



Checkerboard metacommunity structure: an incoherent concept

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Abstract

Checkerboards have emerged as a metaphor to (1) describe mutually exclusive patterns of co-occurrence for ecologically similar species that are geographically interspersed (i.e., checkerboard distributions), and (2) characterize relationships among species distributions along gradients that involve entire metacommunities (i.e., checkerboard metacommunity structure). Critical differences exist in the conceptual foundations that characterize these patterns. Checkerboard distributions are characterized by mutual exclusion of geographically interspersed species, usually pairs of ecologically similar species for which competition prevents syntopy. In contrast, checkerboard metacommunity structures are more restrictive: groups of species must exhibit mutually exclusive distributions, and each of these groups must be spatially independent of all other groups. Consequently, in a checkerboard metacommunity, competition defines one relationship for each species (i.e., that with its mutually exclusive partner), whereas independence characterizes all other interspecific associations. Consequently, a structure designed to be consistent with this concept will conclude that the metacommunity has random rather than checkerboard structure. Indeed, empirical checkerboard metacommunities are quite rare (7 of 766 reported empirical structures), and likely arise because of poor characterization of species ranges due to detection errors (i.e., a preponderance of rare or hard-to-detect species), rather than from underlying ecological mechanisms. Importantly, no ecological mechanism has been identified that is consistent with the concept of negative coherence. Consequently, the evaluation of checkerboards should be restricted to small sets of ecologically similar species for which interspecific interactions may lead to mutual exclusion, and coherence should be used only to evaluate if species distributions are more coherent than expected by chance (i.e., one-tailed tests).

Keywords Competitive exclusion · Environmental gradients · Metacommunity structure · Spatial ecology

Introduction

Checkerboard distributions were conceived to describe relationships between ecologically similar species with geographically interspersed and mutually exclusive distributions (e.g., MacArthur et al. 1972; Diamond 1975). Such patterns

were first described for birds that exhibited interdigitating distributions on small oceanic islands that were not capable of supporting multiple populations of ecologically similar species (MacArthur et al. 1972; Diamond 1975). The mechanisms invoked to explain these patterns were priority effects and competitive exclusion of ecologically similar species by initial colonists. In general, checkerboard distributions have been evaluated for pairs of ecologically similar species, with methods developed to measure patterns of co-occurrence (variance ratio, Schluter 1984; checkerboard score, Stone and Roberts 1990) and to determine if empirical patterns differed from those generated by chance (Ulrich and Gotelli 2013; Connor et al. 2013; Gotelli et al. 2015). Importantly, identification of ecological interactions (e.g., combinations of competition, priority effects, natural enemies, microhabitat variation) as the mechanism responsible for checkerboard distributions requires considerations of the overlap of geographical ranges (i.e., “true checkerboards”), as regional allopatry could result in mutual exclusion (and a lack of

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co-occurrence) due to historical biogeography, habitat specialization, abiotic tolerance, or differential responses to predators or pathogens (Connor et al. 2013). Even when species have coincident geographical ranges, identification of the non-trophic mechanisms that mold patterns of species co-occurrence is difficult (Barner et al. 2018). Moreover, although co-occurrence metrics evaluate patterns of species segregation or aggregation, they do not determine if patterns of segregation represent checkerboard distributions (i.e., geographically interspersed mutual exclusion), as geography is ignored in co-occurrence analyses.

In contrast to this early conception of checkerboard distributions as geographically interspersed pairs of ecologically similar species, the checkerboard metacommunity concept was developed to describe a structure based on the distributions of all species in a metacommunity, which is a set of ecological communities occurring at sites along an environmental gradient that are potentially connected by dispersal (Leibold and Mikkelsen 2002). Two important criteria differentiate these two concepts of checkerboards. First, checkerboard distributions are restricted to ecologically similar species, whereas checkerboard metacommunity structure includes all species in the metacommunity regardless of ecological similarity. Second, checkerboard distributions are based on priority effects and intense competition (or some other combination of ecological mechanisms such as dispersal limitation, natural enemies, microhabitat variation), resulting in interspersed, mutually exclusive distributions for pairs of ecologically similar species (Diamond 1975). In contrast, checkerboard metacommunity structure requires these mechanisms to shape the distributions of multiple pairs of ecologically similar species, with the additional criterion of independence among the distributions of these pairs. The multiple meanings of “checkerboards” has become apparent (Connor et al. 2013; Schmera et al. 2018), requiring careful consideration to distinguish these patterns from each other, as well as the underlying ecological mechanisms, geographical processes, and methods appropriate for detecting each type of pattern.

Metacommunity structure

Metacommunity structure is an emergent property that describes the relationships among species' distributions across an environmental gradient (Leibold and Mikkelsen 2002; Presley et al. 2012). Over the last century, a number of idealized metacommunity structures have been described based on ecological theory, with each structure representing a distinct prediction about the effects of ecological mechanisms on the relationships among species distributions. We briefly describe each of these idealizations and the

ecological mechanism(s) originally proposed to give rise to such structures.

According to the community unit theory, species distributions along gradients result in distinguishable units that are identifiable based on differences in species composition (Clements 1916, 1936; Whittaker 1975). These “Clementian” metacommunities are characterized by coincident range boundaries that delimit compartments (i.e., a set of communities with similar species composition that is distinctive from other such sets of communities; Lewinsohn et al. 2006). In contrast, the individualistic hypothesis posits that local coexistence arises from the adaptation of each species to environmental variation, including biotic and abiotic components (Gleason 1926, 1939; Whittaker 1965, 1975). According to this theory, species distributions and distributional range boundaries should occur idiosyncratically and independently of each other along environmental gradients, forming “Gleasonian” structures that lack compartments (Gleason 1926; McIntosh 1967). Strong interspecific competition coupled with trade-offs in competitive ability may give rise to species distributions and range boundaries that are spaced evenly along environmental gradients (Tilman 1982). Alternatively, strong competition may result in checkerboard patterns characterized by ecologically similar species that have overlapping geographical ranges, but that are not syntopic (Diamond 1975), with distributions of each pair of species being independent of other pairs (Leibold and Mikkelsen 2002). Finally, variation among species in dispersal ability, habitat specialization, or abiotic tolerance, coupled with sequential colonization or extinction, may give rise to nested subsets (Patterson and Atmar 1986). Nested structures are characterized by the ranges of species with more narrow distributions (e.g., specialists or poor dispersers) being contained wholly within those of species with more broad distributions (e.g., generalists or effective colonizers). These associations between mechanisms and structures are those originally proposed when the structures were first identified or conceived by ecologists. However, many mechanisms or combinations of mechanisms could give rise to any of these metacommunity structures, as empirical structures are an emergent property that characterizes associations between the ranges of all species in a metacommunity along a latent environmental gradient. For example, strong environmental filtering could lead to any metacommunity structure, depending on the particular set of responses evinced by species to the dominant environmental gradient, with species ranges potentially forming compartments, forming nested subsets, evincing random associations with each other, or with species responding to multiple environmental gradients.

The framework developed by Leibold and Mikkelsen (2002) distinguishes each of these idealized structures based on three characteristics of species distributions (i.e.,

the elements of metacommunity structure: coherence, range turnover, and range boundary clumping). However, a mismatch exists between the concept of checkerboard metacommunity structure and the methods used to detect it. Methodologically, it is unlikely that checkerboard metacommunity structure can be empirically distinguished from random structure, as the predominant mechanism that molds both random and checkerboard structures is the same. Importantly, this does not necessarily mean that checkerboard metacommunity structures do not exist, only that the proposed methods cannot distinguish those structures from random ones. We review the primacy of coherence in metacommunity analyses, outline the defining criteria of checkerboard metacommunity structure, identify the mismatch between the effects of these criteria and the analytical results considered to be characteristic of checkerboard metacommunities, emphasize the rarity of empirical checkerboard metacommunities, and conclude with implications on analyses of coherence and detection of checkerboard metacommunity structure.

Coherence: the primary element of metacommunity structure

A fundamental assumption in ecology is that the abundances of species along underlying environmental gradients are Gaussian: modal in form with continuous distributions (Gauch and Whittaker 1972; Austin 1985; Blonder 2016). As such, species should occupy a coherent range of sites along environmental gradients (i.e., no gaps or discontinuities should exist in the fundamental niche of a species). For an entire metacommunity to exhibit coherence, the ranges of a preponderance of species must be coherent along the same environmental gradient. The nature of responses to the gradient may differ among species (i.e., the locations or extents of ranges may differ among species), giving rise to a plethora of metacommunity structures. Importantly, each empirical metacommunity structure is defined with respect to a particular latent environmental gradient, which may be defined by axes of ordination, geographical location, species richness and frequency of occurrence, or researcher-defined environmental conditions. Consequently, the same metacommunity may exhibit different metacommunity structure along different gradients.

In general, analyses of metacommunity structure are conducted on site-by-species matrices that have been ordered via reciprocal averaging (Hill 1973). Reciprocal averaging simultaneously optimizes the proximity of species with similar distributions as well as the proximity of sites with similar species compositions in the matrix. In doing so, reciprocal averaging maximizes the coherence of species distributions and the coherence of community compositions,

thereby allowing the distributions of the entire suite of species under consideration to define one or more latent environmental gradients (Gauch 1982; Presley et al. 2009). Imposing particular environmental or spatial gradients can be challenging. Although sites are easily ordered along such gradients, the bases for the ordering of species are more difficult to determine in an unbiased and consistent fashion. More importantly, it is not possible to order sites and species in randomly generated matrices in the same way when employing researcher-defined gradients (e.g., how do you “order” randomly generated sites and species along a spatial gradient?). Consequently, when using a researcher-defined gradient, the empirical matrix is ordered using a different criterion than are the randomly generated matrices on which the null distribution of values is based. This will lead in inflated type I error rates when randomly generated matrices are not ordinated. Alternatively, analyses would be subject to inflated type I or II error rates due to the lack of correspondence between the test statistic (calculated along a researcher-defined gradient) and those generated to evaluate significance that are ordered via reciprocal averaging. Either of these scenarios for researcher-defined gradients results in a comparison of apples (user-defined empirical gradient) to oranges (a null distribution based on randomly generated matrices that are not ordinated or that are ordinated via a different procedure). This is not a problem for tests that use reciprocal averaging as both empirical and randomly generated matrices are ordered using the same procedure (i.e., apples to apples). This coincidence of approach in dealing with empirical and simulated metacommunities is a hallmark of rigorous null model approaches.

The number of embedded absences (i.e., discontinuities in species distributions or in community compositions with respect to a latent gradient) is the basis for evaluation of coherence. This metric represents the number of deviations from “perfect coherence”. This is analogous to the approach used to analyze nested subsets, in which deviations from perfect nestedness are measured after species and communities are rearranged to be as nested as possible along a richness gradient (Ulrich et al. 2009). Empirical deviation from perfect coherence is then compared to a distribution of like values generated via a null model (Leibold and Mikkelsen 2002; Presley et al. 2010). If a metacommunity has fewer embedded absences than expected by chance, it has positive coherence; if it has more embedded absences than expected by chance, it has negative coherence; and if the number of embedded absences is indistinguishable from that generated by random processes, it is non-coherent (Leibold and Mikkelsen 2002).

Coherence is characteristic of 12 of the 14 described metacommunity structures (Presley et al. 2010), including Clementsian, Gleasonian, evenly spaced, and nested structures, as well as their associated quasi-structures. It is

important to recognize that all structures occur somewhere in a 3-dimensional space defined by the 3 elements of meta-community structure (see Fig. 1 of Dallas and Presley 2014), and that the named structures are convenient categories that facilitate the comparison of structures and the identification of processes. Unique combinations of range turnover and range boundary clumping distinguish among coherent structures. Alternatively, if a preponderance of species does not respond to the same environmental gradient, distributions will not form a coherent structure and the metacommunity has “random structure” (Leibold and Mikkelsen 2002). Importantly, this does not necessarily mean that species occur at random with respect to environmental gradients. Rather, if species distributions are associated with different gradients, they would fail to exhibit coherence along a single common gradient (i.e., ranges occur at random with respect to one another, not with respect to environmental variation in general). Finally, negative coherence is indicative of checkerboard metacommunity structure (Leibold and Mikkelsen 2002); a pattern defined by species distributions that have more discontinuities than expected by chance. This overabundance of discontinuities is expected because of the geographical interspersions of mutually exclusive species that form checkerboard distributions (Diamond 1975).

Negative coherence and checkerboards

Two processes are hypothesized to give rise to negative coherence and checkerboard metacommunity structure: (1) mutual exclusion between pairs of ecologically similar species that create interspersed geographical distributions (MacArthur et al. 1972; Diamond 1975), and (2) pairs of mutually exclusive species occurring at random with respect to other such pairs (Leibold and Mikkelsen 2002). The combinations of ecological mechanisms (e.g., priority effects, competition, dispersal limitation, microhabitat variation) that lead to mutual exclusion creates gaps in the environmental distributions of species. This contrasts with the idea that the distributions of species should be continuous along underlying environmental gradients (the basis for positive coherence), and thus in theory could lead to the opposite pattern (negative coherence). If mutually exclusive species pairs exist, but have distributions that are defined by the same environmental gradient, a metacommunity structure with positive coherence manifests (Fig. 1). Using a literal checkerboard pattern as an example, members of mutually exclusive species pairs occur in groups that form two communities that are distinct from one another (Fig. 1a). Consequently, this apparent checkerboard pattern has Clementsian structure (i.e., positive coherence, range turnover, and boundary clumping) with two compartments at the metacommunity level (Fig. 1d). Similarly, if range boundaries are

spaced evenly or occur at random along the environmental gradient, apparent checkerboard patterns (Figs. 1b, c) have evenly spaced (Fig. 1e) or Gleasonian (Fig. 1f) structure, respectively.

Groups of sites that have multiple sets of mutually exclusive species also fail to exhibit checkerboard structure at the metacommunity level. For example, data on breeding birds from the Pearl Archipelago of Panama was used to help develop the concept of checkerboard distributions (MacArthur et al. 1972). However, this metacommunity of 61 species from 17 islands has positive coherence and negative turnover, consistent with nested metacommunity and not checkerboard metacommunity structure (Fig. 2). Clearly, checkerboard distributions based on multiple sets of ecologically similar species do not necessarily result in a checkerboard metacommunity structure when all species in the metacommunity are considered simultaneously.

The two criteria in the definition of checkerboard metacommunity structures (i.e., competitive exclusion and independence among distributions of species pairs) have opposing and unequal effects on coherence. To demonstrate the relative effects of these phenomena, consider a metacommunity of 8 species and 8 sites comprising 4 pairs of mutually exclusive species with independent relationships among all such pairs (i.e., the conceptual definition of a checkerboard metacommunity structure sensu Leibold and Mikkelsen 2002). The ranges of any single pair of mutually exclusive species could be made coherent if we ignored the ranges of the other species (Fig. 3a, b); however, because the ranges of all other species are independent of the mutually exclusive pair that was forced to be coherent, the net effect will be a random structure. In this example, each species has one mutually exclusive partner and 6 species with which its range has a random association, resulting in random associations describing relationships between species distributions 6 times more often than does competitive exclusion. Of course, this is not how reciprocal averaging orders species or communities, but the net effect would be the same for any ordination: the primary structuring mechanism based on the conceptual definition of checkerboard metacommunity structure is randomness. Indeed, the metacommunity in Fig. 3a is non-coherent ($P = 0.700$), indicating random structure. Consequently, this metacommunity designed to be perfectly consistent with the checkerboard metacommunity concept evinces non-coherence and random structure rather than the predicted negative coherence and checkerboard structure!

For metacommunities comprising multiple sets of mutually exclusive species pairs, relative effects of random associations compared to mutually exclusive associations between species in checkerboard metacommunities increases very rapidly, with the proportion of associations that are random defined by the formula $\frac{S-2}{S-1}$, where S is species richness of the metacommunity (Fig. 4). When only 1 pair exists, no

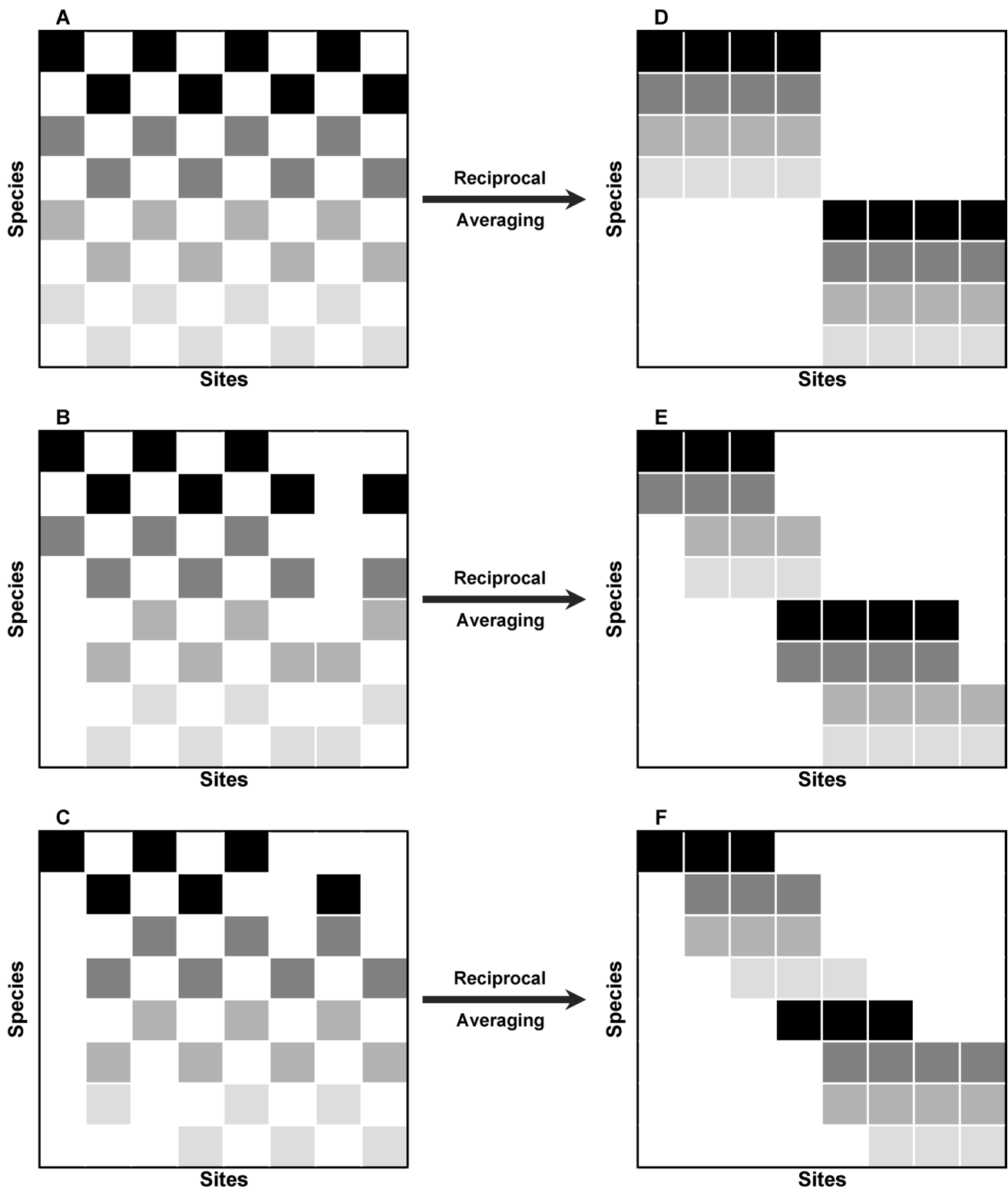


Fig. 1 Examples of a traditional checkerboard patterns (a–c) sensu Diamond (1975) and the metacommunity structures they represent after ordination via reciprocal averaging, including Clementsian (d), evenly spaced (e), and Gleasonian (f) structures. In each of these

cases, the distributions of mutually exclusive species pairs (indicated by colors) are not independent of one another, but exhibit perfect coherence with respect to a common environmental gradient

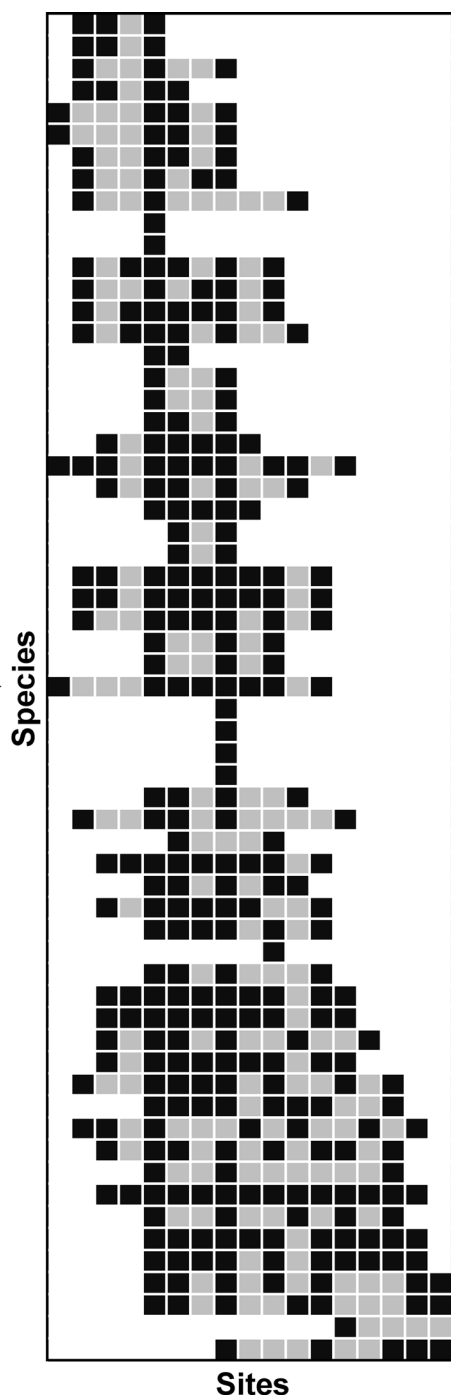


Fig. 2 Distributions of breeding non-marine bird species from the Pearl Archipelago (MacArthur et al. 1972). The metacommunity was ordinated via reciprocal averaging and exhibited positive coherence (Embedded absences=369, $P=0.006$, Mean number of absences from randomly generated matrices=447) and negative turnover (Replacements=6786, $P<0.001$, Mean number of replacements from randomizations=14,453), consistent with nested structure. Black cells represent species presences; gray cells are embedded absences in species distributions

associations are random. However, when 5 pairs exist, each of the 10 species have 1 mutually exclusive association and 8 random associations (i.e., each species has $S - 1$ associations of which $S - 2$ are random). We emphasize that the mismatch between the concept of the checkerboard metacommunity structure and the ability to detect that structure via analysis of elements of metacommunity structure (sensu Leibold and Mikkelson 2002) is not contingent on the use of reciprocal averaging. Regardless of the procedure used to order sites and species, the preponderance of associations between species ranges must be random, making structures that arise from the checkerboard metacommunity concept indistinguishable from the idea that species ranges are not associated with the same environmental gradient (i.e., the definition of random structure). Indeed, the only difference between the conceptual definitions of random and checkerboard structures is that each species in a checkerboard metacommunity has a single mutually exclusive association with another species!

This effect likely explains why empirical checkerboard metacommunity structures (i.e., negative coherence) are rare, representing only 7 of 766 structures reported in 90 studies through April 10, 2019 (Appendix in Supplementary material), a far lower rate than one would expect to represent Type I errors. The 3 cases of checkerboards in free-living taxa represent instances of low matrix fill with rare or difficult to detect species dominating the metacommunity: eurybiont oribatid mites from Holarctic peat bogs (Mumladze et al. 2013), gleanings of animalivorous bats in Costa Rica (Cisneros et al. 2015), and carabid beetles from the Kinzig River in Germany (Tonkin et al. 2016). The remaining 4 checkerboards were observed in parasitic infracommunities, a scale (i.e., the host individual) at which patterns are difficult to detect because they represent depauperate subsamples of component communities (Poulin 1997; Dallas and Presley 2014): helminth infracommunities from *Didelphis aurita* in rural Brazil (Costa-Neto et al. 2018), early larval and pupal stages of spruce budworms (Marrec et al. 2018), and viruses from bats in the Neotropics (Nieto-Rabiela et al. 2018). These “checkerboard metacommunity structures” may represent cases of pervasive detection error, with empirical metacommunities characterized by false absences rather than by independently associated pairs of mutually exclusive species. Such cases would benefit from the application of occupancy modeling via detection error-corrected elements of metacommunity structure (DECEMS, Mihaljevic et al. 2015).

An extensive analysis of pairwise species segregation for birds detected general trends consistent with the above interpretations (Korňan and Svitok 2018). Few pairs of species (<0.3% of all possible species pairs) exhibited species segregation with possible biological significance. Moreover, segregation was more likely to be detected in matrices with

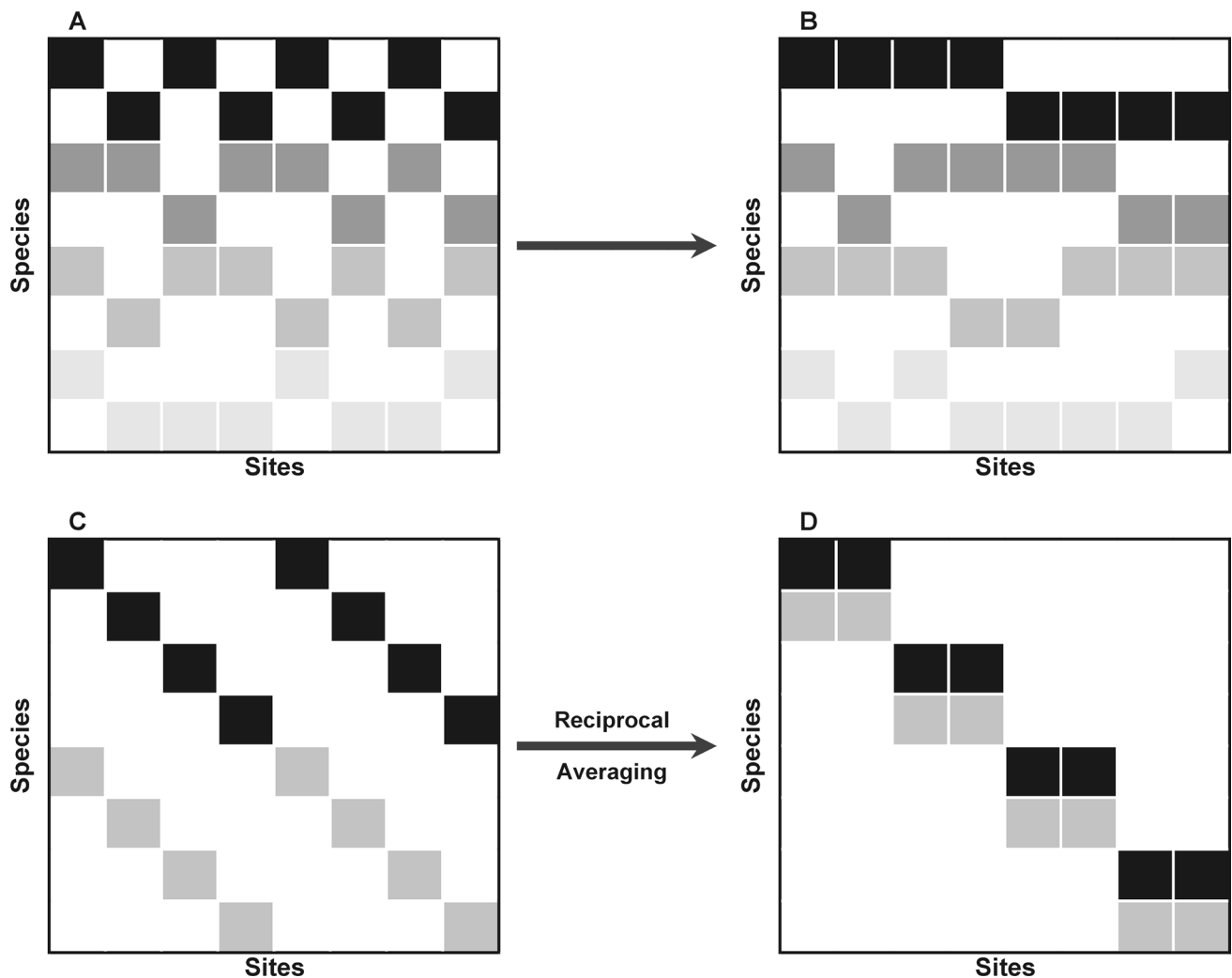


Fig. 3 A metacommunity with four mutually exclusive pairs of species (indicated by colors), whose distributions are associated with different gradients (i.e., whose distributions are independent of one another) (a), and a manual ordination of sites to maximize coherence of one mutually exclusive species pair (black) demonstrating the lack of range coherence in the remaining mutually exclusive species pairs (b). An example with two sets of four mutually exclusive species

whose distributions are associated with the same environmental gradient (c) and an ordination via reciprocal averaging showing that this metacommunity has compartments, resulting in Clementsian structure (d), with the number of compartments equal to the number of species that are mutually exclusive within each set. Mutually exclusive sets of species are indicated by different colors

low fill (similar to metacommunities dominated by hard to detect species) and were less likely to be detected in studies with small plot sizes (i.e., plots that likely represented depauperate subsets of the local community).

Conclusions

Because methods used to quantify elements of metacommunity structure cannot effectively detect checkerboard metacommunity structure as defined conceptually (sensu Leibold and Mikkelsen 2002), we should ask where in nature would we expect to find a metacommunity with several orthogonal

environmental gradients along which the distributions of mutually exclusive species pairs could occur? It is difficult to imagine more than a few such gradients occurring in a single metacommunity. In a montane forest system, there could be multiple independent gradients to which a biota responds: one associated with elevation, one associated with versant (e.g., eastern versus western slopes of a mountain range), and one associated with height above the forest floor. Even if a metacommunity only included 6 species (1 mutually exclusive pair per gradient), random associations between species would be 4 times more common than mutually exclusive ones (i.e., each species distribution would exhibit mutual exclusion with 1 species and have random associations with

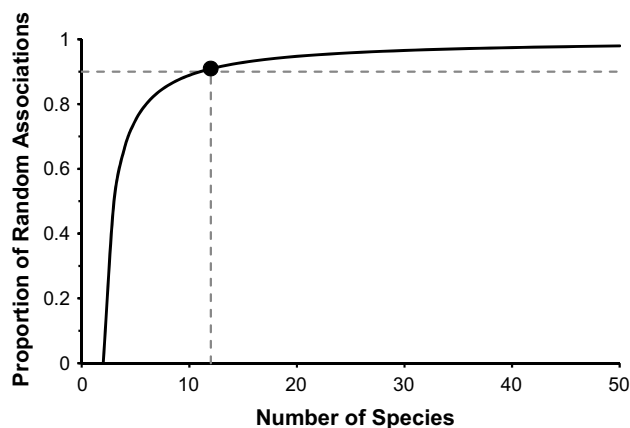


Fig. 4 Relationship between proportion of interspecific associations that are random and the number of species in a metacommunity that comprise mutually exclusive species pairs, when designed to perfectly conform to the theoretical description of a checkerboard metacommunity (Leibold and Mikkelsen 2002). More specifically, each species has $S-1$ associations with other species, and $S-2$ of those associations are random for each species, whereas 1 association is mutually exclusive. Consequently, $\frac{S-2}{S-1}$ describes the proportion of associations between species distributions that are random, where S is the richness of the metacommunity. Perfect checkerboard metacommunities (sensu Leibold and Mikkelsen 2002), comprising 12 or more species are dominated (>90%) by random interspecific associations. Metacommunity with 12 species indicated by a black dot and vertical dashed line, horizontal dashed line indicates 90% of interspecific associations

each of the 4 species whose distributions are associated with other gradients), leading to random metacommunity structure based on analyses of coherence. Multiple pairs of mutually exclusive species associated with each gradient would maintain non-coherence or possibly result in positive coherence if most species distributions were associated with the same gradient (Fig. 1), but additional sets of mutually exclusive species would not contribute to negative coherence.

Currently, no known mechanism is consistent with a metacommunity structure characterized by negative coherence. Although negative coherence may indicate that communities are insufficiently sampled or represent depauperate subsets of the ecological communities of interest, these same phenomena more commonly result in non-coherence. Consequently, negative coherence and non-coherence likely represent a distinction that cannot be detected via analysis of coherence, as they convey the same information about metacommunity structure (i.e., that species distributions are not associated with the same environmental gradient or that communities are insufficiently characterized). As such, the alternative hypothesis to the null of “species distributions have random association with respect to one another” should be “species distributions are molded by a common environmental gradient”,

which represents a one-tailed test for positive coherence characterized by fewer embedded absences than expected by chance. Perhaps mechanisms not yet identified could lead to negative coherence; in such cases two-tailed tests should be used to account for hypotheses that posit negative coherence. However, for the vast majority of circumstances, the current two-tailed approach for analysis of coherence is conservative, with half of the rejection region occurring in a direction from the null hypothesis for which we have no reasonable biological expectation.

In his original treatise of community assembly, Diamond (1975) defined checkerboard distributions as patterns in which “two or more ecologically similar species have mutually exclusive interdigitating distributions”. However, increasing the number of species in a set of mutually exclusive species does not change the fact that if sets of ecologically similar species with mutually exclusive distributions are associated with the same environmental gradient, ordination of that metacommunity will reveal a coherent structure with positive turnover (Fig. 3c, d). As such, checkerboard distributions describe a pattern associated with only a subset of a metacommunity, and likely are best evaluated only for each set of ecologically similar species rather than for entire metacommunities (Ulrich and Gotelli 2013; Connor et al. 2013). Methods already exist that are effective at measuring co-occurrence among groups of ecologically similar species (Schluter 1984; Stone and Roberts 1990) and for evaluating if these patterns differ from random expectations due to regional allopatry (EcoSimR, Gotelli et al. 2015) or as true checkerboards (Connor et al. 2013). Therefore, we recommend that (1) checkerboard distributions, patterns of segregation or aggregation, or true checkerboards should be evaluated only for ecologically similar species as originally proposed by Diamond (1975), and (2) attempts to identify checkerboard metacommunity structure via analysis of coherence should be abandoned because the methodological approach cannot distinguish between conceptual checkerboard and random metacommunity structures.

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Electronic Supplementary Material

Checkerboard Metacommunity Structure: an Incoherent Concept

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Appendix (continued)

| Reference | | Checker | | | Quasi-nested | Evenly spaced | Quasi-evenly spaced | Quasi- | | Quasi-Clementsian |
|---------------------------|-------|---------|--------|--------|--------------|---------------|---------------------|------------|------------|-------------------|
| Authors | Year | board | Random | Nested | | | | Gleasonian | Gleasonian | |
| Gao et al. | 2016 | | | | | | | | 2 | |
| García-Peña et al. | 2016 | | 1 | | | | | 1 | | |
| Gascón et al. | 2016 | | 1 | | | | | | 1 | 1 |
| Guo et al. | 2019 | | 4 | 4 | | | | | 4 | |
| Heino and Alahuhta | 2015 | | | | | | | | 4 | |
| Heino et al. | 2015a | | 2 | 1 | 1 | | 3 | 4 | 4 | 3 |
| Heino et al. | 2015b | | 8 | | 11 | | 5 | 4 | 11 | 5 |
| Heino et al. | 2016 | | 1 | | | | | | 9 | 2 |
| Henckel et al. | 2019 | | | | | | | | 1 | |
| Hernández-Gómez et al. | 2017 | | | | | | | | 1 | |
| Hoverman et al. | 2011 | | | | 1 | | | | | |
| Johnson et al. | 2013 | | | | | | | | 1 | |
| Josefson | 2016 | | | | | | | | | 3 |
| Josefson et al. | 2018 | | 1 | | | | | | 4 | 1 |
| Keith et al. | 2011 | | | | | | | | 2 | |
| Keith et al. | 2013 | | | 1 | | | | | | |
| Keppeler et al. | 2016 | | 1 | | | | | | | |
| Kratochwil et al. | 2009 | | | | 2 | | | | | |
| Kusch et al. | 2005 | | | 6 | 1 | | 9 | 2 | 2 | |
| Leavitt and Fitzgerald | 2013 | | 1 | 1 | | | | | | |
| López-Delgado | 2019 | | 2 | | | | | | 3 | |
| López-Gonzalez and Lozano | 2015 | | | | | | 1 | 1 | | |
| López-Gonzalez et al. | 2012 | | 3 | | 2 | | 1 | | 4 | 1 |
| Maasri et al. | 2018 | | | | | | | | 1 | 1 |
| Marcilio-Silva et al. | 2017 | | | 4 | | | | | | |
| Marrec et al. | 2018 | 2 | 1 | | | | | | | |
| McCauley et al. | 2008 | | | | | | | | | 1 |
| Medina Torres and Higgins | 2016 | | | | | | 1 | 2 | 5 | |
| Meynard et al. | 2013 | | | | | | | | 5 | |
| Mihaljevic et al. | 2018 | | 2 | 3 | | | | | | |

Appendix (continued)

| Reference | | Checker | | | Quasi-nested | Evenly spaced | Quasi-evenly spaced | Quasi- | | Quasi- | |
|---------------------------|------|---------|--------|--------|--------------|---------------|---------------------|------------|------------|-------------|-------------|
| Authors | Year | board | Random | Nested | | | | Gleasonian | Gleasonian | Clementsian | Clementsian |
| Mumladze et al. | 2013 | 1 | | 2 | 1 | | | | 2 | | |
| Newton et al. | 2012 | | | | | | | | 2 | | |
| Nieto-Rabiela et al. | 2018 | 1 | 16 | | | | | | 3 | | 7 |
| Ochoa-Ochoa and Whittaker | 2014 | | | | | | 1 | 2 | 1 | | |
| Pelinson | 2016 | | 2 | 2 | 2 | | | 2 | 1 | | 1 |
| Petsch et al. | 2017 | | 2 | | | | | | 2 | | |
| Presley and Willig | 2010 | | 3 | 4 | | | 1 | 1 | 10 | | 5 |
| Presley et al. | 2009 | | 1 | | | | | 2 | 1 | | |
| Presley et al. | 2011 | | 1 | | | | | | | | 1 |
| Presley et al. | 2012 | | | 1 | | | | | 1 | | 1 |
| Ptatscheck et al. | 2015 | | | | | | | 1 | | | |
| Reardon and Schoeman | 2017 | | 1 | | | | | | | | |
| Richgels et al. | 2013 | | | | | 1 | | | | | |
| Ríos Blanco | 2013 | | 4 | | | 1 | | | | | 2 |
| Ross et al. | 2016 | | | 1 | | | | | | | |
| Ryberg and Fitzgerald | 2015 | | | 1 | | | | | | | |
| Samu et al. | 2018 | | | | | | | | | | 1 |
| Schiesari and Corrêa | 2015 | | | | | | | | | | 1 |
| Shevtsov et al. | 2013 | | 1 | | | | 2 | | 8 | | 4 |
| Tonkin et al. | 2015 | | | | | | | | 3 | | 1 |
| Tonkin et al. | 2016 | 1 | 25 | | 4 | | 24 | 7 | 4 | | 13 |
| Tonkin et al. | 2017 | | 1 | | 1 | | 4 | 3 | 4 | | 2 |
| Tonkin et al. | 2018 | | 8 | | 1 | | 8 | 1 | 4 | | 2 |
| Valanko et al. | 2015 | | 3 | | 1 | | | | | | 4 |
| Vieira | 2015 | | | | 4 | | | | | | 1 |
| Werner | 2007 | | | | | | | | 1 | | |
| Whippo et al. | 2018 | | 1 | | | | | | | | |
| Willig et al. | 2011 | | | | | | | 1 | 1 | | |
| Wojciechowski et al | 2017 | | 1 | | 8 | 2 | 5 | 5 | 4 | | 7 |

Appendix (continued)

| Reference | | Checker | | | Quasi- | Evenly | Quasi- | Quasi- | | Quasi- |
|------------------|------|---------|--------|--------|--------|--------|---------------|------------|------------|-------------|
| Authors | Year | board | Random | Nested | nested | spaced | evenly spaced | Gleasonian | Gleasonian | Clementsian |
| Yeh et al. | 2015 | | 11 | | | | | 1 | | 1 |
| Total | 766 | 7 | 180 | 56 | 65 | 2 | 1 | 80 | 48 | 220 |
| Percent of total | | 0.91 | 23.50 | 7.31 | 8.49 | 0.26 | 0.13 | 10.44 | 6.27 | 28.72 |

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