Ecological Complexity 16 (2013) 9–19

Contents lists available at SciVerse ScienceDirect

Ecological Complexity

journal homepage: www.elsevier.com/locate/ecocom

Original Article

A framework to compare theoretical predictions on trait evolution in temporally varying environments under different life cycles

François Massol [a,b,*]

[a] IRSTEA – UR HYAX, 3275, route de Cézanne – Le Tholonet, CS 40061, 13182 Aix-en-Provence cedex 5, France
[b] UMR 5175 CEFE – Centre d'Ecologie Fonctionnelle et Evolutive (CNRS), 1919 Route de Mende, F-34293 Montpellier cedex 05, France

ARTICLE INFO

Article history:
Received 29 January 2012
Received in revised form 28 May 2012
Accepted 28 May 2012
Available online 27 June 2012

Keywords:
Adaptive dynamics
Evolutionarily stable strategy
Hard selection
Local adaptation
Metapopulation
Soft selection

ABSTRACT

Predicting the evolution of traits such as dispersal or local adaptation, in a variable environment is an important issue in theoretical evolutionary ecology. With concepts such as hard selection *vs.* soft selection or fine-grained *vs.* coarse-grained environmental variability, this issue has attracted much attention, and yet different models seldom agree on qualitative predictions about, *e.g.* the evolution of generalist or specialist strategies, or the occurrence of stabilizing or disruptive selection on studied traits.

Here, I investigate the effect of the order of events in the life cycle on trait evolution in a spatially heterogeneous, temporally varying landscape using a Wright–Fisher island model. I first develop a methodological framework allowing for different life cycles. Then I illustrate the importance of life cycles on selection regimes by looking more closely at the evolution of local adaptation.

Model results show that the occurrence of disruptive selection and bi- or tristability mainly depends on the life cycle, the convexity of the trade-off behind local adaptation, the immigration rate, and the autocorrelation in patch state. With the same forces driving the evolution of local adaptation, different life cycles induce different evolutionary outcomes. Model results highlight the importance of accounting for life cycle specificities when attempting to predict the effects of the environment on evolutionarily selected trait values, as well as the need to check the robustness of evolutionary model conclusions against modifications of the life cycle.

1. Introduction

Predicting the evolution of traits in variable environments has been a classical issue in theoretical evolutionary ecology now for more than fifty years. This issue is central from a population genetics viewpoint because it underlies the whole argument on environmentally maintained polymorphism, *i.e.* the fact that genotypes specialized on different types of environments stably coexist due to frequency-dependent selection. It is also central from a more applied viewpoint since being able to make predictions on adaptation to changing environments is the key to understand how organisms might cope with future changes, *e.g.* climatic changes or habitat fragmentation. For both fundamental and applied reasons, models have been developed to understand how variability in environmental conditions might influence evolutionary trajectories.

Environmental variability can be conceived as both spatial and temporal. On the one hand, environmental variability can be found among sites (*e.g.* ponds with or without insecticide, at different temperatures, with different levels of nutrients, *etc.*). On the other hand, variability in habitat conditions can be a function of time, so that a currently good patch can turn bad for the next generation. It is very tempting to think that different environmental conditions should select for different adaptations in organisms and, hence, should tend to create specialized sister "species" exploiting different environmental conditions regardless of whether variability in habitat conditions is temporal or spatial. However, some early works, such as Levins' coarse-grained habitats *vs.* fine-grained habitats (Levins, 1968, 1979), have proved that the same level of habitat variability might select for two specialized genotypes or a single generalist one, depending on whether each individual experiences several or only one habitat for its entire life. In the 1950s, population geneticists also proposed models to assess the effect of spatial environmental variability on the evolution of traits. More specifically, they focussed on the study of local adaptation polymorphisms maintained by fixed spatial differences in habitat conditions (Christiansen, 1975; Dempster, 1955; Karlin and Campbell, 1981; Levene, 1953; Wallace, 1975). Their results, which have been part of every population genetics handbook ever since, prove that different models can lead to different predictions: whereas Levene's soft selection model allows for protected polymorphisms, Dempster's hard selection model only predicts

---

[*] Corresponding author. Tel.: +33 4 42 66 99 45; fax: +33 4 42 66 99 34.
E-mail address: francois.massol@irstea.fr.

1476-945X/$ – see front matter © 2012 Elsevier B.V. All rights reserved.
http://dx.doi.org/10.1016/j.ecocom.2012.05.004

the dominance of a single genotype, corresponding to the one more adapted to the most abundant habitat.

At some point came the realization that models by Levene, Dempster or others were not dealing with the same situations. For instance, population regulation (*i.e.* the process by which population abundances remain stable) operates in a very different fashion in soft and hard selection models (Christiansen, 1975; de Meeus and Goudet, 2000; de Meeus et al., 1993; Ravigné et al., 2004; Wallace, 1975): under hard selection, propagules are regulated at the landscape level, so that different habitats can emit different amounts of propagules; under soft selection, regulation is local and equally effective among habitats, so that there is no possibility for types specialized in using very productive habitats to overwhelm the whole system. However true these statements may be, it is much more enlightening to interpret differences in model assumptions from a more biological perspective. One such perspective was achieved by Ravigné et al. (2004) who proposed to interpret the models as representing different life cycles: essentially, what happens to individual organisms in these models can be summarized as reproduction, regulation, emigration, and immigration. When regulation occurs just after reproduction, the equations corresponding to the life cycle are those of Levene's model; when regulation occurs in-between emigration and immigration (*i.e.* in the propagule pool), then the life cycle yields Dempster's hard selection model. The last possible case (putting regulation after immigration) yields another different model that Ravigné et al. (2004) have studied at length. Interestingly, Ravigné's third type of model can be classified as either hard or soft depending on whether the model allows for habitat selection (Ravigné et al., 2004).

In spite of the various models that have been brought forth to study the effects of temporal or spatial sources of environmental conditions on evolution of traits such as local adaptation (de Meeus and Goudet, 2000; Dempster, 1955; Levene, 1953; Ravigné et al., 2004), habitat selection (Garcia-Dorado, 1987; Ravigné et al., 2009) or dispersal (Hastings, 1983; Holt, 1985; Kisdi, 2002; Massol et al., 2011), there have been only a few approaches actually tackling both temporal variability and spatial heterogeneity, and most of them focus on the evolution of dispersal (Blanquart and Gandon, 2011; Cheptou and Massol, 2009; Massol and Cheptou, 2011; Mathias et al., 2001; Parvinen, 2002). For traits such as dispersal, it is likely that habitat predictability (McNamara and Dall, 2011), or equivalently habitat temporal coarseness, and the spatial heterogeneity of habitats in the landscape (Hastings, 1983), should both have a say on evolutionary outcomes – and indeed they do (Massol and Cheptou, 2011). However, such results have yet to be extended to the evolution of other important traits affecting fitness, and it is still not clear that results obtained so far on the evolution of dispersal in spatio-temporally variable landscapes (Massol and Cheptou, 2011; McNamara and Dall, 2011) are general laws or depend on the specifics of the life cycle assumed. Results obtained on the evolution of local adaptation (Débarre and Gandon, 2011; Ravigné et al., 2004) suggest, on the contrary, that different life cycles may lead to different evolutionary outcomes. In this paper, I present a general methodological framework to predict the effects of spatio-temporal environmental variability and the order of events in the life cycle on the evolution of life-history traits. As an example, I illustrate present method for local adaptation. By way of studying this general problem, I also aim to show that much care should be taken when describing the assumptions made on life cycles in evolutionary ecology and population genetics model because such models can display much different predictions with a simple swap in life cycle events. Finally, I discuss results in the context of current research aimed at understanding evolutionary reasons for biological diversity.

2. Model

2.1. General principles

Consider the following problem: to predict evolutionary trajectories for a set of traits (vector $\mathbf{X}$) that evolve in a given species, I want to predict whether a given mutant (trait values $\mathbf{X}'$) can invade a landscape filled by a monomorphic resident type (trait values $\mathbf{X}$), *à la* adaptive dynamics (Geritz et al., 1998; Hofbauer and Sigmund, 1990) with clonal reproduction. I assume that the demographics follow Wright–Fisher island model assumptions (discrete time, synchronous reproduction, constant density, dispersal is not distance-limited) with an infinite number of patches containing an infinity of individuals, and can be modeled as simple semelparous life cycles (Ravigné et al., 2004) consisting in four different events. These events are:

- reproduction, noted as event S (or diagonal matrix $\mathbf{D}$ when needed, with entries S_{ij}) whereby local individual densities in patch class i are multiplied by a local growth factor S_{ii};
- environmental change, noted as event E (or matrix $\mathbf{E}$ with entries E_{ij}), which is assumed to be a stochastic process, occurring independently for each patch, and which keeps the expected proportion of patches of each type constant while allowing for autocorrelation in patch type before and after environmental change. Element E_{ij} corresponds to the probability that a patch of class j becomes of class i;
- dispersal, noted as event D (or matrix $\mathbf{D}$ with entries D_{ij}), which potentially accounts for conditional dispersal (different probabilities of emigrating based on current patch type), habitat selection (probabilities to land in patches of a given type may be different from its frequency), and the cost of dispersal. Element D_{ij} corresponds to the proportion of propagules originally in class j that is in class i after the dispersal event; and
- regulation, noted as event R (or diagonal matrix $\mathbf{R}$ with entries R_{ij}), which is assumed to occur independently in each patch. Because each patch contains an infinity of individuals, regulation consists in dividing the number of mutants obtained after all other life cycle events in a given patch by the number of residents obtained after the same steps.

Each event happens only once in the life cycles considered in this study. All individuals follow the same life cycle, *i.e.* the same series of events between birth and death. Because the model assumes non-overlapping generations, this reduces to the order of the four events. By convention, I assume that all life cycles finish with regulation – this convention allows for an easy enumeration of life cycles. Within a given generation, the demographics of the metapopulation are captured by the dynamics of individual mutant densities within each patch class relatively to individual mutant density taken after the last regulation episode. Patch classes are defined based on the level of detail necessary for the computation of regulation factors. In simple cases, patch classes equal patch types (2 classes); in complex cases, patch classes equal the recent history of a patch type, *i.e.* its current and former patch types (hence, 4 classes)

The general methodology developed here consists in finding the expressions for these event matrices. Once expressions for $\mathbf{S}$, $\mathbf{E}$, . . . have been found, these matrices are combined (*i.e.* multiplied) to obtain a next-generation matrix $\mathbf{G}(\mathbf{X}',\mathbf{X})$ that defines the dynamics of the vector of mutant frequencies $\mathbf{Y}_t$ in each patch type:

$$\mathbf{Y}_{t+1} = \mathbf{G}(\mathbf{X}', \mathbf{X}) \cdot \mathbf{Y}_t \qquad (1)$$

Here, the expression for $\mathbf{G}$ is a product $\mathbf{R}(\mathbf{X}) \cdot \mathbf{C}'(\mathbf{X}')$ where $\mathbf{C}'$ is the cycle matrix corresponding to mutant demographics (hence the