

The more you introduce the more you get: the role of colonization pressure and propagule pressure in invasion ecology

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ABSTRACT

Aim We argue that 'propagule pressure', a key term in invasion biology, has been attributed to at least three distinct definitions (with usage of a related term causing additional confusion). All of the definitions refer to fundamental concepts within the invasion process, with the result that the distinct importance of these different concepts has been at best diluted, and at worst lost.

Location Global.

Methods We reviewed pertinent literature on propagule pressure to resolve confusion about different uses of the term 'propagule pressure' and we introduced a new term for one variant, colonization pressure. We conducted a computer simulation whereby the introduction of species is represented as a simple sampling process to elucidate the relationship between propagule and colonization pressure.

Results We defined colonization pressure as the number of species introduced or released to a single location, some of which will go on to establish a self-sustaining population and some of which will not. We subsequently argued that colonization pressure should serve as a null hypothesis for understanding temporal or spatial differences in exotic species richness, as the more species that are introduced, the more we should expect to establish. Finally, using a simple simulation, we showed that propagule pressure is related to colonization pressure, but in a non-linear manner.

Main conclusion We suggest that the nature of the relationship between propagule pressure and colonization pressure, as well as the efficacy of various proxy measures of each, require more detailed exploration if invasion ecology is to continue to develop into a more predictive science.

Keywords

Biological invasions, colonization, null models, propagule pressure.

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INTRODUCTION

Invasion ecology is a fast expanding ecological discipline, with the number of articles on the subject having grown exponentially since the early 1990s (Lockwood *et al.*, 2007). This expansion has resulted in considerable advances in our knowledge and understanding of the invasion process (Kolar & Lodge, 2001; Blackburn *et al.*, 2009a; Davis, 2009). One area where understanding has notably improved is that relating to determinants of establishment success. At the level of individual introduced populations, it is now widely appreciated that the primary determinant of establishment success is propagule

pressure or the number of individuals introduced (Box 1). Propagule pressure is clearly related to the concept of minimum viable population size in conservation biology (Terborgh & Winter, 1980; Traill *et al.*, 2007) and has similar practical consequences. Put simply, the more individuals that are released, the more likely it is that the population will survive environmental or demographic stochasticity, overcome Allee effects or have sufficient genetic variation to adapt to local conditions and thus become self-sustaining (Blackburn *et al.*, 2009b).

Invasion biologists also consider establishment success at the level of biological communities. There has been a host of

published studies comparing exotic species richness across sites and proposing hypotheses to explain the differences. Nearly all of these studies assume that geographical differences in exotic species richness are because of ecological processes that affect the number of species that can establish at a location, such as interspecific interactions, productivity or disturbance (Lockwood *et al.*, 2007). Nevertheless, the concept of 'the more you introduce, the more you get' is also relevant in this context. All else being equal (and ignoring the complication of populations spreading following establishment), one would expect that a site will have more exotic species established if it has had more exotic species introduced (i.e. the subset that failed plus the subset that succeeded).

Confusingly, the number of exotic species that have been released into a specified location has also been termed 'propagule pressure' in the invasion literature (Box 1). Here, we refer to it as 'colonization pressure'. We define colonization pressure as the number of species introduced to a given location, some subset of which will succeed in establishing an exotic population, with the rest failing to do so. Although this terminology is new, the concept clearly is not. Case (1996) was one of the first to note that no location can have more established species than the number of species introduced. Subsequently, Lonsdale (1999) argued that colonization pressure is a pervasive factor unaccounted for in many invasion ecology studies that consider variation in the numbers of exotic species established across locations (although he termed this factor 'propagule pressure'). Wonham & Pachepsky (2006) considered the influence of 'introduction rate' on temporal trends in the rate that invasive species accumulate at a site, where introduction rate is the number of species introduced in any given time period. Chiron *et al.* (2009) concluded that 'community-level propagule pressure', defined as the number of exotic species introduced, was a major driver of the observed variation in the number of established species across Europe. In these contexts, propagule pressure, introduction rate and community-level propagule pressure are all synonyms of colonization pressure. Given that the relevance of the number of exotic species introduced to patterns in the distribution of invasions is increasingly being recognized, it is important to formalize a suitable terminology that clearly differentiates colonization pressure from propagule pressure *sensu stricto* (Box 1).

Having identified colonization pressure as a concept of fundamental importance to invasion biology, we devote the remainder of this article to clarifying how colonization pressure can influence analyses of determinants of invasion success. First, we present evidence for why and how colonization pressure should be included in analyses of invasibility. We proceed to provide examples that show the consequences of failing to consider colonization pressure in studies of exotic species richness other than those concerned with establishment success. We then explore the potential for a relationship between colonization pressure and propagule pressure in exotic assemblages, and what the consequences of such an association might be for studies of establishment success. We

conclude with some brief recommendations about null hypotheses in invasion ecology and the search for proxy measures of propagule and colonization pressure.

ANALYSING COLONIZATION PRESSURE

The key to understanding the role of colonization pressure in driving exotic species richness is recognizing the large asymmetries that exist across locales in the number of species that were introduced (i.e. species that had the chance to establish, whether they ultimately did so or not). The increase in numbers of species introduced may overcome inherent stochasticity in establishment factors such that, at sites with many species introduced, at least one species will coincide with the appropriate conditions for establishment. Nevertheless, a more fundamental reason to include colonization pressure in analyses of exotic species richness is that a positive relationship between the number of species established and introduced is also expected by chance alone (Fig. 1).

This concept is most easily understood by means of a simple example. The island of Maui in the Hawaiian archipelago has 27 exotic bird species established, whereas Mauritius in the Mascarene archipelago has 19 (Blackburn *et al.*, 2008). One can think of several reasons why Maui might be able to support more exotic species, including that the effects of island area, resource availability or interspecific interactions may make it easier to invade. However, Maui has had 47 exotic bird species introduced to it, vs. only 33 for Mauritius. Thus, the probability of success is roughly equal on Maui and Mauritius, at 0.57 vs. 0.58 respectively. This evidence suggests that Maui is not easier to invade than Mauritius, but instead Maui has simply been host to more species introductions. Thus, before considering the ecological factors that might determine the difference in the number of exotic bird species established, it is necessary first to rule out the more prosaic explanation that it is entirely a consequence of colonization pressure.

It is obvious then that to understand why some locations have more exotic species than others, the number of species introduced needs to be taken into account. However, it is incorrect to model the number of established species as a function of colonization pressure, because this is a comparison of $x + y$ vs. y , where y is the number of species that succeeded in establishing, and x is the number that failed. Plotting $x + y$ vs. y will produce a spurious positive correlation (Brett, 2004). Instead, one needs to model the number of established species out of the total number of introduced species as a binomial response variable. The number of exotic species established (with its various determinants) can then be robustly assessed relative to colonization pressure for that particular region (see also Lonsdale, 1999). We thus suggest that a reasonable null hypothesis for all examinations of differences in numbers of established exotic species through time (or across locations) is that observed patterns are produced by colonization pressure alone. Only by discounting this effect, by modelling establishment probability as a function of the number of species introduced, can invasion ecologists invoke mechanistic

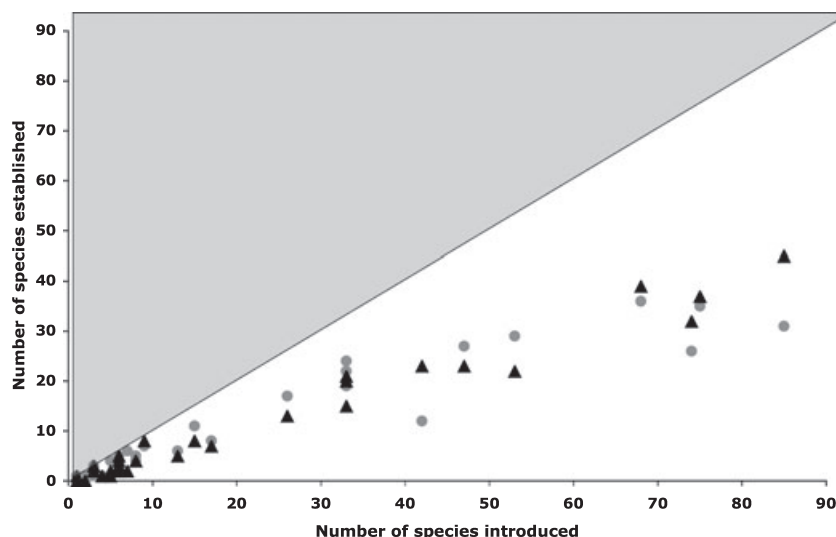


Figure 1 The number of exotic species that establish at a site cannot be greater than the number introduced. Therefore, points cannot occupy the shaded area on the relationship between the two. Points distributed at random in the unshaded area will tend to show a positive relationship by chance alone. The points shown are for birds introduced to 35 islands and archipelagos around the world (filled circles, from data in Blackburn *et al.*, 2008) and for a randomly generated sample of data (filled triangles) with the same number of introduced species per island and the same total number of species successfully established across all islands. Note that while it is interesting that, in the real data, the proportion of species that establish decreases with the number of species introduced, such that the relationship appears saturating, previous analyses (Cassey *et al.*, 2005) suggest that this is more likely to be the result of inter-island differences in propagule pressure than community-level effects on invasibility.

explanations for variation in exotic species richness (invasibility) related to differences in other ecological or evolutionary factors.

SOME CONSEQUENCES OF COLONIZATION PRESSURE

Lonsdale (1999) noted several instances where the effects of colonization pressure temper our conclusions about the role of various ecological drivers of establishment success, including the invasibility of nature reserves vs. pristine areas, and islands vs. continental areas (see also Simberloff, 1995). We highlight two more examples here to illustrate the range of questions that may need explicitly to consider colonization pressure as a null expectation and to show that the importance of colonization pressure is still being overlooked in even the most recent papers.

A common question in invasion ecology is how the rate of invasion has changed through time for a single location. Most temporal trends in numbers of established exotic species show an exponentially increasing accumulation of numbers of exotics (e.g., Cohen & Carlton, 1998; Ricciardi, 2001). At a minimum, comparing these trends across sites indicates which sites accumulate exotic species more rapidly than others. These trends may also indicate something more fundamental about the ecological drivers of invasion rates. For example, an accelerating trend in the increasing number of established exotics could be because of an increase through time in habitat degradation, a change in abiotic conditions, or the synergistic facilitative influence of early arriving exotics on later arrivals.

However, a simple explanation for this pattern is that the rate of exotic species introduction is itself accelerating (Wonham & Pachevsky, 2006). Thus, ecologists cannot use trends in the number of exotic species to indicate something more fundamental about ecological drivers unless information on colonization pressure is also included. We know of no empirical example where colonization pressure has been explicitly considered as a null as we suggest and thus we caution against interpreting existing evidence as favouring any particular ecological hypothesis regarding what determines invasion success.

Our second example of how the effects of colonization pressure may temper conclusions about the invasion process comes from Sax & Gaines (2008) analysis of historical records of plant naturalizations on oceanic islands. Sax and Gaines used these records to assess evidence for different mechanisms whereby the plant assemblages on the islands might be becoming saturated with exotic species. If there is a limit to the number of exotic plant species that an island can house, then the probability that a new species establishes may decrease over time as that limit is approached (colonization-based saturation), or alternatively the establishment of each new species may lead to the extinction of a previous resident so that the limit is not exceeded (extinction-based saturation). Sax and Gaines found that there was no evidence that the rate of establishment was slowing down on the islands in their data or that establishment is leading to extinction. They concluded that there is no evidence for either colonization-based or extinction-based saturation on these islands. They did detect that the slope of the inter-island relationship between the

number of native and number of exotic plant species was consistent across time periods, which they posited suggests that there is something uniform about the relationship between native and exotic species numbers across these islands.

In the absence of information on colonization pressure, however, the processes underlying variation in the richness of exotic species are impossible to identify. While we concur with Sax & Gaines (2008) that there is no evidence for extinction-based saturation in their data, the lack of change in the rate of establishment they observed could be indicative of colonization-based saturation if colonization pressure were increasing over time. Sax & Gaines made this point. However, they failed to note that the reverse is also true: if colonization pressure is decreasing over time, a lack of change in the rate of establishment could mean that an increasing proportion of exotic species become established, indicative of facilitation. The key issue is whether the probability of establishment (y out of $x + y$) is changing over time, rather than simply the number of established species (y). Similarly, the slope of the inter-island relationship between the number of native and number of exotic plant species could simply represent something uniform about where exotic plant species are introduced (c.f. Blackburn *et al.*, 2008).

ARE PROPAGULE AND COLONIZATION PRESSURE RELATED?

The pervasive influence of colonization pressure on establishment success at the level of exotic communities mirrors that of propagule pressure at the population level. In both cases, weight of numbers is the primary driver of establishment success. While propagule pressure and colonization pressure relate to distinct concepts (Box 1), there are reasons to believe that the magnitude of the two may sometimes be related. In situations where introductions can be viewed as the result of a random sampling process (e.g. introductions through ballast water or soil, or as stowaways in traded goods), the number of introduced species should be positively related to the number of introduced individuals because larger samples increase the likelihood that rare species are included, as has long been appreciated for natural assemblages (Preston, 1948). The abundance of the most common species will also be greater in larger samples. This observation suggests that locations that receive more exotic individuals overall will receive more species and have a higher probability that at least some of those species will establish because of their higher associated propagule pressure.

To explore more fully the relationship between propagule and colonization pressure, we constructed a simple simulation of how a source assemblage may be 'sampled' by a transport vector (e.g., a cargo ship), with all entrained individuals eventually being released into an exotic location. To represent a source assemblage, we distributed 1080 individuals across 100 species according to a simple theoretical (but realistic) log series species-abundance distribution (see Cassey *et al.*, 2006). We simulated a transport vector that randomly entrained

individuals from the source assemblage and released them in a single event into an exotic location. In the limit, the transport vector would sample a large enough number of individuals in a single event such that all species from the source assemblage would be represented within the exotic location, with identical abundance distributions at each location. However, it is highly unlikely that any (existing) transport vector could entrain such large numbers of individuals in any single transport event. Thus, of more practical interest is what happens well below this limit to the rate at which propagule and colonization pressure increase as the total number of individuals entrained increases away from very small numbers.

The average results (\pm SD) from 100 simulations are shown in Fig. 2. Colonization pressure shows a decelerating curvilinear relationship to the percentage of individuals released via a single transport event (Fig. 2a). This trend suggests that the number of exotic species released at an exotic location will increase quickly as the overall number of exotic individuals in any given transport event increases, but that the number of new species released will begin to taper as more of the individuals in the source assemblage are released. In contrast, propagule pressure increases in proportion to the percentage of individuals entrained and released (Fig. 2b), meaning that propagule pressure itself is a linear function of the total number of individuals released in a transport event.

The difference in the forms of these two relationships means that, as the percentage in the overall number of exotic individuals released increases, there will be a point where propagule pressure increases at a faster rate than colonization pressure. Our simulations show that propagule pressure will have no relationship to colonization pressure when relatively few individuals are entrained and released in any single transport event (Fig. 2c). Only when higher numbers of individuals are released do propagule pressure and colonization pressure both increase together (Fig. 2c). This relationship suggests that, in any single release event, larger numbers of exotic individuals released will lead to additional established exotic species more through the effect of increasing propagule pressure rather than through increasing colonization pressure.

Note that the actual relationship between colonization and propagule pressure will depend on variation in the species-abundance relationship within the source assemblage from which these exotics are drawn and according to how these are individuals are sampled. For example, transport vectors that preferentially entrain individuals from particular species will probably show very different patterns from the ones we report here. Certainly, in situations where organizations (e.g. acclimatization societies) import specific species for release, there is no statistical reason to expect a positive relationship between colonization pressure and propagule pressure. Nevertheless, it is still possible (but untested) that those organizations that were more zealous in introducing a wide range of exotic species may also have been more zealous in introducing larger numbers of each species released. A careful effort to explore this link between specificity of transport vectors, and propagule and colonization pressure is well warranted and should pay

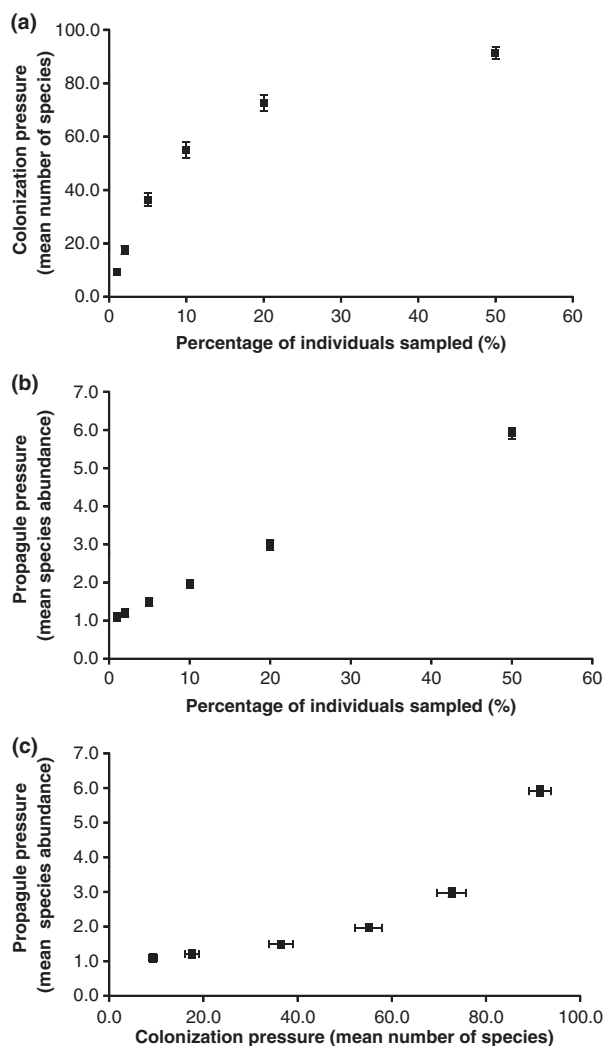


Figure 2 The relationships between (a) the overall percentage of individuals from a source area that are released as exotics and average colonization pressure, (b) overall percentage of individuals released as exotics and average propagule pressure across species and (c) colonization pressure and average propagule pressure; from species abundance distributions with 100 species and 1080 individuals distributed according to a log series model (following methods in Cassey *et al.*, 2006).

large dividends in terms of adding predictive power to efforts of invasion risk assessment.

CONCLUSIONS

In summary, we see two issues that commonly obstruct advancement within the study of invasion ecology. The first is the failure to define terms clearly enough so that their use is consistent across research programmes. This problem has been the topic of several recent papers in invasion ecology (e.g., Davis *et al.*, 2001; Pyšek *et al.*, 2004) and here we contribute to this literature by attempting to clarify the several usages of the term 'propagule pressure'. It is especially confusing that the

term has been used to refer both to the number of individuals introduced at the population level and to the number of species introduced at the community level, because both of these concepts are of fundamental importance to patterns of establishment.

The second and more fundamental issue that commonly obstructs advancement in invasion ecology is the frequent failure to consider the correct null hypothesis when evaluating historical datasets. We suspect that this failure comes in part from a lack of the necessary information from the early stages of the invasion process – previous authors have bemoaned the lack of information on both propagule pressure and colonization pressure, for example. When one does have such information, however, it is clear that patterns are often driven primarily by non-ecological mechanisms. Propagule and colonization pressure both place emphasis on the stochastic nature of the invasion process and an explicit recognition that the very early stages of the invasion process profoundly structure the later stages. In particular, the concept of 'the more you introduce, the more you get' serves as a logical null hypotheses for many aspects of invasion ecology research. A failure to account for this will lead to erroneous conclusions about the influence (or lack thereof) of more deterministic mechanisms that influence invasions. Sometimes, there will be evidence for these deterministic mechanisms and sometimes there will not, but without information on propagule and colonization pressure, it will always be difficult for invasion ecology to achieve a high level of synthesis and predictive power.

Given the importance of propagule pressure and colonization pressure in understanding invasion ecology, but the scarcity of raw data on either, we suggest that a fruitful avenue for future progress may be through the careful exploration of proxy measures of each. The increasing recognition of the role of propagule pressure in invasion ecology is already paying dividends in this regard. Measures such as the amount of ballast water discharged (e.g., Herborg *et al.*, 2007), the regularity with which certain species show up in seed catalogue or within pet stores (Duggan *et al.*, 2006; Cohen *et al.*, 2007; Pemberton & Liu, 2009) and the price that these species command (Dehnen-Schmutz *et al.*, 2007) all show considerable promise as proxies for propagule pressure. Equally compelling are detailed analyses of invasion transport vector behaviour, including building connectivity networks using transportation information (e.g. Tatem & Hay, 2007; Tatem, 2009). Most of these proxies have not been adapted for use in quantifying relative differences in colonization pressure, but the opportunity for their logical extension to that context is apparent.

BOX 1: CONFUSION OVER THE TERM 'PROPAGULE PRESSURE'

Propagule pressure is a key concept in invasion biology, but its importance has been confused by having been applied to more than one concept in the field.

Population-level processes

The most widely used definition of propagule pressure – and the one that we argue has primacy – is simply the total number of individuals introduced at a given location (Williamson, 1996). This total number may be spread across several separate releases or escapes and hence propagule pressure can be viewed as having two components: the number of introduction events (propagule number) and the number of individuals per introduction event (propagule size) (Pimm, 1991; Carlton, 1996; Veltman *et al.*, 1996; Lockwood *et al.*, 2005). Propagule pressure is thus the product of propagule number and mean propagule size, or the sum over all introduction events of the number of individuals liberated.

Propagule pressure has also been used to define a measure of the extent to which established individuals of a species add offspring to the exotic environment. For example, Rouget & Richardson (2003) argued that ‘propagule pressure’ explained why the canopy cover of three invasive tree species was best predicted by the distance of a site from presumed invasion foci. The logic for expecting this association is obvious and essentially the same as for that between propagule pressure *sensu strictu* and establishment success: ecologists are attempting to determine the likelihood of new peripheral populations establishing away from the invasion front or initial invasion foci. We suggest ‘propagule rain’ as a sensible alternative term for this concept.

Community-level process

Propagule pressure has also been defined as the number of exotic species that have been released into a specified location (Lonsdale, 1999; Colautti *et al.*, 2006; Sax & Gaines, 2008). Lonsdale (1999) used this term on the basis of a quote from Williamson (1996): ‘Looking for real differences in invasibility requires looking at the residuals from the relationship between invasion success and propagule pressure’. However, in context, it is apparent that Williamson (1996) is referring exclusively to population-level propagule pressure (as defined above) and, indeed, did not consider the community-level process at all. We propose that the number of exotic species that have been released into a specified location is termed ‘colonization pressure’. This concept is the primary focus of this article.

Reproductive trait

Plant ecologists often refer to the reproductive structures of plants as ‘propagules’. This is not a large impediment to achieving a broad understanding of the role of propagule pressure in invasion ecology, but it does become confusing when propagule pressure is broken into its components, size and number. The ecological literature also refers to the term ‘propagule size’ as the physical dimensions of plant reproductive structures, such as seeds. Seed size has been shown in many cases to play a positive role in establishment success and spread rates for invasive plants (e.g., Richardson & Rejmánek,

2004; Eisenhauer & Scheu, 2008). Small seed size is associated with the production of larger numbers of seeds per adult plant, longer dispersal distances and high initial germination ability. Each of these factors can potentially increase the likelihood of either initial establishment after introduction or new colony establishment during range expansion (Richardson & Rejmánek, 2004) and can act independently of population-level propagule pressure.

The use of ‘propagule size’ to refer to reproductive structures probably originated with plant ecologists unconcerned with invasion biology. Both disciplines have formalized it to such an extent that we do not advocate the creation of a new term to untangle these two concepts. It is nevertheless important for ecologists to recognize that in most studies on the role of propagule pressure in invasion success, propagule size refers to the number of individuals released (or dispersing) and not to the physical dimensions of a reproductive structure.

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