ASSEMBLY RULES: DETERMINISM vs. RANDOMNESS

ASSEMBLY RULES: DETERMINISM vs. RANDOMNESS IN THE FORMATION COMMUNITIES

By

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Abstract

Elucidating the mechanisms structuring communities has been a challenge for community ecology since its beginnings. One theory argues that assembly rules structure communities by means of deterministic mechanisms arising from biological interactions. Another view maintains that patterns seen in community composition and species abundance result from stochastic processes such as migration and extinction. The dilemma has yet not been resolved unambiguously. The main issue is that communities shaped by deterministic mechanisms can produce stochastic patterns via priority effects. The main goal of this study was to determine whether assembly rules structure communities. My strategy was to minimize priority effects by controlling timing of colonization. To do this I used a null community by combining communities of 17 rock pools. This null community was later divided among experimental communities. I conducted three experiments: (1) Experimental communities were exposed to the same external conditions. (2) Communities were exposed to different environments, disturbance, dispersal and habitat heterogeneity. (3) Replicated null communities were connected to allow inter-replicate dispersal. After 4 months, communities (experiment 1) formed alternative states, suggesting the lack of assembly rules control in community structure. The second experiment showed that adding factors results in more alternative states. The increasing number of alternative states among replicate communities indicates that diversified environment and migration are needed to reproduce qualitative patterns observed in nature. The last experiment (3) showed that patterns observed among connected replicate communities resemble patterns that emerged in the presence of biological interactions in unconnected communities. Similarity of patterns between connected and unconnected groups of communities suggest that local biological interactions can be sufficient to structure communities to a considerable degree. Nevertheless, the regional processes appear necessary in their role of supplying species for local communities.

Preface

This dissertation contains three papers, one of which has been submitted to the journal Oecologia. The remaining papers are going to be submitted to relevant scientific journals. All of the papers were coauthored by my supervisor Dr. Jurek Kolasa. Luana Sciullo was the third author of the paper presented in chapter 3. While all the authors contributed ideas and comments to improve the manuscripts, the majority of each paper consists of my own original research.

There is some overlap in the introductory material presented in the general introduction of this thesis (Chapter 1) and all three journal article chapters (Chapters 2-4). This overlap was necessary to set the appropriate context for the thesis and for each or the individual journal articles.

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List of abbreviations and symbols used in figures and text

NMDS:	Non-metric multidimensional scaling
NC:	Null community
BA:	Beakers alone
IB:	Immersed beakers
PM:	Pools mixed
PP:	Pre-mix pools
W:	Connected beakers
WO:	Unconnected beakers
SD:	Standard deviation
ANOSIM:	Analysis of similarity
SIMPER:	Similarity percentage analysis
NSERC:	Natural Sciences and Engineering Research Council
OGS:	Ontario graduate scholarships
COLFUTURO:	Foundation for the Future of Colombia

Chapter 1 : Introduction

BACKGROUND AND RATIONALE

A brief history of the beginnings

Efforts in community ecology are focused on understanding and explaining spatiotemporal patterns in the distribution and abundance of co-existing populations (Chase 2003). There have been more than a few ecological patterns described (Keddy & Weiher 1999, Weiher & Keddy 1995) and also many mechanisms have been identified (McGill 2010, Vellend 2010). However, relating these patterns to the corresponding mechanisms has proven a difficult task (Lawton 1999): ecological communities are a network of the interrelations which involves many elements, factors and mechanisms acting simultaneously and at different scales (Simberloff 2004).

There are two main theories owing to which the exploration of mechanisms has advanced. One of these theories explains the assembly and maintenance of communities as through deterministic local processes (Chase 2005). Local processes include all those aspects in which species' niches are involved. On one side there are the environmental requirements of species or the range of variability of environmental factors that a species can tolerate. On the other side there is the adjustment of niches according to the way other species use resources. This adjustment is effectuated via biological interactions such as competition, predation, mutualism, predation, parasitism, and a suite of indirect interactions.

The alternative theory suggests that the assembly and maintenance of communities results from regional processes. At the ecological time scale, these processes are limited to the migration of species between communities and to local extinction (or extirpation). Because these processes are stochastic by nature, communities assembled in such a way should express that quality in the characteristic signatures of the outcomes they produce. The size of the regional pool of species as well as the size and distance of the host communities to the source become important when explaining patterns observed among communities.

The discussion around which group of processes are more important in the formation and maintenance of communities has spanned almost a century. It may have started with Clements (1916) and Gleason (1927) and their competing theories on plant succession. Succession, as proposed by Clements (1936) refers to the sequential addition and replacement of species in the development of natural communities. According to his theory, different communities followed one another in a directional and predictable way. There, the before-stage facilitates the establishment of the next stage, until a final unique stage, called climax, is reached (Clements 1916, Clements 1936, Connell & Slatyer 1977). This perspective was challenged by Gleason (1927). For him, succession was a result of stochastic events driven by dispersal. Tansley (1935), on the other hand, criticized the existence of a climax state, noting that the final status of communities in a region may vary according to local conditions.

Despite the evidence for Gleason's arguments (Pickett *et al.* 1987), the balance of discussion leaned towards the deterministic view. The reason for this appeared to be the response to the application of the models proposed by Lotka (1932) and Volterra (1926) on the dynamics of two-species competition. The definite proof of the deterministic outcomes predicted by those models came from Gause (1934) . He determined that two species with the same niche could not coexist indefinitely. Gause tested this idea by fitting the Lotka– Volterra equations of two-species competition to the dynamics of competitive exclusion in laboratory populations of *Paramecium*. With these findings known, Hutchison (1959) proposed a niche theory, according to which species coexist thanks to the adjustment of the environmental ranges in which they can subsist. He described the fundamental niche as the spatial or temporal range in which a species can potentially live and the realized niche the as the spatiotemporal range in which a species actually lives in conformity with other species that use to the same type of resources. According to MacArthur and Levins (1967) the result of such niche adjustment is the limiting similarity among species. In other words species in a community have a limit on the overlap of their niches. The idea that interactions limit coexistence (community saturation) led Diamond (1975) to propose assembly rules for communities.

Diamond’s assembly rules

The term Assembly Rules was coined by Jared M. Diamond in 1975 in his treatise Assembly of Species Communities. Diamond constructed a deductive scheme to explain how diffuse competition can lead the assembly of communities by means of certain assembly rules. This scheme is based on his observations of the distribution and abundances of bird guilds on the islands surrounding New Guinea, known as the Bismarck Archipelago.

According to Diamond, even though much of the variance on the distribution of species between islands can be accounted by the balance between migration and extinction rates, much remains that cannot be so accounted. Ultimately, Diamond wrote “Communities are assembled through selection of colonist, adjustment of their abundances and compression of their niches, in part so as to match the combined resource production curve of the island”.

Incidence functions are the main tool Diamond used to support his argumentations. These functions are plots of the incidence (presences of species on islands or sites) against the number of species. The incidence is calculated as the frequency of given species in each of the richness classes of islands. These classes are defined by the number of species: islands with 4-6 species, 7-10, 11-20, etc. An incidence function then, gives the “preferences” of the different species in relation to the richness of the sites.

Comparing the incidence functions of the species in the Bismarck islands, Diamond differentiated 6 distributional categories ranging from high S species to supertramps. High S species are those that mainly inhabit species rich islands and represent K-selection strategies. Supertramps, on the other extreme, are mostly present on species poor islands and represent *r*-selection strategies. Consequently, each species within a guild has a distribution fitting one of the categories generated by the incidence functions. Putting together the incidence functions for a given guild, Diamond observed a series of patterns that in his view represented assembly rules:

1- If one considers all the possible combinations that can be formed form a group of related species, only certain ones of these combinations exists in nature.

2- These permissible combinations resist invaders that would transform them into a forbidden combination.

3- A combination that is stable on a large or species-rich island may be unstable on a small or species-poor island.

4- On a small or species-poor island a combination may resist invaders that would be incorporated on a larger or species-rich island.

5- Some pairs of species never coexist, either by themselves or as a part of a larger combination.

6- Some pairs of species that form an unstable combination by themselves may form part of a stable larger combination.

7- Conversely, some combinations that are composed entirely of stable sub-combinations are themselves unstable.

The evidence supporting competition as the main mechanism behind these rules involves three facts: First, the incidence of supertramps species does not increase with increasing richness. These species are restricted to the poor species island albeit they have capacity to colonize any island, given their dispersal capabilities and lack of specialization. Second, species categorized as supertramps in one archipelago can be categorized differently (e.g., D-tramp or C-tramp) if there are less competitive members of their guilds on other group of islands, and; third, closely related species sometimes display checkerboard distributions.

Lastly, Diamond invokes diffuse competition as the main mechanisms underlying assembly rules. Diffuse competition refers to the "phenomenon of a species that is unable to fit into a community because is excluded by a specific combination of other species". This mechanism acts mainly on related species: in general terms high-S species exclude supertramp species of the same guild by exploiting resources earlier and in excess, which results in a stable community with resistance to invasion.

It is worth mention that despite the rules, Diamond (1975) recognized the existence of variations in community structure among sites with similar environmental conditions, which he believed could be a result of priority effects. This recognition implies that while the basic mechanism structuring communities is deterministic, the different colonization sequences (priority effects) can induce nondeterministic patterns.

The supporters

Most of the support to Diamond´s assembly rules comes from the wealth of information gathered trough several decades of research on small mammal communities (Brown *et al.* 2000, Brown *et al.* 2002, Fox 1987, Fox & Brown 1993, Kelt & Brown 1999).

As with Diamond (1975), diffuse competition was the mechanisms used by M´Closkey (1978) to explain the structure of desert rodent guilds. He noticed that the more diversity within a guild, the more separated the niches where. Conversely, the less the separation between species niches, the more stable or more often observable a specific configuration would be. Hence, guilds with a minimum niche separation – the maximum utilization of resource - were observed while other, probabilistically possible combinations, were transient or absent. From these observations, Fox (1987) formulated a new assembly rule:

"There is a much higher probability that each species entering a community will be drawn from a different functional group (genus or other taxonomically related group of species with similar diets) until each group is represented, before the cycle repeats".

To reach this conclusion, Fox and others (Brown *et al.* 2000, Brown *et al.* 2002, Fox 1987, Fox 1999, Fox & Fox 2000) established the expectancy of favored and unfavored states among functional groups. Functional groups are defined by taxonomic, morphological and functional traits of the members (e.g., insectivores, omnivores, herbivores). Favored states are assemblages in which the number of species present in each functional group tends to differ by no more than one. In contrast, unfavored states will exhibit a larger difference. They found that favored states were observed significantly more frequently than expected if these functional groups had been assembled randomly.

It is striking however than apart from the assembly rules proposed by Diamond (1975) and Fox (1987), explicit assembly rules are scarce (Belyea & Lancaster 1999). Assembly rules have been proposed for plant communities. Examples include guild proportionality, texture convergence (i.e., convergence in the range of values in functional characters across the species present) (Wilson 1999), or trait-environment associations (Weiher & Keddy 1999, Weiher & Keddy 1995). However, these rules either represent patterns instead of rules (in which the mechanism behind the pattern is not explained), or involve some sort of environmental control, whereas the idea underlying the assembly rules is to explain patterns as a result of internal mechanisms (i.e., biological interactions) (Belyea & Lancaster 1999). Most of the literature addressing assembly rules concentrated on finding supporting evidence (or contradictory evidence) for Diamond's and Fox's rules. However, these attempts were faulty in their statistical approach as I explain in the next section.

The opponents

A few years after of Diamond´s publication, Connor and Simberloff (1979) challenged his findings. Their criticism can be summed up in a few basic arguments. Their first objection is that the definitions of the rules are tautological. Consider for example the first and fifth rule:

> "If one considers all the possible combinations that can be formed from a group of related species, only certain ones of these combinations exist in nature".

> "Some pairs of species never coexist, either by themselves or as a part of a larger combination".

According to Connor and Simberloff (1979), these rules are identical: they both refer to the expected result of competition, adjustment of species' niches according to their compatibilities. Species with overlapping niches cannot be together, those that do not overlap, can coexist.

The second problem identified by Connor and Simberloff (1979) is that Diamond does not offer direct evidence for the active exclusion of species by means of competition but relies on circumstantial evidence only.

The last argument against Diamond´s rules is a probabilistic one. Diamond used a null model to prove that although some combinations of species were possible, they were not observed as much as expected. From this observation, he concluded that competition is a factor during the assembly of communities. However, Connor and Simberloff (1979) who used the same null models that Diamond applied, demonstrated that the same patterns can arise by chance alone. Similarly, Fox's rule was criticized on basis of the null model he used (Simberloff *et al.* 1999).

A lengthy discussion spanning several years followed (Colwell & Winkler 1984, Connor & Simberloff 1983, Diamond & Gilpin 1982, Fox & Brown 1993, Fox & Brown 1995, Gilpin & Diamond 1982, Simberloff *et al.* 1999, Stone *et al.* 1996, Wilson 1995a, Wilson 1995b). It was mainly focused on the limitations arising from the presence-absence matrix. Specifically, to create a null model Diamond (1975) and Fox (1987) only put restrictions to the species number for each site but not the frequency of individual species across sites. They did so in order to avoid incorporating patterns that may have resulted from competition – an interaction at the core of the assembly rules thinking – and thus to avoid circular reasoning. According to Wilson (1995a), not including restriction to the frequency of the species gives rise to the Jack Horner effect, which, plainly put, is the demonstration of the obvious. According to Wilson (1995a), Diamond (1975) and Fox (1987) demonstrate that some species are more frequent than others, instead of demonstrating that the proportions of the species within and between guilds are kept constant, as they intended.

Fox and collaborators insist on not including the frequencies of the species in the matrix in order to avoid the Narcissus effect. According to them a test for interspecific competition as the mechanism of exclusion must exclude species frequencies from the model. However, Wilson (1995a) and Simberloff (1999) draw attention to the fact that other factors, not only competition, could be influencing the structure of the community and would be excluded as well form the null model. This leaves us with the dilemma of choosing between the Narcissus effect and the Jack Horner effect. Ultimately, this debate diverted attention away from important issues and delayed progress on detection of assembly rules.

Other approaches

Given that earlier attempts had failed to demonstrate unambiguously the existence of assembly rules, other approaches were explored. This required that the discussion moved away from the effects of biological interactions at the guild level to the community level. Drake (1991) argued that the difficulty of understanding community level dynamics comes in part from the fact that at that moment, most of the studies were focused in small pieces of communities (e.g., guilds). According to him, communities are defined by their connectivity and the dynamics observed within a guild was dependent of connections well beyond the guild level.

One of the attempts to understand the effects of biological interactions at the community level worked under the assumption that if communities were structured by biological interactions (assembly rules), communities should eventually reach a saturation point. Consequently, plotting local against regional richness should reach a maximum asymptotically when that saturation point was reached. In contrast, if biological interactions did not limit the number of species in communities, this saturation point should not be reached and the relationship between local and regional richness should be linear (Shurin *et al.* 2000).

A review of the relationship based on multiple communities revealed that linear local –regional patterns are more common than nonlinear patterns (Lawton 1999). If this is a common pattern, it would suggest a strong control by regional processes in the structuring of communities. However, Lawton's (1999) methodology has been criticized technically and conceptually. Several studies have found that even in cases where biological interactions are indeed a factor, the relationship between local and regional processes can result in a linear relationship (Hillebrand 2005, Shurin 2000, Shurin & Allen 2001, Shurin *et al.* 2000, Srivastava 1999). Finally, even when saturation can be confirmed by means of local-regional richness plots, this would not constitute a direct indication of causality. Similar patterns could be logically assigned to other factors rather than to biological interactions only (Srivastava 1999).

A second line of inquiry into the influence of biological interactions and their role in leading to assembly rules versus regional processes is alternative states. As mentioned before, Diamond (1975) contemplated the possibility of priority effects after he observed alternative states among the bird guilds he studied. It has been established theoretically and empirically that alternative states can be formed as the results of the order in which species colonize communities under a similar environmental regimes (Drake *et al.* 1993, Law & Morton 1993). The assumption is that regional processes such as dispersal add a stochastic element to what otherwise would be a deterministic process, governed by assembly rules. This assumption applies also to alternative states hypothesis. It implies that communities without priority effects, and without significant external modifiers, should converge on a single community state. Research that followed has focused on the exploration of circumstances in which alternative states can form. So far however convergence has not been demonstrated unambiguously (Chase 2003).

Neutral models

It appears that until now most of the attempts to demonstrate deterministic forces in the structuring of communities have been unsuccessful although previous approaches have not exhausted all the alternatives. Other hypotheses exist that postulate the control in the assembly of communities as dependent mostly on regional processes. The most prominent of these are the theory of Island biogeography (MacArthur & Wilson 1963, MacArthur & Wilson 1967) and more recently the unified neutral theory of biodiversity and biogeography (Hubbell 2001).

Island Biogeography theory predicts the equilibrium number of species on islands or patches, taking into account two main parameters, immigration and extinction. Other variables include the distance of the islands to the regional pool and their size (MacArthur & Wilson 1963). However, Island Biogeography was not fully accepted among ecologists probably because it involves processes at evolutionary time. In contrast, ecological processes influencing the coexistence of species reach equilibrium much faster (see Ricklefs 2008). Besides, in an effort to simplify, it ignores the specific characteristics of the species, does not take into account the mechanisms of ecological interactions between species, and colonization and extinction are treated as if they were independent events (Pozo & Llorente 2002). While discussions on the validity of the Island Biogeography theory continued its course, developments in niche theory, limiting similarity, and assembly rules (Diamond 1975, Hutchinson 1959, MacArthur & Levins 1967) biased ecologists' views towards the community control of local composition and dynamics (Ricklefs 2008).

Later however, and in response to the deficiency of answers offered by the local perspective, island biogeography was rescued and revitalized in Hubbell's (2001) neutral theory of biodiversity. His theory assumed that the per capita probabilities of giving birth, dying, migrate and speciate are equal among individuals and species. In assuming so, communities must be seen as resulting from ecological drift (i.e., demographic stochasticity), random migration, and random speciation. As with MacArthur and Wilson's theory, the neutral model met with criticisms, especially its assumption of ecological equivalence (Hubbell 2005, Hubbell 2006). According to Hubbell (2005), due to dispersal and recruitment limitations, the role of biological interactions, mainly competition, is not as strong as in previous models. Evidence for that lies in the fact that character displacement is not a phenomenon of common occurrence (Hubbell 2006).

Hubbell's theory had some success in explaining natural patterns (Bell 2005, Hu *et al.* 2007). However, others have found evidence inconsistent with this theory (Dornelas *et al.* 2006, Fuller *et al.* 2005). Furthermore, some studies have detected that similar patterns can result from both assembly rules based theories and the neutral theory (Chase *et al.* 2005, Chave 2004).

In summary, after much research it is still a matter of controversy whether community structure is primarily driven by local or regional processes (Shurin 2000, Shurin *et al.* 2000), and therefore whether assembly rules exist or not. One of the main issues is that similar patterns can be produced by both. It was my goal to propose and try new approaches that could provide new insights in the issue.

MAIN RESEARCH QUESTIONS

One of the main goals of ecological community research is to elucidate the processes which determine the distribution and abundance of co-occurring species (Chase 2003). As I have outlined in the first part of this introduction, the task has not been easy and still several obstacles are to be overcome. Lawton (1999) in his review on the status of community ecology surrenders to the “overwhelming amount of contingency which has impeded ecologists to find general rules”. I propose a new approach to the problem that builds on and incorporates elements of earlier approaches. I sought to answer the following questions:

1- Are there patterns among communities the result of deterministic processes?
2- Are patterns in natural communities a result of assembly rules arising from biological interactions?
3- If there are such assembly rules, how are they enacted in the context of regional processes?
4- If there are not, are the patterns observed among communities a result of environment or/and regional processes?
5- Are local and regional processes mutually exclusive?

RESEARCH APPROACH

In order to answer these questions I used an experimental approach using a model system comprising natural and constructed microcosms. The rationale behind adopting experimental approach is to break away from examination of patterns observed in realized, natural communities. Such communities make attribution of mechanisms and causes difficult. Instead, I try to strip the community off of many of its tangential and thus confounding patterns and work up from the simplest (discrete unconnected communities developing under the same environmental regime), to the most complex of settings (connected communities, in heterogeneous environment). This stepwise strategy appears to be suitable for separating the roles of biological interactions from those of environment and dispersal in a tractable manner.

The first step was to form a null community, in which priority effects, and the influence of local and regional processes, were minimized. The null community was created by mixing the contents of 17 rock pool communities in a single container. Immediately after mixing the null community was used in three experiments. The first of these experiments consisted in splitting the null community among forty beakers and exposing them to the same environmental regime. With this experiment I wanted to address the question of whether biological interactions are deterministic in character. Any signs of determinism induced by biological interaction would be suggestive of assembly rules.

With the second experiment I wanted to assess the roles of environment and regional processes. Regional processes in the context of this research refer to the influence of dispersal in the structuring of communities. I again divided evenly the null community, this time among three treatments. In one treatment only the physical factors of the pools were evaluated for their capacity to structure communities. The second treatment added water interchange and desiccation. In the third treatment all the above factors were permitted along with dispersal and habitat heterogeneity.

As previously, in the last experiment the null community was divided among forty beakers exposed to the same environment. However, I installed permanent connections in order to facilitate dispersal among twenty of these beakers. The remaining twenty beakers were left without connections. The intention of this experiment was to answer the question whether local processes (biological interactions) and regional processes (dispersal) are antagonistic or complementary.

The formation of alternative states or their absence would be an indicator used to evaluate the degree of stochastic and deterministic influences, respectively. To detect whether alternative states were formed or not, the similarity among the null community samples - the most homogenous of the communities - was set as the delineating criterion. A series of classification and ordination tests were applied to detect alternative states.

STUDY SYSTEM

As a model system we are using a microscopic invertebrate community from rock pools located in Discovery Bay Jamaica. The rock pools are situated in the northwest portion of the Bay in the vicinity of the Discovery Bay Marine Laboratory (Figure 1). These pools are formed as a consequence of rain erosion of carbonate rock (fossilized corals reefs) that constitutes the shore in this area. The average size of the pools is ~ 52 (SD ±20 cm) x 30 cm (SD ± 14 cm), with a mean depth of 13 cm and an average volume of 15 liters. Some pools are separated by a few cm and others by several meters. Since the seashore is not continuous, in some cases pools are isolated from each other by the sea and some are situated on separate rocks. Their elevation above the sea ranges from 1 to 235 cm at high tide (the amplitude of the tide is no bigger than 30 cm). Some of these pools are tidal but the majority are maintained by the rain and occasional wave splash water which results in a mix of fresh, brackish and salt water pools (Romanuk & Kolasa 2001). Most of the 20 other groups of pools are brackish or freshwater and maintained by rain.

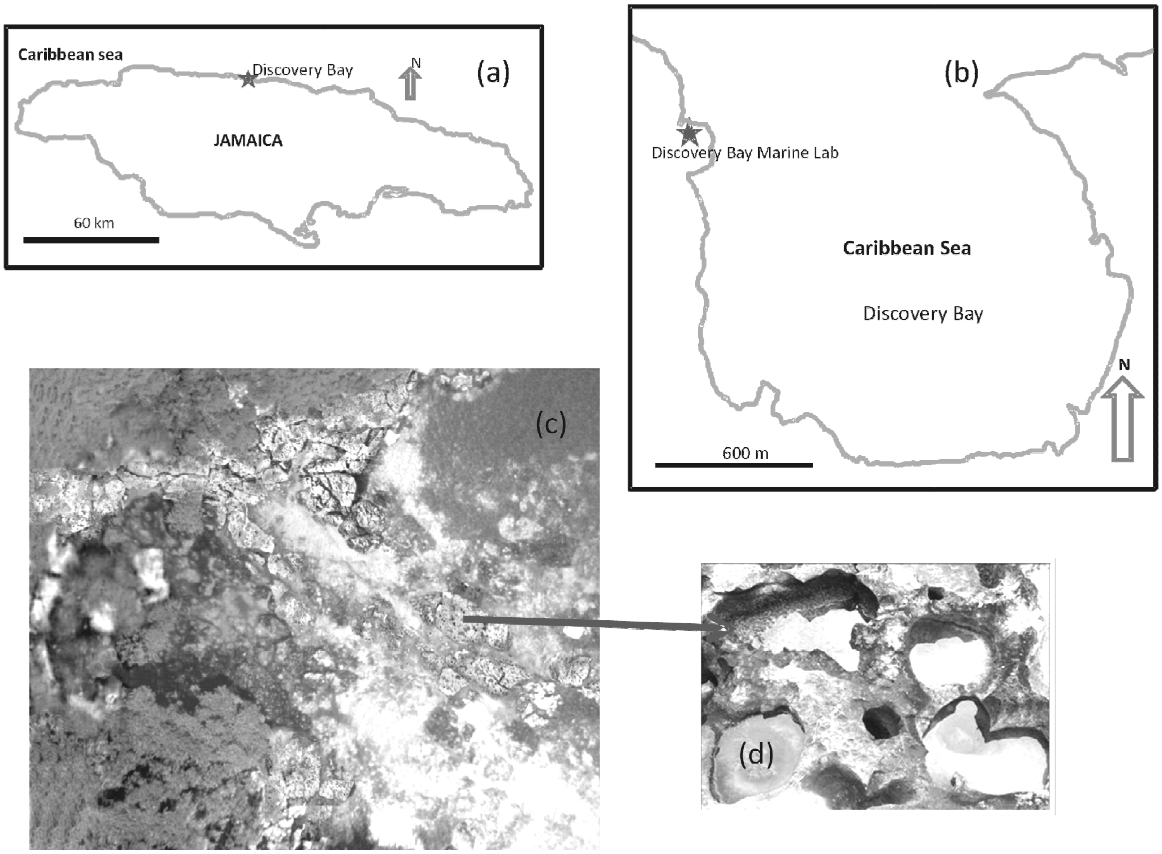

Figure 1. Study site, (a) The island of Jamaica indicating the location of Discovery Bay; (b) Discovery Bay and the location of the Discovery Bay Marine Lab where the rock pools surround; (c) aerial view of the inlet with rock terraces, ~60 m across and; (d) rock pools.

The biological community is represented mostly by small benthic and planktonic animals whose size ranges from 600 µm to 5 mm. So far, over 70 species have been identified on the basis of samples taken each year since 1990 by Jurek Kolasa and his students and collaborators. The animals found include members of different phyla and classes such as Turbellaria (7 spp.), Nematoda (1 spp.), Polychaeta (5 spp.), Oligochaeta (2 spp.), Ostracoda (21 spp.), Copepoda (8 spp.), Cladocera (4 spp.), Decapoda (crab) larvae (1 spp.), Decapoda (shrimps) (3 spp.), Amphipoda (1 spp.), Isopoda (1), and

Insecta (18 spp.). The life cycle of the animals residing in the rock pools range from one week to three months (Kolasa & Romanuk 2005a). These communities nevertheless, are not permanent experience events of desiccation especially in the summer, and more frequently in shallow pools (Therriault & Kolasa 2001).

The character of the communities is heterogeneous in which there are freshwater, brackish and marine communities, and as a whole is more suitably described as a metacommunity of a multi-hierarchy nature (Kolasa & Romanuk 2005a).

THESIS OUTLINE

The dissertation is divided into 5 sections. Chapter 1 contains the general background. In this section the historical developments relevant to the formulation of assembly rules are presented. Next, an explanation follows of how the discovery and formulation of the first assembly rules were reached. Studies supporting and opposing assembly rules are reviewed. The last part of this section consists in brief overview of alternative approaches to the study of assembly rules. Chapters 2-4 are presented as journal articles, each of which is prefaced by a brief rationale for the article.

Chapter 2 (article submitted to Oecologia) contains an article “Biological interactions in the assembly of communities: are they deterministic?” In this chapter it was established that alternative states are formed even when possible priority effects are removed. Alternative states formation in this case indicates either a strong influence of demographic stochasticity (ecological drift) or action of deterministic forces at different scales in time and space. Whatever the reason for the constitution of alternative states, the existence of assembly rules is questioned.

Chapter 3 (article to be submitted) contains an article “Local and regional processes in community assembly”. As a continuation of the previous chapter, I subjected biological interactions to additional environmental and regional variation. I determined that, in order to reproduce patterns observed in natural communities, environmental factors and regional processes must be involved during community assembly.

Chapter 4 (article to be submitted) contains an article “Does dispersal make communities to appear more stochastic?” Earlier, I found (Chapter 3) that regional factors were needed to explain patters observed in natural communities. This finding however raised a new question: are the patterns observed a result of the amplification of the influence of biological interactions or, are they solely the result of the stochasticity involved in regional processes? I concluded that probably the first possibility is the correct answer. However the contribution of regional processes is necessary as a source of species. The more species in the community, the greater the complexity and the degree of stochasticity revealed by communities.

Chapter 5 is the summary of the general conclusions my research led me to.

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Chapter 2 : Biological interactions in the assembly of communities: are they deterministic?

RATIONALE AND OBJECTIVES

As mentioned in the introductory chapter, the search for assembly rules has led to a discussion about the mechanism and processes involved in the structuring of communities that still continues. One of the main issues is that due to priority effects, communities assembled under the control of local processes can result in patterns similar to those described for communities assembled under the control of regional processes. If local processes obey rules of assembly based on niche properties, then local processes are thought to be deterministic. In contrast, dispersal dominates regional processes and thus species assembly is seen as stochastic. However, the determinism exerted by local processes has been difficult to demonstrate unambiguously. The first issue I wanted to address, given its relevance for the identification of assembly rules, has been finding evidence for or against the deterministic outcomes of assembly process. I followed the development of replicated communities under similar environmental conditions. The initial replicated community was a null community in which the effects of priority effects were minimized by means of combining several rock pool communities to form one regional species pool. The logic behind the experiment is that if environment acts as a consistent filter to species membership and if assembly rules arising from biological interactions make a significant contribution, replicated communities should converge towards a unique state. In contrast, if determinism arising from biological interactions is limited (i.e., assembly rules are weak or absent), several alternative states should form among replicated communities. Experimental results do not support deterministic controls at the community level. Alternative states increased in number as time passed. As alternative states could have resulted from different initial conditions included in the communities when the null community was divided among the beakers, I have performed an additional test. To confirm my conclusions on the role of biological interaction structuring communities, I used randomization techniques to derive simulated communities from the null community samples. The first randomization was performed by re-assigning individuals to random communities. Forty such communities showed considerable convergence. The second randomization added a procedure that simulated differential population dynamics. This modification resulted in the formation of alternative states. Results from the simulations confirm our experimental results: differences observed among beaker communities are the results of the dynamics imposed by biological interactions.

ABSTRACT

Local biological interactions are often assumed although not proven to act in deterministic ways. Yet, communities forming under the same environmental conditions rarely converge to a unique community state. Differences in the order of colonization, or priority effects, are commonly identified as the main cause for emergence of alternative states. In order to determine whether biological interactions are truly deterministic when priority effects are minimized, we combined the invertebrate communities of 17 natural rock pools to form a null community (NC). This NC was then divided evenly among 40 plastic beakers (BA) that were exposed to identical (homogenous) environment. Similar NC communities (IB) were immersed in the 17 natural rock pools from which NC was drawn and constituted controls (variable environment although no differences in colonization order). Both sets of communities were left to develop for 4 months. Results showed that BA communities diverged as time passed, with a concomitant reduction in abundance, diversity and richness. Similar results were observed in IB. The experimental results were compared to results obtained from randomized NC communities to determine if small differences in the initial community composition could explain divergence. We found that randomized communities did formed alternative states as observed in the experimental communities. In conclusion, biological interactions were unable to consistently determine community structure and allowed for the diversification of communities under the same environmental conditions. The importance of history, or the order of colonization, has to be re-evaluated if alternative states can originate without its influence.

KEY WORDS

Local processes, biological interactions, alternative states, order of colonization, determinism, stochasticity

INTRODUCTION

Local processes (e.g., competition, environment) are usually assumed as the main force structuring communities deterministically (Bond & Chase 2002, Chase 2007, Jenkins 2006). According to this view, species settling in a local community are first selected from a regional species pool by environmental conditions and the final community membership is refined by biological interactions. The latter is assumed to involve assembly rules (Belyea 2004). Assembly rules were first formulated by invoking competition as a possible factor in the distribution of birds in a group of islands (Diamond 1975). Other studies followed this line of argument and involved small mammals, ants, fish and plants among others (Brown *et al.* 2000, Brown *et al.* 2002,Fox 1987, Gotelli & Mccabe 2002, Kelt *et al.* 1995). However competition-based assembly rules have been questioned (Connor & Simberloff 1979, Diamond & Gilpin 1982, Gotelli & Mccabe 2002, Simberloff *et al.* 1999) and it is common to find opposite conclusions with the same data (Chase 2003, Fukami *et al.* 2005). Despite of these contradictory views ecologists in general have assumed that biological interactions are deterministic, that competition (and predation) is the main mechanism among biological interactions, and that the determinism applies at both, the guild level, in which most of the competition assembly rules theory is based, and at the community level (Chase 2007, Chase & Leibold 2003a, Chase & Leibold 2003b). Consequently, communities assembling from the same pools of species, under the same environmental conditions, should converge to a unique community state - a quorum effect (Jenkins 2006). However this is rarely the case.

Diamond (1975) found that different communities formed under the same environmental conditions and explained this observation as a possible consequence of the order of colonization by the species from the regional species pool. Both, theoretical and empirical studies show that when species come from the same regional pool and assembly takes place in a homogeneous environment, the order of colonization can alter community assembly such that several alternative states may appear (Drake 1990a, Drake 1990b, Drake *et al.* 1999, Shurin *et al.* 2004). Consequently, the order of colonization emerges as a major confounding factor in studies that aim to determine the presence and the effect strength of any biological assembly rule.

Our study intends to minimize the effect of order of colonization in order to isolate the role of biological interactions in the assembly of communities. Specifically, the study aims to determine if biological interactions in the assembly of communities combine into a deterministic process. To do this, we constructed a regional species pool, NC, from which we created replicated communities, placed in a spatially homogenous environment, without any subsequent dispersal allowed. We hypothesized that when the colonization order effects are removed, one of two outcomes is possible. Either the assembly process produces an array of distinctly different communities or such communities will show a considerable degree of structural convergence. We would interpret the first outcome as indicative of the dominant influence of local stochastic processes and the second outcome as indicative of the deterministic processes. Any mix between the two extreme possibilities will indicate relative contributions of the two categories of processes.

METHODS

Study site

We used a micro invertebrate community from a set of rock pools located at Discovery Bay, Jamaica. The average size of the pools is 52 (SD ±20 cm) x 30 cm (SD ± 14 cm), with a mean depth of 12 cm (SD ± 8cm) and an average volume of 17L (SD ± 18.5L). Some pools are separated by a few cm and no pool is separated from the nearest neighbor by more than one meter. Some of the pools are tidal but the majority are maintained by the rain and occasional wave splash water which results in a mix of fresh, brackish and salt water pools (Kolasa & Romanuk 2005b, Romanuk & Kolasa 2001).

The invertebrate community is represented by over 70 species of small benthic and planktonic animals that range in size from 60 µm to 5 mm. The animals belong to different phyla and classes such as Turbellaria (7 spp.), Nematoda (1 spp.), Polychaeta (5 spp.), Oligochaeta (2 spp.), Ostracoda (21 spp.), Copepoda (8 spp.), Cladocera (4 spp.), Decapoda (crab) larvae (1 spp.), Decapoda (shrimps) (3 spp.), Amphipoda (1 spp.), Isopoda (1), and Insecta (18 spp.). The generation times of these animals range from less than one week to three months (Kolasa & Romanuk 2005b). Some communities are permanent while a majority experience events of desiccation, especially in the summer (Therriault & Kolasa 2001).

Experimental approach

To test the hypothesis that communities converge as a result of biological interactions alone we controlled for colonization and habitat differences. First, we created a regional species pool (NC). We accomplished this by mixing the contents of 17 freshwater (i.e., salinity ≤ 5 ppt) pools from the set of 200 rock pools scattered on rocks in an area defined by 50 m radius. We emptied each pool, recorded its volume, and combined its water, sediments, and biological contents in one large container (unchlorinated tap water was added to reach the volume required for the experiments and the controls). The content of the container was vigorously stirred to ensure that all organisms and sediments were distributed evenly during the sampling and transfers to beakers. This NC community was immediately transferred into 40 (500ml) plastic beakers in aliquots of 400 ml. The beakers (BA communities; ‘beakers alone’) were placed outdoors on a platform about 1 m above the ground in partial shade. To allow gas exchange but no invertebrate colonization, each beaker had a lid with a hole sealed with a 63 µm mesh size net. In addition to the primary treatment, we set up a reference system (controls) in order to determine if the variation of natural environmental conditions could affect the resulting community structures in the experimental invertebrates.

Controls consisted of similarly prepared beaker communities (IB; ‘immersed beakers’) that were placed floating in the same rock pools that served as a NC source. The intention was to allow conditions in the control beakers to be similar to physical conditions in the host pool without including possible effects of its heterogeneity due to depth, shape, or sediment distribution. To ensure that the beaker’s lid remained above the water surface, we added a floating device: pipe insulation foam that was installed around the neck of the beaker. Both experiments ran for 4 months.

A set of five samples was taken after the pool water was combined in one large container. These samples represented a composition snapshot of NC at the beginning of the experiments and provided reference values to evaluate community change over time. Individual beakers were sampled once every two months. The samples consisted of 100 ml of water passed through a 63 µm mesh net and the animals retained in the net were preserved in 50% ethanol. Organisms were separated from sediments under a stereomicroscope until more than 95% of the individuals were removed from the sample (Therriault 2002). Subsequently, they were identified and counted.

Data Analysis

To test for the community structure convergence among the beakers a cluster analysis and then a non-metric multi-dimensional scaling (NMDS) were applied to the abundance data. We used this combination of classification and ordination analyses to check for mutual consistency of both representations (Clarke & Warwick 2001). Prior to the analyses, the data were standardized and transformed to the 4th root; this transformation ensures that even the rarest species contribute to the similarity evaluation (Clarke & Warwick 2001).

Both procedures identify natural groups of beaker communities by aggregating communities according to similarity of their composition and abundance. To determine which of these groups were significantly distinct, that is, whether replicated NC communities form alternative states (exhibit quorum effect), we adopted a stringent group defining criterion. The criterion was the maximum similarity that retained NC samples together as one group. Thus, any group of converging states must have contained communities at least as similar as the homogenized NC the experiment had begun with. Graphically this cut off point is represented by circles in the NMDS ordination graph (Figure 3).

We also tested for the significance of the differences between alternative community states (analysis of similarities, ANOSIM) resulting from the cluster and NMDS analyses. Finally, we examined contributions of individual species to the formation of alternative states by using Primer's species analysis (similarity percentage, SIMPER).

Simulated assembly process

A possibility exists that small differences in the initial composition of experimental communities would be sufficient to explain emergence of alternative states. To control for such effects, we have examined an array of simulated communities produced by randomization of the original NC.

Using species abundance data from samples of the initial NC we have created 40 simulated beaker communities. Each beaker received a random number of individuals of each species recorded in NC, with the probability equal to their relative abundance and frequency observed in the actual NC and adjusted to the means observed at the end of the experimental period. This simulated community was then analyzed together with the control samples, two months old communities, and four months old communities for the presence of identifiable groups or quorum effect. Additionally, the simulated community was 'permitted to grow' by raising species abundances to power of 2. This procedure mimicked random differential growth of populations and resulted in species that were initially more abundant in a particular community to increase their relative numbers as compared to the initially rare species.

RESULTS

Species responses

A total of 13 species were recorded during the experiment. They included cladocerans, *Ceriodaphnia rigaudi* Richard 1894 and *Alona davidii*; copepods, *Paracyclops fimbriatus* (Fisher), *Orthocyclops modestus* (Herrick) and *Nitocra spinipes* Boeck; and ostracods, *Candona* sp., *Cypricercus* sp., *Cypridopsis* cf. *mariae* Rome, and *Potamocypris* sp. The remaining 4 species were aquatic stages of three midges, a tanypodid, a chironomid and a ceratopogonid, and of one mosquito *Culex* sp. These species showed different densities and frequencies across samples, with *Potamocypris* dominating (summary in Figure 1).

The five samples representing NC - the combined communities of natural 17 pools - contained 12 of the 13 species listed earlier. In BA communities (beakers alone) only nine out of the total 13 species survived after four months. The losses included insect species, with the exception of the tanypodid midge. The copepod *N. spinipes* also disappeared. In the immersed beakers (IB) 10 species survived but *Culex* sp., tanypodid and ceratopogonid midges disappeared. Species abundance and frequency were positively correlated (Figure 2).

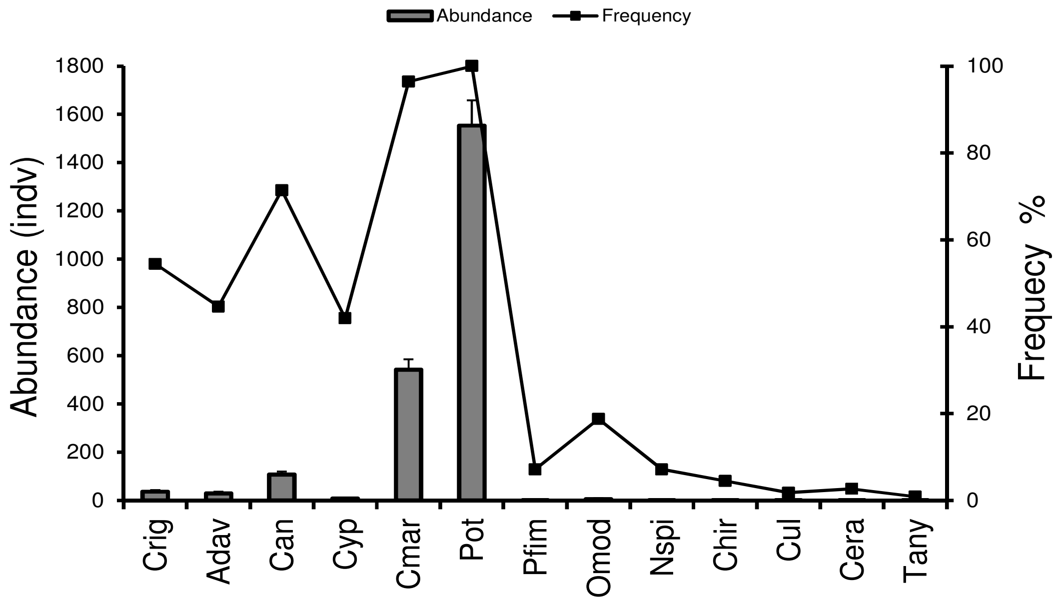

Figure 2-1. Average abundance and frequency of species identified in all the samples. CRIG: Ceriodaphnia rigaudi; ADAV: Alona davidii; CAN: Candona sp.; CYP: Cypricercus sp.; CMAR: Cypridopsis cf. mariae; POT: Potamocypris sp.; PFIM: Paracyclops fimbriatus; OMOD: Orthocyclops modestus; NSPI: Nitocra spinipes; CHI: Chiromid midge; CUL: Culex sp.; CERA: Ceratopogonid midge; TAN: Tanypodid midge. Error bars represent +1 standard error.

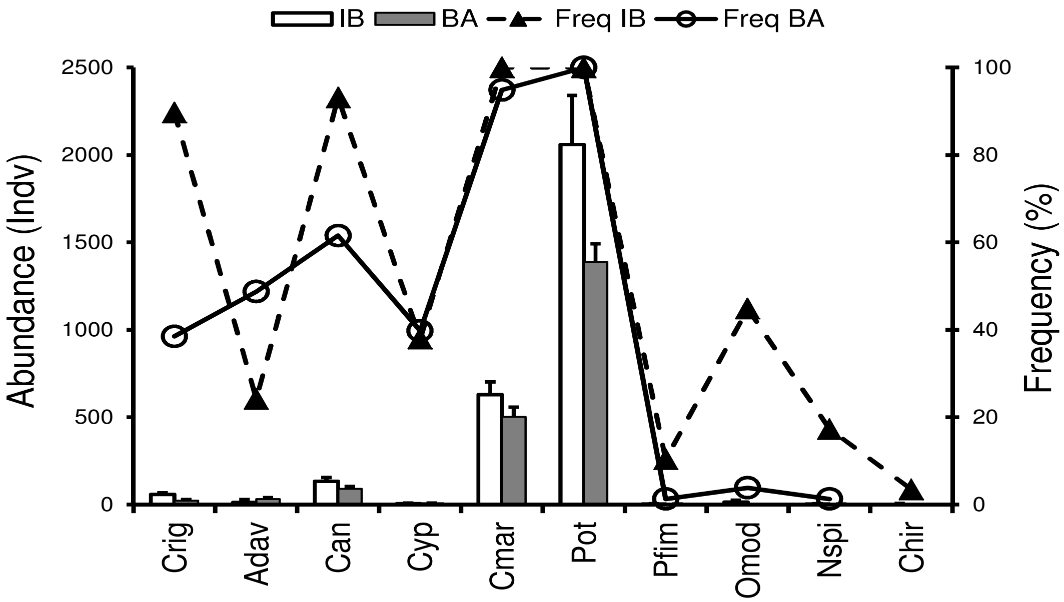

Figure 2-2. Average abundance and frequency of species identified in the beakers alone (BA) and immersed beakers (IB) samples. CRIG: Ceriodaphnia rigaudi; ADAV: Alona davidii; CAN: Candona sp.; CYP: Cypricercus sp.; CMAR: Cypridopsis cf. mariae; POT: Potamocypris sp.; PFIM: Paracyclops fimbriatus; OMOD: Orthocyclops modestus; NSPI: Nitocra spinipes; CHI: Chiromid midge; CUL: Culex sp.; CERA: Ceratopogonid midge; TAN: Tanypodid midge. Error bars represent +1 standard error.

Experiment

Experimental communities diversified over time to form ultimately four alternative states (Figure 3). The similarity value at which the initial NC communities (controls) were retained in the same classification group was 85% (NMDS, stress= 0.1). At this level of similarity one group was identified after two months in BA (BA2, average similarity (as): 90.7%, Figure 3). After fourth months this group split into four different groups representing alternative community states (BA4, as: 91.6%; BA4b, as: 92.2%; BA4c, as: 100% and; BA4d, as: 94.6%; Figure 3). Two beaker communities did not join any group and were designated as BA4out. IB communities formed three alternative states after two months (IB2a, as: 92.4%; IB2b, as: 90% and; IB2c, as: 87.7%; Figure 3), with two beakers as outsiders (IB2out). After four months, these groups changed into two (IB4a, as: 91.3% and; IB4b, as: 91.2%; Figure 3), with four beakers as outliers (IB4out). A chi-square comparison of the two treatments, with IB playing the role of reference system from which expected probabilities were drawn, showed that patterns observed in BA and IB at the end of four months were not different (chi-square= 10.6, 5df, p=0.059). The test results are not exact as some observations were less than 5 but the overall conclusion appears to be sound.

Differences in the abundances among the identified groups, within dates, between dates, and between treatments were significant (ANOSIM, global R: 0,925, p: 0.001). Pair-wise comparisons indicate that all of the differences between formed alternative community states were also significant with a few exceptions where the compared groups had less than 3 members (see Appendix 1).

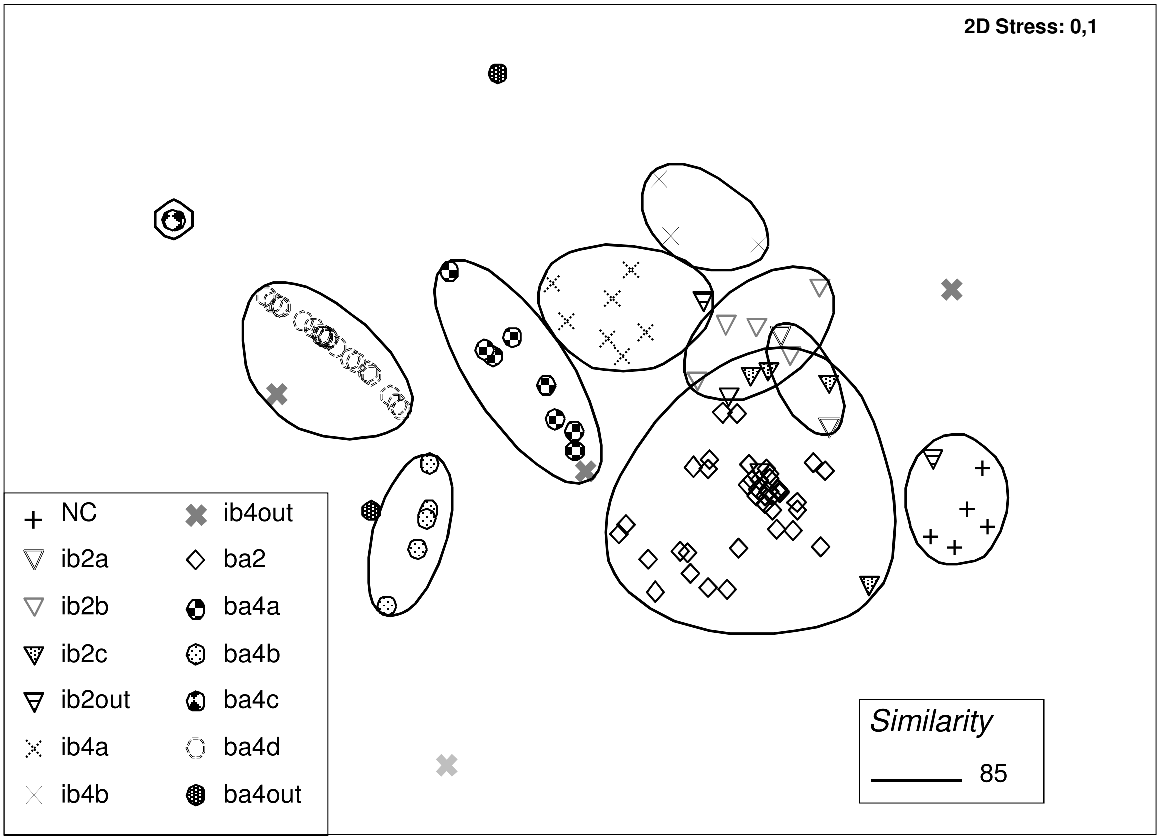

Figure 2-3. Alternative states (circles) formed at the 85% similarity level (see explanation in text) . Group codes: NC - regional species pool; BA – beakers alone; IB – immersed beakers; 2 and 4 – after two and four months, respectively; out - outlier. Stress values <0.1 indicate a suitable ordination without misleading interpretations. Horizontal axis represents NMDS dimension 1 and vertical axis represents NMDS dimension 2.

Species similarity analysis, SIMPER, showed that the species with the greatest contribution (41.3% on average) to the formation of each of the groups were *Potamocypris* sp., followed by *Cypricercus* sp. with 31.5%. These two species were also the most abundant and widely distributed in the beaker communities (Figure 2). The remaining species contributed less than 20% each to the formation of alternative states (Appendix 2).

Four species made major contribution to dissimilarity among groups. Ostracod *C.* cf. *mariae* made the greatest contribution (23.4%), followed by another ostracod, *Candona* sp. (20.1%). A cladoceran, *C. rigaudi* (18%) and copepod *O. modestus* (16.6 %) were two other important contributors to dissimilarity (Appendix 3). Two and four months old communities differed mainly because some species went extinct and abundance of most species declined compared to NC communities. Differences among states in the IB treatment after two months are driven by abundance of *O. modestus, C.* cf. *mariae,* and *A. davidii*. Differences between IB states after four months are driven by abundance of *O. modestus*. Presence/absence of *C.* cf. *mariae* and *Candona* sp. was the major factor in defining differences in BA states after four months. BA and IB states differ mainly because several species disappeared in the BA communities (Appendix 3).

In general, species richness, abundance, and diversity showed decreasing trends from NC over time (Figure 4). Differences were larger between the second and fourth month for BA communities than for the IB communities over the same period. Evenness remained at similar levels during the experiment and across treatments indicating that the community dominance structure remained approximately constant despite other community changes.

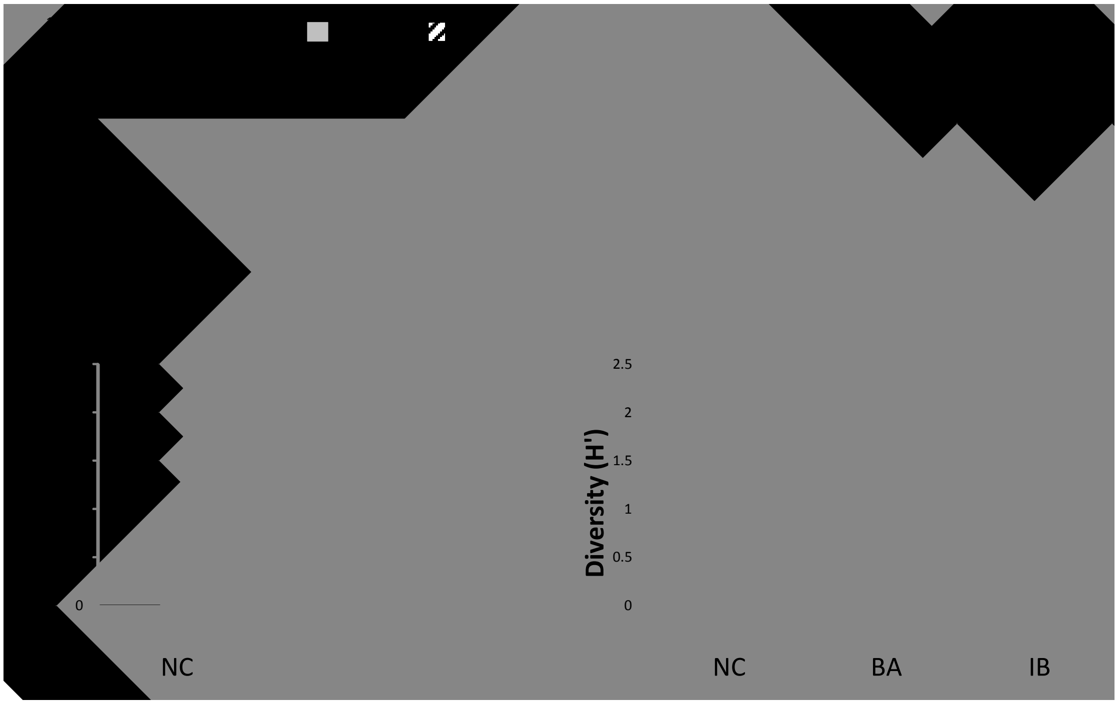

Figure 2-4. Diversity metrics (mean abundance, richness, evenness, and diversity) in experimental treatments at two points in time for beakers alone (BA), immersed beakers (IB) and controls (initial composition, NC). Evenness is Pielou´s (J´) evenness index; Diversity is Shannon-Wiener (H´) diversity index. Error bars represent ±1 standard error.

Simulated communities

NMDS ordination of simulated communities revealed only one group (state) only. This state grouped together, without any outliers, with the original NC samples, and was separated from all other groups at 84% similarity threshold (Appendix 4). When the simulated communities were permitted differential growth of component populations, they fell into 7 groups, with 3 outliers (Appendix 4), with all the groups separated from the control NC at the 87% similarity threshold.

DISCUSSION

Experimental communities in beakers, whether exposed to identical environment (BA) or different combination of physical factors (IB), formed several alternative community states but the community trajectory patterns in these two sets of communities were not significantly different from each other. However, the emerging groupings within each treatment appear unrelated to minor differences in initial conditions. We draw this conclusion from the fact that simulated beaker communities formed only one group under the same analytic regime. When we introduced community differentiation subsequent to the initial randomization, alternative community states similar to those observed in the experimental beakers, were detected. We conclude from this that the alternative states were generated in the process of community development. This may point to a deterministic face of biotic interactions. However, the fact that each of the three sets (simulated, BA, and IB) developed different number of groups strongly suggests that stochastic triggers must have been involved. Below, we relate these findings to earlier research.

Convergence towards a unique community state would indicate a dominant role of deterministic forces in community assembly (or disassembly). Although community structure and local processes have been have been linked for several factors, both biotic and abiotic (see Jocque et al. 2010), convergence has not been proven to occur (Jenkins 2006). Our results are consistent with and add weight to this observation. Absence of convergence in community structure may be due to history (order of colonization and disturbance) on the local community structure (Shurin et al. 2004). However, we removed the effects of the order of colonization, of disturbance, and of dispersal and still did not observe convergence. To the contrary, communities diversified and formed alternative states. The question arises as to the causes.

Alternative states can arise in multiple ways that include colonization preemption by competing species, environmental gradients, or perturbation and random divergence (see Schröder et al. 2005). Given the experimental regime of the BA communities (i.e., homogenous environment), only random factors remain as a possible cause of community divergence. However, a confident attribution of causal role is not simple even if random factors dominate local processes because such factors may induce non-random (deterministic?) cascade of effects. Rather, we propose that random factors initialize modification in the original (NC) community structure. In fact, our simulation appears to confirm the possibility that small random differences in community composition may amplify in experimental communities as community development progresses and lead to formation of alternative community states. Preemption by competing species can be ruled out since all of the species were inserted into all the beakers in the same proportions at the same time. The same can be said for environmental conditions since all of the beakers were exposed to the same environmental regime. Finally, there were no perturbation events known to selectively affect some beakers but not others. Thus, by default, demographic stochasticity becomes a plausible mechanism responsible for the divergence of communities we observed as implied by some theoretical models (e.g., Pascual *et al.* 2001). In such models demographic stochasticity of sufficient amplitude may induce shift of communities from one state to another in a landscape of community states (Beisner et al. 2003). This demographic stochasticity may be further amplified by biological interactions such as competition, predator-prey, mutualism, and many indirect or third order interactions, coupled with environmental changes precipitated by these interactions. Many of these mechanisms can be deterministic at lower levels of community organization (e.g., Fox 1999, Fuller *et al.* 2005) although how these mechanisms interact at the community scale remains unknown (Agrawal et al. 2007).

The question that remains is what happened in the immersed beaker, IB, communities? On the surface those beakers appeared to form a single convergent group, with a few outliers. However, this was not the case. When we compared pattern of group formation between the BA communities and IB communities (chi-square), we found that the latter ‘convergence’ was likely to emerge by chance. This reinforces the idea that stochasticity plays a substantial role in the assembly of communities.

Order of colonization has been proposed on several occasions to explain alternative states. Drake (1990b, 1991) and Law and Morton (1996, 1997) proved both experimentally and theoretically that alternative states can be observed if the order in which species are added changes from one community to another in the same environment. However, our results, particularly those pertaining to the BA communities, suggest that history is just one factor that may trigger emergence of alternative states because biological interactions appear capable of generating alternative states among communities even if these communities remain exposed to the same environmental conditions. However, it has been observed (Donohue *et al.* 2009,Therriault & Kolasa 2001) that the stronger the environmental fluctuations the fewer the number of alternative states. We may have seen the beginning of this process in IB communities where fewer groups formed (although statistically not different from BA communities). Should this be so, the importance of history might depend on the strength of the environmental forcing.

In conclusion, biological interactions were unable to consistently determine community structure and allowed for the diversification of communities under the same environmental conditions. Although deterministic interactions can operate at the guild level, they are not expressed with consistence at the community level. The importance of history, or the order of colonization, has to be re-evaluated if alternative states can originate without its influence.

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Appendix 1

Analysis of similarity (ANOSIM) results. R statistic varies from 0 (indicates agreement with the null hypothesis) to 1 (uniqueness of groups). Group codes: NC - regional species pool; BA – beakers alone; IB – immersed beakers; 2 and 4 – after two and four months, respectively; out – outlier, *non significant.

Groups compared		**R statistic**	**Significance level**
ib2c	**ib2a**	0.5	*0.107
ib2c	**ib2b**	0.472	0.009
ib2c	**ib4a**	0.847	0.002
ib2c	**ib4b**	0.784	0.012
ib2c	**ba2**	0.451	0.003
ib2c	**ba4b**	1	0.002
ib2c	**ba4d**	1	0.001
ib2c	**ba4a**	0.959	0.001
ib2c	**ba4c**	1	0.012
ib2c	**NC**	0.984	0.002
ib2a	**ib2b**	0.782	0.048
ib2a	**ib4a**	1	0.028
ib2a	**ib4b**	1	*0.1
ib2a	**ba2**	0.695	0.004
ib2a	**ba4b**	1	0.048
ib2a	**ba4d**	1	0.004
ib2a	**ba4a**	1	0.022
ib2a	**ba4c**	1	*0.1
ib2a	**NC**	1	0.048
ib2b	**ib4a**	0.895	0.001

Groups compared		R statistic	Significance level
ib2b	**ib4b**	0.815	0.018
ib2b	**ba2**	0.84	0.001
ib2b	**ba4b**	1	0.008
ib2b	**ba4d**	1	0.001
ib2b	**ba4a**	0.961	0.003
ib2b	**ba4c**	1	0.018
ib4a	**ib4b**	0.821	0.008
ib4a	**ba2**	0.945	0.001
ib4a	**ba4b**	1	0.001
ib4a	**ba4d**	1	0.001
ib4a	**ba4a**	0.82	0.001
ib4a	**ba4c**	1	0.008
ib4a	**NC**	1	0.001
ib4b	**ba2**	0.992	0.001
ib4b	**ba4b**	1	0.018
ib4b	**ba4d**	1	0.002
ib4b	**ba4a**	1	0.006
ib4b	**ba4c**	1	*0.1
ib4b	**NC**	1	0.018
ba2	**ba4b**	1	0.001
ba2	**ba4d**	1	0.001
ba2	**ba4a**	0.947	0.001
ba2	**ba4c**	1	0.001
ba2	**NC**	0.974	0.001
ba4b	**ba4d**	0.926	0.001
ba4b	**ba4a**	0.949	0.001
ba4b	**ba4c**	1	0.018
ba4b	**NC**	1	0.008
ba4d	**ba4a**	0.966	0.001

Groups compared		**R statistic**	**Significance level**
ba4d	**ba4c**	0.967	0.003
ba4d	**NC**	1	0.001
ba4a	**ba4c**	1	0.006
ba4a	**NC**	1	0.002
ba4c	**NC**	1	0.018

Appendix 2

Similarity (%) contribution of species to the formed groups (SIMPER) - Values show percent contribution of individual species to group formation. Group codes: NC - regional species pool; BA – beakers alone; IB – immersed beakers; 2 and 4 – after two and four months, respectively; out – outlier. Species abbreviations explained in figure 1 and 2.

Groups/Species	**Cmar**	**Pot**	**Can**	**Cer**	**Cyp**	**Adav**	**Omod**	**Chi**
ib2c	28.8	28.6	18.4	13.2	9.8	>1	>1	>1
ib2a	22.6	28.7	13.8	13.2	>1	8.1	6.8	>1
ib2b	28.4	31.4	20.9	13.7	>1	>1	>1	>1
ib4a	23.4	45.8	14.8	13.9	>1	>1	>1	>1
ib4b	17.2	38.5	15.1	15.8	>1	>1	13.5	>1
ba2	27.5	31.4	17.2	7.1	>1	10.8		>1
ba4b	48.5	51.5		>1	>1	>1	>1	>1
ba4d	73.5	26.5		>1	>1	>1	>1	>1
ba4a	28.1	51.3	20.5	>1	>1	>1	>1	>1
ba4c		100.0		>1	>1	>1	>1	>1
NC	17.5	20.3	13.1	11.5	8.24	10.2	7.2	4.01
Average	**31.5**	**41.3**	**16.7**	**12.6**	**9.0**	**9.7**	**9.2**	**4.0**

Appendix 3

Dissimilarity (%) contribution of species group to group formation (pairwise comparisons; SIMPER). Group codes: NC - regional species pool; BA – beakers alone; IB – immersed beakers; 2 and 4 – after two and four months, respectively; out – outlier; e=equal, i=increased, d=decrease, a=appeared, di=disappeared (from Group 1 to Group 2). Species abbreviations explained in figure 1 and 2.

G1	**G2**	**Nspi**		**Adav**		**Cyp**		**Omod**		**Can**		**Pot**		**Cmar**		**Crig**		**Pfim**		**Tany**		**Chi**		**Cera**		**Cul**	
b2c	**b2a**	0.3		7.8		5.3		4.4		0.4				.26		1		1		1		1		1		1	
b2c	**b2b**	1		1.5		1		8.2		0		0		.7		.5		1		1		1		1		1	
b2a	**b2b**	1.3	**i**	2.3		2	**i**	.6		4.1				.7		.5		1		1		1		1		1	
b2c	**b4a**	1		.1	**i**	2.8		.34	**i**	7.6		3.7		9		.6		1		1		1		1		1	
b2a	**b4a**	7	**i**	1.3	**i**	.6		7	**i**	.7		1		1.6		.4		1		1		1		1		1	
b2b	**b4a**	1		1		6		1.5	**i**	3.2		1.9		8.9		.4		.7		1		1		1		1	
b2c	**b4b**	1			**i**	6		4.2		2.8		2.1		3.7		1		1		1		1		1		1	
b2a	**b4b**	8.1	**i**	2.8	**i**	1.4		4.7		1		.7		0.2		1		1		1		1		1		1	

G1	**G2**	**Nspi**		**Adav**		**Cyp**		**Omod**		**Can**		**Pot**		**Cmar**		**Crig**		**Pfim**		**Tany**		**Chi**		**Cera**		**Cul**	
b2b	**b4b**	1		1				4.9		9.6		1.9		7.7		.2		1		1		1		1		1	
b4a	**b4b**	1		1		2.3		7		.7		1		4.4		1.7		1		1		1		1		1	
b2c	**a2**	1		3.5		1.1		0.5		0.1		0.1		1		7.2		1		1		1		1		1	
b2a	**a2**	1.5	**i**	1.8		5.3		0.1		.1		1		1		5.1		1		1		1		1		1	
b4a	**a2**	1		0		7.1		1		2.8				5.4		1.1		1		1		1		1		1	
b4b	**a2**	1		3		1.4		4		.7		1		7.8		.2		1		1		1		1		1	
b2c	**a4b**	1		.5	**i**	7.5	**i**		**i**	3.5	**i**	.5		1		3.9	**i**	1		1		1		1		1	
b2a	**a4b**	1.3	**i**	4.2	**i**	.3	**i**	1.3	**i**	2.7	**i**	1		.9		2.4	**i**	1		1		1		1		1	
b2b	**a4b**	1		1		1		4.4	**i**	9	**i**	1		.6		6.9	**i**	1		.5		1		1		1	
b4a	**a4a**	1		1		1		1		9.8	**i**	.9		0.6		7.6	**i**	1		.9		1		1		1	
a2	**a4b**	1		2.9	**i**	4.2	**i**	1		1.9	**i**	1		1		7.9	**i**	1		.2		1		1		1	
b2c	**a4d**	1		1		4.7	**i**	1		8.1	**i**	.3		9		0	**i**	1		1		1		1		1	
b2a	**a4d**	0.4	**i**	3.1	**i**	.8	**i**	0.4	**i**	0.8	**i**	1		4.6		0.5	**i**	1		1		1		1		1	
b2b	**a4d**	1		1		1		2	**i**	2.7	**i**	.2		9.4		2.5	**i**	1		1		1		1		1	

G1	**G2**	**Nspi**		**Adav**		**Cyp**		**Omod**		**Can**		**Pot**		**Cmar**		**Crig**		**Pfim**		**Tany**		**Chi**		**Cera**		**Cul**	
b4a	**a4d**	1		1		1		1		6.4	**i**	1		8.8		3.8	**i**	.5	**i**	1		1		1		1	
b4b	**a4d**	1		1		1		7.3	**i**	6.4	**i**	1		.2		8.9	**i**	1		1		1		1		1	
a2	**a4d**	1		9.4	**i**	2	**i**	1		7	**i**	1		8.4		5.2	**i**	1		1		1		1		1	
a4b	**a4d**	1		1		1		1		1		1.7		5.4		1		1		2.9	**i**	1		1		1	
b2c	**a4a**	1		.8	**i**	0.8	**i**	1		0.2		0.5		5.5		9.3	**i**	1		1		1		1		1	
b2a	**a4a**	4	**i**	7.6	**i**	.9	**i**	4	**i**	1		1		0.3		7.7	**i**	1		1		1		1		1	
b2b	**a4a**	1		1		1		8.6	**i**	3.4		.1		6		4.9	**i**	1		1		1		1		1	
b4a	**a4a**	1		1		1		1		5.4		.5		9.5		8.5	**i**	.5		1		1		1		1	
b4b	**a4a**	1		1		.7	**i**	3.5	**i**	1		1		3.4		5.4	**i**	1		1		1		1		1	
a2	**a4a**	1		8.3	**i**	7.8	**i**	1		.7		1		4.3		2.6	**i**	1		1		1		1		1	
a4b	**a4a**	1		1		1		1		1.5		1		7.9		1		1		1		1		1		1	
a4d	**a4a**	1		1		1		1		2.4		1		0.7		1		1		1		1		1		1	
b2c	**a4c**	1		1		1.9	**i**	1		2.8	**i**	.1		3.6	**i**	6.3	**i**	1		1		1		1		1	
b2a	**a4c**	.6	**i**	0.8	**i**	1		.6	**i**	7.1	**i**	1		9.1	**i**	9.9	**i**	1		1		1		1		1	

G1	G2	Nspi		Adav		Cyp		Omod		Can		Pot		Cmar		Crig		Pfim		Tany		Chi		Cera		Cul	
b2b	**a4c**	1				1		1		6.1	**i**	1		5	**i**	8	**i**	1		1		1		1		1	
b2a	**a4c**	.6	**i**	0.8	**i**	1		.6	**i**	7.1	**i**	1		9.1	**i**	6.9	**i**	1		1		1		1		1	
b2b	**a4c**	1		1		1		.6	**i**	6.1	**i**	.2		5	**i**	8	**i**	1		1		1		1		1	
b4a	**a4c**	1		1		1		1		5.4	**i**	1		2.8	**i**	3.5	**i**	1		1		1		1		1	
b4b	**a4c**	1		1		1		1.7	**i**	1	**i**	1		7.3	**i**	3	**i**	1		1		1		1		1	
a2	**a4c**	1		5.6	**i**	.6	**i**	1		1.8	**i**	1		3.7	**i**	2.2	**i**	1		1		1		1		1	
a4b	**a4c**	1		1		1		1		1		3.8		8.8	**i**	1		1		1		1		1		1	
a4d	**a4c**	1		1		1		1		1		1		7.1	**i**	1		1		1		1		1		1	
a4a	**a4c**	1		1		1		1		9.4	**i**	1		5.4	**i**	1		1		1		1		1		1	
b2c	**NC**			8.1		1		2.7		.5		.6		1		.5		1.4		1		2.9		1		.3	
b2a	**NC**			.8		4.5		.5		.9		1		1		1		3.1		1		4.8		.4		.1	
b2b	**NC**	.7		9.7		8.4		.8		1		1		1				.7		1		2.5		.9		.1	
b4a	**NC**	.5		6.6		2.6		2.3		.2		1		.6		.4		.7		1		.4				1	
b4b	**NC**	.4		8.8		1.7		1				.5		0.4		1		.4		1		0.7		.8		.4	

G1	**G2**	**Nspi**		**Adav**		**Cyp**		**Omod**		**Can**		**Pot**		**Cmar**		**Crig**		**Pfim**		**Tany**		**Chi**		**Cera**		**Cul**	
a2	**NC**	.6		.7		.8		7.1		1		1		1		1.7		2		1		3.8		.7		.6	
a4b	**NC**	1		3.3		1		.9		7.7		1		1		5		.6		1		.5		.8		1	
a4d	**NC**	.9		2.3		0.3		.2		6		1		.6		3.9		.2		1				.4		1	
a4a	**NC**	.9		5		2.5		1.1		.8		1		.2		6.9		.5		1		.5		.4		1	
a4c	**NC**	.3		1		.1		.1		4.2		.2		8.5		2.4		.5		1		.2		1		1	
	mean	1.3		6.1		4.1		6.6		0.1		.26		3.4		8.2		.29		.63		0.3		.7		.3	

Appendix 4

NDMS ordinations of simulated communities in the context of experimental communities in controls.

Figure 1, Appendix 4. Simulated communities (grey triangles) based on NC relative abundance structure share group membership with NC controls and are separate from all other groups. Horizontal axis represents NMDS dimension 1 and vertical axis represents NMDS dimension 2.

Figure 2, Appendix 4. Simulated communities (grey triangles) based on random differential change in abundance structure form 7 groups separate from all other groups. Horizontal axis represents NMDS dimension 1 and vertical axis represents NMDS dimension 2.

Chapter 3 : Local and regional processes in community assembly

RATIONALE AND OBJECTIVES

In chapter 2 the absence of effective assembly rules at the community level was established. Patterns however are present in nature. As ample ecological research suggests, environment and regional processes are important for the structuring of communities. However, we wanted to learn what specific influence environment and regional processes have in the assembly of communities. In the experiment implemented here, replicated null communities were exposed to progressively realistic set of factors. These ranged from biological interactions only to varied local environment, along with dispersal and habitat heterogeneity. Comparisons of the resulting communities revealed that only when all these factors were included, patterns among replicated communities matched the level of diversity of those found in the original rock pool communities. The trend observed along the gradient of factors was consistent: similarity among communities within the same treatments declined and the number of alternative states increased. At the most realistic end of the gradient almost all alternative states consisted of individual beaker communities, a condition similar to that observed among original pools prior to the mixing. These results corroborate the joint importance of environment and regional processes in the assembly of communities.

ABSTRACT

Controversy on whether local (deterministic) or regional (stochastic) factors control the structure of communities still persists after decades of research. The main reason for why it has not been resolved may lie in the nature of evidence which largely comes from realized natural communities. In such communities assembly history has left a mark and may support either set of factors. To avoid the confounding effects of assembly history we took an experimental approach which controlled for those effects. We created a null community by mixing 17 rock pool communities. This community was then evenly distributed among treatments representing a gradient of factors from local to regional and its partial disassembly followed. We hypothesized that if communities are structured deterministically, they should converge at the local level (replicate end states should be most similar and the number of alternative states should increase as more realistic factors are allowed to influence the disassembly process). By contrast, if stochastic processes dominate, replicate end states should become less similar and many alternative states should emerge. Our results indicate that stochasticity plays a major role at both local and regional levels. We found no convincing evidence for deterministic community mechanisms tied to species composition. Admittedly, the emergence of groups of replicate communities that are more similar within than the original homogenized null community indicates that some deterministic processes may be involved as well although its contribution appears to be weak.

KEY WORDS

Community assembly, local processes, regional processes, determinism, stochasticity, history,

INTRODUCTION

The assembly of communities from the available species pool has generated two persisting controversies. One concerns the question of whether community assembly is deterministic or stochastic (Belyea & Lancaster 1999, Fukami *et al.* 2005, Lawton 1999, Simberloff 2004). The other concerns the size of contribution of local processes (e.g., competition, environment) versus regional processes (e.g., immigration-emigration) (Jenkins 2006, Jenkins & Buikema 1998, Ricklefs 2008, Shurin 2000, Shurin *et al.* 2000). These questions are closely related since local processes are generally seen as deterministic (regulated by species already present) while regional processes are seen as stochastic (identity of potential colonizers is independent of local conditions) (Hubbell 2006, Jenkins 2006, Jenkins & Buikema 1998).

Local regulation of assembly invokes niche-based or trait-based processes as a key mechanism (Brown *et al.* 2002,Chase 2005, Fargione *et al.* 2003, Fox & Brown 1995, Fox & Fox 2000). According to this perspective, a new community forms from species selected according to their environmental requirements. The selected species are further filtered by assembly rules thought to arise from biological interactions (Belyea

2004, Diamond 1975, Fox 1987). Since environmental and biological filtering operates regardless of the properties of the regional species pool and since the expected outcome is defined by specific conditions and specific species combinations, such processes are seen as deterministic. This proposition is amenable to experimental tests because it allows specific predictions. For example, communities assembling in a homogenous environment and equally accessible to colonizers should follow a common path if the mechanisms are deterministic. Consequently, such communities should proceed to a similar end point state.

In contrast, if regional processes are more important than local processes in the assembly of communities, community structure should be predominantly shaped by stochastic processes such as immigration, order of colonization, extinction and speciation - all of which in turn depend on the size and nature of the regional pool (Hu *et al.* 2007, Hubbell 2006). As a result a set of communities developing in a similar environment should show low similarity among replicate communities and several alternative states.

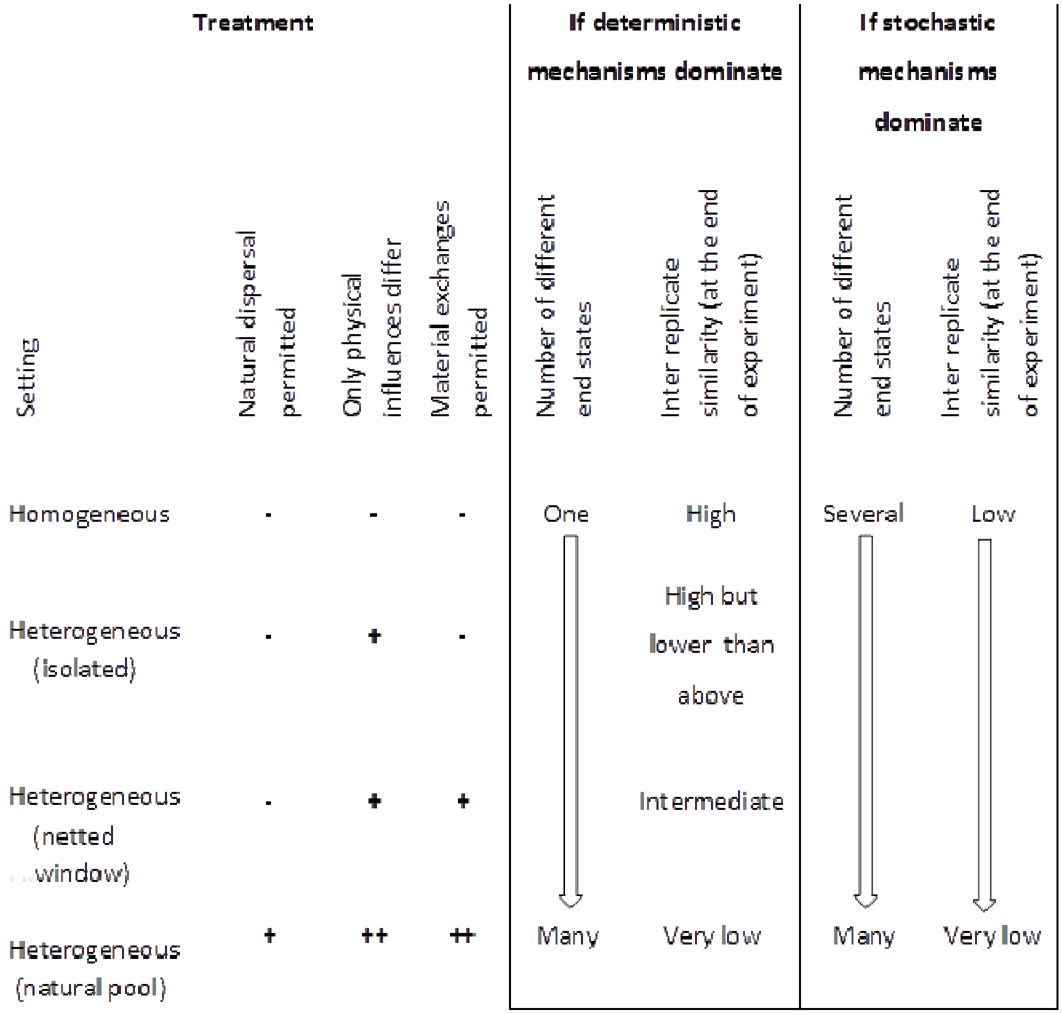
The controversy has arisen from the fact that studies backing up local or regional processes usually rely on realized communities (Mouquet *et al.* 2003). Such communities are the result of multiple factors acting during assembly, but which does not necessarily reflect current conditions (Fukami *et al.* 2005). Furthermore, differences in community trajectory are subsequently adjusted in response to present environmental conditions

(Belyea 2004). Consequently, patterns of assembly in realized communities may be complex and attributing specific mechanisms responsible for their formation difficult.

We propose to test the influence of local and regional processes by an experimental strategy that involves stepwise elimination of confounding influences on assembly. Specifically, we compare (a) naturally assembled communities, (b) communities with no assembly history (all species added at once) and open to subsequent dispersal, (c) communities without history, with limited material exchanges, and without subsequent dispersal, (d) communities without history, dispersal, and material exchanges to (e) communities set in similar environment (homogeneous setting), without history, dispersal, and without material exchanges. To implement this strategy we created a null community (a community of aquatic invertebrates formed from a mix of 17 communities in rock pools) and followed its development through time under different treatments described above. We hypothesized that if local processes are deterministic, a single community state should emerge in the homogeneous setting (all replicate communities should be highly similar), and progressively divergent states should emerge under treatments that allow other influences. If local processes are stochastic, many different community states should emerge in homogeneous settings. Furthermore, in more realistic experimental treatments, such states should reflect the influence and strength of the environmental filters (similarity among community replicates, or inter-replicate similarity, should be lower than in homogeneous setting).

Intermediate levels of realism should result in a set of intermediate patterns (Table 1).

Table 3-1. General outline of treatments and predictions depending on whether community assembly is dominated by deterministic or stochastic mechanisms. "-" symbols mean no; "+" symbols mean yes; "++" symbol refers to fully natural setting where no physical influences or material exchanges are inhibited in any way. Detail description of treatments is given in the Methods section.



	Treatment			If deterministic mechanisms dominate		If stochastic mechanisms dominate	
Setting	Natural dispersal permitted	Only physical influences differ	Material exchanges permitted	Number of different end states	Inter replicate similarity (at the end of experiment)	Number of different end states	Inter replicate similarity (at the end of experiment)
Homogeneous	-	-	-	One	High	Several	Low
Heterogeneous (isolated)	-	+	-	↓	High but lower than above	↓	↓
Heterogeneous (netted window)	-	+	+	↓	Intermediate	↓	↓
Heterogeneous (natural pool)	+	++	++	Many	Very low	Many	Very low

While it is clear that the unobstructed development of communities in the natural setting does not permit discriminating between deterministic and stochastic mechanisms, the decay of their signal should follow different paths and thus assist in drawing inferences.

METHODS

Study site

For the experiments in this study we used invertebrate community from a set of rock pools located at Discovery Bay, Jamaica. The average size of the pools is 52 (SD ±20 cm) x 30 cm (SD ± 14 cm), with a mean depth of 12 cm (SD ± 8cm) and an average volume of 17L (SD ± 18.5L). Some pools are separated by a few cm and others by several meters. Some of the pools are tidal but the majority are maintained by the rain and occasional wave splash water, which produces a mix of fresh, brackish and salt water pools (Romanuk & Kolasa 2001).

The biological community is represented mostly by over 70 small benthic and planktonic animals the majority of which range from 600 µm to 5 mm. The animals found include members of different phyla and classes such as Turbellaria (7 spp.), Nematoda (1 spp.), Polychaeta (5 spp.), Oligochaeta (2 spp.), Ostracoda (21 spp.), Copepoda (8 spp.), Cladocera (4 spp.), Decapoda (crab) larvae (1 spp.), Decapoda (shrimps) (3 spp.), Amphipoda (1 spp.), Isopoda (1), and Insecta (18 spp.). The life cycle of the animals residing in the rock pools may take from less than one week up to three months (Kolasa & Romanuk 2005b). Most rock pool communities experience frequent desiccation, especially in the summer and in shallow pools (Therriault & Kolasa 2001).

Experiments

To implement the strategy outlined in Table 1, in the first step we created a null community - a community of all species available in arbitrarily defined region and with abundance structure approximating regional abundance structure. We created this null community by mixing contents of 17 freshwater (salinity < 5) pools that were selected from the set of pools described above. Before combining the contents of the pools, biotic samples were taken from each pool. At the time the pools were emptied, the volume of water obtained from each pool was measured using graduated buckets. To kill off any remaining freshwater organisms pools were cleaned thoroughly with seawater, and patted dry with a sponge. Subsequently, the null community was placed into the empty pools in volumes matching the original volumes removed. In addition to the null community, two beakers were added into the pool (Figure 1a) filled with 400 ml of the null community mix. One of these beakers had a rectangular hole through its side covered by a fine mesh (125 μm) (Figure 1b); the other beaker was not altered. Both of these beakers had a lid opening covered by a net (63 μm mesh size) to exclude airborne invertebrate propagules (Figure 1a). Forty additional 40 beakers were filled up with the null community mix and placed in a homogeneous environment (outdoors, on a bench).

The above procedures produced treatments described in Table 1 as well as additional reference data sets: (a) naturally assembled pools (pre-mix pools PP); (b) communities in natural pools with no assembly history (all species added at once) and open to subsequent dispersal (pools mixed, PM); (c) communities without history, with limited material exchanges, and without subsequent dispersal (immersed beakers open, IB-open); (d) communities without history, dispersal, and material exchanges to (immersed beakers closed, IB-closed) and; (e) communities set in similar environment (homogeneous setting), without history, dispersal, and without material exchanges (beakers on the outdoor bench, BA). These beakers were screened off to prevent dispersal and experienced no material exchanges. All beakers permitted rain water to seep in through the lid netting.

Samples were taken from the null community mix at the beginning of the experiment, and from each treatment after 4 and 8 months. Contents of the beakers and natural pools were homogenized by stirring the water while sampling for invertebrates.

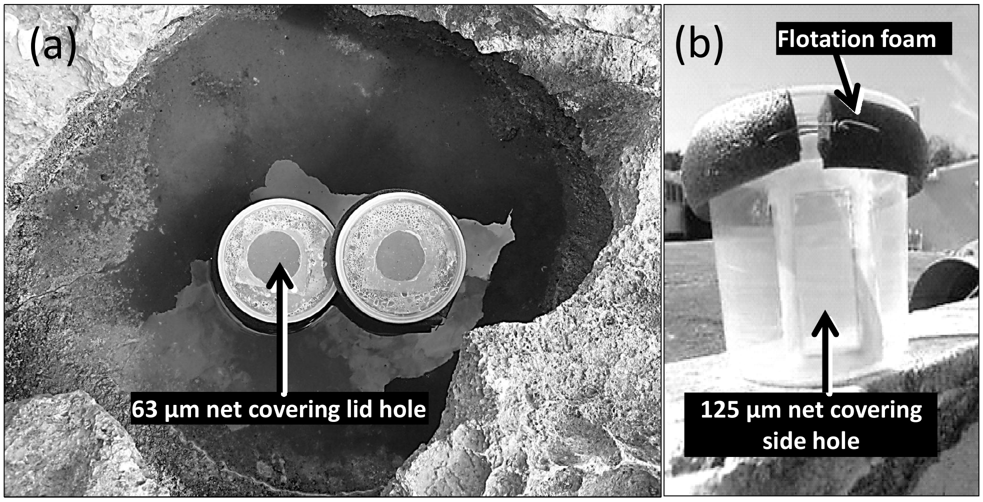


Figure 3-1. (a) Treatments: IB-closed (left beaker), IB-open (right beaker) and PM (pool); (b) detail of a beaker used for the treatment IB-open with a net covered hole for water interchange and foam for floatability.

The 100 ml samples of water were passed through a 63 µm net and the animals retained in the net were transferred into a 50 ml vial with 50% ethanol. In laboratory, organisms were separated using a stereomicroscope following an established visual method in which more than 95% of the individuals are removed from the sample (Therriault 2002), identified and counted.

Data Analysis

The similarity among replicate communities was quantified using Bray-Curtis index after abundance data were fourth root transformed. This transformation downweights high abundance species and allows rare species to contribute more to the overall similarity. The similarity values were used in two ways, one for comparing communities within (inter-replicate) and one for comparing treatments (Kruskall-Wallis test). The similarity values we used for the latter were averages of similarity that each replicate community (beaker or pool) had with all the others in the same treatment.

The second goal was to determine the number of alternative states under each treatment regime. Two stages analysis was followed, first samples were organized according to their similarity with a hierarchical cluster analysis. Group average was used as the cluster mode. The cluster analysis identifies groups of communities by classifying individual communities according to similarity of their composition and abundance. To determine which of these groups were significantly distinct, that is, whether replicated null communities in different treatments formed alternative states, we adopted a stringent group defining criterion. The criterion was the maximum similarity that retained null community samples together as one group. Setting the criterion to a low value results in one group containing all replicates. Setting the criterion to a very high value leads to group breakup. Setting the criterion to the maximum similarity that retains null community samples (initial mix) as a group leads to aggregation of replicates that are more similar than the samples from the original homogenate. Thus, any group of converging states must have contained communities at least as similar as the homogenized null community the experiment had begun with. Following the cluster analysis, and the second stage of the analyses, a non-metric multidimensional scaling (NMDS) ordination was applied. Combining the cluster and ordination tests, confirms the consistency of the grouping in the cluster and, secondly permits an easier graphic interpretation of the results. Graphically this cut off point is represented by circles in the NMDS ordination graph (cf., Figure 3).

RESULTS

Similarity of community states

We found that the levels of inter-replicate similarity formed a gradient entirely consistent with the expectations formulated in Table 1. Specifically, the null community (NC) samples had the highest similarity (88%), communities in natural pools, PP, had the lowest inter-replicate similarity (53%) to each other, and the remaining treatments (PM, IB-open, IB-closed, and BA) showed increasing levels of inter-replicate similarity, respectively (Figure 2).

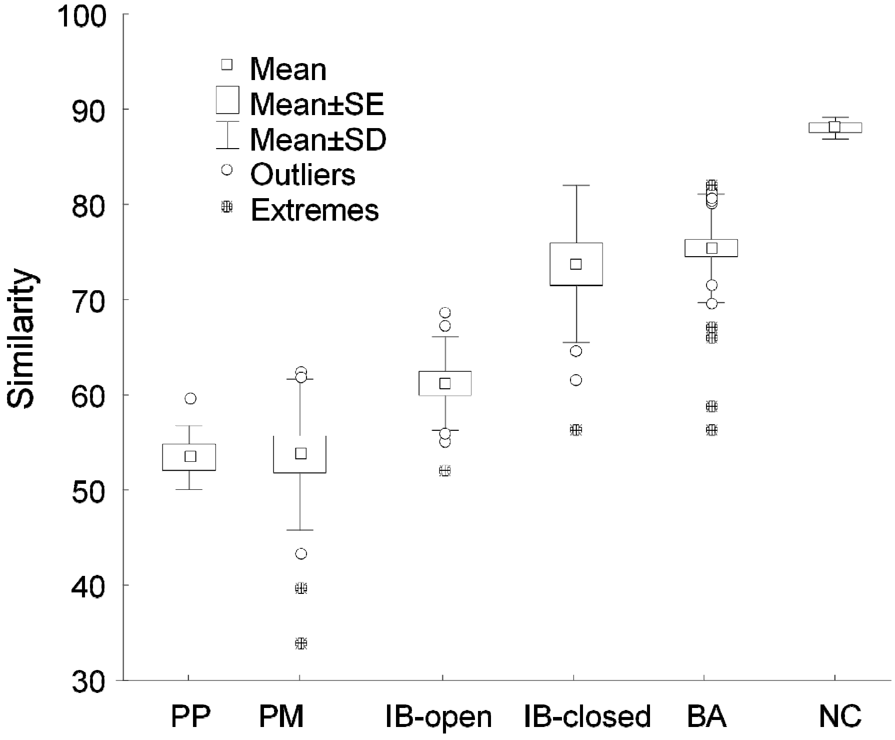


Figure 3-2. Comparison of mean similarity among treatments. Mean similarity values are based on all communities within a single treatment. PP – pre-mix pool communities, PM - communities in natural pools (after they developed from the null community); IB–open immersed beaker communities with material interchange permitted but no dispersal; IB–closed immersed beaker communities without dispersal and material interchange, and BA – beaker communities in homogeneous setting.

Most of the treatments differed significantly from each other and those that did not (Table 2) are consistent with the general pattern nevertheless. Specifically, closed beaker communities in homogeneous setting (BA) were most similar to closed beaker communities immersed in natural pools (IB-closed) and to the null community (NC). Furthermore, pool communities prior to mixing (PP) had the same level of similarity as communities developed from null community in the same set of natural pools (PM) and

IB-open treatment. This convergence indicates the dominant role of the interactions between local and regional processes in natural settings.

Table 3-2. Kruskal-Wallis test comparing similarity between treatments. Numbers are p-values and asterisks indicate significant differences.

	PP	PM	IB-open	IB-closed	BA	NC
PP						
PM	1.000000					
IB-open	1.000000	1.000000				
IB-closed	0.003496*	0.000114*	0.068451			
BA	0.000232*	0.000000*	0.002205*	1.000000		
NC	0.000014*	0.000001*	0.000245*	0.367489	0.359684	

Alternative community states

The trends revealed by the analysis of similarities among replicates of each treatment only tell us that as communities are affected by a progressively more realistic set of factors, their developmental trajectories diverge further away. However, that particular analysis does not answer directly the question of whether the local interactions are dominated by deterministic or stochastic mechanisms. The NMDS analysis of community groupings based on their similarity does offer a tentative answer. We have found that the most isolated replicate communities in homogeneous setting (BA) formed 6 different alternative states, with three beaker communities that were not grouped. The next most isolated group (IB-closed) formed two such groups comprising a total of 10 communities, with the remaining four replicates remaining ungrouped. All other treatments failed to form identifiable groups of replicate communities at the 86% level of similarity shown by the benchmark defined by the NC samples (Figure. 3).

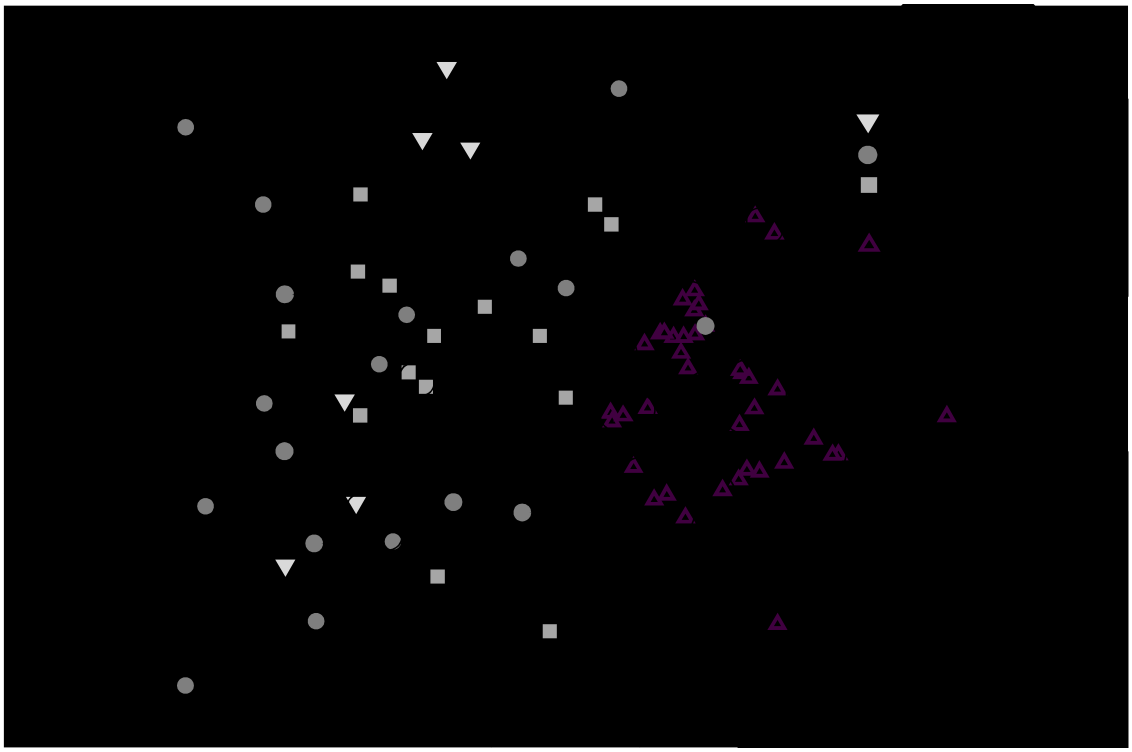


Figure 3-3. Alternative states (circles) formed at the 86% similarity level (see explanation in text) for each of the treatments. Stress values <0.2 indicate an acceptable (significant) ordination. Horizontal axis represents NMDS dimension 1 and vertical axis represents NMDS dimension 2.

Other community trends

On average, replicate community abundances increased over time as compared to null community (NC) with the exception of most isolated communities (BA) (Figure 4). By contrast, richness, diversity, and evenness declined across treatments (Figure 4).

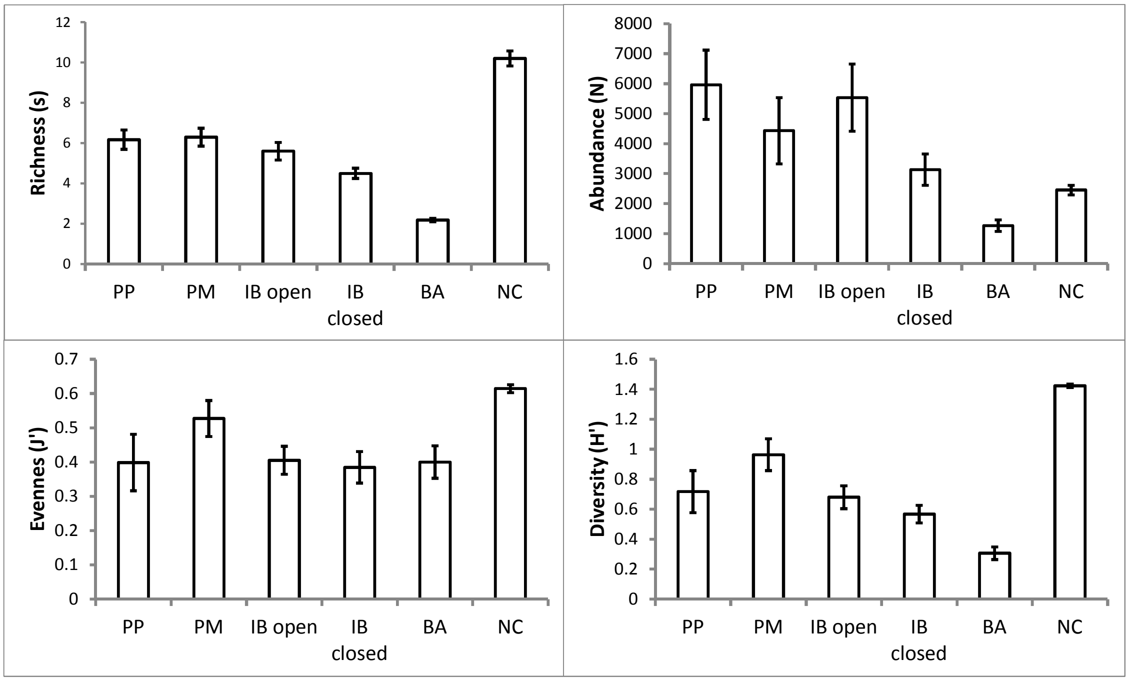


Figure 3-4. State of communities in different treatments at the end of experiment (4 months): mean richness, abundance, evenness, and diversity (bars) and standard error (whiskers) shown.

The composition and abundance of species changed differently in various treatments. Individual species either increased or decreased their relative abundance and frequency compared to NC (Figure 5). A total of 16 species of invertebrates were identified in the null community samples. Most of the individuals were crustaceans: one decapod (larvae) *Sesarma miersi* (Rathbun); two cladocerans, *Ceriodaphnia rigaudi* Richard 1894 and *Alona davidii*; three copepods, *Paracyclops fimbriatus* (Fisher), *Orthocyclops modestus* (Herrick) and *Nitocra spinipes* Boeck; and four ostracods, *Candona* sp., *Cypricercus* sp., *Cypridopsis* cf. *mariae* Rome, and *Potamocypris* sp. The rest of the species where insect larvae represented by three midges: a chiromid, a tanypodid and a ceratopogonid; two mosquitoes, *Culex* sp. and *Anopheles sp.*, and a coleopteran (larvae).

The most abundant of these species were the ostracods *Potamocypris* sp. and *Cypridopsis* cf. *mariae* followed by the cladocerans *C. rigaudi* and *A. davidii*, and ostracod *Candona* sp. Insect larvae and larvae of the crab *S. miersi* were the less abundant. In general, more abundant species showed higher frequencies but both frequency and abundance were more variable in less abundant species (Figure 5).

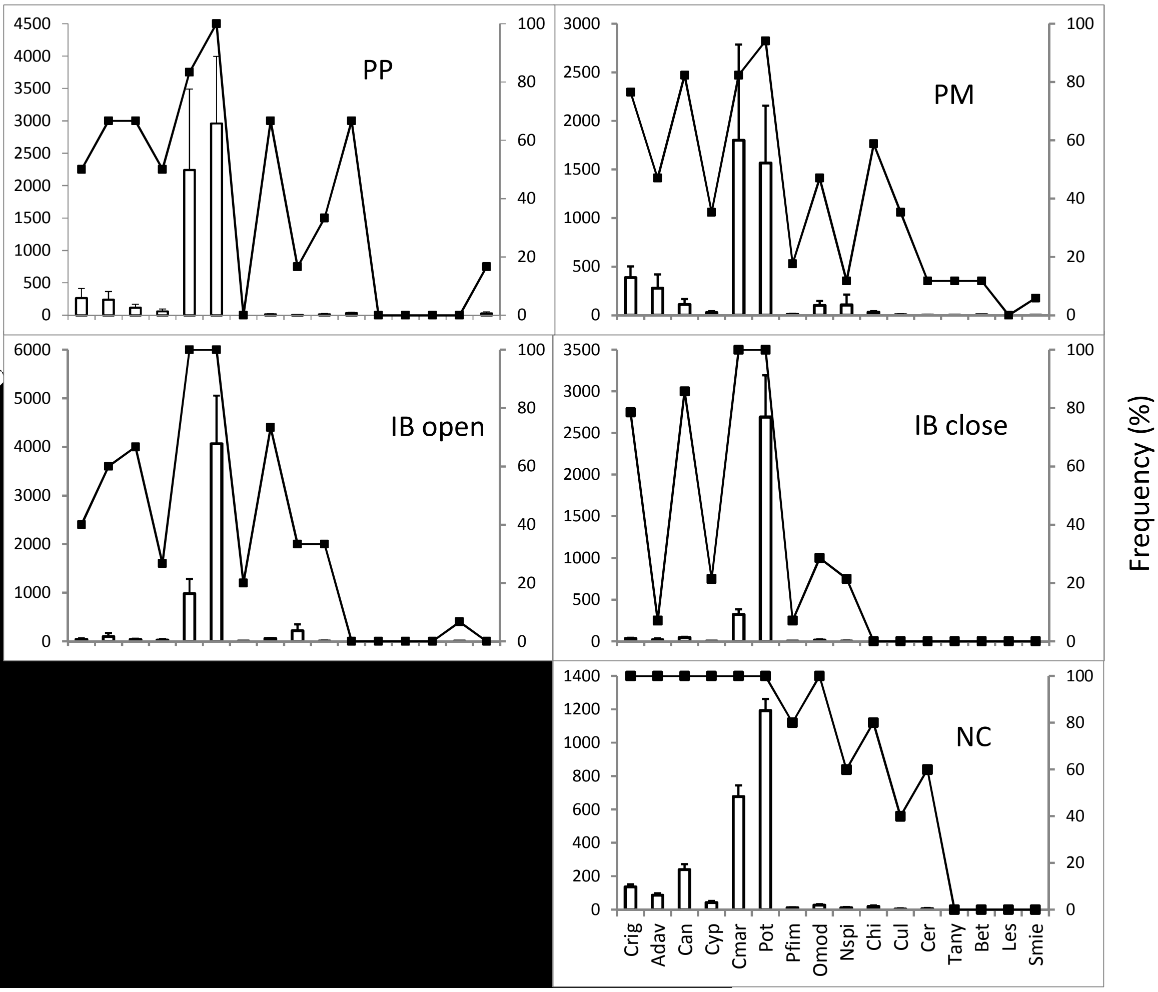


Figure 3-5. Mean abundance and frequency of species in each treatment. PP – pre-mix pool communities, PM - communities in natural pools (from null community); IB–open immersed beaker communities with material interchange permitted; IB –closed immersed beaker communities without migration and material interchange, and BA – beaker communities in homogeneous setting.

DISCUSSION

Communities that formed on a gradient of processes from local to regional scale showed a corresponding gradient in similarity of replicate communities and in the number alternative states. However, contrary to expectations, this pattern did not provide clear delineation between deterministic (local only) to stochastic (regional) factors. Surprisingly, stochastic influences on community development appeared to play a major role in treatments where only local processes were involved. This adheres to the second hypothesis tested.

Results from these experiments have implications on the influence of priority effects an assembly rules in the assembly of communities. First stochasticity among communities in a homogeneous environment without priority effects indicates that the relevance given to this phenomenon is not as important as stated before (Drake 1991, Law & Morton 1996). It is expected then than regardless of the order of species colonization alternative states are formed. This could explain the contradictory findings in which sometimes priority effects were detected an in other instances they were not (Jiang *et al.* 2011, Tilman 2004).

Another important implication is that assembly rules although might exist, do not apply at the level of communities. Most of the evidence that sustains assembly rules comes from guilds (Fox & Fox 2000); however these results have been interpolated at the community level (Simberloff 2004, Simberloff *et al.* 1999, Srivastava 1999, Wilson 1999). Overall, evidence from the BA treatment weakens the argument for deterministic control of local processes that can be attributed to niche differences.

Apart from biological interactions, environment proved to be a source of stochasticity as well. The structure of communities is often linked to environmental local factors (Fukami *et al.* 2005, Houlahan *et al.* 2007, Mutshinda *et al.* 2009), especially among ephemeral ecosystems like the one in this study (Jocque *et al.* 2010). As such, the number of expected alternative states among IB-closed beakers is the same or more than those among BA beakers, this when the scale was adjusted (IB-closed, 17 beakers: BA, 40 beakers). The effects of environment however was more obvious when water interchange was permitted (IB-open treatment). Among IB-open treatment several more alternative states and lower average similarity was observed than in the IB-closed and BA treatments. Water quality parameters have proved to be strong enough as to structure communities in several instances (Cottenie *et al.* 2003,Cottenie 2005,Houlahan *et al.* 2007, Mutshinda *et al.* 2009). An additional factor that may have contributed to differentiation is disturbance. Instances of pool desiccation are not uncommon in the studied system (Therriault & Kolasa 2001). This source of heterogeneity, combined with demographic stochasticity and environmental differences already present, provides a reasonable explanation for a higher number of alternative states and low inter-replicate similarity among IB treatments.

Although biological interactions and environment counted for much of the stochasticity involved in the assembly of the experimental communities, it was not until regional processes (PM treatment) were included that the stochasticity, observed in the natural pools (Pools premixed, PP) was reached. As stated in the introduction, one of the main roles attributed to regional processes is the one of creating priority effects, yet this was overruled given the fact that alternative states appeared without its involvement. However since without the involvement of regional processes diversity decreased, the contribution of species by dispersal to communities should be considered. High richness facilitates the creation of more complex networks among species and also between species and environment. Richness also expands the range of possible responses to disturbance events.

Evidence on the increasing stochasticity with environment and regional processes, reaching patterns observed in natural communities, suggests that environment and regional process are needed to explain patterns and dynamics in realized communities.

In conclusion, we found no compelling evidence for deterministic mechanisms to significantly affect community structure. The emergence of many identifiable groups of assembly end states under homogeneous environmental settings, where only one group should emerge, hints at strong stochastic aspect of the assembly process. Admittedly, the emergence of groups that are more similar within than the original homogenized mix of null community may indicate some deterministic influence although it appears that this determinism is secondary: once a development trajectory is defined by stochastic mechanisms, deterministic processes may lead to a predictable outcome. This logic is further corroborated by the totality of results obtained from the remaining treatments: gradual addition of various external influences leads to a complete breakdown of group formation process. Ultimately, each end point community state is uniquely defined by those influences.

ACKNOWLEDGEMENTS

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Chapter 4 : Does dispersal make communities to appear more stochastic?

RATIONALE AND OBJECTIVES

In Chapter 3 the importance of environment and regional processes in the assembly of communities was established. However, questions remain in how local and regional factors work in conjunction with each other: do the stochastic features of community composition observed in natural communities result from biological interactions? Or, is this due to regional processes only? Another possibility is that both work together and the influence of one is magnified by the effects of the other. In this chapter I want to address these questions. My experimental approach consisted of two groups of communities, one in which the communities were unconnected and another in which the communities were permanently connected. The rationale was that if biological interactions but not the regional processes influence in the creation of alternative states the permanently connected and unconnected beakers should form similar community patterns. Results of this experiment showed that alternative states formed in both, connected and unconnected communities. The formation of alternative states among connected communities provides evidence for a strong influence of the dynamic arising from biological interaction.

ABSTRACT

The contribution of local (e.g., competition) and regional (e.g., dispersal) processes in the structure of communities remains an unresolved issue. It has been usually assumed that local processes are deterministic and regional stochastic. However, recent findings have suggested that stochastic patterns can arise from local processes and be further amplified by dispersal (a regional process). It has been suggested however that dispersal can also homogenize communities. In order to resolve this contradiction we conducted an experiment where the distribution and abundances of species in a group of unconnected communities was compared to a group of connected communities. Each group consisted on replicate communities with identical initial structure. Both groups of communities showed similar patterns that were observed among other non-connected communities. This suggests that biological interactions, demographic stochasticity, or both, exert noticeable control on aspects community structure that reduce similarity among replicate communities and generate alternative states. We speculate that the formation of alternative states enhance potential for species addition. Under this interpretation factors such as dispersal rate and size of the regional pool should also be important in the assembly of communities.

KEY WORDS

Local processes, regional processes, dispersal, determinism, stochasticity

INTRODUCTION

By convention, factors shaping community structure are discussed in terms of local and regional processes (Chase 2005; Hubbell 2006). Local processes tend to be associated with deterministic outcomes arising from largely predictable species interactions and from environmental constraints (Chase 2003). Regional processes tend to be viewed as adding stochastic component to the observed outcomes (from now on ‘community patterns’). The main reasons include priority effects and dispersal limitation (some species never reach a local community or reach it too late) (Hubbell 2005; Hu et al. 2007)

The ability to separate deterministic from stochastic influences is crucial to almost any question community ecologists want to answer (McGill 2010; Vellend 2010). However, our recent work shows that this ability may be limited because local processes alone may produce outcomes with a substantial stochastic signature (Márquez and Kolasa, chapter 1).

Specifically, we found that similarity among replicate communities exposed to the same environment decreased over time. This trend was accompanied by an increase in the number of alternative states. Replicate communities exposed to regional processes tended to diverge even further (Márquez and Kolasa, chapter 2). It thus appears that uneven dispersal in a natural landscape, in combination with physical pool differences, leads to community divergence.

However, theoretical arguments suggest that dispersal should homogenize local communities within a metacommunity (Mouquet et al. 2003; Mouquet and Loreau 2002).To resolve this apparent contradiction, we set up an experiment where dispersal itself is homogenized and applied to initially homogeneous set of communities placed in a homogeneous external environment.

In this experiment, dispersal should homogenize the metacommunity (make local communities more similar) although the magnitude of the effect may depend on dispersal intensity (Cadotte et al. 2005; Cottenie 2005; Mouquet and Loreau 2002).

Empirical separation of the net effect of dispersal on community patterns should provide an informative context for further efforts aimed at understanding trajectories and end states produced locally.

METHODS

Study site

Invertebrates used for the experiment came from a set of natural rock pools located in Discovery Bay, Jamaica. The average size of the pools is 52 (SD ±20 cm) x 30 cm (SD ± 14 cm), with a mean depth of 12 cm (SD ± 8cm) and an average volume of 17L (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 in these rock pools includes over 70 small benthic and planktonic animals, the majority of which range from 600 µm to 5 mm. They belong to different phyla and classes such as Turbellaria (7 spp.), Nematoda (1 spp.), Polychaeta (5 spp.), Oligochaeta (2 spp.), Ostracoda (21 spp.), Copepoda (8 spp.), Cladocera (4 spp.), Decapoda (crab) larvae (1 spp.), Decapoda (shrimps) (3 spp.), Amphipoda (1 spp.), Isopoda (1), and Insecta (18 spp.). The life cycle of the animals residing in the rock pools range from one week to three months (Romanuk and Kolasa 2005). These communities nevertheless, are not permanent and may experience desiccation, particularly in the summer, and more frequently in shallow pools (Therriault and Kolasa 2001).

Experiments

First, a null community was created 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 made 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 equally filled (Figure 1a). The null community mixture was stirred while being distributed into each beaker to ensure that invertebrates added into each were similar in composition and abundance. 20 of the beakers were left unconnected (Figure 1b) and 20 were connected (Figure 1c). The connections consisted of vinyl tubes of ¼ of an inch (6.35mm) inner diameter. The tubes were cut diagonally at the tips to ensure that both bottom dwelling as well as mid water invertebrate species would have access to it. 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 (Figure 1d). The tubes were filled with distilled water and then placed into the beakers. Each container lid had two small openings, one to accommodate the tubes and a second covered by a 63 µm mesh to prevent dispersal but allow for gas exchange. Prior to the experiment, a preliminary test was conducted. A beaker with animals was connected to one containing only water. After a few days, both beakers contained animals from the bottom and mid water indicating the ability for invertebrates to disperse between beakers using the vinyl tubes.

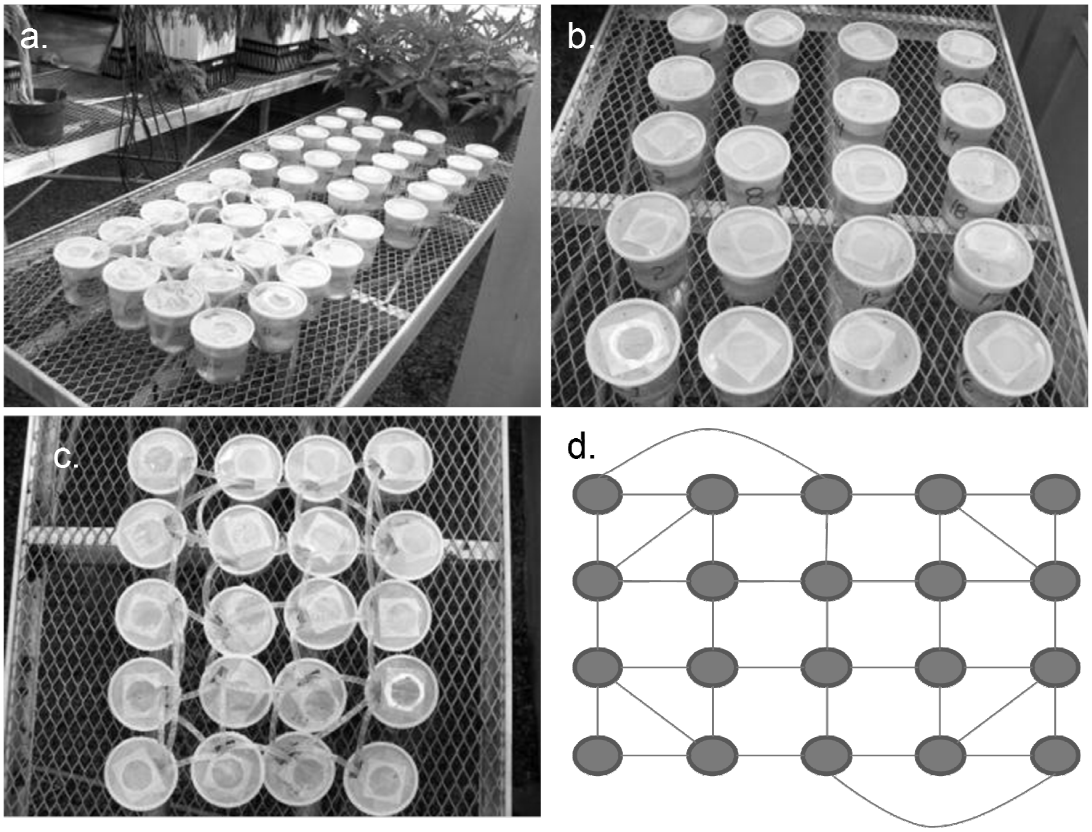

Figure 4-1(a) 40 beakers with the null community; (b) the group of 20 unconnected beakers; (c) the group of 20 connected beakers and; (d) a schematic representation of the connections (lines) between beakers (gray circles).

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.

100 ml samples were taken from each of the beaker communities after stirring beaker contents to homogenize distribution of organisms. 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 ethanol (50-60% in volume). With the use of a stereomicroscope, organisms were separated following an established visual method in which more than 95% of the individuals are removed from the sample (Therriault 2000). After removing and sorting the animals, these 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 of each community to every other community (20*(20-1) values for each treatment). We chose Bray-Curtis similarity because this index value is immune to species missing in any pair of compared communities. Prior to this, abundance data were standardized and fourth root transformed (this transformation permits that even the rarest species contribute to the overall similarity). Analysis followed two stages. First, samples were organized according to their similarity using a hierarchical cluster analysis. Group average was used as the cluster mode.

To determine whether replicated null communities in each of the treatments and dates formed alternative states, we adopted a stringent group defining criterion. The criterion was the maximum similarity that retained null community samples together as one group. Thus, any group of converging samples must have contained communities at least as similar as the homogenized null community the experiment began with. As the second stage of analysis, we applied a non-metric multidimensional scaling (NMDS) ordination. Combining the cluster analysis and ordination tests confirms the consistency of the grouping in the cluster and facilitates visual interpretation of the results. Graphically this cut off point is represented by circles In the NMDS ordination graph, circles encompass communities that lie above the cut off value that separated communities whose intra-group similarity is higher than that of the null community.

RESULTS

Patterns observed among connected and unconnected communities indicate local control by means of biological interactions. Similarity among replicates decreased with time, irrespective of dispersal taking place or not (beakers being connected or not). The higher value of mean similarity was for unconnected beakers in the second month (WO2, 91.3%), followed by the null community (89.5%) and connected beakers in the second month (W2, 89%). After five months, beakers in both treatments (W5, WO5) showed lower values (88.2% and 85.8%, respectively; Figure 1). Concomitantly, the number of outliers and extreme values increased with time among treatments (Figure 1) indicating divergence.

Figure 4-2. Mean similarity among treatments (based on all communities within a single treatment). NC – null community, W – beakers with connections; WO – beakers without connections. Numbers accompanying treatment codes are for samples taken in the second (2) and fifth month (5) of the experiment.

The patterns described above correspond to the ordination where 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 beakers. As for the unconnected beakers, one state was observed in the second month while three were identified in the fifth month (Figure 2).

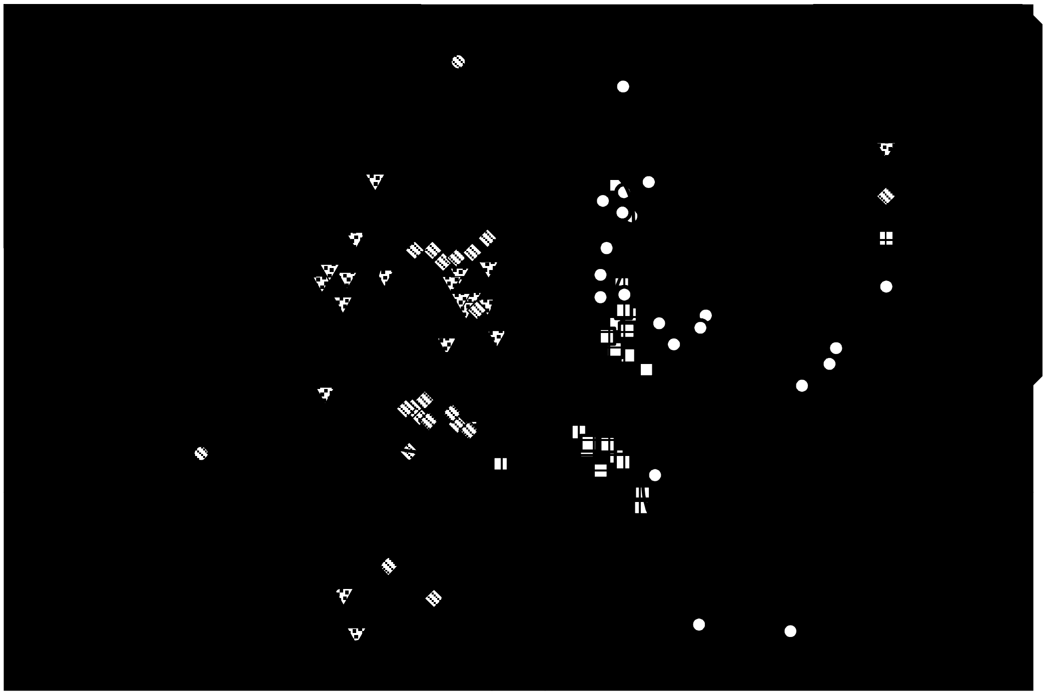

Figure 4-3. Alternative states (circles) formed at the 82% similarity level (see explanation in text) for each of the treatments. Stress values <0.2 indicate an acceptable (significant) ordination. Horizontal axis represents NMDS dimension 1 and vertical axis represents NMDS dimension 2.

DISCUSSION

The results obtained here confirm implicitly 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 and a tendency to form alternative states with 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 (lowering inter-replicate similarity) (Cottenie and De Meester 2004; Cottenie and De Meester 2003; Houlahan et al. 2007; Mutshinda et al. 2009; Shurin et al. 2004). However those authors identified environmental and spatial factors as the main cause of divergence among communities within a metacommunity.

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 conform to previous findings (Brown et al. 2002; Chase 2005; Fox 1987). The new finding however is that the resulting communities did not converge towards a single community state. Presence of alternative states within metacommunities developing within uniform external environment would normally be attributed to the influence of regional processes and the ensuing priority effects (Drake 1990; Morton et al. 2007; Schröder et al. 2005). In this study we showed that alternative states are generated in highly connected communities by means of biological interactions only, where priority effects could not take place.

Some evidence of the control of community assembly by biologic interactions has been established empirically. Shurin (2000) found that in 90% of the cases, species failed to colonize ponds in which the regional species pool was introduced artificially and, presumably, generated a high level of 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. This implies that the existing community impeded colonization by outside species. Resistance to invasion has been proposed as an emergent property in communities in which the accommodation of species according to their niches is the driver of community structure (Belyea and Lancaster 1999; Brown et al. 2002; Gilpin and Diamond 1982). However, contrary evidence, i.e., colonization of established communities is often reported (e.g., Ricciardi 2001; Shurin et al. 2000). Such evidence often comes in a form of a linear relationship between regional and local richness and indicates unsaturated communities.

The conflicting observation that sometimes communities prevent colonization and sometimes favour it could be explained in light of our findings. The formation of alternative states as a result of biological interactions may imply some compositional flexibility, which in turn may imply a degree of openness of at least some of those states to the colonization by outside species. If regional processes increase the number of alternative states, they might also increase the number of assemblages that can be invaded. In such a case the relationship between regional and local richness should lead to a degree of linearity even when community structure is under control of biological interactions (Havel and Shurin 2004; Shurin et al. 2000).

Finally, if priority effects are less relevant than sometimes assumed and alternative states can be formed through biological interactions alone, what is the role of regional processes in the assembly of communities? This is a pertinent question because it is known that the stochastic signature observed in natural assemblages is higher when regional processes are included (Márquez and Kolasa, chapter 2). 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. Lowering similarity among replicate communities and the formation of alternative states in both, connected and unconnected communities are evidence for that. We speculate that the presence of alternative states facilitate species addition potential, which is under the control of regional processes. Under this interpretation factors such as dispersal rate and size of the regional pool should also be important in the assembly of communities. This idea is not new (Hubbell 2006; Ricklefs 2008), however in this case the influence of regional processes depends on local ones.

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Chapter 5 : Conclusions

MAIN CONCLUSIONS

In this thesis I offer new evidence that natural communities controlled by biological interactions do not exhibit deterministic structure. Specifically, communities assembled without priority effects formed alternative community states, which they should not if deterministic processed defined outcomes of assembly. I suggest two probable causes for this result: a) demographic stochasticity (i.e., ecological drift) and b) stochasticity arising from the complexity of deterministic mechanisms. This leads me to conclude that assembly rules are probably absent or undetectable at the community level. This also implies that priority effects are not as important as believed, especially in highly complex systems.

The absence of assembly rules means that patterns observed in nature are dominated by local environment and/or regional processes (i.e., dispersal). This inference was confirmed when the assembly of replicated communities was followed over time. Only when environmental heterogeneity and dispersal were involved, patterns observed in the experimental replicates approached those in the natural system.

Finally, I found that even though environment and dispersal are necessary to explain patterns in natural communities, the tendency among communities to diverge and form alternative states was driven mainly by the influence of biological interactions. Support for this inference is provided by the observation that community patterns among permanently connected communities were not different from those of unconnected communities. Apparently contingent features of natural communities are the result of biological interactions. The latter may be dependent on the environmental and regional context, which can amplify or reduce the differences among communities.

In summary, at the fundamental level, stochastic features of experimental communities are driven mainly by biological interactions, including demographic stochasticity. However, the overall level of stochasticity can be modulated by the properties of the environment and regional processes. In the end, local and regional processes are important in the assembly of and depend on each other in structuring of communities.

DIRECTION OF FUTURE RESEARCH

Regardless of the experimental treatment, divergence of communities turned out to be the general tendency. Consequences of this tendency to follow separate trajectories of development should be further investigated. My results inspire several questions: Does divergence among communities facilitate adaptability to environmental changes? Are alternative states as divergent in functionality as in species composition? Is productivity similar among alternative states?

Finding the relationship between the number of alternative states and the environmental characteristics of a landscape should help us understand the extent of stochasticity generated by biological interactions. Questions come to mind: Which are the characteristic properties of environments associated with both, more than expected and fewer than expected alternative states? Or, along the same line, would the number of alternative states be lower in extreme environments than in hospitable environments?

The role of the frequency and duration of disturbance in the formation of alternative states is another interesting area for further research. When beakers were exposed to desiccation, they showed a tendency to converge. Although I have insufficient evidence to confirm this pattern, frequent and/or long disturbance events have been suggested as a factor driving convergence among communities (Chase 2007,Vanschoenwinkel *et al.* 2010).

My results and general ecological knowledge lead me to speculate that the number of alternative states is a combination of two major ecological gradients. One consists of the external influences that lead to differentiation of species performances (from heterogeneity to probabilities of arrival) that I will call homogeneity-to-heterogeneity gradient. The other relevant gradient describes the environmental forcing along the benign-to-harsh environmental axis (Figure 5-1).

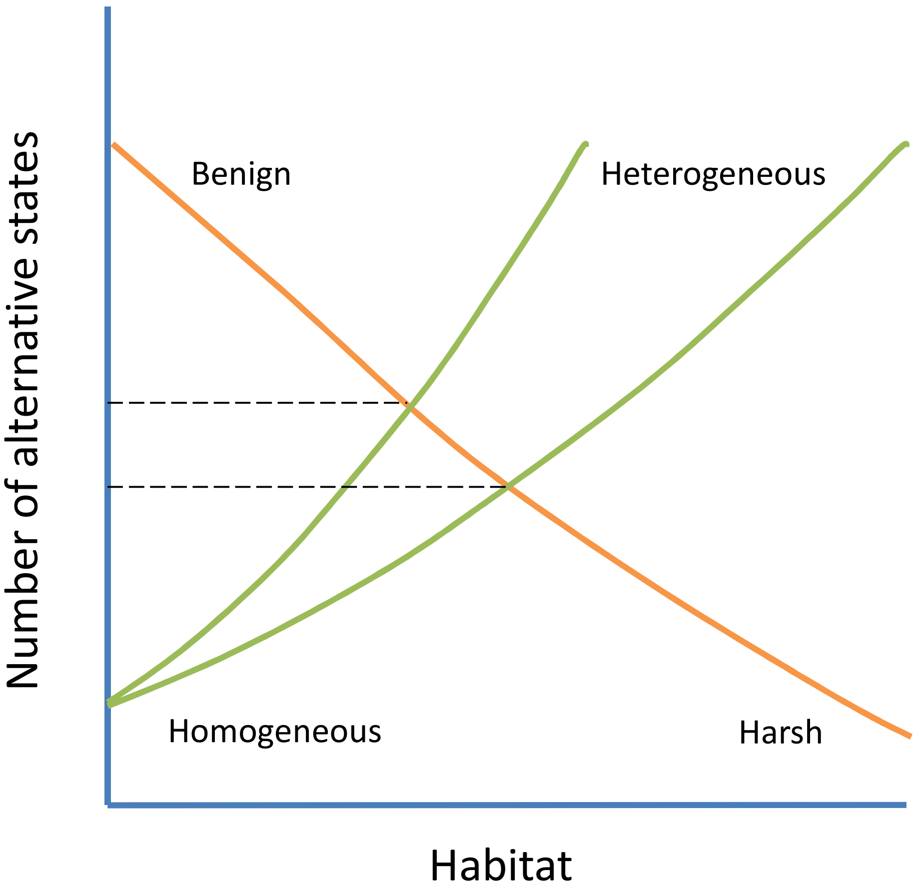

Figure 5-1. A hypothetical interaction of two major ecological gradients influencing the number of expected alternative states. The dotted lines show equilibrium points and the expected number of alternative states given the two combinations of gradients.

Invasion biology could further benefit by the findings I presented here. Questions that should be addressed are: does the formation of alternative states facilitate the invasion of exotic species? How invaders change the odds for the formation of alternative states - would they increase the probability of their formation via augmentation of diversity, or the opposite would happen? What is the proportion of alternative states that remains open to invasions? Is it fixed, or is there usually more of one or the other? What would this depend on?

Metacommunity models should be revisited in the light of my results as well. For example the patch dynamic model specifies that species can coexist if there is a tradeoff between dispersal and competition ability. However, if biological interactions promote occurrence of alternative states, coexistence among species should be observed without such a tradeoff. In the case of the species sorting model, a one to one match between environment and community is expected if we assume that deterministic assembly rules apply. What would be the expectations if they do not?

Neutral theories should be also re-evaluated in light of my findings. In these theories it is assumed that biological interactions are neutral. Consequently the structure of the communities depends only on the properties of regional processes and the properties of the regional pool of species. We can infer from the persistent emergence of alternative states that biological interactions are actually not neutral. The fact that biological interactions, including demographic stochasticity, are able to generate patterns previously claimed as explainable within neutral theories means that assumptions of the latter need revision.

My results suggest that even though biological interactions control the structure of communities, this control is modulated by the influence of regional processes. This line of inquiry should be further investigated.

MANAGEMENT IMPLICATIONS

Findings of my experiments increase management challenges for communities, particularly with regard to restoration ecology. Restoration ecology leans towards the deterministic side of community assembly (Trowbridge 2007). A deterministic assembly implies the existence of assembly trajectories that can be reconstructed to reassemble lost or impaired communities. It also assumes the ability to predict the outcomes and functionality of ecosystems (Belyea 2004). However, the fact that determinism in the formation of communities is absent puts those expectations in question. In restoration ecology, identification of a reference community is crucial to tracking goals as to what community state is to be restored (Lockwood & Samuels 2004). If alternative states are present, identification of a reference community becomes difficult. A solution to this may be setting a set of desirable characteristic of the system to be restored (Trowbridge 2007). However, even if a reference community is established, stochasticity involved in the assembly would make the responses to restoration efforts difficult to predict and assess.

Consequently, management of natural resources should be biased towards conservation rather than restoration after the damage. The arguments for conserving and protecting natural ecosystems and communities gain weight given the potential difficulty of restoring communities that I have mentioned above.

Finally, since divergence towards an increasing number of alternative states seems to be a common feature of ecological systems, conservation and restoration efforts should consider it a quality worthy of preservation. If the common analogy between population genetics and community assembly is true (Vellend 2010), then the preservation and maintenance of diversity (in terms of alternative states) of communities should be a property to keep in mind.

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