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Global dispersal reduces local diversity

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Metapopulation models and stepping-stone models in genetics are based on very different underlying dispersal structures, yet it can be difficult to distinguish the behaviour of the two kinds of models. We demonstrate a striking qualitative difference in the equilibrium behaviour possible with these two kinds of dispersal. If, in a local patch, there are multiple stable equilibria (and consequently an unstable equilibrium), we demonstrate that, for the spatial system with a metapopulation structure, at equilibrium every patch has to be near one of the stable equilibria. This contrasts with the clinal structure possible with a stepping-stone or continuous space model; thus the result can be used to deduce qualitative information about the form of dispersal from observations of allele frequencies.

Keywords: metapopulation; cline; diversity

1. INTRODUCTION

A major question facing both ecologists and geneticists is the interplay between local (in space) dynamics and dispersal in determining gene frequencies or population numbers. A range of dispersal structures can be considered, with exchange only between neighbouring populations representing one extreme, and equal exchange among all populations representing the other extreme. These two extremes can be thought of as idealizations of two concepts of hybrid zones: the more traditional concept in which the hybrid zone is a tension zone (Barton & Hewitt 1985) has only neighbouring populations exchanging individuals, while in a mosaic hybrid zone (Harrison 1990) exchanges among a variety of populations are possible.

Both forms of dispersal have long been used in genetic and ecological models (Hastings & Harrison 1994). Here we will consider genetic or ecological systems where in a single isolated patch there are two stable equilibria. It is well known that with low dispersal rates, and either form of dispersal, such bistable dynamics can lead to global diversity, with different types predominating in different patches (Harrison 1990; Levin 1974; Karlin & McGregor 1972). We will focus here on the role played by the structure of dispersal in determining local (within a subpopulation or patch) diversity in these systems.

Here we will look at systems where, in a single patch, there is more than one stable equilibrium (and hence some unstable equilibria as well). Our goal is to demonstrate that in such systems with equal movement among all patches, all the stable equilibria for the system as a whole have all local populations near one of the stable single patch equilibria. This outcome contrasts to that of a cline or a tension zone, where there is a smooth transition of gene frequencies over space. We will make this condition more precise below. We also note that, although the case of equal exchange will never occur in natural systems, the same result will hold for nearly equal exchange by continuity arguments. We will discuss how this result can be used to draw powerful inferences about the form of dispersal from observations of the distributions of allele or genotype frequencies or population numbers. We consider viability selection against hybrids (see Bazykin 1969; Barton 1979, 1983; Lande 1985; Gavrilets 1997*a*). Our approach can also be used for treating hybrid zones arising from a balance between dispersal and fertility selection against hybrids and/or premating reproductive isolation (Gavrilets 1997*b*; Gavrilets & Cruzan 1998).

Spatial models can be formulated in discrete or continuous space (Hastings & Harrison 1994). For the case of equal exchange it is clear that a discrete space formulation makes the most sense. Although we do extensively explore the local exchange model in this paper, we would view the most reasonable comparison incorporating local movement to be a discrete space formulation with exchange only between neighbouring demes. This avoids many issues which would arise in the continuous space model where boundary conditions would play a major role. In fact, for continuous space the existence of stable solutions which exhibit clines requires either a finite habitat and holding fixed allele frequencies at the boundary, or a region of restricted migration (Levin 1979).

2. A ONE-VARIABLE MODEL FOR ALLELE FREQUENCIES

We begin with a simple model describing the dynamics of a single locus where fixation of either allele is a stable state. This same model can also be used to describe the dynamics of a single species with an Allee effect. We assume that there are n patches, with no underlying spatial variation in dynamics. (Because our major result

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is qualitative, it will also hold if there is small spatial variation in the underlying dynamics.) We will first specify the dynamics at a single location in space, in the absence of exchange between patches. If we let p_i be the allele frequency in a patch labelled i and s be the strength of selection, the approximate continuous-time genetic model for selection at a single locus with underdominance takes the form (Wright 1969)

$$\frac{\mathrm{d}p_i}{\mathrm{d}t} = 2sp_i(1-p_i)(p_i-c), \tag{1}$$

where the parameter c (with $0<c<1$) determines the allele frequency at the unstable interior equilibrium. It is well known that if the patches are arranged in a line, exchange is only allowed between adjacent patches and the exchange rate is small enough, there are stable solutions where the allele frequencies in some patches will be near zero, while the allele frequencies in other patches will be near unity, and there will be a narrow region (a hybrid zone) with allele frequencies at intermediate levels (e.g. Barton 1983).

Our goal is to demonstrate that with the alternative form of exchange, where all patches are assumed equally likely to exchange migrants with all other patches, there are no stable solutions with intermediate allele frequencies in any patch. We will make quantitative our description of intermediate allele frequencies below. We begin by including 'global' dispersal in the selection model (1), obtaining the model

$$\frac{\mathrm{d}p_i}{\mathrm{d}t} = 2sp_i(1-p_i)(p_i-c) + m\left(\sum_{j=1}^{n} p_j/n - p_i\right), \tag{2}$$

which we rewrite as

$$\frac{\mathrm{d}p_i}{\mathrm{d}t} = 2sp_i(1-p_i)(p_i-c) + m(\bar{p}-p_i), \tag{3}$$

where the mean allele frequency over all patches is

$$\bar{p} = \sum_{j=1}^{n} p_j. \tag{4}$$

3. MODEL ANALYSIS

We begin our analysis by considering the steady states of this model. With $\hat{p}_i$ the equilibrium in patch i, we have

$$0 = 2s\hat{p}_i(1-\hat{p}_i)(\hat{p}_i-c) + m(\bar{p}-\hat{p}_i). \tag{5}$$

We observe that if we view the average allele frequency as a parameter, this equation is a cubic in $\hat{p}_i$ and hence has at most three solutions for $\hat{p}_i$. To show that stable solutions have no patches at intermediate frequencies, we will show that at a stable solution no patches are at the intermediate solution of this cubic equation. Look at an equilibrium with n_j patches at allele frequency α_j,

$$n = n_1 + n_2 + n_3, \tag{6}$$

and

$$0<\alpha_1<\alpha_2<\alpha_3<1. \tag{7}$$

We now show that any such equilibrium will be unstable if $n_2>0$.

Stability is determined by the Jacobian matrix for the system (3), evaluated at equilibrium. We denote the local (in space) dynamics as

$$f(p) = 2sp(1-p)(p-c). \tag{8}$$

The form of the Jacobian has n_i rows (for i from 1 to 3) with the diagonal term

$$\left.\frac{\partial f}{\partial p}\right|_{p=\hat{p}_i} -(1-1/n)m, \tag{9}$$

where $\hat{p}_i$ is one of α_1, α_2, or α_3 and with all off-diagonal terms positive. Because the Jacobian matrix has all its off-diagonal terms positive, by reversing all the signs in theorem 2.5.3 (Horn & Johnson 1991, p. 114) we see that all principal minors of such a matrix must be negative for stability (negative eigenvalues). Because every diagonal term is a principal minor, we conclude that stability requires

$$\left.\frac{\partial f}{\partial p}\right|_{p=\hat{\alpha}_2} < (1-1/n)m. \tag{10}$$

If we rearrange this condition as

$$m > \frac{\partial f/\partial p|_{p\hat{\alpha}_2}}{(1-1/n)}, \tag{11}$$

which implies

$$m > \left.\frac{\partial f}{\partial p}\right|_{p=\hat{\alpha}_2}, \tag{12}$$

it is easy to see graphically from figure 1 that it is impossible to have three solutions of the cubic equation (5) and to satisfy equation (11). Thus we conclude that any equilibrium to the model with $n_2>0$, with any patches near the unstable (within a single isolated patch) equilibrium, will be unstable overall.

Because the key steps in this proof are essentially graphical, we can extend this to more complex one-locus (or one-species) models. Additionally, obvious changes in the argument make it apply to an analogous discrete-time model for a single locus. However, we have been unable to extend this result to more than one locus (or species) analytically. However, numerical solutions of an analogous two-locus model demonstrated that the gist of our result holds—at a stable equilibrium of the model the system is 'near' a stable equilibrium in every patch.

4. DISCUSSION

We have shown that a particular kind of equilibrium—patches at intermediate genotype or allele frequencies—cannot be the outcome of a particular kind of dispersal. We can therefore use the contrapositive of this result to claim that observations of natural populations with individual subpopulations at intermediate genotype frequencies cannot be a long-term stable outcome unless migration is restricted or selection varies across space. There have been a number of studies which have focused on the dynamics of 'mosaic' hybrid zones (e.g. Harrison

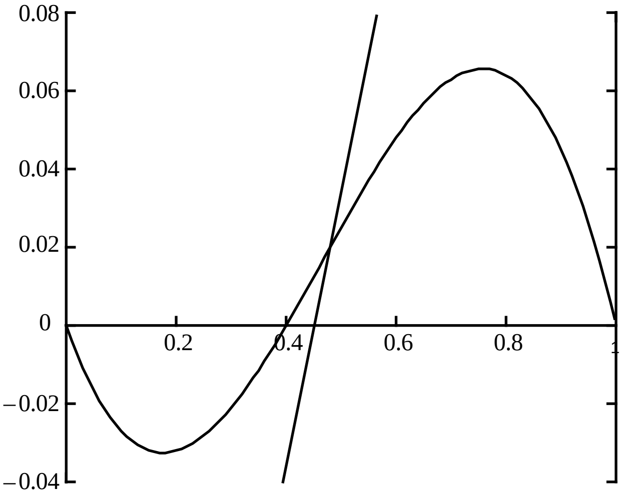

Figure 1. Graphical demonstration that the intermediate solutions to the equation (5) are impossible. Solutions to equation (5) can be found by looking graphically for the intersection of the two curves, $0 = 2s\hat{p}_i(1 - \hat{p}_i)(\hat{p}_i - c)$ and $0 = m(\hat{p}_i - \bar{p})$. The straight line is drawn to satisfy the condition (12) for stability of the intermediate solution. The cubic is drawn for $c = 0.4$. It is clear from the figure that in this case the straight line and the cubic cannot cross three times if the slope of the straight line satisfies the condition (12).

& Rand 1989; Garcia & Davis 1994) for which our results would suggest a limitation on the kind of migration structure. Within the region of intermediate allele frequencies migration must be restricted—long range migration cannot be the rule.

As an example of this we cite the study of Garcia & Davis (1994) on a hybrid zone in the grass shrimp *Palaemonetes kadiakensis* (Palaemonidae). In this study, the authors examine the frequencies of alleles at the GPI and PGM loci, and report a significant number of locations with intermediate gene frequencies (Garcia & Davis 1994, fig. 1 and Appendix 1). We would thus conclude that migration must not be too extensive within those regions where intermediate allele frequencies are present.

Another approach to the problem of relating observations of allele frequencies to migration patterns would be to fit a particular model assuming neutrality (e.g. Tufto *et al.* 1996). We view neither approach as superior, but consider the two approaches as complementary. In many cases the genetic data will not be detailed enough to allow the fit of a particular migration model, and in many cases it is useful to be able to draw general conclusions, as our result will allow.

Our main conclusion on the absence of stable polymorphic equilibria with $n_2 > 0$ (i.e. with any patches at an intermediate allele frequency) is valid for any relationships between fitnesses of homozygotes (that is for any value of c). In a special case of equal fitnesses of homozygotes (that is when $c = 1/2$), we can obtain some additional results. Specifically, it is easy to show that at the symmetrical equilibrium with $n_1 = n_3$ the allele frequencies are

$$p_i = 1/2 \mp \sqrt{(1/4 - m/s)}.$$

This symmetrical equilibrium exists if $m < s/4$ and is locally stable if $m \leqslant s/6$. Note that these conditions are equivalent to the conditions for the existence and stability of polymorphic equilibria in a two-deme model (e.g. Karlin & McGregor 1972). Besides the symmetrical equilibrium the metapopulation model has other non-symmetrical equilibria with $n_1 \neq n_2$ which can be stable. The symmetrical equilibrium is, however, the 'most stable': polymorphic equilibria with $n_1 \neq n_3$ are locally unstable for $m \geqslant s/6$.

From our results we can also draw general conclusions about the relationships among two-patch models, stepping-stone models and metapopulation models with 'global dispersal'. The amount of genetic variation maintained in the metapopulation model is, at most, that in a two-patch stepping-stone model.

In the stepping-stone systems, increasing the number of demes increases the stability of polymorphism. This stability can be characterized in terms of the maximum migration rate m_c still compatible with the maintenance of variation. (For migration rates higher than m_c, polymorphic equilibria are never stable.) For example, with just two demes $m_c = s/6$, with four demes it is $m_c = s/5$ and with a very large number of demes the polymorphic solution described by Bazykin's cline (Bazykin 1969; Barton 1979; Gavrilets 1997*b*) is neutrally stable. In the metapopulation model, the critical migration rate is not higher than in the two-deme system.

In the metapopulation model, there are only two different values of allele frequencies. In contrast, in a stepping-stone model there is a sequence of different allele frequencies (Lande 1985). This means that with global dispersal, allele frequencies (and the levels of genetic variation within demes) are more similar than with local dispersal.

The results which we have discussed here in genetic terms also have analogues in ecology. We essentially show that the form of diversity maintained depends on the structure of dispersal.

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