

Quantifying invasion risk: the relationship between establishment probability and founding population size

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Summary

1. Invasive species usually start out as small colonizing populations that are prone to extinction through demographic stochasticity and Allee effects, leading to a positive relationship between establishment probability and founding population size. However, establishment success also depends on the environment to which species are introduced: for a given species, some locations will be more favourable for establishment than others.

2. We present equations for modelling the expected relationship between establishment probability and founding population size when demographic stochasticity, Allee effects and, for the first time, environmental heterogeneity are operating.

3. We show that heterogeneity in environmental conditions can change the shape of the relationship between establishment probability and founding population size through a disproportionate decline in the probability of establishment in larger populations, the opposite of an Allee effect. This outcome is likely in most empirical data sets relating founding population size to establishment probability, and highlights that unfavourable environments are often the major cause of establishment failures. It also emphasizes the insights that can be gained from applying models with a theoretical underpinning.

Key-words: propagule pressure, biological invasions, non-indigenous species, colonization success, extinction, small populations, population dynamics

Introduction

Invasive species usually start out as small founding populations introduced to new locations. Only some introductions, however, succeed in establishing as persistent populations; many fail to establish and go extinct (Williamson 1996). For a given species, which outcome occurs depends critically on: (i) the size of the founding population (Lockwood, Cassey & Blackburn 2005; Colautti, Grigorovich & MacIsaac 2006; Hayes & Barry 2008; Simberloff 2009), with small populations facing a greater risk of extinction than large populations due to random fluctuations in size resulting from demographic stochasticity and the potential for Allee effects (Dennis 2002; Lande, Engen & Sæther 2003), and (ii) the suitability of the introduction site, with spatial and temporal heterogeneity in environmental conditions meaning some sites will be more favourable for establishment than others (Rejmánek 1989; Schreiber & Lloyd-Smith 2009).

Demographic stochasticity refers to chance events in survival and reproduction that affect individuals independently, along

with fitness differences among individuals (Engen, Bakke & Islam 1998; Lande, Engen & Sæther 2003; Melbourne & Hastings 2008). Demographic stochasticity causes extinction because chance events in individual survival and reproduction lead to random fluctuations in population size. While demographic stochasticity affects all populations, its contribution to population fluctuations declines rapidly as population size increases because in larger populations individual deviations tend to cancel each other out, meaning the risk of extinction associated with demographic stochasticity is much greater in small relative to large populations (Richter-Dyn & Goel 1972; Grevstad 1999; Dennis 2002; Lande, Engen & Sæther 2003; Drake 2004; Melbourne & Hastings 2008).

Establishment probability is also influenced by Allee effects, whereby *per capita* fitness declines as population size decreases (Odum & Allee 1954; Dennis 1989), reinforcing a positive relationship between founding population size and probability of establishment. Allee effects can arise through a variety of mechanisms, including a decline in fecundity if individuals find it increasingly difficult to find mates as populations shrink, or an increase in mortality if individuals in smaller populations become increasingly vulnerable to predation (Courchamp, Berec & Gascoigne 2008; Gascoigne *et al.* 2009). Sufficiently

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strong Allee effects can lead to a threshold population size below which *per capita* growth rates fall below zero, resulting in populations of this size or smaller having a disproportionately low probability of establishing. This will affect the shape of the relationship between establishment probability and founding population size by creating an inflection point in the curve marking a critical threshold population size, below which establishment becomes much less likely (Dennis 2002; Taylor & Hastings 2005).

Invasions also occur in spatially and temporally heterogeneous environments, and differences among locations in factors such as climate, disturbance, nutrient availability and the presence or absence of predators and pathogens will influence whether introduced species succeed in establishing at some locations but fail at others (Shea & Chesson 2002). Data used to explore the factors that influence establishment success typically document the fate of founding populations that have been introduced to different locations (Cassey *et al.* 2004; Mikheyev *et al.* 2008; Sol *et al.* 2012; Rossinelli & Bacher 2014). While founding population size is often the strongest predictor of establishment success or failure (see reviews in Lockwood, Cassey & Blackburn 2005; Colautti, Grigorovich & MacIsaac 2006; Hayes & Barry 2008; Simberloff 2009), once this has been accounted for environmental factors frequently emerge as important (Duncan *et al.* 2001; Forsyth *et al.* 2004). At a broad scale, species introduced to locations more closely matched climatically to their native range are more likely to establish (Blackburn & Duncan 2001; Bacon *et al.* 2014), an observation that underpins the widespread use of species distribution models to forecast invasion risk (Thuiller *et al.* 2005). Even among seemingly homogenous sites, there can be marked variation in establishment outcomes due to substantial fine-scale heterogeneity in environmental conditions (Minton & Mack 2010).

An issue not widely recognized is that environmental heterogeneity, both among and within populations, will influence the expected relationship between establishment probability and founding population size (Bradie, Chivers & Leung 2013). For a given species, consider the fate of founding populations of different size introduced to separate locations. In the absence of spatial or temporal heterogeneity, all populations will experience the same environment and variation in establishment success should be linked to population size through the effects of demographic stochasticity and Allee effects. Now, consider the same situation but with environmental heterogeneity, such that a proportion of introduction sites are unsuitable for establishment and founding populations will go extinct regardless of their size. This will change the shape of the relationship between establishment probability and founding population size by disproportionately increasing the failure rate in large relative to small founding populations. Small populations will go extinct at unsuitable sites, but a proportion would have failed anyway due to demographic stochasticity and Allee effects. Large populations will also go extinct at unsuitable sites but, in contrast to small populations, a greater

proportion would have succeeded otherwise. This outcome occurs when there is spatial (differences among locations in establishment probability) and/or temporal (variation in establishment probability among years at a given location) heterogeneity in environmental conditions because both forms of heterogeneity will lower establishment success independent of population size (Lande, Engen & Sæther 2003).

Our aim in this study is to model the expected relationship between establishment probability and founding population size, a task central to quantifying invasion risk (Leung, Drake & Lodge 2004; Jerde & Lewis 2007; Bradie, Chivers & Leung 2013). To do this, we use existing theory to derive the expected relationship under different conditions: firstly given demographic stochasticity alone and secondly given demographic stochasticity plus Allee effects. We then derive the expected relationship given demographic stochasticity plus environmental heterogeneity in establishment conditions and show that environmental heterogeneity, which will be present in all empirical data sets, can substantially alter the form of the expected relationship and obscure evidence for Allee effects. The fit of the models to data reveals the importance of environmental heterogeneity, highlighting that introduction to unfavourable environments is a major cause of establishment failures.

Derivation of expected relationships

DEMOGRAPHIC STOCHASTICITY

Consider a population in which the mean instantaneous per capita birth and death rates are the same for all individuals and constant over time. Because small founding populations are likely to be well below carrying capacity, we model population growth as a density-independent process such that the population grows according to

$$N_t = N_0 e^{rt} = N_0 e^{(b-d)t} \quad \text{eqn 1}$$

where N_t is population size after time t , N_0 is the founding population size, b and d are the instantaneous per capita birth and death rates, respectively, and r is the intrinsic rate of population growth ($r = b - d$). We assume that the population grows with expectation given by eqn 1 but is subject to fluctuations in size due to demographic stochasticity, which is captured by modelling births and deaths as stochastic events. This describes a stochastic birth–death model, which is suited to modelling the dynamics of small populations because population size is treated as a discrete variable (Dennis 1989).

If the intrinsic rate of population growth is positive ($b > d$), then a founding population will have one of two outcomes: the population will either grow without bound, which we equate to successful establishment, or it will go extinct with probability $(d/b)^{N_0}$ (Kendall 1948; Dennis 1989; Renshaw 1991). Hence, the probability, P_{Est} , that a founding population of size N_0 will establish given positive population growth (i.e. a location suitable for establishment) and demographic stochasticity is:

$$P_{Est} = 1 - \left(\frac{d}{b}\right)^{N_0} \quad \text{eqn 2}$$

Each individual in a founding population has a potential lineage comprising all descendants of that individual. A population becomes extinct when the lineages of all founding members become extinct or, conversely, a population will establish if at least one individual leaves a surviving lineage (Caswell 2001; Fox 2005). The probability p that an individual leaves a surviving lineage is equivalent to the probability that a single founding individual will establish:

$$p = 1 - \left(\frac{d}{b}\right) \quad \text{eqn 3}$$

Combining equations 2 and 3 leads to an expression for the probability that a founding population will establish assuming independent establishment outcomes for individuals in the population (see Leung, Drake & Lodge 2004; Jerde & Lewis 2007):

$$P_{Est} = 1 - (1 - p)^{N_0} \quad \text{eqn 4}$$

Dennis (2002) presents an alternative derivation of eqn 4 by considering a continuous exponential growth model under a diffusion process with intrinsic rate of population growth r and instantaneous variance v arising from demographic stochasticity. From an analysis of first-passage times, the probability that

a founding population of size N_0 will establish is (see eqn 21 in Dennis 2002):

$$P_{Est} = 1 - e^{-\frac{2rN_0}{v}} \quad \text{eqn 5}$$

Equations 4 and 5 are equivalent if we set $2r/v = -\log(1-p)$ (see Leung, Drake & Lodge 2004).

Risk of extinction due to demographic stochasticity is primarily an issue for small founding populations with extinction probability declining rapidly towards zero as population size increases (Lande, Engen & Sæther 2003). This is shown in Fig. 1a, plotting establishment probability against founding population size for different values of p using eqn 4. All of the lines approach an asymptote at 1, which means that, for a given value of p , there will always be a sufficiently large founding population size beyond which establishment is virtually assured.

DEMOGRAPHIC STOCHASTICITY PLUS ALLEE EFFECTS

Dennis (1989) extended the stochastic birth–death model above to include an Allee effect such that the birth rate at time t is multiplied by a factor $N_t/(\theta + N_t)$. An Allee effect is present when $\theta > 0$ corresponding to a disproportionate decline in birth rate in smaller populations. Incorporating this into the stochastic birth–death model generates the expected relationship between establishment probability and founding population size given demographic stochasticity plus an Allee effect (see eqn 4.18 in Dennis 1989):

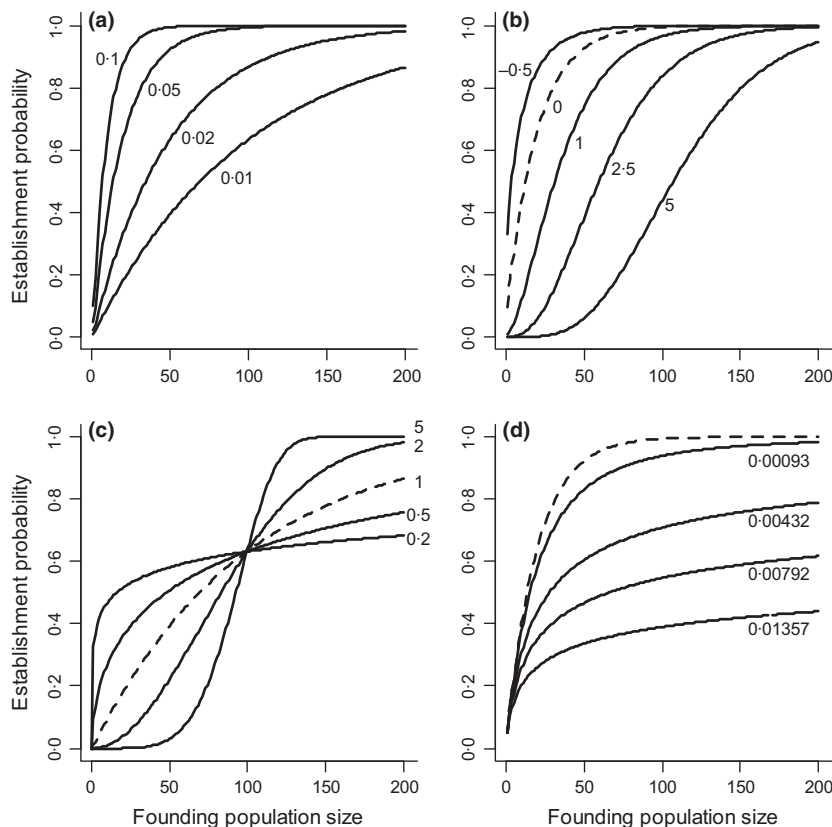


Fig. 1. The expected relationship between establishment probability and founding population size: (a) Under demographic stochasticity (eqn 4) for values of $P = 0.01, 0.02, 0.05$ and 0.1 ; (b) under demographic stochasticity plus Allee effects (eqn 6) for $P = 0.05$ and values of $\theta = -0.5, 0, 1, 2.5$ and 5 . Dashed line is the relationship when $\theta = 0$ corresponding to demographic stochasticity alone; (c) modelled using a Weibull function (eqn 7) with $\alpha = 0.01$ and values of $c = 0.2, 0.5, 1, 2$ and 5 . Dashed line is the relationship when $c = 1$ corresponding to demographic stochasticity alone; (d) under demographic stochasticity plus among-population heterogeneity (eqn 10) for $\bar{p} = 0.05$ and variances $\sigma_{p_1}^2 = 0.00093, 0.00432, 0.00792$ and 0.01357 . Dashed line is the relationship with no among-population heterogeneity ($\sigma_{p_1}^2 = 0$) corresponding to demographic stochasticity alone.

$$P_{Est} = F(N_0, \theta + 1, p) \quad \text{eqn 6}$$

where $F()$ is the cumulative distribution function of a negative binomial distribution with size parameter $\theta + 1$ and probability p . Figure 1b shows how different values of θ alter the relationship between establishment probability and founding population size. A value of $\theta = 0$ is equivalent to demographic stochasticity alone (eqn 4). When $\theta > 0$, there is an inflection in the curve at small population sizes, corresponding to the critical threshold below which populations have a disproportionately lower probability of establishment. Values of $-1 < \theta < 0$ imply the opposite of an Allee effect: a disproportionately lower probability of establishment in larger founding populations (Fig. 1b).

Dennis (2002) suggested modelling Allee effects using a Weibull function to test for an inflection in the curve at small population sizes, an approach adopted by Leung, Drake & Lodge (2004). A Weibull function can be generated from eqn 5 by adding a shape parameter c such that:

$$P_{Est} = 1 - e^{-(\alpha N_0)^c} \quad \text{eqn 7}$$

where $\alpha = 2r/v = -\log(1-p)$ in eqns 4 and 5, respectively. When $c > 1$, the function has a sigmoidal shape similar to eqn 6 with $\theta > 0$ (Fig. 1c). When $c = 1$, the Weibull function simplifies to eqn 5, the relationship under demographic stochasticity alone. Values of $0 < c < 1$ imply the opposite of an Allee effect: a disproportionately lower probability of establishment in larger founding populations. A point of practical importance is that eqn 7 can be rewritten as:

$$\log(-\log(1 - P_{Est})) = c \log(\alpha) + c \log(N_0) \quad \text{eqn 8}$$

This is in the form of a linear model with a complementary log–log link function, with $\log(N_0)$ as the independent variable having slope parameter c and intercept $c \log(\alpha)$. Rearranging the Weibull function as eqn 8 allows us to fit this function to data as a standard generalized linear model.

DEMOGRAPHIC STOCHASTICITY PLUS ENVIRONMENTAL HETEROGENEITY

We have so far modelled the expected relationship between establishment probability and founding population size assuming all populations are governed by the same underlying population growth model. Data on introduction outcomes, however, invariably derive from founding populations introduced to different locations, each of which will have experienced different environmental conditions specific to those locations. This heterogeneity in environmental conditions will mean that the underlying dynamics of each founding population will differ because parameters that affect population growth, such as birth and death rates, will vary from place to place and through time, leading to some locations being more favourable for establishment than others.

We can accommodate heterogeneity in environmental conditions by letting the probability of individual establishment p differ among populations with variation described by a

probability distribution (Bradie, Chivers & Leung 2013). Specifically, we model p_i , the probability of individual establishment in the i th founding population, as drawn from a beta-distribution with parameters α and β :

$$p_i \sim \text{Beta}(\alpha, \beta) \quad \text{eqn 9}$$

The beta-distribution is a natural choice because it constrains p_i to between 0 and 1 (as required for probabilities) and is a flexible distribution able to capture plausible ways in which p_i values might be distributed, including bimodal distributions where some populations have a high and others a low probability of individual establishment.

We can then derive the expected relationship between establishment probability and founding population size. If X_i is the number of individuals in the i th founding population that successfully leave a surviving lineage, then X_i will be binomially distributed with parameters p_i and N_0 . If p_i is beta-distributed, with parameters α and β , then X_i has a compound beta-binomial distribution with parameters N_0 , α and β . From the density function for a beta-binomial distribution, the probability that no individuals establish is $B(\alpha, N_0 + \beta)/B(\alpha, \beta)$, so the probability that at least one individual in a founding population establishes, and therefore that the population succeeds in establishing, is:

$$P_{Est} = 1 - \frac{B(\alpha, N_0 + \beta)}{B(\alpha, \beta)} \quad \text{eqn 10}$$

where $B()$ is the beta-function. From the properties of a beta-distribution, the p_i will have overall mean $\bar{p} = \alpha/(\alpha + \beta)$ and variance $\sigma_{p_i}^2 = \alpha\beta/[(\alpha + \beta)^2(\alpha + \beta + 1)]$.

Figure 1d shows the expected relationship between establishment probability and founding population size under demographic stochasticity plus environmental heterogeneity for fixed \bar{p} but different levels of variation in p_i (obtained by varying α and β in eqn 10). For fixed \bar{p} , greater variation in p_i progressively lowers establishment probability at a given founding population size (Fig. 1d). Under demographic stochasticity alone, extinction is primarily a problem for small founding populations: for a given value of p , there will exist a sufficiently large population size, above which establishment is virtually assured (Fig. 1a). Environmental heterogeneity alters this outcome such that even large founding populations can have a high extinction risk. This occurs because greater heterogeneity in establishment conditions increases the chance of a founding population being introduced to an unfavourable location with a very low probability of individual establishment where populations are likely to fail regardless of their size, disproportionately increasing the failure rate in larger founding populations, the opposite of an Allee effect. Importantly, both spatial and temporal heterogeneity in environmental conditions can produce this outcome because both lower establishment probability regardless of population size (Lande, Engen & Sæther 2003).

We derived eqn 10 explicitly to model the effects of environmental variation on establishment probability. While eqns 6–8 were derived to model Allee effects, they nevertheless can also capture the relationship expected due to environmental

variation, which has a form that is the opposite of an Allee effect (a disproportionate increase in failure rates in larger rather than smaller founding populations). This occurs when $\theta < 0$ for eqn 6, and when $0 < c < 1$ for the Weibull function (Bradie, Chivers & Leung 2013).

Case studies

We fitted these equations to data from two case studies to illustrate how they provide insight into the processes underlying variation in introduction success. The first was a study by Memmott *et al.* (2005) involving 55 experimental introductions of a psyllid biocontrol agent (*Arytainilla spartiophila*) with different founding population sizes (10 introductions of 2, 4, 10, 30 and 90 psyllids and 5 introductions of 270 psyllids; the actual numbers released sometimes differed from these values due to losses associated with transport to the release sites). Introductions occurred at separate release sites located at least 1 km apart, and up to 135 km apart, on South Island, New Zealand. Establishment was deemed successful if psyllids were present when surveyed 5 years after release. We fitted eqns 4, 6 and 10 to these data using maximum likelihood, and the Weibull function as a generalized linear model using eqn 8, in all cases specifying binomial random variation with establishment success or failure as the response variable (see Appendix S1 for R code).

All four models had a comparable fit to the data as judged by the small sample version of Akaike's Information Criterion (AICc: difference between the best and worst fitting model = 5.1, Table 1, Fig. 2). The relationship expected under

Table 1. Fit of different models to the data in Memmott *et al.* (2005) and Sol *et al.* (2012). AIC is Akaike's Information Criterion, and AICc is the small sample version of that. Δ AIC and Δ AICc are the differences in AIC values from the best fitting model for each data set

Model	Equations	AICc	Δ AICc
Memmott <i>et al.</i> (2005)			
Demographic stochasticity	4	69.7	5.3
Demographic stochasticity plus Allee effect	6	64.4	0
Weibull function (Logistic regression + cloglog link)	8	65.0	0.6
Demographic stochasticity plus among-population heterogeneity	10	66.5	2.1
Sol <i>et al.</i> (2012)			
Demographic stochasticity	4	2606.5	1525
Demographic stochasticity plus Allee effect	6	1081.9	0.4
Weibull function (Logistic regression + cloglog link)	8	1081.9	0.4
Demographic stochasticity plus among-population heterogeneity	10	1081.5	0
Sol <i>et al.</i> (2012) Equation 8 + random effects			
Random intercept for species		971.2	
Random intercept & slope for species		971.8	

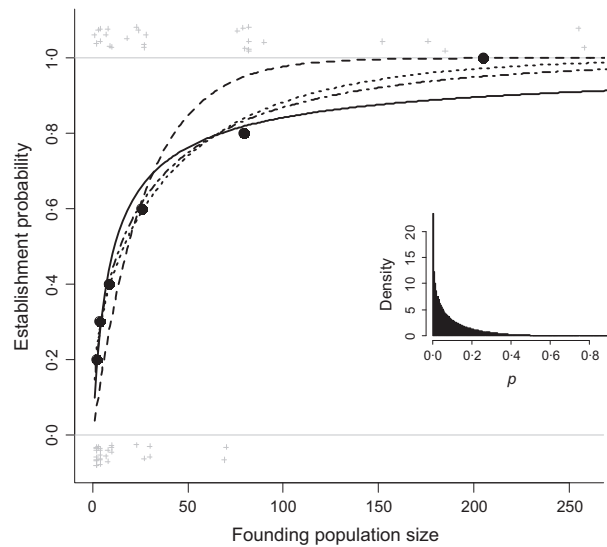


Fig. 2. Data on the outcome of 55 introductions of psyllid populations to New Zealand from Memmott *et al.* (2005). Grey crosses are the raw data showing successful (y -axis values > 1) and unsuccessful (y -axis values < 0) establishment as a function of founding population sizes. Filled circles show the proportion of populations that established for each of the six founding population sizes (2, 4, 10, 30, 90 and 270 individuals). The curved lines show the maximum likelihood fits of different models to the data: dashed line = eqn 4; dotted line = eqn 6; solid line = eqn 10; dotted and dashed line = eqn 8. The inset panel shows the distribution of P values derived from eqn 10.

demographic stochasticity alone (eqn 4) had the poorest fit to the data, while eqn 6 had the best fit. The maximum likelihood value of θ in eqn 6 was < 0 (estimate with 95% confidence interval in square brackets: $-0.54 [-0.89, -0.20]$), implying the opposite of an Allee effect: a disproportionate decline in establishment probability at large population sizes. Equations 8 and 10 fitted the data almost as well as eqn 6 (greatest difference in AICc between these models = 2.1) and were also consistent with a disproportionate decline in establishment probability at larger population sizes: the maximum likelihood value for parameter c in eqn 8 was < 1 (0.55 [0.27, 0.88]), while the distribution of P values estimated from eqn 10 showed substantial variation (inset panel in Fig. 2) with many sites having a very low probability of establishment implying that even large populations would go extinct at some release sites. This fits with the findings in Memmott *et al.* (2005), who observed that introduced populations either went extinct very quickly (within the first year following release, with smaller populations more prone to extinction consistent with demographic stochasticity) or survived, but that some surviving populations subsequently went extinct due to site destruction, which was unpredictable and affected populations regardless of their size.

The second example uses data on the outcome of historical bird introductions from around the world reported in Sol *et al.* (2012). Each observation was the outcome (establishment success or failure) of introducing a species of bird to a particular location, typically a country or large region. We included only observations with data on founding population size, for which

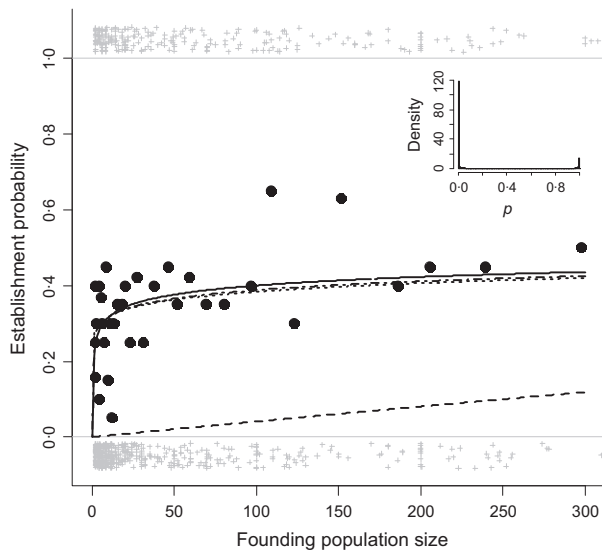


Fig. 3. Data on the outcome of introductions of bird species to locations around the world from Sol *et al.* (2012). Grey crosses are the raw data showing successful (y -axis values > 0.5) and unsuccessful (y -axis values < 0.5) establishment as a function of founding population size. The full data set has 832 observations but only 663 are shown, with the x -axis truncated at a founding population size of 300 individuals to highlight the pattern at small population sizes. Filled circles show the proportion of populations that established for different founding population sizes after population size was ordered and binned into groups each with 20 observations. The curved lines show the maximum likelihood fits of different models to the data: dashed line = eqn 4; dotted line = eqn 6; solid line = eqn 10; dotted and dashed line = eqn 8. The inset panel shows the distribution of P values derived from eqn 10.

there were 832 introductions of 202 species. We expect substantial heterogeneity among populations in individual establishment probabilities because the data are from multiple species and, for many species, multiple introductions each to different locations. There will consequently be at least two sources of among-population variation in individual establishment probability: differences among species (resulting from differences in species-specific demographic parameters and environmental tolerances), and differences among locations within species (due to heterogeneity in environmental conditions). We again fitted eqns 4, 6 and 10 to these data using maximum likelihood, and the Weibull function as a generalized linear model using eqn 8, in all cases specifying binomial random variation with establishment success or failure as the response variable (see Appendix S2 for R code).

The relationship expected under demographic stochasticity alone (eqn 4) fitted the data poorly relative to the other models as judged by AIC (Table 1), while eqns 6, 8 and 10 all fitted the data equally well (greatest difference in AIC between these models = 0.4). The parameter estimates from fitting equations 6, 8 and 10 all implied a disproportionate decline in establishment probability at larger population sizes consistent with substantial among-population heterogeneity in individual establishment probability: the maximum likelihood value of θ in eqn 6 was < 0 (-0.92 [$-0.95, -0.89$]), the value of c in eqn 8 was < 1 (0.11 [$0.06, 0.15$]), and eqn 10 revealed substantial variation in P values among populations, with bimodality in the

distribution indicating that most species at most introduction locations had a very low probability of individual establishment, while a few species were introduced to locations where establishment probability was high (inset panel in Fig. 3). These outcomes were reflected in the shape of the fitted curves (Fig. 3): below about 20 individuals, probability of extinction was strongly linked to founding population size with smaller populations having a higher failure rate, consistent with the outcome we expect due to demographic stochasticity. However, founding populations with between 20 and 300 individuals had a similar probability of establishment (around 0.4) regardless of their size (Fig. 3), implying that processes other than demographic stochasticity and Allee effects, whose influence on establishment probability varies strongly with population size (Fig. 1), were important. Substantial heterogeneity in individual establishment probability could generate this outcome via two processes: (i) species-level differences in individual establishment probability, with some species being inherently poor invaders that failed to establish wherever they were introduced, while others were good invaders with a very high chance of success given founding populations of more than 20 individuals; (ii) heterogeneity in environmental conditions among populations within a species, with some populations being introduced to unfavourable locations, where they failed regardless of population size, while others were introduced to favourable locations where founding populations of more than 20 individuals were likely to succeed.

We can partition these two sources of variation (species-level and population-level heterogeneity) to assess their relative importance: one way to do this is to fit a hierarchical model with species included as a random effect, allowing us to both estimate and account for the among-species variation. While eqn 10 was derived explicitly to model environmental heterogeneity, eqns 6 and 8 fitted the data equally well (Table 1) because both have parameters that allow for a disproportionately lower probability of establishment in larger founding populations. Given that all three equations can capture the form of the relationship, a straightforward approach is to include species as a random effect in eqn 8, which involves fitting a generalized linear mixed model with binomial random variation and a complementary log-log link function, which can be carried out in many standard statistical packages. Equations 6 and 10 are nonlinear and incorporating random effects into these models is not straightforward. We used the ‘lme4’ package in R and compared the fit of two models: the first included a random intercept, and the second a random intercept and a random slope term, for species. Including a random slope term provided no improvement in model fit over a random intercept term alone (increase in AIC = 0.6), but including a random intercept term for species in eqn 8 substantially improved the model fit relative to without (Table 1; reduction in AIC = 110.7). This implies that there is important variation among species in parameter α (a component of the intercept term) but not parameter c (the slope term), which implies significant among-species variation in individual establishment probabilities given that $\alpha = -\log(1-p)$ (Leung, Drake & Lodge 2004).

The level of among-species variation in establishment outcomes (on the complementary log–log scale) is given by the variance term for species in the random effects model, which was 1.68. If this among-species variation accounted for all of the among-population heterogeneity in the data, there would be no further variation in establishment outcomes attributable to environmental heterogeneity, and the relationship between establishment probability and founding population size within species should have the form expected under demographic stochasticity alone along with any Allee effects. That is, having accounted for among-species variation by including species as a random effect in the model, parameter c in eqn 8 should be greater than or equal to one. In contrast, the value of c obtained from the random effects model was still <1 (0.18 [0.12, 0.24]) implying that, having accounted for among-species variation, larger populations still had a disproportionately lower probability of establishment relative to that expected under demographic stochasticity, consistent with significant residual heterogeneity in individual establishment probability that could be attributed to spatial and/or temporal environmental heterogeneity.

Discussion

The relationship between establishment probability and founding population size plays a central role in quantifying invasion risk (Leung, Drake & Lodge 2004; Jerde & Lewis 2007; Bradie, Chivers & Leung 2013): we know, both theoretically and empirically, that larger founding populations are more likely to establish than smaller ones. Indeed, the importance of founding population size in determining invasion outcomes has been the subject of several reviews and it is now recognized that studies routinely need to account for differences in founding population size before considering other factors that might affect establishment success (Lockwood, Cassey & Blackburn 2005; Colautti, Grigorovich & MacIsaac 2006; Hayes & Barry 2008; Simberloff 2009). Our aim was to provide a framework to do this.

Small founding populations face extinction due to demographic stochasticity and Allee effects, and we can derive, from simple population models, the expected relationship between establishment probability and founding population size, given these processes (Fig. 1). We have shown, however, that the presence of spatial and/or temporal heterogeneity in individual establishment probabilities will alter these relationships. Such heterogeneity will be present in data when founding populations are introduced to different locations because local variation in environmental conditions will result in some locations being more favourable for establishment than others. Among-population heterogeneity will also be present in introduction data comprising multiple species due to species-level differences in establishment probability linked to life-history traits and environmental tolerances (Bradie, Chivers & Leung 2013). Empirical data documenting the establishment success or failure of founding populations invariably have one or both of these characteristics and are therefore appropriately analysed using models that allow for among-population heterogeneity.

We derived eqn 10 explicitly for this purpose, but eqn 6 and the Weibull function (eqns 7 and 8) also capture the expected relationship. All three functions provided a similar fit to the data in the two case studies we analysed, and a decision about which to use may depend on the goals of analysis and the ease of fitting. Equation 10 has the advantage of a mechanistic underpinning, and the resulting parameters can be used to infer the distribution of p values (see insets in Figs 2 and 3), which has a direct ecological interpretation. The Weibull function has the advantage of being easy to fit using standard statistical software when expressed in the form of a generalized linear model (eqn 8), and further allows for straightforward partitioning of other sources of variation when these can be included as random effects in a generalized linear mixed model.

Empirical studies analysing the relationship between establishment probability and founding population size have often fitted logistic regression models principally, it seems, because this is a standard way to analyse binary response data (establishment success or failure) rather than because there is an underlying theoretical basis for its use (e.g. Forsyth & Duncan 2001; Drake, Baggenstos & Lodge 2005; Mikheyev *et al.* 2008; Sol *et al.* 2012; Britton & Gozlan 2013). Nevertheless, our results point to logistic regression as a reasonable approach if founding population size is log-transformed. The Weibull function (eqns 7 and 8) can capture the relationship expected under demographic stochasticity alone ($c = 1$), under demographic stochasticity plus Allee effects ($c > 1$) and under demographic stochasticity plus among-population heterogeneity ($0 < c < 1$). With among-population heterogeneity present, the Weibull function fitted the data for the two case studies about as well as eqn 10, which was derived specifically to model this process. When expressed as a generalized linear model (eqn 8), the only difference between fitting a Weibull function and a logistic regression model is replacement of the complementary log–log link with the logit link in the latter. This change in link function may be relatively inconsequential to the model fit, so that in many cases a logistic regression model may provide a similar fit to the data and capture the essential form of the relationship given by eqn 8. For the Memmott *et al.* (2005) data, using a logit link in eqn 8 fitted the data about as well as using a complementary log–log link (AICc = 66.0 and 65.0, respectively), while for the Sol *et al.* (2012) data using a logit link provided a better fit than a complementary log–log link (AIC = 964 and 971, respectively).

Nevertheless, a major advantage of using a complementary log–log link is that the parameters of the fitted model can be interpreted directly in terms of the underlying processes of interest (e.g. the presence of an Allee effect, or among-population heterogeneity depending on the value of parameter c , and the probability of individual establishment for parameter α). The parameters of a logistic regression do not have such a direct interpretation. This is one reason to favour models with a theoretical underpinning: they can provide additional insights into underlying processes. In the case of bird introductions, we could infer that, having accounted for differences among-species in their probability of establishment, larger

founding populations still had a disproportionately lower probability of establishment, consistent with spatial variation in the suitability of sites for establishment and/or temporal variation in establishment conditions (Fig. 1d; Lande, Engen & Sæther 2003). Similar results were obtained in a recent study on parasitic wasps released for biological control (Rossinelli & Bacher 2014).

Moreover, the results imply that such environmental heterogeneity was a major driver of variation in establishment outcomes for birds. While demographic stochasticity could explain the sharp decline in establishment probability in small founding populations (below about 20 individuals), in larger populations establishment probability increased only slowly with founding population size (e.g. the predicted probability of establishment for founding populations of size 100, 1000 and 10 000 was 0.29, 0.41 and 0.55, respectively, having accounted for among-species variation in the random effects model). This abrupt flattening of the curve in populations of >20 individuals is not what we would expect if demographic stochasticity was driving extinctions and implies that the success or failure of most founding populations of more than 20 individuals was driven by factors largely unrelated to their initial size. The implication is that a major cause of establishment failure in birds was that many species were introduced to unfavourable locations where individual establishment probability was low, and this barrier could not be overcome by even large increases in founding population size. The distribution of individual establishment probabilities derived from eqn 10 reinforces this point (see inset panel in Fig. 3), showing that most introductions were to locations with a very low probability of individual success.

Finally, fitting either the Weibull function or eqn 6 has been suggested as a way to test for the presence of Allee effects in introduction data (Dennis 1989; Leung, Drake & Lodge 2004). An Allee effect manifests as an inflection in the curve marking where establishment probability is disproportionately reduced at small population sizes (Dennis 2002; Taylor & Hastings 2005). The outcome we observed in the two case studies was opposite to this: a disproportionate reduction in establishment probability at larger, not smaller, population sizes arising from among-population heterogeneity (see also Bradie, Chivers & Leung 2013; Rossinelli & Bacher 2014). This does not imply that Allee effects were absent in these data, rather that eqn 6 and the Weibull function cannot simultaneously model both an Allee effect (positive density dependence) and among-population heterogeneity (equivalent to negative density dependence) because both equations use a single parameter to specify a pattern consistent with either positive or negative density dependence, but not both. The parameter value, and thus the form of density dependence specified, is likely to reflect the dominant signal in the data. Given that among-population heterogeneity is a feature of introduction data, using these data to test for Allee effects will require modelling the two processes independently.

Contribution

All authors conceived the study. RD derived the equations and performed the analyses. RD wrote the first draft of the manuscript, and all authors contributed substantially to revisions.

Acknowledgements

We thank Jane Memmott for providing us with the original data on psyllid release sizes shown in Fig. 2.

Data accessibility

The data used to construct Fig. 2 were from Memmott *et al.* (2005) and are provided in Appendix S1. The data used to construct Fig. 3 were from Sol *et al.* (2012) and can be downloaded at <http://www.sciencemag.org/content/337/6094/580/suppl/DC1>.

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Received 16 April 2014; accepted 7 October 2014

Handling Editor: Robert Freckleton

Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. Data and R code to produce Fig. 2.

Appendix S2. R code to produce Fig. 3.