Effect of Habitat Selection Behaviour on Parapatric Speciation

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Goal

To investigate and compare the effect of fixed and evolving habitat selection behaviors on parapatric speciation on spatially structured resource landscapes.

Background and motivation

Bewildering diversity is a characteristic of life on all scales from populations to species to communities. Until recently, evolutionary theory postulated that each branching event has required geographic isolation of populations (Provine 2004), in disagreement with Darwin's (1859) view on speciation. But consider bugs and bats and birds. Insects comprise the vast majority of all known animal species, the ca. 1000 bat species comprise almost a fourth of all mammal species, and the ca. 10 000 bird species comprise well over a third of all terrestrial vertebrate species, spread over all habitable corners of the world with countless subspecies. These groups differ from most of their relatives in that they have wings, giving them superior ability to overcome geographical barriers. The notion of geographical isolation alone causing speciation appears to be at odds with the diversity of these highly mobile taxa.

Evolutionary ecologists studying speciation are starting to concentrate on mechanisms other than geography (Dieckmann et al. 2004, Rundle & Nosil 2005), suggesting that sympatric and parapatric speciation might be more prevalent than previously acknowledged (Via 2004). Also empirical evidence is mounting (e.g. Rolan-Alvarez et al. 2004, Cruz et al. 2004, Smith et al. 2005). Theoretically, speciation in panmictic, sympatric populations has been shown to occur due to frequency-dependent selection, if increased phenotypic difference from the phenotype maximizing carrying capacity reduces competition with the maximizing phenotype more than it reduces carrying capacity (Dieckmann & Doebeli 1999). When the model is extended to include space, this constraint is partially relaxed, so that if gene flow across a spatial resource gradient is restricted by limited movement of individuals and ecological interactions operate on sufficiently small distances, speciation occurs even if the effect of competition between different phenotypes exceeds the benefit gained from different resource use (Doebeli & Dieckmann 2003).

However, as noted above, many of the most species-rich taxa are exceptionally good dispersers. The conditions allowing parapatric speciation in the Doebeli & Dieckmann (2003) model become increasingly restricted with such high mobility. Evolution of habitat selection behaviors could be the key to resolving that contradiction.

If habitat selection behavior evolves, and mating requires sufficient proximity between individuals (which is obligatory for animals with internal fertilization and very likely for many other species), habitat selection leads to non-random mating (Rice 1987). Habitat selection can therefore potentially ease theoretical restrictions on non-allopatric speciation. In addition, because mobility combined with habitat selection would facilitate colonization of suitable unused habitat patches and enhance gene flow between similar but spatially separated patches, it could promote the survival and spreading of habitat-specific adaptations, facilitating evolution of pre-mating reproductive isolation via reinforcement. Mobility could thus become a factor facilitating evolutionary branching, instead of restricting it.

Research questions

The overarching question I will address is whether and how habitat selection behaviors affect conditions for parapatric speciation.

I will first concentrate on how the addition of a fixed habitat selection trait, determined by a single population-wide parameter, changes the conditions for parapatric speciation along a one-dimensional resource gradient as considered by Dieckmann & Doebeli (2003; see below). The most important questions here are whether habitat selection allows branching with larger and more frequent individual movements than the original model, and whether mobility with habitat selection could even facilitate branching.

This model will then be extended to allow evolutionary change in the one-dimensional habitat selection trait. Evolution of habitat preference and specialization were earlier argued to be mutually exclusive (de Meeûs et al. 1993), but this is not the case at least when habitat choice is determined pleiotropically by loci responsible for the specialization (Ravigné et al. 2004). The open question here, also raised by Ravigné et al. (2004), is whether the simultaneous evolution can occur if both traits can evolve simultaneously.

Finally, more complex forms of habitat selection behavior will be allowed to evolve in the multi-dimensional trait space provided by evolving neural nets (see below). These behaviors and their effects will be compared to the results from models with fixed and one-dimensional traits. Important questions are whether or not the evolving behaviors utilize the expanded trait space or resemble the simple one-dimensional traits, and whether they lead to different (e.g. faster) patterns of evolutionary branching.

Should these three sub-projects proceed faster than expected, the next goal could be to expand the approach from the effect of habitat selection on gradients to studying evolution in more complex spatially structured resource landscapes. I am already in the process of investigating habitat specialization and speciation in landscapes of two discrete habitat types, with a direct trade-off between utilization of the two resources. Therefore, investigating speciation with habitat selection in two-resource landscapes with different trade-off geometries (de Mazancourt & Dieckmann 2004) is another avenue of interesting research.

Methods and work plan

The work will build on a spatially explicit, individual-based simulation environment already developed, which describes an evolving population of diploid organisms, placed on spatially structured landscape, with the behavior of individuals controlled by neural nets.

The first task is to modify this simulation environment to reproduce the results of Dieckmann & Doebeli (2003) on speciation along linear environmental gradients without habitat selection behaviors. They model the evolution of ecological and mating preference traits – each defined by a number of diploid, diallelic, freely recombining, additive loci. Individuals reside on a two-dimensional landscape, where the ecological phenotype maximizing local carrying capacity changes with the environmental gradient in one direction, according to a steepness parameter. In other words, because of the environmental gradient, the intermediate phenotype is optimal in the middle of the landscape, and the two extreme phenotypes are optimal at the opposite edges of the landscape.

The effective population size experienced by an individual, divided by its phenotype-specific carrying capacity at its location, determines its death rate. This effective population size, in turn, depends on the number, distances, and phenotypes of surrounding individuals: the width of a spatial interaction kernel determines the competitive impact of individuals given distance away, and the width of a phenotypic interaction kernel determines how competition is reduced with increasing phenotypical difference. This leads to locally frequency-dependent selection: the death rate of an individual depends on the phenotypic composition in its neighborhood. In particular, individuals surrounded by others with differing phenotypes can experience a low death rate, even if the absolute number of neighbors is high.

Individuals give birth at a constant rate. Partners are chosen based on phenotypic difference and spatial distance, so that spatial proximity increases and phenotypic difference either decreases (assortative mating) or increases (disassortative mating) the probability of a partner being chosen, depending on the mating character of the choosing individual. Individuals move at a fixed rate, with movement distances drawn from a given distribution.

The outcome of simulations turns out to be affected by three parameters: the steepness of the environmental gradient, the width of the phenotypic interaction kernel, and the expected lifetime movement distance. Under certain parameter combinations the population branches into two species with different resource optima, inhabiting the adjacent halves of the environmental gradient. This branching requires that the environmental gradient is neither too steep nor too shallow, that competition sufficiently decreases with phenotypic difference, and that individual movement in small enough. Interestingly, if the lifetime movement distance is sufficiently small, branching occurs even when competition between different phenotypes is intense, for a wide range of gradient steepness.

In the first stage of the project, fixed habitat selection behaviors will be introduced in the simulation and results will be compared with the original. The fixed habitat selection behaviors planned to be investigated, in order of ascending complexity, are as follows:

1. Avoidance behavior – by altering the magnitude or the rate of movement, individuals exhibit more movement under poorer resource conditions than under good conditions.
2. Positive taxis – movement directions are biased in the direction of the gradient towards better resource conditions. The strength of this bias depends on the currently experienced resource conditions, so that individuals in poorest conditions exhibit the strongest bias.

3. Avoidance and taxis – a combination of the above, so that individuals at locations with poor resource conditions exhibit more movement *and* strongly bias its direction. By contrast, under good conditions individuals move less and more randomly. This combined behavior should lead to rapid convergence to high-fitness locations.

Furthermore, these behavior models can be extended by taking into account the intensity of competition an individual currently experiences, so that individuals tend to move away from intense competition. This would be predicted to facilitate dispersion but also counter frequency-dependent competition. Accordingly, strong competition-driven habitat selection could impede evolutionary branching.

In the next stage of the project, the avoidance strength and taxis accuracy will be allowed to evolve. Initially these behaviors will be set to describe random movement, and the simultaneous evolution of the three traits – specialization, assortativeness, and habitat selection – will be investigated.

Finally, the habitat selection behaviors will be allowed to evolve via the evolution of individual neural nets, while the other aspects of the model will be retained. These nets will receive information about an individual's surroundings, and will process that information into decisions affecting movement. The structure of the neural nets is controlled by an individual's diploid genome (there are two copies of each neuron). When an individual breeds, a haploid gamete is formed by recombination. Another gamete is drawn from the chosen partner individual, and these combine to form the neural net of a new offspring individual. Random mutations can occur with a given probability, providing new alleles to be shuffled by recombination.

Initially the neural nets cause random behavior, but over time selection leads to increasingly appropriate decisions. This setting will allow flexible, nonlinear, and potentially complex habitat selection behaviors to emerge, which would otherwise be difficult to model. More importantly, as the individuals are initially generalists without habitat selection abilities, the issue of simultaneous independent evolution of habitat specialization and preference (Ravigné et al. 2004) is explicitly investigated here in a multi-dimensional trait space.

Relevance and link to ADN's research plan

The effect of habitat selection on speciation should be profound, as it potentially creates genetic polymorphism, spatial segregation, and reduced gene flow within continuous populations (Ravigné et al. 2004). Thorough investigations into this are however only beginning. The planned work builds on research previously carried out by ADN (Dieckmann & Doebeli 2003). Investigating evolving habitat selection behaviors serves as a natural extension of this earlier research. The final part involving multi-dimensional trait spaces and neural net control is an extension into non-linear and flexible behaviors, and will also help to explore evolution on increasingly complex spatial landscape, a line of research that is already in progress in ADN.

Expected output and publications

I anticipate writing a manuscript on the effects of simple habitat selection behaviors during the Summer Program.

The work involving multi-dimensional trait spaces and neural net control, should it proceed smoothly, is also likely to yield a manuscript during or soon after the Program.

After the Program, should we find such collaboration feasible, I would continue working in collaboration with ADN on exploring evolution in more complex landscapes with spatial and temporal resource dynamics.

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