

The Role of Propagule Pressure in Biological Invasions

Daniel Simberloff

Department of Ecology and Evolutionary Biology, University of Tennessee, Knoxville, Tennessee 37996; email: dsimberloff@utk.edu

Annu. Rev. Ecol. Evol. Syst. 2009. 40:81–102

First published online as a Review in Advance on August 27, 2009

The *Annual Review of Ecology, Evolution, and Systematics* is online at ecolsys.annualreviews.org

This article's doi:
10.1146/annurev.ecolsys.110308.120304

Copyright © 2009 by Annual Reviews.
All rights reserved

1543-592X/09/1201-0081\$20.00

Key Words

demographic stochasticity, environmental stochasticity, genetic drift, inbreeding depression, invasion, lag, niche models, propagule, SCOPE

Abstract

Although most studies of factors contributing to successful establishment and spread of non-native species have focused on species traits and characteristics (both biotic and abiotic), increasing empirical and statistical evidence implicates propagule pressure—propagule sizes, propagule numbers, and temporal and spatial patterns of propagule arrival—as important in both facets of invasion. Increasing propagule size enhances establishment probability primarily by lessening effects of demographic stochasticity, whereas propagule number acts primarily by diminishing impacts of environmental stochasticity. A continuing rain of propagules, particularly from a variety of sources, may erase or vitiate the expected genetic bottleneck for invasions initiated by few individuals (as most are), thereby enhancing likelihood of survival. For a few species, recent molecular evidence suggests ongoing propagule pressure aids an invasion to spread by introducing genetic variation adaptive for new areas and habitats. This phenomenon may also explain some time lags between establishment of a non-native species and its spread to become an invasive pest.

1. INTRODUCTION

Many species deliberately or inadvertently introduced to a new region almost certainly fail to survive, and of those that survive, many do not become invasive pests (Jeschke & Strayer 2005, Williamson 1996). These facts have led to a persistent effort to understand why and to be able to predict invasion outcome.

Researchers increasingly recognize that invasions can be divided into two or more stages (e.g., Carlton 1985; Catford et al. 2009; Kolar & Lodge 2001, 2002); the extent to which these must be considered individually depends on the questions asked. Failure of an invasion can occur at any of these stages, and for an introduced species to become invasive it must succeed at all of them. One or more propagules of a species must first become entrained in a transport pathway, then survive the transport voyage, then successfully exit the transport vector, then establish an initial population that may or may not spread and become invasive. For the purposes of this review, all but the last stage can be subsumed into the question of whether a species arrives and establishes a population, while the last stage encompasses the question of whether that population becomes invasive. The great majority of the literature has focused on two approaches to answering both questions, spurred by early classic works on introduced species (Baker 1965, Elton 1958), and formalized in an agenda enunciated in 1983 by the international Scientific Committee on Problems of the Environment, SCOPE (Drake et al. 1989):

1. What characteristics make a species likely to be a successful invader?
2. What characteristics of a local community or environment render it vulnerable (“invasible”) or resistant to invasion?

The SCOPE agenda set the research program in invasion biology for the next two decades (Davis 2006). It is noteworthy that propagule pressure was not mentioned in the SCOPE agenda and has not, until recently, been a very prominent part of this program. Williamson (1996) apparently introduced the term, although the concept was discussed occasionally before this, as is shown below. “Propagule” is variously defined to mean either a group of individuals arriving in a place (the definition used in this review) or any one of these individuals, but the concept of propagule pressure is straightforward. It has two key components: propagule size (the number of individuals in a propagule) and propagule number (the rate at which propagules arrive per unit time). Propagule pressure is the distribution of propagule sizes and the pattern in which propagules arrive. That is, 1000 individuals can arrive in one propagule of size 1000, 100 propagules each of size 10, etc. If they arrive in several propagules, these can arrive at different temporal rates: 1 propagule per year, per decade, per century, etc.

Probably the reason propagule pressure was not prominent in the early rise of invasion biology, even though it seems like an obviously important factor, is that a model attributing invasion success or failure to amount of propagule pressure (rather than the SCOPE factors) is a “null model” (Colautti et al. 2006). It argues that the biological traits of the introduced species and the biological and physical characteristics of the recipient area are less important than simply the rate at which propagules arrive. Null models in ecology have been controversial since their widespread introduction in the 1980s (Gotelli & Graves 1996); recent examples are controversies surrounding the neutral theory of Hubbell (2001) and the mid-domain hypothesis of species richness (Colwell et al. 2004). Some ecologists seem to rebel against the idea that which species coexist may not rest on the traits and interactions of the species. In any event, though propagule pressure was initially not a prominent part of the burgeoning invasion biology literature, the past decade has seen rapidly increased interest in the proposition that propagule pressure is crucially important in determining invasion success and impact (**Figure 1**), perhaps even more important than the two

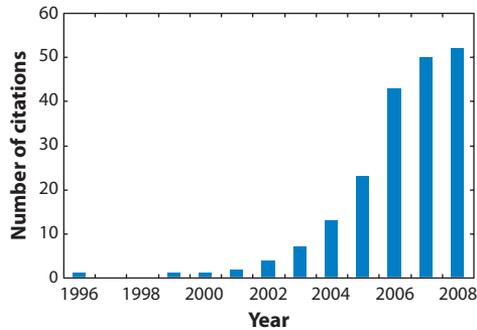


Figure 1

Number of citations found in a search of the ISI Web of Knowledge for articles published between 1996 and 2008 that included “propagule pressure” in the title, abstract, or key words.

factors—species traits and community/environmental traits—suggested in the SCOPE agenda (see Section 2.4).

The few early discussions of propagule pressure assumed that, if it had any influence at all, it would be on the likelihood that an initial introduction would establish an ongoing population (e.g., MacArthur & Wilson 1967). However, a major recent insight is that propagule pressure can also heavily affect the probability that an established introduction will spread and/or become invasive. The various possible impacts of propagule pressure on introductions are best explored by considering the threats and limitations weighing on nonindigenous populations during initial establishment and subsequent spread.

Almost all estimates of propagule pressure have been indirect—deriving from assumed or (rarely) demonstrated correlations between propagule number and readily measured variables [e.g., numbers of nursery catalogs and other indications of horticultural activity (e.g., Mulvaney 2001), area and dates of plantings (e.g., Krivánek et al. 2006), aquarium trade figures (e.g., Semmens et al. 2004), boat and shipping traffic (e.g., Colautti et al. 2003, Schneider et al. 1998, Semmens et al. 2004), and length of roads (e.g., Dullinger et al. 2009)]. Few researchers (e.g., Wonham et al. 2001) have attempted to measure directly the propagule load associated with such pathways. An important recent development is the use of genetic techniques to generate additional estimates of propagule pressure (Section 3 below).

Epidemiological models of the spread of invasions assume that spatial variation in propagule pressure is the driving force behind the spread, but except for one recent publication (Drake & Lodge 2004), such models have not been used explicitly to model propagule pressure per se. In such epidemiological models, spatial distribution of propagule pressure—variation among sites in propagule rain that they receive—has been implicitly modeled in two ways. Classic diffusion models (e.g., Skellam 1951) assume that individuals disperse with equal probability in all directions by random, short movements across a homogeneous landscape. More recent stratified diffusion models (e.g., Hastings 1996, Lewis 1997, Shigesada & Kawasaki 1997) include occasional long-distance “jump” dispersal believed to be important in the spread of many introduced species. Shigesada & Kawasaki (1997) also allowed for greater probability of movement in some directions than in others by adding a term to Skellam’s basic model. Diffusion models have been used with some success to model spread of established invaders (reviewed by Lockwood et al. 2007). This success is assumed to reflect the faithful modeling of propagule pressure, but such models have not been used to attempt to determine explicitly differences in propagule pressure at different points within and outside an established invader’s range.

Gravity models (Fotheringham & O’Kelly 1989) are also employed to explain and/or predict spread of established introduced species. These consider not only characteristics of the source population (e.g., its size) but also those of potential colonization sites (e.g., their distances from sources) and the spatial configuration of sites. Schneider et al. (1998) used a gravity model to assess risk of zebra mussel (*Dreissena polymorpha*) invasion of various Illinois waterbodies, as did Bossenbroek et al. (2001) to predict zebra mussel invasions of uninfested inland lakes of Illinois, Indiana, Michigan, and Wisconsin and to explain existing invasions in these states. The variables measured to estimate propagule pressure were number of boats leaving and arriving at various points plus pairwise distances between points in the former study, and number of boats in each county and locations and areas of lakes in the latter study. The model of Bossenbroek et al. (2001) explained lake occupancy in parts of Michigan and Wisconsin fairly well, but in neither study were propagules actually documented—that is, propagule pressure was simply estimated by the model. Recently, Drake & Lodge (2004) used a gravity model to model propagule pressure explicitly, rather than simply the spread of an invader, in an effort to suggest management approaches for ballast water.

Niche-based distribution models (e.g., Guisan & Thuiller 2005, Peterson 2006) are frequently used to predict the ultimate distribution of introduced species. These have typically incorporated only environmental variables, but several studies have also incorporated variables representing propagule pressure (e.g., Bossenbroek et al. 2001, Dullinger et al. 2009, Foxcroft et al. 2004, Rouget & Richardson 2003). Dullinger et al. (2009) suggest that distributions of introduced species will eventually achieve an equilibrium determined by the environmental suitability of sites, so that, as an invasion proceeds toward that equilibrium, addition of propagule pressure will eventually contribute little to performance of models based on environmental variables. However, Shmida & Wilson (1985) have shown that parts of a plant species’ range may be maintained in spite of unfavorable environment simply by virtue of continuing propagule pressure (which they termed mass effect). Further examples are cited in Section 2.6.

Typically ecotoxicologists seek a dose-response curve to characterize the impact of a chemical on human health (e.g., Felter et al. 1998). Invasion biologists have suggested the same goal for the impact of propagule pressure on establishment success and/or impact (e.g., Lockwood et al. 2005, Ruiz & Carlton 2003)—a sort of invasion analog of the ecotoxicologists’ LD₅₀. This search has been elusive, however (Lodge et al. 2006), partly because there is no simple analog to “dose” (for invasions, it would have to include propagule size, number, and temporal pattern, at least), partly because so many factors weigh on the outcome of an introduction, many of them probabilistically (Sections 2 and 3), and partly because of the inability of invasion biologists to conduct controlled, replicated experiments on more than a handful of species, so few empirical data sets exist on which to base a dose-response curve. However, these few experiments, as well as many observations and models, have yielded a growing understanding of the role of propagule pressure in the trajectories of various invasions.

2. FACTORS AFFECTING PROPAGULE ARRIVAL AND POPULATION ESTABLISHMENT

2.1. Demographic and Environmental Stochasticity

Both successful establishment of an introduced species and the process of extinction of dwindling populations are concerned with the probability that a small population will survive. It is thus not surprising that insights relevant to the role of propagule pressure in invasion success should come from observations, experiments, and theory related to conservation of small populations. Even before the advent of modern invasion biology (roughly the mid-1980s), there was occasional

interest in the notion that the number of individuals in a founding propagule (propagule size) could determine whether a species arriving in a new site would establish a population, and that the rate at which propagules (or groups of them) arrived would affect the probability that the species would ultimately establish or persist once it did establish.

Probably the most influential early expression of this idea was by MacArthur & Wilson (1967) in *The Theory of Island Biogeography*. They deduced on mathematical grounds that individuals of a species must arrive on an island from outside at a certain rate, depending on demographic parameters of the species, in order for a population to persist. This deduction was elaborated by increasingly sophisticated mathematical modeling and incorporated in a phenomenon that came to be termed demographic stochasticity (Lande 1988, Shaffer 1987). Demographic stochasticity is the random fluctuation of population size by virtue of the population's having a finite number of individuals, and it incorporates random fluctuation in such demographic traits as birth rate, death rate, and sex ratio. In a population consisting of a very few individuals, the probability that all will die in the next interval, or that all offspring will be of one sex, is far greater than in a large population. Demographic stochasticity is highly relevant to determining the minimum viable population size for threatened species (see, e.g., Lande 1988, Shaffer 1987) and also to whether a propagule arriving at a new location will found a population. However, the early literature on invasions referred to this matter only sporadically, concentrating instead on species and/or environmental traits favoring successful invasion.

Environmental stochasticity (Lande 1988, Shaffer 1987)—unusual weather events, floods, fires, etc.—is another factor that interacts with propagule pressure. Even a very large propagule can be totally eliminated if it happens to be in the wrong place at the wrong time. A cold snap or a hurricane could kill every individual of a propagule (especially a small one). However, if further propagules continue to be released, the influence of such random events on the ultimate likelihood of establishment is minimized.

As invasion biology matured, several researchers pointed to the key role of chance, in the form of demographic and environmental stochasticity, in determining initial establishment success of introductions (e.g., Crawley 1989, Daehler & Strong 1993). These phenomena are now widely seen as key to puzzling failures of particular introduction attempts (Sax & Brown 2000).

2.2. Propagule Size and Establishment Success

Several cases show that increased propagule size can increase likelihood of establishment (**Table 1**). However, some widespread invasions were founded by surprisingly small propagules, a fact that has led to insights on the relationship of propagule size and number to probability of establishment success. For example, the entire North American population of the widespread introduced European solitary bee *Lasioglossum leucozonium* probably originated from one female (Zayed et al. 2007). Similarly, stocks of the encyrtid wasp *Pauridia peregrina* were propagated from a single female, released in California for biological control purposes, and permanently established (Clausen 1978), while stocks reared from just eight individuals of the encyrtid *Anarhopus sydneyensis*, released in California for biological control, also established (Clausen 1978). Simberloff (1986, 1989) describes other insect species introduced for biological control establishing from very small propagules. In most of these biological control releases, the original propagule was first used to rear populations in captivity from which larger propagules could be released to the field. This procedure might circumvent demographic and environmental stochasticity (though not genetic stochasticity, which is discussed below). However, a number of well-established introductions originated from minute propagules released directly to nature. The classic case is that of the North American muskrat (*Ondatra zibethicus*) in Europe. Three females and two males from Alaska were introduced in 1905

Table 1 Studies indicating positive effect of propagule size (1) and propagule number (2) on establishment of introduced species (additional cases listed by Lockwood et al. 2005)

Taxon	Location and factor	Reference
Biocontrol insects	Canada – 1,2	Beirne 1975
	New York, USA ^a – 1	Grevstad 1999
	New Zealand ^a – 1	Memmott et al. 2005
<i>Aquarius najas</i> (waterstrider)	Finland ^a – 1	Ahloth et al. 2003
Salmonids	Nevada, USA – 1,2	Colautti 2005
Birds	New Zealand – 1,2	Veltman et al. 1996
	New Zealand – 1,2	Duncan 1997
	New Zealand – 1	Green 1997
	New Zealand – 1	Forsyth & Duncan 2001
	Australia – 1	Newsome & Noble 1986
Ungulates	New Zealand – 1	Forsyth & Duncan 2001
Mice	Maine islands, USA ^a – 1	Crowell 1973
<i>Myodes glareolus</i> (bank vole)	Stockholm Archipelago, Sweden ^a – 1	Ebenhard 1989
<i>Holcus lanatus</i> (velvetgrass)	California, USA ^a – 1	Thomsen et al. 2006
Plants	Virginia, USA ^a – 2	Von Holle & Simberloff 2005
<i>Daphnia magna</i>	Laboratory ^a – 1,2	Drake et al. 2005

^aExperimental.

near Prague, Czechoslovakia (Long 2003). By 1914, muskrats numbered 2 million in Bohemia alone and had spilled into Germany and Austria, eventually colonizing most of Europe (although parts of the subsequent spread were aided by other introductions). Similarly, all small Indian mongooses (*Herpestes auro-punctatus*) in the West Indies derived, for many years, from four males and five females from Calcutta, liberated in Jamaica for biological control of rats; descendants of these were subsequently released throughout the Caribbean (Long 2003).

Several recent experiments on the influence of propagule size on probability of establishment resulted in populations founded by minute propagules released directly in the field. Grevstad (1999), by introducing a single gravid female to nature, founded a new population of the beetle *Galerucella californiensis*, a biocontrol agent for purple loosestrife (*Lythrum salicaria*), that was apparently ongoing after three generations. Similarly, Memmott et al. (2005) founded several ongoing (after six years) populations of the psyllid *Arytainilla spartiophila*, used for weed biocontrol, by introducing just two or four individuals in the field. Such examples are not restricted to insects.

Such cases have given rise to what James Carlton (personal communication) has called the Noah fallacy: that a breeding pair (or a mated female; or one individual, for asexual species) suffices for an introduction to take hold and spread. This is not actually a fallacy, as some of the above examples attest: It is theoretically possible for a single pair (or individual) to found a population. However, if we think probabilistically (and invasion biology is largely a probabilistic science), the metaphor of Noah's fallacy is correct in spirit, because for most, if not all, species the probability of such an event is small, even vanishingly small, and larger propagule sizes drastically increase the probability of establishment. Several theoretical treatments predict this increase (e.g., Gabriel & Bürger 1992, Stephan & Wissel 1994), and some experimental research supports it. For example, Grevstad (1999) introduced beetles (*G. californiensis* and *G. pusilla*) onto purple loosestrife at 36 sites with propagule sizes of 20, 60, 180, and 540. She found that both probability of initial population establishment and population growth rate for those populations that did establish increased with increasing propagule size. Memmott et al. (2005) made 55 replicated releases in

the field of 2, 4, 10, 30, 90, and 270 individuals of *A. spartiophila* and found that probability of initial establishment and persistence (only for the first year) increased with propagule size, even though some tiny propagules did establish. Ahlroth et al. (2003) introduced propagules of from 2 to 16 mated female waterstriders (*Aquarius najas*) into 90 Finnish streams and found that probability of population establishment increased with propagule size.

Observations that are not actually experimental (that is, lacking adequate controls and replication) but are drawn from historical introduction records also show that establishment probability increases with propagule size. Pioneering research of this sort was conducted by Beirne (1975) on insects introduced to Canada for biological control. Beirne did not separate propagule size from propagule number, simply tallying total number of individuals of each species introduced, but his results surely implicate total propagule pressure, and probably propagule size, as crucial factors. Of species for which at least 31,200 individuals were introduced, 78% established populations. This statistic fell to 40% when between 5000 and 31,200 individuals were introduced, and to just 10% when fewer than 5000 individuals were introduced. For the subset of species (those introduced to forest habitats) for which individual propagule sizes were available, 60% of species that averaged over 800 individuals per propagule established populations, while only 15% of those with smaller propagules did so.

Similarly, for the 14 ungulate species introduced to New Zealand, releases of propagules smaller than about six individuals were likely to fail while those of larger propagules were likely to succeed (Forsyth & Duncan 2001). Also in New Zealand, of 133 bird species deliberately introduced, data on propagule size and number available for over half (Lockwood et al. 2007) were analyzed by Veltman et al. (1996), Duncan (1997), and Green (1997). All found that establishment probability increased with number of individuals introduced. For example, for species with fewer than 10 individuals released, only 6% established populations, while 36% established when 11–100 individuals were released, and 83% established when more than 100 individuals were released (Green 1997). A similar analysis for birds introduced to Australia yielded similar results: the larger the propagule, on average, the greater the likelihood of establishment (Newsome & Noble 1986). All four species for which more than 500 individuals were released and 11 of the 14 for which between 101 and 500 individuals were released established populations. However, only one of 16 species for which fewer than 20 individuals were released and 6 of 12 for which 21 to 100 individuals were released did so.

2.3. Propagule Number and Establishment Success

Although fewer researchers have explored the role of number of propagules than of propagule size in determining population establishment, some observations suggest propagule number is important (Table 1). The paradigmatic case is that of the Eurasian house sparrow (*Passer domesticus*), introduced to North America. In 1851, eight pairs released in Brooklyn did not establish a population. About 50 birds were released, also in Brooklyn, in 1852, but again establishment failed. Another 50 birds released in 1853, also in Brooklyn, not only established but were the main element in an invasion that eventually covered North America; the house sparrow is now one of the most numerous birds on the continent (Long 1981). As another example, the European red deer (*Cervus elaphus*) was introduced unsuccessfully to New Zealand 31 times before establishment led to spread throughout the entire South Island and much of the North Island (Clarke 1971). Acclimatization societies repeatedly and fruitlessly introduced large propagules of the European rabbit (*Oryctolagus cuniculus*) to New Zealand before one propagule, no larger than the others, led to a disastrous success (Salisbury 1961, Thomson 1922). Sax & Brown (2000) cite other, similar examples.

Among studies of historical records, Beirne (1975) showed that, for biocontrol insects in Canada, ca. 70% of species introduced more than 20 times established populations, compared to about 10% of those introduced fewer than 10 times. For the New Zealand bird data, Veltman et al. (1996) and Duncan (1997) analyzed the separate impacts of propagule size and propagule number, finding that increases in each aspect of propagule pressure increased probability of successful establishment. For instance, Veltman et al. (1996) found that, of unsuccessful introductions, 36% had been introduced only once and 24% only twice, whereas, of successful introductions, only 4% had been introduced just once and 7% just twice. Most of the established birds had been introduced 10 or more times, while all but 3 of the failures had been introduced fewer than 10 times. A similar analysis by Colautti (2005) of the 13 species (16 subspecies) of salmonid fishes introduced into Nevada yielded similar results: Both propagule size and propagule number were significantly, positively associated with successful establishment.

2.4. Relative Importance of Propagule Pressure, Species Traits, and System Traits

For observational (as opposed to experimental) data, part of the apparent influence of propagule pressure (size and number) on success rate may be an artifact of which species people try harder to introduce. Previous reports of successful introduction of a species in other areas may induce people to try to release additional propagules if the first few attempts at a site fail (cf. Beirne 1975), whereas they might not try repeatedly if no successes are known elsewhere. Likewise, it would not be surprising if acclimatization societies (such as those introducing birds to New Zealand) would typically use large propagules of species thought to be “successful colonists” from reports elsewhere, whereas species with no substantial colonization record elsewhere would be introduced with very small propagules, almost as an afterthought, if a few individuals could be inexpensively gathered (cf. Simberloff & Boecklen 1991). However, the experimental studies are not subject to this caveat, and much evidence (cited above) shows a substantial influence of propagule size and number on probability of invasion success.

In fact, several studies have suggested that propagule pressure is, in general, the most important factor in determining establishment success, and that much previous research implicating various SCOPE factors—species traits and recipient ecosystem characteristics—is flawed because propagule pressure was not accounted for (Cassey et al. 2004; Colautti 2005; Colautti et al. 2006; Lockwood et al. 2005, 2007). One approach is to show that direct or indirect measures of propagule pressure are correlated with the factors claimed to predict introduction success. For example, Cassey et al. (2004) assembled all available data on propagule sizes of attempted bird introductions, as well as data on other variables said to affect likelihood of population establishment (body mass, geographical range size, fecundity, degree of diet specialization, degree of habitat specialization, dichromatism, migratory tendency, latitudinal difference between source and target, whether the target is an island or mainland). They analyzed all these data across all species both with and without accounting for phylogenetic relatedness. The key finding was that, except for habitat specialization, all other factors were significantly correlated with propagule size, whether or not phylogeny was taken into account.

The implication of this finding is exemplified by considering a commonplace of invasion biology, tracing back at least to Elton (1958): Introductions are more likely to succeed on islands than on mainland (but see Jeschke 2008, Simberloff 1995). This pattern is usually attributed to the tendency of islands to have fewer species than mainland. However, the fact that island introductions tended to entail larger propagules than mainland ones casts the usual explanation into doubt. It is possible that the correlation between island or mainland status and establishment success is wholly

or largely an artifact of larger propagule sizes on islands. On some islands (e.g., New Zealand), both acclimatization societies and government agencies were particularly assiduous in attempting to introduce birds (Lockwood et al. 2007).

Colautti et al. (2006) conducted a meta-analysis of 79 studies comparing successful invaders with some contrast group (e.g., native species or failed introductions), tabulating 13 species characteristics often felt to correlate with invasiveness and 7 habitat characteristics widely believed to correlate with invasibility. They also broke invasion into two stages, the establishment/spread phase and the abundance/impact stage. Only 29% of the studies considered propagule pressure, but, for those that did, it was the only significant predictor for the establishment stage and was positively associated with success at both the establishment and impact stages. Colautti (2005) simply showed differences in propagule size and number between successfully introduced salmonids in Nevada and failures that were at least as large as differences in various species traits often claimed to contribute to successful establishment.

Von Holle & Simberloff (2005) experimentally tested the relative importance of propagule number and ecological resistance (both biotic and abiotic) to establishment by both native and nonindigenous plants in a Virginia streamside habitat. They varied numbers of propagules (groups of seedlings or small plants) and numbers of species of resident plants in quadrats with different flooding regimes (a key physical trait). Propagule number far outweighed native richness and flooding regime in determining whether an invasion occurred. Many experiments have been conducted to determine the extent to which plants are seed-limited (Turnbull et al. 2000). Most of these have been on native species, possibly because sowing seeds of an introduced plant species into areas unoccupied by that species may be illegal or at least seen as unethical. The relatively few experiments of this sort on introduced plants have generally been conducted in small plots unoccupied by the introduced species within a larger, occupied area, and most of these have had just one sowing density of seeds plus an unsown control treatment (e.g., Foster & Dickson 2004, Sanders et al. 2007). Often a seed-sowing treatment was crossed with a site manipulation (e.g., disturbance of some sort). Many of these experiments show that a particular species can germinate and grow in previously unoccupied sites, suggesting that insufficient propagule pressure could conceivably limit the local occurrence of such species. However, few studies were monitored for a long enough period to determine if self-sustaining populations were established (Turnbull et al. 2000), and this feature, combined with the absence of a range of sowing densities, limits the inferences that can be drawn about the relative importance of propagule pressure, species traits, and site characteristics.

2.5. Mechanisms of Demographic and Environmental Stochasticity

As for why, exactly, increased propagule pressure enhances probability of establishment, demographic stochasticity—chance vicissitudes of demographic parameters such as sex ratio and birth and death rates—must constitute a large part of the answer. As noted above, a very small population has a substantial probability of disappearing for reasons having little or nothing to do with its inherent suitability for biotic or abiotic conditions. Trivially, with only four individuals in one generation (including the founding generation), in sexual species the sex ratio is normally ca. 1:1, so there is a 3% chance that all individuals will be of one sex. For 20 individuals, this probability is only 0.000002. This is to say that very small propagules, or populations that immediately arise from them, may be at great risk of extinction from demographic stochasticity (cf. Lande 1988), but this risk decreases rapidly with increasing propagule size. If a single small propagule is at risk of failure owing to demographic stochasticity, a sequence of propagules may be far more likely to lead to establishment. As Veltman et al. (1996) observe, if the fates of successive identical propagules

are independent and the probability of establishment is p , then the probability that at least one of N propagules will succeed is $1 - (1 - p)^N$. This number can increase rapidly with N .

In sum, increases in both propagule size and propagule number will decrease the likelihood of failure from both demographic and environmental stochasticity, but the roles of the two components of propagule pressure relative to these two risks differ. Environmental stochasticity has an inherent temporal component—a particular disastrous event, like a hurricane, occurs at a particular time and is likely to eliminate every individual even in a large propagule. However, it will not affect subsequent propagules. Thus, propagule number is most likely to lessen risk from environmental stochasticity, even as it may help to compensate for a failure, owing to demographic stochasticity, of a single small propagule. By contrast, increased propagule size is most likely to lessen risk from demographic stochasticity.

Sax & Brown (2000) suggest an additional reason for the differing outcomes of apparently identical propagules and for the role of propagule number. They point to a spatial analog of environmental stochasticity: the differences, even over short distances, of locations in terms of suitability for a particular species. Drawing on the hypothesis (Pulliam 1988) that many sites within most species' ranges are demographic "sinks" and relatively few are "sources" that maintain an entire metapopulation, Sax & Brown (2000) argue that many propagules introduced to the same general region will likely land in unsuitable, sink sites. Increasing numbers of propagules increase the likelihood that at least one will land in a suitable area and become a source. Of course, demographic stochasticity could combine with this phenomenon to produce a range of outcomes for identical propagules. The demographic parameters (e.g., death rate) at different sites may differ, but always probabilistically.

Arrival condition may greatly affect the impact of propagule pressure on probability of establishment (Carlton 1996, Lodge et al. 2006, Verling et al. 2005, Wonham et al. 2001). For many historical instances of disparate results from introduction of apparently similar propagules (see Section 2.3), researchers have speculated on ill health of the failed propagules. For ballast water, propagule load is a function of route, voyage length, ship type, and likely other factors, many of which will also affect the condition of arriving individuals, so that indirect estimates of propagule pressure from number of ship arrivals will err somewhat (Verling et al. 2005). Clearly, varying propagule condition can contribute to apparent demographic stochasticity.

The discussion so far has treated initial establishment of an introduced species. Propagule size and number may have influences beyond establishment—for instance, on ultimate geographic range of an introduced species in its new home. These are discussed in Section 3.

2.6. Limitations of the Role of Propagule Pressure in Establishment

Finally, the facts that propagule pressure is highly correlated with other factors thought to influence establishment and that it was the only significant predictor of establishment success in a meta-analysis (Colautti et al. 2006) do not imply that a sufficiently large propagule, or a sufficiently large number of large propagules, will ensure establishment anywhere of any introduced species. For instance, the European partridge (*Perdix perdix*) was introduced unsuccessfully to New Zealand 24 times, with a minimum total of 676 individuals (Veltman et al. 1996). This failure is perhaps not surprising; the same species has failed in the Hawaiian Islands, Australia, and several European islands a number of times and has never survived in these regions (Long 1981). Exactly why it has such a dismal record is unknown, but surely it is not from lack of introduction effort (propagule pressure). There must also be innumerable releases of various species in regions where the climate is totally unsuitable, so establishment never occurs. Piranhas (*Pygocentrus nattereri*) are routinely taken as aquarium releases in lakes in the northern United States, but they cannot establish because

it is too cold (Fuller et al. 1999). Introductions to southern states may be another matter and, of course, global climate change could change such a perennial failure into an established pest. However, the range of abiotic conditions that a species can tolerate is always bounded. Many agricultural crops are extensively planted in regions where they fail to establish wild populations despite what must be massive propagule pressure. Surely a factor that often contributes to this failure is selection for desirable agricultural traits (e.g., high biomass production) that sometimes comes at the expense of dispersal ability and/or competitiveness.

Sufficient propagule pressure may lead to the illusion of establishment for what is truly a transient species. On Grand Cayman Island, the cultivated fruit tree *Manilkara indica* may be an example (F. Burton, personal communication). It persists for decades in scattered suitable sites, entire stands inevitably dying out during extreme drought or seawater inundation accompanying hurricanes, whereas other stands are initiated by deliberate planting. However, because the species is present at virtually every census interval, it appears to be established. Similarly, the Caribbean brown anole (*Anolis sagrei*) at the northern edge of its introduced U.S. range in Georgia presently probably persists only by the occasional arrival of propagules on northbound automobiles (Campbell 1996; T. Campbell, personal communication). These cases exemplify the “rescue effect” suggested for island biogeography by Brown & Kodric-Brown (1977).

2.7. Climate Change and Propagule Pressure

Persistence maintained by exogenous propagule pressure can be converted to true establishment by changes in biotic or abiotic barriers facing an invader; future global warming could allow *Anolis sagrei* to persist in Georgia without propagules arriving from Florida. The “mass effect” of Shmida & Wilson (1985) could be one means by which a population is maintained solely by propagule pressure until the environment becomes suitable. This is a similar scenario to the source-sink model of Pulliam (1988) discussed above, although the source-sink model applies to a metapopulation established in discontinuous sites, whereas the mass effect model pertains to a single population in a large, continuous range.

Traditional explanations of how climate change will affect rates and impacts of biological invasions (e.g., Hellmann et al. 2008, Stachowicz et al. 2002) rest on the notion that individuals that would have died or been unable to reproduce because of cold temperature will survive and propagate when the climate warms. Growing evidence on the role of propagule pressure suggests a subtler possibility—a smaller propagule size than previously required to have a high probability of establishing an ongoing population. When the physical environment changes, an introduced species that was present only by virtue of exogenous propagule pressure can establish an ongoing, reproductive population, because fewer individuals will be required for establishment (D’Antonio et al. 2001, Thomsen et al. 2006). Thomsen et al. (2006) showed experimentally that varying physical factors reduced the size of a propagule necessary for a high probability of successful establishment of the European grass *Holcus lanatus* in California.

What appears superficially to be gradual spread of an established introduced species by virtue of gradual warming can also be an artifact of unsuspected ongoing propagule pressure; an example is discussed in Section 2.3.

3. SPREAD AND INVASION: PROPAGULE PRESSURE, LAG TIMES, AND GENETICS

3.1. Inbreeding Depression, Drift, and the Genetic Paradox of Invasion Biology

Many examples of Section 2 exemplify a paradox of invasion biology. The foundational principle of conservation genetics is that small population size, in addition to enhancing risk of extinction from

demographic and environmental stochasticity, threatens short-term extinction from inbreeding depression. It also threatens extinction in the longer term from genetic drift, which reduces genetic variation that would allow adaptation to changing environments (Allendorf & Lundquist 2003, Frankham et al. 2002). The bottleneck effect and founder effect of classical genetics are expressions of this phenomenon and have long been invoked to explain deleterious genetic effects in small populations. Yet, many widespread, invasive populations have originated from small propagules.

The paradox may be partly resolved if inbreeding depression is not as universally debilitating as is widely advertised (Allendorf & Lundquist 2003), and theoretical evidence shows its effects are most severe when a formerly large population is suddenly greatly reduced in size and less harmful when a population has always been small or declines gradually (Groom et al. 2006). Another possible resolution of the paradox is that those widespread invasions we observe today that originated from small propagules are simply the small minority that survive. After all, these factors act probabilistically, so one would expect some survivors even if the theory is correct. However, it seems unlikely that inbreeding depression or drift causes most introduction failures. Lande (1988) argues that, for very small populations (the size of most propagules of introduced species), demographic and environmental stochasticity are more likely than genetic factors to cause extinction.

Part of the paradox may be resolved by the fact that some invasive species, even though the size of their initial (and subsequent) propagules is small, receive a continuing flow of propagules, and these may bring increased genetic variation that counters inbreeding depression and drift. Such variation would not easily have been detected until the advent of modern molecular genetics, so only recently has strong evidence for this phenomenon of increased genetic variation from continuing propagule pressure been advanced. Roman & Darling (2007) reviewed evidence from 43 aquatic and marine invaders and found that 27 of them did not have significantly reduced genetic diversity in their introduced ranges; of these, at least 14 had multiple introduction events, and for at least 3 species arrival of propagules has been virtually continuous.

Increased genetic variation from continued propagule pressure may not only stem extinction from inbreeding depression and drift; it could also lead to new genotypes better adapted than those of the initial colonists to the local environment or adjacent ones, thereby enhancing likelihood of persistence and possibly spread (McCauley 1991). A continuing flow of propagules, particularly from a variety of sources, would be a likely means of increasing genetic diversity. Much of the new genetic research yielding information on formerly unsuspected propagule pressure simply documents its occurrence, without providing strong evidence that the new variation is critical to either survival or spread. However, some studies implicate better adaptation.

3.2. Evidence that Propagule Pressure Brings Better-Adapted Genotypes

Research by Saltonstall (2002) strongly suggests that ongoing propagule pressure can adapt an introduced population to different environments and shows that propagule pressure may even render an innocuous species invasive. Common reed (*Phragmites australis*) has been present in the U.S. Southwest for at least 40,000 years and on the Atlantic and Pacific coasts for several thousand years. However, its geographic range and abundance increased greatly in the past 150 years, and it is widely recognized as a highly invasive weed, particularly in disturbed wetlands but even spreading to undisturbed sites (Saltonstall 2002). Using cpDNA sequences, Saltonstall (2002) demonstrated that this expansion probably resulted from invasion by a non-native genotype that has both displaced native genotypes (some of which are now regionally extinct) and spread to areas not formerly occupied by the species. The introduction probably occurred in the early nineteenth century, when soil ballast of ships was widely dumped or used to fill wetlands. The non-native

genotype did not spread rapidly at first but was probably widely distributed during construction of railways and roads in the late nineteenth and early twentieth centuries. Lavergne & Molofsky (2007), using allozyme loci, demonstrate a remarkably similar scenario for invasive reed canary grass (*Phalaris arundinacea*) in North America: Multiple introductions from Europe have led to recombination and the production of novel genotypes in North America, and higher genetic diversity and heritable phenotypic variation than in Europe. These features, in turn, allowed for rapid selection of more invasive genotypes.

A similar explanation seems likely for the expanded range of the highly invasive European green crab (*Carcinus maenas*) in North America (Roman 2006). First recorded in 1817 in the United States in New York and southern Massachusetts, this species gradually spread (taking almost a century) to the Gulf of Maine. However, it did not reach northern Nova Scotia until the 1980s. The most common hypothesis for this slow northward trend is gradual warming of regional surface waters and/or gradual adaptation to colder water through natural selection of existing stocks (e.g., Audet et al. 2003). This explanation aligns with hypotheses linking climate change to the spread of invasive species (Stachowicz et al. 2002) and with the traditional interpretation of invasion success as a function of species and system traits. However, Roman (2006), sequencing a mitochondrial gene, showed that new genetic lineages in the northern part of the crab's Canadian range (part of greater genetic diversity there than in the southern part of the range) probably derived from separate invasions in the 1980s and can survive in colder water than the older lineages from the southern part of the introduced range. The new genotypes probably arrived in ballast water along new shipping routes (Roman 2006).

Finally, intriguing experimental evidence in the waterstrider research by Ahlroth et al. (2003; described above) suggests how genetic variation in founding populations might enhance establishment probability. In their experiments, in addition to propagules being of different size, they were composed of individuals of either one or two source populations found to be distantly related to each other by genetic analysis. In a logistic regression model, both propagule size and number of source populations contributed to establishment: For a given propagule size, establishment probability was always higher for two sources than for one. Ahlroth et al. (2003) examined establishment success before breeding of propagule members, so they were calculating likelihood that at least some individuals would survive to breed, and the logical interpretation of their result is that particular genotypes were better suited than others to survive in the particular streams to which they were introduced. This is an additional effect beyond those usually sought for genetic impacts on the role of propagule size in establishment probability, that is, inbreeding depression and drift.

3.3. Another Paradox: Increased Genetic Variation in Founder Populations

Other research (Table 2) shows that continuing propagule pressure increases genetic variation (and, in some studies, this research demonstrates unsuspected propagule pressure) without demonstrating that the increased variation is important for persistence and/or spread. A prime example is research by Kolbe et al. (2004) on the brown anole, a Caribbean lizard spreading into the continental United States (discussed above). The brown anole first invaded the Florida Keys in the late nineteenth century but did not begin to spread further until the 1940s, and its range has expanded even more rapidly since the 1970s. The expansion is probably due to the slow spread northward of the original introduction plus additional introductions into various areas of peninsular Florida (Campbell 1996). Genetic analysis and phylogenetic reconstruction indicate at least eight separate introductions into Florida and additionally show that two-thirds of the populations in Florida have haplotypes originating from more than one Cuban population, mixing that never occurs in Cuba itself (Kolbe et al. 2004). Most Florida populations therefore have more genetic variation

Table 2 Evidence for positive effect of ongoing propagule pressure on genetic diversity for established introduced species

Taxon	Location	Reference
<i>Carcinus maenus</i> ^a (green crab)	North America	Roman 2006
<i>Phragmites australis</i> ^a (common reed)	North America	Saltonstall 2002
<i>Phalaris arundinacea</i> ^a (reed canary grass)	North America	Lavergne & Molofsky 2007
<i>Anolis sagrei</i> (brown anole)	USA	Kolbe et al. 2004
<i>Undaria pinnatifida</i> (brown alga)	Worldwide	Voisin et al. 2005
<i>Cyclope neritea</i> (gastropod)	Europe	Simon-Bouhet et al. 2006
<i>Dreissena polymorpha</i> (zebra mussel)	North America	Stepien et al. 2002
<i>Bythotrephes longimanus</i> (spiny water flea)	North America	Berg et al. 2002
<i>Gammarus tigrinus</i> (amphipod)	Europe	Kelly et al. 2006
<i>Ambrosia artemisiifolia</i> (ragweed)	France	Genton et al. 2005
<i>Dreissena rostriformis bugensis</i> (mussel)	Eastern Europe	Therriault et al. 2005

^aEvidence of increased adaptation.

than native populations in Cuba and, paradoxically, more recently established introduced populations have more genetic variation than older ones, because the former arose from propagules from multiple sources. It even seems likely that subsequent invasions of this anole to Hawaii and Taiwan came from Florida and not Cuba, because they have combinations of haplotypes found in Florida but not in the native range (Kolbe et al. 2004). This research turns the conventional wisdom on its head that newly established populations of nonindigenous species are automatically genetically depauperate and likely to manifest bottleneck or founder effects. If there is continuing propagule pressure, genetic impoverishment need not always occur.

Ongoing propagule pressure bringing substantial genetic variation is also implicated by isozyme analysis of Eurasian *Capsella bursa-pastoris* (shepherd's purse) in North America (Neuffer & Hurka 1999), in which a minimum of 20 independent introductions were detected. Similarly, mitochondrial DNA analysis demonstrates ongoing propagule pressure in the rapid spread of the brown alga *Undaria pinnatifida* (Voisin et al. 2005). All native Asian populations have low genetic diversity, but these often differ greatly. However, both European and Australasian introduced populations have increased genetic diversity, pointing to multiple introductions. Further, the distribution of haplotypes allowed strong inferences about the nature of these introductions. For instance, in New Zealand, recurrent introductions are implicated, probably inadvertent results of ship traffic. In Europe, both deliberate mariculture introductions and inadvertent introductions by ships have contributed to the spread. As another example, Simon-Bouhet et al. (2006) show, by mtDNA sequence data, that the recent northward expansion of the cryptogenic mollusc *Cyclope neritea*, hypothesized to be due to warming, is probably due instead to propagule pressure, that is, recurrent introductions from several different regions. Also, because this gastropod has no planktonic larval stage and is restricted to an uncommon, discontinuously distributed substrate, this propagule pressure is probably anthropogenic, likely entailing inadvertent movement with the culture of oysters or other shellfish.

Stepien et al. (2002), using randomly amplified polymorphic DNA (RAPDs), found that populations of zebra mussels in North America have surprisingly high genetic variability, implying that there were large numbers of founders and that populations differ substantially from one another, suggesting multiple introductions. The palearctic zooplankter *Bythotrephes longimanus*, invasive in the Great Lakes, manifested a founder effect (heterozygote excess and surprisingly low levels of

among-population variation) in early collections there, but this effect disappeared by 1996 (Berg et al. 2002). Indirect evidence suggests that at least part of this change was due to a continuing influx of propagules from Russia (Berg et al. 2002).

3.4. The Mysterious Lag Time Phenomenon

Many introduced species that ultimately become widespread and invasive do not do so immediately. Rather, the initial population remains small, local, and innocuous for a period that may last decades, then suddenly expands dramatically to become an invasive pest. Salisbury (1953) was perhaps first to remark on this phenomenon, and Kowarik (1995), Crooks & Soulé (1996), and Crooks (2005) have published recent reviews. A variety of explanations have been proposed for lag times both for particular invasions and as a general phenomenon, but many cases remain puzzling.

Salisbury (1953) raised the possibility of a necessary buildup of a sort of “infection pressure” of propagules before an actual invasion can occur but did not elaborate on exactly how low numbers would prevent invasion by an established population. For some bacteria, classic observations accord with the idea of a necessary “infection pressure,” and recent research provides striking insights into a mechanism. For many bacterial species, large populations produce an effect, whereas small populations do not. For instance, outbreak of plant disease can sometimes be predicted from the propagule size at a site (Shrum 1978). This relationship is complicated by the fact that individuals of many potential pathogens can be inactive but still viable and become active given some environmental cue. Ingested human pathogens provide other examples: 180 cells of *Shigella flexneri*, 10^5 cells of *Salmonella typhi*, 10^3 – 10^8 cells of *V. cholerae*, and 10^6 – 10^8 cells of *Escherichia coli* are necessary for pathogenic activity (Collins 1993, Levy 1986). It is possible that many such bacterial effects are mediated by quorum sensing (Liu et al. 2007, Miller & Bassler 2001), a phenomenon recently discovered in an increasing number of bacterial species. Quorum sensing is a means by which bacteria emit chemical signal molecules (autoinducers) that, when a threshold concentration is reached (because of a threshold density of cells), cause an alteration in gene expression. For instance, quorum sensing has been shown to trigger virulence in human pathogens such as *Pseudomonas aeruginosa*, *Staphylococcus aureus*, and *V. cholerae*, as well as the plant pathogens *Agrobacterium tumefaciens* and *Erwinia carotovora*.

Exactly what analog to quorum sensing in bacteria could generate in animals and plants a phenomenon of a necessary threshold density (and, thus, a lag before widespread invasion) is unclear. The Allee effect (Allee 1931) of behavioral ecology is sometimes adduced as a general explanation for lag times in animal introductions (e.g., Shigesada & Kawasaki 1997). Allee effects were initially defined (Allee 1931) as stylized behavior of vertebrates that fails when population density falls below a threshold density, but the concept has been generalized (e.g., Courchamp et al. 1999, Dennis 2002, Lockwood et al. 2007) to encompass any reduction in population growth rates at low population densities. The Allee effect usually invoked to explain either failure of a propagule to establish a population or a lag time before a newly established population spreads is that of individuals having potential problems finding mates (e.g., Veit & Lewis 1996). However, empirical data are rarely, if ever, available to test this hypothesis. Another Allee effect invoked to explain invasion lags for plants is reduced pollination when densities are low, leading to low seed set. The slow early spread of *Spartina alterniflora* from the eastern United States on the Pacific coast is probably partly explicable on these grounds (Davis et al. 2004, Taylor et al. 2004). A likely partial explanation for the lag in the spread of introduced conifer species in South America, relative to spread in other Southern Hemisphere continents, is simply a lag in establishment of extensive plantations that would produce huge quantities of seeds (Simberloff et al. 2010).

Sometimes a lag time can be explained by a subtle change in the environment (Salisbury 1953, 1961), so that a greater area comes to constitute suitable habitat for an introduced species. Another possible explanation for some lag times is “invasional meltdown” (Simberloff 2006, Simberloff & Von Holle 1999), whereby two invasive species facilitate one another’s survival and/or spread, sometimes to the point that the presence of one constitutes an obligate prerequisite for invasion by the other. For example, several non-native fig species were grown in south Florida for decades without reproducing or spreading; the subsequent arrival of the pollinating fig wasp (*Parapristina verticillata*) of *Ficus microcarpus* turned this species into a rapidly spreading invader (Kauffman et al. 1991, McKey & Kauffman 1991).

Although new mutations are sometimes invoked to explain the sudden spread of a formerly quiescent introduced species, evidence for such events is rare, and it seems more of a last-resort explanation when no other explanation comes to mind. There is no doubt that mutations can produce an invasive genotype. For instance, the cold-tolerant aquarium strain of the alga *Caulerpa taxifolia* is able to survive the winters of the northwest Mediterranean, unlike populations from the native range (Meinesz 2001). However, gene flow springing from the arrival of new propagules seems more likely than mutations to be a source for new, invasive genotypes. The cases of the sudden spread after a lag time of the green crab and common reed, discussed above, because they are buttressed by direct genetic evidence for the advent of new genotypes via propagules, strongly implicate lack of adaptive genotypes as the reason for the lag, as well as propagule pressure as the reason for its cessation. Continued use of molecular genetic techniques will likely trace a number of formerly mysterious lags followed by rapid expansion to arrival of new genes in propagules.

Genetic techniques have also been used increasingly to demonstrate the role of continued exogenous propagule pressure, rather than simply diffusion dispersal, in generating range expansion of established introduced species. A good example is ongoing research by Richard Mack and his colleagues (e.g., Bartlett et al. 2002, Novak & Mack 2001) on the history of the spread of Mediterranean cheatgrass (*Bromus tectorum*) to become one of the most widely distributed weeds in North America. Although intracontinental transport (especially with the construction of railways) contributed greatly to dispersal, there were multiple introductions of Mediterranean material, at least seven in western North America and two in the East. Some novel recombinant genotypes occur in North America (Novak & Mack 2001), but it is not yet clear whether they have aided the spread.

4. DISCUSSION AND CONCLUSIONS

Substantial interest in propagule pressure as a determinant of initial successful establishment of non-native species, and of subsequent spread, is relatively recent. However, there is abundant, growing evidence, some of it experimental (**Table 1**), for its importance in establishment and increasing evidence from molecular analyses for its importance in spread of some invaders (**Table 2**). In particular, it is possible that ongoing propagule pressure from new sources can explain some instances of puzzling lag times between establishment and subsequent spread of invaders. Statistical analyses of several large data sets suggest that propagule pressure may, in fact, be even more frequently important in establishment of non-native species than the SCOPE factors customarily viewed as key: species traits of potential invaders and biotic and abiotic characteristics of the invaded ecosystem.

The recognition of the key role of propagule pressure and the availability of molecular tools to document its existence suggest some changes in policy and management approaches that have largely been based on the view that the SCOPE factors are the key determinants of invasions. As a trivial example, several states in the United States bar importation of plant species not already established and/or mandate aggressive attempts to eradicate newly discovered infestations of such

species; however, once a species is well-established, there is no further prohibition on importation of new stock. In light of examples showing invasiveness caused by the arrival of new genes (e.g., common reed, reed canary grass), this policy seems inadequate. More generally, policy should be focused at least as much on restricting pathways for ongoing arrival of propagules (Ruiz & Carlton 2003) as on attacking invasions once they are already under way. Reaser et al. (2009) have recently reviewed a variety of policy implications of accruing information on propagule pressure.

A research approach that would further our understanding of the scope, nature, and importance of propagule pressure for both established and potential invaders, and that could also probably be developed into effective management tools, would be a greatly ramped-up effort to sample exhaustively all propagules carried by various vectors over the entire course of a journey (as by Wonham et al. 2001), especially at the beginning and end of a transport event. Except for ballast water, there is scant direct measurement of propagule arrival, and even for ballast water there is little measurement of decay of propagule pressure through time for pathways traversed by many species en masse. An exhaustive examination of empty sea cargo containers in Australia for insects (Stanaway et al. 2001) stands out as part of such an effort, and even that study has not been replicated. More experiments on the impact of changing sizes, numbers, and spatial and temporal patterns of propagules would surely elucidate the relative importance of propagule pressure and the SCOPE factors. However, as observed above, such experiments with species introduced to new regions (rather than to unoccupied areas within already invaded regions) are possibly immoral and often illegal.

DISCLOSURE STATEMENT

The author is not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

ACKNOWLEDGMENTS

This review was inspired by a workshop, “The link between propagule pressure and nonnative invasion success and impacts,” sponsored by the National Center for Environmental Assessment at the United States Environmental Protection Agency (EPA). I thank Betsy Von Holle for organizing that workshop and later commenting on this manuscript. Martin Nuñez, Mariano Rodriguez-Cabal, and Nathan Sanders provided helpful critiques of the manuscript.

LITERATURE CITED

- Ahlroth P, Alatalo RV, Holopainen A, Kumpulainen T, Suhonen J. 2003. Founder population size and number of source populations enhance colonization success in waterstriders. *Oecologia* 137:617–20
- Allee WC. 1931. *Animal Aggregations: A Study in General Sociology*. Chicago: Univ. Chicago Press, 431 pp.
- Allendorf FW, Lundquist LL. 2003. Introduction: population biology, evolution, and control of invasive species. *Conserv. Biol.* 17:24–30
- Audet D, Davis DS, Miron G, Moriyasu M, Benhalima K, Campbell R. 2003. Geographic expansion of a nonindigenous crab, *Carcinus maenas* (L.) along the Nova Scotian shore into the southeastern Gulf of St. Lawrence, Canada. *J. Shellfish Res.* 22:255–62
- Baker HG. 1965. Characteristics and modes of origin of weeds. In *The Genetics of Colonizing Species*, ed. HG Baker, GL Stebbins, pp. 147–72. New York: Academic
- Bartlett E, Novak SJ, Mack RN. 2002. Genetic variation in *Bromus tectorum* (Poaceae): differentiation in the eastern United States. *Am. J. Bot.* 89:602–12

- Beirne BP. 1975. Biological control attempts by introductions against pest insects in the field in Canada. *Can. Entomol.* 107:225–36
- Berg DJ, Garton DW, MacIsaac HJ, Panov VE, Telesh IV. 2002. Changes in genetic structure of North American *Bythotrephes* populations following invasion from Lake Ladoga, Russia. *Freshw. Biol.* 47:275–82
- Bossenbroek JM, Kraft CE, Nekola JC. 2001. Prediction of long-distance dispersal using gravity models: zebra mussel invasion of inland lakes. *Ecol. Appl.* 11:1778–88
- Brown JH, Kodric-Brown A. 1977. Turnover rates in insular biogeography: effects of immigration on extinction. *Ecology* 58:445–49
- Campbell TS. 1996. Northern range expansion of the brown anole (*Anolis sagrei*) in Florida and Georgia. *Herpetol. Rev.* 27:155–57
- Carlton JT. 1985. Transoceanic and interoceanic dispersal of coastal marine organisms: the biology of ballast water. *Oceanogr. Mar. Biol. A. Annu. Rev.* 23:313–71
- Carlton JT. 1996. Pattern, process, and prediction in marine invasion biology. *Biol. Conserv.* 78:97–106
- Cassey P, Blackburn TM, Sol D, Duncan RP, Lockwood JL. 2004. Global patterns of introduction effort and establishment success in birds. *Proc. R. Soc. London Ser. B (Suppl.)* 271:S405–8
- Catford JA, Jansson R, Nilsson C. 2009. Reducing redundancy in invasion ecology by integrating hypotheses into a single theoretical framework. *Divers. Distrib.* 15:22–40
- Clarke CMH. 1971. Liberations and dispersal of red deer in northern South Island districts. *N. Z. J. Forest Sci.* 1:194–207
- Clausen CP. 1978. *Introduced Parasites and Predators of Arthropod Pests and Weeds: A World Review. Agriculture Handbook 480.* Washington, DC: U.S. Dep. Agric.
- Colautti RI. 2005. Are characteristics of introduced salmonid fishes biased by propagule pressure? *Can. J. Fish. Aquat. Sci.* 62:950–59
- Colautti RI, Grigorovich IA, MacIsaac HJ. 2006. Propagule pressure: a null model for biological invasions. *Biol. Invasions* 8:1023–37
- Colautti RI, Niimi AJC, van Overdijk DA, Mills EL, Holeck K, MacIsaac HJ. 2003. Spatial and temporal analysis of transoceanic shipping vectors to the Great Lakes. In *Invasive Species. Vectors and Management Strategies*, ed. GM Ruiz, JT Carlton, pp. 227–246. Washington, DC: Island
- Collins CH. 1993. *Laboratory-acquired Infections.* Oxford: Butterworth-Heinemann. 3rd ed.
- Colwell RK, Rahbek C, Gotelli N. 2004. The mid-domain effect and species-richness patterns: What have we learned so far? *Am. Nat.* 163:E1–23
- Courchamp F, Clutton-Brock T, Grenfell B. 1999. Inverse density dependence and the Allee effect. *Trends Ecol. Evol.* 14:405–410
- Crawley MJ. 1989b. Chance and timing in biological invasions. See Drake et al. 1989b, pp. 407–23
- Crooks JA. 2005. Lag times and exotic species: the ecology and management of biological invasions in slow-motion. *Écoscience* 12:316–29
- Crooks J, Soulé ME. 1996. Lag times in population explosions of invasive species: causes and implications. In *Proc., Norway/UN Conf. Alien Species*, ed. OT Sandlund, PJ Schei, A Viken, pp. 39–46. Trondheim, Norway: Directorate Nature Manage. Norwegian Inst. Nature Res.
- Crowell KL. 1973. Experimental zoogeography: introductions of mice to small islands. *Am. Nat.* 107:535–58
- Daehler CC, Strong DR Jr. 1993. Prediction and biological invasions. *Trends Ecol. Evol.* 8:380
- D’Antonio C, Levine J, Thomsen M. 2001. Ecosystem resistance to invasion and the role of propagule supply: a California perspective. *J. Mediter. Ecol.* 2:233–45
- Davis HG, Taylor CM, Lambrinos JG, Strong DR. 2004. Pollen limitation causes an Allee effect in a wind-pollinated invasive grass (*Spartina alterniflora*). *Proc. Natl. Acad. Sci. USA* 101:13804–7
- Davis MA. 2006. Invasion biology 1958–2005: the pursuit of science and conservation. In *Conceptual Ecology and Invasion Biology*, ed. MW Cadotte, SM McMahon, T Fukami, pp. 35–64. Dordrecht, Netherlands: Springer
- Dennis B. 2002. Allee effects in stochastic populations. *Oikos* 96:389–401
- Drake JA, Mooney HA, diCasta F, Groves RH, Kruger FJ, et al. 1989a. Preface. See Drake et al. 1989b, pp. xxiii–xxiv
- Drake JA, Mooney HA, diCasta F, Groves RH, Kruger FJ, et al., eds. 1989b. *Biological Invasions: A Global Perspective.* Chichester, UK: Wiley

- Drake JM, Baggenstos P, Lodge DM. 2005. Propagule pressure and persistence in experimental populations. *Biol. Lett.* 1:480–83
- Drake JM, Lodge DM. 2004. Global hot spots of biological invasions: evaluating options for ballast-water management. *Proc. R. Soc. London Ser. B* 271:575–80
- Dullinger S, Kleinbauer I, Peterseil J, Smolik M, Essl F. 2009. Niche based distribution modelling of an invasive alien plant: effects of population status, propagule pressure and invasion history. *Biol. Invasions* doi: 10.1007/s10530-009-9424-5
- Duncan RP. 1997. The role of competition and introduction effort in the success of passeriform birds introduced to New Zealand. *Am. Nat.* 149:903–15
- Ebenhard T. 1989. Bank vole (*Chethrionomys glareolus* (Schreber, 1780)) propagules of different sizes and island colonization. *J. Biogeogr.* 16:173–80
- Elton CS. 1958. *The Ecology of Invasions by Animals and Plants*. London: Methuen
- Felter SP, Dourson ML, Patterson J. 1998. Assessing risks to human health from chemicals in the environment. In *Handbook of Environmental Risk Assessment and Management*, ed. P Calow, pp. 9–23. Oxford: Blackwell Sci.
- Forsyth DM, Duncan RP. 2001. Propagule size and relative success of exotic ungulate and bird introductions to New Zealand. *Am. Nat.* 157:583–95
- Foster BL, Dickson TL. 2004. Grassland diversity and productivity: the interplay of resource availability and propagule pools. *Ecology* 85:1541–47
- Fotheringham AS, O’Kelly ME. 1989. *Spatial Interaction Models: Formulations and Applications*. Dordrecht, Netherlands: Kluwer
- Foxcroft L, Rouget M, Richardson DM, Fadyen SM. 2004. Reconstructing 50 years of *Opuntia stricta* invasion in the Kruger National Park, South Africa: environmental determinants and propagule pressure. *Divers. Distrib.* 10:427–37
- Frankham R, Ballou JD, Briscoe DA. 2002. *Introduction to Conservation Genetics*. Cambridge: Cambridge Univ. Press
- Fuller PL, Nico LG, Williams JD. 1999. *Nonindigenous Fishes Introduced into Inland Waters of the United States*. Bethesda, MD: Am. Fish. Soc.
- Gabriel W, Bürger R. 1992. Survival of small populations under demographic stochasticity. *Theor. Pop. Biol.* 41:44–71
- Genton BJ, Shykoff JA, Giraud T. 2005. High genetic diversity in French invasive populations of common ragweed, *Ambrosia artemisiifolia*, as a result of multiple sources of introduction. *Mol. Ecol.* 14:4275–85
- Gotelli NJ, Graves GR. 1996. *Null Models in Ecology*. Washington: Smithsonian Inst.
- Green RE. 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
- Grevstad FS. 1999. Experimental invasions using biological control introductions: the influence of release size on the chance of population establishment. *Biol. Invasions* 1:313–23
- Groom MJ, Meffe GK, Carroll CR, eds. 2006. *Principles of Conservation Biology*. Sunderland, MA: Sinauer. 3rd ed.
- Guisan A, Thuiller W. 2005. Predicting species distributions: offering more than simple habitat models. *Ecol. Lett.* 8:993–1009
- Hastings A. 1996. Models of spatial spread: Is the theory complete? *Ecology* 77:1675–79
- Hellmann JJ, Byers JE, Bierwagen BG, Dukes JS. 2008. Five potential consequences of climate change for invasive species. *Conserv. Biol.* 22:534–43
- Hubbell SP. 2001. *The Unified Neutral Theory of Biodiversity and Biogeography*. Princeton, NJ: Princeton Univ. Press
- Jeschke JM. 2008. Across islands and continents, mammals are more successful invaders than birds. *Divers. Distrib.* 14:913–16
- Jeschke JM, Strayer DL. 2005. Invasion success of vertebrates in Europe and North America. *Proc. Natl. Acad. Sci. USA* 102:7198–202
- Kauffman S, McKey DB, Hossaert-McKey M, Horvitz CC. 1991. Adaptations for a two-phase seed dispersal system involving vertebrates and ants in a hemiepiphytic fig (*Ficus microcarpa*: Moraceae). *Am. J. Bot.* 78:971–77

- Kelly DW, Muirhead JR, Heath DD, MacIsaac HJ. 2006. Contrasting patterns in genetic diversity following multiple invasions or fresh and brackish waters. *Mol. Ecol.* 15:3641–53
- Kolar CS, Lodge DM. 2001. Progress in invasion biology: predicting invaders. *Trends Ecol. Evol.* 16:199–204
- Kolar CS, Lodge DM. 2002. Ecological predictions and risk assessment for alien fishes in North America. *Science* 298:1233–36
- Kolbe JJ, Glor RE, Schettino LR, Lara AC, Larson A, Losos JB. 2004. Genetic variation increases during biological invasion by a Cuban lizard. *Nature* 431:177–81
- Kowarik I. 1995. Time lags in biological invasions with regard to the success and failure of alien species. In *Plant Invasions: General Aspects and Special Problems*, ed. P Pysek, K Prach, M Rejmánek, M Wade, pp. 15–38. Amsterdam: SPB Acad.
- Krivánek M, Pysek P, Jarosik V. 2006. Planting history and propagule pressure as predictors of invasion by woody species in a temperate region. *Conserv. Biol.* 20:1487–98
- Lande R. 1988. Genetics and demography in conservation. *Science* 241:1455–60
- Lavergne S, Molofsky J. 2007. Increased genetic variation and evolutionary potential drive the success of an invasive grass. *Proc. Natl. Acad. Sci. USA* 104:3883–88
- Levy SB. 1986. Human exposure and effects analysis for genetically modified bacteria. In *Biotechnology Risk Assessment*, ed. J Fiksel, VT Covello, pp. 56–74. New York: Pergamon
- Lewis MA. 1997. Variability, patchiness, and jump dispersal in the spread of an invading population. In *Spatial Ecology: The Role of Space in Population Dynamics and Interspecific Interactions*, ed. D Tilman, P Kareiva, pp. 46–69. Princeton, NJ: Princeton Univ. Press
- Liu Z, Stirling F, Zhu J. 2007. Temporal quorum sensing induction regulates *Vibrio cholerae* biofilm architectures. *Infect. Immun.* 75:122–26
- Lockwood JL, Cassey P, Blackburn T. 2005. The role of propagule pressure in explaining species invasions. *Trends Ecol. Evol.* 20:223–28
- Lockwood JL, Hoopes MF, Marchetti MP. 2007. *Invasion Ecology*. Malden, MA: Blackwell
- Lodge DM, Williams S, MacIsaac HJ, Hayes KR, Leung B, et al. 2006. Biological invasions: recommendations for U.S. policy and management. *Ecol. Appl.* 16:2035–2054
- Long JL. 1981. *Introduced Birds of the World*. New York: Universe Books
- Long JL. 2003. *Introduced Mammals of the World*. Wallingford, UK: CABI Publ.
- MacArthur RH, Wilson EO. 1967. *The Theory of Island Biogeography*. Princeton: Princeton Univ. Press
- McCauley DE. 1991. Genetic consequences of local population extinction and recolonization. *Trends Ecol. Evol.* 6:5–8
- McKey DB, Kauffman SC. 1991. Naturalization of exotic *Ficus* species (Moraceae) in south Florida. In *Proc. Symp. Exotic Pest Plants*, ed. TD Center, RF Doren, RL Hofstetter, RL Myers, LD Whiteaker, pp. 221–36. Washington, DC: U. S. Dep. Inter./Natl. Park Ser.
- Meinesz A. 2001. *Killer Algae*, 2nd ed. Chicago: Univ. Chicago Press
- Memmott J, Craze PG, Harman HM, Syrett P, Fowler SV. 2005. The effect of propagule size on the invasion of an alien insect. *J. Anim. Ecol.* 74:50–62
- Miller MB, Bassler BL. 2001. Quorum sensing in bacteria. *Annu. Rev. Microbiol.* 55:165–99
- Mulvaney M. 2001. The effect of introduction pressure on the naturalization of ornamental woody plants in south-eastern Australia. In *Weed Risk Assessment*, ed. FD Panetta, JG Virtue, RH Groves, pp. 186–193. Collingwood, Victoria, Aust.: CSIRO Publ.
- Neuffer B, Hurka H. 1999. Colonization history and introduction dynamics of *Capsella bursa-pastoris* (Brassicaceae) in North America: isozymes and quantitative traits. *Mol. Ecol.* 8:1667–81
- Newsome AE, Noble IR. 1986. Ecological and physiological characters of invading species. In *Ecology of Biological Invasions*, ed. RH Groves, JJ Burdon, pp. 1–20. Cambridge: Cambridge Univ. Press
- Novak SJ, Mack RN. 2001. Tracing plant introduction and spread: genetic evidence from *Bromus tectorum* (cheatgrass). *BioScience* 51:114–22
- Peterson AT. 2006. Uses and requirements of ecological niche models and related distributional models. *Biodivers. Inform.* 3:59–72
- Pulliam HR. 1988. Sources, sinks, and population regulation. *Am. Nat.* 132:652–61
- Reaser JK, Meyerson LA, Von Holle B. 2009. Saving camels from straws: How propagule pressure-based prevention policies can reduce the risk of biological invasion. *Biol. Invasions* 10:1085–98

- Roman J. 2006. Diluting the founder effect: cryptic invasions expand a marine invader's range. *Proc. R. Soc. London Ser. B* 273:2453–59
- Roman J, Darling JA. 2007. Paradox lost: genetic diversity and the success of aquatic invasions. *Trends Ecol. Evol.* 22:454–64
- Rouget M, Richardson DM. 2003. Inferring process from pattern in plant invasions: a semimechanistic model incorporating propagule pressure and environmental factors. *Am. Nat.* 162:713–24
- Ruiz GM, Carlton JT. 2003. Invasion vectors: a conceptual framework for management. In *Invasive Species. Vectors and Management Strategies*, ed. GM Ruiz, JT Carlton, pp. 459–504. Washington, DC: Island Press
- Salisbury EJ. 1953. A changing flora as shown in the weeds of arable land and waste places. In *The Changing Flora of Britain*, ed. JE Lousley, pp. 130–39. Oxford: Bot. Soc. Br. Isles
- Salisbury EJ. 1961. *Weeds and Aliens*. London: Collins
- Saltonstall K. 2002. Cryptic invasion by a non-native genotype of the common reed, *Phragmites australis*, into North America. *Proc. Natl. Acad. Sci. USA* 99:2445–49
- Sanders NJ, Weltzin JF, Crutsinger GM, Fitzpatrick MC, Nuñez MA, et al. 2007. Insects mediate the effects of propagule supply and resource availability on a plant invasion. *Ecology* 88:2383–91
- Sax DF, Brown JH. 2000. The paradox of invasion. *Global Ecol. Biogeog.* 9:363–71
- Schneider DW, Ellis CD, Cummings KS. 1998. A transportation model assessment of risk to native mussel communities of zebra mussel spread. *Conserv. Biol.* 12:788–800
- Semmens BX, Buhle ER, Salomon AK, Pattengill-Semmens CV. 2004. A hotspot of non-native aquarium fishes: evidence for the aquarium trade as an invasion pathway. *Mar. Ecol. Prog. Ser.* 266:239–44
- Shaffer ML. 1987. Minimum viable populations, coping with uncertainty. In *Viable Populations for Conservation*, ed. ME Soulé, pp. 69–86. Cambridge: Cambridge Univ. Press
- Shigesada N, Kawasaki K. 1997. *Biological Invasions: Theory and Practice*. Oxford: Oxford Univ. Press
- Shmida A, Wilson MV. 1985. Biological determinants of species diversity. *J. Biogeogr.* 12:1–20
- Shrum RD. 1978. Forecasting of epidemics. In *Plant Disease*, vol. 2, ed. JG Horsfall, EB Cowling, pp. 223–38. New York: Academic
- Simberloff D. 1986. Introduced insects: a biogeographic and systematic perspective. In *Ecology of Biological Invasions of North America and Hawaii*, ed. HA Mooney, JA Drake, pp. 3–26. New York: Springer-Verlag
- Simberloff D. 1989. Which insect introductions succeed and which fail? See Drake et al. 1989b, pp. 61–75
- Simberloff D. 1995. Why do introduced species appear to devastate islands more than mainland? *Pac. Sci.* 49:87–97
- Simberloff D. 2006. Invasional meltdown six years later: important phenomenon, unfortunate metaphor, or both? *Ecol. Lett.* 9:912–19
- Simberloff D, Boecklen W. 1991. Patterns of extinction in the introduced Hawaiian avifauna: a reexamination of the role of competition. *Am. Nat.* 138:300–327
- Simberloff D, Nuñez MA, Ledgard NJ, Pauchard A, Richardson DM, et al. 2010. Spread and impact of introduced conifers in South America: lessons from other southern hemisphere regions. *Austral Ecol.* In press
- Simberloff D, Von Holle B. 1999. Positive interactions of nonindigenous species: invasional meltdown? *Biol. Invasions* 1:21–32
- Simon-Bouhet B, Garcia-Meunier P, Viard F. 2006. Multiple introductions promote range expansion of the mollusk *Cyclope neritea* (Nassariidae) in France: evidence from mitochondrial sequence data. *Mol. Ecol.* 15:1699–711
- Skellam JG. 1951. Random dispersal in theoretical populations. *Biometrika* 38:196–218
- Stachowicz JJ, Terwin JR, Whitlatch RB, Osman RW. 2002. Linking climate change and biological invasions: ocean warming facilitates nonindigenous species invasion. *Proc. Natl. Acad. Sci. USA* 99:15497–500
- Stanaway MA, Zalucki MP, Gillespie PS, Rodriguez CM, Maynard GV. 2001. Pest risk assessment of insects in sea cargo containers. *Aust. J. Entomol.* 40:180–92
- Stephan TS, Wissel C. 1994. Stochastic extinction models discrete in time. *Ecol. Model.* 75/76:183–92
- Stepien C, Taylor CD, Dabrowska KA. 2002. Genetic variability and phylogeographical patterns of a non-indigenous species invasion: a comparison of exotic vs. native zebra and quagga mussel populations. *J. Evol. Biol.* 15:314–28

- Taylor CM, Davis HG, Cívile JC, Grevstad FS, Hastings A. 2004. Consequences of an Allee effect in the invasion of a Pacific estuary by *Spartina alterniflora*. *Ecology* 85:3254–66
- Therriault TW, Orlova MI, Docker MF, MacIsaac HJ, Heath DD. 2005. Invasion genetics of a freshwater mussel (*Dreissena rostriformis bugensis*) in eastern Europe: high gene flow and multiple introductions. *Heredity* 95:16–23
- Thomsen MA, D’Antonio CM, Suttle KB, Sousa WP. 2006. Ecological resistance, seed density and their interactions determine patterns of invasion in a California coastal grassland. *Ecol. Lett.* 9:160–70
- Thomson GM. 1922. *The Naturalisation of Animals and Plants in New Zealand*. Auckland: Cambridge Univ. Press
- Turnbull LA, Crawley MJ, Rees M. 2000. Are plant populations seed-limited? A review of seed sowing experiments. *Oikos* 88:225–38
- Veit RR, Lewis MA. 1996. Dispersal, population growth, and the Allee effect: dynamics of the house finch invasion of eastern North America. *Am. Nat.* 148:255–74
- Veltman CJ, Nee S, Crawley MJ. 1996. Correlates of introduction success in exotic New Zealand birds. *Am. Nat.* 147:542–57
- Verling E, Ruiz GM, Smith LD, Galil B, Miller AW, Murphy KR. 2005. Supply-side invasion ecology: characterizing propagule pressure in coastal ecosystems. *Proc. R. Soc. London Ser. B* 272:1249–57
- Voisin M, Engel CR, Viard F. 2005. Differential shuffling of native genetic diversity across introduced regions in a brown alga: aquaculture vs. maritime traffic effects. *Proc. Natl. Acad. Sci. USA* 102:5432–37
- Von Holle B, Simberloff D. 2005. Ecological resistance to biological invasion overwhelmed by propagule pressure. *Ecology* 86:3212–18
- Williamson M. 1996. *Biological Invasions*. London: Chapman & Hall
- Wonham MJ, Walton WC, Ruiz GM, Frese AM, Galil BS. 2001. Going to the source: role of the invasion pathway in determining potential invaders. *Mar. Ecol. Prog. Ser.* 215:1–12
- Zayed A, Constantin SA, Parker L. 2007. Successful biological invasion despite a severe genetic load. *PLoS ONE* e868(Issue 9):1–6



Contents

Associational Resistance and Associational Susceptibility: Having Right or Wrong Neighbors <i>Pedro Barbosa, Jessica Hines, Ian Kaplan, Holly Martinson, Adrianna Szczepaniec, and Zsafia Szendrei</i>	1
The Importance of Ecological and Phylogenetic Conditions for the Occurrence and Frequency of Sexual Cannibalism <i>Shawn M. Wilder, Ann L. Rypstra, and Mark A. Elgar</i>	21
Abundant Genetic Variation + Strong Selection = Multivariate Genetic Constraints: A Geometric View of Adaptation <i>Bruce Walsh and Mark W. Blows</i>	41
Responses of Humid Tropical Trees to Rising CO ₂ <i>Christian Körner</i>	61
The Role of Propagule Pressure in Biological Invasions <i>Daniel Simberloff</i>	81
Nongenetic Inheritance and Its Evolutionary Implications <i>Russell Bonduriansky and Troy Day</i>	103
The Ecology and Evolution of Microbes that Manipulate Host Reproduction <i>Jan Engelstädter and Gregory D.D. Hurst</i>	127
Spontaneous Mutation Accumulation Studies in Evolutionary Genetics <i>Daniel L. Halligan and Peter D. Keightley</i>	151
Geologic and Biologic Controls on the Evolution of Reefs <i>Wolfgang Kiessling</i>	173
Molecular Estimation of Dispersal for Ecology and Population Genetics <i>Thomas Broquet and Eric J. Petit</i>	193
Flower Evolution: The Origin and Subsequent Diversification of the Angiosperm Flower <i>Chelsea D. Specht and Madelaine E. Bartlett</i>	217

Is There a Latitudinal Gradient in the Importance of Biotic Interactions? <i>Douglas W. Schemske, Gary G. Mittelbach, Howard V. Cornell, James M. Sobel, and Kaustuv Roy</i>	245
Evolution of Placentas in the Fish Family Poeciliidae: An Empirical Study of Macroevolution <i>B.J.A. Pollux, M.N. Pires, A.I. Banet, and D.N. Reznick</i>	271
Gene Flow and Isolation among Populations of Marine Animals <i>Michael E. Hellberg</i>	291
Latex: A Model for Understanding Mechanisms, Ecology, and Evolution of Plant Defense Against Herbivory <i>Anurag A. Agrawal and Kotaro Konno</i>	311
What Salamanders Have Taught Us About Evolution <i>David B. Wake</i>	333
The Evolutionary Genetics of Emerging Viruses <i>Edward C. Holmes</i>	353
Belowground Herbivory and Plant Defenses <i>Nicole M. van Dam</i>	373
The Causes and Consequences of Compensatory Dynamics in Ecological Communities <i>Andrew Gonzalez and Michel Loreau</i>	393
Evolution and Ecology of Species Range Limits <i>Jason P. Sexton, Patrick J. McIntyre, Amy L. Angert, and Kevin J. Rice</i>	415
Woody Plant Diversity, Evolution, and Ecology in the Tropics: Perspectives from Seasonally Dry Tropical Forests <i>R. Toby Pennington, Matt Lavin, and Ary Oliveira-Filho</i>	437
Comparative Genomics on the <i>Drosophila</i> Phylogenetic Tree <i>Nadia D. Singh, Amanda M. Larracuente, Timothy B. Sackton, and Andrew G. Clark</i>	459
Genetic Consequences of Range Expansions <i>Laurent Excoffier, Matthieu Foll, and Rémy J. Petit</i>	481
Stoichiometrically Explicit Food Webs: Feedbacks between Resource Supply, Elemental Constraints, and Species Diversity <i>Spencer R. Hall</i>	503
Changing Ecology of Tropical Forests: Evidence and Drivers <i>Simon L. Lewis, Jon Lloyd, Stephen Sitch, Edward T.A. Mitchard, and William F. Laurance</i>	529

Systematic and Biogeographical Patterns in the Reproductive Biology of Scleractinian Corals <i>Andrew H. Baird, James R. Guest, and Bette L. Willis</i>	551
Effects of Natural Enemy Biodiversity on the Suppression of Arthropod Herbivores in Terrestrial Ecosystems <i>Deborah K. Letourneau, Julie A. Jedlicka, Sara G. Bothwell, and Carlo R. Moreno</i> ...	573
Statistical Phylogeography <i>L. Lacey Knowles</i>	593
The Nitrogen Paradox in Tropical Forest Ecosystems <i>Lars O. Hedin, E.N. Jack Brookshire, Duncan N.L. Menge, and Alexander R. Barron</i>	613
The Role of Animal Pollination in Plant Speciation: Integrating Ecology, Geography, and Genetics <i>Kathleen M. Kay and Risa D. Sargent</i>	637
Rates of Evolution <i>Philip D. Gingerich</i>	657
Species Distribution Models: Ecological Explanation and Prediction Across Space and Time <i>Jane Elith and John R. Leathwick</i>	677
Mycorrhizal Symbioses and Plant Invasions <i>Anne Pringle, James D. Bever, Monique Gardes, Jeri L. Parrent, Matthias C. Rillig, and John N. Klironomos</i>	699
Indexes	
Cumulative Index of Contributing Authors, Volumes 36–40	717
Cumulative Index of Chapter Titles, Volumes 36–40	721
Errata	
An online log of corrections to <i>Annual Review of Ecology, Evolution, and Systematics</i> articles may be found at http://ecolsys.annualreviews.org/errata.shtml	