Demography of source–sink populations and the evolution of ecological niches

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Summary
The demography of populations living in variable environments is an important factor molding the evolution of ecological niches, for it determines the relative strength of selection pressures on adaptations to different habitats. Here I consider a coarse-grained environment consisting of two habitat types and investigate how the selection pressure on reproductive success in different habitats depends on their quality and frequency and the dispersal pattern. The results suggest that selection on adaptations to optimal habitats will usually be stronger than on adaptations to poor habitats and the ecological niche will thus tend to be an evolutionarily conservative character. It is because under the habitat choice or limited dispersal that seem to prevail in natural populations, more individuals encounter the better habitat than would be expected solely on the basis of its relative area. This bias results in reduced selection pressure on reproductive success in the poorer habitat. With habitat choice or limited dispersal, selection pressure on reproductive success in the poorer habitat may exceed that on reproductive success in the better habitat only if the poorer habitat is much more frequent in the environment than the better habitat and the difference in their quality is not large.

Keywords: demography; dispersal; ecological niche; evolution; heterogeneous environments; natural selection; source–sink populations

Introduction
Natural environments are heterogeneous. Populations encounter variation in abiotic conditions, resources and the abundance and type of competitors, predators and parasites. In spatially heterogeneous environments some habitats are rare and some common, some are good, some less good and some completely unsuitable. If the environment is coarse grained (Levins, 1968), differences in habitat quality translate into differences in performance and reproductive success of individuals encountering different habitats, unless perfect and cost-free habitat choice is possible, resulting in the ideal free distribution (Fretwell and Lucas, 1970). Differences in habitat quality will therefore usually result in a source–sink population structure (Pulliam, 1988) with net emigration of individuals from better (source) habitats and net immigration into poorer (sink) habitats. In source habitats reproduction exceeds mortality; in sinks the opposite is true.

Habitat quality sets limits to the ecological niche of an organism: the (fundamental) niche consists of habitats in which the population could persist without immigration, i.e. in which reproduction exceeds mortality at low density. Because most populations will attain a higher density most of the time, with some density-dependence operating, it is possible for a suboptimal habitat within the niche to be a sink (c.f. Pulliam, 1988). The subpopulation in a sink is kept above the local carrying capacity (Holt, 1985) and would decline if cut off from the source but would not necessarily become extinct.

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Habitat quality, as meant above, is not a property of the habitat itself, but depends on the interactions of the environmental conditions with the adaptations of the organism. An interesting question is, under what circumstances is a population likely to evolve new adaptations to a habitat initially outside the fundamental niche, so that its quality as perceived by the organism increases and it is finally included in the niche? Or, when is an adaptation to a suboptimal habitat close to the niche edge likely to become eroded, so that the habitat finally falls out of the niche? The answers to these questions depend on genetics and physiology (how much genetic variation is present, to what extent can the phenotype expressed in different habitats vary independently, what are the costs of the new adaptation) and on ecology and demography which determine the sensitivity of the overall fitness to performance in particular habitats and, thus, the direction and strength of selection pressure. In this paper I concentrate on the demographic aspect, asking how selection pressure on reproductive success in different habitats is affected by their abundance and quality and by dispersal among them.

Recently Holt and Gaines (1992) have considered an environment consisting of two equally frequent habitats connected by symmetric dispersal. They have shown that under complete mixing, fitness is equally sensitive to reproductive success in both habitats, but if dispersal is limited (i.e. more than 50% of offspring remain in their natal habitat) selection on reproductive success is always stronger in the source than in the sink habitat. In turn Kawecki and Stearns (1993) have shown that under complete mixing selection pressure on life history characters expressed in a given habitat increases with its frequency (cf. also Via and Lande, 1985). Here I generalize those results to a coarse-grained environment consisting of two types of habitats with arbitrary frequencies. I consider two extreme migration patterns: passive limited dispersal and perfect habitat choice and ask how the strength of selection pressure in a habitat depends on frequency of that habitat, current performance of the population in it and on the dispersal pattern.

The model

Consider a population with discrete generations living in an environment consisting of two kinds of habitats connected by dispersal. Dispersal can take place either at an early juvenile stage or at the adult stage before reproduction; in any case it is assumed that the reproductive success of an individual is affected only by one habitat, the one in which it spends most of its life (a coarse-grained environment; Levins, 1968). The dynamics of the population is described by the equation

\[
\begin{bmatrix}
    N_1(t + 1) \\
    N_2(t + 1)
\end{bmatrix} =
\begin{bmatrix}
    R_1 m_{11} & R_2 m_{21} \\
    R_1 m_{12} & R_2 m_{22}
\end{bmatrix}
\begin{bmatrix}
    N_1(t) \\
    N_2(t)
\end{bmatrix}
\]

where \( N_i(t) \) denotes the number of individuals in habitat \( i \) at the beginning of generation \( t \) (after migration), \( \overline{R}_i \) is the mean reproductive success in habitat \( i \) and \( m_{ij} \) is the proportion of offspring originating from habitat \( i \) that migrate to habitat \( j \). The reproductive successes in the two habitats will in general depend on density. With density dependence, the population may attain an equilibrium or undergo cyclic or chaotic fluctuations, depending on the particular form of population limitation (Caswell, 1989). Here I restrict my attention to cases where the population attains a stable ecological equilibrium, with a constant density and stable distribution of offspring among habitats.

The selection on the reproductive successes in this population can be described by a version of Lande’s (1982) model (Caswell, 1989)

\[
\frac{\Delta \bar{R}_1}{\Delta \bar{R}_2} = \frac{1}{\lambda} \begin{bmatrix} G_{11} & G_{12} \\ G_{12} & G_{22} \end{bmatrix} \begin{bmatrix} \partial \lambda / \partial \bar{R}_1 \\ \partial \lambda / \partial \bar{R}_2 \end{bmatrix}
\]