

LETTER

Distance-limited dispersal promotes coexistence at habitat boundaries: reconsidering the competitive exclusion principle

Florence Débarre* and

Thomas Lenormand

Centre d'Écologie Fonctionnelle et Évolutive, CNRS – UMR 5175, 1919 Route de Mende, F-34293

Montpellier Cedex 5, France

*Correspondence: E-mail:

florence.debarre@cefe.cnrs.fr

Abstract

Understanding the conditions for the stable coexistence of different alleles or species is a central topic in theoretical evolution and ecology. Different causes for stable polymorphism or species coexistence have already been identified but they can be grouped into a limited number of general processes. This article is devoted to the presentation and illustration of a new process, which we call 'habitat boundary polymorphism', and which relies on two key ingredients: habitat heterogeneity and distance-limited dispersal. Under direct competition and with fixed population densities, we show that this process allows for the equilibrium coexistence of more than n types in a n -habitat environment. Distance-limited dispersal indeed creates local maladaptation at habitat edges, which leaves room for the invasion of more generalist alleles or species. This mechanism provides a generic yet neglected process for the maintenance of polymorphism or species coexistence.

Keywords

Allele polymorphism, cline, exclusion rule, generalist, habitat, habitat fragmentation, intermediate heterogeneity hypothesis, landscape complementation, spatial heterogeneity, specialist, species diversity.

Ecology Letters (2011)

INTRODUCTION

For more than 40 years, the question of the maintenance of genetic polymorphism or of species coexistence has been central in both theoretical ecology and evolution. Formal models addressing these two issues share strong mathematical similarities and processes described in population genetics models are often successfully applied in community ecology models and reciprocally. Given the large literature devoted to this topic, it is difficult to survey in detail all models which have been developed to address the issues of allele polymorphism and species coexistence. Focusing only on deterministic effects, six main mechanisms, which are not mutually exclusive, can be identified (Haldane & Jayakar 1963b; Karlin & McGregor 1972; Amarasekare 2000). A stable polymorphism may be maintained: (1) by recurrent mutations (Haldane 1927), or introduction of new species (Vellend 2010), (2) by heterozygote advantage (Haldane 1926), (3) by frequency dependence in favour of rare types [negative frequency dependent selection (Lewontin 1958; Haldane & Jayakar 1963a)], which might be caused by trophic interactions with parasites or predators (Janzen 1970; Connell 1971); (4) by density-dependence, when intertype competition is weaker than intratype competition (Lotka-Volterra competition), (5) by a competition-colonization trade-off (Tilman 1994) or other trade-off across sexes (Kidwell *et al.* 1977), or life stages (Scudo 1967), (6) last, and perhaps most commonly, by migration when different types are favoured in different habitats (Haldane 1930; Wright 1931; Nagylaki 1975; Felsenstein 1976) [and the concept was imported in ecology by Loreau & Mouquet (1999)]. Processes (1) to (5) correspond to local processes [although process (5) is implicitly spatial]; and (6) to a spatial process. We focus here on the latter situation.

Tightly associated to the question of polymorphism is the concept of habitat. In theoretical models, different habitats are most often

characterized by different selective conditions. In absence of frequency and density dependence on fitness, and with haploid selection (which is equivalent to competition between two species in an ecological setting), it is widely acknowledged that a maximum of n alleles (species) may be deterministically maintained in n habitats (Karlin & McGregor 1972; Strobeck 1979; Nagylaki & Lou 2001; Nagylaki 2009) (and see (Armstrong & McGehee 1980), in the case where resources are abiotic and densities fixed, as in the present study), which is equivalent to Gause's exclusion principle in ecology (Hardin 1960). However, in a recent study, Lou & Nagylaki (2006) found 'unexpected, complex phenomena' when studying the evolution of the frequencies of three alleles, in a spatially and temporally continuous model. In particular, they indicate that an internal equilibrium (i.e. an equilibrium with the three alleles at positive frequencies) may sometimes occur with homogeneous and isotropic migration. This possibility raises many new questions. The first is whether such an internal equilibrium is stable. If it is, it would be important to understand the processes, to identify which environmental situations favour this equilibrium and finally to evaluate the spatial distribution of the different alleles at equilibrium.

In this article, we address these questions. First, can more than n alleles (or species) be maintained in n habitats in absence of processes (1) to (5)? We will see that this is possible, and we illustrate this result with $n = 2$ habitats. Second, why is it so? We will see that with limited dispersal, the very concept of habitat depends not only on patterns of selection but also, crucially, on the distance to the boundary between habitats, so that additional generalists may be stably maintained close to habitat boundaries. We term this mechanism habitat-boundary polymorphism. Third, we will determine how this process varies under different but related models (one vs. two spatial dimensions, different habitat transitions and different dispersal kernels). Finally, we will discuss why this process has been overlooked for so long.

MODELS

The population

We model a haploid, asexually reproducing population of fixed density, living in an environment containing two different habitats. This fixed total density, N , is the same at each spatial location. Time is continuous and our model is deterministic. We use the word *type* to refer either (and equivalently) to an allele or to a species. The mechanism which we model indeed applies in both situations and with the same equations; the underlying hypotheses, however, differ. If alleles are considered, our model is valid for haploid individuals, or for diploid individuals and co-dominance at the selected locus. If species are considered, we have to assume that all individuals of a given species share the same phenotype (Vellend 2010) (i.e. there is no intraspecific variation). We also have to assume that species only differ by their adaptation to one or the other habitat; there are competitors at the same trophic level and they have the same migration parameters. We assume that the fitness of an individual depends on both its type and on the habitat where it lives: $r_i(x)$ is the fitness of an individual of type i living at location x . Its fitness therefore depends on the habitat type at location x . We have :

$$r_i(x) = \begin{cases} \rho_i^A & \text{if } x \text{ in habitat A} \\ \rho_i^B & \text{if } x \text{ in habitat B} \end{cases} \quad (1)$$

ρ_i^A and ρ_i^B being constant. At location x and at time t , the mean fitness is

$$\bar{r}(x, t) = \sum_i r_i(x) p_i(x, t) \quad (2)$$

where $p_i(x, t)$ is the proportion of type- i individuals in the population located at x , at time t . Selection happens locally, but the individuals can change places, according to a migration kernel. A migration kernel is the probability density function of the parent-offspring distance. We assume that migration is not biased towards one direction (i.e. migration is isotropic: the mean of the migration kernel is 0), and that it is independent of the location (i.e. homogeneous). In particular, this passive dispersal means that habitat boundaries are not perceptible to the dispersing individuals (Fagan *et al.* 1999). Finally, in the absence of migration, only one type, the fittest, is eventually fixed in each habitat. We illustrate this model in different environmental setups. In all cases, there are two adjacent habitats, A and B, in proportions q and $1 - q$ respectively. The quality of the two habitats does not change with time; their edges are infinitesimally thin, so that the change of habitat is a step function (Strayer *et al.* 2003).

Continuous space 1-D

The first setup we consider consists of two habitats along a single spatial dimension (see Fig. 1a). The environmental boundaries are periodic (of period $2S$); thus, this environment may be viewed as being circular. Migration is modelled as a diffusive process and the standard deviation of the migration kernel, σ , fully characterizes migration (Turchin 1998). We define $p_i(x, t)$ as the proportion of type- i individuals in the population located at x , at time t . The model reads

$$\frac{\partial p_i}{\partial t} = \left(\frac{r_i(x)}{\bar{r}(x, t)} - 1 \right) p_i(x, t) + \frac{\sigma^2}{2} \frac{\partial^2 p_i}{\partial x^2} \quad (3)$$

Note that diffusion is an approximation because only the mean and variance of the migration kernel are considered: higher moments of

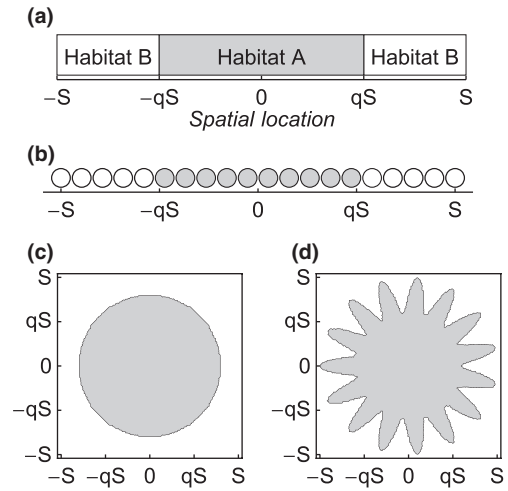


Figure 1 Different environment configurations. (a) 1-D continuous environment. (b) 1-D stepping stone. (c) 2-D continuous environment, circular [$a = b = 0$, $R = S\sqrt{2/\pi}$, see eqn (4)]. (d) 2-D continuous environment with more edges ($a = 0.2$, $b = 15$, $R = S\sqrt{2/\pi}$).

the distribution are neglected. Nagylaki (1975) used a slightly different model, which is obtained by assuming a logistic regulation of total number (Crow & Kimura 1970). Our results are robust to the choice of density regulation [Fig. S1 is the equivalent of Fig. 3a with model (3) without the \bar{r} denominator, like in Nagylaki (1975)]. This model is solved numerically using the NDSolve function in Mathematica (Wolfram Research, Inc. 2008).

Continuous space 2-D

The two dimensional (2-D) version of the spatially continuous model is similar. The boundaries between the two habitats are periodic (of period $2S$ in each direction). The environment may thus be viewed as being toric. In two dimensions, there is more freedom to model the shape of the transition between the two environments. We consider either a circular habitat edge (Fig. 1c) or a flower-like boundary (tortuous habitat edge, sensu Strayer *et al.* (2003), Fig. 1d). The equation of the boundary (in polar coordinates) reads:

$$r = R + aS \sin(b\theta), \quad (4)$$

where R is the mean radius of the habitat, b the number of oscillations (b must be odd) and a their amplitude ($a = 0$ corresponding to a circular habitat).

We use the same reaction-diffusion model as in a 1-D environment, but in two-dimensions (x and y stand for the two-spatial dimensions and t for time):

$$\frac{\partial p_i}{\partial t} = \left(\frac{r_i(x, y)}{\bar{r}(x, y, t)} - 1 \right) p_i(x, y, t) + \frac{\sigma^2}{2} \frac{\partial^2 p_i}{\partial x^2} + \frac{\sigma^2}{2} \frac{\partial^2 p_i}{\partial y^2} \quad (5)$$

This model is solved numerically using the NDSolve function in Mathematica (Wolfram Research, Inc. 2008).

Stepping stone

In order to build a spatially discrete version of the model, we use a stepping stone model made of a linear set of k patches. Each patch consists of one habitat only (see Fig. 1b); q k contiguous patches consist of habitat A and $(1 - q)k$ of habitat B. We model dispersal

with a discrete kernel. We use a binomial kernel (B) to model distance-limited dispersal, a uniform kernel (U) to model non-distance limited dispersal and mixtures of both for intermediate cases. More specifically, we design two kernels, K_1 and K_2 , which are intermediates between the binomial (B) and the uniform (U) kernels:

$$K_1 = 0.65B + 0.35U \quad (6a)$$

$$K_2 = 0.35B + 0.65U \quad (6b)$$

The kernels B , K_1 , K_2 and U have the same variance but have increasing kurtosis. With the stepping-stone model, a sufficient number of patches is required to obtain a clinal pattern. If the number of patches is too low, the model behaves like a two-patch model. This model is solved using the `deSolve` function in R (R Development Core Team 2010; Soetaert *et al.* 2010).

Two-patch model

Finally, we compare our results to the results obtained with the classical two-patch model, where one patch consists of habitat A (and represents a fraction q of the total available space) and the other of habitat B (in proportion $1 - q$). Individuals migrate from one patch to another and the migration rate is μ . Let p_i^j be the frequency of individuals of type i in habitat j ; the dynamics read (see appendix C in Débarre & Gandon (2010) for the derivation of the model):

$$\frac{dp_i^A}{dt} = \left(\frac{p_i^A}{\bar{p}^A} - 1 \right) p_i^A + \mu(1 - q)(p_i^B - p_i^A) \quad (7a)$$

$$\frac{dp_i^B}{dt} = \left(\frac{p_i^B}{\bar{p}^B} - 1 \right) p_i^B + \mu q(p_i^A - p_i^B) \quad (7b)$$

where

$$\bar{p}^j = \sum_j p_i^j p_i^j \quad (8)$$

Note that this model can also apply to a metapopulation where a fraction q of patches consist of habitat A and the remaining $1 - q$ of habitat B, with island migration (i.e. any patch can be reached with the same probability).

RESULTS

Habitat boundary polymorphism: the basic mechanism

The basic mechanism of habitat boundary polymorphism occurs in all the models we tested provided two basic conditions are met. The first is that dispersal is spatially limited, meaning that it vanishes at sufficiently long distance. The second is that ecological conditions are coarse-grained (Levins 1968), meaning that they vary at a larger spatial scale than the typical dispersal distance. These two conditions are obviously not very restrictive. To understand what is going on, it is sufficient to focus on the simplest model, the 1-D continuous environment (Fig. 1a).

When only two types, each adapted to one habitat, compete in a 1-D continuous environment containing two habitats, the outcome is either the maintenance of one type or the coexistence of the two types (Nagylaki 1975). When the two types coexist (which happens provided migration is below a threshold), their frequencies vary gradually and

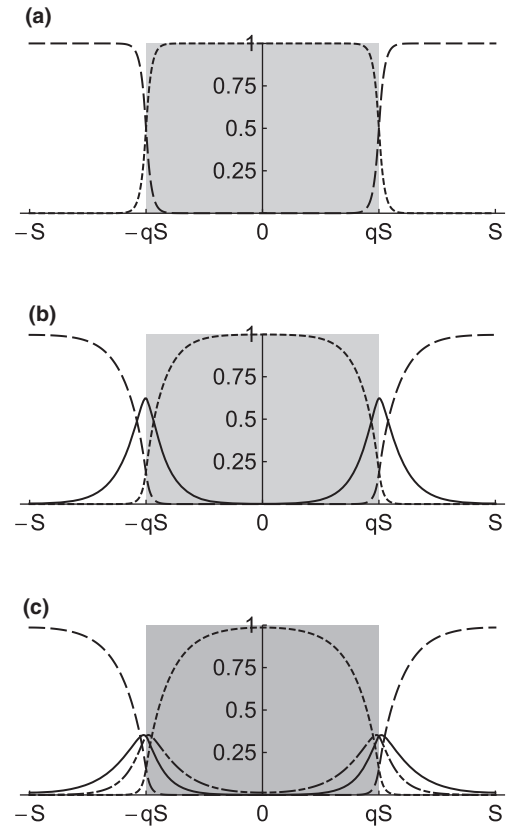


Figure 2 Equilibrium frequencies, for the competition between two (a), three (b) and four (c) types, in the 1-D continuous environment. Long dashed line: species 2, specialist in habitat B; Dotted line: species 1, specialist in habitat A; Full line: species 3, generalist; Dot-dashed line: species 4, other generalist. Parameters: (a, b, c): $p_1^A = 1, p_1^B = 0, p_2^A = 0, p_2^B = 1, q = 1/2, \sigma = 0.025$; (b): $p_3^A = p_3^B = 0.95$, (c): $p_3^A = 0.975, p_3^B = 0.925, p_4^A = 0.925, p_4^B = 0.975$.

form a clinal pattern (see Fig. 2a). In particular, this means that the degree of maladaptation and polymorphism are high around the boundary between the two habitats. If we now focus on the competition between three types, we see that a third type may be maintained at a stable equilibrium on top of these two previous types (see Fig. 2b), a phenomenon that has remained largely overlooked. This third type is necessarily more generalist, in the sense that it is an inferior competitor to each specialist type in its own habitat (see conditions 9a and 9b, type 3 being the generalist), but that it presents a better average fitness than each of them (condition 9c).

$$p_3^A < \max(p_1^A, p_2^A) \quad (9a)$$

$$p_3^B < \max(p_1^B, p_2^B) \quad (9b)$$

$$\int r_3(x) dx > \max\left(\int r_1(x) dx, \int r_2(x) dx\right) \quad (9c)$$

As one might expect, the generalist type is maintained close to the habitat boundary, where maladaptation is high when only two specialists are present. This phenomenon is intuitively understood by the fact that, with distance-limited dispersal, types present close to the habitat boundary are the ones which are the most likely to switch between habitats in the next generations, which gives generalist types an advantage in this area. Figure 3(a) shows the parameter range

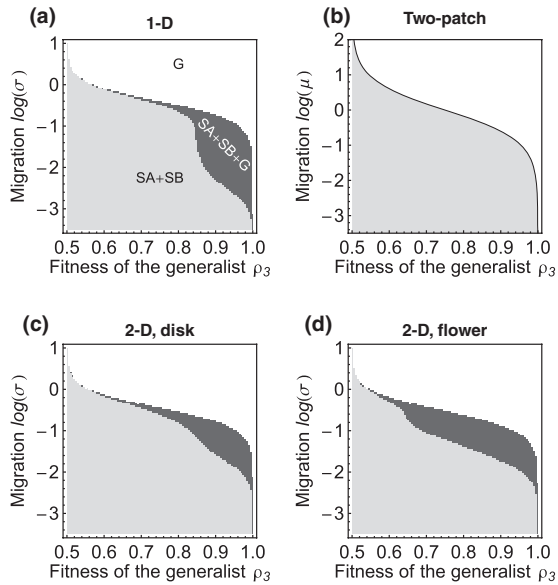


Figure 3 Coexistence areas at equilibrium, for various environments, as a function of the generalist's fitness ($\rho_3^A = \rho_3^B$), and the migration range σ (a, c, d) or migration rate μ (b) (note the log scale). Dark grey: the three types coexist (SA + SB + G), Light grey: the two specialists coexist (SA + SB), White: only the generalist (G). The parameters of the specialist types are the same as in Fig. 2: $\rho_1^A = 1, \rho_1^B = 0, \rho_2^A = 0, \rho_2^B = 1; q = 1/2$. The equation of the boundary in (b) is $\mu = 1/(2\rho_3 - 1) - 1$. Subfigures (a, c and d) are obtained by numerical resolution of eqn (3) (subfigure a) and eqn (5) (subfigure c and d); a type is assumed to have disappeared when its global frequency is below 1%. Subfigure (b) is obtained analytically [stability study of model (7)], and confirmed by numerical resolutions.

where the three types coexist in this model. In particular, we see that the three types coexist for intermediate migration rates (dark grey area) and that the parameter range where this three-type coexistence exists gets larger when the fitness of the generalist increases (provided it remains below 1, otherwise the generalist obviously always outcompetes the two specialists). Note that we chose to illustrate this result with a symmetrical environment ($q = 1/2$) but that the result still holds in asymmetrical environments (see Fig. S3 where $q = 0.3$).

Robustness of the process

First, we inquired whether this habitat boundary polymorphism is a unique feature of spatially continuous models. As a check, we investigated the conditions for the coexistence of three types in a stepping-stone environment containing two habitats. We find similar results. Figure 4(a) shows for instance that the three types can coexist in a 1-D discrete environment containing only two different habitats, with a binomial dispersal kernel. This process is therefore not due to the continuity of the environment. We also checked that the results were not artifacts due to symmetry in fitnesses (Fig. S2), nor to symmetry in the environmental configuration (Fig. S3), and finally to the assumption of equal migration kernels among types (Fig. S4).

Second, we checked that this process was not specific to a 1-D situation. To do so, we investigated the conditions for three-allele coexistence in 2-D environments. In a first 2-D model, we considered a circular habitat edge (Fig. 1c). In a second one, we considered a more tortuous habitat edge (Fig. 1d). Three-type coexistence occurs in these 2-D models. Figures 3(c,d) illustrate the parameter range where

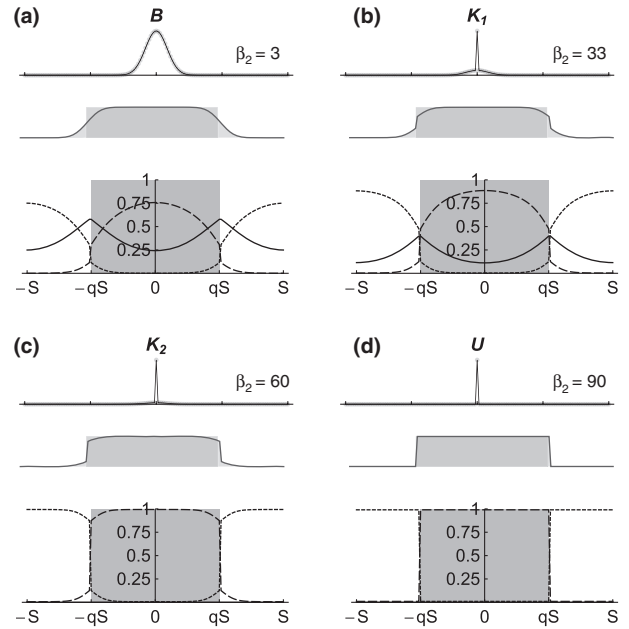


Figure 4 Stepping stone model for various kernel shapes: (a) Binomial kernel B , (b) Intermediate K_1 , (c) Intermediate K_2 , (d) Uniform kernel U . All kernels have the same variance ($\sigma^2 = 0.0068$) but have different kurtosis (β_2). In each subfigure, from top to bottom: kernel shape, perceived habitat, equilibrium frequencies of the three types. Parameters: $\rho_1^A = 1, \rho_1^B = 0, \rho_2^A = 0, \rho_2^B = 1, \rho_3^A = \rho_3^B = 0.95, q = 1/2, \sigma = 0.025, k = 149$ patches.

the two specialists and the generalist coexist. As this coexistence is due to maladaptation of the specialists near the habitat edges, we expect that more edges (given the same proportion of both habitats) widen the parameter space where the three types coexist. With a more tortuous habitat edge, and everything else being equal, the parameter range of three-type coexistence is larger (compare Figs 3d with 3c).

Third, we investigated how this process varies with different dispersal kernels. As the advantage of the generalist type near the habitat boundary crucially depends on the fact that dispersal is distance-limited, we predicted that three-type coexistence should be more difficult with a dispersion kernel having a higher kurtosis. Indeed, a higher kurtosis for the same variance of the kernel means that a higher fraction of individuals do not move but that the moving individuals disperse at larger distance. At the extreme, if our reasoning is correct, a three-type polymorphism cannot occur with a uniform kernel U , where migrating individuals have the same chance to disperse to any location of the environment. This intuition is backed up by the fact that with such a kernel, the model becomes mathematically equivalent to a two-patch model, where a maximum of two types can coexist (see Figs 3b and 4d). As a check, we investigated the impact of having a more kurtotic kernel for a given variance. To do so, and because diffusion methods are not appropriate in this case, we used the stepping stone model with four kernels of increasing kurtosis (B, K_1, K_2, U , see Models). It is interesting to note that these four kernels would yield the same results under the diffusion approximation because in this case, only the mean and variance of the kernels are taken into account. Our results fully confirm the prediction and the interpretation: as expected, it is harder to obtain coexistence between the three types when the kurtosis of the kernel increases (Fig. 4). This contrasts with the results of Snyder &

Chesson (2003), who found that moments higher than the variance of the dispersal kernel do not influence the conditions for species coexistence.

Fourth, it is important to note that no hypothesis of weak selection has been made to derive the model's equation (this assumption is commonly made in population genetics models). As a consequence, the process we describe is not an artifact of this type of approximation.

Finally, we tried to determine whether more than three types may be maintained by this process. To do so, we tried different combinations of fitness parameters, and found that up to four types could coexist in a 1-D environment, discrete or continuous. Figure 2c illustrates such a situation with an example. Four-type stable polymorphism can occur when there are two generalists close to the habitat boundary; one generalist a little more specialist to habitat A and the other a little more specialist to habitat B. Still, we also found that the parameter range allowing for a four-type polymorphism was very narrow. Thus, how many alleles can coexist in a spatially explicit environment with n habitats and distance-limited migration remains an open question; we can conjecture that more types can coexist, but that it occurs in a vanishingly small parameter range (and therefore, matters little in terms of biology). In any case, this question is unlikely to be solved using numerical solutions.

DISCUSSION

Habitat boundary polymorphism

The migration-selection balance is a very powerful mechanism to maintain genetic polymorphism (Wright 1931). Similarly in an ecological context, the migration-competition balance (Loreau & Mouquet 1999) can substantially increase diversity around habitat boundaries. In both cases, these processes have been recognized for a long time; however, they are systematically envisioned with a limit at equilibrium of n types in n habitats. In this article, we show that with spatially limited dispersal, generalist types may additionally be maintained at equilibrium at habitat boundaries. Our model is as simple as possible: it is deterministic, the population is haploid, the habitats are saturated and only direct competition is considered. In the absence of migration, only one type gets fixed in each habitat. The individuals compete locally; the best competitor is the one which produces most offspring. In our model, where migration is distance limited, coexistence arises due to maladaptation of the specialist types near the habitat boundaries. This maladaptation allows more generalist types to invade near the habitat boundaries. We term this process 'habitat boundary polymorphism'. As it works under generic assumptions, it is thus likely to occur in a very large array of ecological conditions.

When intra- and interspecific competitions have the same intensity, as is the case in our model, never more than two species can coexist in a two-patch model (Karlin & McGregor 1972), and see Fig. 3(b). As this principle generalizes to n species in n habitats when the number of subpopulations equals the number of habitats (Strobeck 1979; Nagylaki 2009), this result is often taken for granted even in more complex situations. Consequently, most studies do not even investigate the conditions for coexistence of more than n alleles in an n habitat environment [but see (Lou & Nagylaki 2006)], or focus on island migration only, which explains why the habitat boundary polymorphism had not been highlighted previously.

Habitat boundaries: diversity hotspots

Even considering the coexistence of two types, it is well established that intermediate distance-limited dispersal promotes polymorphism near habitat boundaries [(Nagylaki 1975), and see Fig. 2a]. The process which we present here further increases this effect since additional types may be maintained at these boundaries. Thus, our results reinforce the view that habitat edges are expected to be important either in terms of genetic variation within species or in terms of diversity. Note that we do not mean that high habitat fragmentation favours diversity: the habitats have indeed to be wide enough for specialist types to maintain (increasing the grain of the environment is equivalent to decreasing the range of dispersal in our model). We show in fact that there is a non-monotonic effect of increased fragmentation on species diversity, which can account for the diversity of trends observed in empirical studies on the effects of habitat fragmentation *per se* (Fahrig 2003). Due to scaling effects, indeed, the vertical axes in Fig. 3 can be replaced by the grain of the environment, low (resp. high) migration being equivalent to coarse (resp. fine) grain. With this interpretation, we see that an intermediate grain maximizes diversity, and this result gives a theoretical backup to the 'intermediate heterogeneity hypothesis', whereby biodiversity is most favoured under intermediate heterogeneities (Tscharntke *et al.* 2005; Fahrig *et al.* 2010). Importantly, this finding does not undermine the idea that other mechanisms may promote diversity on habitat edges. In particular, habitat edges may extend spatially and define additional ecotone habitats (contrary to our model where edges do not have any thickness: the two habitats are adjacent, there is no intermediate habitat in-between). Ecotones may favour distinct ecotone-specialist types. What our model stresses though is that it is not necessary to consider a specific ecotone habitat (with a spatial extent) to maintain additional types: the process that we present here already generates polymorphism beyond the n habitats- n types baseline. This idea is related to 'landscape complementation' (Dunning *et al.* 1992), whereby a species requires different habitat types throughout its life-cycle (as demonstrated e.g. for leopard frogs, see Pope *et al.* 2000). Whether patterns of increased diversity near edges arise due to the presence of ecotone habitats or to habitat boundary polymorphism remains to be clarified, the latter being more likely with sharp ecological transitions between habitats.

Mechanisms for the maintenance of polymorphism

There are many mechanisms which may promote stable polymorphisms (see Introduction). Our result adds one mechanism to this list. Distance-limited dispersal can generate maladaptation close to habitat boundaries (but not elsewhere), opening a new niche for generalist types to invade. Such a phenomenon has never been described before and is fundamentally different from the usual migration-selection balance, which was originally described with an island model (Haldane 1930; Wright 1931). In the usual n -types n -habitat island model, increased dispersal can only result in having fewer types maintained at equilibrium: with zero dispersal indeed, the n types are all fixed in their habitats; increasing dispersal can only reduce the number of types maintained at equilibrium below n , or in the best case maintain it at n . On the contrary, we find that intermediate dispersal can actually promote the maintenance of more than n types.

Implications for field studies

In real situations, it is difficult to determine which mechanisms are responsible for the maintenance of polymorphism. The first difficulty is to show that the observed polymorphism is stable. In fact, the most important mechanism promoting polymorphism or diversity beyond the n types- n habitats baseline is certainly non-equilibrium dynamics. For instance, in a genetic context, allele replacement takes time and the flow of newly arising alleles can be high enough to sustain much more polymorphism than what would be expected under equilibrium conditions [for a detailed field situation where the dynamic of such allele replacements is documented see Labbe *et al.* (2009)]. In addition, there is often a striking parallel between models involving environmental selection and selection against hybrids (Bazykin 1969). In particular, the clinal patterns expected under both types of selection are often indistinguishable (Kruuk *et al.* 1999). The pattern which we describe herein with a generalist type maintained at the habitat boundary probably echoes of an analogue situation in a hybrid zone where a compatible ('generalist') type may coexist with incompatible types, which forms a buffer zone around the boundary between the two types. Interestingly, such a phenomenon is documented in contact zones between chromosomal races in mice (Searle *et al.* 1993; Britton-Davidian *et al.* 2000).

Regarding species coexistence, it is often hard to distinguish between the effects of the diversity and amounts of habitats in the landscape [also referred to as compositional heterogeneity (Fahrig & Nuttle 2005; Fahrig *et al.*, 2010) or habitat variability (Duelli 1997)] and of changes in the amount of habitat edges (configurational heterogeneity or habitat heterogeneity), both being often confounded in studies on fragmentation (Fahrig 2003). Our study however shows the importance of disentangling the two, as they differently affect species coexistence, and should stimulate empirical work aiming at discriminating between habitat amounts and edge effects in patterns of diversity.

Environmental grain and perceived habitat

However, our study has also a more fundamental consequence on the notion of habitat or niche. In models where dispersal is not distance dependent (e.g. in island models), the number of habitats can be clearly and quite conveniently defined as the number of distinct selective conditions. This number may be lower than the actual number of subpopulations. For instance, in an island model with n populations, a fraction p of them may share the same selective conditions. However, when dispersal is distance limited, the number of habitats is less clearly related to the number of distinct selective conditions. Everything depends on the scale of dispersal relative to the scale of environmental heterogeneity. This fact is also a well known issue, most often described in terms of 'environmental grain' (Levins 1968). At one extreme, fine grain refers to the case where dispersal occurs at much larger distance than environmental heterogeneity, whereas coarse grain refers to the opposite extreme. This finding is a useful idea, but it can also be misleading, as our study shows. With two selective conditions, fine grain is usually synonymous with having one averaged selective condition (and only one generalist allele maintained at equilibrium) while coarse grain is usually synonymous with having two distinct selective conditions (and two specialist allele maintained at equilibrium). Thus, in the fine-coarse grain continuum, one is tempted to conclude that with

two selective conditions, the number of alleles maintained at equilibrium will always be either one or two. In fact, as we show, there is an intermediate grain where more than two alleles may be maintained. This result can easily be understood in terms of 'perceived habitat' in a given location (plotted in Fig. 4). Here, 'perceived' means that, because of future or past dispersal, the selection of an individual experiment is in fact spatially averaged around the individual's current position. This 'perceived habitat' smoothly changes when approaching an environmental transition. Thus, even if there are only two selective conditions (two habitats) changing abruptly at a given location, perceived selection changes smoothly and defines a continuum of perceived habitats where additional alleles may persist at equilibrium.

Overall, because our results both challenge and improve concepts of environmental grain and habitats, they have a fundamental importance for ecology and ecological genetics.

ACKNOWLEDGEMENTS

We thank François Massol for critical comments on the manuscript, Lenore Fahrig and Sylvain Gandon for insightful discussions.

REFERENCES

- Amarasekare, P. (2000). The geometry of coexistence. *Biol. J. Linn. Soc.*, 71, 1–30.
- Armstrong, R.A. & McGehee, R. (1980). Competitive exclusion. *Am. Nat.*, 115, 151–170.
- Bazykin, A.D. (1969). Hypothetical mechanism of speciation. *Evolution*, 23, 685–687.
- Britton-Davidian, J., Catalan, J. & Belkhir, K. (2000). Chromosomal and allozyme analysis of a hybrid zone between parapatric Robertsonian races of the house mouse: a case of monobrachial homology. *Cytogenet. Genome Res.*, 96, 75–84.
- Connell, J. (1971). On the role of natural enemies in preventing competitive exclusion in some marine animals and rain forest trees. In: *Dynamics of Populations* (eds Boer, P.J.D. & Gradwell, G.R.) Chapter. Center for Agricultural Publication and Documentation, Wageningen, pp. 298–312.
- Crow, J.F. & Kimura, M. (1970). *An Introduction to Population Genetics Theory*. Harper & Row, New York.
- Débarre, F. & Gandon, S. (2010). Evolution of specialization in a spatially continuous environment. *J. Evol. Biol.*, 23, 1090–1099.
- Duelli, P. (1997). Biodiversity evaluation in agricultural landscapes: an approach at two different scales. *Agric. Ecosyst. Environ.*, 62, 81–91.
- Dunning, J., Danielson, B. & Pulliam, H. (1992). Ecological processes that affect populations in complex landscapes. *Oikos*, 65, 169–175.
- Fagan, W.F., Cantrell, R.S. & Cosner, C. (1999). How habitat edges change species interactions. *Am. Nat.*, 153, 165–182.
- Fahrig, L. (2003). Effects of habitat fragmentation on biodiversity. *Annu. Rev. Ecol. Evol. Syst.*, 34, 487–515.
- Fahrig, L. & Nuttle, W. (2005). Population ecology in spatially heterogeneous environments. In: *Ecosystem Function in Heterogeneous Landscapes* (eds Lovett, G.M. and Jones, C.G., Turner, M.G. & Weathers, K.C.) Chapter. Springer-Verlag, New York, pp. 95–118.
- Fahrig, L., Baudry, J., Brotons, L., Burel, F.G., Crist, T.O., Fuller, R.J. *et al.* (2011). Functional landscape heterogeneity and animal biodiversity in agricultural landscapes. *Ecol. Lett.*, 14, 100–111.
- Felsenstein, J. (1976). The theoretical population genetics of variable selection and migration. *Annu. Rev. Genet.*, 10, 253–280.
- Haldane, J.B.S. (1926). A mathematical theory of natural and artificial selection, part III. *Math. Proc. Cambridge*, 23, 363–372.
- Haldane, J.B.S. (1927). A mathematical theory of natural and artificial selection, part V: selection and mutation. *Math. Proc. Cambridge*, 23, 838–844.
- Haldane, J.B.S. (1930). A mathematical theory of natural and artificial selection, part VI: isolation. *Math. Proc. Cambridge*, 26, 220–230.
- Haldane, J.B.S. & Jayakar, S. (1963a). Polymorphism due to selection depending on the composition of a population. *J. Genet.*, 58, 318–323.

- Haldane, J.B.S. & Jayakar, S. (1963b). Polymorphism due to selection of varying direction. *J. Genet.*, 58, 237–242.
- Hardin, G. (1960). The competitive exclusion principle. *Science*, 131, 1292–1297.
- Janzen, D. (1970). Herbivores and the number of tree species in tropical forests. *Am. Nat.*, 104, 501–528.
- Karlin, S. & McGregor, J. (1972). Polymorphisms for genetic and ecological systems with weak coupling. *Theor. Popul. Biol.*, 3, 210–238.
- Kidwell, J.F., Clegg, M.T., Stewart, F.M. & Prout, T. (1977). Regions of stable equilibria for models of differential selection in the two sexes under random mating. *Genetics*, 85, 171–183.
- Kruuk, L.E.B., Baird, S.J.E., Gale, K.S. & Barton, N.H. (1999). A comparison of multilocus clines maintained by environmental adaptation or by selection against hybrids. *Genetics*, 153, 1959–1971.
- Labbe, P., Sidos, N., Raymond, M. & Lenormand, T. (2009). Resistance gene replacement in the mosquito *Culex pipiens*: fitness estimation from long-term cline series. *Genetics*, 182, 303–312.
- Levins, R. (1968). *Evolution in Changing Environments: Some Theoretical Explorations*. Princeton University Press, Princeton, NJ.
- Lewontin, R.C. (1958). A general method for investigating the equilibrium of gene frequency in a population. *Genetics*, 43, 419.
- Loreau, M. & Mouquet, N. (1999). Immigration and the maintenance of local species diversity. *Am. Nat.*, 154, 427–440.
- Lou, Y. & Nagylaki, T. (2006). Evolution of a semilinear parabolic system for migration and selection without dominance. *J. Differ. Equ.*, 225, 624–665.
- Nagylaki, T. (1975). Conditions for the existence of clines. *Genetics*, 80, 595–615.
- Nagylaki, T. (2009). Evolution under the multilocus Levene model without epistasis. *Theor. Popul. Biol.*, 76, 197–213.
- Nagylaki, T. & Lou, Y. (2001). Patterns of multiallelic polymorphism maintained by migration and selection. *Theor. Popul. Biol.*, 59, 297–313.
- Pope, S., Fahrig, L. & Merriam, H. (2000). Landscape complementation and metapopulation effects on leopard frog populations. *Ecology*, 81, 2498–2508.
- R Development Core Team (2010). *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria. Available at: <http://www.R-project.org>. ISBN 3-900051-07-0. Last accessed 6 January 2011.
- Scudo, F.M. (1967). Selection on both haplo and diplophase. *Genetics*, 56, 693–704.
- Searle, J.B., Navarro, Y.N. & Ganem, G. (1993). Further studies of a staggered hybrid zone in *Mus musculus domesticus* (the house mouse). *Heredity*, 71, 523–531.
- Snyder, R.E. & Chesson, P. (2003). Local dispersal can facilitate coexistence in the presence of permanent spatial heterogeneity. *Ecol. Lett.*, 6, 301–309.
- Soetaert, K., Petzoldt, T. & Setzer, R.W. (2010). Solving differential equations in R: Package deSolve. *J. Stat. Softw.*, 33, 1–25.
- Strayer, D.L., Power, M.E., Fagan, W.F., Pickett, S.T.A. & Belnap, J. (2003). A classification of ecological boundaries. *BioScience*, 53, 723–729.
- Strobeck, C. (1979). Haploid selection with n alleles in m niches. *Am. Nat.*, 113, 439–444.
- Tilman, D. (1994). Competition and biodiversity in spatially structured habitats. *Ecology*, 75, 2–16.
- Tscharntke, T., Klein, A.M., Kruess, A., Steffan-Dewenter, I. & Thies, C. (2005). Landscape perspectives on agricultural intensification and biodiversity ecosystem service management. *Ecology Letters*, 8, 857–874.
- Turchin, P. (1998). *Quantitative Analysis of Movement: Measuring and Modeling Population Redistribution in Animals and Plants*. Sinauer Associates Inc, Sunderland.
- Vellend, M. (2010). Conceptual synthesis in community ecology. *The Quarterly Review of Biology*, 85, 183–206.
- Wolfram Research, Inc. (2008). *Mathematica Edition: Version 7.0*. Wolfram Research, Inc., Champaign, IL.
- Wright, S. (1931). Evolution in Mendelian populations. *Genetics*, 16, 97.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Figure S1 Equivalent of Fig. 3(a), with Nagylaki (1975) equation [i.e. eqn (3) without the \bar{r} denominator].

Figure S2 Equivalent of Fig. 3(a), changing the parameters of the second specialist type: $\rho_2^A = 0.1$, $\rho_2^B = 0.9$. The new intermediate grey area correspond to the coexistence of the specialist type 1 and of the generalist. There is no three-type coexistence when $\rho_3 > \rho_2^B$ because the generalist becomes better adapted to the second environment than the second specialist (right of the dashed line).

Figure S3 Equivalent of Fig. 3(a), in an asymmetrical environment where $q = 0.3$. The intermediate grey area correspond to the coexistence of the specialist of the most frequent habitat (2) and of the generalist.

Figure S4 Equivalent of Fig. 2(b), when the migration parameters differ among types. The thicker grey line shows the total population density. New parameters: $\sigma_1 = 0.0075$, $\sigma_2 = 0.05$, $\sigma_3 = 0.01$.

As a service to our authors and readers, this journal provides supporting information supplied by the authors. Such materials are peer-reviewed and may be re-organized for online delivery, but are not copy-edited or typeset. Technical support issues arising from supporting information (other than missing files) should be addressed to the authors.

Editor, Jean-Michel Gaillard

Manuscript received 27 September 2010

First decision made 29 October 2010

Manuscript accepted 8 December 2010