

Stochastic impediments to biological diversification

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Goal

To devise a theoretical framework for understanding the impacts of demographic and environmental variation on evolutionary branching.

Background and motivation

Speciation is evolution at the grandest scale. Speciation is the mechanism responsible for generating the astounding biodiversity that is the most salient feature of life on Earth, and one of our most threatened and irreplaceable resources. Speciation is also one of the greatest mysteries of evolution, occurring primarily on scales of space and time beyond our experimental reach, and through a delicate interplay of events from the molecular shifting of nucleotides to the geologic shifting of mountains and rivers. For organisms with sexual reproduction, the process of speciation must account for the genetic isolation of incipient species, and speciation models must therefore embrace genetic dynamics (Coyne & Orr 2004). Accounting for this genetic dimension of speciation has been achieved largely at the expense of simplifying, or ignoring altogether, speciation's ecological dimension. The latter results from the complex features and interactions that distinguish species from one another and that enable a rich diversity of species to persist.

The importance of ecological interactions in speciation has been acknowledged for some time (the concept of reinforcement goes back to Dobzhansky and Wallace), yet few studies have had more influence in highlighting the ecological basis for speciation than that by Dieckmann and Doebeli (1999), which brought the nascent theory of mutation-limited long-term phenotypic evolution known as 'adaptive dynamics' to the attention of empirical and theoretical evolutionary ecologists. While genetic dynamics are addressed in this study, at its heart lies an ecological model for the evolutionary branching of a phenotypic trait describing competitive interactions: in the course of adaptation, this trait approaches an evolutionary branching point, i.e., an attractor of the evolutionary dynamics of a single morph that, once reached through directional selection, naturally leads to the emergence of a diverging dimorphism through frequency-dependent disruptive selection. In this project, we will focus on the dynamics around such evolutionary branching points. While ignoring genetic details for a start, we will extend previous work by focusing on the impacts of stochastic processes on the evolutionary dynamics leading to biological diversification.

Almost all quantitative theories of evolution have relied on stochastic models to address the impacts of chance events – such as mutations, births, deaths, and environmental changes – that affect the evolutionary process (Fisher 1937; Lande 1979; Coyne & Orr 2004). Adaptive dynamics theory typically considers two sources of stochasticity: random mutations and the loss of advantageous mutants to chance extinction while their numbers are small. What these models typically do not consider is

demographic stochasticity of resident populations (resulting from intrinsic fluctuations through stochastic birth and death events in finite populations of discrete individuals) and environmental stochasticity (resulting from external fluctuations in the environmental conditions a population experiences).

Several recent studies have tried to overcome these limitations. Claessen et al. (2007, 2008) explore simulations of evolutionary branching in small populations and found that demographic stochasticity can delay or halt diversification. Johansson and Ripa (2006) explored the impact that correlated environmental stochasticity has on diversification. They assume that as populations diverge, the environmental influences upon them become less similar. They demonstrate that this correlation can facilitate coexistence early in the process of branching, and as it weakens, the chance that a branch is lost increases. While these studies make an excellent start, a more general theory and mathematical framework is needed to untangle and quantify the multitude of effects stochasticity has on evolutionary branching.

Research questions

How do demographic and environmental stochasticity influence the process of evolutionary branching? What is the waiting-time distribution for evolutionary branching to persist under these stochastic processes?

Methods and work plan

We consider a general model of evolutionary branching in a one-dimensional trait and examine it through a series of approximations. We assume individuals are born at rate b and die at rate d . These rates may depend on the number N of resident individuals, on their traits x , and on a fluctuating environment E . Upon birth, an individual faithfully inherits the trait value of its parent with probability $1 - \mu$. With probability μ , it experiences a mutation: its trait value is then drawn from a normal distribution around that of its parent. This results in a stochastic processes with two components: a demographic jump process on the positive integers N describing the population's size, and a mutational jump process on the continuous trait x .

While easy to implement numerically, this model is not directly amenable to analytical study. In an effort to make the analysis tractable, we will therefore consider several biological limits before relaxing the associated simplifying assumptions. First, we can choose functions for b and d ensuring that the total population is large at demographic equilibrium, so extinction of the entire population and fixation of deleterious mutations can be ignored. Second, we can assume that mutations are rare (mutation-limited evolution), so the resident population is close to its equilibrium when new mutations arise. Third, we can assume that variations in the environment E are negligible.

Based on these assumptions, we can divide the process of evolutionary branching into four stages and calculate the resultant distribution of waiting times until persistent evolutionary branching:

- Starting from a monomorphic resident population in the vicinity of the branching point, we first calculate the waiting time for a mutation to occur that, together with the resident trait, falls within the region P_2 of dimorphic trait space that allows for the mutual invasibility of each morph by the other and therefore contains all pro-

tected dimorphisms. When the resident population is situated exactly at the branching point, all mutations fall into P_2 , but when the resident population has not yet converged to the branching point, mutational steps have to exceed a minimum size to enter P_2 .

- Even though a mutant entering P_2 experiences a positive growth rate, it must establish itself by reaching a population size that makes chance extinction unlikely. From the first stage, we know the probability density of mutants entering P_2 . For each such mutant, we can determine the probability that it escapes initial chance extinction.
- Having survived initial chance extinction, the mutant finds itself in a dimorphic population. As the resident trait and the mutant trait are very similar, and since both lie near the branching point, the frequency-dependent selection promoting their coexistence is very weak, so that the random drift of their relative frequency readily leads to the loss of mutant or resident before further mutations allow the dimorphism to widen.
- In a fourth stage, the now established populations undergo a random walk of their trait values in P_2 . Should this random walk hit the boundary of P_2 , one morph goes extinct and the entire process must start again. By calculating the probability that the dimorphic random walk escapes the boundary, we can thus quantify the fourth and final stage of evolutionary branching.

Combining results for each stage, we can determine the distribution of waiting times until persistent evolutionary branching.

Relevance and link to EEP's research plan

This work is directly relevant to EEP's project on *Adaptive Dynamics Theory*, by extending the analysis of evolutionary branching to include the effects of demographic and environmental stochasticity.

Expected output and publications

The results of this research will be submitted as a jointly authored paper to a peer-reviewed international scientific journal in the area of ecology and evolution.

References

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