refer to it as the 'dose-response curve', where dose is propagule size or number and the response is establishment probability (Figure 2). In most of the research summarized

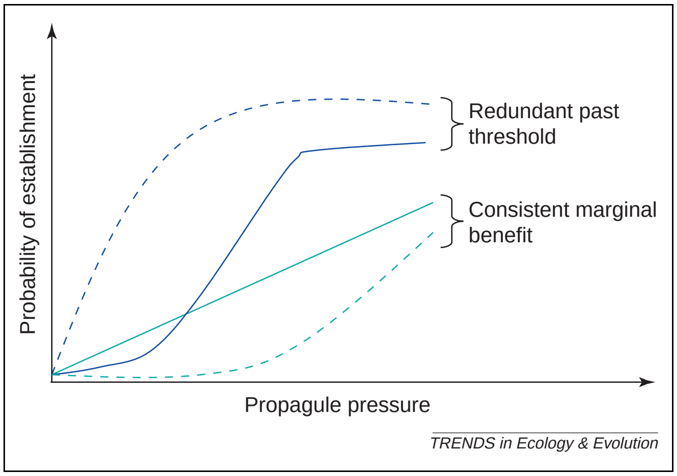

Figure 2. The dose-response curve of biological invasions [20], where dose is propagule pressure and the response is probability of establishment. Variability in the shape of the curve is of considerable practical interest [20]. Exponential (green dashed) or linear (green solid) responses suggest that there is a consistent marginal benefit to either releasing (e.g. biocontrol or conservation reintroductions), or prohibiting the release (regulatory control of transportation vectors), of every individual. A dose-response curve that contains thresholds (blue lines) suggests that, beyond a certain propagule size, effort expended to prohibit or encourage the release of more individuals is redundant.

within Table 1, the authors were unable to (or did not) portray propagule pressure or establishment probability as continuous variables (but see [23,24]). Thus, we have a poor idea as to the true shape of this relationship or to factors that affect it (although see Figure 2).

In addition, we do not have a clear understanding of the relative roles of number of individuals released versus the number and spatial configuration of release events. These measures of propagule pressure are likely to have unique relationships with establishment probability. Propagule size serves to overcome stochastic and inverse density-dependent forces, whereas propagule number serves to reduce the influence of negative forces that are spatially structured (e.g. climate or biotic interactions). Under what circumstances does one element of propagule pressure become more important than the other? The answer dictates how society might best regulate the flow of goods such that the more crucial element to propagule pressure (whatever that turns out to be) is reduced [22]. For example, Drake and Lodge [25] identified global hotspots of marine and estuarine invasion, constructed a ship traffic transportation network model, and estimated the future rate of invasion under three different management scenarios. They concluded that reducing the average probability of an individual ship causing an invasion is more effective for reducing the rate of biotic homogenization than is eliminating key ports that were significant donor centers for the global spread of invasive species.

Whether propagule number and size function in either a synergistic or independent manner with respect to one another also needs to be considered. The answer to this question will determine the best approach to modeling the role of propagule pressure in invasion research, and will dictate the design of experimental analyses that incorporate differences in propagule pressure between treatments.

Genetic variability and evolution

Second, we suggest that the relationship between propagule pressure and genetic diversity deserves greater attention than it has received, because it might be more complex than is commonly appreciated. Typically, we think of incipient non-native populations as having low genetic variability. These few founding individuals contain only a fraction of the total heterozygosity observed in their native population, and the inter-mating of the few founding individuals leads to substantial genetic drift (e.g. [26]). Experience with the conservation of very small populations gives us plenty of evidence that such low levels of genetic variation will decrease the probability of non-native population establishment [27]. We expect that increased propagule pressure will serve to increase genetic variability in the incipient non-native population, and thereby increase the chances of establishment (e.g. [14]).

Recent work by Kolbe and colleagues [28] indicates that, if propagules are coming from different native source areas and that these native populations show spatial genetic structure, genetic diversity can be increased over that observed within any of the native populations. For non-native populations of the lizard *Anolis sagrei,* this increase resulted from the inter-mingling of distinct native haplotypes within the non-native populations in Florida [28]. Such infusions of novel genetic material might provide the variation (genetic and phenotypic) for the non-native population to establish successfully and begin expanding its range after relatively long lag phases. It might also provide unprecedented opportunities for novel genetic recombination within the non-native population, with the accompanying possibility of evolutionary shifts in key life-history or morphological characters [28].

The prevalence with which increasing propagule pressure serves to increase genetic variation over native values is currently difficult to know because of the relatively limited number of studies of the genetics of non-native populations. It is possible that increased genetic variation within the non-native range will boost the probability of establishment well beyond what we would expect if we were to discount problems of low genetic variability, and might also account for variation in establishment success that propagule pressure fails to explain. However, finding increased genetic variation in the non-native population is dependent on a transportation vector that effectively 'samples' from across the native range of the species. Not all vectors will act in this manner, and not all native populations are spatially structured such that sampling would add novel genetic material. Finally, this is also an example of how the study of propagule pressure might tie together previously disparate research threads. The increase in genetic variability that accompanies increased propagule pressure should enhance establishment success as well as the potential for the non-native to expand its range and cause ecological harm.

Location and species-specific effects

Third, we suggest investigation of how the shape of the dose-response curve varies depending on the condition of the recipient location, the species (or group) under consideration, or the nature of interactions between newly arriving species and those already established [19]. Several authors have highlighted the role of disturbance in influencing establishment success. D'Antonio and colleagues [21] suggest that any location can be invaded by non-native individuals given the appropriate conditions (see also [29]). The more disturbed the location (e.g. experiencing physiological stress or resource flux), the lower the propagule pressure necessary to enable successful establishment of the non-native population, and vice versa. Crawley [30] suggested a similar role for life history, whereby some species have traits that enable them to establish successfully even if released as small propagules, whereas others would require substantial propagule pressure for successful establishment. Certainly, although propagule size and establishment success are correlated within bird families, they are not correlated across families, suggesting that different taxa respond differently to increases in numbers released [16].

It is also possible that non-native populations that have already established can influence the propagule pressure that is necessary for later introductions of other non-native species to succeed. Some non-native species have large effects on resources or biotic interactions within the native community. The presence of these non-native species represents a form of disturbance and, just as with physical disturbances, the presence of these species might enable newly arriving non-natives to establish successfully with low propagule sizes or numbers [21]. A similar effect could be realized through synergistic or mutualistic interactions between existing non-natives and new non-native arrivals [31]. These examples illustrate that the influence of location- and species-level effects on establishment will indirectly influence the relationship between propagule pressure and establishment success. This will often lead to seemingly odd results, whereby similar numbers of individuals of the same species do not always ensure success across locations (e.g. [16]).

Experimental investigations of the dose-response curve

Fourth, and following on from above, there is a clear need for experimental investigations to address explicitly the role of propagule pressure in explaining the probability of establishment success. Because the dose-response curve can vary substantially according to the physical and biological context of the introduction, retrospective analyses are inherently limited and cannot provide causative connections between propagule pressure and other relevant factors. Currently, most experiments add species (usually plants) to plots that differ in one or more elements that are thought to be important for establishment success (e.g. native species richness or disturbance level) and follow the fate of these potential invaders through time (e.g. [32,33]). However, almost without exception, the number of individuals (seeds) 'released' is held constant and the 'release event' (seed additions) occurs only once at the beginning of the experiment. The results relating to the influence of species- and location-specific effects on propagule pressure suggest that the outcome of these experiments would be quite different if propagule size, propagule number, or both, are varied in a nested or crossed design with other factors considered of importance. The results from such experiments should serve to delineate clearly how the dose-response curve responds to variations in biophysical elements, number of native species and intensity of competition, predation, or mutualism.

Conclusions

Elucidating the factors that determine introduction success involves disentangling the influence of characteristics of the species and environment, and the idiosyncrasies of specific introduction events [4]. From the array of possibilities available, propagule pressure is emerging as a single consistent correlate of establishment success. Propagule pressure can explain not only why some introductions succeed when others fail, but also why introduction success is so idiosyncratic. However, although propagule pressure has good explanatory power, its predictive ability is untested. Being able to explain which species have already become biological invaders does not imply that we can predict which species will be the new invaders [34]. An important step now is to assess whether propagule pressure has the power to predict the future as well as it explains the past.

References

1 Blackburn, T.M. and Duncan, R.P. (2001) Determinants of establishment success in introduced birds. *Nature* 414, 195–197
2 Carlton, J.T. (1996) Pattern, process, and prediction in marine invasion ecology. *Biol. Conserv.* 78, 97–106
3 Rouget, M. and Richardson, D.M. (2003) Inferring process from pattern in plant invasions: a semimechanistic model incorporating propagule pressure and environmental factors. *Am. Nat.* 162, 713–724
4 Duncan, R.P. *et al*. (2003) The ecology of avian invaders. *Annu. Rev. Ecol. Syst.* 34, 71–98
5 Cassey, P. (2002) Life history and ecology influences establishment success of introduced land birds. *Biol. J. Linn. Soc.* 76, 465–480
6 Lever, C. (1996) *Naturalized Fishes of the World*, Academic Press
7 Colautti, R.I. and Mac Isaac, H.J. (2004) A neutral terminology to define 'invasive' species. *Div. Dist.* 10, 143–146
8 Grosholz, E.D. and Ruiz, G.M. (1996) Predicting the impact of introduced species: lessons from the multiple invasions of the European green crab. *Biol. Conserv.* 78, 59–66
9 Simberloff, D. (1989) Which insect introductions succeed and which fail?. In *Biological Invasions: A Global Perspective* (Drake, J.A. *et al*., eds), pp. 61–75, John Wiley & Sons
10 Williamson, M. (1996) *Biological Invasions*, Chapman & Hall
11 Akcakaya, H.R. *et al*. (1999) *Applied Population Ecology*, Sinauer Press
12 Brown, J.H. and Kodric-Brown, A. (1977) Turnover rates in insular biogeography: effect of immigration on extinction. *Ecology* 58, 445–449
13 Hanski, I. (1989) Metapopulation dynamics: does it help to have more of the same? *Trends Ecol. Evol.* 4, 113–114
14 Ahlroth, P. *et al*. (2003) Founder population size and number of source populations enhance colonization success in waterstriders. *Oecologia* 137, 617–620
15 Simberloff, D. (2000) Forewood. In *The Ecology of Invasions by Animals and Plants* (Elton, C.S.), pp. vii–xiv, University of Chicago Press
16 Cassey, P. *et al*. (2004) Global patterns of introduction effort and establishment success in birds. *Biol. Lett.* 271, S405–S408. DOI: 10.1098/rsbl.2004.0199
17 Schoener, T.W. and Schoener, A. (1983) The time to extinction of a colonizing propagule of lizards increases with island area. *Nature* 302, 332–334
18 Ehrlich, P. (1986) Which animal will invade? In *Biological Invasions of North America and Hawaii* (Mooney, H.A. and Drake, J.A., eds), pp. 79–92, Springer-Verlag
19 Kolar, C.S. and Lodge, D.M. (2001) Progress in invasion biology: predicting invaders. *Trends Ecol. Evol.* 16, 199–204

20 Cassey, P. *et al*. (2005) Lessons from the establishment of exotic species: a meta-analytical case study using birds. *J. Anim. Ecol.* DOI: 10.1111/j.1365-2656.2005.00918.x
21 D'Antonio, C. *et al*. (2001) Ecosystem resistance to invasion and the role of propagule supply: a California perspective. *J. Med. Ecol.* 2, 233–245
22 Ruiz, G.M. and Carlton, J.T. (2003) Invasion vectors: a conceptual framework for management. In *Invasion Vectors* (Ruiz, G.M. and Carlton, J.T., eds), pp. 459–504, Island Press
23 Griffith, B. *et al*. (1989) Translocation as a species conservation tool. Status and strategy. *Science* 245, 477–480
24 Pimm, S.L. (1991) *The Balance of Nature?*, University of Chicago Press
25 Drake, J.M. and Lodge, D.M. (2004) Global hotspots of biological invasions: evaluating options for ballast-water management. *Proc. R. Soc. Lond. Ser. B* 271, 575–580
26 Baker, A.J. and Moeed, A. (1987) Rapid genetic differentiation and founder effect in colonizing populations of common mynas (*Acridotheres tristis*). *Evolution* 41, 525–538
27 Frankham, R. *et al*. (2004) *A Primer of Conservation Genetics*, Cambridge University Press
28 Kolbe, J.J. *et al*. (2004) Genetic variation increases during biological invasion by a Cuban lizard. *Nature* 431, 177–181
29 Davis, M.A. *et al*. (2000) Fluctuating resources in plant communities: a general theory of invisibility. *J. Ecol.* 88, 528–536
30 Crawley, M.J. (1986) The population biology of invaders. *Philos. Trans. R. Soc. Lond. Ser. B* 314, 711–731
31 Simberloff, D. and Von Holle, B. (1999) Positive interactions of nonindigenous species: invasional meltdown? *Biol. Inv.* 1, 21–32
32 Foster, D.L. (2001) Constraints on colonization and species richness along a grassland productivity gradient: the role of propagule availability. *Ecol. Lett.* 4, 530–535
33 Von Holle, B. and Simberloff, D. (2004) Testing Fox's assembly rule: does plant invasion depend on recipient community structure? *Oikos* 105, 551–563
34 Williamson, M. (1999) Invasions. *Ecography* 22, 5–12
35 Bierne, B.P. (1975) Biological control attempts by introductions against pest insects in the field in Canada. *Can. J. Entomol.* 107, 225–236
36 Hopper, K.R. and Roush, R.T. (1993) Mate finding, dispersal, number released, and the success of biological control introductions. *Ecol. Entomol.* 18, 321–330
37 Grevstad, F.S. (1999) Experimental invasions using biological control introductions: the influence of release size on the chance of population establishment. *Biol. Inv.* 1, 313–323
38 Marchetti, M.P. *et al*. (2004) Alien fishes in California watersheds: characteristics of successful and failed invaders. *Ecol. Appl.* 14, 587–596
39 Duncan, R.P. (1997) The role of competition and introduction effort in the success of passeriform birds introduced to New Zealand. *Am. Nat.* 149, 903–915
40 Sol, D. and Lefebvre, L. (2000) Behavioural flexibility predicts invasion success in birds introduced to New Zealand. *Oikos* 90, 599–605
41 Green, R.E. (1997) The influence of numbers released on the outcome of attempts to introduce exotic bird species to New Zealand. *J. Anim. Ecol.* 66, 25–35
42 Duncan, R.P. *et al.* Factors affecting the release, establishment and spread of introduced birds in New Zealand. In *Biological Invasions in New Zealand* (Allen, R.B. and Lee, W.G., eds), Springer (in press)
43 Veltman, C.J. *et al*. (1996) Correlates of introduction success in exotic New Zealand birds. *Am. Nat.* 147, 542–557
44 Duncan, R.P. *et al*. (2001) High predictability in introduction outcomes and the geographical range size of introduced Australian birds: a role for climate. *J. Anim. Ecol.* 70, 621–632
45 Newsome, A.E. and Noble, I.R. (1986) Ecological and physiological characters of invading species. In *Ecology of Biological Invasions* (Groves, R.H. and Burdon, J.J., eds), pp. 1–20, Cambridge University Press
46 Duncan, R.P. and Blackburn, T.M. (2002) Morphological overdispersion in game birds (Aves: Galliformes) successfully introduced to New Zealand was not caused by interspecific competition. *Evol. Ecol. Res.* 4, 551–561
47 Forsyth, D.M. *et al.* Climatic suitability, life-history traits, introduction effort and the establishment and spread of introduced mammals in Australia. *Conserv. Biol.* 18, 557–569
48 Crowell, K.L. (1973) Experimental zoogeography: introductions of mice to small islands. *Am. Nat.* 107, 535–558
49 Ebenhard, T. (1989) Bank vole (*Chethrionomys glareolus* (Schreber, 1780)) propagules of different sizes and island colonization. *J. Biogeogr.* 16, 173–180
50 Forsyth, D.M. and Duncan, R.P. (2001) Propagule size and the relative success of exotic ungulate and bird introductions to New Zealand. *Am. Nat.* 157, 583–595
51 Wolf, C.M. *et al*. (1998) Predictors of avian and mammalian translocation success: reanalysis with phylogenetically independent contrasts. *Biol. Conserv.* 86, 243–255
52 Bossenbroek, J.M. *et al*. (2001) Prediction of long-distance dispersal using gravity models: zebra mussel invasion of inland lakes. *Ecol. Appl.* 11, 1778–1788