Local versus regional processes and the control of community structure

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Abstract: The contribution of local (e.g., competition) and regional (e.g., dispersal) processes in the structure of communities remains an unresolved issue. In general, a tendency to assume local processes to be deterministic and regional to be stochastic dominates, although it is challenged. Fortunately, it can be cast as a testable proposition: if correct, the degree of determinism in the final community structure might indicate which process is more prominent in the control of community structure. However, recent findings have also suggested that stochastic patterns can arise from local processes and that dispersal can homogenize communities, which would make them appear deterministic irrespective of the mechanism involved. To evaluate these competing expectations we conducted an experiment where the initial communities had the same composition and species abundances. We hypothesized that if local processes dominate, then arrays of communities will show divergence of community structures whether connected by dispersal or not (i.e., being fully isolated). Alternatively, if regional processes dominate, the dispersal connected communities should converge while isolated ones should not. We found, however, that both groups of experimental communities showed similar patterns of change - a decline in similarity and a tendency to diverge. This suggests that biological interactions, demographic stochasticity, or both, exert noticeable control over community structure such that they reduce similarity among replicate communities and diversify their final states. We speculate that these mechanisms enhance potential for species additions, particularly in conjunction with factors such as dispersal and the size of the regional species pool.

Introduction

By convention, factors shaping community structure are discussed in terms of local and regional processes (Chase 2005, Hubbell 2006). Although controversial, community ecologists tend to associate local processes with deterministic outcomes arising from largely predictable species interactions and from environmental constraints (Chase 2003). In contrast, they view regional processes as stochastic. The latter implies that the final structure of a community depends on the distance from and size of the regional pool of species (Hubbell 2005, Hu et al. 2007).

Although contrasting structures are expected from each set of processes, local processes have also been shown to lead to patterns of species composition and relative abundance that appear stochastic (Márquez and Kolasa 2013). The regional view explains these patterns as due to priority effects (Law and Morton 1993, Drake et al. 1994). However, priority effects are not a prerequisite for the formation of diverse outcomes such as alternative states among communities (Márquez 2011). Recently we found that similarity among replicate communities exposed to the same environment decreased over time (Márquez and Kolasa 2013). Some of the suggested mechanisms included demographic stochasticity or/and small initial differences in the abundance of the populations (Márquez and Kolasa 2013). Other possible mechanisms for the observed differentiation could include intra-guild predation, random extinction of top predators or size dependent predation (Borrvall and Ebenman 2006, Verdy and Amarasekare 2010)

Under the scenario in which both local and regional processes produce stochastic community patterns, their individual contributions to the structure of the community are hard to determine. However, since theoretical and empirical studies suggest that strong dispersal homogenizes local communities within a metacommunity (Mouquet and Loreau 2002, Mouquet et al. 2003, Cadotte 2006, Altermatt et al. 2011), contrasting effects may arise depending on whether local or regional processes structure communities. Assuming that homogenization of community structure is inevitable when dispersal is strong (although see Scotti et al. 2013 for simulation-based arguments to the contrary), we conducted an experiment in which two sets of highly similar communities were left to develop under a homogenous external environment. We established permanent connections in one set of these communities while we left the other set unconnected. We propose that (1) if unconnected and connected communities develop alternative states to a similar degree, then biological interactions can be implicated in structuring communities, and (2) if connected communities converge into a single community state, then regional processes can be interpreted as being able to overcome the stochastic contribution of biological interactions.

Given the departure of these assumptions from the commonly espoused views, a theoretical resolution of the problem is not readily available. However, empirical separation of the net effect of dispersal on community patterns should prove informative. At the very least, it should provide context for further efforts aimed at understanding why development trajectories of individual communities diverge. More interest-

ingly, it should also help in understanding why such divergence leads to identifiable community end states attributable to local processes.

Methods

Study site

Invertebrates used for this experiment came from a set of natural rock pools located in Discovery Bay, Jamaica. The average size of the pools is 52 cm (SD ±20 cm) x 30 cm (SD ± 14 cm) with a mean depth of 12 cm (SD ± 8 cm) and an average volume of 17 L (SD ± 18.5L). Some pools are separated by a few centimeters and others by several meters. Some of these pools are tidal but the majority are maintained by rain and occasional wave splash which results in a mix of fresh, brackish and salt water pools (Romanuk and Kolasa 2005).

The biological community inhabiting these rock pools includes over 70 small benthic and planktonic animals, ranging in size from 600 μm to 5 mm. The animals belong to different phyla and classes such as Turbellaria (7 species), Nematoda (1), Polychaeta (5), Oligochaeta (2), Ostracoda (21), Copepoda (8), Cladocera (4), Decapoda larvae (1 crab species), Decapoda (3 shrimps), Amphipoda (1), Isopoda (1), and Insecta (18 species). The life cycles of the animals residing in the rock pools range from one week to three months (Romanuk and Kolasa 2005). Individual rock pool communities may experience desiccation, particularly in the summer, and more frequently in shallow pools (Therriault and Kolasa 2001).

Previous studies on the rock pools community had identified trophic relationships for some of the species (Therriault and Kolasa 2001, Beisner and Romanuk 2005). For example,

larger ostracods, like *Candona* sp., are top predators feeding on several trophic levels that range from cladocerans (herbivores), other ostracods (detritivores), down to detritus. Insects such as mosquitoes feed on phytoplankton, protozoans, and detritus, while beetles are predatory. Most midges, however, feed also on filamentous algae and detritus, while some are predatory.

Experiments

First, we created a null community in which neither local nor regional factors have had any influence. This was to ensure that none of the patterns observed at the conclusion of the experiment could be attributed to priory effects or dispersal limitation. The null community was created by mixing the contents of cultured invertebrate communities originally retrieved from 26 rock pools and subsequently maintained in separate beakers in laboratory. Conditioned tap water was added to complete the volume (~20 liters) needed for the experiments. Immediately following the formation of the null community, 40 half-liter beakers were filled with equal volumes containing the null community (Fig. 1a). The null community mixture was stirred while being distributed into each beaker to ensure that composition and abundance of invertebrates added into each was similar. Twenty beakers were left unconnected (Fig. 1b) and twenty were connected (Fig. 1c). The connections consisted of vinyl tubes 6.35 mm in inner diameter. The tubes were cut diagonally at the tips to ensure that both bottom dwelling as well as mid water invertebrates would have access. Under this configuration most of the beakers had four connections with the exception of the beakers at the corners of the array. Of these, two corner beakers had three connections and the other two corners had only two connections (Fig. 1d). Initially, the tubes were filled with
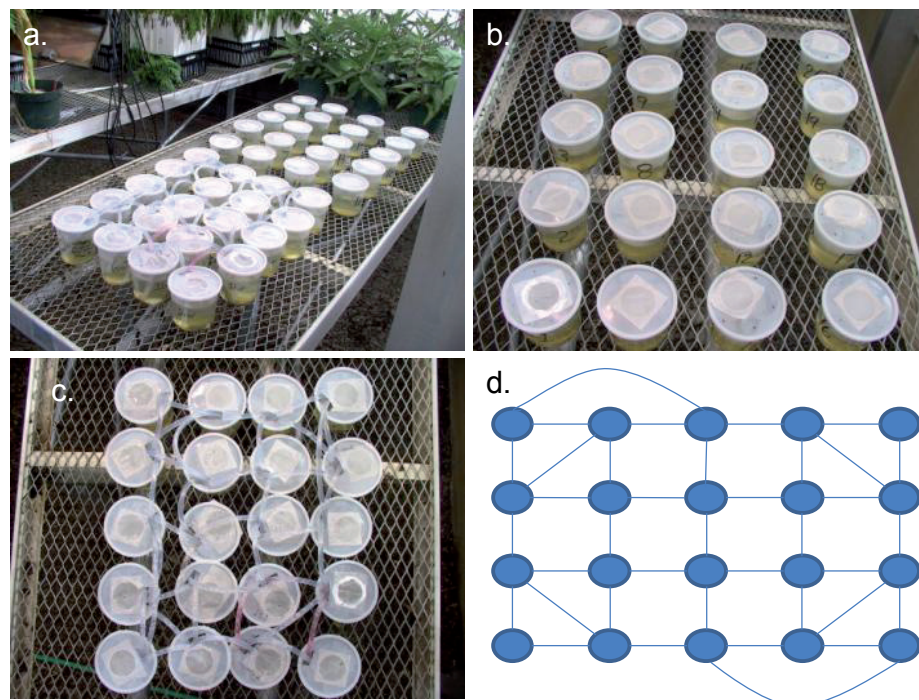

Figure 1. (a) 40 beakers with the null community; **(b)** the group of 20 unconnected beakers; **(c)** the group of 20 connected beakers and; **(d)** a schematic representation of the connections (lines) between beakers (gray circles).

distilled water. Each beaker had a lid part of which had an opening covered by a 63 μm mesh to prevent dispersal and allow gas exchanges. The connected beakers had an extra opening in the lid to accommodate the tubes. Prior to the experiment, we conducted a preliminary test to determine if tubes were effective means for animal dispersal. We connected two beakers, one with animals to one without. After a few days, both beakers contained animals from the bottom and mid water indicating the ability for invertebrates to disperse between beakers via corridors offered by the vinyl tubing.

The experiment was run in a greenhouse located at McMaster University. The communities were allowed to adjust and respond to treatments for 5 months. Samples were taken on three occasions: (1) at the start of the experiment (the null community), (2) after 2 months, and (3) at the conclusion of the experiment after 5 months – a sufficient time to capture changes in populations of experimental organisms whose Life cycle ranges from one week to no more than three months (Romanuk and Kolasa 2005). From each of the beakers after stirring the contents to homogenize distribution of organisms we took 100 ml of water. Once collected, the samples were passed through a 63 μm net and any animals retained in the net were transferred into a 50 ml vial with 50% ethanol. After sampling, 100 ml of distilled water was added to each beaker. With the use of a stereomicroscope, organisms were separated following an established visual method in which more than 95% of individuals are removed from the sample (Therriault and Kolasa 2000). After removing and sorting the animals, they were identified and counted.

Data analysis

In order to detect the level of homogenization or divergence among the connected (W) and the unconnected (WO) groups of beakers, we calculated Bray-Curtis similarity. Prior to this, abundance data were standardized and fourth root transformed (this transformation permits that even the rarest species contribute to the overall similarity). The analysis followed two steps. First, samples were organized according to their similarity using a hierarchical cluster analysis (using group average as the cluster mode). This analysis forms groups of samples according to their similarity regardless of the treatment. To determine which of these groups formed alternative states, we adopted a stringent group defining criterion using the null community as reference. Specifically, we used maximum similarity value at which the ordination retained all the null community samples together as one group. Thus, any group of converging samples with the same or higher similarity than the homogenized null community was considered to represent an alternative state. Consequently, only communities that converged to become more similar than those manually homogenized would become members of such groups.

As the second step of analysis, we performed a non-metric multidimensional scaling (MDS) ordination. Combining the cluster analysis and ordination tests has an advantage of confirming the consistency of groupings produced by the cluster analysis and facilitates visual interpretation of the results.

Graphically, communities forming an alternative state(s) and remaining communities are delineated by ellipses in the MDS ordination graph. Communities encompassed by the ellipses share values of similarity that lie above the cut off value that kept null community samples together. Both analyses were performed using PRIMER 6. To test whether these alternative states were different from each other, we applied an analysis of similarities (ANOSIM protocol in PRIMER 6).

Finally, a Similarity Percentage (SIMPER protocol in PRIMER 6) analysis was run in order to identify the species contribution to the differences between alternative states. Furthermore, this analysis allowed identifying changes in structure of each group of alternative state communities over the duration of the experiment.

Results

Generally, community similarity among replicates decreased with time, irrespective of whether dispersal was allowed or not, with one exception. After two months, unconnected communities (WO2) showed the highest similarity, followed by connected communities (W2). After five months, both treatments (W5, WO5) showed declines in intercommunity similarity (Fig. 2a). Furthermore, declines were quite uneven among individual replicates as evidenced by an increase in standard deviation of similarity values within treatments (Fig. 2b). The number of outliers and extreme values also increased with time (Fig. 2a). Together, all these measures point to a tendency of communities to diverge from each other regardless of the treatment.

The above patterns are further corroborated by an ordination which showed that the number of alternative states increased as time passed. For example, two alternative states were detected in the connected beakers in the second month. In the fifth month, when similarity decreased, four alternative states were recorded. Two of these alternative states consisted in individual communities. In unconnected communities, patterns were somewhat different. After two months, only one alternative state was observed in the second month and four were identified in the fifth month (Fig. 3). Again, two of these alternative states corresponded to individual beakers. ANOSIM tests indicate that all of the alternative states containing more than one member communities were significantly different from each other (Appendix 1).

Result from the SIMPER analysis showed that of the seven species in the experiment, the two with the most contribution to the formation of each of the groups were ostracods *Potamocypris* sp. (38%) followed by *Cypricercus* sp. with 20.2%. The remaining species contributed less than 20% each to the formation of alternative states (Appendix 2). This is expected since both of the species were the most abundant and thus ubiquitous in all the states (Fig. 4).

Three species made major contribution to dissimilarity among groups. Ostracod *Candona* sp. made the greatest contribution (27%), followed by cladocerans, *Alona davidii* (Richard) (24.9%) and *Ceriodaphnia rigaudi* Richard 1894 (19.7%). These species presented mid to low abundances in the
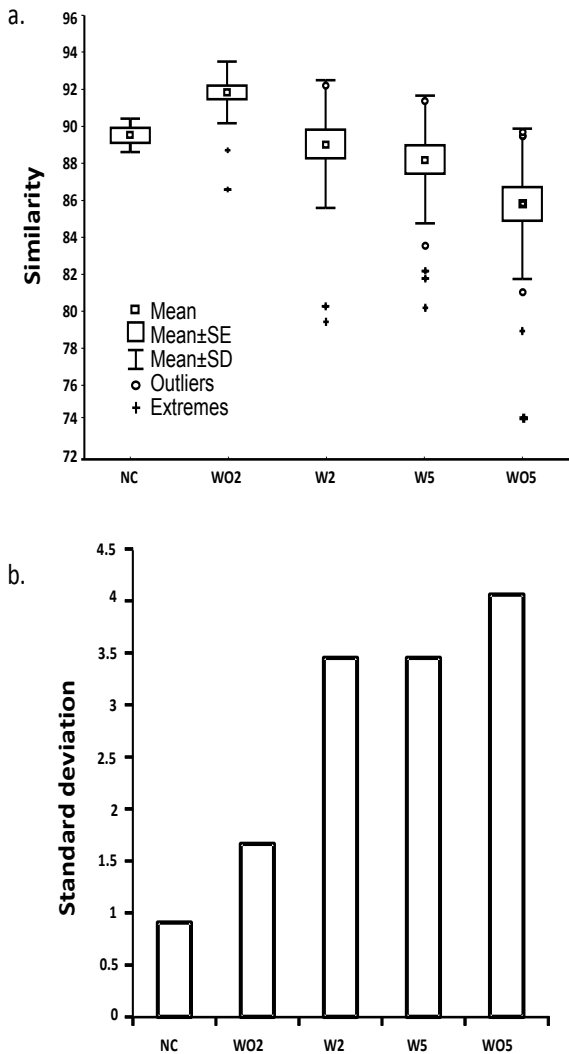
Figure 2. Mean similarity among treatments **(a)** and standard deviations **(b)** - based on all communities within a single treatment. NC – null community, W – communities with connections, WO – communities without connections. Numbers accompanying treatment codes are for samples taken in the second (2) and fifth month (5) of the experiment.

groups so they were most prone to extinction. Consequently, the combination of presence/absence and changes in abundance of these three species were pivotal for the differentiation of alternative states. Ostracods *Cypricercus* sp. (18.3%) and *Cypridopsis* cf. *mariae* Rome (17.9%) were two other important contributors to dissimilarity (Appendix 3, Fig. 4). Two and five months old connected communities differed mainly because some species went extinct and abundance of most species declined compared to NC communities, however a cladoceran *A. davidii* increased its abundance in most instances. In unconnected communities, all species showed declines in abundance through the second and fifth month, with *A. davidii* going extinct. Species abundances declined faster in unconnected communities in the first two months except for one species, ostracod *Cypricercus* sp.. Differences between connected and unconnected communities in the fifth month were due mainly to the extinction of *A. davidii*. The other species remained generally less abundant in the unconnected communities (Appendix 3, Fig. 4).

Discussion

Our results confirm indirectly the role of biological interactions as one of the most important factors structuring communities. Both groups of communities, connected and unconnected, showed a decrease in similarity, a tendency to form alternative states, and an increased rate of change over time. Others have also reported that local processes can override the influence of regional processes in generating multiple alternative states and divergence in community structure (i.e., lowering inter-replicate similarity) (Cottenie and De Meester 2003, 2004, Shurin et al. 2004, Houlahan et al. 2007, Mutshinda et al. 2009). Nevertheless, those authors identified environmental and spatial factors as the main cause of divergence among communities within a metacommunity (Michels et al. 2001).

We feel that our experiment provided more direct evidence for the dominance of local biological processes over regional processes in a homogeneous environment. To this extent our results concur with previous findings by Fox
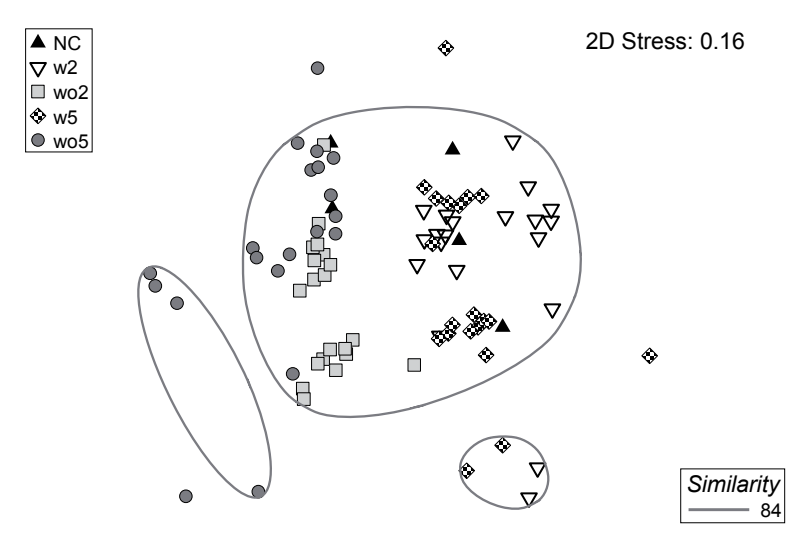

Figure 3. Alternative states (ellipses) formed at the 84% similarity level (see explanation in text) for each of the treatments. Stress values <0.2 indicate an acceptable (significant) ordination. Horizontal axis represents MDS dimension 1 and vertical axis represents MDS dimension 2.
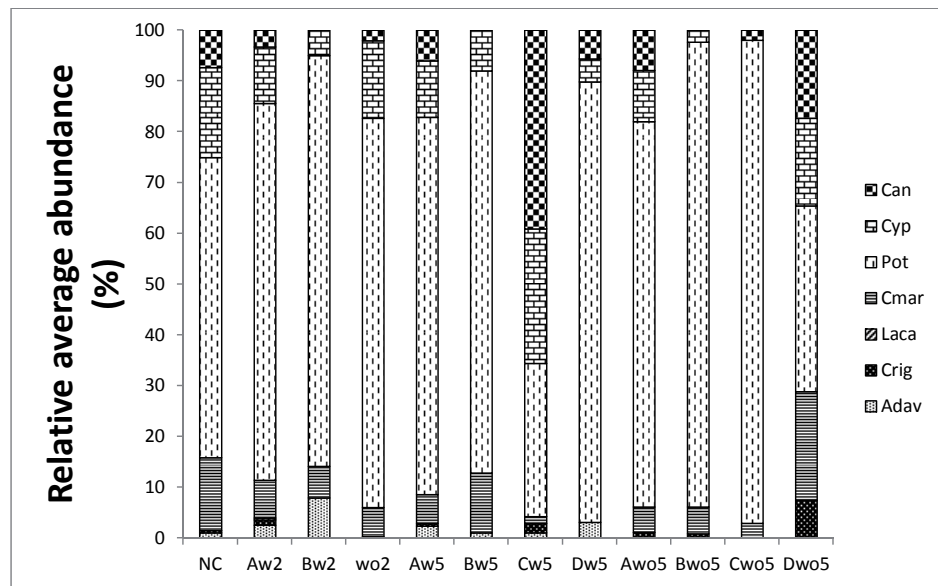
Figure 4. Relative average abundance (%) of each one the species in each of the resulting alternative states. NC – null community, W – communities with connections; WO – communities without connections. Numbers accompanying treatment codes are for samples taken in the second (2) and fifth month (5) of the experiment. Letters A, B, C, D indicate alternative states among treatments. Species abbreviations are: Cmar = *Cypridopsis* cf. *mariae* Rome; Pot = *Potamocypris* sp.; Can = *Candona* sp; Cyp = *Cypricercus* sp; Adav = *Alona davidii* (Richard); Crig = *Ceriodaphnia rigaudi* Richard 1894; Laca = *Leydigia acanthocercoides.*

(1987), Brown et al. (2002), and Chase (2005). The new finding, however, is that the resulting communities did not remain in a single community state. Presence of alternative states in a metacommunity developing under uniform external environment was usually attributed to the influence of regional processes and the ensuing priority effects (e.g., Drake 1990, Morton et al. 1996, Schröder et al. 2005). We provide indirect evidence that alternative states can be generated in connected and unconnected communities by means of biological interactions only (as no external environmental factors could possibly differentiate community structures in replicates).

The most probable interactions among species in the communities were predation and competition; also demographic stochasticity should have played a role. *Potamocypris* sp. and *Cypridopsis* sp. feed on detritus (Beisner and Romanuk 2005) - the most obvious resource in the experimental communities. These species started as the most abundant populations in the community but they declined the most and suffered from many local extinctions suggesting competition. These declines influenced deeply similarity levels among communities. *Candona* sp. being the top predator in the experimental communities (Beisner and Romanuk 2005) occurred initially in low density. Even though it has resources to feed on and no competition, it was not able to survive in all the replicates, especially in the unconnected communities where rescue effects were not possible (Fig. 4). Most probably, its extinction or decrease in abundance among unconnected community replicates was due to demographic stochasticity. For example, Powell and Boland (2009) corroborate such effects and show how individual-level interactions can propagate to community trophic structural outcomes at small population densities. Such propagation can lead to divergence of emerging

structure as observed in our experiment. Finally, cladocerans *A. davidii* and *C. rigaudi* are mainly algal consumers (Beisner and Romanuk 2005). Given the water quality conditions in the beakers, phytoplankton populations should decrease over time due to nutrients being locked up in organic matter. Low food resources, and presumably competition, it is probably why these species declined and went extinct in some replicates. Notably, *A. davidii* was present in most of the replicates of the connected communities, while *C. rigaudi* survived much better in the unconnected set. These differences are most easy to explain in terms of biological interactions. Some evidence of the control of community assembly by biological interactions has been established empirically. Shurin (2000) found that in 90% of the cases species failed to colonize ponds to which the regional species pool was introduced artificially and, presumably, generated a high level of species saturation. Cottenie et al. (2003) found that a mix of the communities of two pools introduced in one of them resulted in the same community structure as the original occupying that pool. His result implies that the existing community impeded colonization by outside species. Resistance to invasion has been proposed as an emergent property of communities in that it controls accommodation of invading species and thus it becomes the driver of community structure (Gilpin and Diamond 1982, Belyea and Lancaster 1999, Brown et al. 2002). However, contrary evidence, i.e., a successful colonization of established communities by new species is often reported (e.g., Ricciardi 2001, Shurin et al. 2000).

The conflicting observation above that sometimes communities prevent colonization and sometimes favour it could be explained in light of our previous (Márquez and Kolasa 2013) and present findings. The formation of alternative

states as a result of biological interactions may imply a degree of compositional flexibility, which in turn may imply a degree of openness to the colonization by outside species, at least for some of the alternative community states.

Finally, if priority effects are less relevant than sometimes assumed and alternative states can form through biological interactions alone, what is the role of regional processes in the assembly of communities? This is a pertinent question because we earlier found that the stochastic signature observed in natural assemblages is higher when regional processes are included (Márquez and Kolasa 2013). Since some of the communities in a metacommunity could be open to invasion, the contribution of regional processes might be to enhance the number of species present in local communities (Cadotte 2006). A local increase in the number of species leads to more ways in which species can relate to each other and thus augment stochastic outcomes driven by biological interactions alone.

In summary, our experiment suggests that biological interactions exert noticeable control on community structure. Progressive loss of similarity among replicate communities and the formation of alternative states in both connected and unconnected communities are evidence for that control. We speculate that the presence of alternative states enhances potential for further addition of species. This enhancement does not negate the role of regional processes where factors such as dispersal rate and size of the regional pool also contribute to the assembly of communities. The idea that regional processes contribute to the assembly of communities is not new (Hubbell 2006, Ricklefs 2008), however the influence of regional processes depends on community attributes and states produced by the local interactions.

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Electronic supplements

Appendix 1. ANOSIM results for the pairwise comparisons of the similarity among alternative states.

Appendix 2. SIMPER results showing contribution of each of the species to the similarity among alternative states.

Appendix 3. SIMPER results showing contribution of each of the species to the dissimilarity between each of the alternative states.

The file may be downloaded from www.akademiai.com.