Ilkka Hanski: The legacy of a multifaceted ecologist

The interplay between immigration and local population dynamics in metapopulations

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Stochastic models of closed populations predict eventual extinction with certainty. Consequently, their behavior is often characterized by the quasi-stationary state, i.e. the long-term distribution of population sizes conditional on non-extinction. In contrast, models which allow for immigration exhibit a regular stationary state. At the limit of a low immigration rate, a population is expected to alternate between three states: the quasi-stationary state of a closed population, the extinction state, and the transient phase during which a newly arrived immigrant either establishes a new population or fails to do so. We develop this argument into a simple and intuitive framework that can be used to assess the effect of immigration in a general class of population models. We exemplify the framework for models in which immigrants arrive either singly or in groups, for models with an Allee effect, for models with environmental stochasticity, and for models leading to metapopulation dynamics.

Introduction

If a sequence of adverse events drives a closed population to extinction, it will never recover as there are no individuals to produce new ones, and thus stochastic models of closed populations predict eventual extinction with certainty. Depending on the model structure, forms of stochasticity incorporated, and the parameter regime, the expected time to extinction may range from the time scale of individual life times to astronomically long time scales (Lande 1993, Nåsell 2001, Grimm & Wissel 2004, Melbourne & Hastings 2008, Ovaskainen & Meerson 2010). In cases where the expected time to extinction is long relative to the life times of individuals, it is rele-

vant to examine the nature of population dynamics before the eventual extinction takes place. Mathematically, such behavior is characterized by the quasi-stationary distribution q, i.e. the probability distribution of population sizes conditional on the system having not gone extinct yet, after long enough time so that the influence of the initial population size has vanished (Darroch & Seneta 1967, Gyllenberg & Silvestrov 1994, 2008, Ovaskainen 2001). If the initial population size is sampled from the quasi-stationary state, the time until extinction is exponentially distributed under very general conditions, and thus the mean time to extinction τ is a sufficient statistic for prediction the distribution of extinction times (Grimm & Wissel 2004).

In the real world, populations are subject to emigration and immigration and consequently they are not closed. If a population goes extinct, immigrants originating from extant populations may re-colonize the patch, leading to colonization–extinction dynamics in mainland–island systems (MacArthur & Wilson 1963, 1967, Brown & Kodric-Brown 1977) or metapopulation dynamics in patch networks (Hanski 1999). Further, immigrants from surrounding populations can contribute to the dynamics of existing local populations both demographically and genetically. In particular, a continuous immigration process can lead to a reduced extinction rate (Dey & Joshi 2013), termed the *rescue effect* by Brown and Kodric-Brown (1977). Mathematically, the introduction of immigration, with no matter how small a rate, prevents the extinction state of zero population size of being an absorbing state (e.g. Matis & Kiffe 1999). In this case, the long-term behavior of the system can be characterized by the stationary state p describing the long-term probability distribution of population sizes. The zero state p_0 of this distribution measures the fraction of time that the system is found extinct. As discussed above, in models without immigration $p_0 = 1$, whereas in models with immigration $p_0 < 1$.

A variety of mathematical and numerical methods is available for computing either exactly or approximately quantities such as the mean time to extinction and the stationary and quasi-stationary distributions (Darroch & Seneta 1967, Gyllenberg & Silvestrov 1994, 2008, Ovaskainen 2001, Doering *et al*. 2005, Ovaskainen & Meerson 2010). One starting point is the master equation, which is a set of differential equations describing the time evolution of the vector containing the probabilities by which the population is of a given particular size. The master equation can be solved numerically or approximated by a diffusion approximation (Lande *et al*. 1998, Drake & Lodge 2006) or by the Wentzel-Kramers-Brillouin (WKB) approximation (Assaf & Meerson 2010). Another starting point is the moment-generating function, which produces an infinite hierarchy of equations (for the mean, variance, skew, etc.), which can be solved approximately with moment-closure methods (Matis & Kiffe 1999, 2004). In

the context of island biogeography, MacArthur and Wilson (1963) used the latter approach to derive equations for the mean and variance for the number of species expected to be found from an island.

Understanding the influence of immigration on local population dynamics is relevant in the context of mainland–island models (MacArthur & Wilson 1967, Brown & Kodric-Brown 1977), for predicting biological invasions (Drake & Lodge 2006), and for assessing the metapopulation dynamics of a set of local populations connected by dispersal (Hanski 1999). While the mean time to extinction and quasi-stationary state are central parameters for predicting the fate of an established (meta)population, the influence of immigration, in particular the process of colonization, also depends on the probability of reaching the established state (Grimm & Wissel 2004), called the establishment curve if considered a function of initial population size (Drake & Lodge 2006). Since the pioneering works of island biogeography (MacArthur & Wilson 1963, 1967, Brown & Kodric-Brown 1977), the influence of immigration on local dynamics has been studied from several points of view: immigration may stabilize chaotic behavior (Ruxton 1995, Stone & Hart 1999), it may sustain populations in sink patches (Eager *et al*. 2014), and influence demographic (Matis & Kiffe 1999, 2004) and genetic (Robert *et al*. 2003) population dynamics and consequently metapopulation dynamics (Lande *et al*. 1998). Intuitively, if the immigration rate is much smaller (or conversely, much larger) than the extinction rate, the population is likely to be extinct (or conversely, extant) for the majority of time. If the two rates are comparable, the system is expected to exhibit colonization–extinction dynamics.

In this paper, we build on the work by Lande *et al*. (1998) to develop a general and intuitive framework for exploring the connections between closed population models and corresponding models with immigration. We illustrate this framework for mainland–island models, starting with a version of the stochastic logistic model, and then moving to more general models by adding environmental stochasticity (Lande 1993), Allee effects (Dennis 2002) and the possibility of immigrants arriving in groups. Finally,

we relax the assumption of a constant immigration rate by considering a metapopulation model in which the immigration rate in a focal patch depends on the population sizes in the other habitat patches. In particular, we illustrate how the knowledge of three parameters that characterize the behavior of a closed population model (mean time to extinction, mean population size conditional on non-extinction, and the probability of successful establishment when starting from a low population size) can be used for deriving a stochastic patch occupancy model (SPOM) that mimics the behavior of the individual based model (IBM) at the level of colonization–extinction dynamics.

## Influence of immigration to local population dynamics

We focus on stochastic population models formulated at the level of discrete individuals rather than models which approximate population density as a continuous variable, thus including demographic stochasticity by construction. Further, we consider models that can be described as a continuous time Markov process, thus allowing for overlapping generations. In single-step models of a closed population, the only allowed transitions are births ($n \rightarrow n + 1$, with rate λ_n) and deaths ($n \rightarrow n – 1$, with rate μ_n) of individuals. In more general models, multiple births or deaths may take place at the same time, the former e.g. due to a litter size distribution (Matis & Kiffe 2004), and the latter e.g. due to environmental stochasticity inducing the simultaneous death of several individuals (Cairns *et al*. 2007).

While the framework to be developed here is of general nature, we start from a stochastic version of the Verhulst model (Nåsell 2001) in which the per-capita birth rate $\lambda_n/n = B$ is independent of the current population density n, whereas the per-capita death rate $\mu_n/n = D(1 + n/N)$ increases with population density. The system size parameter N represents the population size in which the death rate is doubled from the density-independent rate D. The deterministic skeleton of this model, which ignores demographic stochasticity, reads as

$$\frac{dn}{dt} = (B - D)n - D\frac{n^2}{N}.$$

The deterministic model has two fixed points: one at the extinct state $n^* = 0$ and the other one at the carrying capacity $n^* = K := (B/D – 1)N$. If the non-trivial equilibrium state is positive (i.e., if $B > D$), it is stable, and thus the deterministic model converges to the carrying capacity if starting from any positive initial density. In the stochastic variant of the model, the mean time to extinction is exponentially long, assuming that the system is above the deterministic extinction threshold ($B > D$). If the system is below the extinction threshold ($B < D$), the expected time to extinction is very short (Nåsell 2001). The mean time to extinction, starting from any initial population size, can be computed exactly for any single-step model (Doering *et al*. 2005). However, in the general case the exact formula is too complex to provide analytical insights, and thus simpler formulae for large N approximations are often applied in practice (Ovaskainen & Meerson 2010).

We add immigration to the stochastic logistic model by assuming that immigrants arrive at a rate r, thus modifying the birth rate to $\lambda_n = Bn + r$. While this model has been treated before using the cumulant truncation analysis (Matis & Kiffe 1999) and is actually simple enough to be solved exactly (Meerson & Ovaskainen 2013), we continue here with a heuristic approach. Our aim is to simplify the full model into a stochastic patch occupancy model (SPOM; Moilanen 1999) consisting of just two states, the occupied state ($o = 1$) and the extinct state $o = 0$. Assuming that the population size reaches the quasi-stationary state rapidly after the colonization, the transition rate from occupied to empty ($o = 1 \rightarrow o = 0$) equals $e = 1/\tau$, where τ is the mean time of the closed populations model. Less trivially, how should the colonization ($o = 0 \rightarrow o = 1$) rate c be computed? As new individuals arrive at rate r, at first sight the choice $c = r$ may seem reasonable. However, this would overestimate the effective colonization rate, as during the transient period after the immigrant arrives the population size is expected to be small, and thus the extinction risk is greater than after the population has reached the quasi-stationary state (Grimm & Wissel 2004). To account for the transient, we
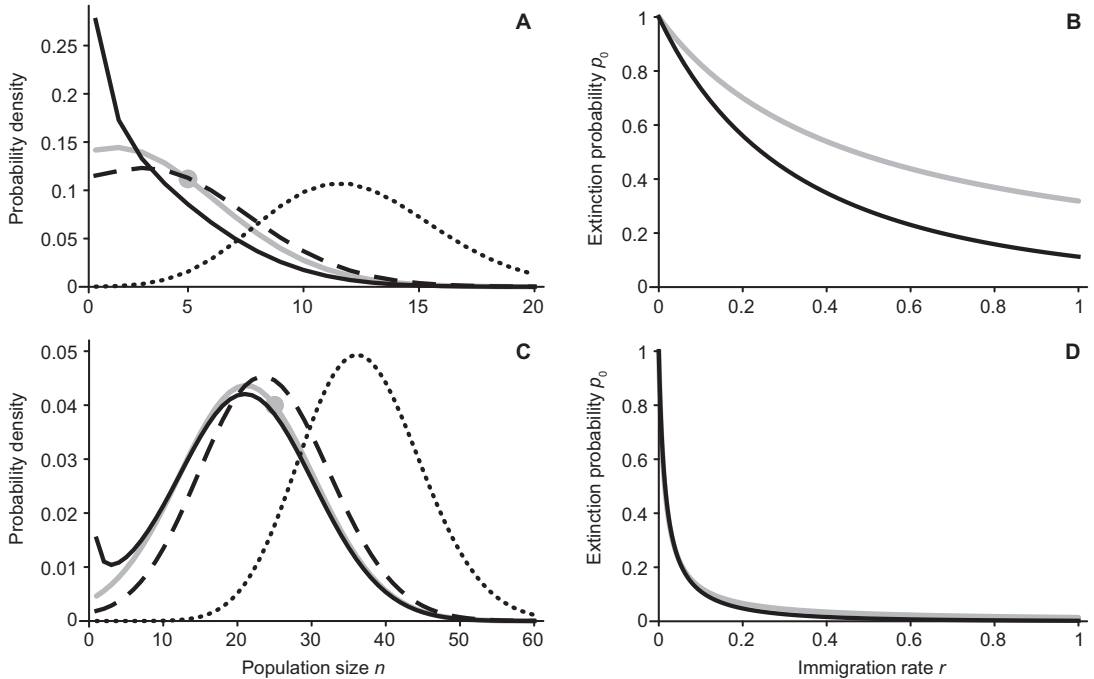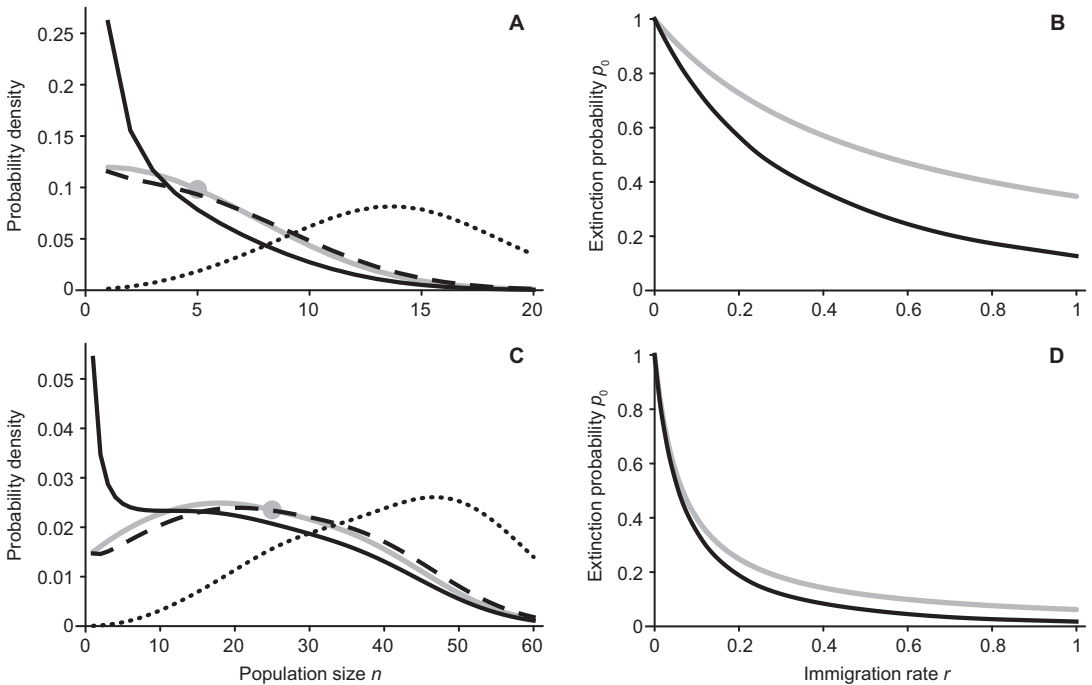
Fig. 1. The behavior of the stochastic logistic model with and without immigration. (**A** and **C**) The quasi-stationary distributions of the model without immigration (gray lines) and the stationary distributions (truncated for positive population sizes) of the model with immigration, assuming the immigration rates of $r = 10^{-4}$ (black solid lines), $r = 1$ (black dashed lines) and $r = 10$ (black dotted lines). The large gray dots depict the carrying capacity of the deterministic model. (**B** and **D**) The probability p_0 of finding the patch empty in the model with immigration, the black line showing the exact result and the gray line the prediction by Eq. 1. In **A** and **B**, the carrying capacity parameter N is set to 10, whereas in **C** and **D** to 50. Other parameters are $B = 1.5$ and $D = 1$.

follow Lande *et al*. (1998) by letting s_n denote the probability that the population goes extinct before establishment (i.e., before reaching the quasi-stationary state) if starting from a low number of n individuals. To compute s_n, we utilize the fact that the system is at low density and thus density dependence can be ignored. Without density dependence, the population persists indefinitely if it has a positive growth rates and escapes the transient phase. This yields a simple and well-defined method for computing s_n without the need to define an arbitrary level of abundance at which the immediate risk of extinction is negligible (Drake & Lodge 2006). For the logistic stochastic model, a simple calculation (Meerson & Ovaskainen 2013) shows that $s_n = (D/B)^n$, which result was given also by Nisbet and Gurney (1982). After an immigrant arrives, the population thus goes either soon extinct with probability $s_1 = D/B$ or establishes with probability $1 - D/B$, yielding the effective

colonization rate estimate $c = r(1 - s_1) = r(1 - D/B)$. The stationary probability of finding the system extinct (i.e., one minus the incidence of occupancy, Hanski 1994), is

$$p_0 = \frac{e}{e+c} = \frac{1}{1+c\tau} = \frac{1}{1+r(1-D/B)\tau}. \quad (1)$$

At the limit of a large carrying capacity ($K \gg 1$) and a low immigration rate ($r \ll 1$), Eq. 1 can be shown to hold in mathematically rigorous manner (Meerson & Ovaskainen 2013). For small carrying capacity or large immigration rate, the influence of the immigration rate on local population dynamics is more complex (Fig. 1). If the carrying capacity K is small, the population has a high extinction risk (Fig. 1B) and consequently the population spends much time at the extinct state or in the transient state from immigration to extinction (Fig. 1A). With a very high immigration rate r, the continuous influx of immigrants is partly able to counter-
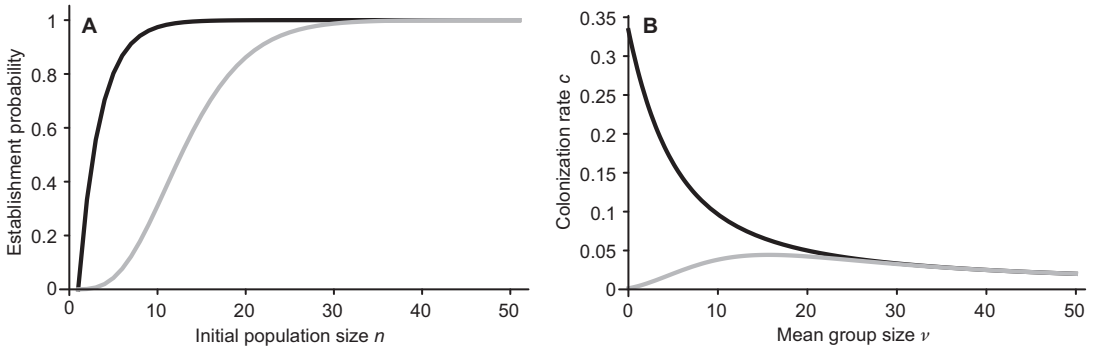
Fig. 2. The behavior of the stochastic logistic model with catastrophes, with and without immigration. This figure is identical to Fig. 1, but shows the behavior of logistic model supplemented with catastrophes. Parameter values as in Fig. 1 except for $D = 0.8$, $\rho = 0.4$ and $\theta = 0.5$.

act the effects of density-dependent mortality (Fig. 1A–C), and thus the system stays much above the carrying capacity.

The heuristic derivation presented above for the stochastic logistic model allows one to examine the interplay between local dynamics and immigration also in more complex models. As an example, we next add to the stochastic logistic model environmental stochasticity in the form of a birth-death-catastrophe model (Cairns *et al.* 2007). Thus, we assume that on top of the baseline death rate of the stochastic logistic model, catastrophes appear at a rate ρ. When a catastrophe takes place, each individual dies with probability θ, and thus the number of deaths is binomially distributed with parameters n and θ. As the catastrophes influence the entire population simultaneously, the population undergoes large fluctuations, as reflected by the wide stationary distribution of population sizes (Fig. 2). Consequently, under environmental stochasticity also large populations have a non-negligible extinction risk unlike in models with demographic stochasticity only (Figs. 1 and 2). Figure 2 suggests

that the intuitive approximation of Eq. 1 (with c and τ computed numerically) holds also in this model at the limit of low immigration rate and low extinction risk. Further, the quasi-stationary distribution of the closed population model predicts well the stationary distribution of the model with immigration, assuming that the transient phase from immigration to establishment is short so that the system reaches the quasi-stationary state soon after colonization, and that immigration rate is low so that immigrants do not influence much the local population size when the system is occupied (Fig. 2).

As another example, we return to the model without environmental stochasticity, but assume the population exhibits an Allee effect, so that the per-capita growth rate is not maximized at low density. Allee effects have been shown to play an important role in slowing the establishment and spread of non-native species (Tobin *et al.* 2011). Following earlier work (Matis & Kiffe 1999, Dennis 2002, Meerson & Ovaskainen 2013), we modify the per-capita birth rate to $\lambda_n/n = Bn/(n + n_0)$, so that for $n_0 > 0$ it increases with popu-

Fig. 3. The behavior of the stochastic logistic model with an Allee effect, and individuals arriving in groups. (**A**) The probability $1 - s_n$ by which the population will establish if starting from an initial population size of n. (**B**) The colonization rate c (Eq. 2) as a function of the mean group size ν. The black lines represent a model without an Allee effect ($n_0 = 0$) and the gray lines a model with an Allee effect ($n_0 = 5$). Other parameters are $N = 50$, $B = 1.5$ and $D = 1$.

lation size asymptotically to the value of B. In the part of the parameter space that allows for persistence, the deterministic counterpart of this model has three fixed points, which we denote by $n^* = 0$, $n^* = n_c$ and $n^* = K$. Here K is the carrying capacity which the population reaches if it starts from an initial population size that is larger than the critical population size n_c. If the initial population size is smaller than n_c, the population declines to extinction ($n^* = 0$), which state is stable in this model unlike in the model without the Allee effect. In the stochastic model, the Allee effect modifies the probability of establishment as (Meerson & Ovaskainen 2013) $s_1 = 1 - (1 - D/B)^{n_c+1}$ thus greatly reducing it as the deterministic drift downwards at low population sizes makes it difficult to reach the critical population size n_c during the establishment phase.

Let us then counteract the Allee effect by modifying the immigration process so that the individuals arrive in groups instead of arriving singly. Let r_n denote the rate at which groups of size n arrive, so that the total immigration rate is $r = \sum_n r_n n$. As $1 - s_n$ is the probability of successful establishment if starting from population size n, the rate of successful establishment becomes $c = \sum_n r_n (1 - s_n)$. We assume that group sizes are Poisson distributed with mean ν, so that the arrival rate of groups (of any size) is r/ν, where the mean arrival rate r is kept at a constant value independently of the parameter ν. Assuming no Allee effect ($n_0 = 0$), it is easy to see (Meerson & Ovaskainen 2013) that the colonization rate is

$$c = \frac{1 - e^{-\nu(B-D)/B}}{\nu} r. \qquad (2)$$

We note that at the limit of $\nu \to 0$, it holds that $c \to r(1 - D/B)$, thus reproducing the above result for the stochastic logistic model with independently arriving migrants. Increasing the group size increases the establishment probability per colonization attempt (Fig. 3), but this comes with the cost immigration events taking place less frequently as the per-capita arrival rate r is kept constant. In the model without an Allee effect, the colonization rate (Eq. 2) decreases monotonically with ν, and thus the colonization rate is maximized if the individuals arrive singly. However, an Allee effect changes the balance, as now the colonization rate is maximized with group size somewhat larger than the critical population size n_c (Fig. 3). This result is similar to that of Soubeyrand and Laine (2017), who found that an intermediate group size of dispersing propagules maximizes metapopulation persistence in the presence of an Allee effect.

Influence of immigration on metapopulation dynamics

The above examples relate to mainland-island situations with a fixed immigration rate. We next relax this assumption by considering a metapopulation persisting in a balance between local extinctions and recolonizations. To do so, consider a

network of habitat patches, each of which follows the stochastic logistic model with environmental stochasticity but without an Allee effect. To allow for recolonization, we assume that a newborn individual migrates from patch i to patch j with probability ε_{ij}. Our aim is to approximate the full individual based model (IBM) with a stochastic patch occupancy model (SPOM), in which the dynamic variable is the vector o of occupancy states, with $o_i = 0$ if patch i is empty and $o_i = 1$ if it is occupied. We denote for patch i by τ_i the mean time to extinction, by $1 - s_{1i}$ the probability of successful establishment by a single immigrant, and by $\overline{n}_i$ the mean population size, averaged over the quasi-stationary distribution, each of which we computed numerically with a master equation approach. The question that we address here is whether these three parameters (τ_i, s_{1i}, $\overline{n}_i$), all of which are properties of a closed population model, are sufficient for predicting metapopulation dynamics at the patch occupancy level. Proceeding as above, we assume that the extinction rate of patch i can be approximated by $e_i = 1/\tau_i$ and that the colonization rate of patch i can be approximated by $c_i = r_i(1 - s_{1i})$. In this case the immigration rate r_i is a dynamic variable, which we approximate by $r_i = B\sum_j \varepsilon_{ji}\overline{n}_j o_j$. Figure 4 illustrates that the dynamics of such constructed SPOM well coincide with the occupancy dynamics of the IBM. Note that in this example the patch network is heterogeneous with much variation in carrying capacity, and consequently with much variation in mean time to extinction.

Discussion

In this paper, we have presented a simple but general framework to link individual, population and metapopulation level processes. To do so, we have first examined how the addition of a constant immigration rate leads to colonization–extinction dynamics in stochastic population models. As a first approximation, the extinction rate can be derived from the mean time to extinction of the corresponding model without immigration, and the colonization rate can be derived as the product of the immigration rate and the probability of establishment after an immigrant arrives (Lande *et al*. 1998, Meerson & Ovaskainen 2013). We

have illustrated that this approximation holds at the limit of low immigration rate for many kinds of models, including models with environmental stochasticity, Allee effects, and immigrants arriving singly or in groups. We have then extended the viewpoint from mainland–island models to metapopulation models by assuming that immigration rate is not constant, but that it depends on the states of the other populations and the movement rates of individuals between the populations.

Conceptually, the link from the individual-level processes of births, deaths and movements to the metapopulation level processes of extinctions and colonizations is evident. On the one hand, local extinction appears when the last individual of a population dies, and thus the local extinction rate depends on the functional forms and parameters of the model describing local population dynamics. On the other hand, recolonizations depend on the availability of source populations, on the migration rates between the populations, and on the probability than migrants will reach an empty patch and successfully establish a local population (Lande *et al*. 1998). Metapopulation models that combine local population dynamics and migration have been developed both in the deterministic (e.g. Hastings & Wolin 1989, Gyllenberg & Hanski 1992) and stochastic (e.g. Ovaskainen & Hanski 2004, Harrison *et al*. 2011, Eriksson *et al*. 2014) frameworks, but the complexity of such models has made it difficult to obtain analytical insights. Consequently, much of metapopulation ecology has been developed in the context of patch occupancy models (SPOMs), which ignore transient dynamics after colonization and thus classify the population sizes simply to two classes, occupied or empty (Hanski 1999). Our work provides a link between individual-based models and SPOMs by using the results derived for mainland-island populations as a building block. In particular, we have shown how SPOMs can be derived for heterogeneous patch networks from three key parameters that can be derived (analytically or numerically) from a mainland-island model (extinction rate of established populations, establishment probability following an immigration event, and mean population size), and the dispersal rates among populations. Our simulations have demonstrated that such constructed SPOM
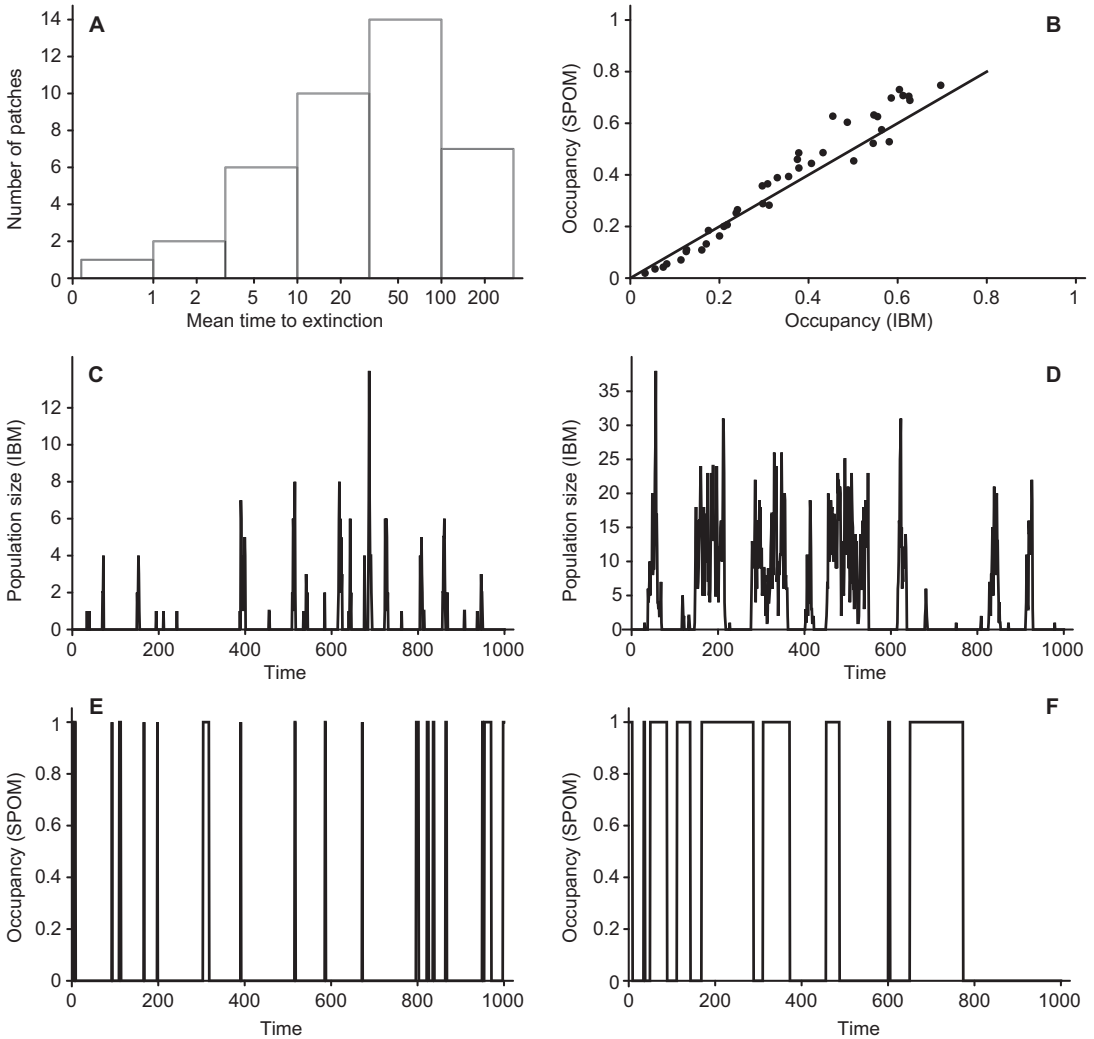
Fig. 4. A comparison between an individual-based model (IBM) of metapopulation dynamics and its stochastic patch occupancy model (SPOM) approximation. The model is the logistic stochastic model with environmental stochasticity described in the main text, with 40 patches with carrying capacities $N = 1, 2, 3, …, 40$, and the other parameters being identical for all patches: $B = 1.5$, $D = 0.8$, $\rho = 0.2$ and $\theta = 0.5$. We assume that the newborn individuals emigrate from their natal patch with probability 0.005, in which case they migrate to a patch selected with equal probability among all the other patches. (**A**) The distribution of extinction times over the patches. (**B**) The comparison of the patch-specific occupancy probabilities between the IBM and the SPOM, both based on a simulation of the quasi-stationary state (at the metapopulation level) during 10 000 time units. (**C** and **D**) The dynamics of the IBM for patches with carrying capacities of $N = 5$ and of $N = 20$, respectively. (**E** and **F**) The dynamics of the SPOM for the same patches. For both models, the population dynamics were simulated with the Gillespie algorithm (Gillespie 1977).

can well approximate an individual-based model in a heterogeneous patch network.

Acknowledgements

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