



Metapopulation mirages: Problems parsing process from pattern

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ABSTRACT

Ecological models attempting to unite the concepts of biodiversity and biogeography have been used to describe and predict the distribution and abundance of species. Two mechanistic hypotheses, the neutral model and the community-level metapopulation model, have the potential for direct comparison. However, there is potential for incorrectly inferring the underlying mechanisms of observed data if the hypotheses have similar descriptive ability. In this paper, we simulated a range of abiotic island-mainland system and biotic community structure variables following the mechanisms underlying these two hypotheses in order to compare model descriptive ability relative to each other and to a null model. We found that the null and metapopulation models could accurately describe data created under their respective assumptions for many of the simulated system structures. The neutral model generally failed to describe data created under neutral conditions relative to the null model. Modelling also revealed limitations of these mechanistic models identifying conditions where metapopulation dynamics would be inferred but were not occurring, and failing to detect metapopulation dynamics where it was actually occurring. To help alleviate this problem, we also identified sets of conditions where metapopulation dynamics, if it is actually occurring, could be distinguished from null or neutral models. Such systems have moderate variability in distance to mainland, density of mainland species and island area, as well as low to moderate numbers of islands and species (10–50). Simulations demonstrated the potential to distinguish unified models under certain conditions, but there are also conditions where models are equivalent and where the model that best described the data was not consistent with the underlying mechanism. These shortcomings may lead to incorrect conclusions regarding mechanisms presumed to be producing observed patterns in species abundance and distribution.

1. Introduction

Understanding and predicting the distribution and abundance of species lies at the heart of Ecology (Andrewartha and Birch, 1954). Thus, it is not surprising that ecologists have developed a variety of hypotheses to explain patterns in species richness and abundance. Several of these hypotheses are referred to as “unified hypotheses” in their attempt to unify the fields of biodiversity and biogeography. McGill (2010) identified six unified hypotheses: Hubbell, 2001 Unified Neutral Theory of Biodiversity and Biogeography, the metapopulation-derived hypothesis developed by Hanski and Gyllenberg (1997); Gauch and Whittaker’s continuum hypothesis (1972); Storch et al. (2008) fractal hypothesis, the cluster Poisson hypothesis (Morlon et al., 2008; Plotkin and Muller-Landau, 2002; Stoyan and Stoyan, 1994), and the maximum entropy hypothesis (Harte, 2008; McGill, 2006). Subsequent to McGill (2010) review there have been additional attempts at unifying the concepts of biodiversity and biogeography and extensions of these hypotheses (e.g. Borregaard et al., 2016; Connolly et al., 2017; May

et al., 2013; May et al., 2016; Rosinell and Harmon, 2013; Whittaker et al., 2008). These competing hypotheses all describe patterns of biodiversity and hold promise for predicting the distribution and abundance of species and potentially for understanding the biological mechanisms thought to produce these patterns (Cabral et al., 2017; Jones et al., 2011; Leidinger and Cabral, 2017).

A limitation of current unified hypotheses is that there have been few quantitative comparisons among them (Jones et al., 2011). Evaluation often has been limited to qualitative analysis of a single hypothesis (e.g., McGill et al., 2006) and less commonly between or among hypotheses (e.g., McGill, 2010). Where quantitative comparisons exist, the studies generally have tested a single hypothesis within a taxon versus a null model, in contrast to testing competing hypotheses (e.g., Matter et al., 2002; McGill, 2006). Quantitative comparison among all unified hypotheses is difficult due to the inherent dissimilarities among them, including the spatial and temporal scale of investigation, mechanisms influencing distribution and abundance assumed, and underlying theories used to develop the hypotheses. However,

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comparisons can be made among unified hypotheses derived from similar theory.

Two of the unified hypotheses can be used to investigate the same community scale structure and were similarly derived. Both the unified neutral and metapopulation hypotheses incorporate similar mechanisms and are derived from the theory of island biogeography (MacArthur and Wilson, 1967) to produce patterns of species incidence and abundance. Assuming these mechanisms, small and/or isolated areas of habitat would have lower colonization and higher extinction rates compared to larger, less isolated areas, producing a positive relationship between species richness and area and a decreasing relationship between species richness and isolation (Hanski and Gyllenberg, 1997; Matter et al., 2002). These two hypotheses have the potential to be useful for ecological studies because of the limited set of mechanisms, but their performances have not been directly compared.

The general background of the two unified hypotheses used in this paper, neutral and metapopulation, are briefly described here, but are described in detail elsewhere including their derivations (Hanski and Gyllenberg, 1997; Hubbell, 2001; Matter et al., 2002; May et al., 2013; May et al., 2016; McGill, 2010; Rosindell et al., 2011; Rosinell and Harmon, 2013). The two unified models can only be compared within an island-mainland system for a variety of reasons detailed in the model descriptions. Island-mainland systems historically have served as important models to study ecological theories and continue to be important for elucidating mechanisms driving biodiversity (Warren et al., 2015).

1.1. Neutral model

The neutral hypothesis is considered neutral because all individuals in the community are assumed to have identical migration, birth, and death rates. The interactions among species at the level of individual organisms is also considered equal. The hypothesis' mechanisms, such as colonization, extinction, and speciation, determine species richness and are assumed to be equal for all individuals and in the community (Hubbell, 2001). Specifically, the neutral hypothesis describes both local and regional (metacommunity) patterns of relative abundance and can include the mechanisms of random migration, speciation, as well as ecological drift. While the neutral hypothesis has application over evolutionary time, it also can be applied to biodiversity patterns in island-mainland systems over ecological time, which is the focus of this study. The neutral hypothesis also follows a zero-sum dynamics assumption; there is a constant number of individuals in a system with equal birth and death rates (Hubbell, 1979; Hubbell, 2001). Under these assumptions, the distribution and abundance of species can be predicted from the relative abundance of each species in the community.

The neutral hypothesis has been used to predict the distribution and abundance of different taxa, such as tropical trees, marine invertebrates, temperate herbaceous plants, birds, fish, and insects (Fuller et al., 2004; He, 2005; Hubbell, 2001; McGill, 2003; McGill, 2006; McGill et al., 2007; Pandolfi, 1996; Terborgh et al., 1996), but generally has not been applied to island-mainland systems despite its flexibility to be used in these systems (Leidinger and Cabral, 2017; Rosindell and Phillimore, 2011). Previous studies generally only evaluated this hypothesis for a single island and for fragmented habitat patches (Fuller et al., 2004; He 2005; Hubbell 2001; McGill 2003; McGill, 2006; McGill et al., 2007; Pandolfi 1996; Rosindell and Harmon 2013; Terborgh et al., 1996). A unified hypothesis should not be taxon-specific, but rather have the ability to universally applied to any ecological communities. Few studies have tested the neutral hypothesis in an island-mainland system and tests generally have only considered a single taxon (Leidinger and Cabral et al., 2017; Rosindell and Phillimore, 2011).

McGill (2006) reviewed multiple sets of empirical tests and found that all failed to support the neutral model. Despite that the

development of the neutral model was done with single island data (Hubbell, 2001), none of these empirical tests were done in an island-mainland setting using multiple islands. The distribution patterns of such a system may vary from patterns seen for a single sample or habitat patch. One example is a study done by Leigh et al. (1993) on islands of Gatun reservoir in Central Panama which was the same system where Hubbell (2001) collected the data that the neutral hypothesis was based on. The authors indirectly tested neutrality for the same taxa as well, mature tropical tree species, and found that some species were lost more rapidly than expected by random extinction on the six smallest islands. Hubbell (2001) found neutrality for data collected on one of the largest islands of Gatun reservoir, Barro Colorado Island. Therefore, evaluating the assumption of neutrality for all islands in a multiple island-mainland setting may yield different results than if it was studied in a single island setting, or a subset of island sizes (Bowers and Matter, 1997; Connor et al., 2000). Differences in community structure may also occur depending on the sampling scale. Gaston and Matter (2002) found the relationship between the number of individuals of a species and area can change depending on whether sampling was at a habitat-specific patch level versus a general sampling area. Similarly, neutrality may also be scale dependent since it operates on the level of the individual. Since the neutral hypothesis was originally derived using islands as patches, it may be more appropriate to test it in island systems.

1.2. Metapopulation model

The second unified hypothesis is the metapopulation hypothesis which scales up predictions made for single species to the community-level. Thus, this model can be used to describe species incidence as well as species richness. The metapopulation hypothesis was developed assuming island-mainland conditions, i.e., there is a mainland that is a source of species that (re)colonize islands (Hanski and Gyllenberg, 1997). Therefore, comparative tests are only valid under island-mainland conditions. The metapopulation hypothesis assumes that species richness (S) for a given island is determined by a balance of local extinction occurring on islands and (re)colonization from a mainland species pool (R):

$$\log \frac{S_{j/R}}{1 - S_{j/R}} = a + \bar{x} \log A_j - \bar{\alpha} d_j, \quad (1)$$

where A is the area and d the distance from the mainland of island j , and \bar{x} and $\bar{\alpha}$ describe the mean extinction risk and the mean migration ability of species in the community, respectively (Hanski and Gyllenberg, 1997; Matter et al., 2002). The parameter a is an amalgam of mean population density, the scaling of extinction risk with area, and a constant parameter.

This “bottom-up” approach, scaling a population-level hypothesis to the community-level, is potentially beneficial because extinction and recolonization are viewed from the species level. Species richness is then determined by summing incidence for individual species on an island. As opposed to the neutral hypothesis, species in the metapopulation model are not treated equally but instead have individual estimates using the following the incidence (P) function for species i on island j :

$$P_{ij} = \frac{e^{K_{ij}}}{e^{K_{ij}} + 1} \quad (2)$$

where K_{ij} is the logit-transformed species-specific incidence:

$$K_{ij} \log \frac{P_{ij}}{1 - P_{ij}} = \log c + (1 + x_i) \log w_i + x_i \log A_j - \alpha_i d_j \quad (3)$$

where α_i describes the migration ability of species i in the community and w_i is the constant density of species i (Hanski and Gyllenberg, 1997; Matter et al., 2002). c is a constant parameter.

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