

INVASION GENETICS: THE BAKER AND STEBBINS LEGACY

The influence of numbers on invasion success

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Abstract

The process by which a species becomes a biological invader, at a location where it does not naturally occur, can be divided into a series of sequential stages (transport, introduction, establishment and spread). A species' success at passing through each of these stages depends, in a large part, on the number of individuals available to assist making each transition. Here, we review the evidence that numbers determine success at each stage of the invasion process and then discuss the likely mechanisms by which numbers affect success. We conclude that numbers of individuals affect transport and introduction by moderating the likelihood that abundant (and widespread) species are deliberately or accidentally translocated; affect establishment success by moderating the stochastic processes (demographic, environmental, genetic or Allee) to which small, introduced populations will be vulnerable; and affect invasive spread most likely because of persistent genetic effects determined by the numbers of individuals involved in the establishment phase. We finish by suggesting some further steps to advance our understanding of the influence of numbers on invasion success, particularly as they relate to the genetics of the process.

Keywords: birds, inbreeding, invasive species, population dynamics

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Introduction

Hindsight is a wonderful thing. It is easy to look back with a critical eye on the best research produced by previous generations and feel good about oneself by observing only the shortcomings. A case in point is Baker & Stebbins' (1965) edited Proceedings of the First International Union of Biological Sciences Symposia on General Biology. It is titled *The Genetics of Colonizing Species*, but the then state of the art means that it contains little focus on molecular genetics, and mainly considers ecological and quantitative genetics, and phenotypes assumed to have a genetic basis. It is also not always obvious what is meant by a 'colonizing species', and indeed, three different types of such species are identified (Mayr 1965). The

bulk of the discussion in Baker & Stebbins (1965) relates to species we would now term non-native or alien (i.e. species whose presence in a region is attributable to human actions, which have enabled them to overcome fundamental biogeographical boundaries; Richardson *et al.* 2011), and their volume is recognized as a classic text of invasion biology. Yet, to the eye of the modern invasion biologist, there are some glaring omissions that serve to highlight how far the field has come over the last half century. Perhaps the most important of these is the lack of appreciation that invasion biology is primarily a succession of numbers games.

The process by which an alien species invades can be divided into a series of consecutive stages: transport (beyond native range limits), introduction (into the wild in a new environment), establishment (of a viable alien population) and finally (invasive) spread (Blackburn *et al.* 2011). Recognition that the number of individuals

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matters greatly to this process arose from developments in conservation biology, where it had become apparent that the persistence of small populations depends fundamentally on population size (Caughley 1994). Initially, the importance of numbers was largely considered in terms of establishment success, but it was quickly realized that the number of individuals matter at all invasion stages. Thus, abundant native species are more likely to be entrained in a transportation mechanism and later released into a new location (Blackburn & Duncan 2001). Species more abundant in captivity are also more likely to be released (Cassey *et al.* 2004a; Chang *et al.* 2009). Introduced populations are more likely to establish if more individuals are released (higher 'propagule pressure', which is the sum over all release events of the number of individuals released to form a population, sometimes also termed 'introduction effort': Cassey *et al.* 2004b, 2005; Lockwood *et al.* 2005; Hayes & Barry 2008; Blackburn *et al.* 2009; Simberloff 2009), and populations introduced with higher propagule pressure, or that produce more offspring in the new environment, are more likely to spread (Duncan *et al.* 1999, 2001; Caswell *et al.* 2003; Signorile *et al.* 2014). Several chapters in Baker & Stebbins mention numbers in the context of colonization by alien species, but primarily as a consequence of invasion, not as a cause (e.g. Birch 1965; Fenner 1965; Fraser 1965; Harper 1965; Sakai 1965). None presage the prominence this issue has now achieved. Today, the key questions are not about whether numbers influence invasion success, but how.

The invasion stage that has received most attention in terms of the influence of numbers is establishment. Most alien populations start out at very small numbers (Blackburn *et al.* 2009; fig. 3.1). Population dynamic theory and conservation practice both demonstrate that small populations are more likely to go extinct, on average, than larger populations (see any ecology or conservation text book). We would expect extinction risk to vary with population size for alien as well as for native populations, and so it is no surprise to find that propagule pressure is generally strongly positively correlated with establishment success (Lockwood *et al.* 2005; Colautti *et al.* 2006; Hayes & Barry 2008; Blackburn *et al.* 2009; Simberloff 2009). Nevertheless, small populations are vulnerable to a variety of processes, including demographic stochasticity, environmental heterogeneity, Allee effects and genetic effects (Morris & Doak 2002; Cassey *et al.* 2014). We might expect the precise mechanisms underlying the relationship between numbers of individuals and persistence to differ for native and alien populations. For example, the importance of environmental heterogeneity or Allee effects may differ for species new to a location vs. species with a long evolutionary history in that environment. The role of genetic

effects may also differ for populations structured by natural vs. anthropogenic processes. To date, few studies have explored the influence of propagule pressure on alien population establishment in ways that allow us to discriminate between the actions of these different processes.

Here, we review evidence that helps us to understand how the broad positive relationship between numbers and invasion success might be driven, considering all stages in the invasion process. In the spirit of Baker & Stebbins (1965), we highlight how numbers might interact with genetic effects where possible. However, as Ernst Mayr noted in his concluding remarks to the Proceedings, 'I am sure every ecologist here realizes that he (*sic*) really ought to know more about genetics', and that very much applies to the three of us.

Numbers, transport and release

The early stages of the invasion pathway concern which species are transported beyond the limits of their native geographic ranges and which of these species are subsequently liberated into new environments. In many cases, the first evidence that species have been transported and released outside their native ranges comes when free-living individuals are observed within a new environment. Hence, most studies of these early stages of invasion concatenate transport and release. A basic dichotomy in classification at these early invasion stages is whether individuals are moved intentionally or unintentionally by humans (Lockwood *et al.* 2013). Either way, the number of individuals in the native population matters.

Examples of accidental transport and release include individuals caught up in the ballast (soil or water) of ships, within the packing material used for dry cargo, or as hitchhikers living beside or within a purposefully traded species (Mack 2003; Hulme *et al.* 2008; Hulme 2009). Under these circumstances, individuals of alien species find themselves entrained in a transport vector essentially at random. Species more prevalent in their native environment are by chance alone more likely to be unintentionally transported (Hulme 2009) and more likely to be present in those samples in higher numbers (Wonham *et al.* 2001). Species that have adapted to human-altered habitats may be more likely to be transported by accident than species that shun anthropogenic environments (Hufbauer *et al.* 2012), but we would still expect accidental transport to concern more abundant species in these environments. The same processes apply also to intraspecific variation, such that higher frequency genotypes (and phenotypes) are more likely to be captured for transportation and release (Nei *et al.* 1975). In sum, accidental transport and introduction filter out rarity. Random sampling processes also result in larger numbers of individuals per species

being introduced as the size of the sample increases (Lockwood *et al.* 2009), which has further consequences for the probability that an alien species will establish a viable population once released.

The same is true for many species deliberately transported and released. Species may be intentionally moved for a variety of reasons, including as game animals, ornamental plants or animals, as biocontrol agents, or for the purposes of conservation (Lockwood *et al.* 2013). Identity will clearly matter in such cases—not all plants are equally desirable as ornamentals, for example (Pyšek *et al.* 2003)—but the availability of species for capture and transport typically matters too. Thus, birds transported from the UK to New Zealand tended to be species that are abundant and resident in the UK (Blackburn & Duncan 2001). Similarly, parrots that are transported outside their native ranges tend to be widespread species, and widespread and abundant parrot species are more likely to be released or escape into novel regions (Cassey *et al.* 2004a). While nonrandomness in the taxonomic composition of species has revealed that certain types were preferentially moved (e.g. wildfowl, game birds; Blackburn & Duncan 2001), the species introduced were nevertheless those that were the most readily available and easily obtained (Fig. 1). Abundant species tend also to be widespread (Gaston & Blackburn 2000) and so likely to be available for collection at a wide range of locations. For any given species, higher frequency genotypes and phenotypes are again more likely to be moved. Thus, with the acknowledgement that some deliberately transported species are rare in their native range, we should expect commonness to also be favoured in the deliberate movements of species.

These transport filters have consequences for subsequent invasion stages, as they determine which species become exposed to novel environments (Cassey *et al.* 2004a). Common, widespread species are common and widespread for a reason. While it is still not obvious if we can identify the actual underlying processes with much confidence, the breadth or typicality of species' environmental requirements or tolerances seem likely to be important determinants of establishment success and subsequent invasive spread (Gaston 1994, 2003; Gaston & Blackburn 2000). Alternatively, species that have adapted to human-altered habitats may be more likely to be both transported and able to exploit conditions they find on release (into other human-altered habitats; Hufbauer *et al.* 2012). Either way, the early stages of the invasion process may be selecting for species that are pre-adapted to cope with conditions they will encounter in the new location (Chapple *et al.* 2012). This may in part explain why establishment success is surprisingly high in at least some groups of alien spe-

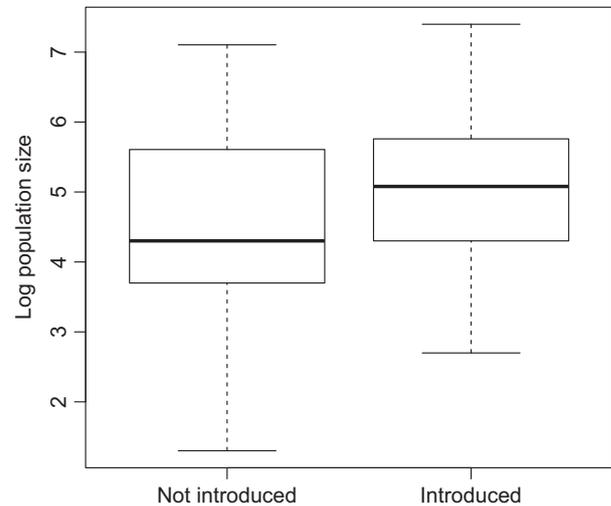


Fig. 1 Boxplot showing variation in estimates of the global population for wildfowl (Order Anseriformes) species that have or have not ever been introduced to areas beyond the limits of their native geographic range. A binomial general mixed linear model (with a random effect for genus to account for nonrandomness due to taxonomy) shows that population sizes are larger for species that have a history of introduction than for those that do not (estimate \pm standard error = 0.64 ± 0.19 , $N = 153$, $P < 0.001$). Data on population size were those used in Blackburn & Duncan (2001), while a list of introduced wildfowl species came from the Global Avian Invasions Atlas (GAVIA) database (E. Dyer & T. M. Blackburn, unpublished).

cies (e.g. Williamson 1996; Gaston *et al.* 2003; Jeschke 2008). Random sampling processes also result in larger numbers of individuals per species being introduced as the size of the sample increases, which has further consequences for the probability that an alien species will establish a viable population once released (Lockwood *et al.* 2009).

Numbers and establishment success

Once an alien species is released into a novel environment, the individuals must found a self-sustaining population to be considered 'established' (Lockwood *et al.* 2013). The probability that this will happen is higher for alien populations that are founded by relatively large numbers of individuals. If these individuals are released over more than one location, or at more than one time, the probability of establishment may also be higher. These relationships result because the perils of small population size tend to ensure that populations with few founders will eventually become extinct (Lockwood *et al.* 2005; Hayes & Barry 2008; Blackburn *et al.* 2009; Simberloff 2009). Demographic stochasticity, environmental stochasticity, Allee effects and genetic

effects are all likely to play a role in increasing the chances that a small population will fail to establish. However, the actual contribution of each of these processes in the context of invasions is as yet unresolved. We are nevertheless gaining insights into these relationships from the increasing application of theoretical models of invasion dynamics to empirical data. These models show that different processes are expected to produce different relationships between propagule pressure and establishment success.

Duncan *et al.* (2014) derived the expected relationship between establishment probability and the number of individuals released for populations under the influence of demographic stochasticity, Allee effects and among-population environmental heterogeneity in establishment conditions. They assumed that founding populations initially were composed of far fewer individuals than the location's carrying capacity, and noted that a population will establish if at least one individual leaves a surviving lineage (Caswell 2001; Fox 2005). Under demographic stochasticity alone, the probability of establishment, P_{est} , for a newly introduced population of size N_0 is as follows:

$$P_{est} = 1 - (1 - P)^{N_0} \quad \text{eqn 1}$$

where P is the probability that each individual leaves a surviving lineage. Demographic stochasticity affects all populations, and so Duncan *et al.* (2014) used eqn 1 as the base to which to add additional effects. They incorporated Allee effects by adding a term that models changes in the birth rate at different population sizes: a disproportionate decline in birth rate at low population sizes is expected under Allee effects. They incorporated among-population environmental heterogeneity by modelling variation in the probability of individual establishment, P , across different locations as drawn from a beta distribution.

Duncan *et al.* (2014) tested the fit of these different models to data for 55 experimental releases of the alien psyllid *Arytainilla spartiophila* to New Zealand for the purposes of biocontrol (Memmott *et al.* 2005). The data were best fit by the model of establishment success as a function of demographic stochasticity plus Allee effects, although the model of demographic stochasticity plus among-population heterogeneity also fitted the data reasonably well. Establishment success was relatively poorly predicted by demographic stochasticity alone. However, the best fitting model revealed that establishment probability per individual was actually proportionately lower at large population sizes, not at small population sizes as expected under a classic Allee effect. Duncan *et al.* (2014) found similar effects for global data on the outcome of bird species introductions (using data in Sol *et al.* 2012), with disproportionately lower

per individual success rates when large numbers of birds were released.

These models suggest that variation in establishment success can broadly be explained by two processes. First, the decline in success at small propagule pressures (the left hand side of Fig. 2) is consistent with the effects of demographic stochasticity. Second, the disproportionate decline in success (per individual released) for larger releases suggests that success here is being driven by factors largely unrelated to the initial size of a population. This would be expected if populations are being introduced to areas that are unsuitable for their establishment, regardless of how many individuals are involved. Interestingly, Memmott *et al.*'s (2005) data showed substantial variation in the probability that each individual leaves a surviving lineage (P ; see inset panel in Fig. 2), with many sites having a very low probability of establishment. This observation implies that even

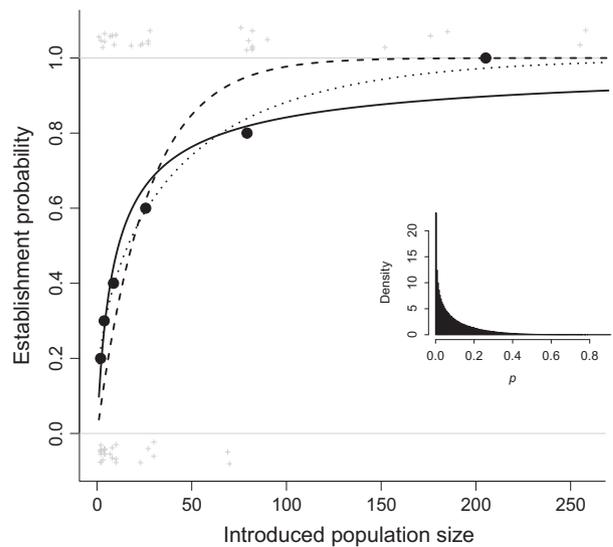


Fig. 2 Establishment probability vs. introduced population size for 55 of psyllid populations released in New Zealand. Introductions spanned a range of population sizes (10 introductions of 2, 4, 10, 30 and 90 psyllids and 5 introductions of 270 psyllids) and were considered successful if populations were still present after 5 years. Grey crosses are the raw data showing successful (y -axis values >1) and unsuccessful (y -axis values <0) establishment as a function of introduced population size, while the filled circles show the proportion of populations that established for each population size. The curved lines show the maximum-likelihood fits of different models to the data: dashed line = demographic stochasticity alone; dotted line = demographic stochasticity plus Allee effects; solid line = demographic stochasticity plus among-population heterogeneity. The inset panel shows the distribution of probabilities that each individual leaves a surviving lineage, P , for different populations modelling among-population heterogeneity. From Duncan *et al.* (2014), based on data in Memmott *et al.* (2005).

large populations of psyllids were destined to go extinct at some of the release sites. Indeed Memmott *et al.* (2005) noted that while small introduced psyllid populations tended to go extinct very quickly (consistent with demographic stochasticity), surviving populations were then prone to extinction due to site destruction, which affected populations regardless of their size.

Duncan *et al.* (2014) explored establishment probability as a function of the number of individuals released, but ignored the fact that this number can be arrived at in a number of different ways. In particular, N total individuals may derive from one large or several smaller release events (Lockwood *et al.* 2005). Different release configurations will clearly influence the relative impacts of demographic stochasticity vs. Allee effects (and environmental suitability), but the precise outcome is likely to be influenced by how these effects are manifested. Hopper & Roush (1993) suggested that multiple, small releases may be more likely to establish than a single large one under environmental heterogeneity, because increasing the number of releases increases the probability that one of those will coincide temporally or spatially with favourable environmental conditions. This argument has subsequently been confirmed by a variety of models (e.g. Haccou & Iwasa 1996; Grevstad 1999; Haccou & Vatutin 2003). Conversely, simulations by Cassey *et al.* (2014) found that the probability of establishment was negatively correlated with the number of separate release events, and the time between them, even under conditions of extreme (interannual) environmental variability. They attributed their results to the fact that a single, large release will grow more quickly in population size, and hence is more capable of riding out harsh environmental conditions, while less likely to be reduced to a level where demographic and typical Allee effects are relevant. However, Cassey *et al.* (2014) modelled releases distributed in time, but not in space. Multiple releases to different locations may enhance the probability that some of those released individuals encounter a favourable environment simply because these conditions are more variable across space than through time at a single location (cf. Haccou & Iwasa 1996; Haccou & Vatutin 2003; Duncan *et al.* 2014).

The number of individuals released, and how they are released, is also likely to determine the impacts of genetic stochasticity in alien populations. Smaller releases are likely to have lower genetic diversity, and higher likelihoods of population bottlenecks, genetic drift and inbreeding, all of which can cause declines in mean fitness (Fig. 3; Frankham *et al.* 2004). These founder effects will be exacerbated if the population remains small for a number of generations (Nei *et al.* 1975). All of these effects may decrease the probability that an alien species will establish a self-sustaining population.

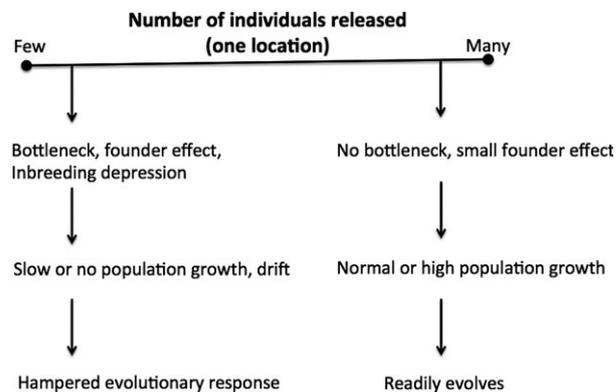


Fig. 3 Flow chart of the cause-effect sequence of events whereby low propagule pressure results in low genetic variation, slow population growth causing further genetic erosion and finally a dampened ability to evolve to new conditions in the alien range. Contrast this outcome to the sequence of events expected when propagule pressure is high. Any one of the events in this sequence can add to the likelihood that an initially small founder population will probably go extinct due to genetic issues.

Releasing a given number of individuals in several small releases distributed across space (or time) may exacerbate these problems by forcing the population through a series of smaller bottlenecks. Alternatively, it has been suggested that multiple releases may promote establishment by providing a 'genetic rescue effect' (*sensu* Carlson *et al.* 2014) by supplementing genetic diversity, especially in cases where supplementary individuals come from different source populations (Sakai *et al.* 2001; Brook 2004). While alien populations are expected to sample only a proportion of the genetic variation present in their native range (see e.g. Dlugosch & Parker 2008), there are prominent examples where local alien populations are genetically more diverse than local source populations (e.g. Kolbe *et al.* 2004). Individuals deriving from diverse donor locations may not only increase genetic diversity and reduce the likelihood of bottlenecks, but may also trigger novel outcrossing events that can increase the adaptive potential of an introduction (Novak & Mack 2005), or import novel genetic variation that allows evolutionary rescue. Conversely, they may also lead to outbreeding depression.

Dlugosch & Parker (2008) reviewed studies of genetic variation in introduced vs. native ranges, finding data for 80 alien species from a range of taxa. While they found some examples where genetic diversity was higher in the alien range, in most populations it was lower. The average loss of diversity was estimated at between 5.8% and 32.7%, depending on the molecular marker. However, the extent of this loss was smaller for populations that had resulted from multiple

introduction events. These patterns would be expected under a genetic rescue effect, but could also be explained if multiple introductions tended to have higher propagule pressures. This is certainly the case for bird introductions to New Zealand, where number of individuals of a species released at a location is highly positively correlated with the number of releases ($r = 0.73$, $N = 92$, $P < 0.001$; from data used by Blackburn *et al.* 2013). Dlugosch & Parker (2008) do not control for this effect, but a subsequent meta-analysis of animal and plant introductions showed that genetic diversity tends to be higher for alien populations deriving from multiple introductions, controlling for the number of individuals introduced (Uller & Leimu 2011). Nevertheless, these analyses do not inform about the influence of genetic effects on establishment success, as they do not include genetic data for failed introductions (these are considerably more difficult to come by). A field experiment by Ahlroth *et al.* (2003) does suggest that genetic composition may be important: they found that the likelihood of successful colonization increased with propagule pressure for introduced water striders populations, but that colonization success was higher, for a given propagule pressure, when founders came from two vs. one source populations. Nevertheless, the maximum number of founders introduced by Ahlroth *et al.* (2003) was only 16. Even releases involving few individuals can sample much native genetic diversity (Novak & Mack 2005; see also Roman & Darling 2007), suggesting that genetic effects may be relevant only to the smallest releases.

The population model of establishment success explored by Cassey *et al.* (2014) supports this interpretation. They included genetic effects by modelling inbreeding depression and identified four factors that were influential in determining establishment in their simulations: net reproductive rate per female, the number of individuals released, the influence of extreme environmental events and the strength of inbreeding effects. The genetic effects were the smallest of the four. Inbreeding had negligible effects on establishment probability in cases where success or failure is more or less guaranteed on the basis of other modelled parameters, but could tip the balance towards failure for populations with intermediate chances of establishment. Overall, their models found that a single release was always more successful than multiple releases, all else being equal, even under conditions of extreme environmental variability. One large release grew more quickly, was less likely to be reduced to a population size where demographic, genetic and Allee effects come into play and could exploit favourable conditions when they occurred. All that spreading out the release of more individuals did, in terms of establishment success, was

to delay their reproductive contribution to future generations (Cassey *et al.* 2014). However, their model did not incorporate negative density dependence, and so it is possible that multiple releases may matter more for populations that are highly constrained in size.

Alien populations are not fixed entities, but can evolve to meet challenges of novel environments to which they are not pre-adapted (Sakai *et al.* 2001). Adaptation that occurs rapidly enough that a population recovers from environmentally induced demographic effects that otherwise would have caused extinction is termed 'evolutionary rescue' (Gomulkiewicz & Holt 1995; Gonzalez *et al.* 2013; Carlson *et al.* 2014). The recent growth of interest in evolutionary rescue is largely driven by attempts to understand the likely responses of species to rapid, anthropogenic environmental change (Gonzalez *et al.* 2013), but it is clearly also relevant to biological invasions (e.g. Holt *et al.* 2005). The likelihood that evolutionary rescue occurs will also be influenced by propagule pressure, because the size of a population is generally positively related to the rate at which it can adapt, and to the maximal rate of environmental change to which it can adapt (Lanfear *et al.* 2014). Larger populations may also take more time to decline to the size at which extinction due to stochastic processes is likely, although this will depend also on the degree of maladaptation (Holt *et al.* 2005), and hence the rate of population declines (Carlson *et al.* 2014). Moreover, the likelihood of evolutionary rescue is higher for populations with greater standing genetic variation available for selection to act upon (Bell 2013; Carlson *et al.* 2014), which also should be positively related to propagule pressure.

Evolutionary rescue may be influenced by how individuals are released. Multiple releases may promote evolutionary rescue if the additional propagules import novel genetic material or increase opportunities for mutations (Carlson *et al.* 2014). Once again, however, it is not obvious that these benefits would be greater than if the population derived from a single release of the same total number of individuals. Conversely, multiple releases may hamper evolutionary rescue if the immigrants bring maladaptive genes into the population (e.g. Schiffrers *et al.* 2013), which could eliminate fitness gains made from adaptation in the original release. This suggests that, in some cases, multiple releases may actually reduce the likelihood of establishment by an alien population, although we are not aware of any examples of this.

Models and analyses of historical data on establishment success have been informative about the potential and actual influence of numbers introduced, but we are now at a point where the most useful development would be more experimental tests of the processes

concerned. There is a small but growing number of such studies (Grevstad 1999; Ahlroth *et al.* 2003; Drake *et al.* 2005; Memmott *et al.* 2005; Fauvergue *et al.* 2007; Bailey *et al.* 2009; Bell & Gonzalez 2009; Gertzen *et al.* 2011; Hufbauer *et al.* 2013; Szucs *et al.* 2014). Experiments that manipulated the genetic composition of individuals introduced to locations (e.g. microcosms, enclosures) in different numbers and multiples of events could be particularly rewarding in distinguishing the influence of genetic, demographic and Allee effects. Recent studies by Hufbauer *et al.* (2013) and Szucs *et al.* (2014) that manipulated the numbers and genetic composition of insects introduced to experimental arenas are an excellent first step. For example, Szucs *et al.* (2014) demonstrated that establishment success in populations of *Tribolium* beetles depended on founder size but not on their genetic provenance (inbred to outbred), although subsequent population growth was depressed at low founder sizes for inbred lines.

Numbers and alien species spread

The influence of numbers on the process of invasion continues beyond the establishment phase to influence how far alien species spread across the new environment. Here, numbers affect spread (invasiveness) in two broad ways.

First, populations that produce more offspring in the new environment are more likely to spread more widely across it (Caswell *et al.* 2003). For example, successful plant invaders tend to be more fecund compared to their native congeners or related taxa, and to alien congeners with different degrees of invasiveness (Pyšek & Richardson 2008). Bird species with life history traits associated with higher fecundity (and higher rates of population growth) have larger alien geographic range sizes in both New Zealand (Duncan *et al.* 1999) and Australia (Duncan *et al.* 2001). This relationship may arise if the process of spread in a new environment is functionally equivalent to a sequence of establishment events (Blackburn *et al.* 2011). Under this analogy, an alien species that has established a sustainable population at a 'beachhead' in a new environment then spreads by establishing further populations at new locations, at each of which the same challenges that faced the original introduction are overcome. Just as the number of individuals in the initial introduction is of fundamental importance to that first establishment, so too is the number of individuals that reach subsequent locations a key determinant of the likelihood of establishes there. All else being equal, increasing local abundance boosts the number of propagules available for dispersal to new, unoccupied locations. If higher fecundity increases a population's local abundance, then a

relationship between fecundity and spread would be expected.

Second, populations introduced to the new environment in larger numbers are not just more likely to establish a viable population there, but are also more likely to spread more widely across it (e.g. Duncan *et al.* 1999, 2001). Thus, the influence of propagule pressure appears to extend beyond the establishment phase, also to determine alien range size. Propagule pressure is argued to affect establishment success because it helps populations to overcome the consequences of Allee effects, and of demographic, environmental and genetic stochasticity (Fig. 3, see above). Population and conservation biology tell us that the first three of these processes quickly lose their threat to a population's persistence as it grows away from small numbers. The residual influence of propagule pressure therefore seems most likely to act through the continued impacts of genetic effects.

Alien species typically pass through a small population bottleneck on the pathway to establishment, and the concomitant declines in genetic diversity and increases in the likelihood of inbreeding can affect fitness over extended time frames (Fig. 3). For example, a review of genetic variation in established alien bird species found that more severe bottlenecks reduced genetic variability in the resulting populations, relative to the native range (Merilä *et al.* 1996). Briskie & Mackintosh (2004) used data on the breeding success of alien bird species established in New Zealand to demonstrate that rates of hatching failure were a negative function of the number of individuals introduced. Their data suggest that increases in failure rates are mainly expressed in populations for which fewer than 100 individuals were introduced (Fig. 4). Given that the species analysed by Briskie & Mackintosh (2004) were introduced in the middle of the nineteenth century, their data suggest that the fitness consequences of passing through a population bottleneck are still being expressed more than a century after the bottleneck occurred. An alternative outcome is that prolonged inbreeding will allow harmful genetic mutations to be expressed and that these mutations will then be 'purged' from the population via selection (Frankham *et al.* 2004). If this situation pertains in alien invasions, we should expect that some alien populations established with few individuals, and whose populations remained low but persistent for long periods, will eventually begin to express higher fitness. For example, Facon *et al.* (2011) showed that inbred individuals of the ladybird *Harmonia axyridis* from the native range showed greater inbreeding depression than individuals from alien populations, suggesting that recessive deleterious mutations had been purged from the latter.

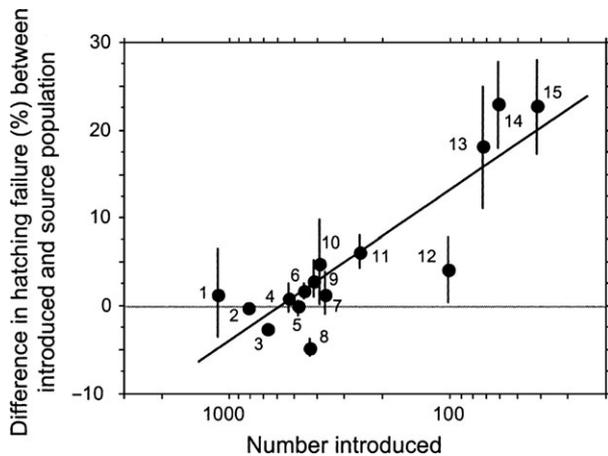


Fig. 4 The relationship between the number of birds introduced and relative hatching failure rate (the difference between the failure rate in the alien and native source populations) for alien bird species established in New Zealand. Species introduced in smaller numbers show a larger increase in failure rates in the alien relative to the native population. Species are as follows: (1) *Callipepla californica*; (2) *Turdus merula*; (3) *Sturnus vulgaris*; (4) *Fringilla coelebs*; (5) *Carduelis carduelis*; (6) *Carduelis flammea*; (7) *Passer domesticus*; (8) *Alauda arvensis*; (9) *Turdus philomelos*; (10) *Emberiza citrinella*; (11) *Prunella modularis*; (12) *Chloris chloris*; (13) *Acridotheres tristis*; (14) *Branta canadensis*; and (15) *Corvus frugilegus*. From Briskie & Mackintosh (2004).

The fitness consequences of bottlenecks for alien species may affect the dynamics of their populations. For example, the experimental work of Szucs *et al.* (2014) showed that populations of *Tribolium* that establish from low propagule pressures grow more slowly if those founders are inbred, while dispersal rates in these populations increase with genetic diversity. Their results imply that population growth and spread following establishment can both be driven by genetic processes. Similarly, Signorile *et al.* (2014) studied alien grey squirrel (*Sciurus carolinensis*) populations at four locations in Europe. They found that genetic variation across these populations increased with founder population size and that there was a positive relationship between founder population size and the rate of population spread. A common feature of the population growth curves of alien populations is a lag phase, defined as a period of slow population growth followed by a marked increase in the rate of growth (Shigesada & Kawasaki 1997; Williamson *et al.* 2005; Aikio *et al.* 2010; Aagaard & Lockwood 2014). The lag phase may be a simple consequence of the form of population growth curves, but may also reflect the time taken for the population to produce the necessary adaptations to allow spread (Crooks & Soulé 1999). If so, losses of genetic variation that result from low propagule pressure and subsequent slow population growth may pro-

mote longer lag phases by reducing the genetic diversity available for selection to act upon.

The sampling effect of bottlenecks may also reduce the likelihood that individuals with appropriate adaptations to allow spread are introduced to a new location (McCauley 1991) (Fig. 4). For example, Zenni *et al.* (2014) showed that range expansions by alien *Pinus taeda* resulted from an interaction between the genetic provenance of the introduced individuals and the climate in the alien range. These invasions are led by plants with a genotype that conveyed higher fitness in the alien range, which suggests that the invasions would have at best proceeded more slowly had this genotype not been initially introduced. Such effects may also influence the extent of the alien range size.

The impacts of introduction history can have long-term effects through genetic stochasticity, but as with the effects of demographic and environmental stochasticity, these impacts are likely to decrease as an alien population grows and spreads. Selection may, depending on the precise conditions, purge exposed deleterious recessive alleles, weakening inbreeding depression over time (Frankham *et al.* 2004). Dlugosch & Parker (2008) found some evidence that the proportional change in genetic diversity in alien relative to native populations shows a U-shaped relationship to the length of time that an alien species has been established, at least for species established from multiple introduction events (but see Uller & Leimu 2011). Allelic richness decreased with time across populations up to around 80–100 years after first introduction, but then started to increase again. Dlugosch & Parker (2008) argued that drift and strong selection were likely to have caused a loss of within-population genetic diversity in the initial phase of establishment, for all initially established alien populations, given their associated slow population growth. However, as these alien populations increased in numbers and became more connected through dispersal (integrating more across multiple populations at multiple introduction sites), genetic diversity would begin to increase again (Fig. 5). This relatively higher genetic diversity can then be preserved during population expansion (when populations might be expected to go through a series of bottlenecks with each new colonization event or suffer from gene surfing by deleterious alleles; Edmonds *et al.* 2003), probably as a result of frequent long-distance dispersal events (e.g. Berthouly-Salazar *et al.* 2013).

Based on the evidence we present above, we suggest that the degree to which alien species will show a U-shaped pattern in diversity is dependent on at least two factors: (i) numbers of individuals initially released and (ii) the degree of genetic structure in the native range and how the transport process ‘samples’ this

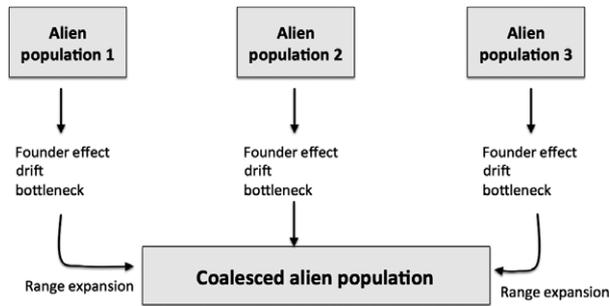


Fig. 5 A visual explanation of the U-shaped genetic diversity pattern shown by Dlugosch & Parker (2008). Multiple, independently founded alien populations lose genetic diversity (the down-slope of the U), but eventually coalesce to form one large, panmictic population, thereby increasing the total genetic diversity (the up-slope of the U). The depth of the U is dependent on the number of individuals released at each location and the degree to which the transport mechanism 'sampled' individuals representing divergent genetic backgrounds.

variation (Fig. 5). These two factors essentially determine the 'down' and 'up' of the U-shape, respectively. All available evidence suggests that the loss of genetic variation at the time of founding is dependent on propagule pressure. This manifests through founder effects and bottlenecks, but can also result from the synergistic effect of these factors dictating long periods of slow population growth leading to drift. Thus, the smaller the propagule pressure for any of the initially established populations of an alien species, the steeper and deeper the drop into the bottom of the U-shape. Once these independently established populations begin to exchange individuals, they establish gene flow, effectively homogenizing any existing differences in genetic variation across populations. If the initial populations are effectively drawn from a single panmictic native source, the rise in diversity in the alien range from gene flow will be minor; gene flow in this case will only be overcoming the effects of randomly sampling alleles from a single large population. However, if the initial populations are founded by individuals taken from across the native range, and there is a high degree of geographic genetic structure in this range, the rise up the U-shape will be steeper. In this case, gene flow effectively represents admixture whereby alleles from divergent sources are intermixing in a single population.

Conclusions

Looking through the older literature on invasions, it is not that surprising that none of the contributors to Baker & Stebbins (1965), or any of the other early works on invasion biology (e.g. Elton 1958; Drake *et al.* 1989),

recognized the importance of numbers of individuals on the dynamics of biological invasions. The arguments we proffer here result from an intense interest in small population dynamics within conservation biology and the ability to track the loss (and gain) of genetic diversity that accompanied transformative genetic technologies. Each of these lines of inquiry really only produced their insights from the late 1980s and early 1990s. What they bring to invasion biology is the fundamental insight that numbers matter at all stages of the invasion process. We have reviewed evidence for these effects above, but we also hopefully have highlighted gaps in our understanding of them, especially as they relate to the influence of genetic diversity. Below we summarize what we see are the three next steps to pushing our understanding past its current position and associated debates.

First, empirical studies clearly show the profound influence that the transportation and release stage of invasions have on the genetic composition of alien species and that the number of individuals transported strongly mediates these effects. However, such studies are few in number, and their insights have not apparently penetrated a good portion of the invasion literature as yet. For example, Dlugosch & Parker (2008) were able to source information on differences in genetic diversity between 80 alien and native populations. They found some consistent patterns, but there was also much variation present. Knowledge of the transport dynamics behind each of these introduction events, including the number of individuals released across spatial and temporal scales, could explain much of this variation. As yet, there have been very few attempts to make these connections. Given the potential for knock-on effects of low genetic diversity across all invasion stages, we suggest that these connections will prove insightful relative to our understanding of invasion dynamics.

Second, the general influence of propagule pressure on establishment success is well supported across species and ecosystems (Lockwood *et al.* 2005; Colautti *et al.* 2006; Hayes & Barry 2008; Simberloff 2009). The more individuals released, the more likely an incipient alien population is to persist. The mechanisms behind this relationship are easy to speculate upon, and we detail them above, but they have only recently been actively under investigation. For example, recent modeling and empirical evidence strongly suggests that the relationship between numbers released and establishment is an increasing but asymptotic function (see e.g. Fig. 2). One under-explored possibility is that variation is influenced by genetic variability on population growth, either manifest as inbreeding depression (very low numbers) or admixture (very high numbers). The

existence and location of these effects would be likely to vary across species, for example according to their life history traits. There is a clear need to explore genetic and other mechanisms behind the role of numbers released on establishment success, including the synergistic interactions of these mechanisms with one another.

Finally, the link between propagule pressure and subsequent invasive spread sits squarely within the realm of genetics. There is some evidence that low genetic variability within an alien population can limit its potential to adapt to novel conditions in the new range, cause lasting negative effects on survival and reproduction or trigger a behavioural change that is maladaptive in the new range. There is also evidence that some invasive populations have benefited from the purging of deleterious alleles as a consequence of passing through a bottleneck at introduction, while some invasive populations have higher genetic diversity than in the native range as a result of admixture and hybridization. There is considerable room for exploration in this area, and we suggest that future investigations explicitly consider the link between 'standing' genetic variation in an alien species and the number of individuals (and the source of these individuals) in producing this variation. Making these connections will provide crucial insight into our basic understanding of the role of genetic variation in species' range sizes, but more practically into our ability to predict which newly introduced alien species may go on to become invasive.

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