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How propagule size and environmental suitability jointly determine establishment success: a test using dung beetle introductions

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Abstract Both the size of founding populations (propagule size) and environmental suitability are known to influence whether a species newly introduced to a location will establish a self-sustaining population. However, these two factors do not operate independently: it is the interaction between propagule size and environmental suitability that determines the probability an introduced population will establish. Here I use the example of dung beetle introductions to Australia to illustrate the importance of this interaction. I first describe equations that model establishment success jointly as a function of propagule size and environmental suitability. I then show how these equations provide insight into the different outcomes observed in two dung beetle species widely introduced to Australia. In one species, variation in propagule size had relatively little influence on establishment success due to large variation in environmental suitability, leading to an essentially bimodal outcome: sites were either very suitable for establishment and introductions succeeded, or sites were unsuitable and introductions failed regardless of propagule size. For the second species, there was much less variation among locations in environmental suitability, leading to propagule size having a strong influence on establishment success. These examples highlight how the interaction between environmental suitability and founding population size is central to determining the probability an introduced species will establish.

Introduction

Two factors play a key role in determining whether a species newly introduced to a location will establish a self-sustaining population. First, is the degree to which the environment at the introduction site is suitable for the species that is introduced. Spatial variation in climate, the availability of resources, and the presence of predators and competitors mean that some sites will be more suitable for the persistence of a given species than others (Rejmánek 1989; Blackburn and Duncan 2001; Peterson 2003). Temporal variation in these factors may also mean that at a given site some time periods are more favourable for establishment than others (Davis et al. 2000; Shea and Chesson 2002). Second, the size of the introduced founding population (propagule size) plays a role because stochastic processes result in population size fluctuations, which are more likely to lead to establishment failure (i.e., local extinction) in small relative to large founding populations (Lande 1993; Grevstad 1999a; Fauvergue et al. 2012; Duncan et al. 2014).

Importantly, it is the interaction between these two factors that is central to understanding how and why introduced species establish (D'Antonio et al. 2001; Rouget and Richardson 2003; Leung and Mandrak 2007; Miller et al. 2014). This is because the relationship between founding population size and establishment probability can vary as a function of environmental suitability: at locations where suitability is high few founding individuals may be required for a population to establish, while more individuals are required for success at sites of low suitability. This will cause the shape of the relationship between establishment success and founding population size to vary as a function of environmental conditions, and it is the resulting interaction between these factors that determines the probability of population establishment (D'Antonio et al. 2001). Although this interaction has been identified and modelled using species occurrence data (Rouget and Richardson 2003;

Leung and Mandrak 2007; Eschtruth and Battles 2011) no studies have clearly demonstrated its importance for population establishment in the field. Studies of plant populations have shown that the form of the relationship between the number of seeds added to plots (initial population size) and the number of seedlings that recruit varies depending on environmental conditions (Thomsen et al. 2006; Miller et al. 2014) but these studies have not assessed population establishment. Greenhouse and laboratory studies of insect introductions have shown strong effects of both founding population size and environmental suitability on establishment success, but no evidence of a significant interaction between the two (Hufbauer et al. 2013; Szűcs et al. 2014).

My aim in this paper is to use the outcome of dung beetle introductions to Australia to demonstrate the importance of the interaction between founding population size and environmental suitability in explaining population establishment. Dung beetles were purposefully introduced to Australia to speed up recycling of cattle dung in pastures and rangelands. Records documenting the outcome of these introductions provide a unique opportunity to test models of population establishment because data on founding population size and establishment success are available for numerous introductions at release sites spanning a wide range of environments. In addition, there have been recent advances in developing models that capture how environmental suitability and founding population size should jointly determine establishment success (Leung et al. 2004; Leung et al. 2012; Duncan et al. 2014). Because these models have a basis in demographic theory (Duncan et al. 2014) they can potentially provide new insights into the processes underpinning population establishment. This is particularly relevant to insect biocontrol introductions where establishment success rates have been low (Beirne 1985). Uncovering the reasons for establishment failure can inform future release programmes as well as providing fundamental insights into what drives population establishment (Fauvergue et al. 2012).

A framework for jointly modelling propagule size and environmental variation

Small founding populations are prone to extinction due to fluctuations in size resulting from demographic and environmental stochasticity. From a simple model of population growth in which fluctuations in population size result from demographic stochasticity alone, we can derive an equation for the probability, P_{Est}, that a founding population will establish based on the number of individuals in the founding population, N_0, and the probability that a single founding individual will establish by producing a surviving lineage, p (Leung et al. 2004; Duncan et al. 2014):

$$P_{\mathrm{Est}} = 1 - (1 - p)^{N_0} \tag{1}$$

Environmental variation will also affect founding populations in at least two ways. First, for a given species spatial variation in factors such as climate, resource availability, and the presence of competitors and predators, will mean that some locations are more suitable for establishment than others, such that p differs from place to place. Second, at a given location environmental conditions, and thus p, can vary through time, such that populations could fail to establish at otherwise suitable locations due to unfavourable conditions at the time of introduction. Spatial and temporal variation in environmental conditions thought to affect establishment probability can be included in equation 1 by modelling p as a function of environmental covariates (Leung and Mandrak 2007; Leung et al. 2012). While modelling spatial variation in environmental suitability is often straightforward, modelling temporal variation is harder because we often lack data on how the environment has varied over time at a given location, and thus the conditions that an introduced population encountered at the time of introduction (but see Norris et al. 2002).

A second approach to incorporating environmental variation is to specify a more general model that allows for variation in p, both spatially and temporally, that is captured using a probability distribution. If variation in p can be described with a beta distribution, having parameters α and β, then we can derive from equation 1 the probability that a founding population will establish given both demographic stochasticity and environmental variation (Duncan et al. 2014):

$$P_{\mathrm{Est}} = 1 - \frac{\mathrm{B}(\alpha, N_0 + \beta)}{\mathrm{B}(\alpha, \beta)} \qquad (2)$$

where B( ) is the beta function, and p is drawn from a beta distribution with mean $\bar{p} = \alpha / (\alpha + \beta)$ and variance $\sigma_p^2 = \alpha\beta / [(\alpha + \beta)^2(\alpha + \beta + 1)]$. Here, $\bar{p}$ could be considered the average environmental suitability of a location, which we can model as a function of environmental covariates. The advantage of equation 2 over equation 1 is that by including the variance term we capture any additional environmental variation, both spatial and temporal, not captured by the environmental covariates. Hence, when there is important variation in establishment conditions not accounted for by measured environmental variables, we expect equation 2 to provide a better fit to the data than equation 1.

Fitting these equations to data requires observations on the outcome of introductions (whether a population established or not) to different locations, and associated data on founding population size (N_0) and environmental characteristics. To make the link between data and model more concrete, I illustrate this approach using dung beetle introductions to Australia as an example. My aim is not to explore in detail the environmental conditions favouring population establishment in dung beetles. Rather it is to show how the framework described above can be used to model establishment as the joint outcome of founding population size and differences among sites in environmental suitability, and to highlight the importance of the interaction between these two factors. To do this I focus on modelling how establishment success varies along a single environmental gradient.

Methods

I used data on the outcome of dung beetle introductions to Australia that occurred between 1969 and 1984 (Tyndale-Biscoe 1996). During this period the Commonwealth Scientific and Industrial Research Organisation (CSIRO) in Australia carried out continent-wide introductions of dung beetles with the aim of establishing populations in pasture and rangelands to speed up the process of cattle dung recycling. Forty-three species of dung beetle were imported to Australia, primarily from South Africa, reared in the laboratory and then introduced into the wild. Introductions involved releasing a species at a site, with founding populations ranging in size from 4 to 7380 individuals.

I analysed introduction data for two species, *Onthophagus gazella* and *Onitis alexis*, with these species chosen to illustrate different ways in which environmental suitability and founding population size can interact to determine population establishment. I extracted the 391 records for these two species for which the location (latitude and longitude), outcome of the introduction (whether the population established or not), and the number of individuals in the founding population were recorded. Dung beetle introduction sites were usually revisited on several occasions following release to monitor the outcome, with the average time between introduction and last site visit being just over 4 years. If a species was found at the introduction site during the last visit, I scored the introduction as successful (the population established); if absent, I scored the species as having failed to establish at that location.

Differences in site suitability based on climate are potentially important in determining whether dung beetle populations established or not because releases occurred across Australia (Fig 1) at locations spanning a wide range of climates from tropical to cool temperate to arid. In addition, other factors that might have limited distribution were controlled for: released individuals were free from parasites and diseases because laboratory reared populations were carefully screened for these, and beetles were released at locations where their primary resource, dung, was abundant (Duncan et al. 2009). I therefore focussed on quantifying how establishment success varied along climatic gradients.

To quantify climatic conditions at each introduction site, I extracted climate data from a global meteorological dataset that gridded the world into 10' x 10' latitude–longitude grid cells (New et al. 2002). This dataset contained mean monthly values for a range of meteorological data, including temperature and precipitation, for each grid cell. I converted these monthly values into 16 variables that are commonly used in ecological studies to characterize climate at a given location: mean annual temperature; temperature of the coolest month; temperature of the warmest month; annual temperature range; mean temperature of the coolest quarter; mean temperature of the warmest quarter; mean temperature of the wettest quarter; mean temperature of the driest quarter; annual precipitation; precipitation of the wettest month; precipitation of the driest month; coefficient of variation of monthly precipitation; precipitation of the wettest quarter; precipitation of the driest quarter; precipitation of the coolest quarter; and precipitation of the warmest quarter. Each dung beetle introduction site was assigned the climate variables associated with the 10' x 10' grid cell in which the release took place.

For each species, I identified the climate variable that best explained whether dung beetle introductions succeeded or failed to establish. To do this, I fitted logistic regression models with establishment success or failure as the response variable and each of the 16 climate variables (log transformed) as univariate explanatory variables, and chose the climate variable that produced the lowest model AIC. My aim here was to identify a single climate gradient along which establishment probability varied so I could explore the interaction between climate suitability, founding population size and establishment success.

I fitted equations 1 and 2 to the data for each species to model the relationship between establishment probability and founding population size (propagule size models), with the response variable being whether an introduction with founding population size N_0 established or not. I fitted these models using maximum likelihood, treating establishment outcome as a Bernoulli random variable. Equation 2 has two unknown parameters, α and β, and it is helpful to reparameterise these in terms of the mean probability of establishment, $\bar{p} = \alpha / (\alpha + \beta)$, and a precision parameter, $\phi = \alpha + \beta$, where smaller values of ϕ imply higher variance because $\sigma_p^2 = \bar{p}(1 - \bar{p}/(1+\phi))$ (Ferrari and Cribari-Neto 2004).

I included climate as a covariate by modelling either p (equation 1) or $\bar{p}$ (equation 2) as a function of the climate variable selected for each species, using a logit transformation to constrain p to between zero and one:

$$\log\left(\frac{\bar{p}}{1-\bar{p}}\right) = \beta_0 + \beta_1 \log(\text{climate parameter}) \tag{3}$$

I jointly modelled the effects of founding population size and climate (propagule size + climate models) by combining either equations 1 & 3 or equations 2 & 3. The model combining equations 1 & 3 has two unknown parameters: β_0 and β_1 are intercept and slope terms, respectively, describing how the probability of individual establishment varies with respect to the climate variable on the logit scale. The model combining equations 2 & 3 has a precision parameter, ϕ, which allows for additional variation in p not accounted for by the climate variable.

For each species, I used AIC to compare the fit of six models to the data, with the best-fitting model having the lowest AIC (Burnham and Anderson 2001). I included a logistic regression model with no explanatory variables (intercept only) as a null model for comparison, which models establishment probability as the same across all sites. The other five models were: the two propagule size models (eqns. 1 & 2); a logistic regression model that included the climate variable (intercept + climate) to assess the importance of climate suitability alone; and the two joint models in which propagule size and climate interact because the influence of one variable depends on the magnitude of the other: propagule size + climate (eqns. 1 & 3) and propagule size + variability + climate (eqns. 2 & 3).

AIC allows the fit of different models to the data to be compared but does not evaluate overall model performance. A model can have low AIC relative to other models but still fit the data poorly. I used the area under the curve of the receiver operating characteristic plot (AUC) to assess the ability of each model to correctly discriminate establishment success from failure. An AUC value of 0.5 indicates a model performs no better than chance, while a value of 1 indicates perfect discrimination (Swets 1988). I interpreted AUC values following the recommendation in Araujo et al. (2005) as: excellent AUC >0.90; good 0.80> AUC <0.90; fair 0.70> AUC <0.80; poor 0.60> AUC <0.70; fail 0.50< AUC >0.60.

In all cases the response variable was whether introductions of each species established or not and climate variables were log-transformed. The logistic regression models were fitted in R version 3.1.2 (R Development Core Team 2013) using the function ‘glm’, while the propagule size and propagule size + climate models were fitted in R using maximum likelihood with function ‘optim’.

Results

There were 293 introductions of *Onthophagus gazella* of which 223 established (success rate = 0.76) with a marked geographical pattern to the distribution of successes and failures: below 30 degrees latitude most introductions failed (success rate: 29/88 = 0.33), while above 30 degrees latitude most succeeded (success rate: 194/205 = 0.95; Figure 1). *Onitis alexis* had fewer introductions (98) and a lower overall success rate (46/98 = 0.47), with no clear geographical pattern to the distribution of successes and failures.

Propagule size models

Introductions of *O. gazella* involved founding populations ranging in size from 53 to 7380 individuals. Equation 1 (propagule size with demographic stochasticity alone) provided a poor fit to the data relative to equation 2 (propagule size with demographic stochasticity and environmental variability; see Table 1). Nevertheless, the fit of equation 2 revealed that establishment probability was only weakly related to propagule size, such that small founding populations had a similar probability of establishment to large ones (Figure 2a). Indeed, the AUC value for equation 2 (0.55) indicated a failure to discriminate establishment success and this model had an almost identical AIC to the null intercept model (Table 1), implying that propagule size explained little variation in establishment outcomes. The α and β parameters in equation 2 describe the beta distribution of p values most consistent with the data. This distribution was bimodal (Fig 2c), implying that most locations had either a very high or low probability of individual establishment success.

Introductions of *Onitis alexis* involved founding populations ranging in size from 60 to 2000 individuals. Fitting equations 1 or 2 to these data lowered AIC by at least 9 points relative to the null intercept model (Table 1), suggesting propagule size had significant explanatory power with larger founding populations having a higher probability of establishment (Fig. 2b). Equations 1 and 2 provided a similar fit to the data (difference in AIC = 2.4) implying that patterns in establishment success were consistent with the outcome we would expect under demographic stochasticity alone without additional environmental variability, although the AUC values for both models indicated a poor ability to discriminate establishment success from failure. The distribution of p values from equation 2 most consistent with the data implied that all locations had a relatively low probability of individual establishment: the mean value of p was 0.0019 with most values <0.004 (Fig 2d).

Climate models

The climate variable most strongly related to introduction outcome for *Onthophagus gazella* was mean temperature of the wettest quarter. In contrast to propagule size this was strongly linked to establishment success (Fig. 3a) with inclusion of this variable resulting in a substantial reduction in AIC (Table 1; the AIC of the intercept + climate model is almost 100 less than the intercept and propagule size models, implying a much better fit to the data) and an AUC value of 0.96, indicating an excellent ability to discriminate establishment success from failure. There was a sharp transition in establishment success along the temperature gradient: at mean temperatures below 15 degrees all 37 introductions of *O. gazella* failed, while at mean temperatures above 25 degrees all 172 introductions succeeded (Fig. 3a).

The climate variable most strongly related to introduction outcome for *Onitis alexis* was annual rainfall. Inclusion of this variable reduced AIC by 3.5 relative to the null intercept model, suggesting relatively weak explanatory power, reinforced by an AUC value of 0.64 indicating a poor ability to discriminate. Nevertheless, the 95% confidence interval (CI) for the rainfall parameter excluded zero (on the logit scale, parameter estimate and [95% CI] = -1.37 [-2.61 to -0.22]), with lower annual rainfall associated with a higher probability of establishment (Figure 3b).

Joint models

Equations that jointly modelled the effect of propagule size and climate provided the best fit to the data for both *Onthophagus gazella* and *Onitis alexis* as judged by both AIC and AUC (Table 1). For *Onthophagus gazella* eqns. 2 & 3 fitted the data substantially better than eqns.

1 & 3 (difference in AIC = 44.8) implying that inclusion of the precision term to model additional environmental variability was important, although this resulted in only a slight increase in AUC (Table 1). For *Onitis alexis*, in contrast, the model without additional environmental variability (eqns. 1 & 3) provided an almost identical fit to the data as the model with this variability (eqns. 2 & 3), with both models having a fair ability to discriminate establishment success from failure (AUC 0.72-0.73).

Fitting eqns. 2 & 3 to the data revealed how individual establishment probabilities changed along the climate gradients (Fig. 4a, c). For *Onthophagus gazella,* individual establishment probability was close to zero at locations with a mean temperature of the wettest quarter less than about 15 degrees, but increased sharply at higher mean temperatures. For *Onitis alexis,* individual establishment probability was low across the rainfall gradient, increasing slightly at locations with lower annual rainfall. The slope parameter β_1 in equation 3 describes the extent to which individual establishment probability varies with respect to the climate parameters. For both species, the 95% CI for this parameter excluded zero (on the logit scale) in all joint models, implying we can be confident that suitability for establishment varied along these climate gradients (for *Onthophagus gazella*: slope parameter = 8.6 [2.7 to 14.5], for *Onitis alexis* slope parameter = -1.14 [-2.11 to -0.17]; 95% CI calculated from 1000 bootstrap samples using eqns. 2 & 3).

Figures 4c & d show how founding population size and climatic conditions together determine establishment probability using the parameter estimates from the propagule size + variability + climate models (eqns. 2 & 3). Fig. 4d illustrates how establishment probability can depend on the interaction between environment and propagule size. At low propagule sizes, for example, establishment probability for *Onitis alexis* varied little along the rainfall gradient but was more strongly dependent on rainfall at larger propagule sizes.

Discussion

This study highlights the importance of understanding the interaction between propagule size and environmental suitability in determining the likelihood that an introduced species will establish at a new location. While variation in the size of founding populations, and measures related to this, are often among the strongest predictors of introduction outcomes (Cassey et al. 2005; Lockwood et al. 2005; Simberloff 2009), not all studies show strong effects of propagule size on establishment success (Schoener and Schoener 1983; Nuñez et al. 2011). This might be expected where environmental variation is sufficiently large to overwhelm the effects of differences in founding population size. In the case of *Onthophagus gazella* there was no apparent effect of propagule size on establishment probability (Fig 2a) due to the sharp gradient in environmental suitability associated with mean temperature, such that most introductions were to locations where individuals had either a very high or low chance of establishing. Introductions to locations with very low individual establishment probability were assured of failure, while introductions to sites with high individual establishment probability were virtually assured of success independent of founding population size across the range of propagule sizes in this study. For *Onthophagus gazella* this meant there was only a narrow window in mean temperature of the wettest quarter, somewhere in the range 15-20 degrees C, where individual establishment probability was neither too low nor too high to essentially guarantee an outcome, and hence where variation in propagule size could have a measurable effect, although this effect was evident only at small propagule sizes (Fig. 4c). The observation that even large founding populations still had a relatively low probability of success at sites with intermediate mean temperatures (Fig. 4c) suggests the influence of an additional unknown or stochastic environmental variable, which was reflected in the model including environmental variability (eqns. 2 + 3) being the best-fitting (Table 1).

For *Onitis alexis*, in contrast, environmental suitability was low, but not so low as to ensure failure, across all locations, meaning that differences in propagule size then had a measureable effect on the probability of establishment (Fig 2b). These outcomes are contingent on the range of propagule sizes included in this study (50 – 7380 individuals). We might have expected a relationship between establishment probability and propagule size to have been more apparent given a greater range in propagule sizes, particularly if smaller founding populations had been included.

The extent to which establishment outcomes appear strongly governed by environmental conditions is likewise dependent on the interplay between environmental variation and propagule size (D'Antonio et al. 2001; Eschtruth and Battles 2011). Among locations, establishment success may be only weakly linked to environmental suitability if propagule sizes are small because at low propagule size stochastic fluctuations can be a major cause of extinction, such that populations fail regardless of how suitable the environment is. This was evident for *Onitis alexis* where, at low propagule sizes establishment probability varied little along the rainfall gradient but was more strongly dependent on rainfall at larger propagule sizes (Fig 4d). Similarly, at very high propagule sizes founding populations may be large enough to ensure success at all locations despite substantial differences in environmental suitability. This occurs when sheer weight of numbers can essentially guarantee that at least one founding individual in a population will establish even at sites of low suitability (Von Holle and Simberloff 2005; Hollebone and Hay 2007). Consequently, the environmental factors most strongly governing site suitability and establishment success may be most apparent at intermediate levels of propagule size.

A take-home message is that the outcome we observe - whether introduced populations establish at some locations but not others – is highly dependent on the interplay between environmental suitability and propagule size (D'Antonio et al. 2001; Rouget and

Richardson 2003; Thomsen et al. 2006). Furthermore, the outcome of this interplay is species-specific and contingent on both the range of environments sampled, and hence the extent to which locations differ in suitability, and the range of propagule sizes included in the study (Fig. 4). Depending on the combination of these factors different studies could find weak or strong effects of propagule size, and/or weak or strong effects of environmental conditions on establishment outcomes. Given this, our approach should switch from seeking correlates of establishment success using standard additive models, where the aim is often to identify a subset of statistically significant explanatory variables, to fitting models that explicitly capture the manner in which variables such as environmental suitability and propagule size interact to jointly determine establishment outcomes. Models that aim to capture these processes, including equations 2 and 3, provide a way to reconcile the conflicting findings of different studies and to develop better predictive tools to describe the outcomes we expect under a wide range of conditions (Leung and Mandrak 2007; Bradie et al. 2013; Duncan et al. 2014).

Equation 2 alone contains information on the importance of environmental variability in the expected distribution of p values as measured by parameters α and β. For *Onthophagus gazella* this distribution was bimodal, implying that most introductions occurred at sites with either high or low suitability, reflected in the steep gradient in individual establishment probability associated with variation in mean temperature in the wettest quarter (Figs. 3a, 4a). For *Onitis alexis* the distribution of p values implied that most locations had low suitability with little variation among them, reflected in a comparatively low probability of individual establishment across the annual rainfall gradient with no sharp transitions. Hence, even in the absence of environmental data that might underlie variation in introduction outcomes, equation 2 alone can reveal important information about variation in environmental suitability among locations.

I have focused on how demographic stochasticity, environmental variation, and founding population size affect establishment success. In addition, Allee effects can play a critical role in the dynamics of small founding populations (Dennis 2002; Courchamp et al. 2008; Fauvergue et al. 2012). Allee effects arise when individual fitness declines with decreasing population size (Odum and Allee 1954; Stephens et al. 1999), which means the probability of individual establishment, *p*, will vary with founding population size, being lower in smaller populations. Sufficiently strong Allee effects will cause the relationship between founding population size and establishment success to be sigmoidal, with an inflexion point defining a critical size threshold below which founding populations have a much lower probability of establishing (Dennis 2002; Taylor and Hastings 2005). The joint models I fitted can in principle detect an Allee effect but only in the absence of strong environmental variation (Duncan et al. 2014), which was not the case here. A more complex model would be needed to simultaneously model the effects of founding population size, environmental variation and Allee effects on population establishment. Even then, detecting Allee effects in the dung beetle data could be challenging given the lack of small founding populations (<50 individuals) where we expect Allee effects to be strongest.

Previous studies have shown that propagule size is an important factor determining whether insect populations establish following introduction to new locations (Beirne 1985; Hopper and Roush 1993; Grevstad 1999b; Memmott et al. 2005). The results of this study extend these findings to show that, for a given species, the relationship between propagule size and establishment probability is not fixed but will between locations depending on environmental suitability. This understanding could help improve the outcome of intentional insect introductions for biocontrol purposes by matching propagule size with site conditions to ensure a desired probability of success given a limited number of individuals for release. It also provides a promising way to incorporate demographic processes into species distribution models by explicitly modelling the interaction between propagule availability and environmental suitability (Guisan and Thuiller 2005).

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Table 1. Comparison of the fit of six candidate models to data on establishment success or failure for two dung beetle species introduced to Australia. *n* is the number of parameters estimated in each model, AIC is the Akaike Information Criterion measuring the fit of each model to the data, with smaller values indicating a better fit, ΔAIC is the difference in AIC between each model and the best fitting model in the candidate set (highlighted in bold for each species), and AUC is the area under the curve of the receiver operating characteristic plot.

Species	**Model**	***n***	**AIC**	**ΔAIC**	**AUC**
Onthophagus gazella	Intercept	1	324.2	202.4	0.5
	Propagule size (eqn. 1)	1	391.0	269.2	0.55
	Propagule size + variability (eqn. 2)	2	324.4	202.6	0.55
	Intercept + climate	2	124.7	2.9	0.96
	Propagule size + climate (eqns. 1 + 3)	2	165.9	44.1	0.94
	Propagule size + variability + climate (eqns. 2 + 3)	3	**121.8**	**0**	**0.96**
Onitis alexis	Intercept	1	137.5	15.9	0.5
	Propagule size (eqn. 1)	1	125.7	4.1	0.65
	Propagule size + variability (eqn. 2)	2	128.1	6.5	0.65
	Intercept + climate	2	134.0	12.4	0.64
	Propagule size + climate (eqns. 1 + 3)	2	**121.6**	**0**	**0.73**
	Propagule size + variability + climate (eqns. 2 + 3)	3	121.8	0.2	0.72

Figure Captions.

Fig. 1 Locations where introductions of *Onthophagus gazella* and *Onitis alexis* occurred in Australia between 1969 and 1984. The maps marked Successful show where introduced populations established following release, the maps marked Failed show where introduced populations failed to establish. The dotted line is at latitude 30 degrees south.

Fig. 2 (a), (b) Data on the outcome of introductions of *Onthophagus gazella* and *Onitis alexis* to Australia in relation to propagule size. 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 size. Filled circles show the proportion of introductions that established for different propagule sizes after propagule size was ranked and binned into groups. The dashed lines show the maximum likelihood fits of equation 1 to the data, and the solid lines show the maximum likelihood fits of equation 2. **(c), (d)** The distribution of p values (the probability a single individual leaves a surviving lineage) derived from parameters α and β in equation 2.

Fig. 3 (a), (b) Data on the outcome of introductions of *Onthophagus gazella* and *Onitis alexis* to Australia in relation to climate variables. Grey crosses are the raw data showing successful (y-axis values > 1) and unsuccessful (y-axis values < 0) establishment as a function of climate variables. Filled circles show the proportion of introductions that established for different values of each climate variable after each climate variable was ranked and binned into groups each with 20 observations. The solid lines show the fit of logistic regression models to the data.

Fig. 4 (a), (b) The relationship between invasibility and climate variables for *Onthophagus gazella* and *Onitis alexis* and: **(c), (d)** Probability of establishment as a function of both climate and propagule size from the fit of equations 2 and 3 to the data.

Figure 1

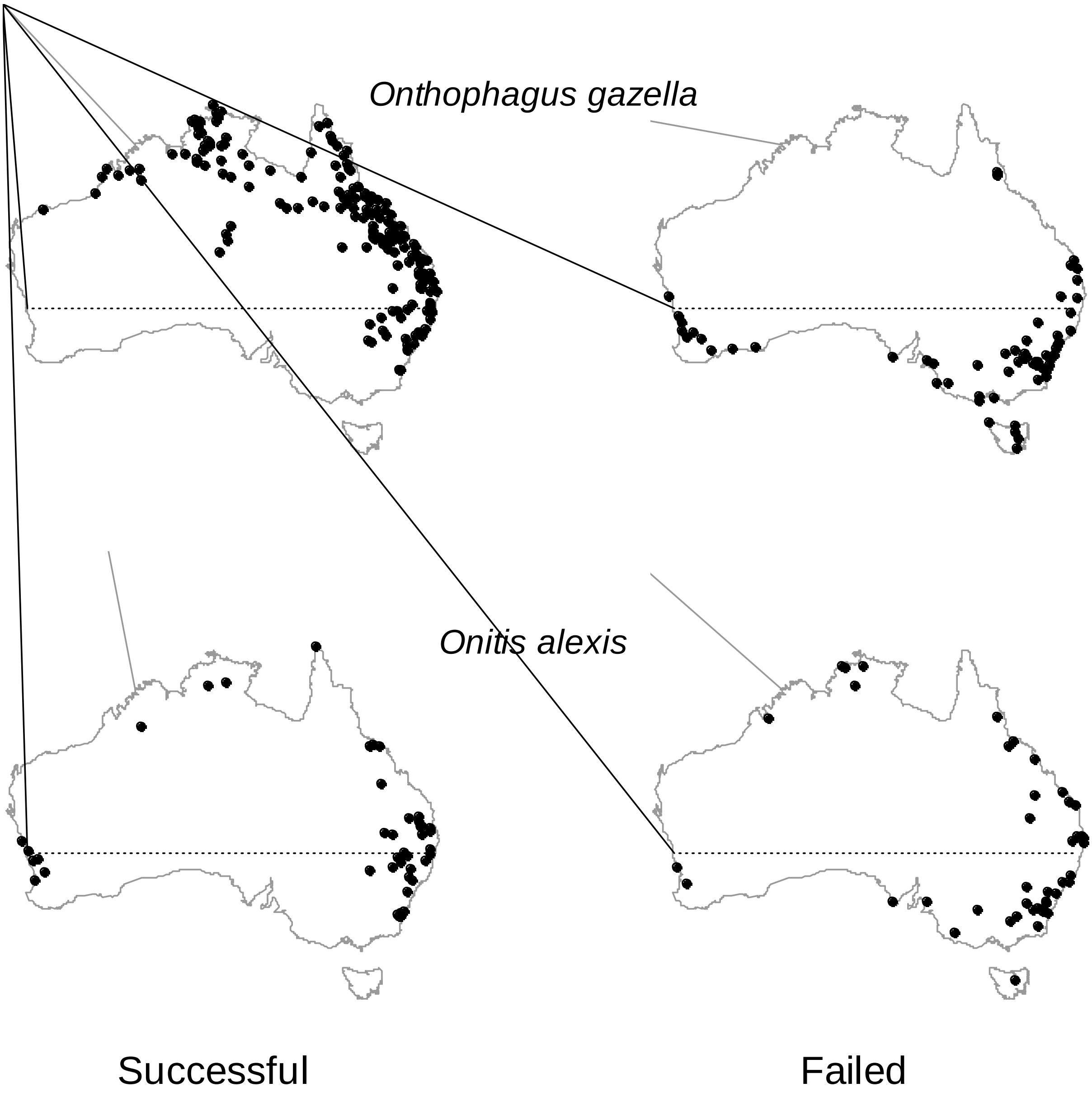
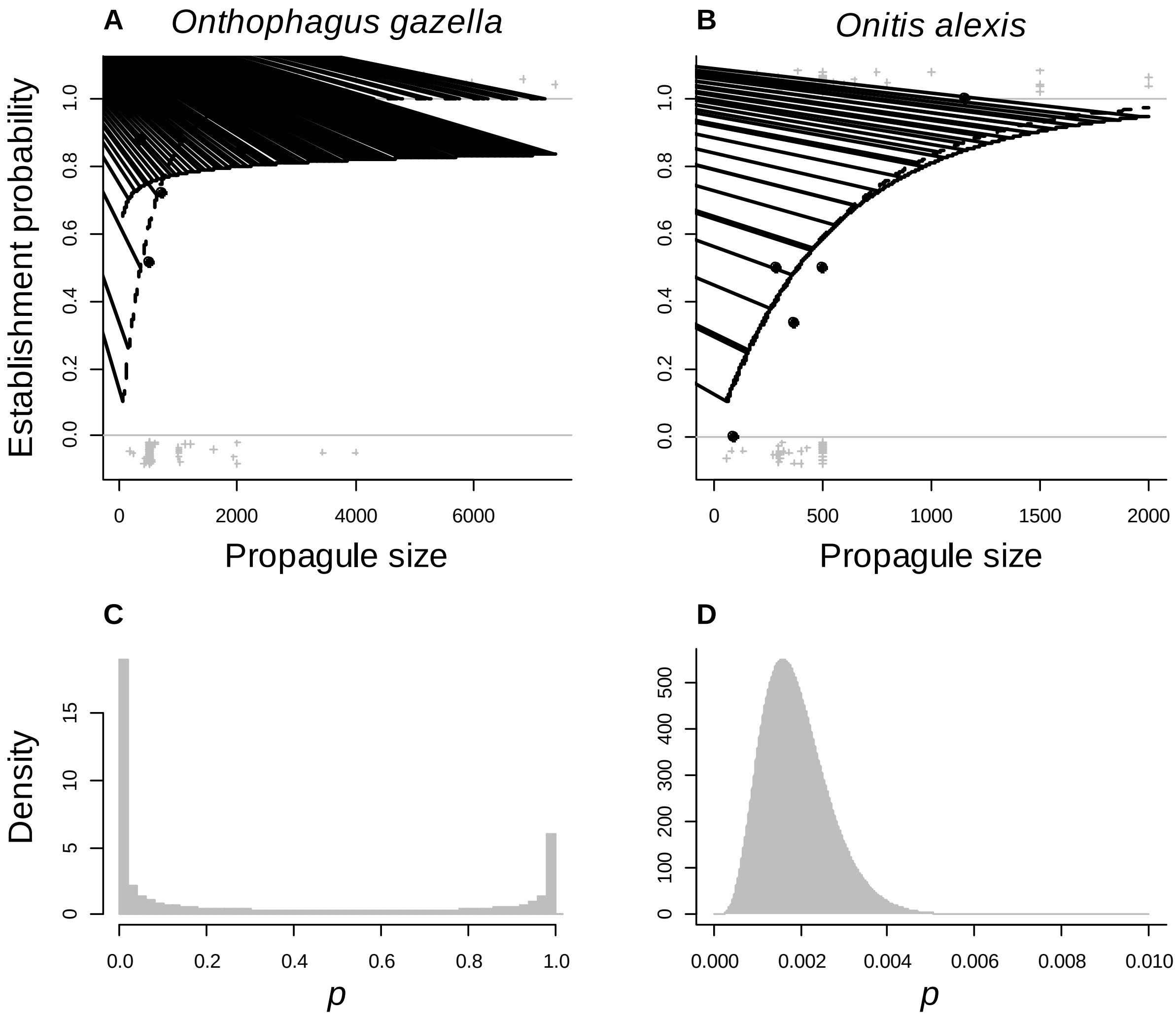


Figure 2



A
Onthophagus gazella
B
Onitis alexis
Establishment probability
0.0
0.2
0.4
0.6
0.8
1.0
0
2000
4000
6000
Propagule size
0
500
1000
1500
2000
Propagule size
C
D
Density
0
5
10
15
0.0
0.2
0.4
0.6
0.8
1.0
p
0
100
200
300
400
500
0.000
0.002
0.004
0.006
0.008
0.010
p

Figure 3

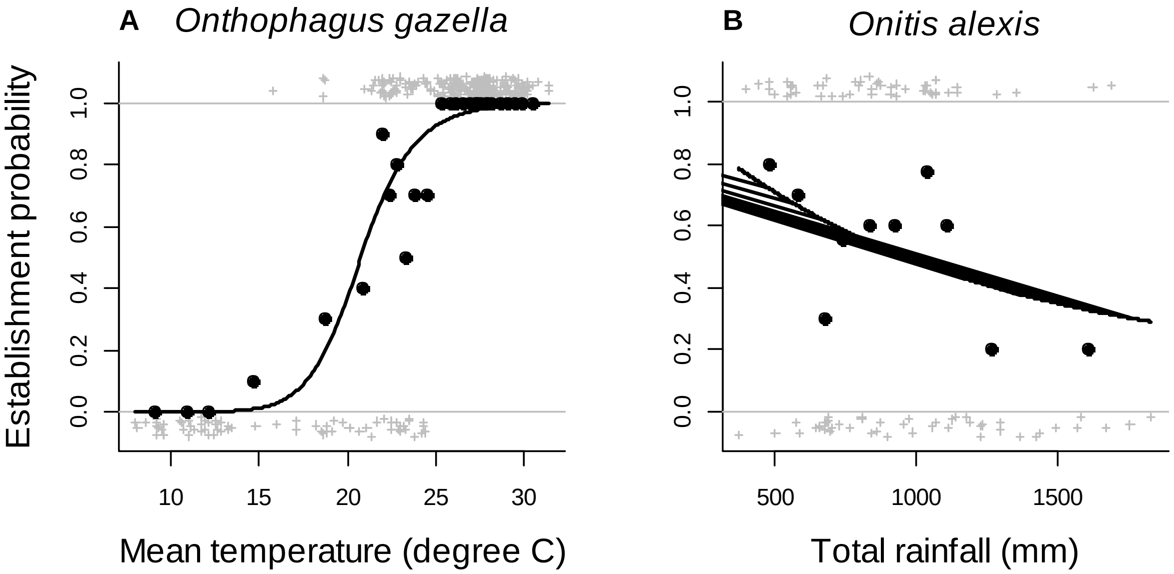
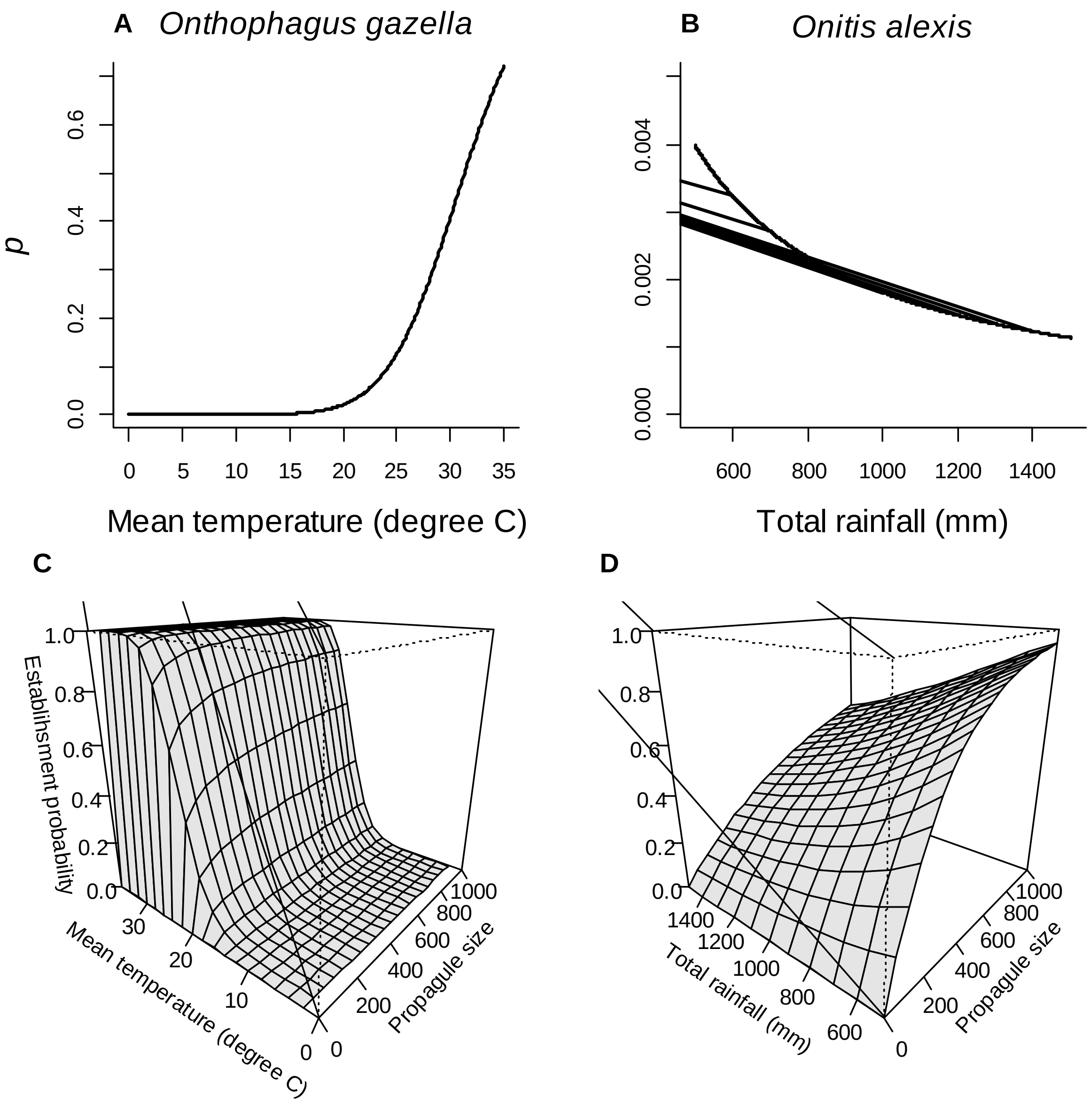

A
Onthophagus gazella
B
Onitis alexis
Establishment probability
0.0
0.2
0.4
0.6
0.8
1.0
10
15
20
25
30
Mean temperature (degree C)
500
1000
1500
Total rainfall (mm)

Figure 4


A
Onthophagus gazella
p
0.0
0.2
0.4
0.6
0
5
10
15
20
25
30
35
Mean temperature (degree C)
B
Onitis alexis
0.000
0.002
0.004
600
800
1000
1200
1400
Total rainfall (mm)
C
Establishment probability
1.0
0.8
0.6
0.4
0.2
0.0
30
20
10
0
Mean temperature (degree C)
0
200
400
600
800
1000
Propagule size
D
1.0
0.8
0.6
0.4
0.2
0.0
1400
1200
1000
800
600
Total rainfall (mm)
0
200
400
600
800
1000
Propagule size