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Evolution in heterogeneous populations: From migration models to fixation probabilities

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ABSTRACT

Although dispersal is recognized as a key issue in several fields of population biology (such as behavioral ecology, population genetics, metapopulation dynamics or evolutionary modeling), these disciplines focus on different aspects of the concept and often make different implicit assumptions regarding migration models. Using simulations, we investigate how such assumptions translate into effective gene flow and fixation probability of selected alleles. Assumptions regarding migration type (e.g. source-sink, resident pre-emption, or balanced dispersal) and patterns (e.g. stepping-stone versus island dispersal) have large impacts when demes differ in sizes or selective pressures. The effects of fragmentation, as well as the spatial localization of newly arising mutations, also strongly depend on migration type and patterns. Migration rate also matters: depending on the migration type, fixation probabilities at an intermediate migration rate may lie outside the range defined by the low- and high-migration limits when demes differ in sizes. Given the extreme sensitivity of fixation probability to characteristics of dispersal, we underline the importance of making explicit (and documenting empirically) the crucial ecological/ behavioral assumptions underlying migration models.

1. Introduction

Evolution and adaptation occur through the initial spread and fixation of new alleles and genotypes in natural populations. How invasion and fixation occur is central to our understanding of adaptation to novel environments as well as to the maintenance of genetic diversity or co-evolutionary dynamics (Gandon et al., 1996; Thrall and Burdon, 1997; Turner and Elena, 2000; Morgan et al., 2005). Such information is also particularly important to prevent the spread of viruses or genes for drug and pesticide resistance (Munster et al., 2007; Tyutyunov et al., 2008).

The dynamics and probability of fixation for new alleles obviously depend on local population size and selection coefficients, but also on connectivity with other populations, which may differ in size and selective pressures (Tachida and Iizuka, 1991, Gavrilets and Gibson, 2002, Whitlock, 2003, Whitlock and Gomulkiewicz, 2005, Vuilleumier et al., 2008; see review by Patwa and Wahl, 2008). Migration rate, in particular, has been shown to strongly affect fixation probabilities in structured and heterogeneous populations (Kimura, 1970; Tachida and Iizuka, 1991; Barton, 1993; Gavrilets and Gibson, 2002; Whitlock, 2003).

Migration (or dispersal) is in fact increasingly recognized as a key issue in many disciplines of population biology, such as population genetics, evolutionary modeling, metapopulation dynamics, or behavioral ecology (e.g. Clobert et al., 2001). These different disciplines, however, clearly focus on different aspects of the concept, and have therefore different views of what migration means and why it matters. How the "migration" concept of a behavioral ecologist translates into something useful for a population geneticist is not always clear.

According to population geneticists, the quantity of interest to predict gene dynamics and evolutionary processes is the *effective backward migration rate*, m_{ij}^{B}, which measures the proportion of reproducers in deme j that originated from deme i. This, together with drift and patterns of local selection, will determine the spread and fixation of new alleles. However, the main determinants of gene flow (in particular how forward dispersal rate translates into effective backward migration rate) are not of primary concern for this discipline, and neither are the proximate or ultimate causes of dispersal.

Evolutionary models of migration, by contrast, focus on ultimate causes (i.e. the selective forces driving forward dispersal). Fitness costs (e.g. mortality during dispersal) and fitness benefits (e.g. effective reproduction as an immigrant) are balanced in order to derive evolutionary stable patterns of dispersal (i.e. those that maximize inclusive fitness). Provided dispersal costs are not too high, it should result in ideal free distributions (Fretwell and Lucas, 1970), in which individual benefits equalize over the landscape. Given that benefits are density dependent, this should induce a balanced dispersal, in which immigration matches emigration (McPeek and Holt, 1992; but see Leturque and Rousset, 2002).

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Metapopulation dynamics focuses on the demographic consequences of dispersal, and often assumes a constant (species-specific) forward migration rate. How this rate translates into backward dispersal rates will depend on dispersal costs and distance between populations (Vuilleumier and Perrin, 2006), but also on their size or productivity (for a constant rate, large populations send more migrants than small ones Hanski, 1999; Hanski and Ovaskainen, 2000). Differences in sizes or productivity may result in large asymmetries, leading to source-sink metapopulation systems (Pulliam, 1988; Morris, 1991).

Behavioral ecology, finally, focuses on proximal causes, both in terms of emigration (e.g. which ecological or demographic circumstances motivate or refrain individual decisions to disperse?) and immigration (e.g. which social circumstances facilitate or prevent successful settlement?). Depending on the patterns of local competition, territoriality, or kin cooperation, a given forward migration rate may translate into very diverse effective backward migration rates (e.g. Danchin et al., 2008).

Reliable empirical estimates of dispersal rate and gene flow are scarce. Mark-recapture studies may provide information on forward or backward migration rates (White and Garrott, 1990; Lee, 1992; Bennetts et al., 2001), but not on gene flow, and are often limited to local scales (long-distance migrants are usually missed; Koenig et al., 1996; Nathan et al., 2003). Genetic assignment methods may detect long distant migrants, but not effective gene flow. Genetic estimates of population structure (F_{ST}) have been used to evaluate gene flow, but provide very crude estimates subject to many biases (Whitlock and McCauley, 1999). New methods are emerging to estimate effective migration rates between populations (e.g. Beerli and Felsenstein, 2001) but are not yet in a position to clarify the relationships between forward and effective backward migration rate. Such relationships are clearly complex functions that depend on interactions between population structure and species-specific behavioral features.

In this paper we investigate such relationships under a variety of settings, in order to contrast and explore the consequences of diverse assumptions commonly found in the migration literature in terms of gene flow and fixation. We ask in particular how forward migration rate (a quantity documented by behavioral ecologists and implemented in metapopulation models) may translate into effective gene flow and fixation probability (the quantity of importance for population geneticists) when local populations vary in size and selective pressures. In order to do this, a first step is to properly characterize the main features of dispersal processes.

2. Characterizing migration

Migration might be characterized by its rate, type, and pattern. *Migration rate* is the proportion of individuals in a population that are migrants. A distinction has to be made (Karlin, 1982) between forward migration rate m_{ij}^F (or emigration rate) which measures the proportion of individuals from deme i that migrate to deme j, and backward migration rate m_{ij}^B (or immigration rate) which measures (after dispersal) the proportion of individuals in deme j originating from deme i. Effective backwards migration rate refers to those immigrants which successfully reproduce in their new population. For a given emigration rate, the absolute number of emigrants relates to the size or productivity of source populations. How these emigrants translate into an immigration rate depends on the size of the receiving population relative to the source, on population structure (fragmentation), as well as on migration pattern (e.g. island vs. stepping stone). Whether immigrants will generate an effective gene flow will be conditional on their successful settlement, and whether this gene flow will translate into fixation will also depend on local population size and selective pressures.

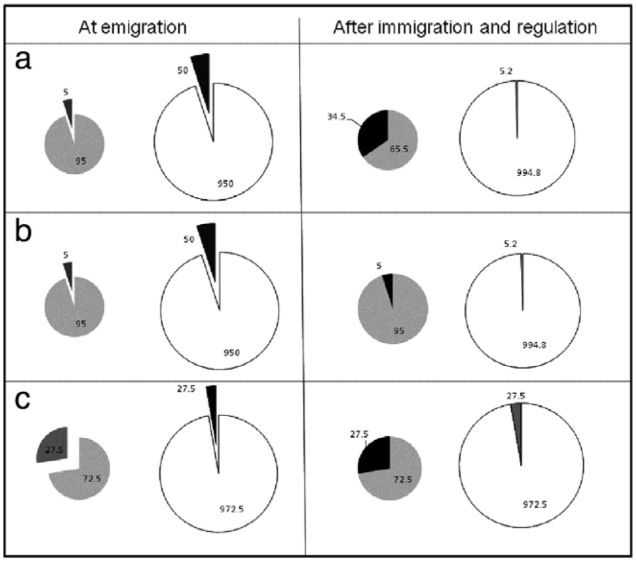

Fig. 1. Two-demes metapopulation systems showing the effects of different migration types ((a) source-sink, (b) resident pre-emption and (c) balanced dispersal) on emigration (left) and effective immigration (right). Parameter values set to $N_1 = 100$, $N_2 = 1000$, and average emigration rate $m^F = 0.05$. Detail values for migration rates are presented in Table 1.

To investigate these relationships we will contrast three *migration types* (Fig. 1) reflecting assumptions commonly found in different fields of population biology. In the first type (Fig. 1(a), Table 1) the emigration rate is assumed constant (i.e., independent of local deme size and productivity, so that large and productive demes send more emigrants than small and/or less productive demes), and settlement probability is assumed identical for immigrants and residents. When populations differ in size or productivity, this will result in a *source-sink* dynamics, where immigration exceeds emigration in smaller and/or less productive demes (Pulliam, 1988; Holt, 1996; Holt and Gomulkiewicz, 1997; Kawecki, 2000; Peck et al., 2000; Bolnick and Nosil, 2007). The smaller demes are actually better referred to as relative sinks, since they would be viable even without immigration (Kawecki, 2008).

In the second type (Fig. 1(b), Table 1), emigration rate is also assumed constant and independent of local deme size or productivity, but residents benefit from a competitive advantage over immigrants, and settle in priority (Danchin et al., 2008). Formally, only the spots left by emigrants are available for immigrants. Immigration thus exactly balances emigration in small demes, but not in large ones, in which emigration still exceeds immigration. This type will be referred to as *resident pre-emption*.

The third type is the *balanced dispersal* underlying ideal-free-distribution models (Fretwell and Lucas, 1970; McPeek and Holt, 1992; Diffendorfer, 1998) (Fig. 1(c), Table 1), in which immigration exactly compensates emigration in every deme ($m_{ij}^F = m_{ji}^B$). The absolute numbers of immigrants and emigrants are equal for all demes ($m_{ij}^F N_i = m_{ji}^F N_j$), so that large and/or more productive demes show smaller per capita emigration-and immigration rates.

Regarding *migration patterns*, finally, we will contrast the two classical models most frequently found in the literature, which can be considered as the extrema of a continuum of isolation by distance. On one hand, the island model (Wright, 1943) considers n equivalent demes homogeneously connected through a common pool of migrants, so that any emigrant individual has the same probability of reaching any of the $n - 1$ other non-natal demes. On the other hand, the linear stepping-stone model (Kimura and Weiss, 1964), assumes that migrants can only reach the neighboring demes.