



Adaptive diversification in heterogeneous environments



Olivier David^{a,*}, Christian Lannou^b, Hervé Monod^a, Julien Papaïx^c, Djidi Traore^a

^a MaIAGE, INRA, Université Paris-Saclay, 78350 Jouy-en-Josas, France

^b UMR 1290 BIOGER, INRA, Thiverval Grignon, France

^c UR 546 BioSP, INRA, Avignon, France

ARTICLE INFO

Article history:

Received 7 October 2016

Available online 7 December 2016

Keywords:

Adaptation
Adaptive dynamics
Migration
Multivariate evolution
Spatial heterogeneity
Structured populations

ABSTRACT

The role of environmental heterogeneity in the evolution of biological diversity has been studied only for simple types of heterogeneities and dispersals. This article broadens previous results by considering heterogeneities and dispersals that are structured by several environmental factors. It studies the evolution of a metapopulation, living in a network of patches connected by dispersal, under the effects of mutation, selection and migration. First, it is assumed that patches are equally connected and that they carry habitats characterized by several factors exerting selection pressures on several individual traits. Habitat factors may vary in the environment independently or they may be correlated. It is shown that correlations between habitat factors promote adaptive diversification and that this effect may be modified by trait interactions on survival. Then, it is assumed that patches are structured by two crossed factors, called the row and column factors, such that patches are more connected when they occur in the same row or in the same column. Environmental patterns in which each habitat appears in each row the same number of times and appears in each column the same number of times are found to hinder adaptive diversification.

© 2016 Elsevier Inc. All rights reserved.

1. Introduction

Adaptive diversification is the evolution of different types of organisms under the effects of evolutionary forces such as selection and mutation (Doebeli, 2011). In natural populations, it may play a role in the evolution of biological diversity (Kocher, 2004; Johnson, 2007). In agrosystems, it may allow some genotypes to have higher performances in some environments (Rhoné et al., 2008; Gautier et al., 2009) but also some pathogens to better develop on some hosts and possibly to be more damaging (Pariaud et al., 2009; REX Consortium, 2013; Fabre et al., 2015). In medicine, it may be involved in the emergence of drug resistance (REX Consortium, 2013; Roemhild et al., 2015). It is therefore important to identify the circumstances that promote diversification.

Biotic and abiotic conditions are often variable within environments. Various features of this environmental heterogeneity may influence adaptive diversification. The overall level of heterogeneity generally promotes diversification, although intermediate

levels sometimes maximize diversification propensity (Meszéna et al., 1997; Geritz et al., 1998; Doebeli and Dieckmann, 2003; Débarre et al., 2013; Haller et al., 2013). When geographical sites are equally connected by dispersal, balancing the frequencies of the habitats resulting from environmental heterogeneity promotes diversification (Geritz et al., 1998). When dispersal is more important between neighboring sites, gradients and landscapes isolating populations into large spatially continuous habitats promote diversification (Débarre and Gandon, 2010; Birand et al., 2012; Haller et al., 2013; Papaïx et al., 2013). When dispersal is more important within groups clustering patches than between groups, diversification is hindered by making within-group habitat distributions equal (Papaïx et al., 2013).

Most theoretical works on the role of environmental heterogeneity in adaptive diversification have studied the influence of a single environmental factor. However, the complexity of environments makes it likely that many factors are involved in adaptive diversification (Poisot et al., 2011; Laughlin and Messier, 2015). For example, such factors could be related to temperature, rainfall, soil type, host genotype, etc. Gavrillets and Vose (2005) studied how populations adapted to their environment when habitats were characterized by several environmental factors and were assigned to patches with equal probabilities. However, habitat factors may be associated in a landscape in various ways: they may

Abbreviations: ES, evolutionary singularity.

* Correspondence to: Unité MaIAGE, Bât. 210, INRA, Domaine de Vilvert, 78352 Jouy-en-Josas Cedex, France.

E-mail address: Olivier.David@inra.fr (O. David).

vary independently between patches or they may be correlated. An exploration of the consequences of the relationships between habitat factors is needed.

Most theoretical studies of the diversifying effects of environmental heterogeneity have considered simple models of dispersal, in particular models in which dispersal rates are constant, decay with spatial separation or depend on an environmental factor. However, dispersal may be more complex in reality (Karlin, 1982). For example, plant pathogens may be dispersed by air, rain, water, soil, or by vectors such as animals, pollen, microbes, people, and machinery (West, 2014). The spread of human diseases may depend on the clustering of hosts into species or age classes (Sloan et al., 2011; Johnson et al., 2015). Animal diseases may spread between farms at a regional scale through animal movements due to animal trade (Beaunée et al., 2015). An exploration of the interactions between environmental heterogeneity and various forms of dispersal would be welcome.

In this article, we study how environmental heterogeneity promotes the gradual evolution of polymorphism when this heterogeneity and dispersal depend on several factors. We consider a population of individuals living on a network of patches holding different habitats (Section 2). We restrict ourselves to models that are sufficiently simple to be analyzed analytically. We study how the allocation of habitats to patches influences diversification when habitats are characterized by several factors and when patches are equally connected by dispersal (Section 3). Then, we study how it influences diversification when dispersal depends on two crossed factors (Section 4).

2. Model

2.1. Individuals and environment

Individuals are characterized by a vector $x = (x_1, \dots, x_d)^T$ of $d \geq 1$ continuous adaptive traits, where T denotes transposition. They are assumed to reproduce asexually and to have the same trait vector x as their parent, unless mutations occur.

The environment comprises P patches, each holding K individuals, with K sufficiently large that demographic stochasticity can be neglected. Each patch belongs to one habitat among H possible ones. Each habitat is characterized by a vector $\beta = (\beta_1, \dots, \beta_d)^T$, that corresponds to the optimal phenotype for this habitat. As will be detailed below, the growth of a juvenile in this habitat is optimal if $x = \beta$. The allocation of habitats to patches is called an environmental pattern.

2.2. Life cycle

Juvenile dispersal. Juveniles are assumed to disperse after birth. A proportion $m_{i'}$ of juveniles move from patch i' to patch i during a life cycle, with $\sum_i m_{i'} = 1$ and $m_{i'} = m_{i'i}$. All patches are assumed to be connected.

Growth and selection. After dispersal, a juvenile either develops into an adult or dies. The proportion $g(x, \beta)$ of juveniles with trait vector x in a habitat selecting for phenotype β that become adults is assumed to have a d -dimensional normal shape (Geritz et al., 1998; Doebeli and Ispolatov, 2010)

$$g(x, \beta) = \alpha \exp\left(-\frac{(x - \beta)^T B (x - \beta)}{2}\right),$$

with $d \times d$ inverse variance–covariance matrix B , that is symmetric and positive definite. An individual is more adapted to a habitat when its phenotype is closer to the optimal phenotype of this habitat. The normal shape of $g(x, \beta)$ imposes a trade-off between the growths in the habitats: adaptation to a habitat causes maladaptation to the other habitats. The non-diagonal elements of B quantify the interactions between traits on juvenile

development. When B is diagonal, $\ln(g(x, \beta))$ is simply a sum of trait contributions

$$\ln(g(x, \beta)) = \ln(\alpha) - \sum_{j=1}^d B_{jj}(x_j - \beta_j)^2/2,$$

where $B_{jj'}$ is the element of B in row j and column j' . When B has some non-zero non-diagonal elements, $\ln(g(x, \beta))$ also involves contributions from pairs of traits, i.e. the sum $-\sum_{j < j'} B_{jj'}(x_j - \beta_j)(x_{j'} - \beta_{j'})$, so that traits interact.

Density regulation. After growth, density dependence makes the size of each patch equal to K .

Reproduction. Finally, each adult gives birth to f juveniles before dying. Thus generations are non-overlapping.

No other assumptions are done at this stage but later when we address some specific issues.

2.3. Adaptive dynamics

We use the adaptive dynamics framework (Geritz et al., 1998; Diekmann, 2004). Let us consider a monomorphic resident population, i.e. a population in which all the individuals have the same trait vector x . The population evolves thanks to the recurrent fixation of mutants. Mutations are assumed to be rare so that the population has time to reach its demographic equilibrium between mutation events. They are also assumed to have small effects so that evolution is gradual.

Adaptive dynamics is based on the definition of an invasion fitness that indicates if a mutant can invade a resident population. To define fitness, the initial demography of a mutant population is approximated by a matrix model (Appendix A). Invasion fitness is then defined as the dominant eigenvalue of the projection matrix. The mutant is assumed to replace the resident when its fitness is larger than one and to go extinct when its fitness is smaller than one.

Evolutionary singularities (ESs) are evolutionary equilibria. It is shown in Appendix D that our model has a unique ES that is equal to

$$\hat{x} = \sum_h p_{1\dots d}(h) \beta(h),$$

where $p_{1\dots d}(h)$ is the frequency of habitat h , i.e. the proportion of patches with this habitat, and $\beta(h)$ is the optimal phenotype of habitat h . This ES depends on the environmental pattern through habitat frequencies only.

An ES \hat{x} is attracting (or convergence stable) if the resident trait converges to \hat{x} by gradual evolutionary changes. It is shown in Appendix E that \hat{x} is an attractor. In the following sections, we study how environmental heterogeneity destabilizes \hat{x} when habitats and dispersal are patterned by factors.

3. Diversification in multi-dimensional environments

Multi-dimensional habitats. Environments are likely to exert selection pressures through several variables in nature. Thus we assume that habitats are multi-dimensional in the sense that they are characterized by d factors. Here each factor has two levels, so that there are 2^d possible habitats, that are denoted by the row vectors $h = (h_1, \dots, h_d)$, where $h_j = 1, 2$ is the level of the j th factor for $j = 1, \dots, d$. The optimal phenotype of habitat h is assumed to be equal to $\beta(h) = ((-1)^{h_1}, \dots, (-1)^{h_d})^T \theta$, where θ is a positive scalar. The j th factor influences the j th component of $\beta(h)$ and thus exerts a selection pressure on the j th trait, but it may also affect other traits through trait interactions. The discrepancy between habitats h and h' can be quantified by the distance

$$\sqrt{(\beta(h) - \beta(h'))^T B (\beta(h) - \beta(h'))}. \quad (1)$$

Download English Version:

<https://daneshyari.com/en/article/5760582>

Download Persian Version:

<https://daneshyari.com/article/5760582>

[Daneshyari.com](https://daneshyari.com)