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A minimum stochastic model evaluating the interplay between population density and drift for species coexistence

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ABSTRACT

Despite the general acknowledgment of the role of niche and stochastic process in community dynamics, the role of species relative abundances according to both perspectives may have different effects regarding coexistence patterns. In this study, we explore a minimum probabilistic stochastic model to determine the relationship of populations relative and total abundances with species chances to outcompete each other and their persistence in time (i.e., unstable coexistence). Our model is focused on the effects drift (i.e., random sampling of recruitment) under different scenarios of selection (i.e., fitness differences between species). Our results show that taking into account the stochasticity in demographic properties and conservation of individuals in closed communities (zero-sum assumption), initial population abundance can strongly influence species chances to outcompete each other, despite fitness inequalities between populations, and also, influence the period of coexistence of these species in a particular time interval. Systems carrying capacity can have an important role in species coexistence by exacerbating fitness inequalities and affecting the size of the period of coexistence. Overall, the simple stochastic formulation used in this study demonstrated that populations initial abundances could act as an equalizing mechanism, reducing fitness inequalities, which can favor species coexistence and even make less fitted species to be more likely to outcompete better-fitted species, and thus to dominate ecological communities in the absence of niche mechanisms. Although our model is restricted to a pair of interacting species, and overall conclusions are already predicted by the Neutral Theory of Biodiversity, our main objective was to derive a model that can explicitly show the functional relationship between population densities and community mono-dominance odds. Overall, our study provides a straightforward understanding of how a stochastic process (i.e., drift) may affect the expected outcome based on species selection (i.e., fitness inequalities among species) and the resulting outcome regarding unstable coexistence among species.

1. Introduction

For many decades, models have been proposed to describe and explain observed patterns in species abundances (Etienne and Olff, 2005; Fisher et al., 1943; Hubbell et al., 1999; MacArthur, 1957, 1960; Preston, 1948, 1962), and several different mechanisms have been elected as drivers of biological diversity variation in space and time. Much of ecology is built on the assumption that species differ in their niches. Studies have shown that species may differ in their use of multiple limiting resources (Tilman, 1982; Tilman et al., 1986), their ability to colonize disturbed sites (Grubb, 1977), and their response to temporal fluctuations in the environment (Ziebarth et al., 2010). Current knowledge claims that stable coexistence can occur when niche differences cause species to limit their populations more than they limit others - stabilizing effect (Chesson, 2000). One good example of the effect of stabilizing process is the role of population abundance (i.e., relative frequency) in reducing population average per capita growth rates (Adler et al., 2007), making a species to suppress itself faster relative to a competing species.

Neutral theory directly challenges the niche paradigm by proposing that high diversity of many natural communities can be achieved assuming species equivalences. However, it does not imply that the world is in fact neutral. Instead, it does suggest

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progress can be made incorporating neutral perspective (Rosindell et al., 2012). The idea that neutral processes regulate ecological communities (Bell, 2001; Hubbell, 2001) has had a profound effect on ecology (Chave, 2004), but this remains contentious (Gaston and Chown, 2005). Data-driven studies refute some aspect of neutral patterns or processes (Gilbert and Lechowicz, 2004; McGill, 2003; Turnbull et al., 2005; Wootton, 2005), denying that neutral dynamics can produce observable ecological patterns. Similarly, completely niche-based explanations have failed to adequately explain extant community patterns (Chave, 2004; Holyoak and Loreau, 2006). Consequently, several studies have attempted to reconcile neutral and niche dynamics (Adler et al., 2007; Chave, 2004; Gravel et al., 2006; Holyoak and Loreau, 2006; Tilman, 2004). The divergence and reconciliation between neutral and niche dynamics can be described viewing coexistence mechanisms as either equalizing or stabilizing (Adler et al., 2007; Chave, 2004). Stabilizing coexistence describes species differences that result in reduced niche overlap, thus minimizing the impact of fitness inequalities on competitive interactions. Equalizing mechanisms promote similarities in species responses (i.e. fitness equivalency), reduces the rate of competitive exclusion, and promote coexistence from weak stabilizing mechanisms. Thus, fitness inequalities between species may drive competitive exclusion and can be approximated by species average growth rate differences (Chesson, 2000). In general, the species with the highest average fitness displaces all competitors in the absence of niche differences.

Despite the achievements observed in past years about the role of different mechanisms driving community dynamics (MacDougall et al., 2009), the community ecology theory has been perceived as a mess (Vellend, 2010) and the recognition of general process that drives ecological communities can help to elucidate its determinant factors. Assuming the most general level, patterns in the composition and diversity of species—the subject matter of community ecology—are influenced by only four classes of process: selection, drift, speciation, and dispersal (Vellend, 2010, 2016). Drift is the result of random sampling during the process of birth, death, and reproduction, while the presence of selection can be understood as differences in fitness among species.

Selection is ubiquitous in the ecological literature, it constitutes the core of the niche theory and is present in examples of resource partitioning (Tilman et al., 1986), consequences of environmental heterogeneity on community dynamics (Harrison et al., 2006), trait-based community ecology (McGill et al., 2006) and others. However, even when statistical signatures of selection are strong and clear (e.g., composition-environment relationships), a great part of the variation in the community composition remains unexplained (Soininen, 2014). This demonstrates that even when selection is important, it does not exclude the influence of other factors, such as drift (McPeek and Gomulkiewicz, 2005), or even their interaction. For example, fitness inequalities can lead one population to dominate the community after a specific period (Adler et al., 2007). However, more individuals to “trade” in a finite and resource-conserved system can balance the chances of success that govern demographic properties, if these demographic properties are also influenced by stochasticity. Therefore, initial population abundance could work as an equalizing, by reducing the fitness inequalities, rather than stabilizing mechanism, promoting coexistence. Within some plant populations, the balance between stochastic forces and frequency-dependent mating largely governs style morph frequencies in heterostylous populations. Studying clonal species of *Eichornia Azurea*, Cunha et al. (2014) found that deviations from equal morph ratios often result from founder events and unfavorable conditions for sexual reproduction. Therefore, differences in sub-populations abundances would be preeminent compared to the reproductive value (i.e. fitness) of different morphs in determining population dynamics due to stochastic effects.

In this study, we were not focused on the evaluation of the predictions of the Neutral Theory of Biodiversity (Hubbell, 2001) on community dynamics, which has been extensively studied in the ecological literature. Instead, we aimed to provide an explicitly functional formulation of how population relative abundances, system support capacity and fitness inequalities affect species probability to outcompete each other and their persistence in time under the influence of drift. Therefore, our aim is to provide a simple mathematical formulation to show the interplay between population density and the stochastic recruitment of individuals in closed systems. We could show with our study the relationship between populations total and relative abundances and the probability of species to dominate each other. We also showed how population relative abundance could work as an equalizing mechanism, diminishing fitness inequalities among species and influencing unstable coexistence among species, here defined as persistence in time of all species. Our model, overall, provides a straightforward understanding of the role of drift and how it changes with species relative abundances. We also provide examples and experimental designs that could be used to confirm or test model predictions.

2. Materials and methods

2.1. A minimum stochastic model

To test our predictions, we used a simple probabilistic model with stochastic demography. This model can be visualized as an alternative interpretation for the formulas that would apply to classic neutral models, but reduced to 2 species with no speciation and with constant selection among species. The community assembly follows a random demographic process in a hypothetical two species, A and B, system. Each species has specific chances to lose one individual or to reproduce, gaining one individual, at each time step. Once species are at a site, the abundance of each will be proportional to the total number of individuals at that point in time. The number of individuals in the system is conserved, representing a closed system, and thus it is always constant and equal to the system carrying capacity K, a zero-sum neutral assumption (Hubbell, 2001). When one individual dies in the community, it is replaced by a new individual of the competing population, simulating a lottery model (Coad et al., 2013; Shinen and Navarrete, 2014) among competing populations. This situation could describe an exploitative competition scenario between two species where some resources are finite and allocated in the biomass of the organisms inhabiting this system. When one individual dies the newly available resources is used by the other species to build a new individual. This assumption strongly simplifies the model structure by directly relating reproduction and death probabilities, but may cause the model to be apart from the biological evidence governing species recruitment. In general, when two species compete, instead, any individual has a probability of contributing through reproduction to the population of the species it belongs to, and any of them, a probability of dying. Even though our model simplification may cause deviations from biological systems, or is appropriate just to very specific biological scenarios (where competition occurs only at a spatial or temporal boundary separating the two species), the model results would still show how drift effects, due to relative population densities, would affect species dominance odds under distinct selection scenarios. Therefore, we can simplify the probability of success of species A over species B, or vice-versa, as it chances to survive and reproduce with a single probability parameter, representing the fitness differences