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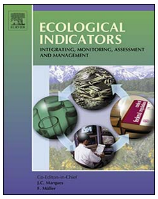

On the reliability of the Elements of Metacommunity Structure framework for separating idealized metacommunity patterns

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ABSTRACT

The Elements of Metacommunity Structure (EMS) framework originally suggested by Leibold and Mikkelson (2002) in Oikos is a popular approach to identify idealized metacommunity patterns (i.e. checkerboard, nested, evenly spaced, Clementsian, Gleasonian), and hereby to infer the existence of structuring processes in metacommunities. Essentially, the EMS framework consists of the rearrangement of the sites-by-species incidence matrix followed by a series of tests for coherence, turnover and boundary clumping in species distributions. Here, we give a critical evaluation of the EMS framework based on theoretical considerations and simulations. We found that user defined site ordering may influence the coherence test (number of embedded absences) depending also on the ordering of species, and therefore we argue that the application of user-defined matrix rearrangement has strong limitations. The recommended ordering by correspondence analysis is sensitive to matrix structure and may even include arbitrary decisions in special cases. Further, we revealed different meanings of the checkerboard pattern and showed that negative coherence is not necessarily associated with this as assumed in the EMS framework. Also, the turnover test cannot always detect nested pattern, because turnover and nestedness are not necessarily the opposite endpoints of a continuum. We argue that the boundary clumping test can only be used for separating Clementsian, Gleasonian and evenly spaced patterns if sites are ordered along a real environmental gradient rather than a latent one identified by correspondence analysis. We found that the series of tests in the EMS framework are burdened by anomalies and that the detection of some metacommunity patterns is sensitive to type II error. In sum, our findings suggest that the analytical methodology of the EMS framework, as well as the conclusions drawn from its application to metacommunity studies require careful reconsideration.

1. Introduction

Detecting and understanding drivers of metacommunity structure are key issues in community ecology with significant legacy (Mittelbach, 2012). Early ecologists have already inferred the existence of structuring forces from the community patterns observed. For instance, Clements (1916), the pioneer of North American plant ecology, viewed plant communities as coherent units with discrete boundaries formed in response to environmental factors (*Clementsian pattern*). In contrast, Gleason (1926) argued that species have distinct ecological characteristics and therefore individualistic responses to underlying environmental gradients (*Gleasonian pattern*). *Evenly spaced pattern* occurs in systems with trade-offs in fitness in different environments, resulting in a spatial distribution with evenly dispersed populations (Tilman, 1982). Intense interspecific competition may generate *checkerboard pattern* where pairs of species are mutually exclusive (Diamond, 1975). Finally, *nested pattern* occurs when species poor communities consist of subsets of species occurring in richer communities (Patterson and Atmar, 1986). These cases have been regarded as idealized types of metacommunity pattern (Ulrich and Gotelli, 2013; Heino et al., 2015) and have received increasing attention due to their theoretical interpretation (Carvalho et al., 2013; Ulrich and Gotelli, 2013).

The development of metacommunity theory provided a conceptual framework for ecologists to disentangle underlying drivers (niche based species sorting, dispersal, drift, see Vellend 2010, Shipley et al., 2012) of multisite communities (Leibold et al., 2004). Some of the approaches

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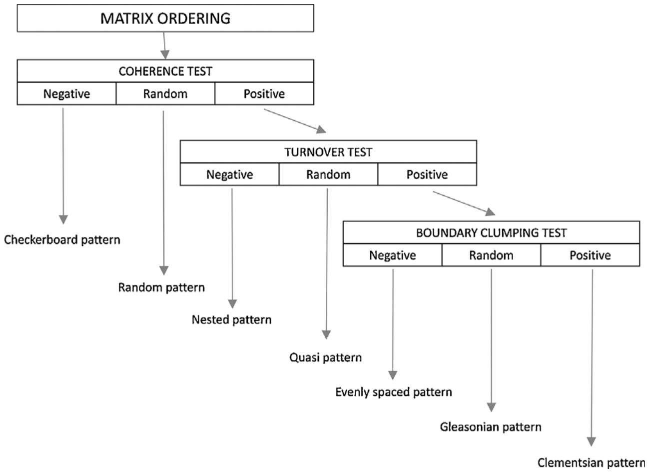

Fig. 1. Diagrammatic representation of the Elements of Metacommunity Structure (EMS) framework following Leibold and Mikkelson (2002) and Presley et al. (2010).

use multispecies distribution patterns for inferring the existence of structuring ecological forces. No doubt that the "elements of metacommunity structure" approach suggested by Leibold and Mikkelson (2002) and its upgrade (Presley et al., 2010, hereafter referred to as EMS framework) provide a very popular methodology developed for this purpose.

The EMS framework includes the rearrangement of the sites-by-species incidence matrix followed by three tests (Fig. 1), each related to a given element of metacommunity structure. First, the rows and the columns of the matrix are ordered along the first axis of correspondence analysis (CoA) to discern variation in response to a latent environmental gradient. According to Leibold and Mikkelson (2002, p. 241), the simultaneous ordering of sites and species has three purposes: (1) it often minimizes the number of interruptions in species' ranges (number of embedded absences), (2) it provides a basis for judging whether a given metacommunity is nested, or dominated by turnover (high number of species replacements), and (3) it defines the boundaries of species' ranges (boundary clumping). Consequently, matrix rearrangement via CoA has strong impact on the assessment of each element of metacommunity structure. Note that although this procedure is recommended for general use, the EMS framework also allows user-defined matrix ordering. Secondly coherence, the first element of metacommunity structure is defined as the number of embedded absences in the matrix and its significance is examined using null model tests. Following the study of Gotelli (2000), species richness of sites is kept constant in the recommended null model (Presley et al., 2010). If coherence is negative (the number of embedded absences is significantly higher than expected by chance) then the EMS framework detects checkerboard pattern. If the number of embedded absences does not differ significantly from a randomly generated value (coherence is random) then the EMS framework indicates a random pattern. If coherence is positive (the number of embedded absences is lower than expected by chance) then the matrix should be examined for turnover. Turnover, the second element of metacommunity structure, is measured as the number of times one species replaces another between two sites (i.e. number of replacements) for each possible pair of species and for each possible pair of sites. If turnover is negative (the number of replacements is lower than expected by chance) then the EMS framework reveals a nested pattern, if turnover is random the EMS detects quasi pattern (see Presley et al., 2010), and if turnover is positive (the number of replacements is higher than expected by chance) then the EMS framework suggests the existence of Clementsian, Gleasonian or evenly spaced patterns. These latter three are separated from each other by examining the boundary clumping of species ranges, the third element of metacommunity structure, using the Morisita test. If clumping is positive (Morisita I is significantly larger than 1.0) then the EMS framework detects Clementsian pattern; if clumping is negative (Morisita I is significantly lower than 1.0) evenly spaced pattern is indicated, and if clumping is random (Morisita I does not significantly differ from 1.0) then the pattern is thought to be Gleasonian.

There is, however, much controversy about the relative merits of the EMS framework. Gotelli and Ulrich (2012, p. 178), for instance, noted that species segregation and aggregation examined in the coherence test "might be the different sides of the same coin" and that rearranging the matrix (i.e. the reordering of sites by correspondence analysis) "does not alter any of the underlying information on species occurrences in the matrix". By examining the power of different null model algorithms, Gotelli and Ulrich (2012) found that a segregation measure was not exactly opposite in its behavior to a nestedness measure, suggesting that nested and segregated patterns (i.e. evenly spaced, Gleasonian and Clementsian) are not necessarily mutually exclusive as implied by the turnover test in the EMS framework. The same authors repeated this comment later and also argued that "The frameworks proposed by Leibold and Mikkelson (2002), and Presley et al. (2010) implicitly assume that measures of coherence, turnover, and boundary clumping describe orthogonal, independent properties of matrices. But if the measures are strongly correlated, some of the proposed cells in their classification frameworks may be redundant or not achievable. Leibold and Mikkelson (2002) recognized this problem and noted that they were able to identify empirical matrices that fit each of the five different scenarios they described" (Ulrich and Gotelli, 2013, p. 3). A more recent paper stated that the efficiency of the EMS framework is heavily dependent on data quality (Mihaljevic et al., 2015, see also Gotelli and Graves, 1996; Ulrich and Gotelli, 2013) and suggested the use of occupancy models to at least partly overcome this problem. These models allow an estimation of predicted occupancy at each sample site and thus make it possible to distinguish between the probability of a species occurring at a site and the probability of a species being detected at a site in which it does occur (Mihaljevic et al., 2015). These critical comments, however, did not prevent community ecologists from using the methodology even further. The EMS framework has still been used increasingly both in terrestrial and aquatic realms for finding the best fit to idealized metacommunity patterns (Dallas and Presley, 2014; de la Sancha et al., 2014; Heino et al., 2015). However, the reliability of the method in discerning idealized (meta) community patterns has not been tested as yet.

To fill this methodological gap, this paper examines the performance of the EMS framework. Combining theoretical aspects with simulation approaches we go through this approach step by step and inspect how the rearrangement of the matrix, the output of individual tests as well as their series influence the success of analysis. We examined also the robustness of the methodology to increasing noise in the data, as well as the practice of researchers in revealing the importance of environmental factors structuring metacommunity patterns.

2. Methods

To guarantee unambiguous answers, we first carefully review terms and procedures related to the EMS framework. We discuss possible interpretations of terms and evaluate the performance of different procedures. In case of equivocal use of any term or procedure, we attempt to clarify the situation by suggesting a solution.

We calculated the following indices: the number of embedded absences (the index of coherence test, Leibold and Mikkelson, 2002; Presley et al., 2010), the number of mutually exclusive species pairs (Diamond, 1975), turnover (the index of turnover test, Leibold and Mikkelson, 2002; Presley et al., 2010). As nestedness is not defined in the EMS framework, we used two nestedness measures, the relativized nestedness (N_{rel}, Podani and Schmera, 2011) and the site-order independent version of NODF (Almeida-Neto et al., 2008) called as $NODF_{max}$ (Podani and Schmera, 2012; Ulrich and Almeida-Neto, 2012).