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Impact of stochasticity in immigration and reintroduction on colonizing and extirpating populations

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ABSTRACT

A thorough quantitative understanding of populations at the edge of extinction is needed to manage both invasive and extirpating populations. Immigration can govern the population dynamics when the population levels are low. It increases the probability of a population establishing (or reestablishing) before going extinct (EBE). However, the rate of immigration can be highly fluctuating. Here, we investigate how the stochasticity in immigration impacts the EBE probability for small populations in variable environments. We use a population model with an Allee effect described by a stochastic differential equation (SDE) and employ the Fokker–Planck diffusion approximation to quantify the EBE probability. We find that, the effect of the stochasticity in immigration on the EBE probability depends on both the intrinsic growth rate (r) and the mean rate of immigration (p). In general, if r is large and positive (e.g. invasive species introduced to favorable habitats), or if p is greater than the rate of population decline due to the demographic Allee effect (e.g., effective stocking of declining populations), then the stochasticity in immigration decreases the EBE probability. If r is large and negative (e.g. endangered populations in unfavorable habitats), or if the rate of decline due to the demographic Allee effect is much greater than p (e.g., weak stocking of declining populations), then the stochasticity in immigration increases the EBE probability. However, the mean time for EBE decreases with the increasing stochasticity in immigration with both positive and negative large r. Thus, results suggest that ecological management of populations involves a tradeoff as to whether to increase or decrease the stochasticity in immigration in order to optimize the desired outcome. Moreover, the control of invasive species spread through stochastic means, for example, by stochastic monitoring and treatment of vectors such as ship-ballast water, may be suitable strategies given the environmental and demographic uncertainties at introductions. Similarly, the recovery of declining and extirpated populations through stochastic stocking, translocation, and reintroduction, may also be suitable strategies.

1. Introduction

Species colonization and extirpation have been known since the birth of ecology. These can occur through natural processes, but their rates have been accelerated recently due to human activities (Simberloff, 2009). Some colonizing species become invasive (Colautti and MacIsaac, 2004; Vale´ry et al., 2008), meaning that they expand beyond their native range and increase in numbers potentially changing the existing structures and functions of the exotic habitats, and imposing trickledown effects, detrimental or beneficial, to the habitat dependents (Keller et al., 2007). Indeed, the next invader and its effects are largely unknown. Similarly, we do not know the effect of the next species going extinct.

Invasive species keep expanding their range (Sorte et al., 2010), some threatening indigenous species (Sanderson et al., 2009), and becoming a major threat to biological diversity (Lockwood et al., 2005). They are estimated to be a cause of the endangerment of 48% of the species listed under the US Endangered Species Act (ESA) (Czech and Krausman, 1997; Wilcove et al., 1998), and are estimated to cost the US economy more than $120 billions a year (Pimentel, 2009). Although one can argue that humans are not in a position to morally judge their impact on the ecology of the systems, we can all agree that some invasive species have become a nuisance (Lovell et al., 2006), whereas the extinction of a species may come with a price (Wilson et al., 2011).

Thus, if we are to control the colonization of non-indigenous species that rapidly propagate through human-mediated vectors and become invasive in novel habitats (Lovell et al., 2006; Simberloff, 2009), we need to know how the immigration dynamics affect their colonization potential. Similarly, if we are to stock declining indigenous populations preventing them from going

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extinct, or if we are to reintroduce extirpated indigenous populations (IUCN, 2010; Snyder et al., 1996), that are subject to unknown stochastic factors, we need to know how the immigration dynamics affects their persistence and re-colonization potential. In this paper, we address the aspect of how *stochasticity in immigration* affects the population dynamics and the outcomes.

Propagule pressure is a main driver of colonization (Colautti et al., 2006; Simberloff, 2009). For example, non-indigenous marine species such as diaptomid copepods, *Pseudodiaptomus inopinus, P. marinus,* and *P. forbesi* have been invading the west coast of North America from their native habitats in Japan through human-mediated vectors such as ship ballast water discharge (Cordell et al., 2008). The Canadian Aquatic Invasive Species Network (CAISN, 2011) has developed a research program to estimate their propagule pressure, so as to assess the risks of population establishment. To control unwanted colonization, efforts are made to reduce human-mediated immigration (Olenin et al., 2011).

On the reinforcement of populations against going extinct, science-based relocation (Sheean et al., 2011), translocation (Weeks et al., 2011) and assisted colonization programs (Seddon, 2010) are becoming increasingly popular. For example, indigenous species from the Superfamily Diaptomidae, *Hesperodiaptomus shoshone*, have been extirpated from their native habitats in alpine lakes after fish-stocking (Sarnelle and Knapp, 2004). Kramer et al. (2008) have carried out re-colonization experiments to investigate the constraining factors of the *H. shoshone*'s population recovery. To sustain such endangered, threatened or declining species, efforts are made to artificially replenish populations by captive breeding and stocking (Paragamian and Hansen, 2011; Thomas et al., 2010), and to recover extirpated populations that by reintroductions (IUCN, 2010; Lorenzen et al., 2010).

In the contexts of both the spreading of colonizing populations through natural or human-mediated propagule pressure, and stocking or reintroduction of declining populations, we observe that the dynamics of a population where the propagules are flowing into a habitat as *immigration* in general. Armstrong and Seddon (2007) have proposed that, the knowledge gained from colonization dynamics of invasive species can be used to improve the success of stocking and reintroduction programs of declining or extirpating populations.

Cordell et al. (2009) have sampled large densities of non-indigenous species in ballast water from ships entering Puget Sound. However, most species found in ballast-water discharge are not known to have colonized yet. Numerous control treatments, such as mid oceanic exchange of ballast water (NOAA technical memorandum, 2007; Simard et al., 2011), chemical treatments (Nanayakkara et al., 2011) and temperature treatments of ballast water tanks (Quilez-Badia et al., 2008) are deployed to control immigration (Olenin et al., 2011) and thus to minimize colonization risks. Yet, not all ships carry the same densities of species at all times. They are subject to variation (see data in Cordell et al. (2009)). Moreover, there is no guarantee that such control treatments can reduce risks to zero. Hence, deploying costly methods uniformly or arbitrarily to reduce immigration may not be economically optimal when the immigration is variable. If we know how stochasticity in immigration impacts the chances of colonization in the presence of other stochastic factors such as environment and demography, then we can calibrate the manner in which these treatments should be deployed to make them more effective in reducing the invasion risks to acceptable levels. The optimal control methods to decrease the spread have been investigated from the economic standpoint by Finnoff et al. (2010).

Endangered, threatened, or declining populations are commonly associated with negative intrinsic growth rates, and some of these populations are stressed by unknown and unpredictable stochastic factors (Morris and Doak, 2002). Few efforts in stocking and reintroductions have been successful in sustaining declining or endangered populations (Noël et al., 2011; Rasmussen et al., 2009; Schooley and Marsh, 2007; Wada et al., 2010). Noël et al. (2011) has indicated that failures of close to 50% were evident in the reintroduction of 50 populations of 7 wetland species. Godefroid et al. (2011) have shown that the causes for 34% of the failures in reintroductions were not known, while 8% were due to known unexpected changes in the habitats. Some failures have been attributed to the environmental stochasticity (Vincenzi et al., 2012). Schaub et al. (2009) have suggested incorporating demographic stochasticity in making decisions when to end release programs so as to guarantee success.

Often there is unaccounted stochasticity apparent in the population densities and in the timing of stocking and reintroductions (e.g., see data in Shute et al. (2005)). However, in the presence of environmental and demographic variations, we do not yet know how the variation in stocking or reintroduction rates will impact the subsequent colonization or re-colonization success. If we were to know this, then we could strategize stocking and reintroduction schemes to optimize their positive effects. To our knowledge, there have been no analyses to date, on the effects of variability in stocking, translocations, or reintroductions in determining establishment success of declining populations.

The probabilities associated with the colonization and extirpation of populations are commonly quantified using stochastic differential equations (SDE) and diffusion approximations through Fokker–Planck equations (FPE) (Dennis, 2002; Morris and Doak, 2002; Ovaskainen and Meerson, 2010). Dennis (2002) has used the Fokker–Planck diffusion method (as in Gardiner (2004)) to quantify the probability of a population size *first hitting one arbitrary threshold before another.* Drake and Lodge (2006) have used the same mathematical method of first passage probability to quantify the probability of a population *first* becoming a nuisance species (or establishing) *before* going extinct (EBE probability) incorporating a model with continuous immigration, and shown that an increase in the rate of immigration increases the EBE probability under stochastic demographic conditions. However, the impact of *stochasticity in immigration* on the EBE probability has not yet received enough attention.

Here, the *extinction threshold* is defined on the assumption that, the species go functionally extinct below a lower population density. Assumptions on the existence of such quasi-extinction thresholds is standard in population viability analyses (Morris and Doak, 2002; Dennis, 2002). However, when the immigration is continuous and indefinite in time, we note that, any population realization that hits even a zero density level can later replenish from extirpation. Of course, the imposition of ecologically meaningful population thresholds on a model is only an approximation to the more complex full system. It is certainly possible that, a population that drops below the extinction threshold can also recover through stochastic effects alone.

Taylor and Hasting (2005) have described how a *strong demographic Allee effect* (Courchamp et al., 2008) will force the per capita population growth rate to become negative below a low population threshold. This threshold, defined as the Allee threshold, also can be used as an extinction threshold for quantifying the EBE probability when the immigration is continued indefinitely. This is because, we note that, the negative growth rate caused by the demographic Allee effect, due to individuals being unable to replace themselves, can counteract the rate of immigration at low population levels and creates a functional extinction threshold. There is empirical evidence to support the assertion that populations introduced at a level below a demographic Allee threshold tend to go extinct (e.g. Kramer et al. (2008)). Kramer et al. (2009) have found substantial evidence for Allee effects in animal populations. In 69%

of 91 studies, there was conclusive evidence for a component Allee effect, the demographic Allee effect, or both. Out of those studies, 23 showed the presence of the demographic Allee effect, in which, 7 showed a critical density below which the population growth rate was negative, that is, the presence of the strong demographic Allee effect. Yet, Gregory et al. (2010) have concluded that there was relatively a high potential for the demographic Allee effects in the populations they studied, but only few cases were observed across many taxa.

In the case of declining and extirpated populations, where often the stocking is carried out only until the population either gets established or is gone extinct, we can investigate the impact of stochasticity in stocking on the EBE probability similar to invasive species. Thus, here we define *immigration* broadly as natural and human-mediated introductions through vectors, translocations, relocations, and artificial replenishment of populations through captive breeding and release into habitats.

In the context of invasive species (assuming populations of high fitness, or having large and positive intrinsic growth rates given the environment), we investigate how stochasticity in immigration continues to impact the EBE probability of an initial population impulse that exceeded the extinction threshold. In the context of declining (or endangered or threatened) populations (assuming populations of low-fitness, or having large and negative intrinsic growth rates given the environment), we investigate how the stochasticity in stocking or reintroduction continues to impact the EBE probability of an existing population. To make our model realistic, we allow for Allee effect, demographic stochasticity and environmental stochasticity in the population dynamics (see Lande et al. (2004) for details) although our main focus is the impact of stochasticity in immigration.

2. Model

First, we analyzed a deterministic exponential Allee model for the case where stochasticity is not present in the immigration. Next, we incorporated environmental, demographic, and immigration stochasticity into the model, heuristically, and solved the corresponding Fokker–Planck diffusion equation for the EBE probabilities for the cases with and without stochasticity in immigration under two scenarios: species moving into (A) favorable habitats (i.e., where the intrinsic growth rate is large and positive), for example, colonizing high-fitness populations as in the case of invasive species, and, (B) unfavorable habitats (i.e. where the intrinsic growth rate is large and negative), for example, stocking low-fitness populations as in the case of endangered, threatened, or declining populations.

We solved the FPE for the cases incorporating (i) all three types of stochasticity (environmental, demographic and immigration) using a finite-difference numerical method (Grasselli and Pelinovsky, 2008), and the cases specific to (ii) demographic and immigration stochasticity, and (iii) immigration stochasticity, analytically. We also derived the equation that yields the moments of first passage times for the population first hitting the establishment threshold before the extinction threshold, or the time for EBE, and analyzed the impact of stochasticity in immigration on mean time for EBE.

Deriving SDEs heuristically from their counterpart deterministic models has been a major concern in the theoretical ecology literature. The suitability of the SDE formulations, whether to use Ito (Mao, 1997) or Stratonovich (1963), has been thoroughly discussed by Turelli (1977) followed by Ricciardi (1986) and more recently by Braumann (2007, 2008). Ricciardi (1986) following up on Turelli (1977) has shown that if the system is intrinsically a continuous growth process in a random environment, then it should be modeled using the Stratonovich formulation followed by appropriate calculus. Goel and Richter-Dyn (2004) have used this approach to investigate stochastic models in biology in the case when the underlying processes are continuous in time. If a process is discrete in time, then the Ito SDE formulation may be more appropriate (Ricciardi, 1986). Population viability analysis models commonly use the Ito formulation (Dennis, 2002; Morris and Doak, 2002). An invasive species study by Drake and Lodge (2006) also used the same formulation. We also used the Ito one. For generality, the results are mathematically comparable regardless of which method is used, so that the specific method may only be relevant when fitting the model to real data to calibrate parameters (Braumann, 2007).

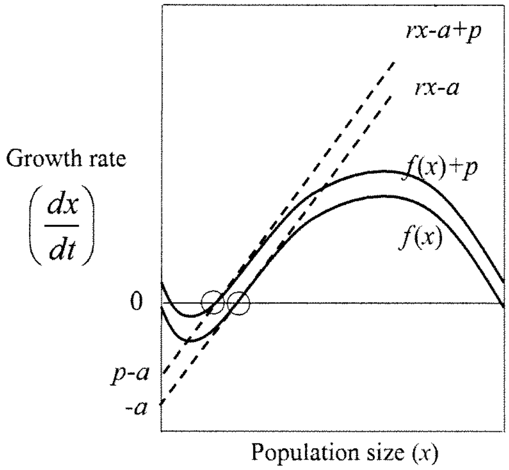


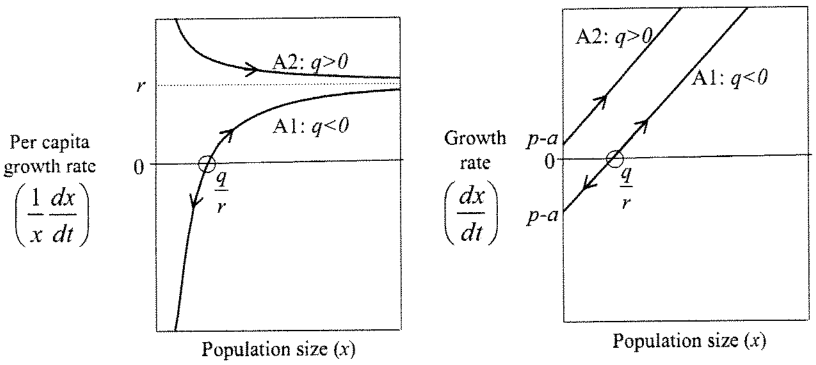
Fig. 1. Population models $\frac{dx}{dt} = f(x)$, and, $\frac{dx}{dt} = f(x) + p$, with dashed lines for the cases linearized at $\frac{dx}{dt} = 0$.

Deterministic population model

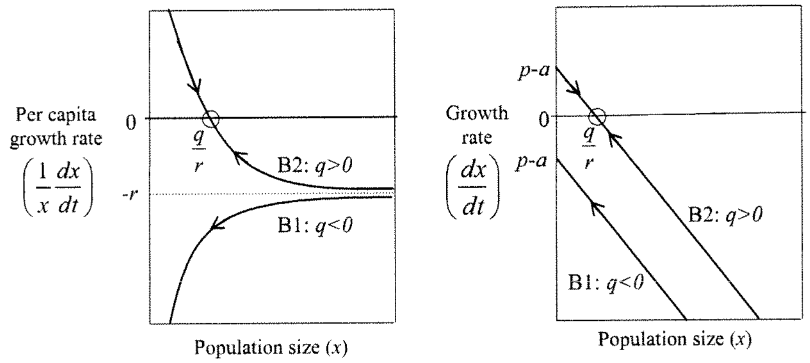
We write the growth rate of a population having density x as $dx/dt = f(x) + p$, where $f(x)$ is the average rate of population growth, and p is the mean rate of immigration into the population. Function $f(x)$ can take various linear (e.g. density-independent) and non-linear (e.g. density–dependent) forms.

Here, we do not intend to investigate the case at $x = 0$, or at high values limited by the population density. Our modeling focus is to investigate the dynamics of a population far below the level of density dependent regulation. Thus, we take the linearized form of the model near the low population equilibrium (the Allee threshold), where $dx/dt = 0$ (Fig. 2). Thus, the model reduces to a simple Malthusian form, such that, $f(x) = rx - a$, and, we write $dx/dt = rx - a + p$. Here, r is the intrinsic growth rate of the population that depends on the individuals' responses to environmental parameters, which was defined as r_m in Fagan et al. (2010). The parameter a is the rate of loss due to individuals that cannot, on average, replace themselves resulting from the demographic Allee effect (the simplest Allee form described in Gregory et al. (2010)). Depending on whether $r > 0$ (scenario A) demonstrating high-fitness, or $r < 0$ (scenario B) demonstrating low-fitness, we consider that, the habitats the species are introduced to, or living in, are either *favorable* or *unfavorable* to the population on average (Sibly and Hone, 2002). Thus, invading species commonly show $r > 0$, and endangered, or declining, populations commonly show $r < 0$. We define the net inflow rate to be $q = p - a$. Thus, note that, a reduces the per capita growth rate to be negative at low population densities, and p counteracts it as an opposing force to raise the per capita growth rate to be positive (Fig. 1).

Fig. 2(a) illustrates the situation when habitats are favorable ($r > 0$, scenario A). If the demographic Allee effect is strong ($a > p$, scenario A1), then the per capita growth rate becomes negative at population levels that fall below the Allee threshold ($x < q/r$), an unstable equilibrium below which population eventually tends to



(a) Scenario A (favorable habitats where $r > 0$).



(b) Scenario B (unfavorable habitats where $r < 0$).

Fig. 2. Dynamics of deterministic population model $\frac{1}{x}\frac{dx}{dt} = r + \frac{q}{x}$ when net-flow rates (q) and intrinsic growth rates (r) are positive and negative. Here, $q = p - a$.

zero. For initial values of $x > q/r$, the population tends to any high arbitrary level. We note that, when $a < p$ the Allee threshold is removed (scenario A2). Therefore, for the scenario $r > 0$, the Allee threshold exists only if $a > p$.

Fig. 2(b) illustrates the situation when habitats are unfavorable ($r < 0$, scenario B). If the Allee effect is weak ($a < p$, scenario B2), then the per capita growth rate becomes positive at small $x < q/r$, and negative at $x > q/r$, with $x = q/r$ being a stable equilibrium. In scenario B1 ($a > p$), the per capita growth rate remains negative as x is varied. In summary, when $r < 0$ (scenario B), the population may persist in a low equilibrium density or tend to zero depending on whether $a < p$ (scenario B2) or $a > p$ (scenario B1), respectively. The low equilibrium density occurs solely due to the forcing by propagules continuously flowing into the system and exceeding the negative growth rate caused by the demographic Allee effect.

The two scenarios above, $r > 0$, and $r < 0$, suggest that if $a > p$ (scenario A1 and B1), we may define a functional extinction threshold that is forced by a strong demographic Allee effect, because the negative net per capita growth rate of the population near zero drives the population to extinction. By way of contrast, scenarios A2 and B2 have positive net per capita growth rates at small population levels. Hence, the idea of a functional extinction threshold does not make sense for scenarios A2 and B2, when the propagule flow is continuous and indefinite. However, in practical situations (such as the stocking of declining populations), assuming the existence of an extinction boundary may make sense for all scenarios, including A2 and B2, as human intervention can halt propagule flow wherever the population hits any arbitrary lower threshold.

Hence, in the context of colonizing populations ($r > 0$), the probability of population *establishing before going extinct* (EBE probability) may have biological relevance limited to scenarios A1. In the context of endangered populations ($r < 0$), if stocking, translocation, or reintroduction is carried out only *until* the population hits either the establishment or a functional extinction threshold, then EBE probability has a practical relevance in scenarios B1, B2, and A2.

Stochastic population model

Based on the deterministic counterpart, we modeled the corresponding SDE heuristically, incorporating environmental, demographic and immigration stochasticity. Thus, we write the growth process characterized by the stochastic dynamical equation satisfied by the population x as

$$dx = \alpha(x)dt + \beta(x)dW \qquad (1)$$

(as in Dennis (2002)). Here, we have the infinitesimal mean of the process, $\alpha(x) = rx + q$, and $\beta(x) = \sqrt{\sigma_e^2x^2 + \sigma_d^2x + \sigma_p^2}$, where $\sigma_e^2x^2$, σ_d^2x and σ_p^2 are the infinitesimal variances in the population fluctuations corresponding to the environment (see Ricciardi (1986)), demography (see Feller (1951)), and immigration. Here, $dW \sim N(0, dt)$. The differential of the diffusion process of x is formulated in terms of Ito stochastic integral as in Dennis (2002) and Drake and Lodge (2006). Tier and Hanson (1981) studied the case where demographic and environmental stochasticity are incorporated together into a SDE population model, which was later used by Drake and Lodge (2006) to investigate invasive species populations. Here we further extended the idea to incorporate immigration stochasticity.

We note that, the processes involving propagules flowing into a system, either natural or human-mediated, can be Poisson (e.g. Drury et al. (2007) and Jerde and Lewis (2007)). In our paper, we assume this processes to be Gaussian allowing the immigration to be over-dispersed. We assume the same properties of stochasticity in immigration in the event of replenishment of declining populations by stocking, translocation or reintroduction. Such assumptions also simplify the formulation of the SDE into a form that satisfies the FPE, and can be analytically solved for EBE probabilities.

Diffusion approximation for EBE probabilities

We note that, the transition probability density $P(x_0, t)$ for a population at *initial* position (x_0) and time $(-t)$, given that the final position and time are *fixed*, for Eq. (1), satisfies the backward FPE. Solving the backward FPE, we can calculate the probability of a population remaining between, or exiting, two fixed population levels, such as establishment and extinction thresholds. Thus, we can write the backward FPE that satisfies the SDE in Eq. (1) as,

$$\partial_t P(x_0, -t) = A(x)\partial_x P(x_0, -t) + \frac{1}{2}B(x)\partial_{xx} P(x_0, -t) \tag{2}$$

where the diffusion coefficient is $B(x) = 2(\beta_e x^2 + \beta_d x + \beta_p)$, and $2\beta_e = \sigma_e^2$, $2\beta_d = \sigma_d^2$ and $2\beta_p = \sigma_p^2$ are the spectral densities of the zero average Gaussian processes corresponding to environmental, demographic, and immigration stochasticity, and the drift coefficient is $A(x) = \alpha(x)$.

We define $G(x_0)$ as the *probability of the population first hitting an arbitrary establishment threshold* (x_d) *before first hitting an arbitrary extinction threshold* (x_e), (EBE probability) assuming initial position $x_d > x_0 > x_e$. Here, $G(x_0)$ satisfies the time-homogeneous version of Eq. (2) That is,

$$A(x_0)\partial_{x_0} G(x_0) + \frac{1}{2}B(x_0)\partial_{x_0 x_0} G(x_0) = 0 \tag{3}$$

with boundary conditions, $G(x_d) = 1$, and $G(x_e) = 0$ (Gardiner, 2004). We solved the general case above using a finite-difference numerical method (Grasselli and Pelinovsky, 2008). However, note that, the EBE probability exists in ecological reality only if the upper and lower thresholds are functionally establishment and extinction thresholds, which is true in the scenarios A1, and B1. This would also hold for scenarios A2 and B2, if stocking is stopped once the population realization hits the functional extinction threshold.

An analytical solution for the special case of the FPE in Eq. (3), with demographic and immigration stochasticity alone, yields EBE probability with initial population at x_0 to be as follows.

$$G(x_0) = \frac{E(x_0) - E(x_e)}{E(x_d) - E(x_e)}. \tag{4}$$

Here, $E(x_i) = (bx_i + c)^k {}_1F_1\left(k, k+1; \frac{-r}{b^2}(bx_i + c)\right)$, $b \equiv \sigma_d^2/2$, $c \equiv \sigma_p^2/2$, $k = \left(\frac{rc}{b^2} - \frac{q}{b}\right) + 1$, and x_i denotes x_0, x_e, and x_d. ${}_1F_1$ is the Kummer confluent hypergeometric function of the first kind (Slater, 1960) of the form, ${}_1F_1(a, b, z) = 1 + \frac{az}{b} + \frac{(a)_2 z^2}{(b)_2 2!} + \cdots + \frac{(a)_n z^n}{(b)_n n!}$ s.t. $a_n = a(a+1)(a+2)\cdots(a+n)$ (see Appendix A for derivation). An analytical solution for the special case of Eq. (3) with immigration stochasticity alone yields the EBE probability with initial population at x_0 to be Eq. (4) with $E(x_i) = Erf_z\left(\frac{q + rx_i}{\sigma_p\sqrt{r}}\right)$ (see Appendix A for derivation). Here, *Erfz* is the error function (Abramowitz and Stegun, 1972), and x_i takes subscript values $i = 0, e, d$.

The point of changing the impact of immigration stochasticity on EBE

The point at which the direction of impact of stochasticity in immigration on the EBE probability switches, satisfies the condition, $\frac{\partial G(x_0)}{\partial \sigma_p} = 0$. Thus for the case where immigration stochasticity alone is present (Eq. (4)), the equation to be satisfied by the parametric combination is as follows.

$$\left(\frac{(q + rx_o)\, e^{k_0} - (q + rx_e)\, e^{k_e}}{(q + rx_d)\, e^{k_d} - (q + rx_e)\, e^{k_e}}\right) - \left(\frac{E(x_0) - E(x_e)}{E(x_d) - E(x_e)}\right) = 0. \tag{5}$$

Here, $k_i = \frac{(q + rx_i)^2}{r\sigma_p^2}$, and $E(x_i) = Erf_z\left(\frac{q + rx_i}{\sigma_p\sqrt{r}}\right)$, with subscript values $i = 0, e, d$. Here, Erf_z is the error function (Abramowitz and Stegun, 1972), and x_i takes subscript values $i = 0, e, d$.

First passage time

We define $T_n(x_d, x_0)$ as the nth *moment of the first passage time, given that the population size first hit an arbitrary establishment threshold*, x_d, *before an arbitrary extinction threshold*, x_e. That is, we denote $T_n(x_d, x_0)$ as the nth moment of first passage time for EBE assuming the initial position of the population density is at $x_d > x_0 > x_e$ for the scenarios A1, and B1.

Thus, the function $T_n(x_d, x_0)$ satisfies,

$$\begin{aligned} &A(x_0)\partial_{x_0} G(x_0) T_n(x_d, x_0) + \frac{1}{2}B(x_0)\partial_{x_0 x_0} G(x_0) T_n(x_d, x_0) \\ &\quad = -nG(x_0) T_{n-1}(x_d, x_0) \end{aligned} \tag{6}$$

(see Appendix B for derivation). The boundary condition at $x_0 = x_d$ is determined by $G(x_d) = 1$, $T_n(x_d, x_d) = 0$, and hence, $G(x_d)T_n(x_d, x_d) = 0$. The boundary condition at $x_0 = x_e$ is determined by $G(x_e) = 0$, and hence, $G(x_e)T_n(x_d, x_e) = 0$. The cases $n = 1, 2$ yield the mean and the second moment of first passage times respectively. Thus, a special case of the equation above, that is when $n = 1$, yields the mean time for EBE as in Gardiner (2004).

We solved the mean time for EBE iteratively using a finite-difference numerical method (Grasselli and Pelinovsky, 2008) by incorporating the solutions given in Eq. (4) for $G(x_0)$ in Eq. (6). This can be extended to scenarios A2 and B2 if the stocking is stopped once the population realization hits a functional extinction threshold.

3. Results

EBE probability of colonizing $(A1 : r > 0, p < a)$ *or declining* $(B1 : r < 0, p < a)$ *populations*

Solutions to the time homogeneous Eq. (3), based on the range of parameter values given, show that increased stochasticity in immigration decreases the EBE probability in populations in high fitness, or populations introduced to favorable habitats $(r > 0)$ (e.g. invasive populations) (Fig. 3). Increased stochasticity in immigration increases the EBE probability of populations in low fitness, or in unfavorable habitats $(r < 0)$ (e.g. endangered or declining populations) further amplifying the effect caused by the environmental and demographic stochasticity on the EBE probability. The percentage effect is generally higher at low and moderate environmental and demographic stochasticity, and greater when the initial population size is nearing the extinction threshold for $r > 0$, and greater when the initial population size is nearing the establishment threshold for $r < 0$ (Fig. 4).

EBE probability of declining populations given that immigration (stocking) is ceased when the population realization hits a threshold $(B2 : r < 0, p > a)$

Fig. 5(a) shows that the stochasticity in stocking (immigration) decreases the EBE probability in scenario B2 $(r < 0, q > 0)$ when q is large and positive (resulting from large p with fixed demographic Allee effect a), given that stocking is ceased when the population hits a threshold. Stochasticity in immigration increases EBE probability when q is large and negative. However, Fig. 5(b) shows that, the point at which the direction of the impact of stochasticity in immigration on EBE probability changes sign, is shifting towards large and negative r given that q is positive and large, and shifting towards small and positive r given that q is negative and large. This suggests that the direction of the impact of stochasticity in immigration on EBE probability cannot be determined by the sign of the intrinsic growth rate or net propagule flow alone when their signs are opposite.

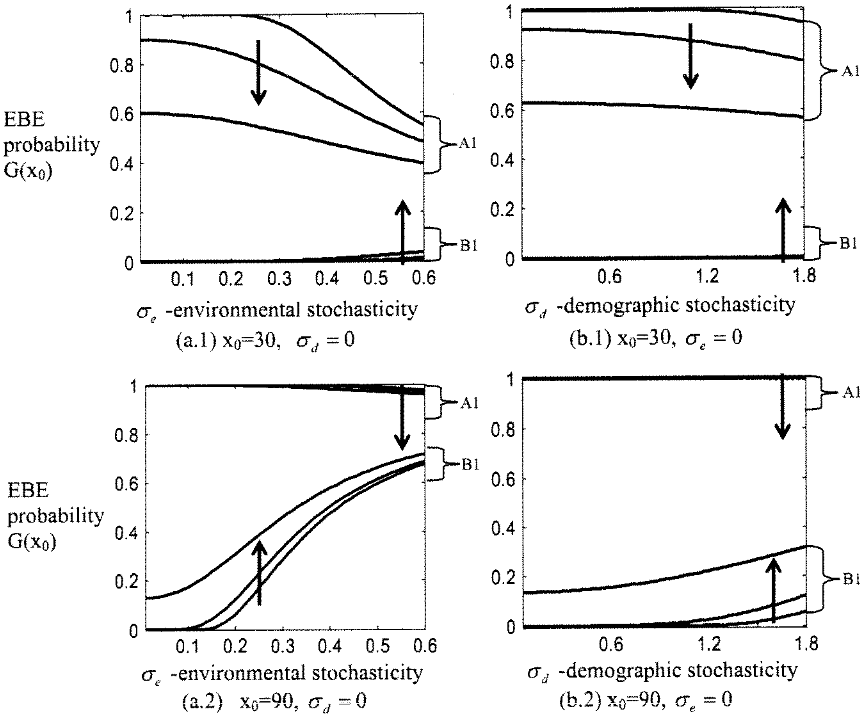


Fig. 3. Probability of a population *establishing before going extinct*, $G(x_0)$, with respect to increasing (a) environmental stochasticity, and (b) demographic stochasticity. Initial population size is at x_0. Net propagule flow rate $q = -4$ (such that $p < a$). (A1) Favorable habitats ($r = 0.4$); (B1) unfavorable habitats ($r = -0.4$). Red: propagule flow, $\sigma_p = 0$ (that is without propagule flow stochasticity); green: $\sigma_p = 10$; blue: $\sigma_p = 20$. Other parameters are: extinction threshold $x_e = 10$, establishment threshold $x_d = 100$. Arrows show the direction of the impact of stochasticity in propagule flow on the EBE probability. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

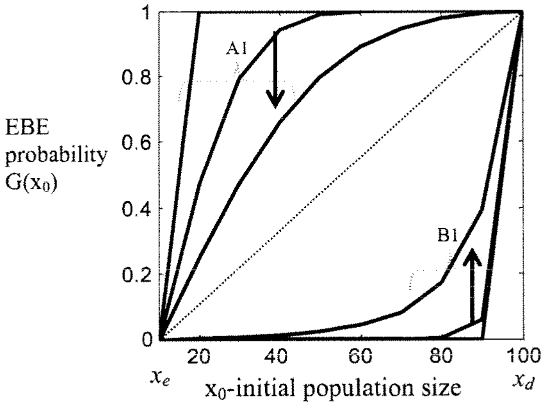


Fig. 4. Probability of a population *establishing before going extinct*, $G(x_0)$, with respect to increasing initial population size at x_0. (A1) Favorable habitats ($r = 0.4$), (B1) unfavorable habitats ($r = -0.4$). Net propagule flow rate $q = -4$ (such that $p < a$). Red: propagule flow, $\sigma_p = 0$ (that is without propagule flow stochasticity); green: $\sigma_p = 10$; blue: $\sigma_p = 20$. Other parameters are: environmental stochasticity, $\sigma_e = 0$, demographic stochasticity $\sigma_d = 0$, extinction threshold $x_e = 10$, establishment threshold $x_d = 100$. Probability converges to the diagonal dotted line for higher σ_p. Note that, for the case of propagule flow stochasticity alone is present, $G(x_0) - > \left(\frac{x_0 - x_e}{x_d - x_e}\right)$, which is the diagonal line, that is, for $\sigma_p \to \infty$ (Appendix A). Arrows show the direction of the impact of stochasticity in propagule flow on the EBE probability.(For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Fig. 6, which was drawn based on the cases satisfying Eq. (5), indicates that, the stochasticity in immigration decreases the EBE probability when $r > 0$ and $q > 0$ (scenario A2), or, when q is positive and large enough compared to negative r, or r is positive and large enough compared to negative q. That is, in general, when the net population growth rate remains positive. The stochasticity in immigration increases the EBE probability when $r < 0$ and $q < 0$, or when r is negative and large enough compared to positive q, or q is negative and large enough compared to positive r. That is, in general, when the net population growth rate remains negative. Thus, we note that, when r and q have opposite signs, we cannot predict the direction of the impact of immigration stochasticity on the EBE probability by examining their signs alone, unless we calculated the critical point at which the switching occurs.

It follows that, in general, when the EBE probability becomes large, either due to high intrinsic growth rate, or high mean immigration rate given low intrinsic growth rate, the stochasticity in immigration tends to decrease the EBE probability. When the EBE probability becomes small due to large and negative intrinsic growth rate at low immigration rates, then the stochasticity in immigration tends to increase the EBE probability.

Mean time for population establishment before extinction

Fig. 7, drawn based on Eq. (6), indicates that the log mean time for EBE decreases when the immigration is stochastic regardless of whether the population is introduced to, or existing in, a favorable ($r > 0$) or an unfavorable ($r < 0$) habitat. This effect, simulated for the case with environmental stochasticity, is qualitatively the same had we incorporated the demographic stochasticity.

4. Discussion

Our results show that the *stochasticity in immigration* decreases the probability of populations that are of high fitness, or introduced to favorable habitats, or having high positive intrinsic growth rates, such as the colonizing invasive populations, *establishing before going extinct* (the EBE probability). This effect counteracts the EBE probability increased by high mean immigration rates that were shown in Drake and Lodge (2006). The decrease in the EBE probability resulting from the immigration stochasticity is

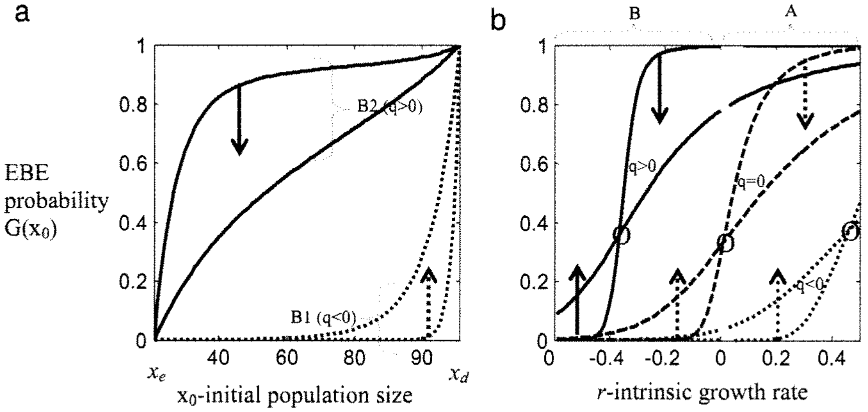


Fig. 5. (a) Probability of a population *establishing before going extinct*, $G(x_0)$, with respect to increasing initial population size. Here, $q = -20$ (dotted lines, such that $p < a$ scenario 1), and $q = 20$ (solid lines, such that $p > a$ scenario 2), $r = -0.3$. Green: $\sigma_p = 10$; blue: $\sigma_p = 20$. This shows the effect of stochasticity in propagule flow on the EBE probability when q is turning to positive ($p > a$) from negative ($p < a$), that is when p is increased from a small value given that the demographic Allee effect, a is fixed. (b) $G(x_0)$ with respect to intrinsic growth rate for the same scenarios as above, with $x_0 = 40$. Dashed lines depict the case for $q = 0$ (that is, $p = a$). Circled are the points at which the direction of the impact of propagule flow stochasticity on the EBE probability changes sign. For both illustrations above, the other parameters are: environmental stochasticity, $\sigma_e = 0$, demographic stochasticity $\sigma_d = 0$, extinction threshold $x_e = 10$, establishment threshold $x_d = 100$. Arrows show the direction of the impact of stochasticity in propagule flow on the EBE probability. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

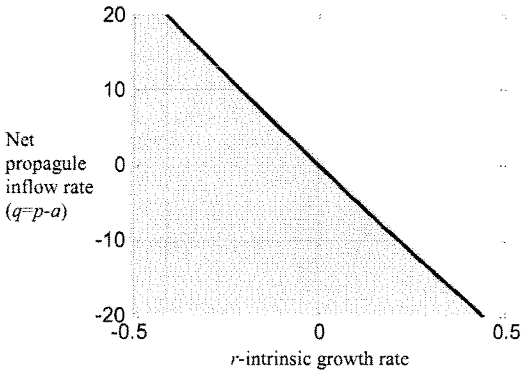


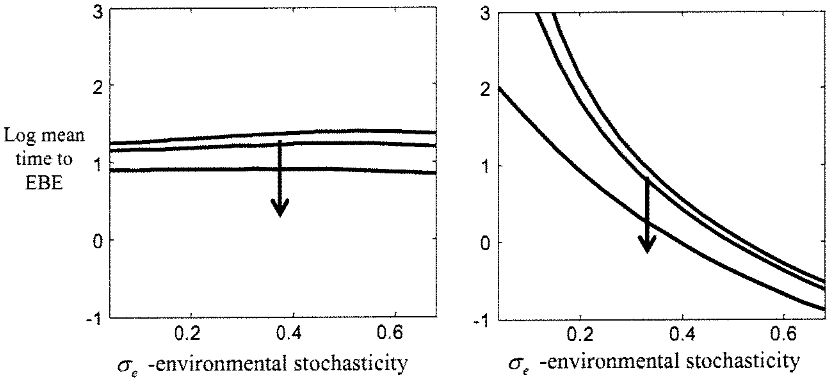
Fig. 6. The solid line (which is slightly non-linear) depicts the parametric combination of intrinsic growth rate (r) and net propagule flow rate (q) at which the direction of impact of stochasticity in propagule flow on EBE probability changes sign satisfying Eq. (5). Shaded area depicts the combinations where the stochasticity in propagule flow increases the EBE probability, non-shaded area depicts where it decreases the EBE probability. When r and q take opposite signs, whether the EBE probability increases or decreases depends on their specific values. The other parameters are: environmental stochasticity, $\sigma_e = 0$, demographic stochasticity, $\sigma_d = 0$, propagule flow stochasticity, $\sigma_p = 5$, extinction threshold $x_e = 10$, establishment threshold $x_d = 100$.

amplified further by the environmental and the demographic stochasticity. The percentage amplification is stronger when the population is closer to the extinction threshold.

However, we indicated that the EBE probability can be defined ecologically meaningfully either, when the demographic Allee effect (if existed) exceeds the immigration rate allowing a functional extinction threshold to exists, or otherwise, if the immigration can be stopped by an intervention after the population reached a threshold below which the extinction is the most likely scenario. If the immigration rate exceeds the demographic Allee effect removing the existence of a functional extinction threshold, continuation of immigration then results in the population to replenish from any lower threshold driving the population to become colonized eventually. As we have little control over the invasive species propagating into new habitats, especially in the cases such as propagules of marine invasive copepods discharged into ecologically tolerable habitats through ship ballast water (Cordell et al., 2008, 2009), the above scenario of inevitable-colonization can often be a reality.

The impact of stochasticity in immigration on the EBE probability is qualitatively and quantitatively the same as the probability of a population *first hitting an arbitrary upper threshold before an arbitrary lower threshold* regardless of the knowledge of the ecological nature of the boundaries. Thus, the results of the EBE probabilities are the same as the first passage probabilities. It follows that, if the immigration of invasive species is made to fluctuate by human-mediation, keeping the average the same, then we may predict the chance that the population first reaching a high population level (and get established) before a low level (and go extinct) would be less than the case had the flow of propagules remained steady (or uniform, or without stochasticity). Supposing if a functional extinction threshold did not exist (at the given rate of immigration and the demographic Allee effect), then the population eventually gets colonized inevitably regardless of the fluctuations we would create in the flow of propagules or in the immigration. Therefore, an advantage for an invasive species management will be the case if an extinction threshold does exist without our knowledge. Thus, implementing strategies to fluctuate the expected propagule flow (as opposed to, keep it steady or uniform) regardless of the knowledge of the existence of an extinction threshold seems benevolent to the management as it creates a chance to reduce the establishment probability of an invading population. Hence, the impact of stochasticity in immigration on colonization may be incorporated into decision-making formula for stochastic controlling of, for example, invasive marine species propagated through ship ballast water, especially when strategizing and developing monitoring programs for mid oceanic exchange of ship ballast water (NOAA technical memorandum, 2007; Simard et al., 2011), and ballast water discharging regulations, chemical treatments (Nanayakkara et al., 2011), and temperature treatments of ballast water tanks (Quilez-Badia et al., 2008). Although, the policies can be designed and implemented to lower the mean discharge rate of propagules to achieve better results, as an alternative, the same result may be obtained by altering the stochasticity in the propagule flow rate, while keeping the mean discharge rate the same.

Programs are implemented to stock or reintroduce declining populations through captive breeding and release, and artificially replenish populations before they go extinct (Fraser, 2007; Seddon et al., 2007; Bell et al., 2008). Our results indicate that increased stochasticity in stocking (or translocations, or reintroductions) increases the EBE probability in declining populations in stochastic



(a) Scenario A1.

(b) Scenario B1.

Fig. 7. Mean time for population *establishing before going extinct*, $T_n(x_d, x_0)$, with respect to increasing environmental stochasticity. (a) In favorable habitats ($r = 0.4$, $x_0 = 30$). (b) In unfavorable habitat ($r = -0.4$, $x_0 = 90$). Red: propagule flow stochasticity, $\sigma_p = 5$; blue: $\sigma_p = 10$; green: $\sigma_p = 20$. Other parameters are: extinction threshold $x_e = 10$, establishment threshold $x_d = 100$, and net propagule flow rate $q = -4$. Arrows show the direction of the impact of stochasticity in propagule flow on log mean time to EBE. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

environments and demographic conditions compared to the case when stocking is steady (or uniform), given that either the intrinsic growth rate is large and negative, or the negative growth rate caused by the demographic Allee effect is stronger than the stocking rate. This effect is stronger in terms of percentage-increase when the population is nearing the establishment threshold.

However, when the mean stocking rate becomes large resulting in a high EBE probability, then the stochasticity in stocking, in turn, can decrease the EBE probability. This suggests that, the direction of the effect of stochasticity in stocking on the EBE probability depends on the mean rate of stocking in relation to the demographic Allee effect and the intrinsic growth rate of the population. Thus, if we are to make a decision as to whether to amplify or de-amplify the stochasticity in stocking in order to increase the EBE probability under practical circumstances, then we will need to assess the critical point at which the direction of the impact on EBE switches as we have shown under the results section. However, it may be more effective to begin reintroductions with regulated stochasticity, and later turn it into a steady flow with subsequent increase in population densities. Under the right conditions, increasing the stochasticity at low average stocking rate may be a low-cost strategy compared to increasing the average stocking rate, as both may yield the same result.

Studies that quantified the effect of stochasticity in reintroductions, translocations, or stocking on population establishment success have not been found in the literature. Apparently, some data in reintroduction and stocking studies (e.g., Verspoor and de Lea´niz (1997) and Shute et al. (2005)) shows unplanned variations in the release of propagules. Shute et al. (2005) indicated reintroduction success of 4 species of fishes in Abrams Creek, Tennessee, apparently indicating high variations in stocking. Similarly, Verspoor and de Lea´niz (1997) indicated stocking success of Scottish Atlantic salmon in two Spanish rivers. Yet, their data do not seem to have enough information to be able to test the effect of stochasticity in immigration on the establishment success. A well-designed experiment can be implemented to test our hypothesis more concretely.

We have also found that, the stochasticity in immigration decreases the mean time for a population *establishing before going extinct* (mean time for EBE) in both high- and low-fitness populations. Thus, the management of invasive species has an interesting theoretical trade-off as to whether to lower the EBE probability, and thus risks, by increasing the immigration stochasticity, or to increase the mean time for the population establishment by decreasing the immigration stochasticity after a population is detected in a novel habitat. In the case of stocking declining populations, we have observed that the increase in stochasticity in stocking decreases the mean time for the population establishment. Thus, it is complementing the increase in probability of the population *establishing before going extinct* when the mean stocking rate is low. However, care must be taken as the risk of these decisions is high because the mean stocking rate can become large without our knowledge far exceeding the demographic Allee effect, thus causing the stochasticity in stocking to suppress the EBE probability. The knowledge of the critical point at which the impact on the EBE probability switches direction may be crucial in making those decisions. However, we need to test our hypotheses using empirical studies before application.

In a nutshell, the study suggests that the stochasticity in immigration, together with the environmental and the demographic stochasticity, suppresses the colonization potential of invading populations, yet increases the reestablishment potential of declining populations in general. Either way, it seems to serve the interests of ecological management, and help producing low cost strategies.

Further developments may include improving the model to reflect periodic variation in environmental forcing with stochasticity in immigration, which may be a scenario much evident in marine habitats. It may enable us to analyze the stochastic impacts on the cases with time-dependent introductions.

Acknowledgments

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Appendix A

Special case: EBE probabilities of population in the presence of demographic and immigration stochasticity

Here, we solve Eq. (3) in the main text, $A(x)\partial_x G(x) + \frac{1}{2}B(x)\partial_{xx}G(x) = 0$ for the case $A(x) = rx+q$, and, $B(x)/2 = (bx+c)$, where we denote $b \equiv \sigma_d^2/2$, and $c \equiv \sigma_p^2/2$.

We substitute x by $z = \frac{1}{b}\ln(bx + c)$, thus, $x = \frac{1}{b}[\exp(bz) - c]$, $dx = (bx + c)dz$.

Thus, we can write Eq. (3) as $\partial_{zz}G(z) + \left(\frac{r}{b}e^{bz} + \left(q - \frac{rc}{b} - b\right)\right) \partial_z G(z) = 0$ as, $\partial_{xx}G(x) = \frac{1}{(bx+c)^2}\left(\partial_{zz}G(z) - b\partial_z G(z)\right)$, and, $\partial_x G(x) = \frac{1}{(bx+c)}\partial_z G(z)$.

Thus, it follows from (Polyanin and Zaitsev, 2003, 2.1.3-27) that the transformation of an equation of the above form with substitutions, $\xi = e^z$ Polyanin and Zaitsev (2003, 2.1.3-27) leads to the equation of the form, $\xi^2\partial_{\xi\xi}G(\xi) + \left(\frac{r}{b}\xi^b + \left(q - \frac{rc}{b} - b + 1\right)\right) \xi\partial_\xi G(\xi) = 0$, in Polyanin and Zaitsev (2003, 2.1.2-146).

Substitutions $\zeta = \xi^b$ and, $W(\zeta) = G(\xi)\zeta^{-k}$, where $k = \frac{1}{b}\left(\frac{rc}{b} - q + b\right)$ leads to the equation of the form $b^2\zeta\partial_{\zeta\zeta}W(\zeta) + \left(r\zeta + b\left(\frac{rc}{b} - q + b\right) + b^2\right)\partial_\zeta W(\zeta) + \frac{r}{b}\left(\frac{rc}{b} - q + b\right)W(\zeta) = 0$ in Polyanin and Zaitsev (2003, 2.1.2-108). Transforming into the Kummer's equation (Polyanin and Zaitsev, 2003, 2.1.2-108), it yields the general solution following Polyanin and Zaitsev (2003, 2.1.2-70)

$$W(\zeta) = C_1 {}_1F_1\left(k, k+1, \frac{-r}{b^2}\zeta\right) + C_2\zeta^k {}_1F_1\left(0, 1-k, \frac{-r}{b^2}\zeta\right)$$

where $k = \frac{1}{b}\left(\frac{rc}{b} - q + b\right)$, and, ${}_1F_1(a, b, z) = 1 + \frac{az}{b} + \frac{(a)_2 z^2}{(b)_2 2!} + \cdots + \frac{(a)_n z^n}{(b)_n n!}$ s.t. $a_n = a(a+1)(a+2)\cdots(a+n)$, which is the confluent hypergeometric function of first kind (for more details: Slater (1960) and Abramowitz and Stegun (1972)).

Thus, we can write, $W(\zeta) = C_1 {}_1F_1\left(k, k+1, \frac{-r}{b^2}\zeta\right) + C_2\zeta^k$.

By reverse transformation, $\zeta = \xi^b$ and, $W(\zeta) = G(\xi)\zeta^{-k}$, it yields,

$$G(z) = C_1 e^{bkz} {}_1F_1\left(k, k+1; \frac{-r}{b^2}e^{bz}\right) + C_2.$$

Substituting for x for z, we get,

$$G(x) = C_1(bx+c)^k {}_1F_1\left(k, k+1; \frac{-r}{b^2}(bx+c)\right) + C_2.$$

Applying boundary conditions, $G(x_d) = 1$, and $G(x_e) = 0$, it yields, $G(x_0) = \frac{E(x_0) - E(x_e)}{E(x_d) - E(x_e)}$, where, $E(x_i) = (bx_i + c)^k {}_1F_1\left(k, k+1; \frac{-r}{b^2}(bx_i + c)\right)$ for x_k denoting x_0, x_e, and x_d. Here, $k = \left(\frac{rc}{b^2} - \frac{q}{b}\right) + 1$.

Special case: EBE probabilities of population in the presence of immigration stochasticity

Here, we solve Eq. (3) in the main text, $A(x)\partial_x G(x) + \frac{1}{2}B(x) \partial_{xx}G(x) = 0$ for the case $A(x) = rx + q$, and, $B(x)/2 = c$, where we denote $c \equiv \sigma_p^2/2$.

Thus, equation, $A(x)\partial_x G(x) + \frac{1}{2}B(x)\partial_{xx}G(x) = 0$ has a general solution,

$$G(x) = \int_x C \exp\left(-\int_{x''} \frac{2A(x')}{B(x')}dx'\right)dx''$$

where C is a constant. After applying boundary conditions at $x_0 = x_d$ determined by $G(x_d) = 1$, and at $x_0 = x_e$ determined by $G(x_e) = 0$, we obtain,

$$G(x_0) = \frac{E(x_0) - E(x_e)}{E(x_d) - E(x_e)}$$

where, $E(x_i) = Erf_Z\left(\frac{q + rx_i}{\sqrt{2cr}}\right)$, or can also be expressed in terms of confluent hypergeometric function of first kind, as $E(x_i) = (q + rx_i) {}_1F_1\left(\frac{1}{2}, \frac{3}{2}, -\frac{(q+rx_i)^2}{2rc}\right)$. Here, x_i for subscript $i = 0, e, d$, and Erf_z is the error function.

Note that, $G(x_0) -> \left(\frac{x_0 - x_e}{x_d - x_e}\right)$ for $c \to$ inf.

Appendix B

Moment generating function of passage times of the population first hitting an upper boundary before a lower boundary

Following the methods in Gardiner (2004), here, we derive the nth *moment* of time for a population initially at x_0 in (x_d, x_e) to exit through an upper boundary x_d before first hitting a lower boundary x_e.

We define the total probability that population initially at $(x_0, 0)$ exited through x_d at time t given by the time integral of the probability current at x_d by

$$\begin{aligned} q_{x_d}(x_0, t) &= -\int_0^t dt' J(x_d, t' \mid x_0, 0) \\ &= \int_0^t dt' \left\{ -A(x_d)P(x_d, t' \mid x_0, 0) \right. \\ &\quad \left. + \frac{1}{2}\partial_{x_d}\left[B(x_d)P(x_d, t' \mid x_0, 0)\right] \right\}. \end{aligned}$$

Here, $P(x_d, t' \mid x_0, 0)$ is the transition probability density function that satisfies FPE corresponding to SDE Eq. (1). We let the time that population leaves (x_d, x_e) be T. Thus the probability that population has exited at time t given that it exited through x_d be

$$\Pr(T_{x_d} < t) = \frac{q_{x_d}(x_0, t)}{q_{x_d}(x_0, \infty)}.$$

Here, $q_{x_d}(x_0, t)$ is the probability that population exited through x_d at time t.

We note that $P(x_d, t' \mid x_0, 0)$ satisfies a backward Fokker–Planck equation.

From here onwards, we ignore subscript zero that indicates the initial position as a variable.

Thus,

$$\begin{aligned} &A(x)\partial_x q_{x_d}(x, t) + \frac{1}{2}B(x)\partial_{xx}q_{x_d}(x, t) \\ &= -\int_0^t dt'\partial_{t'}J(x_d, t' \mid x_0, 0) = -J(x_d, t' \mid x_0, 0) \\ &= \partial_t q_{x_d}(x, t). \qquad (B.1) \end{aligned}$$

Note that, for the time-homogeneous case (letting, $t \to \infty$) the above Eq. (B.1) reduces to Eq. (3) in the main text, that is, $A(x)\partial_x G(x) + \frac{1}{2}B(x)\partial_{xx}G(x) = 0$, such that, $G(x) \equiv q_{x_d}(x, \infty) = \int_0^\infty dt' J (x_d, t' \mid x, 0)$, which is the probability that population establishing before going extinct (or first hitting x_d before first hitting x_e) with boundary conditions, $G(x_d) = 1$, and $G(x_e) = 0$.

We write the mean exit time, given that population exits through x_d as

$$T_1(x_d, x) = \int_0^\infty t\partial_t \Pr(T_{x_d} < t)dt.$$

This is because, $\Pr(T_{x_d} < t)$ is the cumulative density function that population exited before time t of the probability density function, $\partial_t \Pr(T_{x_d} < t)$, that population exited at time t given that it exited through x_d.

Thus, we write the nth moment of the exit time, given that population exited through x_d as

$$\begin{aligned} T_n(x_d, x) &= \int_0^\infty t^n\partial_t \Pr(T_{x_d} < t)dt \\ &= \int_0^\infty t^n\partial_t\left(\frac{q_{x_d}(x, t)}{q_{x_d}(x, \infty)}\right)dt = \frac{\int_0^\infty t^n\partial q_{x_d}(x, t)}{G(x)}. \end{aligned}$$

After integration by part,

$$T_n(x_d, x) = \frac{\int_0^\infty [\partial t^n q_{x_d}(x, t) - nq_{x_d}(x, t)t^{n-1}\partial t]}{G(x)}.$$

Here we find, $\int_0^\infty \partial t^n q_{x_d}(x, t) = 0$, thus, it yields,

$$T_n(x_d, x)G(x) = -n \int_0^\infty q_{x_d}(x, t)t^{n-1}\partial t. \tag{B.2}$$

Multiplying Eq. (B.1) by t^{n-1}

$$\begin{aligned} &A(x)\partial_x t^{n-1} q_{x_d}(x, t) + \frac{1}{2}B(x)\partial_{xx} t^{n-1} q_{x_d}(x, t) \\ &\quad = t^{n-1}\partial_t q_{x_d}(x, t) = \partial_t t^{n-1} q_{x_d}(x, t) - (n-1) q_{x_d}(x, t)t^{n-2}. \end{aligned}$$

Integrating w.r.t t from 0 to infinity,

$$\begin{aligned} &A(x)\partial_x \int_0^\infty t^{n-1} q_{x_d}(x, t)\partial t \\ &\quad + \frac{1}{2}B(x)\partial_{xx} \int_0^\infty t^{n-1} q_{x_d}(x, t)\partial t \\ &\quad = \int_0^\infty \partial t^{n-1} q_{x_d}(x, t) - (n-1)\int_0^\infty q_{x_d}(x, t)t^{n-2}\partial t. \end{aligned}$$

As $\int_0^\infty \partial t^{n-1} q_{x_d}(x, t) = 0$, it yields,

$$\begin{aligned} &A(x)\partial_x \int_0^\infty t^{n-1} q_{x_d}(x, t)\partial t \\ &\quad + \frac{1}{2}B(x)\partial_{xx} \int_0^\infty t^{n-1} q_{x_d}(x, t)\partial t \\ &\quad = -(n-1)\int_0^\infty q_{x_d}(x, t)t^{n-2}\partial t. \end{aligned}$$

Substituting Eq. (B.2) on the above, and denoting $x = x_0$, finally it yields,

$$\begin{aligned} &A(x_0)\partial_{x_0} G(x_0)T_n(x_d, x_0) + \frac{1}{2}B(x_0)\partial_{x_0x_0} G(x_0)T_n(x_d, x_0) \\ &\quad = -nG(x_0)T_{n-1}(x_d, x_0). \end{aligned} \tag{B.3}$$

The boundary condition at $x_0 = x_d$ is determined by $G(x_d) = 1$, $T_n(x_d, x_d) = 0$, and hence, $G(x_d)T_n(x_d, x_d) = 0$. The boundary conditions at $x_0 = x_e$ is determined by $G(x_e) = 0$, and hence, $G(x_e)T_n(x_d, x_e) = 0$. The cases $n = 1, 2$ yield the mean and the second moments of first passage times respectively. By substituting $G(x_0)$ from the solution to Eq. (3) (main text), we solve Eq. (B.3) above numerically for $T_n(x_d, x_0)$ for the nth moment of first passage time iteratively for the population first hitting an upper threshold x_d, before a lower threshold x_e.

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