

How likely is speciation in neutral ecology ?

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Patterns of biodiversity predicted by the neutral theory rely on a simple phenomenological model of speciation. To further investigate the effect of speciation on neutral biodiversity, we analyze a spatially-explicit neutral model based on population genetics. We define the metacommunity as a system of populations exchanging migrants use this framework to introduce speciation with little or no gene flow (allopatric and parapatric speciation). We find that with realistic mutation rates, metacommunities driven only by neutral processes cannot support more than a few species. Adding natural selection in the population genetics of speciation increases the number of species in the metacommunities and generate patterns of species distribution similar to those predicted by Hubbell's neutral theory of biodiversity.

Keywords: Neutral theory, speciation, metacommunity, allopatry, parapatry, graph theory

I. INTRODUCTION

How patterns of biodiversity arise through ecological and evolutionary processes is a central question in modern ecology. According to Hubbell's neutral theory of biodiversity (NTB), patterns of biodiversity such as species-abundance distributions can be explained by the balance between speciation, dispersal and random extinction. The neutral theory provides a good fit to species distribution curves, and it has been extended in several ways. The neutral theory has been shown to be flexible enough to fit nearly any distribution, but it is often regarded as a valid starting point and an interesting null hypothesis for community ecology.

While a lot has been said about the assumption of ecological equivalence, much less attention has been given to the speciation mode, which is sometime seen as the theory's weakest point. In recent years, some studies altered the speciation model within neutral ecology. However, nothing has been done to relate the theory to population genetics and known models of speciation, despite the fact that, as Etienne et al. noted, such a mechanistic model could eventually force us to reject neutrality. The neutral theory with point speciation has also been criticized for predicting too many rare species, too many young species, and for assuming a direct relationship between abundance and speciation. With random-fission, the neutral theory predicts less rare species, but the resulting species abundance curves result in a worst fit.

In this article, we introduce a neutral theory of biodiversity with a speciation model derived from population genetics. We emphasize the role of allopatric and parapatric speciation. Speciation modes are most often distinguished according to the level of gene flow between the diverging populations. Allopatric speciation occurs when the new species originates from a geographically isolated population. By contrast, sympatric speciation is often defined as speciation without geographical isolation, in short, when the diverging populations share the same location. Lastly, parapatric speciation covers the middle ground between these two extremes.

In the original neutral theory's formulation, Hubbell presented two models of speciation, point-speciation and

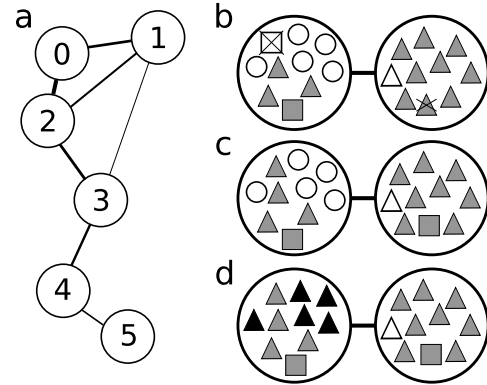


FIG. 1. The metacommunity as a graph of local communities. Each community is connected by dispersal to one or more communities.

random-fission speciation. Both are phenomenological individual based models. In the case of point-speciation, a newly recruited individual is selected at random and undergoes speciation. In the case of random-fission, the whole species is divided in two at random. In both cases, the probability of speciation of a given species is directly proportional to abundance and independent of dispersal. Hubbell associates the point-speciation model with sympatric speciation, and the random fission model with allopatric speciation. Some rare forms of sympatric speciation are indeed similar to the point speciation model, namely polyploid speciation, but most sympatric speciation events involve a population being divided in two by non- geographical factors. Also, as neither models take gene flow into consideration, neither can distinguish sympatric and allopatric speciation events.

While theoretical models have shown sympatric speciation to be possible, empirical studies have uncovered only a very few solid cases and much of the theory is controversial. Despite the growing acceptance of sympatric speciation as a plausible cause of speciation, most speciation events are still thought to occur with limited gene flow. Allopatric and parapatric speciation events are more common, but modelling them require some details about the spatial structure of the metacommunity. We chose to base our model on the most common forms of

speciation despite the increased complexity of a spatially-explicit framework. We find that with realistic parameters, metacommunities cannot support more than a few species when the genetics of speciation is assumed to be neutral. We also considered a simple alternative pseudo-selection model by adding natural selection at the genetic level, but keeping the ecological equivalence assumption at the individual level. This approach shows that the rates of speciation typical of the NTB cannot be obtained without selection pushing mutations to fixation.

II. MODEL

We model speciation with the Bateson-Dobzhansky-Muller model (BDM) in which reproductive isolation is the consequence of the accumulation of incompatible alleles. While the BDM model is simple, we have many empirical and theoretical reasons to believe that speciation events often follow a similar scheme. We use a two-loci and two-alleles version of the model where sexual reproduction is ignored. Each population starts with the ab haplotype fixed. The allele at the first locus, a , mutates to A , and the allele at the second locus, b , mutates to B . Both mutate at the same rate μ . We follow Gavrillets and ignore back mutations. Alleles a and B are incompatible, so the path from ab and AB can be seen as a process with three states: