Does colonization asymmetry matter in metapopulations?

Séverine Vuilleumier* and Hugh P. Possingham

The Ecology Centre, University of Queensland, Brisbane, Queensland 4072, Australia

Despite the considerable evidence showing that dispersal between habitat patches is often asymmetric, most of the metapopulation models assume symmetric dispersal. In this paper, we develop a Monte Carlo simulation model to quantify the effect of asymmetric dispersal on metapopulation persistence. Our results suggest that metapopulation extinctions are more likely when dispersal is asymmetric. Metapopulation viability in systems with symmetric dispersal mirrors results from a mean field approximation, where the system persists if the expected per patch colonization probability exceeds the expected per patch local extinction rate. For asymmetric cases, the mean field approximation underestimates the number of patches necessary for maintaining population persistence. If we use a model assuming symmetric dispersal when dispersal is actually asymmetric, the estimation of metapopulation persistence is wrong in more than 50% of the cases. Metapopulation viability depends on patch connectivity in symmetric systems, whereas in the asymmetric case the number of patches is more important. These results have important implications for managing spatially structured populations, when asymmetric dispersal may occur. Future metapopulation models should account for asymmetric dispersal, while empirical work is needed to quantify the patterns and the consequences of asymmetric dispersal in natural metapopulations.

Keywords: asymmetric dispersal; metapopulation; population modelling; Monte Carlo simulation

1. INTRODUCTION

Metapopulations exist as a dynamic tension between local extinctions and the colonization of empty patches (Levins 1969). Dispersal and associated colonization events determine the distribution of organisms in a metapopulation (Fretwell & Lucas 1970), the spatial dynamics of the metapopulation (Hanski 1999) and genetic variation among and within populations (Wright 1943).

Dispersal is a process at the interface of ecology, population genetics, ethology and evolution. In metapopulation ecology, dispersal or migration refers to the overall process of individual movements, while colonization means a successful dispersal event from an occupied patch to an empty patch (Hanski 1999). In this paper, we use the term dispersal to mean the general process of individuals leaving a habitat patch and travelling, potentially, to other habitat patches; colonization refers, specifically, to an individual or a group of individuals successfully establishing a new population in a previously empty patch.

Measuring and understanding how colonization events occur is a major empirical challenge in metapopulation ecology (Hansson 1991; Doebeli & Ruxton 1998; Hanski & Ovaskainen 2000). One issue that has rarely been considered is the possibility that dispersal events and hence, colonization probabilities are biased in one direction rather than perfectly symmetric.

Traditionally, spatial population models, whether they are genetic or demographic, assume that dispersal between subpopulations is symmetric (Dias 1996; Hanski 1999; Whitlock & Mccauley 1999). This is assumed despite the fact that asymmetric dispersal and colonization can affect metapopulation dynamics and evolution (Kawecki & Stearns 1993; Kawecki 1995; Holt 1996*a,b*; Lundy & Possingham 1998; Saether *et al.* 1999; Whitlock & Mccauley 1999; Kawecki & Holt 2002). Moreover, the few models that have considered asymmetric dispersal make the simplifying assumption that the number of patches is very small, usually two (Pulliam & Danielson 1991; Lundy & Possingham 1998; Kawecki & Holt 2002; Amarasekare 2004).

There is considerable evidence for asymmetric dispersal. Indeed, given that perfectly symmetric dispersal would require perfectly symmetric environments along all the axes, asymmetric dispersal may well be the norm. Asymmetry in dispersal arises from a combination of environmental factors and the dispersal behaviour of species, i.e. whether a species is more passive or active disperser (Diffendorfer 1998). At one extreme, passive dispersers are influenced by directional dispersing agents such as ocean currents, river currents or prevailing winds (Watkinson 1985; Pulliam 1988; Holt 1996*a*; Honnay *et al.* 2001). In rivers, the direction of dispersal is predominantly downstream leading to an accumulation of genetic diversity in populations located in the lower reaches of a river—as discovered for fish (Hernandez-Martich & Smith 1997) and plant species (Friedman & Stein 1980; Gornall *et al.* 1998). Wind is known to be an important factor for sand dune plants (Keddy 1981) and shifts in temperature isotherms induced by climate change may lead to asymmetric dispersal of species towards the poles and higher altitudes (review by Walther *et al.* 2002).

At the other extreme, active dispersers are affected by environmental heterogeneity and fragmentation (Pulliam

*Author and address for correspondence: Fish ecology and evolution, Eawag, Seestrasse 79, 6047 Kastanienbaum, Switzerland (severine.vuilleumier@eawag.ch).

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1988; Holt 1996*a*; Koenig *et al.* 1996). Differences in habitat quality may lead to an asymmetric flow of individuals (Pulliam 1988), as is the case for brook charr (*Salvelinus fontinalis*; Fraser *et al.* 2004). Spatial structures within the matrix may guide or potentially inhibit movement from one direction (Haddad 1999; Wiens 2001) and produce asymmetric dispersal (Haddad 1999). In addition, social interactions may affect dispersal and habitat selection (summary in Reed & Dobson 1993) and therefore, leads to asymmetric dispersal between two populations. Finally, by differentially altering the quality of patches, humans may induce asymmetric connectivity between habitat patches.

In this paper, we developed a simulation model to answer three questions about the role of asymmetric colonization in metapopulation dynamics. First, what is the effect of asymmetric colonization on metapopulation persistence and patch occupancy? Second, how does asymmetric dispersal affect the relationship between persistence and the number of habitat patches, M, and per patch colonization probability, c? Finally, how do isolated patches, donor-only and recipient-only patches, and donor–recipient and recipient–donor (defined in §2*a*) affect metapopulation viability? We also analyse the ability of simple metapopulation theory to approximate systems with asymmetric dispersal by comparing our results obtained with symmetric and asymmetric systems with those predicted by classical metapopulation models.

2. MATERIAL AND METHODS

First, we describe the metapopulation simulation model, the procedure to create the symmetric and asymmetric metapopulation system and the metapopulation dynamic. Second, a mean field approximation of the system is created to provide a point of comparison for the simulation system.

(a) *Simulation model*

The metapopulation model has 100 habitat patches. To build the metapopulation dynamic, we used an object-oriented programming approach (Downing & Reed 1996). We considered two types of object: habitat patches and the directional connections between them. Each habitat patch can potentially be connected to any other patch, leading to 9900 possible one-way connections. The connections can be active or not. The habitat patches can be empty or occupied. Occupied patches can undergo local extinction and colonize empty habitat patches. The probability of extinction is the same for every population according to a fixed probability. Colonization events occur from an occupied patch to an empty patch, only if the connection between them is active. As connections have a direction, in asymmetric cases, one connection links two patches and in symmetric cases two connections link connected patches, one in each direction.

We generated 2000 metapopulation systems where all connections are symmetric and 2000 with asymmetric connections. Each system varies according to the number and position of connections, which are created in two steps. First, we select the number of connections in the system at random; second, we assign randomly the positions of the connections in the system. Thus, initially, all potential connections are inactive. To provide, on an average, the same one-way and two-ways connections in the asymmetric and symmetric case, respectively, a random uniformly distributed number selects the number of connections
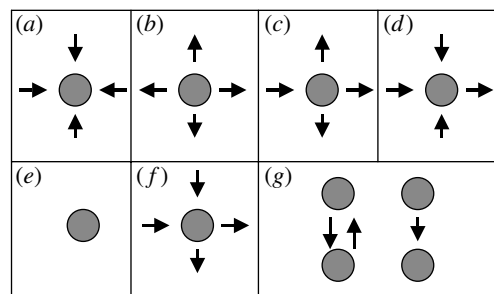

Figure 1. Classification of the habitat patches according to the number of connections that enter or leave a habitat patch. (*a*) Recipient-only and (*b*) donor-only have all connection that enter or, respectively, leave the habitat patches. (*c*) Donor–recipient and (*d*) recipient–donor have a positive, negative balance, respectively, of connections entering in the habitat patch. (*e*) Isolated patches do not have connections. (*f*) Equally donor–recipient patches have the same number of connections entering and leaving the habitat patches. (*g*) Pairs of patches have in common one or two connections and no connections to other patches.

among the half of the number of all possible one-way connections in the system. These connections are activated in a different manner for the symmetric and asymmetric cases. For the asymmetric case, the one-way randomly selected connections are activated. For the symmetric case the one-way randomly selected connections are activated and for each connection the opposite one-way connection is also activated, leading to a symmetric system of connections. We repeat this process 2*y* times for the asymmetric case and *y* times for the symmetric case, as each symmetric connection is actually two asymmetric connections. For the asymmetric case with only one-way connections, we classified patches into several types: isolated patches, recipient-only, donor-only, recipient–donor, donor–recipient, equally donor–recipient patches and isolated pairs of patches (figure 1). Note that we do not define these patches according to their ability to sustain a population or their demographic properties (Pulliam 1988; Morris 1991; Watkinson & Sutherland 1995; Kawecki & Holt 2002), but according to the kinds of connections entering and leaving a patch. Isolated patches have no connections in or out and do not count towards the count of patches, M, in the metapopulation. Recipient-only are patches that only have connections leading to them and donor-only are patches that only have connections leading away from them. A recipient–donor or donor–recipient patch has more directional connections that enter or leave that patch than vice versa. Equally donor–recipient patches have the same amount of leaving and entering directional connections (NB. The sum of patches in these four categories must be the sum total of all patches). Isolated pairs of patches are only connected to each other by one or two connections; hence either both are equally donor–recipient or one is a donor-only and the other a recipient-only.

The metapopulation dynamic is simulated using a stepwise process in which extinction precedes colonization. At the beginning of the simulation, all habitat patches are occupied. At each time-step, extinction events occur with a fixed per patch probability of $e = 0.5$. The per connection colonization probability, c, is the chance an occupied patch colonizes an empty patch to which it is connected. At the beginning of the simulation a colonization probability between 0 and 1 is randomly selected from a uniform distribution. In one
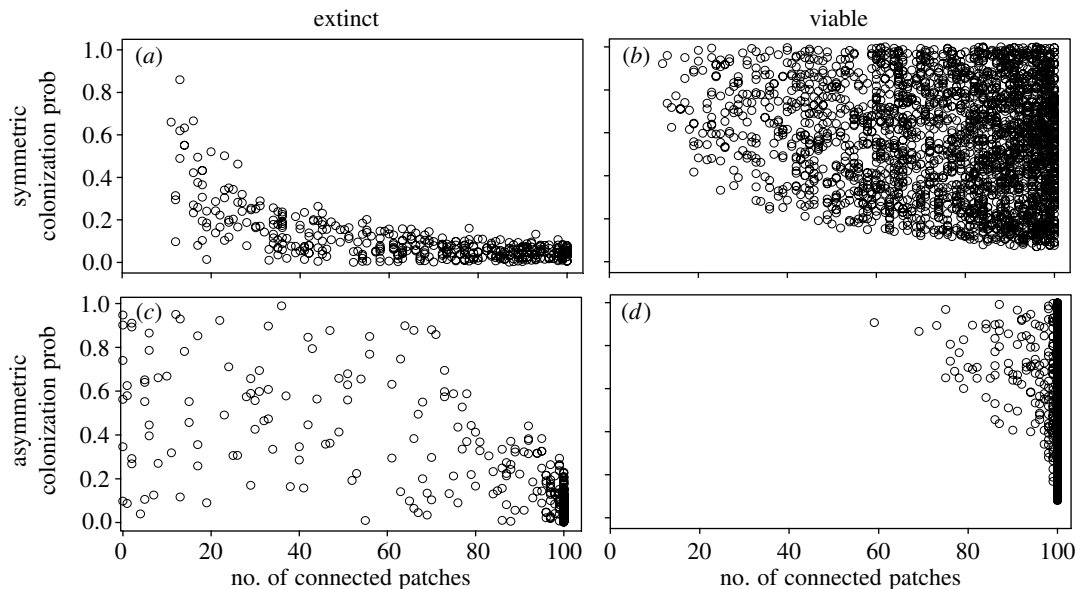
Figure 2. Whether or not a metapopulation is viable as a function of the number of connected habitat patches, M, and the per connection colonization probability, c, in symmetric and asymmetric systems. The results from simulations are presented for when the system is (*a* and *b*) symmetric and (*c* and *d*) asymmetric.

time-step a newly occupied patch cannot cause the colonization of an empty patch.

We call 'viable', a metapopulation that does not go extinct after 1000 time-steps. For both the symmetric and asymmetric connectivity patterns, we generate 2000 metapopulation systems with different patterns of connection. Then, we simulate the extinction and colonization processes as described above. At the end of each simulation, we determine if the system is extinct and the following parameters are recorded: the value of the colonization probability, the number of occupied patches, the number of connections, the number of isolated patches, the number of recipient-only, donor-only, donor–recipient, recipient–donor and the number of pairs of patches.

(b) *Mean field approximation for the metapopulation model*

To develop a simple and differential equation for population model, we use the following modified version of a standard metapopulation model ([Levins 1969](#)). In this analytical model, the rate of change of occupied patches, dp/dt, is driven by the colonization of empty patches minus the per patch local extinction rate e, where M is the total number of patches. To determine the net colonization rate, we multiply the per connection colonization rate, c, by the average number of patches to which each patch has an outgoing connection, μ_c, weighted by the fraction that are empty, $(1-p/M)$; which assumes there are no spatial autocorrelations in patch occupancy). This yields a mean field approximation for the metapopulation dynamics

$$\frac{dp}{dt} = c\mu_c p\left(1 - \frac{p}{M}\right) - ep, \tag{2.1}$$

which has a locally stable fixed point

$$p^* = M\left(1 - \frac{e}{c\mu_c}\right). \tag{2.2}$$

Therefore, the system should be deterministically viable if the expected per patch colonization rate is greater than the per patch extinction rate

$$\mu_c c > e. \tag{2.3}$$

For every simulation run, we can use the mean field approximation to determine whether or not the system is viable equation (2.3) and the approximate number of occupied patches if it is viable equation (2.2). The parameters for the mean field approximation are determined from the simulations as follows: the colonization and extinction rates are simply the colonization and extinction probabilities, c and e; the number of patches, M, is 100 minus those that are not connected to any other patch (the isolated patches), and the mean number of outgoing connections per patch is the total number of one-way connections, divided by the number of non-isolated patches.

3. RESULTS

Asymmetric colonization dramatically changed the range of per connection colonization probabilities, c, and connected patches, M, under which the metapopulation can persist (figure 2).

Under symmetric colonization (figure 2*a* and *b*), extinction occurred under two conditions. First, when the number of connected patches was approximately under 20 for all, but the highest colonization probabilities. The minimum number of connected patches in a viable metapopulation was 12 with a mean number of connections per patch of 10.3 and a per connection colonization probability of 0.92. Second, extinction occurred when the colonization probability was below 0.1; the symmetric metapopulation with the smallest value of the colonization probability was $c = 0.07$, with a large number of connected patches, 96 and high connectivity, 85.2 connections per patch.

When colonization was asymmetric (figure 2*c* and *d*), extinction occurred at any colonization probability if the number of connected patches was below 60. Extinction always occurred if the colonization rate was below 0.07 (figure 3). Metapopulations were viable only when over 70 patches were connected and if the colonization probability was low, less than 0.4, almost all the patches needed to be connected.

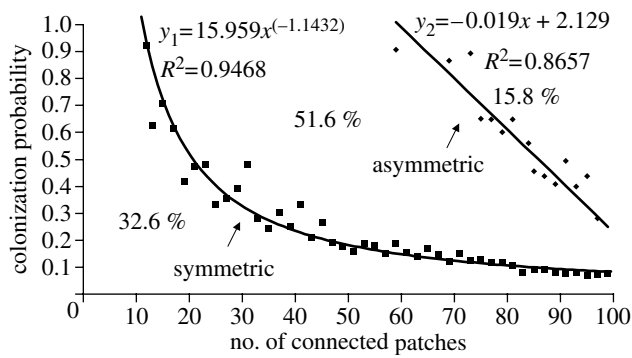Since the number of total directional connections was the same for symmetric and asymmetric cases, most

Figure 3. The threshold combinations of colonization probability and number of connected patches that distinguish between viable and extinct cases for the symmetric and asymmetric systems. The percentage of parameter space for which the metapopulation is viable in the asymmetric case is 15.8%, the difference in the area of parameter space where systems are viable for symmetric and asymmetric systems is 51.6% and the area of the parameter space where the metapopulation goes extinct for both systems is 32.6%.

asymmetric metapopulations had all 100 patches connected. Even so, the probability of extinction under asymmetric dispersal was twice as frequent as when dispersal was symmetric. Metapopulation persistence appeared to be very sensitive to whether flow between populations was directional or not.

The parameters sets that distinguish between the viable and extinct systems in both the symmetric and asymmetric case are presented in figure 3. The fractions of colonization probability, c and patch number, M, parameter space where *both* symmetric and asymmetric systems were viable or extinct was 15.8 and 32.6%, respectively. The difference between these two curves represents the discrepancy between the predictions of the two systems. If we assumed that an asymmetric metapopulation system had symmetric connectivity, then for over 50% of parameter combinations we would falsely infer that the system is viable, when it is inviable.

Figure 4a presents the mean percentage of donor-only, donor–recipient, recipient-only, recipient–donor, equally donor–recipient and isolated patches in an asymmetric metapopulation system for viable and extinct cases. For both, the proportion of donor–recipient and recipient–donor was high (94% for the viable case and 71% for the extinct case), but the proportion of donor-only and recipient-only differed significantly (*t*-test, $p < 0.0001$) and reached 12% when a metapopulation is inviable and was less than 0.5% when the metapopulation is viable. The viable asymmetric systems were composed almost entirely of donor-only and recipient-only. The proportion of habitat patches that did not contribute to the metapopulation dynamic, namely the isolated, recipient-only and paired patches in symmetric and asymmetric metapopulation systems are presented compared to the proportion that contributed to the dynamic in figure 4b. In the symmetric case, a system could be viable with less than 80% of patches contributing; in the asymmetric case the number of patches that may contribute to the metapopulation had to be greater than 95% for the system to be viable.

Figure 5 shows the fraction of patches occupied at the end of each simulation compared to the fraction predicted by the mean field approximation equation (2.3) using
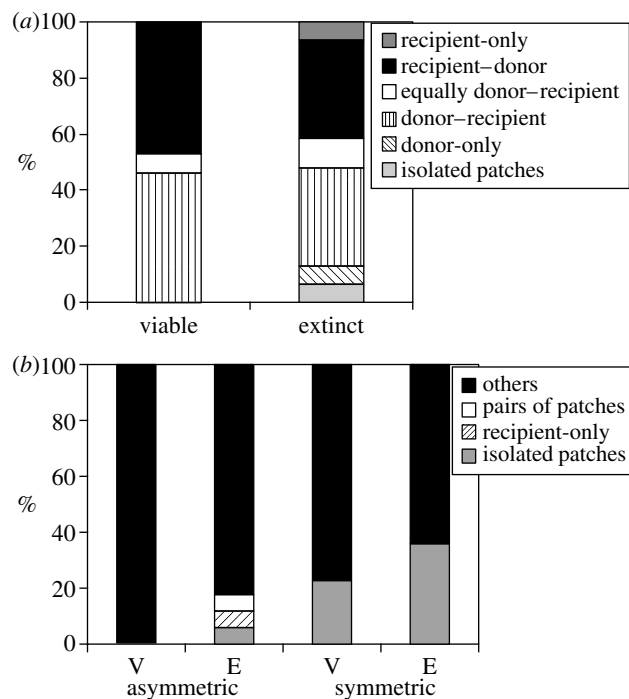

Figure 4. (*a*) The mean portion of donor-only, donor–recipient, recipient-only, recipient–donor, equally donor–recipient and isolated patches in viable and extinct asymmetric metapopulation system and (*b*) the proportion of isolated, donor-only and paired patches in the metapopulation.

the parameter values (colonization rate, number of connected patches and number of connections per patches) from the simulation. The mean field approximation provided a good prediction of the final fraction of occupied patches where dispersal is symmetric ($R_{Pearson} = 0.998$, $p < 0.0001$). This was not true for the asymmetric metapopulation system where the final fraction of occupied patches predicted by the simulation was significantly higher than predicted by the mean field approximation ($R_{Pearson} = 0.638$, $p < 0.0001$).

4. DISCUSSION

The simulation metapopulation models are essential for understanding the dynamics of spatially structured populations (Hanski 1999). They have proved valuable for conservation and management of species (Drechsler & Wissel 1998; Hanski & Ovaskainen 2000). Our results suggest that such models are unreliable for predicting metapopulation dynamics when there is asymmetric dispersal. Given that we have no simple theory for metapopulation dynamics where connectivity is asymmetric we suggest that an object-oriented simulation approach is currently the best platform for understanding the dynamics of metapopulations with asymmetric dispersal and large number of patches.

Our simulations suggest three main conclusions about metapopulations with asymmetric dispersal. First, asymmetric connectivity increases the chance that metapopulations will not be viable. If we were to erroneously assume that a system with asymmetric dispersal was symmetric, then it is very likely that we would overestimate the viability of such a system. This has important consequences in metapopulation management and conservation. Second,
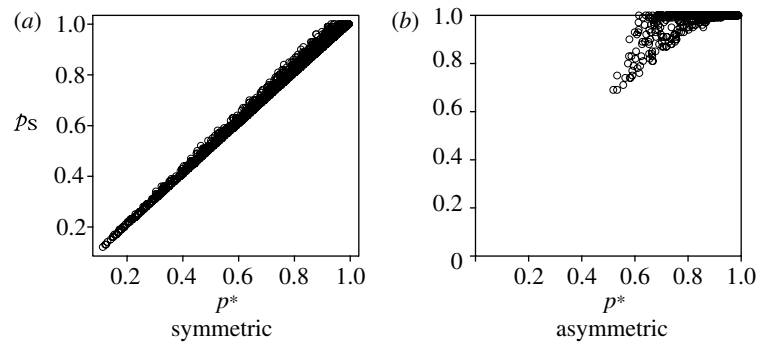
Figure 5. Comparison of the predicted proportion of occupied habitat patches obtained with the mean field approximation of the system p^* in equation (2.2) with those obtained by the simulation p_S when the metapopulation is viable, for (a) the symmetric and (b) asymmetric cases.

the critical factors that determine the viability of asymmetric and symmetric metapopulation systems are different. The number of connected patches largely determines metapopulation viability in an asymmetric system, while it is the colonization probability in symmetric systems. This has alarming implications for ecological management because increasing connectivity, a well-known management recommendation for decreasing the negative effects of fragmentation is unlikely to lead to an increase in metapopulation viability when dispersal is asymmetric. Third, the number of patches involved in the system is a determinant of viability for symmetric and asymmetric metapopulations. However, for asymmetric systems, the number of donor-only and recipient-only, as well as the number of pairs of patches, has a significant negative impact on metapopulation viability. We were not able to show an important effect of the presence of donor–recipient and recipient–donor.

In this paper, we only consider the extreme situation in which the entire metapopulation is either totally asymmetric or symmetric. In the natural environment, we may expect metapopulations to lie on a continuum between these extreme cases. Intermediate asymmetric systems may lead to specific spatial structures that provide a longer or shorter persistence. Future work should address other situations found in natural environments such as partial asymmetry (Kudoh & Whigham 1997, 2001; Donahue *et al.* 2003) or temporal asymmetry (Boughton 1999; Walther *et al.* 2002). In both cases, we anticipate an increase in extinction probability with increasing asymmetry.

Ecologists have long recognized that spatial heterogeneity can change the dispersal pattern of a species, but few models have been used in the field of ecology and conservation that take into account asymmetric dispersal. Models and concepts related to asymmetric dispersal arise mainly from evolutionary and genetic fields (Morris 1991; Kawecki 1995; Dias 1996; Case & Taper 2000; Lebreton *et al.* 2000; Fraser *et al.* 2001; Kawecki & Holt 2002). Methods providing indirect estimates of the number of migrants when gene flow is asymmetric are currently available (Beerli & Felsenstein 2001) and commonly applied (Imbert & Lefèvre 2003; Fraser *et al.* 2004). However, in the metapopulation literature, symmetric dispersal is invariably assumed without comment. This leap of faith occurs despite the fact that we know little about real dispersal patterns in heterogeneous landscapes (Koenig *et al.* 1996; Diffendorfer 1998). This paper shows

that the tacit assumption of symmetric dispersal has dramatic consequences on our ability to predict and manage metapopulations.

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