



Research article

How to design trait-based analyses of community assembly mechanisms: Insights and guidelines from a literature review



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ABSTRACT

One of the fundamental challenges in ecology is to identify the signature of assembly mechanisms resulting from patterns of community composition. For this purpose, the trait-based approach has promoted the analysis of functional trait distributions within communities. Until now, much attention has been paid to the design of appropriate null models and the definition of relevant functional metrics for inferring community assembly mechanisms from trait distributions. However, less consideration were given to the set of methodological choices preceding the statistical analysis – i.e. from designing a sampling scheme to measuring traits – and how likely they influence the conclusions drawn, as this may subject the analysis to methodological biases. In this regard, a comprehensive perspective on how the overall set of methodological choices influence the inference of community assembly mechanisms is needed.

We extensively reviewed recent studies that have addressed animal and plant community assembly by applying a trait-based null model approach. We analyzed how the set of methodological choices in these studies depended on the mechanisms of interest and how they could influence the conclusions drawn by the authors. We found that methodological choices only weakly depended on the hypothesized assembly mechanisms studied by the authors, especially because the two main assembly mechanisms hypothesized, i.e. environmental filtering and limiting similarity, were often tested based on a common experimental design. In contrast, the detection of assembly mechanisms was strongly dependent on the sampling scale, the type of data, the origin of trait values and the delineation of the reference species pool, while less affected by the null model and the functional metrics chosen. These results underline plausible methodological biases in favor of the detection of certain mechanisms to the detriment of others. In addition, there was a significant relationship between the predominant mechanisms concluded by the authors and the type of organism used as biological model, suggesting either that the methodological choices depend on a common strategy used by the different authors when studying similar biological models, or that the methodological choices depended on certain particular properties of the organisms.

From this extensive review, we highlight major conceptual and methodological issues that need to be addressed in trait-based null model approaches. We synthesize the methodological choices relevant to study several assembly mechanisms while minimizing methodological biases. We then derive practical guidelines and emphasize the importance of spatial structure in sampling strategy and null model design, because of the scale-dependent signatures of ecological processes.

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1. Introduction

One of the fundamental challenges in ecology is to understand community assembly by identifying the signature of underlying mechanisms. Current theories basically consider two distinct sets of mechanisms to explain community assembly patterns. Neutral theory postulates that communities result mainly from a stochastic balance between dispersal of individuals and local demography, and that niche differences do not influence fitness differences among individuals (Hubbell, 2001; Munoz and Huneman, 2016). Niche theory conversely postulates that community assembly is determined by adaptive variations among species, reflecting niche differences (Keddy, 1992; Belyea and Lancaster, 1999; HilleRisLambers et al., 2012). Our study is part of the framework of niche theory, especially because the trait-based approach aims to identify causal relationships between community assembly mechanisms and their functional signatures. It assumes that differences in biological attributes, i.e. functional traits, influence the relative fitness of coexisting species (Violle et al., 2007). In recent years, the trait-based approach has gained momentum based on the idea that the diversity of functional traits conveys the signature of niche-based ecological processes driving ecosystem and community dynamics (McGill et al., 2006). In this study, we address the various methodological choices that have been proposed within the trait-based framework. Based on a comprehensive review of studies that have addressed the signatures of niche-based mechanisms using a trait-based null model approach, we critically assess the influence of methodological choices on the detection of the major niche-based community assembly mechanisms.

Niche-based mechanisms influencing community assembly can be due to abiotic constraints, such as environmental filtering, whereby species are selected depending on the match between their niche preferences and the environmental conditions (Weiher and Keddy, 1995) and biotic interactions, such as competition, whereby species with similar niches compete for the same resources and undergo competitive exclusion (Hardin, 1960), thus potentially leading to either niche differentiation – limiting similarity principle (Abrams, 1983) – or competitive dominance (Mayfield and Levine, 2010; see Table 1 for details). However, other biotic interactions can also contribute to community assembly,

such as facilitation (Bruno et al., 2003). These niche-based mechanisms combine over a hierarchy of spatial scales and yield scale-dependent signatures (Munoz and Huneman, 2016; Fig. 1). With the development of trait-based approaches, diverse statistical frameworks have been proposed to infer basic community assembly mechanisms from local and regional trait distributions (Pillar et al., 2009; Pausas and Verdú, 2010; Götzenberger et al., 2012).

To detect the signature of entangled ecological drivers, the trait-based approach is generally associated with a particular null model (thereafter named trait-based null model approach, see for instance Kraft et al., 2008). The distribution of trait values in a given community is compared to the distribution of trait values of numerous communities randomly generated under a specific null hypothesis. The null hypothesis considers the absence of a particular niche-based mechanism, whereas the alternative hypothesis acknowledges the influence of this particular mechanism on the trait distribution. Randomization procedures are thus designed to generate ‘null communities’ following a specific null hypothesis and, in this context, statistical properties of the randomization procedure depend on the sampling design and the functional metrics used. Therefore, the efficiency of the trait-based null model approach relies on both: (i) data acquisition (collecting information on species occurrence or abundance in sampling sites at a specific spatial scale and obtaining trait values following relevant protocols) – and (ii) data analysis (analyzing trait distribution patterns to determine whether they show the signature of a particular niche-based mechanism). Until now, much attention has been paid to appropriately choose and combine null models and functional metrics for data analysis (e.g. Mouchet et al., 2010; Mason et al., 2013; but see Supplementary Appendix A for details on the methodological choices), while the influence of data acquisition strategy has received far less interest. As a consequence, some recent criticisms have emphasized that methodological choices are not always suited to grasp the spatial scaling of niche-based mechanisms (Villéger et al., 2008; de Bello et al., 2012; Götzenberger et al., 2016). In light of these criticisms, the conclusions of studies using the trait-based null model approach are potentially subject to methodological biases (Hardy, 2008; Mouchet et al., 2010; Mason et al., 2013). Therefore, how the overall combination of method-

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