

Speciation through sexual selection in spatially heterogeneous environments

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Goal

To investigate how frequency-dependent local interactions can induce mating domains in spatially heterogeneous environments, thus causing speciation through sexual selection and the evolution of assortative mating.

Background and motivation

Speciation in sympatry has received considerable attention because, unlike for speciation in allopatry, the lack of population subdivision means that reproductive isolation must be achieved in the presence of persistent gene flow. One mechanism that is thought to be capable of creating reproductive isolation in sympatry is frequency-dependent disruptive selection combined with reinforcement through selection against maladapted hybrids. Such disruptive selection could act on an ecological trait, as in Dieckmann and Doebeli (1999), or on a sexually selected trait via divergent Fisherian runaway, as in Higashi et al. (1999). While it has been shown that species produced via frequency-dependent disruptive natural selection can stably coexist (Dieckmann and Doebeli 1999), it is not known whether sexual selection is capable of generating equivalently stable species. Even though ecologically heterogeneous environments are known to stabilize such species (Lande 1982; Payne and Krakauer 1997), corresponding studies are surprisingly few and leave open many questions that deserve to be explored. Furthermore, there are no theoretical studies so far examining sexual selection in heterogeneous environments that are neutral with respect to natural selection, such as environments that are heterogeneous in local carrying capacity and/or growth rates. Without such studies, it is difficult to assess the relative importance of sexual selection in speciation and the evolution of assortative mating.

Lande (1982) analyzed the joint evolution of geographic variation in female mating preferences and secondary sexual characters in males in an ecologically heterogeneous environment and found that sexual selection tended to enhance spatial population structure, to a larger extent than would be expected under natural selection alone. Payne and Krakauer (1997) suggested that Lande's model, as well as the non-spatial models presented by Kirkpatrick (1982) and Seger (1985), always result in eventually homogeneous populations when applied to ecologically homogeneous environments with constant diffusion. They then showed that, if diffusion was not constant, but dependent on local conditions, spatially structured populations could emerge even in the absence of environmental heterogeneity. In particular, they showed that when the dispersal of males was inversely proportional to their mating success, spatially heterogeneous populations and assortative mating could evolve, resulting in segregated mating domains individually characterized by the co-occurrence of mutually compatible mat-

ing traits. However, while this was not explicitly stated in their paper, it turns out that the spatial population structures reported by Payne and Krakauer (1997) were in fact only transitory, and only applied before one mating domain eventually replaced all others. The authors also showed that, in the presence of an ecological gradient, population structure became more pronounced. It has since been shown that mating-dependent dispersal is not the only mechanism capable of leading to such evolutionary outcomes (Dieckmann 2004).

A number of important questions emerge from these results, the primary one being: How do the spatial dynamics of mating traits affect long-term population structure and the evolution of assortative mating when situated in spatially heterogeneous environments? In other words, How much environmental heterogeneity is required for stably maintaining mating domains in which different mutually compatible combinations of mating traits prevail and across which hybridization will be rare? A number of follow-up questions are discussed below.

Research questions

The focus of this research project will be to investigate how frequency-dependent local interactions between different mating types (Payne and Krakauer 1997; Dieckmann 2004) can induce spatial structure and the evolution of assortative mating in spatially heterogeneous environments. More specifically, we will try to answer the following questions:

- How do environments implying spatial heterogeneity in the local amplitudes of carrying capacities and/or growth rates affect the emergence and persistence of mating domains under frequency-dependent local effects on mobility (Payne and Krakauer 1997)?
- How do environments requiring local adaptation, such as those in Lande (1982), affect the emergence and persistence of mating domains?
- How do results extend to frequency-dependent local effects on fecundity and mortality (Dieckmann 2004)?
- How do results differ when temporal variations in environmental heterogeneity are considered?
- How do results differ when the considered environments are two-dimensional instead of one-dimensional?

It may also be worthwhile investigating environments in which there is an ecological advantage of rarity. This will tend to discourage the evolution of assortative mating, and thus compete with the selection created by the aforementioned mechanisms.

Methods and work plan

We will focus on developing and investigating stochastic individual-based models and may, time permitting, eventually examine the possibility of approximating these through deterministic continuum models.

We will begin by extending an existing individual-based model (Doebeli and Dieckmann 2003) with the first aim of reproducing the main results reported by Payne and Krakauer (1997). In particular, we will show that in homogeneous environments the negative dependence of dispersal in males on their mating success can be a suffi-

ciently strong force to generate mating domains. We will then show that these spatial structures do not persist over evolutionary time, as one mating domain eventually replaces all others. Next, we will show how environments (i) implying spatial heterogeneity in the local amplitudes of carrying capacities and/or growth rates or (ii) requiring local adaptation stabilize otherwise transient mating domains. Following ideas presented in Dieckmann (2004) we will also investigate the effects of frequency-dependent mortality and frequency-dependent fecundity.

After exploring spatial environmental structures described by linear gradients, we will examine more complex heterogeneities. For example, Lande (1982) considered three spatial environmental structures that could be investigated: a one-step, a two-step (comprising of a one-step up and a one-step down), and an environment periodically changing in space.

It will be important to compare results in one-dimensional space with those in two dimensions, since it has been suggested that, in the absence of spatial environmental structure, mating domains deteriorate more quickly in two dimensions than in one (Dieckmann, unpublished). This effect results from domain boundaries encroaching on convex domains; a phenomenon that naturally cannot occur in a single spatial dimension.

We will also investigate temporal variation, both on its own and in combination with spatial heterogeneity. This could be done in one of two ways, both of which are likely to provide interesting results. First, spatial patches could experience some probability of extinction during each generation. Re-colonization would then occur via dispersal. This will increase the overall level of stochasticity in the model, and will likely reduce the persistence of mating domains. Alternatively, the spatial environmental structure could fluctuate in time, so that, for example, a patch could gradually oscillate between having high or low carrying capacity, or between favoring one local adaptation or another. It is not clear a priori how such variation will affect results.

We plan to consider two mechanisms of assortative mating, in order to be consistent with previous models. In the “fixed relative-preference” mating scheme, a female with preference strength a , is a times more likely to mate with a male bearing the desired trait than with a male not bearing that trait (Kirkpatrick 1982). A more general approach is the “best of N ” scheme, in which a female surveys N males before choosing a mate. Again she is a times more likely to choose a male with the desired trait (Seeger 1985). In one extreme, for $N = 1$, the “best of N ” scheme corresponds to random mating, whereas in the other extreme, when N approaches the size of the whole population, the “best of N ” and the “fixed relative-preference” schemes become equivalent. Possible extensions here include considering the evolution of a , or male and female mating traits that are coded for by multiple loci and that are thus subject to segregation and recombination. The latter has been suggested by Bridle et al. (2000) as a worthwhile extension of the model in Payne and Krakauer (1997).

Our tentative plan is to further investigate interesting results from the individual-based models with the help of an approximate analytical continuum model. However, without such results having yet been assembled and the feasibility of such approximations having been scrutinized, it is not realistic to speculate about the details of such a model.

Relevance and link to EEP's research plan

This project is an extension of work that was developed at IIASA. I will be using the adaptive dynamics framework to extend the individual-based models developed in Doebeli and Dieckmann (2003). This project will thus make contributions to EEP's research project on *Adaptive Dynamics Theory*. Furthermore, our model will contribute to EEP's research project on *Evolving Biodiversity* by investigating the conditions under which ecologically similar species may or may not arise and coexist over evolutionary time.

Expected output and publications

This work will be a part of my PhD thesis and is intended for publication as a co-authored article in an international scientific journal.

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