HABITAT SPECIALIZATION AND METACOMMUNITY

THE ROLE OF LOCAL AND REGIONAL PROCESSES ALONG THE GRADIENTS

OF HABITAT SPECIALIZATION FROM A METACOMMUNITY PERSPECTIVE

By

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ABSTRACT

Emergence of the metacommunity concept has explicitly recognized the interplay of local and regional processes. The metacommunity concept has already made a substantial contribution to the better understanding of the community composition and dynamics in a regional context. However, long-term field data for testing of available metacommunity models are still scarce and the extent to which these models apply to the real world remains unknown and some of their assumptions untested. Tests conducted so far have largely sought to fit data on the entire regional set of species to one of several metacommunity models, implicitly assuming that all species, members of the metacommunity, can be modelled in the same manner (using a single model). However, species differ in their habitat use to the extent that such uniform treatment may be inappropriate. Furthermore, in testing the metacommunity models, all metacommunity studies relay on snapshots of species distribution to assess the relative importance of local and regional processes. However, snapshot patterns may be insufficient for producing a reliable picture of metacommunity dynamics and processes shaping it. I hypothesised that the relative importance of local (competition, predation or abiotic filtering or constraints) and regional (interaction of populations with landscape, migration or dispersal) processes may vary with species' traits, including habitat specialization. The perception of importance of local and regional processes in structuring community composition obtained via static approach may vary from that obtained by considering the temporal

dynamics of component species. My general approach used a model system comprising natural rock pools microcosms. I have also employed experimental approach in the laboratory. I found that different metacommunity models suit for different groups of habitat specialization. I also found this to be true whether the analyses are based on snapshot data or describing temporal dynamics of species populations. These results suggest that a metacommunity system exhibits an internal differentiation of structuring processes. Specifically, from the metacommunity perspective, the dynamics of habitat specialists are best explained by a combination of species sorting and mass effects models, while that of habitat generalists is best explained by patch dynamics and neutral models.

Key words: habitat specialization, habitat generalists, habitat specialists, population synchrony, temporal turnover, metacommunity

PREFACE

This dissertation contains four papers that either have been published in the primary literature or have been submitted to journals to be considered for publication. Among the four, three papers were coauthored with my supervisor, Dr. Jurek Kolasa and a committee member, Dr. Karl Cottenie (University of Guelph), and one of the papers was coauthored with my supervisor Dr. Kolasa, only. While Dr. Kolasa and Dr. Cottenie contributed ideas and comments to improve these manuscripts the majority of each paper consists of my own original research. The general procedures we used was that I would develop idea and collect data, analyze them and develop each paper into a coherent document first, and the Dr. Kolasa and Dr. Cottenie would make suggestions on how the manuscript might be improved, much in the way peers comment on the work of a colleague.

I have co-authored one publication during the course of my thesis research:

Pandit, S.N., J. Kolasa, and K. Cottenie 2009. Contrasts between habitat generalists and specialists: an empirical extension to the basic metacommunity framework. Ecology: Vol. 90, No. 8, pp. 2253-2262.

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distance being removed; E|S is the pure environmental synchrony with the effect of distance has being removed; S is the distance between pairs of pools; S|E is the pure distance effect with the effect of environmental synchrony being removed. Bold numbers indicate significant values at $p<0.05$ level.

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List of abbreviations and symbols used in figures and text

AD	Average density
ANOVA	Analysis of variance
B	Niche breadth
CCA	Canonical Correspondance
CCF	Cross correlation function
C_{obs}	The number of species that colonized in the interval $[i, i+1]$
DBML	Discovery Bay Marine Laboratory, University of West Indies, Jamaica
df	Degree of freedom
$\delta_{i,t}$	Cross correlation coefficient
E	Variation explained by environmental variables
E|S	Variation explained by pure environmental variables (contribution of S removed)
EC events	The mean number of combined colonization and extinction events in a pool
EF	Environmental fluctuation
E_{obs}	The number of species that become extinct
EØS	Variation shared by environmental and spatial variables

ES	Correlation coefficients obtained through cross correlation functions between the value of salinity between a site i and site j (environmental synchrony).
EV	Environmental variability
F	F statistics
mL or ml	Mililiter
$N_{i,t}$	Population size of species *i* in each microcosm at time t
$N_{i,t+1}$	Population size of species *i* in each microcosm at time t_{+1}
OMI	Outlying Mean Index
ppt	Parts per thousands
r^2	Correlation coefficient
RDA	Redundancy Analysis
$r_{i,t}$	Population growth rate
RS	Regional population synchrony
RMSTOL	Root mean square standard deviation across four axes.
S	Variation explained by spatial variables
s	Species richness
S|E	Variation explained by pure spatial variables (contribuation of E removed)
SD	Standard deviation

SE	Standard error
S_i	The number of species observed in a pool in year i
$Slope_{PS.E}$	Slope between population synchrony and environmental synchrony
$Slope_{PS.S}$	Slope between population synchrony and distance
SS	Sum of squared deviations from the mean
TTS	Species temporal turnover
TTS_{mean}	The mean species turnover for each pool

CHAPTER 1

Introduction

BACKGROUND AND RATIONALE

A central question in community ecology is "What processes shape a community structure in a site?" Species number (alpha diversity), relative abundance of its constituent species (community structure), and their interactions with one another are examples of the fundamental structural properties of a community (e.g., Roughgarden and Diamond 1986, Tokeshi 1999, Cottenie et al. 2003). For a long time, studies in community ecology focused on a single scale of a local community and usually treated species sharing the same habitat location as if they were isolated from other local communities (Leibold et al. 2004). Within those other local communities, populations were also assumed to interact internally by affecting one another's species birth and death rates, as modeled by population dynamics models such as the Lotka-Volterra models (e.g., May 1973, Pimm and Lawton 1978, McCann et al. 1998, Leibold et al. 2004). Consequently, much attention has been focused on interactions among the population within a habitat, with the assumption that such interactions are a fundamental force that regulates community structure (Ricklefs and Schluter 1993, Cottenie et al. 2003, Beisner et al. 2006, Ricklefs 2008). It has been recognised, however, that dispersal of some species among habitats influences the persistence of species in a community (Chase et al. 2005, Holyoak et al. 2005). For example, species interactions can occur in a network of local communities where they affect colonisation probabilities and extinction

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patterns at larger scales than those typically considered in the case of a closed, local

community (Leibold et al. 2004). Thus, in recent years, community ecology has moved

towards improving the understanding of larger systems, or sets of local systems, as

opposed to focusing on the temporal dynamics of a local community (Leibold et al. 2004,

Hastings 2005, Beisner et al. 2006). Such sets of local systems acquired their own name:

Metacommunity. Metacommunity is defined as a set of local communities observed in

discrete habitats such as islands, lakes, forest patches that are linked by dispersal of

multiple potentially interacting species (see Figure 1-1, Wilson 1992, Leibold et al. 2004,

Holyoak et al. 2005). A collection of
models, statistical approaches, assumptions
about relevant factors, and the notion that
processes occurring in a local community
affect the dynamics of communities nested
in a larger landscape and vice versa are
jointly known as metacommunity theory or
framework.

Figure 1-1. Aerial view of islands, with arrows that indicate species dispersal linkages among islands.

Within metacommunity theory one

thus assumes that fundamental structural properties of a community are governed not only

by local factors (such as productivity, predation, competition, resource constraints,

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disturbance frequency), but also by regional factors (such dispersal, regional species pools and speciation) (e.g., Gaston and Blackburn 2000, Ricklefs 1987, Cornell and Lawton 1992, Cottenie et al. 2003, Cottenie 2005). These two local and regional factors play an important role in structuring community composition in different ways. Regional factors determine the number and identity of species reaching the habitat. Environmental factors determine which species establish and persist locally (e.g., Leibold et al. 2004, Cottenie 2005, McCauley 2007). Thus, ecological systems are best understood and studied in the context of where the systems are located in space relative to each other (e.g., Legendre 1993, Turner 1998, Magunson and Kart 1999, Cottenie 2003) and whether dispersal pathways for the different species in the system exists or not (Cottenie 2003). Leibold et al. (2004) and Chase et al. (2005) also highlighted the importance of dispersal of species by suggesting that dispersal of species among habitats can affect the dynamics and community structure in local habitats. Thus, within the metacommunity framework, both local and regional processes are considered to be important forces in structuring community composition in discrete and spatially distributed habitat patches (e.g., Leibold et al. 2004, Holyoak et al. 2005, Ellis et al. 2006, Harrison and Cornell 2008, Jones et al. 2008, Paradise et al. 2008. Lindo and Winchester 2009).

Depending on the relative importance of local and regional processes, four metacommunity models are proposed to account for species diversity patterns at local and

regional scales (Cottenie 2005). Metacommunity models (patch dynamics, species sorting, mass effects, and neutral) have different assumptions and predictions, by fitting which of the models fits best a particular subset of data; it is possible to make a prediction of species distribution and abundance in a fragmented landscape. Despite the fact that the relative roles of local and regional processes have been studied extensively, understanding the roles of local and regional processes in generating community level patterns has proven to be more challenging (Shurin and Allen 2001, Havel and Shurin 2004, Rajaniemi et al. 2006). The challenge arose because studies report mixed results as to which factors are more important in structuring of a community, especially in lakes or other aquatic systems. In some cases (e.g., Pinel-Alloul et al. 1995, Cottenie et al. 2003, Cottenie 2005, Vanschoenwikel et al. 2007), environmental variables dominated over spatial factors, whereas in others (e.g., Shurin et al. 2000, Cottenie 2005) spatial factors were more important in determining community structure. In some of the cases, both of these processes are found to be important in structuring community composition (e.g., Cottenie 2005, Vanshoeninkel et al. 2007).

Beisner et al. (2006), Vanshoeninkel et al. (2007) and others also found mixed results when they examined the interplay between local and regional processes for different groups of species of the same ecosystem, with the prediction that different groups of species respond to different processes. For example, Beisner et al. (2006) found

that a crustacean zooplankton community was controlled by both spatial and local processes in both overland and water dispersal, the fish community was structured by spatial processes but only when lakes are connected, and variation of phytoplankton species did not depend significantly on either local or regional factors. Thus, understanding the roles of local and regional processes in generating community level patterns seems to be more challenging.

Another fact that has a potential to affect metacommunity dynamics is species habitat specialization. Species differ in their habitat use where some show broad environmental tolerances (habitat generalists), while others have very specific and narrow environmental tolerances (habitat specialists). As local performance as well as dispersal my differ among species of different specializations, variation in the relative importance of the processes that affect community composition may be also affected by proportions of generalist and specialist species in a set of habitats considered as a metacommunity. Habitat specialists are more likely to be governed by habitat availability than generalists (Munday et al. 1997, Bean et al. 2002). Thus, the importance of local vs. regional processes in determining species distribution and abundance of species may differ depending on their ecological specialization: specialists may respond more readily to local processes, particularly habitat characteristics, while generalist species may appear to respond more to regional spatial factors, particularly to distance between patches.

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However, as important and promising as this broad question may be, it has not been investigated before. Consequently, I decided to focus on investigating the importance of species' traits in determining metacommunity dynamics. The approach I took was to attempt to fit one of several existing metacommunity models to a large data set. As I have mentioned previously, metacommunity models differ in their assumptions and predictions as to the relative importance of local and regional factors. By determining which model fits better the data set available to me, I hope to shed light on the mixture of underlying forces that affect the metacommunity of interest. In metacommunity research, tests of metacommunity models conducted so far have largely sought to fit data on the entire regional set of species to one of several metacommunity models. Such tests implicitly assumed that all species, members of the metacommunity, can be modelled in the same manner (using a single model). However, species differ in their habitat use to the extent that such uniform treatment may be inappropriate.

Furthermore, most of prior metacommunity studies failed to take temporal patterns into account because most tests of metacommunity relay on snapshot patterns of species distributions and abundance in order to detect and assess the relative importance of local and regional processes. However, because community composition and population densities fluctuate continuously in space and time (e.g., Connell and Sousa 1983, Horne and Schneider 1995); snapshot patterns may be insufficient for producing a

reliable picture of metacommunity dynamics and processes shaping it. Thus, in this thesis I explore the role of local and regional processes in the temporal dimension of population dynamics along the gradient of habitat specialization, and compare the results obtained from snapshot and continuous patterns data used in tests. Moreover, communities with higher species richness imply more interaction than the communities with less species richness (e.g., Tilman and Downing, 2004). Species richness (diversity) could confound the results. Thus I further explore whether the results and inferences pertaining to the above problems depends on species diversity.

So far, I have identified two deficiencies of the current metacommunity theory and practice that may have important effect on past and future tests of specific models and thus on the progress of understanding of factors determining metacommunity dynamics. One deficiency is related to the potential differences between dynamics of habitat specialists and generalists. The other deficiency is related to the nature of data used in tests (static vs. dynamic). The main thrust of my research was in response to these deficiencies. To address the two deficiencies of the metacommunity framework, I developed two hypotheses. 1) The relative importance of local and regional processes may vary with species' traits in terms of habitat specialization and within a metacommunity system such that generalist species dynamics may be dominated by dispersal factors while that of specialists by environmental factors. If this hypothesis is

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correct, then suitability of different metacommunity models will differ among species with of different habitat specialization. 2) The perception of importance of local and regional processes in structuring community composition obtained via static approach may vary from those obtained by considering the temporal dynamics of component species.

The goal of the research is to expand and modify metacommunity framework in such way that it provides a better way of examining spatial dynamics of communities. Specifically, I aim to determine whether metacommunity models are capable of dealing with species of different specialization and whether it is sufficient to use short-term data or whether a long-term dynamics data are required for a satisfactory test of models.

Habitat specialization or species' traits

Species differ in the range of environmental conditions that they can live and reproduce at. Species that are restricted to a small area of the multidimensional habitat space are considered specialists, while the generalists are those species which are not so restricted (Kolasa and Waltho 1998). Any collection of species is likely to exhibit a gradient of specialization traits. At the extremes, these two species categories have different population dynamics (Kolasa and Li 2003). For example, variation in population density is higher in habitat specialists than in generalists (Kolasa and Li 2003). Similarly, habitat specialists use smaller habitat units, which are nested within the larger ones

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(Kolasa and Pickett 1989). Species which use smaller habitat units tend to have lower population densities as a consequence of decreased efficiency in finding suitable patches and mortality during dispersal (Kolasa and Romanuk 2005). Furthermore, habitat availability appears to control habitat specialists more than generalists (e.g., Munday et al. 1997, Bean et al. 2002). Recognition of such differences implies the need for different predictions for specialist versus generalist dynamics under different metacommunity models.

The metacommunity models and its assumptions

As mentioned above, the metacommunity framework has only recently emerged by combining concepts of classical community ecology and metapopulations. It incorporated ideas about the immigration and extinction of species from community ecology and ideas about the role of dispersal from metapopulation models. The main goal of metacommunity framework is to aid in the understanding biodiversity dynamics in fragmented landscapes. Despite the recognition of importance of regional processes to community composition, which was first introduced through Island Bio-geography theory (MacArthur and Wilson 1963, 1967), the Island Bio-geography theory appeared to be insufficient when dealing with community composition and dynamics of multiple habitat patches where no mainland source of colonists exists (e.g., Tilman 1994, Tilman et al. 1994, Karieva and Wennergren 1995, Cottenie et al. 2003, Holyoak et al. 2005). This is

because Island Bio-geography theory stated that species richness in a habitat being a function of the habitat size and the distance to "mainland" habitat, from which other species migrate. Furthermore, the metapopulation concept provides new insight to spatial dynamics for only one species occupying as set of habitat patches (Levins 1969). However, species do not typically exist in isolation; rather they exist as participants in complex web interactions within ecological communities. To reflect the need to consider both the local interactions among species and the influence of other locations with related communities, metacommunity models have been developed to close the gap between island biogeography and metapopulation models. Applying metacommunity theory to natural patterns of variation in community structure requires considerable empirical work (e.g., Leibold and Miller, 2004, Urban et al. 2008). Prior metacommunity research has concentrated primarily on formulating theoretical models consisting of competitors (e.g., Amarasekare et al. 2004). Only some of the models have been empirically tested, including neutral models (e.g., Bell 2001, Hubbell 2001, reviewed by Chave 2004, McGill et al. 2006) and the effect of competition and colonization trade-offs on species coexistence (e.g., Levine and Rees 2002, Mouquet et al. 2004, Yu et al. 2004, Cadotte 2007). Other metacommunity studies have examined the role of connectivity and dispersal between patches (Gonzalez et al. 1998, Gonzalez and Chaneton 2002, Forbes and Chase 2002), the effects of dispersal and predation at local and metacommunity scales (Kneitel and Miller 2003, Cadotte 2006a and Cadotte 2006b), or have used spatial

position of a habitat patch relative to other patches as a proxy for dispersal and decomposed variation in community structure into that explained by either environmental or spatial processes (Cottenie 2005).

Four metacommunity models (neutral, patch dynamics, species sorting, and mass effects) exist that differ in their assumptions and predictions as well as the relative importance that each places on environmental and spatial processes involved in structuring the communities within the system (see Figure 1-2). Neutral model assumes that species and the environment within communities are functionally equivalent, where the communities are characterized as dispersal limited and species are lost due to stochastic extinction (Amarasekare 2003, Leibold et al. 2004, reviewed in Chave 2004, Cottenie 2005). Therefore, communities conforming to neutral model will be structured by spatial processes only (Cottenie 2005).

Patch dynamics model assumes spatial homogeneity of environmental conditions among patches (local communities) but, in contrast to the neutral model, assumes trade-offs between competition and dispersal (species is either a good competitor or a good disperser), and that extinctions are both stochastic and deterministic (Leibold et al. 2004). Consequently, communities conforming to this model are also structured by spatial processes only (Cottenie 2005).
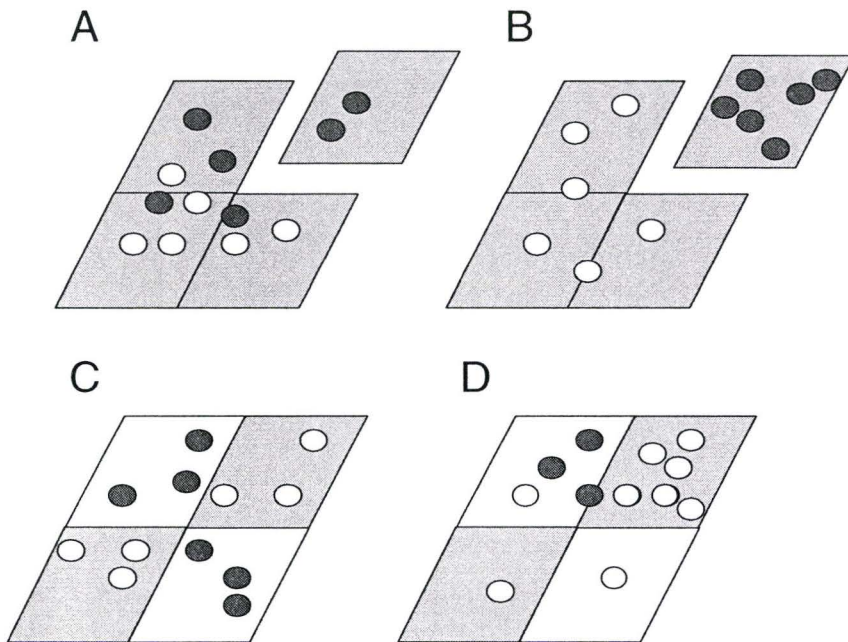
Figure 1-2. Illustration of the assumptions of metacommunity models. Boxes represent patches, and each cluster of 4 patches represents a metacommunity. Metacommunity has homogeneous environmental conditions when shading is uniform and heterogeneous when it contains both white and gray patches. Different color circles within the patches represent the individuals of different species. A, B, C and D represent Neutral, Patch dynamics, Species Sorting and Mass Effect models, respectively.

Species sorting model differs from the previous models because the species sorting model emphasizes the importance of local environmental factors. It assumes that the environment is heterogeneous and forms a gradient of conditions. When dispersal is sufficient, species sort themselves along an environmental gradient such that a species persists in its favored environment (e.g., Tilman et al. 1982, Chesson 2000, Chase and Leibold 2003, Cadotte 2006). Mass effects model (Holt 1993, Mouquet and Loreau 2002, Mouquet et al. 2005) also assumes that the environment is heterogeneous, but differs from the species-sorting model in terms of dispersal rates, which are high enough to alter population abundances through source-sink dynamics.

The metacommunity models and predictions of diversity patterns

Since assumptions in these metacommunity models vary, predictions of diversity patterns on a local and regional scales made by the models also vary (Chase et al. 2005). Neutral model predicts that when dispersal rates increase, beta-diversity (site-to-site compositional variation) should decrease (Hubbell 2001, Bell 2001), and regional richness (total diversity in a group of patches) should decrease (Table 1-1, Chase et al. 2005). Local diversity (diversity of a patch) increases with an increasing rate of dispersal. In the extreme, a very high dispersal rate or a highly homogeneous dispersal pattern (species have an equal chances of reaching any local community within a landscape)
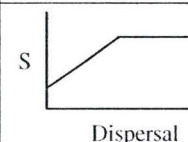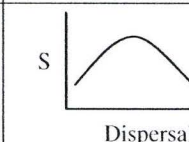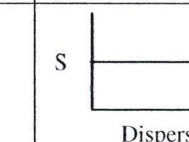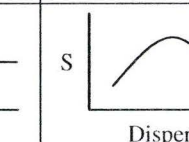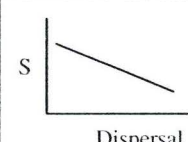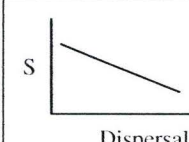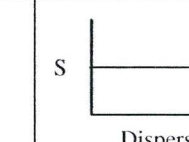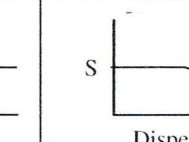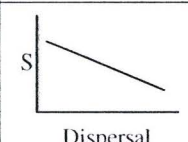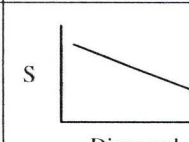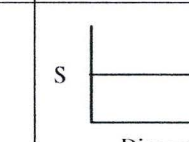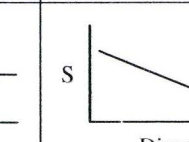
should result in a constant local diversity because no differences along the local communities would develop (Chase et al. 2005, Holyoak et al. 2005).

Patch dynamics models predict that local diversity should be hump- shaped (Mouquet et al. 2002) as a function of dispersal rate. This simply means that, as dispersal increases, local diversity also increases but, after reaching a peak, it will decline. Beta and gamma (regional) diversity should decrease with increased dispersal rates because local displacements occur more rapidly under the condition of high dispersal and, ultimately, fewer species manage to persist in the metacommunity as a whole (Chase et al. 2005).

Species sorting models predict that local, regional and beta-diversity will not be affected as a positive function of dispersal (Chave and Leigh 2001). Like the patch-dynamics model, the mass effects model predicts that local diversity increases with increasing dispersal and then decreases (hump- shaped) (Mouquet and Loreau 2003). This change in the effect of dispersal on local diversity happens because species can persist in habitats where they are not favoured due to mass effects until species that are better regional competitors arrive, which is facilitated by higher dispersal rate, and eliminate the prior residents (Chase et al. 2005). Regional diversity will not be affected at low to intermediate dispersal rates, but the diversity decreases at high dispersal rates (Mouquet and Loreau 2003, Chase et al 2005). The mechanism for this decrease is similar to the mechanism operating locally: locally competitively inferior species are displaced by

superior species that spread regionally (Chase et al. 2005). Consequently, beta diversity also decreases when the rates of dispersal increase (Mouquet and Loreau 2003, Chase et al. 2005).

Table 1-1. Simplified predictions of the local, regional and beta diversity changes as a function of dispersal rate by the four generalized metacommunity models

Effects	Model predictions			
	Neutral	Patch dynamics	Species sorting	Mass effects
Dispersal effects: local diversity				
Dispersal effects: regional diversity				
Dispersal effects: Beta diversity				

MAIN RESEARCH QUESTIONS

As explained above, the metacommunity models have been recently developed to aid in understanding of regional and local species composition and density as well as their spatial dynamics in a fragmented landscape. The predictions and assumptions of these

models differ. Therefore, it is important that an appropriate model is chosen for a natural system of interest to management or conservation. However, deficiency in empirical testing of these models makes a selection of an appropriate model difficult. In applied ecology, if a model fitted to a natural system is incorrect, it may lead erroneous decisions about network development (corridor between habitats) or improvement of habitat conditions. Therefore, thorough testing of the models using empirical data is most desired (Leibold et al. 2004). However, most of the studies tested these models with the assumption that all species are subject to the same factors over one set of sites. As I have mentioned above, different groups of species, such as habitat generalists and specialists, perform differently in different habitats that constitute a fragmented landscape of interest.

Given the importance and novelty of the metacommunity models, the relatively low level of testing that they were subjected to, and the need of conceptual refinement and increased realism, I formulated a central question to guide my efforts in this area.

The main questions of my research are: Can a single metacommunity system exhibit an internal differentiation of structuring processes for different groups of species in terms of species' traits? Would accounting for systematic difference in species traits, as captured by the general gradient of species habitat specialization, improve our understanding of metacommunity dynamics and fitting procedures for metacommunity

models? I have developed additional and specific questions in the chapters of the thesis to answer this main research question.

RESEARCH APPROACH

To pursue the questions articulated above, my general approach combined several methodologies and took advantage of the available data. On the empirical side, I used a model system comprising natural microcosms. Most work in the area of metacommunity ecology faces limitations due to the nature of available data. Because I used microcosms, I was able to use a rich data set on distribution and abundance of species across numerous discrete habitats and ample data on the spatial arrangement of these habitats and their physico-chemical properties. The second component of my approach is theoretical. With several metacommunity models available, each with different set of specific predictions, it is possible to use them in two main modes. One is to use the available data to test the models – a task that, given the paucity of tests in the literature, would contribute to improving the metacommunity theory. The other is to use the models to test new hypotheses concerning important factors that are not yet the part of the theory. In this case I focused on the consequences of species specialization and its role in our ability to apply metacommunity theory to natural systems. My approach required a range of specific methodologies. To test the fit of the models, I have compared the amount of

variance in the data for the different groups of species (habitat generalists, specialists and combination of both groups of species) to model qualitative predictions. In order to make groups based on habitat specialization, I computed niche breadth (B) of species based on the uniformity of species distribution among the 49 pools. I selected five species with the greatest niche breadths (as generalists) and five species with the lowest niche breadths (as specialists). However, the number of selected species (five) is arbitrary. I also examined the consistency of my tests by comparing results of model fitting based on short-term and long-term data. Finally, to incorporate long-term population dynamics and make it relevant to metacommunity considerations, I used a new procedure that involved calculation of synchrony among individual populations. In addition to the reliance of the natural microcosms, I have also employed experimental approach in the laboratory. Population variability in the field is inherently noisy and therefore experiments aimed to control factors others than those of direct theoretical interests (Cottenie 2005, Pandit et al. 2009). Moreover, field data were collected only once a year, which provided limited information on the temporal dynamics of the species because their generation time is short.

STUDY SYSTEM

Most of my research was conducted using invertebrate species from a rock pool metacommunity as a model system. The system consists of a diverse set of pools located on the north Coast of Jamaica (Figure 1-3, Figure 1-4, 18^0 28' N, $77^0$25'). All pools are located within a 25 m radius, with considerable variation in environmental characteristics among pools. Due to the small area of the metacommunity, it can be assumed that any species found in one pool can potentially reach any other pools under study. The island-like nature of the pools in the rock creates well defined habitat boundaries within unsuitable terrestrial matrix of dry rock. I expect some dispersal of species between the pools either through active dispersal, passive or vector processes, which make the system meet the metacommunity criterion. Although the system I investigate is small in comparison to many natural systems of interest to humans, use of microcosms as model systems can make significant contributions to ecological and conservation studies (e.g., Srivastava et al. 2004).

For the study, I used the data collected earlier by Prof. Kolasa and his colleagues from the 49 rock pools from 1989 on. The 49 rock pools are situated on the fossil reef (see Figure 1-4). The study was restricted to pools that were no less than 500 ml in volume. The rock pool size ranges from 13 to 105 cm in width and length, and varies from 1 to 37 cm in depth (mean depth = 12.8 ± 8.3 SD). Volumes were highly diversified

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and range up to 115 liters, with a mean of 12 ± 21 SD. On average, a rock pools located within 1 m of the nearest neighbor, and none is separated by more than 5 m from the nearest neighbor. Their elevation above sea level range from 1 to 235 cm (mean = 76.6 ± 80.1 SD) at high tide, with the tide rarely exceeding 30 cm. A few pools are tidal (although tidal flooding was not daily), but most are maintained by atmospheric precipitation and, very occasionally, wave splash water (detail about the study area are in Kolasa et al. 1996).

Rock pool biotic communities consist of micro-organisms, periphyton, phytoplankton, zooplankton, benthic invertebrates, and crab and insect larvae (Romanuk and Kolasa 2001).

Over 70 meio-invertebrate species have been identified in the rock pool system: Turbellaria (7), Nematoda (1), Polychaeta (5), Oligochaeta (2), Ostracoda (20), Copepoda (6), Cladocera (5), Decapoda larvae (5), Amphipoda (1), Isopoda (1), and Insecta (18). In total, over 400,000 individuals were collected and identified.
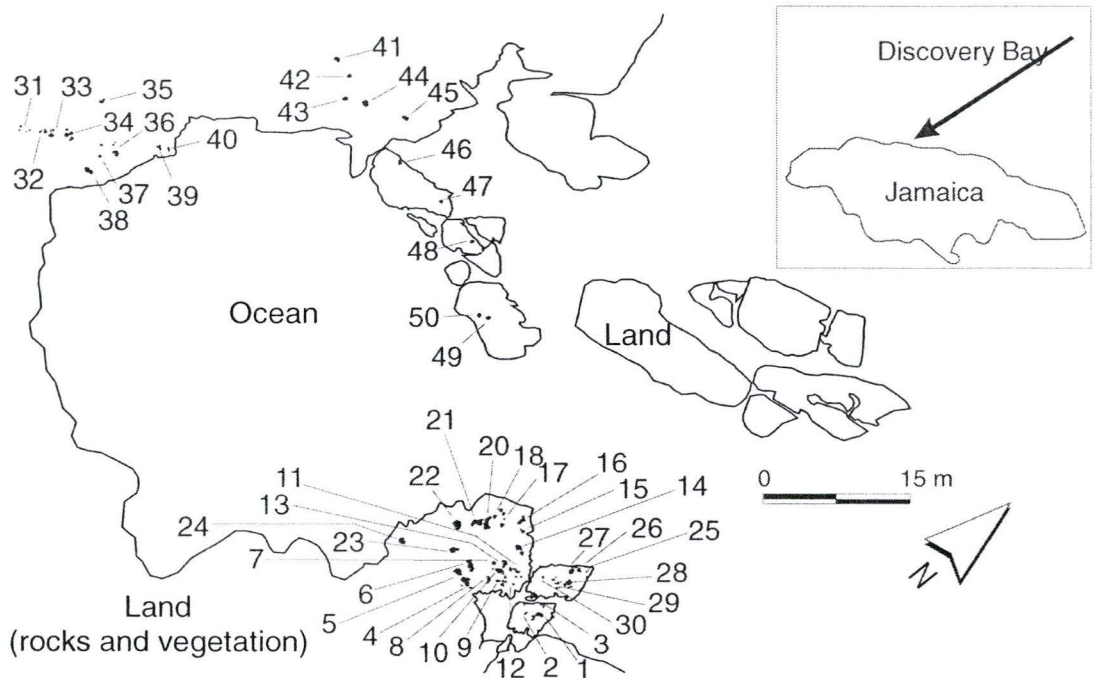
Figure 1-3. Location of the study area and 49 rock pools (numbered) at the Discovery Bay

Marine Laboratory (DBML), University of West Indies, Jamaica. Arrow indicates the

approximate location of the study site in Jamaica.

Figure 1-4. Coastal rock with a mixture of freshwater and saline pools near Marine Lab at the Discovery Bay coast, Jamaica. The photograph shows a landscape of rock pools near pool 45 in Figure 1-1. Photo: J. Kolasa.

THESIS OUTLINE

This dissertation is divided into 6 sections. Chapter 1 contains the general backgrounds, general overview of the role of local and regional processes and its implication in metacommunity models, main research questions and research approach. Chapter 1 also reviews various theoretical attempts at explanation of the importance of local and regional processes in metacommunity. Chapters 2-5 are presented as journal articles, each of which is prefaced by a brief rationale for the article.

Chapter 2 (a manuscript accepted in Ecology, in press) contains an article "contrast between habitat generalists and specialists: an empirical extension of the basic metacommunity frameworks". In this chapter I showed that a metacommunity system can exhibit an internal differentiation of structuring processes, with habitat specialists governed predominantly by environmental factors and habitat generalists governed mainly by spatial factors. The dynamics of habitat specialists are best explained by a combination of species sorting and mass effects, while that of habitat generalists are best explained by patch dynamics and neutral models.

Chapter 3 (a manuscript submitted to Journal of Animal Ecology) contains an article "Species richness and environmental fluctuation affect population synchrony in a metacommunity". This chapter explores the comparative role of environmental

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fluctuation in the temporal population dynamics among generalist, specialist and intermediate species. I showed that population synchrony in a metacommunity was higher between specialist species than generalist when environmental fluctuation was high. The metacommunity with higher species richness had low level of population synchrony.

Chapter 4 (a manuscript in preparation) contains an article "Opposite effects of environmental variability and species richness on temporal turnover of species: differences between specialists and generalists". I reported that the species temporal turnover varied between the different groups of species. Environmental variability (EV) induced greater temporal turnover among specialists than generalists. Species temporal turnover decreased with species richness and that the effect of richness (biodiversity) was consistent for generalists and specialists.

Chapter 5 (a manuscript in preparation) contains an article "the role of regional and local processes in the temporal population dynamics of species along a gradient of habitat specialization in a rock pool metacommunity". In this manuscript I reported that species of different habitat specialization show systematic differences with respect to local processes involving environmental characteristics but fail to show such difference with respect to regional processes involving distance, at least when long-term dynamics is concerned.

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Chapter 6 is the general conclusion and discussion of the results presented in this dissertation.

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CHAPTER 2

Contrasts between habitat generalists and specialists: an empirical extension to the basic metacommunity framework

This chapter was published in Ecology (partial citation follows) and is published here with permission of Ecological Society of America (ESA, Appendix). This chapter has been re-formatted to maintain consistency throughout the thesis.

Pandit, S. N., J. Kolasa, and K. Cottenie 2009. Contrasts between habitat generalists and specialists: an empirical extension to the basic metacommunity framework. Ecology: Vol. 90, No. 8, pp. 2253-2262.

RATIONALE AND OBJECTIVES

The main goal of this dissertation is to find out whether species specialization affects inferences as to which structuring processes dominate in determining community composition within a metacommunity system. Because metacommunity models have different assumptions and predictions, by finding which of the models fits best a particular subset of data, it is possible to make inferences as to which underlying processes govern the distribution and abundance of species in a fragmented landscape. The major difference among the models involves relative importance of spatial vs local factors. Spatial factors may include any variable that affects exchanges of propagules among individual communities. Local factors may include any variable that affects the colonization, survival, and reproduction of a species at a site. Specific objective of this chapter is to test whether species with different habitat specialization respond to the different factors (local or regional); and to expand metacommunity theory by incorporating species' traits into the selection of metacommunity models. My general approach was to use the observation data on rock pool metacommunity and to compare the proportion of variation in species distributions and abundance explained by environmental versus spatial factors. I found that:

- Regional processes were important for generalists and explained on an average 27% of variation in their abundance, whereas

- Local processes were important for specialists and explained on an average 35% of variation in their abundance, and

- Dynamics of habitat specialists is best explained by a combination of species sorting and mass effects, while that of habitat generalists is best explained by patch or neutral models.

These results suggest that metacommunity can exhibit complicated dynamics.

ABSTRACT

Emergence of the metacommunity concept has made a substantial contribution to better understanding of the community composition and dynamics in a regional context. However, long-term field data for testing of available metacommunity models are still scarce and the extent to which these models apply to the real world remains unknown. Tests conducted so far have largely sought to fit data on the entire regional set of species to one of several metacommunity models, implicitly assuming that all species operate similarly over the same set of sites. However, species differ in their habitat use. These differences can, in the most general terms, be expressed as a gradient of habitat specialization (ranging from habitat specialists to habitat generalists). We postulate that such differences in habitat specialization will have implications for metacommunity dynamics. Specifically, we predict that specialists respond more to local processes, and generalists respond to regional spatial processes. We tested these predictions using natural microcosm communities for which long-term (9-year) environmental and population dynamics data were available. We used redundancy analysis to determine the proportion of variation explained by environmental and spatial factors. We repeated this analysis to explain variation in the entire regional set of species, in generalist species only, and in specialists only. We further used ANOVA to test for differences in the proportions of explained variation. We found that habitat specialists responded primarily

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to environmental factors, and habitat generalists responded mainly to spatial factors. Thus, from the metacommunity perspective, the dynamics of habitat specialists are best explained by a combination of species sorting and mass effects, while that of habitat generalists are best explained by patch dynamics and neutral models. Consequently, we infer that a natural metacommunity can exhibit complicated dynamics, with some groups of species (e.g., habitat specialists) governed according to environmental processes, and other groups (e.g., habitat generalists) governed mainly by dispersal processes.

Key words: Habitat specialists, habitat generalists, habitat specialization, metacommunity models, patch dynamics, species sorting, mass effects, neutral models, variance partitioning

INTRODUCTION

Recent advances in ecological theory explicitly recognize the interplay between local environmental and regional processes in structuring local communities. Regional processes determine the number and identity of species reaching a habitat, while local environmental processes (including biotic interactions) determine which species establish and persist there (McCauley 2007). Based on the relative importance of the two processes, and some additional assumptions, four kinds of metacommunity models have been proposed: species sorting, mass effects, patch dynamics, and neutral (reviewed in Leibold and Miller 2004; Holyoak et al. 2005, Cottenie 2005).

The species sorting model (Leibold et al. 2004) emphasizes the importance of local environmental factors. It assumes that the environment is heterogeneous and forms a gradient of conditions. When dispersal is sufficient, species sort themselves along an environmental gradient so that species persist in their favored environments (e.g., Tilman et al. 1982, Chesson 2000, Chase and Leibold 2002, Cadotte 2006). Species sorting has occurred in a wide range of systems (e.g., Gilbert and Lechowicz 2004, Kolasa and Romanuk 2005, Miller and Kneitel 2005, Cottenie 2005, Ellis et al. 2006). The mass effects model (Holt, 1993; Mouquet and Loreau 2002, Mouquet et al. 2005) also assumes heterogeneous environment, but applies when dispersal rates are high enough to alter

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population abundances through source-sink dynamics. Mass effects are also frequently observed in nature (Cottenie 2005, Miller and Kneitel 2005). The neutral models (Hubbell 2001, Chave 2004) assume that the environment is homogeneous and individuals have equal abilities to settle and succeed locally. Further, it assumes that dispersal is limited and species loss is likely to occur due to stochastic extinction (Amarasekare 2003). Finally, the patch dynamics model describes at least two types of regional communities where limited dispersal is important. The first, classical type of patch dynamics, assumes spatial homogeneity of environmental conditions among patches (local communities) but, in contrast to the neutral models, assumes trade-offs between competition and dispersal, and that extinctions are both stochastic and deterministic (Leibold et al. 2004). The second type of patch dynamics model also assumes environmental homogeneity but additionally it assumes strong priority effects where the order of colonization caused by different dispersal rates among species (either due to fixed species traits such as in the first type, or by chance) leads to different and stable communities (Shurin et al. 2004).

Applying metacommunity theory in general, or the four metacommunity models in particular, to natural patterns of variation in community structure requires considerable empirical work (Leibold and Miller, 2004). Prior metacommunity research has concentrated primarily on formulating theoretical models consisting of competitors

(Amarasekare et al. 2004). Only some of the models have been empirically tested (see Ellis et al. 2006), including the neutral models (Bell 2001, Hubbell 2001, McGill et al. 2006) and the effect of competition and colonization trade-offs on species coexistence (Levine and Rees 2002, Mouquet et al. 2004, Yu et al. 2004, reviewed by Ellis et al. 2006, Cadotte 2007). Other metacommunity studies have examined the role of connectivity and dispersal between patches (Gonzalez et al. 1998, Gonzalez and Chaneton 2002; Forbes and Chase 2002), the effects of dispersal and predation at local and metacommunity scales (Kneitel and Miller 2003, Cadotte 2006), or used spatial position as a proxy for dispersal and decomposed variation in community structure into that explained by either environmental or spatial processes (Cottenie 2005).

The above studies tended to associate one single model with the whole metacommunity, without making any systematic distinction among different categories of species. However, some species show broad environmental tolerances (habitat generalists), while others have very specific and narrow environmental tolerances (habitat specialists) and these two species categories have different population dynamics (Kolasa and Li 2003). For example, variation in population density is higher in habitat specialists than in generalists (Kolasa and Li 2003). Similarly, habitat specialists use smaller habitat units, which are nested within the larger ones (Kolasa and Pickett 1989). This has another consequence because species which use smaller habitat units tend to have lower

population densities as a consequence of decreased efficiency in finding suitable patches

and mortality during dispersal (Kolasa and Romanuk 2005). Habitat availability appears

to govern habitat specialists more than generalists that utilize a broader range of habitat

types (Munday et al. 1997; Bean et al. 2002). When the availability of habitat, whether

aquatic, terrestrial or biotic (e.g., mutualists), is altered dramatically, its effect should be

higher on abundance of habitat specialists (Vazquez and Simberloff 2002), as observed in

many communities (see in Julliard et al. 2004, Swihart et al. 2003, Cleary and Genner

2004, Munday 2004). Habitat specialists are more susceptible to extinction then

generalists when habitat conditions are altered, and increasing levels of habitat loss and

fragmentation raise concern about the future of these species (Tilman et al. 1994, Travis

2003). Recognition of such differences implies the need for different predictions about

specialists versus generalists dynamics under different metacommunity models.

We postulate that dispersal will play a lesser role in explaining the distribution of

habitat specialists, whose distribution and variation are instead more likely to depend on

habitat properties (Kolasa and Romanuk 2005). In contrast, habitat generalists should be

more strongly affected by distances between sites than by habitat properties. Thus, we

hypothesize that environmental variables will account for more of the explained variation

in the abundance and spatial distribution of habitat specialists, while spatial variables

based only on site location (which we use as proxy measures of dispersal) will explain

relatively more of the variation in habitat generalists. To test these hypotheses, we used a model system of 49 natural rock pools inhabited by 69 invertebrate species. The available data set consisting of nine sets annual records of species abundance and physical attributes of rock pools allowed us to determine how consistently different metacommunity models applied over time and to consider the interplay between theoretical constructs and the natural variation of different categories of species.

METHODS

Study site

We conducted the study along the ocean shoreline at the Discovery Bay Marine Laboratory, University of the West Indies, on the northern coast of Jamaica (18^0 28' N, 77^0 25' W, Figure 1-3). For the study, we selected 49 rock pools (Figure 1-3) with a volume of no less than 500 ml, situated on fossil reef, within a 25 m radius of mixed land and sea environment. The pools in this small area had varying environmental characteristics. The rock pools used in this study ranged from 13 to 105 cm in width and length, and 1 to 37 cm in depth (mean depth = 12.8 ± 8.3 SD). Volumes ranged from 0.5 L to 115 L (mean = 12 L ± 21 SD). On average, the rock pools were located within 1 m of the nearest rock pool, and none were separated by more than 5m from the nearest pool. Their elevation above sea level ranged from 1 to 235 cm (mean = 76.6 ± 80.1 SD) at high

tide, with the tide rarely exceeding 30 cm. A few pools received some tidal influx (although tidal flooding did not occur daily), but most were maintained by atmospheric precipitation and, very occasionally, ocean spray.

Sampling design

Annual surveys were carried out between December 28 and January 11 from 1989 to 2008 and once in early June, in 1997. However, no data were collected in winter of 1995. We measured pool temperature, salinity, dissolved oxygen concentration, pH, turbidity and specific conductivity, usually on the day of biotic sample collection or one day prior, using a multiprobe sondes (DataSonde from Yellow Springs Instruments, Yellow Springs, Ohio or Hydrolab Corporation, Austin, Texas, USA). Biotic samples were collected by taking 500 ml of water from each pool after stirring the pool to dislodge organisms from its sides and bottom and to homogenize their distribution. Each pool water sample was then filtered through a 63μm net to separate invertebrates, which were immediately transferred to a 50-ml vial and preserved in 50% ethanol. The biotic samples were sorted, identified, and counted in the laboratory using dissecting and compound microscopes.

Although invertebrate samples have been collected from the rock pool system for more than a decade, identification and enumeration of the full set of invertebrate samples for all 49 pools has only been completed for nine years at this time. We used all 9 years

of available data in our analyses. A total of 69 species were collected including ostracods (20 species), copepods (including two harpacticoid and three cyclopoid species), cladocerans (5 species), worms (15 species, including oligochaetes, polychaetes, and turbellarians), aquatic insects (18 species), and other crustaceans (6 species). The abundance data used in the analyses are expressed as the total number of individuals collected in a 500 ml sample of pool water on a given sampling date.

Habitat specialization

Among the 69 species, 45 were rare and found only once or twice in the study area in the entire 9 years of sampling. Due to their limited occurrence, these species might appear to be specialized even if they are not and we therefore excluded them from the analysis. For the remaining common 24 species that were included in further analyses, we used Levins' approach (Levins 1968) to measure their habitat specialization (niche breadth) by computing:

$$B_j = 1 / \sum_{i=1}^{N} P_{ij}^2$$

where B_j= niche breadth, P_{ij} = the proportion of the individuals of species j in resource state i. We explicitly chose this method because it determines habitat specialization based on niche breadth (B) as a function of uniformity of the distribution of species abundance among the resource states for a community at hand (Levins 1968, Colwell and

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Futuyma 1971). Since we defined "resource state" as one habitat patch or rock pool in

this study, irrespective of local environmental conditions or spatial locations, the

calculated niche breadth is not directly related to the environmental variables within the

pools or to the spatial location of the different pools relative to one another in the

landscape. This independence of the niche breadth measure from environmental and

spatial variables was a necessary condition to prevent potential circularity of inferences.

The niche breadth properties are provided in Appendix 2-1.

General descriptive statistics of the 24 common species used in the study are

provided in Appendix (Table Appendix 2-2). Niche breadth for the 24 species ranged

from 2.50 to 32.72. Species with higher niche breadth values were those that used a

broader range of resource states. Thus, species with higher and lower values of niche

breadth can be considered generalists and specialists, respectively. We arbitrarily selected

5 species with the greatest niche breadths (as generalists) and 5 species with the lowest

niche breadths (as specialists) for further analysis. The former included *Sesarma miersi*

(Rathbun), *Culex* sp., *Paracyclops fimbriatus* (Fischer), *Nitocra spinipes* Boeck, and

Ceriodaphnia rigaudi Richard, (niche breadth: from 21.21 to 32.72). The specialists

included two copepods (a cyclopoid sp. and a harpacticoid sp.), two worms (a nematode

and a dorvilleid polychaete), and one dipteran larva (family Dolichopodidae), with niche

breadths from 2.50 to 6.43. There was no significant relationship between average

density and niche breadth ($r^2 = 0.06$, slope = 0.03, p value for slope >0.21), suggesting

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that both the specialists and generalists contain a mix of abundant and rare species.

Species, environment, and spatial matrices

To determine whether environmental constraints or spatial dynamics better describe the metacommunity in discrete habitats, we partitioned the variation in species abundance among various environmental and spatial variables per sampling period. Specifically, we characterized local sites (rock pools) using species data, corresponding environmental data, and data describing spatial relationships among the rock pools.

a. Species data

We created species abundance matrices for the selected habitat generalists, habitat specialists, and all 24 species for each of 9 annual surveys. The species data sets were transformed using Hellinger transformations prior to ordination analysis (see Legendre and Gallagher 2001, Peres-Neto et al. 2006).

b. Environmental data

Romanuk and Kolasa (2002) have shown that water temperature, salinity, dissolved oxygen concentration, and pH strongly influence community composition in the rock pool system. Consequently, we used these four physicochemical parameters, along with rock pool volume and elevation (which have not been included in previous studies of the rock pools but which may shape community composition), in our analyses.

These six variables comprised the environmental matrix for each year. Average values were used whenever multiple measurements were taken in a given year.

c. Spatial data

We assumed that the spatial configuration of pools may affect rates of dispersal in various ways, with distance between pools playing a central role. To create a matrix for further analyses, we measured X and Y coordinates of the central point of each pool using an aerial map. We arbitrarily assigned 0,0 at the lower left corner of the map to create the coordinate origin. For the data set with the X–Y coordinates, the initial set of spatial variables consisted of all terms of a third-order polynomial of the two coordinate variables. The third order polynomial function helps to detect more complex spatial features in the species data set than a linear function (see Ripely 1981, Borcard et al. 1992).

Statistical analysis

We used redundancy analysis (RDA) (Borcard et al. 1992, Cottenie 2005, Vanschoenwikel et al. 2007) to determine the proportion of variation explained by environmental and spatial factors. We used a forward selection procedure on the full set of six environmental and nine spatial variables to construct an explanatory model for rock pool metacommunity structure and to determine which environmental and spatial variables explained invertebrate community abundances. The amount of variation in

species abundance that was explained uniquely by the spatial variables and environmental variables of the rock pools was compared. When testing for unique effects of spatial configuration, all selected environmental variables were used as covariables, a procedure that removes the contribution of those variables to the explained variance. Similarly, when testing for a unique effect of environment, all selected nine spatial variables were used as covariables. The total variation in community composition was partitioned into four components ([E], [S], [E|S] and [S|E], see Table 2-1). The statistical significance of these different components was evaluated by Monte Carlo permutations tests (1000 permutations under the reduced model). All RDA analyses were completed with CANOCO for Windows 4.5 (ter Braak and Šmilauer, 2002).

To determine whether the relative importance of local (environment) versus regional (spatial) factors differed for species with different habitat specializations, we performed similar tests separately on habitat generalists and specialists, for each sampling year. We used all nine years of data. Since the typical generation time of the species in our system is ~ 2-14 days (Romanuk et al. 2006), and the average time between sampling periods is 10.5 months, temporal autocorrelation between species abundances at these time scales will be minimal, and we treated the obtained variation components as independent estimates in our statistical tests. Treating years as replicates enabled the use of ANOVA to test for differences in the proportion of variation explained by pure

environmental and pure spatial components for each group of species. Furthermore, we used factorial ANOVA to determine interactions between species specialization groups and the components (pure spatial and pure environmental).

RESULTS

Overall, we found that both the spatial configuration and the environmental conditions of the rock pools affect invertebrate community structure (Table 2-1 and Figure 2-1). For all 24 species, the variation in species abundance was better explained by the pure spatial (~24% variation) than by the pure environmental component (~14% variation). The contribution of these two components were significantly different (ANOVA, $F_{1,16} = 40.91$, $p<0.001$).

The same pattern emerged when we restricted the analysis to habitat generalists only. Here, environmental variables also contributed less than spatial variables to the explanation of community variation. The pure environmental component accounted for only about 12% of the variation, while the pure spatial component explained about 27% of the variation. The contributions of pure spatial and environmental components were significantly different (ANOVA, $F_{1,16} = 32.77$, $p<0.001$).

A different picture emerged when we restricted the analysis to habitat specialists only. A combination of both pure environmental and pure spatial processes explained

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52% of the variation in species abundance, with the pure spatial component being a less influential contributor than the environmental component. These two components were also significantly different (ANOVA, $F_{1,16}$= 16.35, p<0.001).

In addition to significant differences between the contribution of spatial and environmental variables observed within each group of species, factorial ANOVA revealed a significant interaction ($F_{2,48}$ = 32.4, p<0.000) between specialization and the pure spatial and environmental components (Figure 2-1). This means that as species specialization increases, a notable shift takes place from the greater importance of spatial to the greater importance of environmental variables in determination of species' local abundance.

While the patterns exhibited by habitat specialists and generalists were consistent across sampling years, we further evaluated the importance of the six environmental variables for each group of species (all species, habitat generalists, and habitat specialists) in each sampling year. Overall, there was a significant effect of both elevation and salinity on invertebrate community structure in most years (Table 2-1). However, most of the environmental variables (elevation, salinity, temperature and oxygen) contributed significantly to the explanation of variation in the community composition of the specialists, but only elevation and occasionally some other variables were significant for the generalists.

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Table 2-1. Variance partitioning among environmental and spatial variables for the three sets of data (all 24 species, habitat specialists, and habitat generalists) for each of the nine years of study of the rock pools metacommunity located at the DBML. Abbreviations: E = variation explained by environmental variables; S = variation explained by spatial variables; E|S = variation explained by pure environmental variables (contribution of S removed); and S|E = variation explained by pure spatial variables (contribution of E removed). Bold indicates the value is significant at $p \leq 0.05$. (Actual p values are given in Appendix 2-2).

Years	Group of species	Variance explained (%)			
		E	S	E|S	S|E
1989 Dec.	All species	**31.1**	**41.9**	14.7	**25.5**
1990 Jan.		**30.1**	**45.1**	14.1	**29.1**
1991 Jan		**28.2**	**37.7**	**15.7**	**25.2**
1992 Jan.		**30.1**	**45.1**	14.1	**29.2**
1993 Jan.		**30.1**	**32**	**16.6**	18.5
1994 Jan.		19.1	**30.8**	13.6	**25.3**
1997 Jan.		**38.2**	**38.5**	**17.4**	**17.8**
1997 Jun.		**31.1**	**46.9**	10.5	**26.2**
1998 Jan.		**32.5**	**43.4**	10.8	**21.8**
Average		30.1	40.2	14.2	24.3
1989 Dec.	Habitat generalists	**30.7**	**47**	12.5	**28.3**
1990 Jan.		**27.3**	**46.6**	7.9	**27.1**
1991 Jan		**32.1**	**44.5**	10.7	**20.1**
1992 Jan.		**32.4**	**55.2**	14.3	**37.1**
1993 Jan.		**31.5**	**30.9**	**20**	**29.3**
1994 Jan.		18.7	**35.4**	14.7	**33.9**
1997 Jan.		**42.9**	**49.9**	10.2	17.2
1997 Jun.		**29.1**	**50.1**	8.6	**29.5**
1998 Jan.		**36.3**	**44.5**	11.4	19.6
Average		31.2	44.9	12.3	26.9
1989 Dec.	Habitat specialists	**44.5**	23.1	**35.2**	14.4
1990 Jan.		**45.1**	23.6	**35**	13.4
1991 Jan.		**26.3**	24.1	**22**	19.8
1992 Jan.		**40.1**	22.1	**31.7**	13.7
1993 Jan.		**37.8**	21.6	**36.9**	19.7
1994 Jan.		**30.5**	**32.7**	12.8	10.6
1997 Jan.		**65.9**	**29.3**	**44.9**	**24.1**
1997 Jun.		**71.9**	**30.9**	**48.4**	**27.5**
1998 Jan.		**64**	23.7	**48.6**	8.3
Average		47.3	25.7	35.1	16.8

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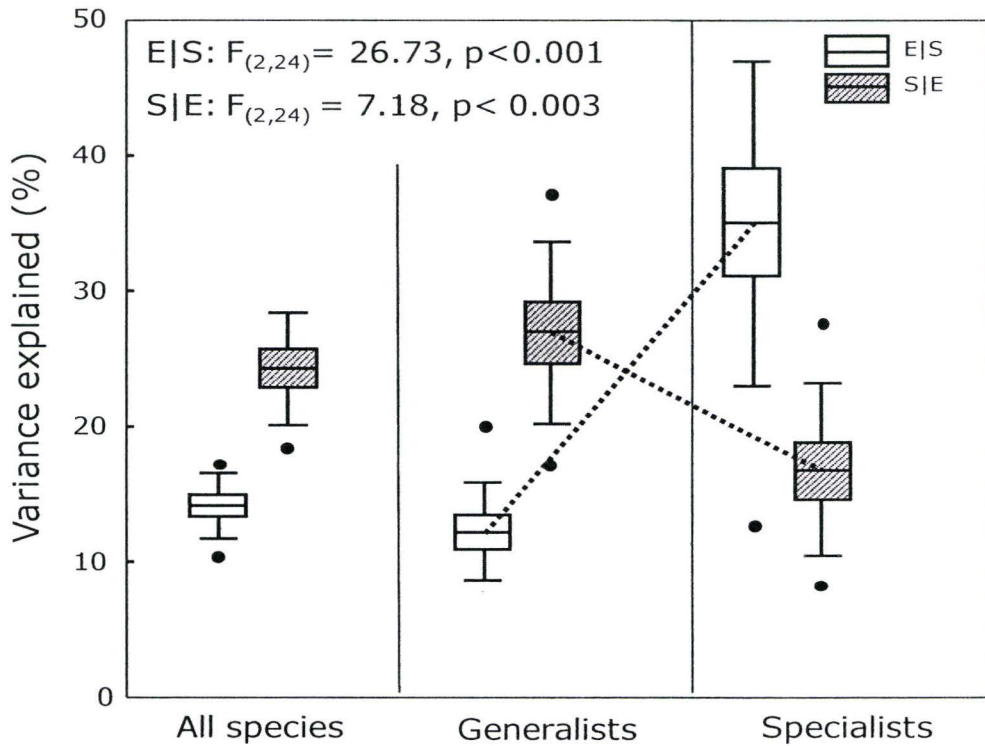
Figure 2-1. The relative contribution of pure environment (E|S) and pure spatial (S|E) components in explaining the variation in abundance of three species groups for the different sampling periods. Boxes represent the inter quartile range, the central bar represents the mean, the whiskers represent the standard error, and the points are outliers outside 1.5 times the distance of the inter quartile range. Dotted lines connect mean values of explained variation and illustrate a significant interaction effect between species specialization groups and the components (E|S and S|E).

Table 2-2. Relative contribution (percentage of total variation) of each of six environmental variables for the community structure of three species groups: all species, habitat generalists and habitat specialists. Only p-values ≤ 0.05 are reported.

Years	Temp. %	p	Salinity %	p	Oxygen %	p	pH %	p	Volume %	p	Elevation %	p
All species												
1989 Dec.	1		3		8	0	2		3		14	0
1990 Jan.	1		3		7	0	3		2		14	0
1991 Jan.	4		15	0	1		1		2		5	0.04
1992 Jan.	2		5	0.04	3		5	0.04	2		13	0
1993 Jan.	3		6	0.03	3		2		1		15	0
1994 Jan.	5	0.03	2		1		1		2		8	0.01
1997 Jan.	8	0	5	0.04	4	0.05	5	0.04	2		14	0
1997 Jun.	2		9	0	1		1		1		17	0
1998 Jan.	5	0.01	2		2		2		5	0.03	16	0
Generalists												
1989 Dec.	0		1		4		4		2		20	0
1990 Jan.	0		3		4		5	0.05	1		14	0
1991 Jan.	3		5	0.05	2		0		2		20	0
1992 Jan.	1		3		2		6	0.03	2		18	0
1993 Jan.	5	0.03	1		7	0	4		1		13	0
1994 Jan.	3		1		3		0		2		9	0
1997 Jan.	5	0.05	3		0		7	0.01	6	0.03	21	0
1997 Jun.	3		4		3		3		1		15	0
1998 Jan.	2		3		6	0.03	5	0.04	1		19	0

Specialists

1989 Dec.	5	0.04	23	0	6	0.03	1		0	9	0.01
1990 Jan.	5	0.04	24	0	5	0.04	1		1	9	0.01
1991 Jan.	19	0	2		1		2		0	2	
1992 Jan.	0		12	0	10	0	6	0.04	1	11	0
1993 Jan.	2		14	0	9	0	7	0.01	0	6	0.04
1994 Jan.	8	0	8	0.01	6	0.05	6	0.05	1	1	
1997 Jan.	31	0	7	0.01	14	0	1		1	12	0
1997 Jun.	32	0	6	0.02	21	0	1		1	10	0
1998 Jan.	34	0	8	0.01	9	0	2		1	10	0

DISCUSSION

Our results show that both environmental and spatial processes play roles in structuring species communities in the rock pools metacommunity. However, which of these processes is important depends on the degree of habitat specialization. The expectations that variation of the abundance of habitat generalists would be more influenced by the spatial distribution of pools and that that of specialists would be more influenced by the local environmental condition of the pools were upheld by our analyses. Several studies on zooplankton communities that have used a similar approach to partitioning of variation into different components produced mixed results regarding which factors (regional or environmental) are important in determining community structure. In some cases (e.g., Pinel-Alloul et al. 1995, Cottenie et al. 2003, Vanschoenwikel et al. 2007), environmental variables dominated over spatial factors, but in others (e.g., Cottenie 2005), spatial factors were more important in determining community structure. Given our results, it is possible that the systems studied by other authors had a different ratio of specialists to generalists. Such differences might account for the different results and conclusions and thus underscore the need to recognize species specialization as a dimension relevant to testing metacommunity models. Ellis et al. (2006) also found it difficult to satisfactorily fit any single metacommunity model to a natural community.

Our analysis has shown that environmental variables, salinity and elevation in particular, explain a significant portion of the variation in the total abundance of rock pool invertebrate species. Salinity has previously been shown to affect both species diversity (Jorcin 1999) and variation in species abundance (Therriault 2001). Since rock pools span a range of salinity concentrations from freshwater to seawater, salinity concentration (or its variability) might be expected to affect individual species differently, depending on their tolerances. In fact, we found that salinity strongly influences species composition of specialists and of all species combined, but play a less important role for generalists. Elevation, on the other hand, was important in explaining the community composition for all three groups of species. While differences in elevation among pools seem small (approx. 0- 2.5 m above sea level), pools at lower elevation are more often disturbed by ocean spray, wave action, or occasional flooding. In addition, pools at higher elevation received relatively more shade from nearby trees than pools at lower elevation. These factors may affect water temperature or rates of leaf litter accumulation in the pools, both of which may affect species composition and abundance. Previous studies have shown that elevation, nutrients, and disturbances strongly affect zooplankton community composition (e.g., Rautio 1998). Consequently, the range of variation in environmental conditions created through elevation might reasonably be expected to affect species differentially. Of the remaining physicochemical variables most were significant in explaining distribution and abundance of specialists in most

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study years, but not in generalists or all species combined, except on few occasions. Since both species groups, specialists and generalists, were analyzed based on the same sample size (number of pools), we conclude that environmental variables influence specialists much more than they influence generalists.

The above examination of the relative importance of local and regional processes for generalists and specialists indicates that different metacommunity models (Leibold et al. 2004, Cottenie 2005) apply best to different categories of species and at different times. Among these, the species sorting model expects that species composition is affected by local environmental factors (Cottenie 2005). This model appears suitable for habitat specialists, for which environmental variables were most important. Our results therefore support the inference that species sorting was the most important process in determining the structure and dynamics of specialists in this system. However, on two sampling occasions, both spatial and environmental factors were significant predictors of the variation in specialist abundance. This suggests that a combination of factors played roles in determining abundance patterns, as postulated by species sorting and mass effects or dispersal limitation models (e.g., Cottenie 2005).

When generalists were considered alone, the relative importance of the various metacommunity-shaping processes changed. Spatial variables became important, with patch dynamics or neutral models being the more appropriate for six out of nine years. The patch dynamics model could explain the observed patterns if habitat generalists are

better dispersers in the landscape and/or if they were better able to persist in any given location as a consequence of strong priority effects. In addition, habitat generalists might be structured by neutral dynamics, since the environment must seem relatively more homogeneous to generalist than to specialist species. In one of the nine years, both environmental and spatial variables significantly explained variance in generalist abundance, suggesting that a combination of processes associated with species sorting and mass effect or dispersal limitation models were occasionally important for generalists. Thus, the distribution and variation of generalists in a metacommunity are mainly explained by patch dynamics or neutral models, and occasionally by the mass effects model. This variability in model suitability may be due to seasonal or annual changes in the severity of environmental conditions in the rock pool system. For example, the absence of rain for a few weeks may deepen the gradient of salinity, temperature, and desiccation frequency, and/or change the spatial environmental regime. The magnitude of such changes may be in excess of the tolerance ranges of generalists in some pools, causing them to respond to local physicochemical conditions rather than to regional structuring processes.

The variation patterns for all species are a combination of the patterns exhibited by both the habitat specialists and generalists. This suggests a mechanism to the decision tree proposed by Cottenie (2005), who equated the presence of both environmental and spatial signals to a combination of processes associated with species sorting and mass

effects models. The current results suggest that one way of obtaining such a signal is by having one subset of species being strongly influenced by environmental processes and another subset of species is strongly influenced by dispersal processes.

Approximately half of the variation in the abundance of both groups (habitat generalists and specialists) was left unexplained by the environmental and spatial variables. This amount of unexplained variation is fairly common in ecological studies since variation in species abundance data is often very high (ter Braak and Šmilauer 1998; Cottenie 2005). This may be due to stochastic variation in species population growth rates, other important environmental variables not included in the study, biotic interactions, a mismatch in the temporal resolution of environmental and biological data, or any combination of the above. For example, we have no data on bacterial dynamics, which may be linked to the performance of invertebrate species. Furthermore, short-term variation in physicochemical factors may have escaped our monitoring regime but affected densities of invertebrate later, at the time of their collections.

In conclusion, as hypothesized, we found that environmental processes better explained variation for habitat specialists than for habitat generalists. This finding points to the composite nature of metacommunity dynamics, where different categories of species show interactions with different dimensions of the environmental template. This has several important implications. First, the differentiation between different species extends the current metacommunity framework to potentially different metacommunity

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models for different groups of species within a metacommunity. Second, further progress in testing and applying the current metacommunity models requires that differences in ecological species traits, particularly those pertaining to habitat specialization, be examined before conclusions are made about model suitability. Another recent metacommunity oriented study (Schlesinger et al. 2008) obtained a similar result. They demonstrated that urbanization stressors affect the richness of bird groups differently depending on their life history traits (cavity versus open nesters). Also, longer time series of data are desirable to avoid spurious model evaluations. Otherwise, fitting one metacommunity model for all species in a metacommunity may lead to faulty inferences about both the characteristics of a metacommunity in question and the validity of the model. Since one of the goals for fitting a metacommunity model is to make predictions about dynamics of species, fitting a model that is inappropriate for a significant number of species is likely to lead to wrong predictions.

Our findings also have some implications beyond metacommunity theory and tests. For example, biodiversity conservation may need to recognize the need of specialists for the specific habitat attributes. By contrast generalists seem to respond more to patch configuration and connectivity. Such differential responses to habitat properties and habitat configuration may impose different selective pressures and require different adaptations for survival and dispersal among specialists and generalists inhabiting the same community. Thus, one approach to biodiversity conservation may be insufficient to

accomplish two somewhat separate conservation goals of maintaining diversity inclusive of different categories of species.

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APPENDIX 2.1

Niche breadth calculations and properties

Although several other measures are available to quantify habitat specialization (i.e., niche breadth in our context) such as species distribution along environmental gradients (e.g., Dolédec et al. 2000) or species co-occurrences data (Fridley et al. 2007), we explicitly chose the Levins' approach because it determines habitat specialization based on a particular measure of niche breadth (B). Here B is a function of uniformity of distribution of species abundance among the resource states for a community at hand (Levins 1968, Colwell and Futuyma 1971). This method assigns different niche breadths even for species that have the same overall abundance in the landscape of patches if one species is uniformly distributed (generalist) while the other shows clumped distribution (specialist). Further, B is independent of the environmental, biological and spatial variables measured for the rock pool metacommunity because we defined "resource state" as one habitat patch or rock pool in this study. The calculated niche breadth is not directly related to the environmental variables within the pools, or the spatial location of the different pools relative to each other in the landscape. This is a necessary condition to avoid circular arguments.

Thus this method is most suitable given our aim to assess the effects of spatial and environmental variables on metacommunity dynamics. Other methods are burdened with features that might compromise our inferences. The method we chose is commonly used in many ecological studies to quantify habitat specialization (e.g., Feldhamer et al. 1993, Fugi et al. 2008). Finally, to verify that the Levins' measure adequately captures species specialization, we calculated niche breadth based on environmental variables alone using Canonical Correspondence (CCA) and found it was reasonably well correlated with the former. While we cannot use the CCA based niche breadth in our variance partitioning analysis for the reasons stated above, the convergence of the two methods reinforces the suitability of the Levins' measure.

$y = 1.96x + 46.16$

$R^2 = 0.47$, $p < 0.001$

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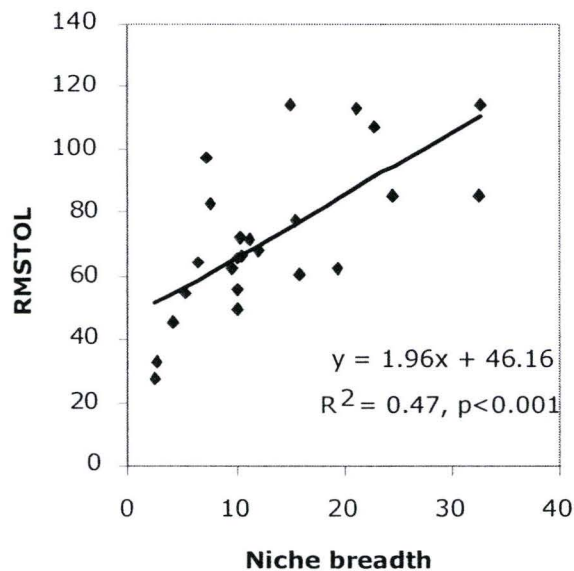
Figure Appendix 2-1. The relationship between tolerances (root mean square standard deviation across four axes, RMSTOL) and niche breadth calculated by Levins' method (1968). The RMSTOL was obtained for each species using CANOCO's Canonical Correspondence Analysis from four significant CCA axes.

Table Appendix 2-1. Descriptive statistics of the data set. AD represents average density of each species across all years and pools, SE: standard error; Min: minimum density, Max: maximum density.

Species name	AD	SE	Min	Max	Niche
Sesarma miersi Rathburn	6.23	1.03	0	149	32.72
Culex sp.	3.38	0.56	0	71	32.52
Paracyclops fimbriatus (Fischer)	2.49	0.48	0	73	24.42
Nitocra spinipes Boeck	93.1	59.2	0	10845	22.81
Ceriodaphnia rigaudi Richard	61	12.8	0	1895	21.21
Cypridopsis cf. mariae Rome	62.2	13.7	0	2004	19.26
Candona sp.	6.02	1.48	0	227	15.84
Potamocypris sp.	184.2	20.9	0	3243	15.48
Orthocyclops modestus (Herrick)	92.9	23.4	0	6195	15.12
Tanypodid sp.	3.06	0.86	0	191	12.08
Alona davidii	34.7	10.2	0	2160	11.31
Heterocypris sp.	19.16	5.78	0	1325	10.66
Cytheromorpha sp.1	12.65	3.86	0	831	10.39
Leidigia leidigi	1.91	0.59	0	91	10.13
Cypricercus sp.	11.11	3.45	0	803	10.1
Oligochaete sp.	9.3	2.89	0	636	10.08
Gyratrix hermaphroditus	3.76	1.2	0	322	9.57
Polychaete T	0.62	0.22	0	46	7.61
Metis sp.	2.1	0.77	0	164	7.32
Dipteran sp.	0.15	0.06	0	14	6.44
Dorsovilleid polychaete	1.99	0.43	0	111	5.3
Copepod sp.	30.5	14.9	0	3986	4.14
Nematode sp.	84.9	27.1	0	8390	2.72
Copepod sp. 2	4.45	2.81	0	854	2.5

Table Appendix 2-2. Variance partitioning among environmental and spatial variables for the three sets of data: all 24 common species (all species), habitat specialists, and habitat generalists for each of the nine years of study of the 49 rock pools located at the DBML. Abbreviations: E= variation explained by environmental variables; S= variation explained by spatial variables; E|S= variation explained by pure environmental variables (contribution of S removed); and S|E= variation explained by pure spatial variables (contribution of E removed). 100-[E+S|E] = unexplained variation, EøS= variation shared by environmental and spatial variables. The significance was determined from Monte Carlo permutations test under the reduced model from partial RDA.

Years	Groups	Variance explained (%)									
		E	p	S	p	E|S	p	S|E	p	EøS	100-[E+S|E]
1989 Dec.		31.1	0.00	41.9	0.00	14.7	0.47	25.5	0.00	16.4	43.4
1990 Jan.		30.1	0.00	45.1	0.00	14.1	0.56	29.1	0.00	16.0	40.8
1991 Jan		28.2	0.00	37.7	0.00	15.7	0.02	25.2	0.00	12.5	46.6
1992 Jan.		30.1	0.00	45.1	0.00	14.1	0.19	29.2	0.00	16.0	40.7
1993 Jan.	All species	30.1	0.00	32.0	0.00	16.6	0.02	18.5	0.07	13.5	51.4
1994 Jan.		19.1	0.11	30.8	0.00	13.6	0.48	25.3	0.02	5.5	55.6
1997 Jan.		38.2	0.00	38.5	0.00	17.4	0.03	17.8	0.02	20.8	44.0
1997 Jun.		31.1	0.00	46.9	0.00	10.5	0.82	26.2	0.01	20.6	42.7
1998 Jan.		32.5	0.00	43.4	0.00	10.8	0.39	21.8	0.00	21.7	45.7
Average		30.1		40.2		14.2		24.3		15.9	45.7
1989 Dec.		30.7	0.00	47.0	0.00	12.5	0.48	28.3	0.00	18.2	41.0
1990 Jan.		27.3	0.00	46.6	0.00	7.9	0.76	27.1	0.00	19.4	45.6
1991 Jan	Habitat generalists	32.1	0.00	44.5	0.00	10.7	0.20	20.1	0.05	21.4	47.8
1992 Jan.		32.4	0.01	55.2	0.00	14.3	0.19	37.1	0.00	18.1	30.5
1993 Jan.		31.5	0.00	30.9	0.00	20.0	0.02	29.3	0.01	11.5	39.2

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1994 Jan.		18.7	0.11	35.4	0.00	14.7	0.23	33.9	0.00	4.0	47.4
1997 Jan.		42.9	0.00	49.9	0.00	10.2	0.38	17.2	0.17	32.7	39.9
1997 Jun.		29.1	0.01	50.1	0.00	8.6	0.86	29.5	0.03	20.5	41.4
1998 Jan.		36.3	0.00	44.5	0.00	11.4	0.32	19.6	0.07	24.9	44.1
Average		31.2		44.9		12.3		26.9		19.0	41.9
1989 Dec.		44.5	0.00	23.1	0.17	35.2	0.00	14.4	0.24	9.3	41.1
1990 Jan.		45.1	0.00	23.6	0.15	35.0	0.00	13.4	0.30	10.1	41.5
1991 Jan		26.3	0.01	24.1	0.19	22.0	0.02	19.8	0.24	4.3	53.9
1992 Jan.		40.1	0.00	22.1	0.70	31.7	0.02	13.7	0.89	8.4	46.2
1993 Jan.	Habitat specialists	37.8	0.00	21.6	0.41	36.9	0.00	19.7	0.09	0.9	42.5
1994 Jan.		30.5	0.01	32.7	0.00	12.8	0.56	10.6	0.95	17.7	58.9
1997 Jan.		65.9	0.00	29.3	0.05	44.9	0.00	24.1	0.05	21.0	10.0
1997 Jun.		71.9	0.00	30.9	0.04	48.4	0.00	27.5	0.04	23.5	0.6
1998 Jan.		64.0	0.00	23.7	0.16	48.6	0.00	8.3	0.42	15.4	27.7
Average		47.3		25.7		35.1		16.8		12.3	35.8

APPENDIX 2-1: LITERRATURE CITED

(Only those in the Appendix but not in the main paper are included here)

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CHAPTER 3 :

Species richness and environmental fluctuation affect population synchrony in a metacommunity

This chapter has been submitted in the Journal of Animal Ecology (partial citation follows). This chapter has been re-formatted to maintain consistency throughout the thesis.

Pandit, S.N., J. Kolasa, and K. Cottenie. Species richness and environmental fluctuation affect population synchrony in a metacommunity. *Journal of Animal Ecology* (*Submitted*)

RATIONALE AND OBJECTIVES

The chapter departs from the prevailing practice where most tests of metacommunity rely on snapshot patterns of species distributions and abundance in order to assess the relative importance of local and regional factors. In contrast, I thought that, because populations fluctuate continuously in space and time, snapshot patterns may be insufficient for producing a reliable picture. To see if my conclusions from Chapter 2 as to the differences in application of models to specialist species vs. generalist species hold under continuous change of population size, I needed an experimental laboratory approach. The main reason for the experimental approach is the relative ease with which populations can be monitored as opposed to a natural setting. Because the metacommunity models differ in predictions with respect to effects of local environmental conditions on species performance, I needed two sets of variables to satisfy the requirement for model fitting: continuous population data and variation in environmental conditions. In addition I needed to mimic dispersal. Specifically, the objective of this chapter had three objectives. One was to explore that comparative role of environmental fluctuation in temporal population dynamics among generalist, specialist and intermediate species. The second objective was to test some aspects of the relationship between environmental variation and synchrony. The third objective was to

see if the results and inferences pertaining to the above problems depend on species diversity.

My general approach was to look at population synchrony. By using population synchrony, which is a correlation between population sizes in two locations, and by introducing controlled dispersal, I have effectively employed a metacommunity perspective. However, according to much research synchrony and environmental variation can be related in various ways. Furthermore, species richness is believed to stabilize communities. My experiment allows me to examine its contribution and impact on synchrony. I compared the level of population synchrony in a factorial design including low and high diversity treatments and different magnitudes of environmental fluctuations for different species (generalist, intermediate and specialist). I found that:

- Population synchrony in a metacommunity was higher in a specialist than generalist species when environmental fluctuation was high.

- The metacommunity with higher species richness had low level of population synchrony.

These results confirm that environmental factors have different impact on species with different specialization when seen through snapshot or temporal dynamics lens. Species richness reduces the effects of environmental fluctuations on population synchrony.

ABSTRACT

Fluctuations of local populations may show a degree of synchrony when they experience significant dispersal (local populations are a metapopulation) or correlated environmental variability, or concurrent predation. Potentially, synchrony may be an important variable in multispecies systems but its nature and implications have not been explicitly examined. Because the number of coexisting metapopulations (richness) is known to affect population variability (stability) of community members, we assume that in addition to dispersal and external factors, the presence of other species (metacommunity) may affect population synchrony as well. Further, it might do so differently under different regimes of environmental fluctuation, EF. We hypothesized that spatial synchrony of population among the patches should be higher in a low richness metacommunity than in a metacommunity with high richness. Additionally, we predict that synchronization is more likely when environmental fluctuation becomes high, but with the specific effect increasing with species sensitivity to fluctuating environmental factors. We examined the synchronizing effects of environmental fluctuation on three invertebrate species of dissimilar specialization in experimental metacommunities of variable richness. We used three levels of EF by manipulating salinity of the culture media. We found that species responded differently to EF treatments: high EF enhanced population synchrony for the specialist and intermediate species but not for the generalist

species. Furthermore, monocultures exhibited higher population synchrony than metacommunities of 2-4 species. Our findings emphasize that the magnitude of environmental fluctuation and species richness interact. It suggests that in natural communities the presence of other species may alter the expected effects of environmental fluctuation on population synchrony. Importantly, our results suggest that biotic diversity may actually stabilize metapopulations through disrupting synchrony.

Key words: species richness, population synchrony, metacommunity, environmental fluctuations, cross correlation function, habitat specialization gradient

INTRODUCTION

Understanding the causes and processes of species extinction is one of important goals of ecology. Population synchrony, simultaneous rise and fall of population abundances in disjoint patches, is thought to be one of the processes of species extinction because it reduces the probability of effective rescue from neighbouring patches (e.g., Ruxton 1994, Paradis 1997). According to prior research, an increase in migration rates among patches (Heino 1997, Lande et al. 1999, Ripa 2000), large scale correlated environmental variability (Moran 1953, Royama 1992, Hudson and Cattadori 1999) and predation and predator switching (e.g., Ims and Andreassen 2000) act alone or together to synchronize fluctuations among populations occupying different but adjacent locations. Population synchrony has been found to occur in many taxa, including birds (e.g., Paradis et al. 1999 and 2000), fishes (e.g. Cattanéo et al. 2003, Tedesco et al. 2004) insects (e.g., Hanski and Woiwod 1993, Myers 1998), and mammals (e.g., Moran 1953, Sinclair et al. 1993, Hudson and Cattadori 1999). In spite of empirical evidence for the role of some of these factors, other studies failed to support the proposition that population synchrony is driven by correlation among the shared local density-independent factors such as climatic, edaphic, or anthropogenic factors (Ranta et al. 2006, p. 81).

Most synchrony studies are conducted in the metapopulation framework with explicitly and implicitly assuming that the populations of constituent species fluctuate

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independently of each other irrespective of the richness and composition of a community (Loreau and Mazancourt 2008). However species richness is known to affect population variability (stability) of community members and any population is also affected by other local processes, including broader community dynamics (via species interactions) as well as spatial or regional processes (e.g., dispersal from regional pool species) (Holyoak et al. 2005). Recognition of the potential importance of regional and local factors implies the need for evaluation of their relative importance to species synchrony in a metacommunity framework since theoretical studies (e.g., Heino et al. 1997, Earn et al. 2000) predicted that synchrony in the fluctuation of populations increases the risk of global metapopulation extinction.

The metacommunity framework addresses the issues of dispersal and species interactions (Leibold et al. 2004) and it focuses on the temporal dynamics and stability of communities of a set of multi-habitats or multi-communities rather than of single community. Metacommunity is defined as a set of local communities that are linked by dispersal of at least one species (Holyoak et al. 2005). Thus, the metacommunity framework offers a context for considering jointly metapopulations of different species in the interplay between local and regional processes. Recent theoretical work (Koelle et al. 2005) indicated that population synchrony induced in a metapopulation did not materialize at metacommunity scale, that is, it did not synchronize other members of the metacommunity. They showed that decrease in effective between-patch distance may

impede population synchrony because of the effect this change has on the migration patterns of other species. Possibly, the presence of other species affects response of a population to migration and environmental fluctuations by reducing the expected level of its synchrony with other populations.

Leibold and Mikkelson (2002) further indicate that temporal coherence (population synchrony) may also vary along an environmental gradient. Moreover, a recent study has shown (Pandit et al. 2009) that species with different traits display different dynamics within the same metacommunity. Habitat generalists respond more to spatial factors while specialist species respond more to local environmental factors. Since the response of a habitat specialist to environmental fluctuation could be potentially different from the response of a generalist, we hypothesized that level of synchrony would be affected by species traits. We further hypothesized that higher species richness implies more complex interactions, and we predicted that population synchrony in communities of low species diversity would be higher than in high diversity communities. Additionally, we predicted that synchronization should be greater when magnitude of environmental fluctuation is high, with the size of the effect depending on species tolerance to environmental factors. We tested the above hypotheses experimentally in artificially assembled aquatic metacommunities.

Our general approach was to look at synchrony in a metacommunity context. Specifically, we compared the level of population synchrony in a factorial design including low and high diversity treatments and different magnitudes of environmental fluctuations. Additionally, we examined the responses of three categories of species represented by one species each: a generalist, a specialist, and a species with an intermediate degree of specialization (the intermediate species in short).

METHODS

Experimental organisms

The experiment was conducted using four species: *Daphnia magna*, *Ceriodaphnia rigaudi*, *Potamocypris* sp. and *Nitocra spinipes*. The first species was collected from an old laboratory culture while the remaining three species were originally collected from tropical rock pools, Jamaica (detailed information in Kolasa et al. 1996) and then cultured in our laboratory. *Ceriodaphnia*, *Potamocypris* and *Nitocra spinipes* are among the most widespread and abundant species in Jamaican rock pools. These four species have high reproductive output and short generation times. Generation times can be substantially reduced at high average water temperature (Gillooly 2000). Based on Gillooly (2000) and Romanuk et al. (2006), average generation times for all species used in our experiment would range from 2 - 20 days.

Microcosm system

The experiment was executed in plastic cups that were 8 cm in diameter and 15 cm deep. The cups were filled with medium to a depth of 10 cm (volume 500 ml), which is the average size of our natural rock pools (Jamaican rock pools). The medium used for the experiment was prepared with concentration of 96 mg $NaHCO_3$, 60 mg $CaSO_4$, 60 mg $MgSO_4$ and 4 mg KCl in one liter distilled water (as suggested by Weber 1993). The single-cell green algae (*Chlorella*) cultured in five liter glass jar using distilled water and nutrients under sunlight. The algae were used as food for the experimental species. The density of the algae was estimated in hemocytometer to ensure consistent amounts of food provided. Saline solution for the experiments was prepared using analytical grade NaCl.

We linked populations into a metacommunity by weekly collecting 10 ml water samples with organisms from communities within each cluster of 4 communities (see design below, fig. 3-2), mixing all the samples together in one container and then returning 10 ml of water containing the mixture of propagules to the individual communities in each cluster of four communities.

Experimental design and sampling

We chose 3 species with different habitat specialization (*Daphnia*, *Ceriodaphnia* and *Potamocypris* sp.). We first tested the population dynamics of the three species at

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different salinities. We reared them separately in media with different salinity

concentrations (0, 2, 4 and 6ppt), over 3 weeks (June 3-June 24, 2007) to determine and

choose appropriate levels of salinity to create effective but non- destructive amplitude of

environmental fluctuations. A total of 12 microcosms (4 salinity levels × 3 replications)

were set up for each species to a total of 36 experimental microcosms. Initially, fifty

individuals of each species were placed in each experimental microcosm. Sampling

started 2 days after the beginning of the experiment by gently stirring water with a glass

stirrer and then taking three aliquots of 50-mL in volume from each experimental

microcosm at two days interval. The organisms were counted using a dissecting

microscope and then returned unharmed to their respective experimental microcosms.

Similarly, after enumeration, medium was replaced in each microcosm with fresh

medium of same salinity every 7 days. Food was added with the new medium as 50 ml

water with algae at concentration of 1.5×10^6 cells/ml.

The individuals of *Ceriodaphnia* and *Daphnia* survived in the salt concentration

of 6 ppt, but their density decreased at salinity of 6 ppt (Figure 1) to the point that

population of *Ceriodaphnia* disappeared after 14 days. In contrast, the density of

Potamocypris did not change in elevated salinity of 6 ppt. Thus, we defined

Potamocypris as a generalist, *Ceriodaphnia* as a specialist and *Daphnia* as a species with

an intermediate degree of salinity tolerance or specialization. We also used *Nitocra*

spinipes. Nitocra spinipes is a common harpacticoid species found in brackish water (0.5

to 30 ppt of salinity), with high reproductive output and short generation time (Steinarsdóttir and Ingólfsson 2004).

Based on the above experience, we chose to use three amplitudes of environmental fluctuation in the main experiment. In that experiment we alternated microcosm salinity and medium every 7 days. We used the following fluctuation regimes:

1) No fluctuation (and control); no change of salinity, always 0 ppt.

2) Low amplitude of environmental fluctuation (or Low EF); alternating between 0 ppt and 3 ppt every 7 days.

3) High amplitude of environmental fluctuation (or high EF); alternating between 0 ppt and 6 ppt every 7 days.

The main experiment was set up as an unbalanced factorial design, with four levels of species richness (in eight species combinations) and three amplitudes of environmental fluctuation (Figure 3-2).
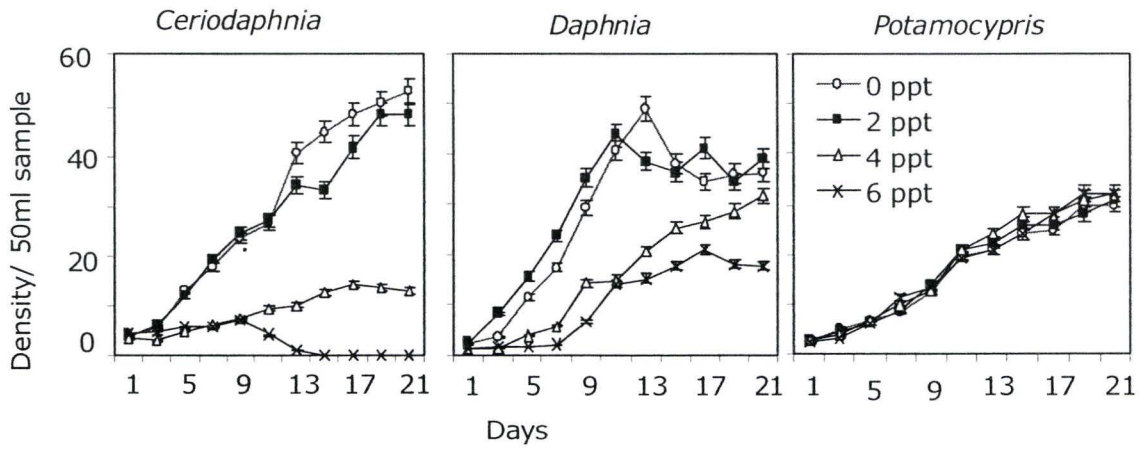
Figure 3-1. Population abundance of *Ceriodaphnia*, *Daphnia* and *Potamocypris* under different salt concentrations. Points are the mean ± standard error based on three replicates.

Among the eight species combinations we had three single-species microcosms (*Daphnia*, *Ceriodaphnia* and *Potamocypros*), three two-species combinations microcosms (*Daphnia* + *Ceriodaphnia*; *Daphnia* + *Potamocypris; Potamocypris* + *Ceriodaphnia*), one three-species combination (*Daphnia* + *Potamocypris* + *Ceriodaphnia*). In addition, we used one four-species combination using *Nitocra* (*Daphnia* + *Potamocypris* + *Ceriodaphnia* + *Nitocra*).

Community of each microcosm started with 100 individuals. When a microcosm contained more than one species, all species were initially introduced in equal proportions. Microcosms were sampled weekly, before salinity manipulations, by gently stirring the water with a glass stirrer and using a 50 ml dip container. We collected three aliquots of 50-mL in volume from each experimental microcosm weekly, counted individuals of each species with a dissecting microscope and we averaged the counts. We returned the individuals to their respective experimental microcosms following enumeration. The experiment was conducted in the laboratory at room temperature (24-25^{0}C) from August 5 to October 28, 2007. However, sampling started one week later, on the 12th of August. Light was provided for 12 hours per day by 2 fluorescent 40 W tubes placed 38 cm above the experimental microcosms. We changed the position of microcosms randomly every week to reduce possible effects of differences in the intensity of light on the microcosms.
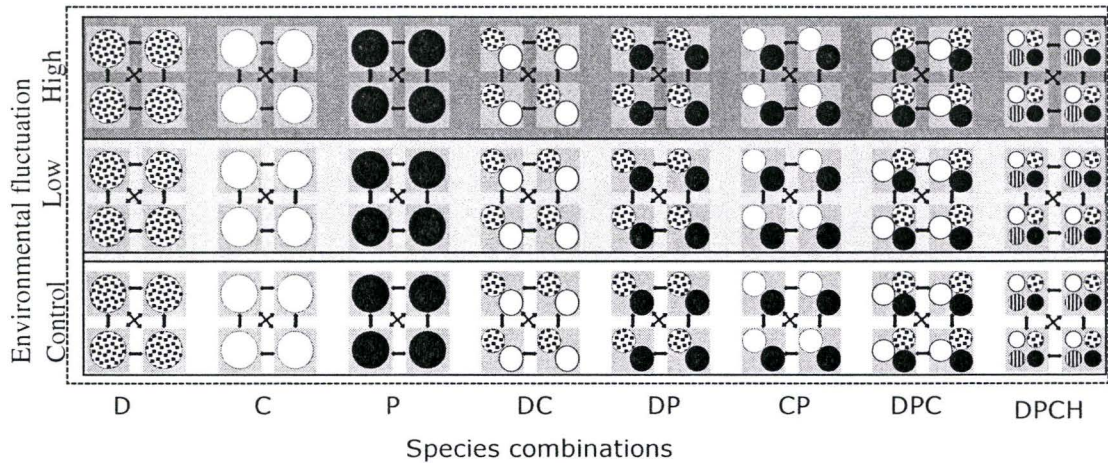
Figure 3-2. Experimental design: D, P, C and H represent *Daphnia magna*, *Ceriodaphnia sp.*, *Potamocypris sp.* and *Nitocra spinipes* respectively. Squares represent patches (microcosms), and each cluster of 4 patches is a metacommunity. Circles within the patches represent species, each shading patterns represents a different species. Patches with circle of one, two, three, and four shading patterns represent one, two, three, or four species, respectively. Similarly, size of the circle represents the initial number of introduced individuals of each species. The largest size represents 100 individuals and the smallest size 25 individuals. When a microcosm contained more than one species, all species were initially introduced in equal proportions.

Statistical analysis

First, for each species, we calculated the population growth ($r_{i,t}$) over time for each patch (microcosm) as differences between successive population estimates for each patch of each metacommunity in each environmental fluctuation treatment, such that $r_{i,t} = [((N_{i,t+1})-(N_{i,t}))/(N_{i,t})]$, where $N_{i,t}$ is the population estimate in each microcosm i at time t. As a measure of synchrony, we used cross-correlation coefficients, $\delta_{i,j}$, for each pair-wise combination of microcosms based on $r_{i,t}$ (Bjørnstad et al. 1999) within its four microcosms metacommunity. Noise in species data in ecological studies is often very high (ter Braak and Šmilauer 1998). Thus calculating cross-correlation coefficients ($\delta_{i,j}$) based on growth rates (r_t) can avoid the problems with long-term trends in the data associated with calculating synchrony based on measures of abundance (Liebhold et al. 2004). Thus, for each EF treatment and species richness, there were 6 cross-correlation coefficients since there were 4 patches (microcosms) in each metacommunity. We averaged these 6 cross correlation coefficients to obtain the synchrony per experimental unit (the metacommunity). For each species, we used the average cross-correlation coefficients for each metacommunity that contained that particular species: e.g. for *Daphia* (abbreviated as D) these were the D, DC, DP, DPC, and DPCH metacommunities (Fig 3-2). We decided to use this unbalanced but replicated design because of time constraints. Counting the individuals throughout the experiment to ensure that sampling did not affect the population dynamics with these fast generation times was the limiting

factor. We were unable to implement a completely balanced design due to the sample processing limitation because, for consistency, it was necessary to count all the samples within a short time frame.

RESULTS

Time series of population density showed that population size of all three species varied in time in all six treatments (Figure 3-1). Population synchrony in within individual metacommunities showed different pattern for the generalist as compared to the specialist and the intermediate species (Table 3-1). For all 3 species, although the interaction between EF and the species richness (SR) was not significant, the EF and SR affected differentially to species of different specialization (Table 3-1).

Population synchrony within individual metacommunities was significantly higher among the different EF treatments for intermediate and specialist species than for the generalist species (Table 3-1, Fig. 3-4). The effect of richness was surprisingly clear. Population synchrony significantly declined with species richness for all species in all experimental metacommunities (Fig. 3-4).

We found no correlation between the average density and the species richness for any of the three species (*Daphnia*: $r^2 = 0.63$, $p = 0.10$; *Ceriodaphnia*: $r^2 = 0.29$, $p = 0.34$ and *Potamocypris*: $r^2 = 0.05$, $p=0.71$), suggesting that the calculated population synchrony was not an artifact of population dynamics being dominated by the increase in density.
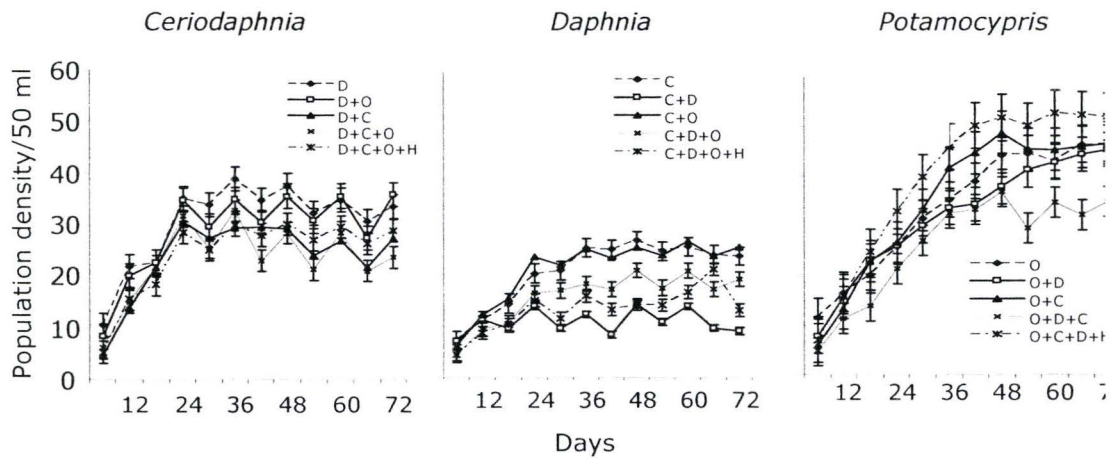
Figure 3-3. Population densities through the course of the experiment for three species. The points are the averaged population size of each metacommunity ± standard error based on three environmental fluctuation treatments for each species combination scenario.

Table 3-1. General linear models (two-ways ANOVA table) for the effects of species richness and amplitude of environmental fluctuations (EF) on population synchrony among the patches (microcosms) for three species.

Species	Effects	*SS*	*df*	*MS*	*F*	*p*
Ceriodaphnia sp. (specialist)	EF	0.064	2	0.032	9.936	**0.047**
	Species richness	0.121	3	0.04	12.5	**0.033**
	EF × Species richness	0.039	6	0.006	2.04	0.298
	Error	0.009	3	0.003		
Daphnia magna (intermediate)	EF	0.054	2	0.027	19.32	**0.019**
	Species richness	0.091	3	0.03	21.55	**0.015**
	EF × Species richness	0.002	6	0	0.301	0.901
	Error	0.004	3	0.001		
Potamocypris sp. (generalist)	EF	0	2	0	0.07	0.931
	Species richness	0.039	3	0.013	31.8	**0.008**
	EF × Species richness	0.003	6	0	1.27	0.456
	Error	0.001	3	0		
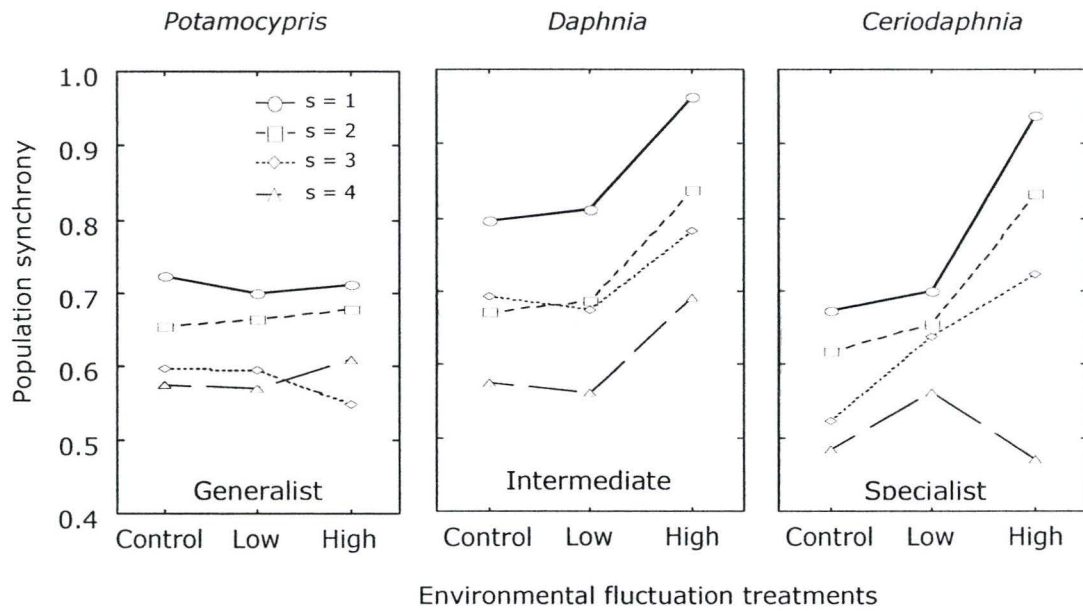
Figure 3-4. Two-ways interactions (species richness and the magnitude of environmental fluctuations) for three studied species. Lines with different patterns represent the metacommunity of different species richness. s represents species richness.

DISCUSSION

Our study shows that processes involved in formation of metacommunities may challenge the current metapopulation paradigm because they involve two important aspects, each capable of systematic interference with the traditional expectations of metapopulation dynamics. One is differences in habitat specialization. The other is the effects of species richness, presumably affecting the nature of inter-specific interactions.

Specifically, we found that both species richness and the amplitude of environmental fluctuations affect population synchrony in patches of a metacommunity. However, population synchrony differed depending on ecological specialization. Our expectation that population synchrony would be higher in metacommunities exposed to high environmental fluctuations was upheld for the specialist and intermediate species, but not for the generalist. Differences in the degree of population synchrony in the experimental metacommunities may result from differences in the species tolerance to the fluctuating factor (salinity in this case). Previous studies predicted that the degree of synchrony depends on the relative strength of the environmental fluctuation (e.g., Ranta et al. 1997a), with stronger fluctuation producing higher synchrony. However, our study suggests that the degree of synchrony also depends on how a particular species perceives the strength of the environmental fluctuation, with lower levels of environmental

fluctuation required to alter the population dynamics of specialist and intermediate species than those of generalist species. Consequently, one should not expect the equal level of synchrony for all species forming the metacommunity.

Moran (1953) assumed that populations would synchronize to the same degree as the environment but we found that population synchrony never matched the level of synchrony of environmental fluctuation for any of the species. Our result is in agreement with findings by others who conducted research in natural (Grenfell et al. 1998) and experimental (Benton et al. 2001, Fontaine et al. 2005) communities. For example, Grenfell et al. (1998) examined synchrony in populations of feral sheep on two neighboring islands where no dispersal between islands existed and found that an environmental correlation of ~0.9 was required to produce the observed population synchrony of 0.685. Similarly, experiments involving soil mites revealed levels of synchrony of about 0.75 even when environmental noise was perfectly correlated among patches (Benton et al. 2001). Although the strength of the salinity fluctuation treatment was strong enough to change the population dynamics for specialist species in our experiment, the population fluctuations of the species showed only an average 79% correlation between population growth rates. Our study is different from the Benton's study because we introduced dispersal (metacommunity framework), even though the synchrony achieved by the populations was far from complete. This mismatch between population synchrony and environmental correlation may be the consequence of the dual

nature of strong environmental noise as explained by Ranta et al. (1997b) - while strong correlated environmental noise may create synchrony in population fluctuations on the one hand, it may also modify or disrupt typical patterns in population dynamics over the long term.

The study further shows that species richness affects level of population synchrony. In fact, for all three species (generalist, intermediate and specialist), synchrony was higher in monocultures than it was in metacommunities with more species, suggesting that higher species richness results in interactions that introduce a degree of contingency, which indeed disrupts the synchronization of populations among communities. This is supported by the fact that population variability is often relatively higher (i.e., populations are less stable) in communities with higher species richness (e.g., Ives 1995, Doak et al. 1998, Gonzalez and Descamps 2004) even though community variability (in terms of biomass) is low (McCann 2000). In fact, the growth response of each species to the environmental fluctuation depends not only directly on the environmental fluctuations, but also indirectly, through changes in the abundances of each of the species in the community (Ives 1995). For instance, compensatory effects – where an increase in the population of one species results in a decline in the population of the other – are frequently observed in plant and animal communities with higher species richness (e.g., Naeem and Li. 1997, Bai et al. 2004). As such, the dynamics of the monoculture populations and those in multispecies communities might be expected to

differ because, in monocultures, the density of the one species may decline rapidly under harsh environmental condition but recover rapidly once favorable conditions are restored, without any impact of inter-specific competition or facilitation. By contrast, a metacommunity is more likely to include species with a range of environmental tolerances that will allow them to respond differently to environmental fluctuations. If these species compete or participate differently in a food processing chain, recovery of species abundances may follow different paths, disrupting any synchrony among populations that environmental fluctuation might generate. A similar argument has been made by Chase et al. (2005).

Small populations follow inherently less predictable growth paths due to stochastic variation in demographic rates (e.g., reproductive success) of the few individuals (Reed 2008). Population synchrony might also be negatively influenced by population size via density vagueness (Melbourne and Hastings 2008). Hypothetically, density of individual species might decline in the experiment with the increasing number of species due to resource partitioning. However, we found no relationship between density and species richness in the experimental metacommunities. We thus conclude that the population synchrony was not systematically affected by density. Therefore, the only factor we are able to identify as disrupting synchrony is species richness.

The observation that correlated environmental fluctuation has differing effects on synchrony of species of different specialization but the same dispersal regime has implication for how we may interpret dynamics of different species in the context of metacommunity. We have shown earlier (Pandit et al. 2009) that habitat specialists are structured according to species sorting dynamics and habitat generalists according to either neutral or patch dynamics. Therefore, many species in communities that conform to the species sorting type of dynamics (e.g., Leibold et al. 2004, Ellis et al. 2006) should be synchronized primarily by synchrony of the important environmental variables. Many species in communities that conform to patch or neutral dynamics models should be much more influenced by dispersal and its factors affecting dispersal such as spatial configuration, connectivity, dispersal barriers among patches (Cottenie 2005). This study shows that the population dynamics of specialist seems to be described better by species sorting models since fluctuation of population sizes of the species are governed by environmental factor.

Furthermore, the synchronizing role of environment (specialists) and dispersal (specialists and generalists) can be reduced by increasing metacommunity species richness as discussed earlier. Consequently, one should expect different metacommunity dynamics under different levels of species richness. Differences in metacommunity dynamics due to richness may introduce variation into the performance of applicable metacommunity models.

Our findings have potentially some conservation implications. If population synchrony tends to be higher among specialists than generalists in habitats with spatially correlated EF, this raises a serious concern. Theoretical studies (e.g., Heino et al. 1997, Earn et al. 2000) have already shown that higher synchrony increases the risk of global metapopulation extinction, which adds one more factor to the increased vulnerability of specialists. However, we show that effects of synchrony declines when species richness increases. If confirmed in natural systems, the effect of richness may have positive implications in reducing the risk of extinction of habitat specialists.

To summarize, as we hypothesized, metacommunities composed of monocultures exhibited high levels of population synchrony (temporal coherence) for all species but the pattern of synchrony differed among species depending on two factors: habitat specialization and species richness. The latter factor reduced synchrony of local populations irrespective of specialization.

ACKNOWLEDGEMENTS

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CHAPTER 4 :

Opposite effects of environmental variability and species richness on temporal turnover of species: differences between specialists and generalists

This chapter has been prepared for publication in *Ecological Research* (partial citation follows). This chapter has been re-formatted to maintain consistency throughout the thesis.

Pandit, S. N. and J. Kolasa. Opposite effects of environmental variability and species richness on temporal turnover of species: differences between specialists and generalists. Planned for *Ecological Research.*

RATIONALE AND OBJECTIVES

I previously showed that a metacommunity can exhibit an internal differentiation of structuring processes. Chapter 3 showed that the effect of environmental fluctuation is higher for a specialist species than a generalist, when continuous dynamics of single populations are concerned. In contrast, this paper aims to complement those earlier results. The main goal of this chapter is to explore the role of environmental variability in temporal dynamics of community structure, with a particular attention to distinction between specialists and generalists. Furthermore, species richness is believed to stabilise communities. I further explore the effects of species richness in temporal dynamics of community structure. Community structure (i.e., species composition and abundance) changes over time at a site (temporal turnover) as a consequence of both local and regional processes. However, the temporal turnover of species can be a function of habitat specialization and environmental variability. To examine these possible relationships I used again the observation data from Jamaican rock pool system.
I found that:

- Turnover among specialists was much higher as compared to generalists,

- Environmental variability induced more temporal turnover for specialists than generalists,

- Species temporal turnover decreased with species richness and that the effect of richness (biodiversity) was consistent for generalists and specialists

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These results suggest that temporal dynamics (temporal turnover) of specialists is tied more to variability of the environment as to compare to habitat generalists. These results emphasize the complex nature of community response to environmental change along a gradient of richness and species specialisation.

ABSTRACT

Understanding the patterns of species turnover is an important issue for biodiversity conservation. Many studies examined change in species composition between habitats but not so at a single location over time (temporal turnover), particularly in conjunction with species traits such as habitat specialization of species. In communities where habitat specialization is a result of constraint by abiotic variables, specialists are likely to respond to environmental characteristics more than generalists and thus their variation should be correlated with habitat variation more than that of generalists. Consequently, we hypothesized that specialists undergo higher temporal turnover than generalists in the presence of environmental variability (EV). We tested these predictions using natural microcosm communities for which long term environmental and community data were available. We compared temporal turnover between a group of generalist species and a group of specialists. We used standard deviation of salinity over time to represent EV for each pool. We chose salinity because prior studies show that it has a dominant effect on species presence and abundance. We further obtained the mean number of combined colonization and extinction events (EC events) for each species in individual pools. We assessed the effect of EV on the EC events for each of 24 species by linear regression. We found that the species temporal turnover varied between the different groups of species. Environmental variability (EV) induced greater temporal turnover among specialists than generalists. We further found

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that species temporal turnover decreased with species richness and that this effect was similar for generalists and specialists. Overall, our study supports the hypothesis and emphasizes the complex nature of community response to environmental change along a gradient of richness and species specialization.

Key words: species temporal turnover, habitat generalists, habitat specialists, habitat specialization, CE Events, colonisation and extinction

INTRODUCTION

Understanding the patterns of species turnover is an important issue in biodiversity conservation (e.g., Buckely and Jetz 2008, McKnight et al 2007). Most studies examined turnover of species composition between habitats (spatial turnover) (e.g., Buckely and Jetz, 2008, La Store and Boecklen 2005, Davies et al 2005, Krauss et al. 2003b, Brown et al. 2001, Oberdorff et al. 2001, Arnott et al. 1999, Rice et al. 1983; Schoener and Spiller 1987). Temporal turnover in a single location received less attention (Wernberg and Goldberg 2008). Temporal turnover may, however, suggest important factors affecting dynamics of species composition. For example, Buckely and Jetz (2008) found different taxa to vary in spatial turnover rates, which they attributed to differential response of these taxa to environmental conditions. Findings like those of Buckley and Jetz (2008) imply that understanding turnover of species would improve by following local (within the pool) temporal dynamics of species that differ in their relationship with environment. In the most general terms such differences occur along a gradient of habitat specialization. Theoretical studies corroborate this idea. Shurin (2007) explored a model according to which environmental heterogeneity and species specialization interact to govern species turnover. Importantly, Chalcraft et al. (2004), who studied plant species, found that local turnover did not show scale-dependency but spatial turnover did. Their observation implies that conclusions based local turnover patterns may be more reliable and general.

Earlier studies showed that, in a model system of natural aquatic microcosm communities, specialization affects variation of population density, with higher variation in habitat specialists than in generalists (Kolasa and Li 2003, Kolasa and Romanuk 2005). Similarly, in that system, distribution and variation of specialist species depended more on environmental characteristics of habitat but significantly less so for generalist species (Pandit et al. 2009). These observations suggest that environmental variability of a site may also affect change in community composition over time (temporal turnover). Not all studies point in the same direction; however Thuiller at al. (2007) examined vegetation composition of Cape Coast floristic region of South Africa and concluded that biological attributes of species did not influence their turnover. Notwithstanding, given the amply documented differences between specialists and generalists in sensitivity to environmental conditions, we hypothesize that temporal turnover should be higher among specialists than generalists in the presence of significant environmental variability (EV). A factor that could confound the test of the hypothesis is species richness. Recent research (e.g., Kathryn et al. 2001, Ives et al. 2003) has shown that communities with higher species richness often show greater stability of biomass or abundance. It is plausible to expect that greater stability correlates negatively with temporal turnover. Theoretical studies postulate specific mechanisms for linking species richness and compositional turnover on a site. For example, Shurin's 'biotic' model (Shurin 2007) provides a potential explanation for this link by assuming feedbacks between richness

and colonization and extinction rates. Therefore, to test the hypothesis, we examined the effect of habitat variability and richness on temporal turnover of species. Specifically, we used long-term data on composition, abundance, and distribution of aquatic invertebrates inhabiting 49 natural rock pools as well as parallel data on the physical conditions in the pools. We asked the following questions: 1. Does the rate of turnover vary between generalists, specialists? 2. Does the rate temporal turnover decrease when the number of species increases? and 3. How does the influence of environmental variability on temporal turnover vary along the gradient of habitat specialization? Depending on the question, we contrasted two groups of species, habitat specialists and habitat generalists, or used regressions where specialization was a continuous variable. In some analyses all the species were combined and used as another group for comparison with the specialization groups.

Although our analysis involves abiotic aspects of the environment only, other species or functional groups can also vary and affect turnover of species of interest. For example, La Sort and Boecklen (2005) found that changes in avian communities were, among many factors, correlated with the expansion of common species.

METHODS

Data source and preparation

The study is based on a system of 49 natural rock pools present in Jamaica, near Discovery Bay Marine Laboratory. These pools are small water bodies, with variable physico-chemical regimes (Pandit et al. 2009, Kolasa et al. 1996). They are occupied by over 70 species of aquatic invertebrates. We used 9 annual sets of data on distribution and abundance of these species as well as data on environmental conditions in 49 rock pools. Physico-chemical conditions that we consider are salinity, temperature, pH, and oxygen concentration. Among the 69 species found, 45 were rare and found only once or twice in the study area over the entire 9 sampling dates. The remaining 24 species were included in further analyses.

Species specialization

We quantified habitat specialization of species by means of Levins' approach (Levins 1968; see Pandit et al. 2009 for details). Levins' approach assigns higher niche values to species that use a broader range of resource states. We call them habitat generalists in contrast to habitat specialists whose niche breadth values are low. Using the niche values we divided these species into a group of 12 generalists and 12 specialists and used these groups in the examination of the effects of species specialization on turnover.

Biological and physical measurements

In order to test the hypotheses, we needed several derived variables to characterize temporal change in species presence and in composition of communities as well as environmental variability in each of 49 rock pools. We describe these variables under subheadings below.

Biological factors

We used two measures to capture the variation in species presence and composition. Species turnover summarizes mean compositional difference between adjacent censuses. The mean number of colonization and extinctions (the EC events) characterizes dynamics of a single species over time.

a. Turnover in species composition

We quantified species temporal turnover (TTS) as the inter-annual turnover in species composition. For each pool and separately for generalists and specialists, we calculated percent of temporal turnover in species composition between pairs of consecutive years (Davies et al. 2005) according to:

$$TTS\,(\%) = \frac{C_{obs} + E_{obs}}{S_i + S_{i+1}} \times 100$$

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where S_i is the number of species observed in a pool in year i, C_{obs} is the number of species that were recorded in a pool in year $i+1$ but not seen in year i (i.e., the number of species that colonized in the interval $[i, i+1]$ and E_{obs} is the number of species that were recorded in year i but that were not seen in year $i+1$ (i.e., the number of species that became extinct). This is similar to beta-diversity (Sørensen dissimilarity index), which reflects the compositional dissimilarity between years as the likelihood that a species will occur in just one year (e.g., Veech et al. 2002). We calculated the turnover for only those years that were separated from adjacent year by no more than 12 months.

Some analyses (see section: statistical analysis) relied on the TTS values while other required using their means over time. The mean species turnover for each pool was obtained from $TTS_{mean} = \sum_{0}^{n} TTS / N$

where, *TTS* is the temporal turnover in species composition from year to year of a single pool, N is the number of times that *TTS* was calculated (N=6). This calculation produced 49×3 values representing mean turnover for each of 49 pools and three groups of species separately.

b. Number of colonizations and extinctions

We characterized individual species by counting the number of colonizations and extinctions (colonization-extinction events, CE events) that they underwent in a single

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pool over the span of the study. To enable meaningful comparisons among species that occupied different number of pools, we used mean values of CE events.

d. Species richness

We calculated mean species richness of each pool over sampling years, as

$$S_{mean} = \sum_{0}^{n} S / N$$

Where S is the number of species collected in a pool, N is the number of annual censuses ($N=9$).

Physical factors (Environmental variability, EV)

We used standard deviation of salinity over time to represent EV for each pool. Although data on other environmental variables were available, we chose salinity because salinity was the best predictor of community composition in the system of rock pools (e.g., Therriault and Kolasa 1999).

Statistical analyses

To test whether temporal turnover in species composition vary between generalists and specialists, we used a factorial ANOVA where specialization groups and year-to-year intervals as factors and the temporal turnover rate in species composition as

a dependent variable. We further examined the effects of species richness on the temporal turnover. We did so by regressing the mean temporal turnover values (TTS_{mean}) against the mean species richness of each pool, separately for the three group species.

In order to test for the effects of environmental variability on temporal turnover, we used the mean CE events of individual species in each pool. We assessed the importance of EV on the CE events for individual species by linear regression. This resulted in 24 regressions that linked directly EV and CE events but not EV and specialization. Thus, to determine whether species specialization and EV were linked, we regressed the slopes of the above regressions against species niche breadth values.

RESULTS

Turnover among specialists was much higher as compared to generalists and all 24 species analyzed jointly (Figure 4-1). However, the species turnover did not differ between different year-to-year intervals nor was there any interaction between the species groups and years (Table 4-1).

Furthermore, species turnover systematically increased with the increase in EV (Table 4-2). However, the relation was significant for four species only (see Table 4-2). In one species, temporal turnover (CE) decreased with the increase in EV.

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To determine the immediate cause of the difference between specialists and generalists, we regressed the mean value of EC events against EV using 49 pools to obtain 24 species specific regression statistics. Subsequently, we plotted the slope values of these regressions as a function of niche breadth (Fig. 4-2). Although the majority of individual regressions were not statistically significant, we found a general relationship that EC events were positively correlated with EV among specialists but that this relationship dissolved for generalists.

As hypothesized, species temporal turnover declined in pools with higher species richness for all three groups of species (Fig. 4-3). The rate of turnover decline did not differ among the groups even though the intercept did, which corroborates the results presented in Figure 4-3 that specialists undergo higher rates of change.

Table 4-1. Effects of different groups of species (generalists, specialists and all 24 species) and year (pairs of years) on temporal species turnover. (General linear model: factorial ANOVA).

	SS	df	MS	F	p
Years	0.606	5	0.121	1.526	0.179
species groups	8.133	2	4.066	51.155	**<0.001**
Years × species groups	0.512	10	0.051	0.644	0.776
Error	57.155	719	0.079		
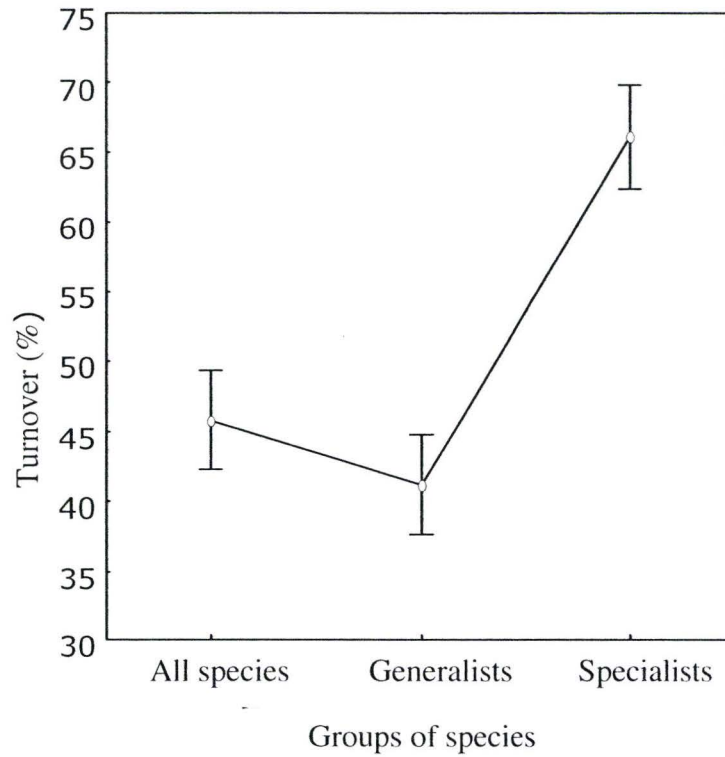
Figure 4-1. Mean and standard error of the temporal turnover of different groups of species in 49 rock pools ($F_{2,719} = 51.155$, $p<0.001$, one-way ANOVA).

Table 4-2. Slope and Pearson correlation coefficient, r, of the relationship between mean number of colonization and extinction events, CE events, and environmental variability, EV.

Code	Scientific name of the species	Relationship between CE and EV		
		Slope	r	p
Alon	*Alona davidii*	0.029	0.144	0.557
CrabL	*Sesarma miersi* Rathburn	-0.065	-0.426	**0.005**
Cyc9	Copepod sp.	0.060	0.308	0.214
CycL	*Orthocyclops modestus* (Herrick)	-0.022	-0.150	0.321
CycM	*Metis* sp.	0.165	0.737	**0.003**
CycS	*Paracyclops fimbriatus* (Fischer)	0.035	0.253	0.142
Daphn	*Ceriodaphnia rigaudi* Richard	0.055	0.313	0.178
Dipter	Dipteran larvae	0.078	0.255	0.450
Gyratr	*Gyratrix hermaphrodites*	-0.032	-0.304	0.148
Harp	*Nitocra spinipes* Boeck	-0.062	-0.329	0.329
HarpM	Copepod (genus, species, unidentified)	0.087	0.333	0.192
Leid	*Leidigia leidigi*	0.080	0.344	0.404
Mos1	*Culex* sp.	-0.024	-0.150	0.391
Nema	Nematode sp.	0.032	0.179	0.263
Oligo	Oligochaete sp.	-0.050	-0.338	0.063
Ost1	*Cypridopsis cf. mariae* Rome	0.076	0.390	**0.021**
Ost2	*Heterocypris* sp.	0.008	0.044	0.810
Ost4	*Cytheromorpha* sp.	0.028	0.223	0.487
Ost5	*Candona* sp.	0.132	0.595	**0.007**
Os5A	*Cypricercus* sp.	0.085	0.429	**0.008**

Ost6	*Potamocypris* sp.	0.042	0.211	0.203
PolyT	Polychaete T	0.041	0.284	0.305
PolyJ	Dorsovilleid polychaete	0.115	0.452	0.091
Tany	Tanypodid sp.	0.000	0.000	0.999
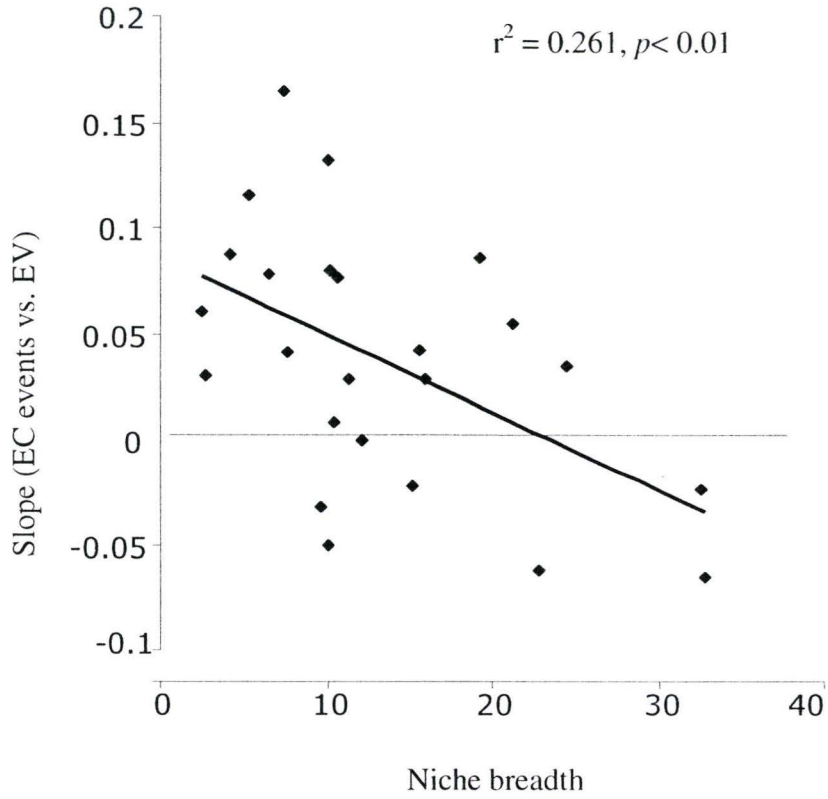
Figure 4-2. The relationship between the slope of regression [between extinction and colonization (mean EC events) and environmental variability, EV] and specialization of 24 species.
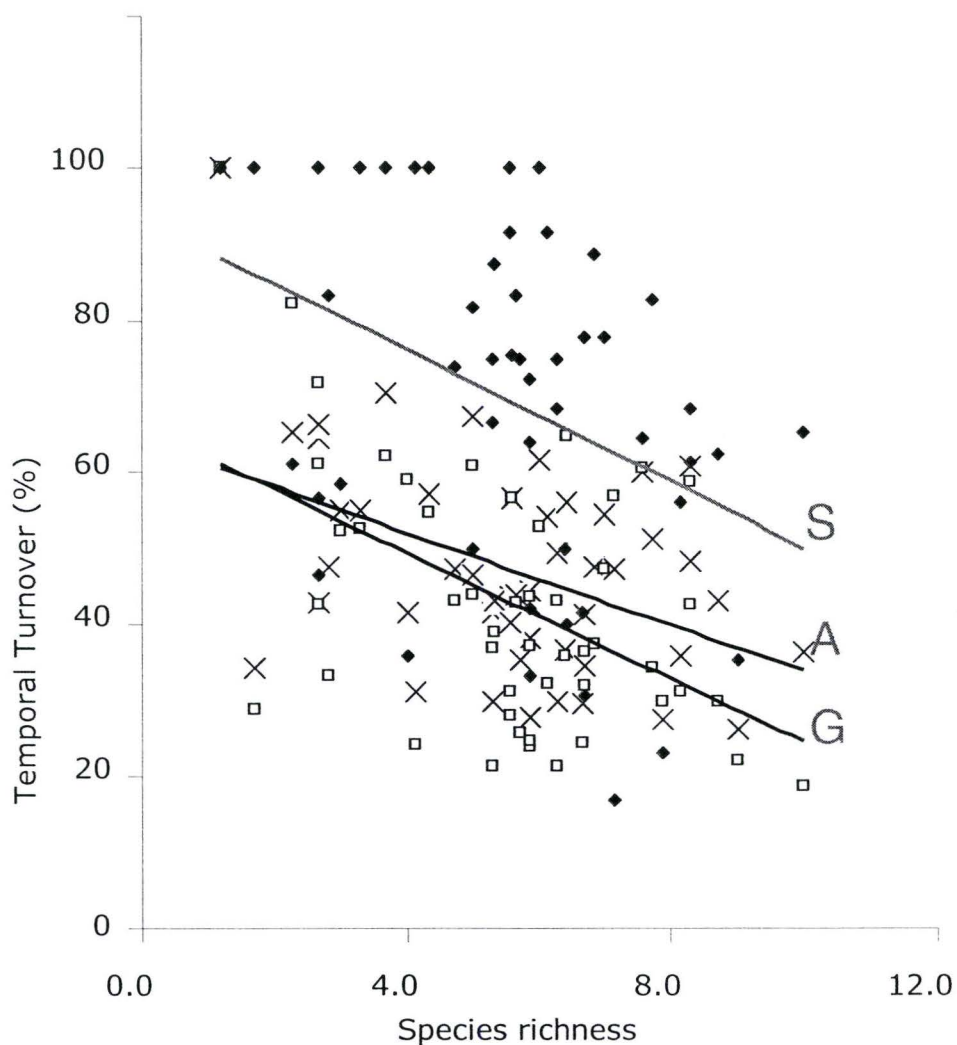
Figure 4-3. Linear relationship between temporal species turnover and species richness in a cluster of 49 pools for the group of species (all species, generalists and specialists). S, A and G represent specialists, all species and generalists, respectively. All trends are significant (all species: r = -0.432, p = 0.002, generalists: r = -0.48, p = 0.0004; and, specialists: r = -0.37, p = 0.007).

DISCUSSION

In general, this study shows that species temporal turnover varies between the different groups of species in a rock pools metacommunity. The prediction that higher environmental variability would induce high temporal species turnover in the groups of specialists more than generalists, or the entire community, was upheld by our analysis. Similarly, the hypothesis that the rate of species temporal turnover decreases as species richness increases was accepted for the rock pool invertebrate communities. Independently, both results have also been postulated by theoretical models developed by Shurin (2007). This convergence of theoretical and empirical work may suggest considerable generality of findings.

Differences in performance of specialists and generalists are corroborated amply in the literature. Specialists show higher turnover under the conditions of higher environmental variability because they have low environmental tolerances (Kolasa and Romanuk 2005, Krauss et al. 2003b), low dispersal abilities, higher mortality during dispersal, lower efficiency to colonize through failure to find suitable habitats (Kolasa and Romanuk 2005). Saether et al. (2006) also mentioned that specialist species often suffer more relative to generalists from changes in environmental conditions. Fischer and Stocklin (1997) as well as Boulinier et al. (2001) also found that colonization and extinction rate in specialists is higher than in generalists.

Although we found one species (*Sesarma miersi*) whose EC events declined with environmental variability, and whose slope departs from 0, it is possible that environmental variability can stabilize generalists under certain circumstances. For example, such stabilization (absence of extinctions) could occur when environmental variability exceeded tolerance levels of its competitors or predators. In sum, our study suggests that the relative importance of EV in determining temporal turnover is a function of habitat specialization; with habitat specialists exhibiting greater constraints by local conditions and greater responsiveness to their variation than generalist species.

Our findings might be biased if the groups of species that we compared differed significantly in mean species density. This is because species with lower densities should experience higher rates of local extinctions (Hanski 1999). However, the groups were not different with respect to density (simple ANOVA) and hence we assumed that the turnover was not systematically affected by density. As a result, environmental variability remains the only factor that we are able to identify as responsible for higher temporal turnover of specialists.

In addition to the effect of environmental variability and species specialization, we also found that temporal turnover correlated negatively with species richness. Plausibly, this observation represents an echo of a more general finding that richness correlates with greater community stability (e.g., Tilman and Downing 1994, Doak et al.

1998, Loreau et al. 2001, Shurin et al. 2007). We find that the temporal turnover often declines as average species richness increases, indicating that more diverse communities have lower temporal turnover (greater stability) in species composition (e.g., Tilman 1994, Ives et al. 1999, Vogt et al. 2006, Shurin et al. 2007). It is possible that, if a pool represents a suitable habitat for a finite number of species, an increase in turnover will automatically lead to lower species richness and thus to a negative relationship between the two variables. Another potential explanation was offered by Shurin (2007) who invoked feedbacks between species richness and turnover. Such feedbacks could operate by denying success to potential colonists when richness is high or by rescuing and protecting resident species via internal propagule banks.

In general, the link between richness and temporal turnover is potentially an important aspect of management and conservation strategies. The full understanding of the underlying mechanisms will, however, require further studies. The observation that the temporal turnovers of species rates are higher for specialists than generalists across the range of richness values may offer a clue to the mechanisms involved. The rate of temporal turnover varies between generalists, all species and specialists, however more similar between all species combined and generalists, and more different between the all species and specialists. Studying only on all species, without differentiating the groups of species based on habitat specialization, may be misleading, and influence decision-making in conservation planning. The tight linking of environment and species turnover

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suggests that communities with specialists may be particularly susceptible to environmental variation or climate change, since higher variability in environmental conditions is expected due to global warming. But its effects disappear when looking at entire community species. Thus it is an urgency to recognize species specialization as a dimension relevant to the prediction of community dynamics in biodiversity conservation.

ACKNOWLEDGEMENTS

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CHAPTER 5 :

The role of local and regional processes along the gradients of habitat specialization in a metacommunity framework

This chapter has been prepared for publication in *Ecology Letters* (partial citation follows). This chapter has been re-formatted to maintain consistency throughout the thesis.

Pandit, S.N., J. Kolasa. and K. Cottenie: The role of local and regional processes along the gradients of habitat specialization in a metacommunity framework. Planned for *Ecology Letters.*

RATIONALE AND OBJECTIVES

In the previous chapters, using experimental data and data from a rock pool invertebrate community, I found that a system composed of discrete habitats can exhibit an internal differentiation of structuring processes, with habitat specialists governed predominantly by environmental factors and habitat generalists governed mainly by spatial factors. In addition to these findings, the effect of environmental variability on both population synchrony and temporal turnover is higher for specialist than generalist species. However, my research presently in the previous chapter did not examine joint contribution and interactions between spatial variables and temporal dynamics of species. Chapter 2 examined only stationary patterns. Chapter 3 reported on the results of an experiment involving dynamics of few species only. Chapter 4 focused on changes of local communities and on differences between specialists and generalist. This Chapter completes the picture by adding the spatial component explicitly. The objective of this chapter is to examine whether temporal dynamics of specialists is tied more to variability of the environment as compared to habitat generalists who are hypothesized to respond more to spatial factors than to environmental ones. I developed and tested specific predictions addressing this above question using natural microcosms communities for which a long-term (9 year) environmental and population dynamics data were available. I found:

- The effect of environmental variability was increasing with the specialization (synchrony among specialists was correlated more with synchrony of physical variables in the same pools).

- Although the effect of spatial variables was lesser, it was still consistent with the hypothesis that synchrony of generalists should be affected more by distance among local populations.

Overall, the study suggests that species of different habitat specialization show systematic differences with respect to local processes involving environmental characteristics but show fewer difference with respect to regional processes involving distance, at least when long-term dynamics is concerned.

ABSTRACT

Most tests of metacommunity rely on snapshot patterns of species distributions and abundance. However populations fluctuate in space and time making snapshot patterns insufficient for revealing a complete picture. For example habitat generalists and specialists respond to environmental variation differently. Thus, environmental variation may induce significant changes in metacommunity dynamics. Specifically, we hypothesized that variability of environment affects specialists more and that its influence will be expressed by increased synchrony among populations of specialists, as opposed to habitat generalists, in response to correlated (synchronized) variation in environmental factors. We found that population synchrony of 24 invertebrate species (natural rock pools in Jamaica) increased with habitat specialization in response to environmental synchrony measured as synchrony in variation of salinity. However, distance among pools, which affects dispersal, was negatively correlated with population synchrony, irrespective of species specialization. Since only specialists show increasing synchrony with environmental synchrony, and both are negatively correlated with distance, we infer that generalists must be synchronized by dispersal while specialists by environmental forcing. This reinforces the idea that direct tests of metacommunity models will be difficult.

INTRODUCTION

Depending on the importance of the regional (dispersal, regional species pool) and local (species interactions, local effects of habitat on species performance; both direct and indirect) processes, several metacommunity models have been proposed to account for species diversity patterns at local and regional scales (Cottenie 2005). These models have a potential for providing a general framework for ecological processes in discrete and fragmented habitats but their tests have been few and largely limited to data set spanning short time frames. Irrespective of the model (the mass effects, species sorting, neutral models and patch dynamics; e.g., Leibold et al. 2004, Cottenie 2005), tests focused on determining which model applies to a particular community. However, communities and population fluctuates in space and time (e.g., Connell and Sousa 1983, Horne and Schneider 1995) making snapshot patterns potentially deficient for determining which model, if any, applies to a particular metacommunity. For example, earlier work (Pandit et al. 2009, Azeria and Kolasa 2008) shows that habitat generalists and specialists respond to environmental variation differently. If so, environmental variation as it differentiates species responses along the habitat specialization gradient may induce significant changes in metacommunity dynamics at different times. Indeed, variable metacommunity dynamics might present a major challenge to testing the general

metacommunity framework and specific models.

Recently, we found that environmental factors govern population dynamics of species with greater habitat specialization while spatial factors (distance and isolation effects on dispersal) govern primarily habitat generalists (Pandit et al. 2009). Given these findings, we hypothesized that variability of environment affects specialists more and that its influence will be expressed by increased synchrony among populations of specialists, as opposed to habitat generalists, in response to correlated (synchronized) variation in environmental factors. In general, population synchrony arises as a consequence of correlated environmental fluctuation, dispersal (e.g., Hoopes et al. 2005), and predation and prey-switching behavior among habitat patches in a fragmented landscape (e.g., Ydenberg 1987, Ims and Steen 1990, Ims and Andreassen 2000, Huitu et al. 2003, Li et al. 2005). Population synchrony offers two means for gaining insights into metacommunity workings: it allows for better evaluation of contribution of regional scale processes (dispersal vs. environmental forcing) and enhances the ability to draw inferences from temporal and spatial dynamics.

Our hypothesis assumes that environmental variability influences temporal dynamics of habitat specialists more than it does generalists because specialists tend to be more constrained by local conditions (cf. Azeria and Kolasa 2008). In contrast, habitat generalists experience the landscape as relatively more homogenous and thus may be less responsive to local constraints. This difference, therefore, should promote the importance

of distance among populations in determining population synchrony of generalists.

We tested these predictions in a model system of 49 rock natural rock pools inhabited by 69 invertebrate species for which long-term (9 year) environmental and population dynamics data are available. The data span tens to hundreds of generations for most of the constituent species (Kolasa and Romanuk 2005). We also know that the variable physical environment in these pools induce dynamic responses in community structure at local and regional scales (Kolasa et al. 1996, Therriault and Kolasa 2000).

METHODS

Study site

The study included 49 rock pools with volumes greater than 500mL within a 25m radius along the northern coast of Jamaica, at the Discovery Bay Marine Laboratory, University of the West Indies (18^0 28' N, 77^0 25' W, Figures 1-3, 1-4). All rock pools were located within 1 m of the nearest rock pool, on average, and none were separated by more than 5m from their closest neighbor. Despite their close proximity, the environmental characteristics of the 49 rock pools are quite variable. The rock pools used in this study ranged from 13 to 105 cm in width and length, and 1 to 37 cm in depth (mean depth = 12.8 ± 8.3 SD). Volumes ranged from 0.5 L to 115 L (mean = 12 L ± 21 SD). Elevation above sea level ranged from 1 to 235 cm (mean = 76.6 ± 80.1 SD) at high

tide, with the tide rarely exceeding 30 cm. A few pools received some tidal influx (although tidal flooding did not occur daily), but most are maintained by atmospheric precipitation and ocean spray.

Sampling design

Annual surveys were carried out between December 28 and January 11 from 1989 to 2008 (with the exception of 1995) and once in early June, in 1997. Standard abiotic surveys were usually conducted on the day of biotic sample collection (or one day prior) using a multiprobe sonde (DataSonde from Yellow Springs Instruments or Hydrolab Corporation) and included measurements of pool temperature, salinity, dissolved oxygen concentration, pH, turbidity and specific conductivity. Samples of the resident invertebrate communities were obtained by passing 500 ml of pool water through a 63μm net after stirring the pool to dislodge organisms from pool surfaces and to homogenize the distribution of the invertebrates in the water column. Invertebrate samples were immediately preserved in 50% ethanol and were later sorted, identified, and counted in the laboratory using dissecting and compound microscopes.

Although invertebrate samples were being collected from the rock pool system for more than a decade, identification and enumeration of the full set of invertebrate samples for all 49 pools has only been completed for nine years at this time. We used all nine

years of available data in our analyses. A total of 69 species have been identified to date, including ostracods (20 species), copepods (including two harpacticoid and three cyclopoid species), cladocerans (5 species), worms (15 species, including nematodes, oligochaetes, polychaetes, and turbellarians), aquatic insects (18 species), and other crustaceans (6 species). Of the 69 species, 43 were found only once or twice in the study area: These species were considered rare and were excluded from the analysis. Thus, 24 species were used for our analyses. Abundance data are presented as the total number of individuals of a species collected in a 500 ml sample of pool water on a given sampling date.

Habitat specialization

Habitat specialization was computed for the 24 species using two methods, one independent (based on Levins' (1968) approach) and the other dependent (based on OMI approach (Dolédec et al. 2000)) of measured environmental factors. Levins' approach expresses specialization as niche breadth (*B*) where a species' niche breadth is a function of the uniformity of the distribution of its abundance among the various resource states for a community at hand (Levins 1968, Colwell and Futuyma 1971). Here, we define "resource state" as one habitat patch (rock pool), irrespective of local environmental conditions or spatial locations of the different pools relative to one another in the landscape. The OMI approach (Dolédec et al. 2000) determines habitat specialization as

"species tolerances" based on the amplitude of the distribution of each species along environmental gradients observed at sampling sites. Low tolerance values indicate that a species is distributed across habitats within a narrow range of conditions (specialist species), while high values imply that a species is distributed across habitats with varying broad range environmental conditions (generalist species). R software was used to calculated habitat specialization using the OMI method (R Development Core Team 2000, with package ADE4: niche).

Environmental and spatial matrices

The environmental gradient in the rock pools was defined by combining the four environmental factors (salinity, temperature, pH, and the concentration of dissolved oxygen) using principle components analysis (we did not include elevation or pool volume in our analyses since these do not vary temporally). Average values were used whenever multiple measurements of environmental variables were taken in a given year. But when biological samples were available for a given pool but some environmental variables were not available, we substituted missing data by the inter-annual mean.

Redundancy analysis (RDA) and principal component analysis helped identify salinity as the dominant variable determining composition and influencing abundances of metacommunity members. Consequently, we chose salinity as the meaningful indicator

of synchronous variation in environmental conditions. To quantify how similar (synchronous) a pair of pools is with respect to environmental variability we calculated log-zero cross correlation functions between the values of salinity between site i and a site j (environmental synchrony).

To asses the effects of distance on population synchrony, we $\log(x+1)$ transformed distances between pools to create a distance matrix between pairs of pools.

Population and environmental synchrony

In order to evaluate contribution of regional scale processes as compared to local processes we calculated population synchrony for all 24 individual species in all combinations of pool pairs they occurred in. We used lag-zero cross-correlation functions (CCF) (Ranta et al. 1998, Koenig 1999, Paradis et al. 2000, Leibhold et al. 2004) for all 9 years species abundance data (Dec. 1989, Jan 1990, Jan. 1991, Jan. 1992, Jan 1993, Jan 1994, Jan 1997, Jun 1997 and Jan 1998).

Regional synchrony of the rock pools metacommunity for each of 24 species was calculated. Regional or overall synchrony of each of 24 species was defined as the mean of the cross correlation coefficients (CCC). We used a bootstrapping approach to test whether regional synchrony or overall synchrony in the metacommunity for each species differed significantly from zero using the Randomization and Bootstrap programs

available from www.uvm.edu/~dhowell/StatPages/Resampling/Resampling.html. A

bootstrapping approach to computing the mean CCC was required because the data from

the same pools are used to compute several CCCs in the metacommunity, making the

individual CCCs dependent. For each species, the standard error of the mean CCC

(SE_{Boot}) was calculated using 1000 means generated from 1000 samples with

replacement. If the 95% confidence interval (with mean $CCC \pm 2 \times SE_{Boot}$) of the mean

CCC did not include zero, then we accepted that the mean CCC is significantly different

from zero (Paradis et al. 2000), indicating synchrony among populations of different

pools.

We used distance decay relationships to assess whether population synchrony

declined as a function of 1) decrease in environmental synchrony and 2) increase

geographic distance. In addition, we found that the environmental conditions were

spatially correlated ($r^2 = 0.04$, $p<0.0001$), raising concerns about collinearity in the data.

Consequently, we examined the unique effects of distance and environmental synchrony

on population synchrony. In order to examine unique effects of environmental synchrony

on population synchrony, we first obtained the residuals from the relationship between

environmental synchrony (y axis) and distance (x axis) between pairs of pools. We then

regressed population synchrony against so obtained residuals. Similarly, we examined the

unique effect of distance between patches by regressing population synchrony against the

residuals of the relationship between distance (y axis) and environmental synchrony (x axis).

Thus, we assessed the effects of four components (environmental synchrony (E), space [S], pure environmental synchrony [E|S] and pure spatial [S|E]) on population synchrony for each of the 24 species. The absolute value of the slope and Pearson correlation coefficient (r) were obtained for each species using all possible pairs of pools in the metacommunity for each of the following relationships: 1) population synchrony and E (slope$_{PS.E}$ and r$_{PS.E}$). 2) population synchrony and S (slope$_{PS.S}$ and r$_{PS.S}$), 3) population synchrony and E|S (slope$_{PS.E|S}$ and r$_{PS.E|S}$), and 4) population synchrony and S|E (slope$_{PS.S|E}$ and r$_{PS.S|E}$). Finally, we examined how the slope and correlation coefficient, r, varied for each of these four relationships across the specialization gradient (using separately both Levins' niche breadth and OMI tolerance) to evaluate the effects of distance and environmental synchrony on population synchrony.

RESULTS

1. Regional synchrony

Regional synchrony is a mean of population synchrony values for all pool pairs in which a species occurred. Only 13 of 24 (~54%) species showed regional synchrony that differed from zero. When significant population synchrony was observed, it was generally weak, with mean CCC ranging from -0.045 to +0.161.

2. Population synchrony, environmental correlation and distance

Synchrony in population size vs. synchrony in salinity values

Population synchrony tended to increase with the increasing environmental (salinity) synchrony. The slope of this relationship (slope$_{ps,e}$) varied between -0.012 and + 0.46. About two thirds of the species showed a positive relationship between population and salinity synchrony, but the relationship was significant for six species only. This was true both before and after the effects of distance on environmental synchrony were removed (Table 5- 2). For about one third of the species, population synchrony tended to decrease with increasing salinity synchrony, but only one species showed a significant negative relationship.

Table 5-1. Regional synchrony for 24 common species of rock pool invertebrates, where n is the number of cross-correlation coefficients for a given species (CCCs); RS is the regional population synchrony (the mean of all CCCs); SE_{boot} is the standard error of the regional synchrony calculated using the bootstrapping method. Significant RS cases (different from zero at the 5% confidence level) appear in bold.

Code	Scientific name of species	n	RS	SE$_{boot}$
Alon	*Alona davidii*	170	**0.126**	0.035
CrabL	*Sesarma miersi* Rathburn	890	0.004	0.012
Cyc9	Copepod (genus species, unidentified)	110	**0.107**	0.046
CycL	*Orthocyclops modestus* (Herrick)	903	0.016	0.02
CycM	*Metis* sp.	90	0.056	0.041
CycS	*Paracyclops fimbriatus* (Fischer)	543	0.022	0.017
Daphn	*Ceriodaphnia rigaudi* Richard	172	0.051	0.033
Dipter	Dipteran larvae	63	0.036	0.049
Gyratr	*Gyratrix hermaphroditus*	209	**0.051**	0.026
Harp	*Nitocra spinipes* Boeck	1021	**0.085**	0.013
HarpM	Copepods (genus species, unidentified)	91	**0.137**	0.047
Leid	*Leidigia leidigi*	21	0.114	0.088
Mos1	*Culex* sp.	427	**0.161**	0.02
Nema	Nematode sp.	584	**0.077**	0.016
Oligo	Oligochaete sp.	376	**0.067**	0.02
Ost1	*Cypridopsis cf. mariae* Rome	420	**0.045**	0.021
Ost2	*Heterocypris* sp.	478	**0.06**	0.019
Ost4	*Cytheromorpha* sp.	55	-0.045	0.046
Ost5	*Candona* sp.	75	0.037	0.046
Os5A	*Cypricercus* sp.	522	**0.093**	0.02
Ost6	*Potamocypris* sp.	661	0.024	0.017
PolyT	Polychaete T	105	**0.144**	0.044
PolyJ	Dorsovilleid polychaete	108	**0.149**	0.044
Tany	Tanypodid sp.	486	0.001	0.017

Synchrony in population size vs. distance between pools

The relationship between population synchrony and distance ($slope_{ps,d}$) varied from +0.05 to -0.36 and from +0.06 to – 0.25 before and after removing the effects of environment on synchrony, respectively (Table 5-2). Population synchrony tended to decline with increasing distance between pools for the majority of species, but the relationship was significant for only nine and six species before and after removing the effects of environment on distance, respectively. Only one species (Poly J) showed significant population synchrony with both environmental synchrony and distance.

3. Effects of distance and environmental synchrony on population synchrony along the habitat specialization gradient

In general, population synchrony was significantly higher in pools where variation of salinity was synchronized (environmental synchrony). However, the effects of environmental synchrony on population synchrony decrease as a function of niche breadth. The effect of environmental synchrony on population synchrony drop to 0 for generalist species irrespective of the method used to measure niche breath (Fig. 5-2).

Table 5-2. Slope of the relationship between population synchrony (PS), environmental synchrony (ES), and distance (S) for pairs of pools for all 24 species, where PS is a mean population synchrony in all pairs of pools a species occurs; ES is environmental synchrony (correlation of salinity values) without the effects of distance being removed; E|S is the pure environmental synchrony with the effect of distance has being removed; S is the distance between pairs of pools; S|E is the pure distance effect with the effect of environmental synchrony being removed. Bold numbers indicate significant values at $p < 0.05$ level.

Code	Scientific name of the species	Slope			
		PS vs. ES	PS vs. S	PS vs. E|S	PS vs. S|E
Alon	*Alona davidii*	0.111	-0.103	0.087	-0.088
CrabL	*Sesarma miersi* Rathburn	0.022	**-0.06**	0.005	**-0.06**
Cyc9	Copepod sp.	0.232	-0.158	0.202	-0.114
CycL	*Orthocyclops modestus* (Herrick)	-0.071	**-0.15**	**-0.11**	**-0.17**
CycM	*Metis* sp.	0.093	0.053	0.098	0.06
CycS	*Paracyclops fimbriatus* (Fischer)	0.064	**-0.12**	0.041	**-0.11**
Daphn	*Ceriodaphnia rigaudi* Richard	0.146	**-0.14**	0.132	-0.125
Dipter	Dipteran larvae	0.012	0.104	0.044	0.115
Gyratr	*Gyratrix hermaphroditus*	**0.218**	-0.062	**0.215**	-0.008
Harp	*Nitocra spinipes* Boeck	-0.041	-0.039	-0.054	-0.05
HarpM	Copepods (genus species, unide)	**0.375**	-0.231	**0.346**	-0.178
Leid	*Leidigia leidigi*	-0.115	-0.245	-0.051	-0.237
Mos1	*Culex* sp.	-0.014	**-0.15**	-0.054	**-0.16**
Nema	Nematode sp.	-0.043	0.024	-0.038	0.017
Oligo	Oligochaete sp.	0.041	-0.057	0.023	-0.053
Ost1	*Cypridopsis cf. mariae* Rome	0.046	-0.033	0.038	-0.026
Ost2	*Heterocypris* sp.	**0.099**	-0.039	0.094	-0.019
Ost4	*Cytheromorpha* sp.	0.053	-0.039	0.051	-0.037
Ost5	*Candona* sp.	-0.011	-0.033	-0.017	-0.036
Os5A	*Cypricercus* sp.	**0.161**	**-0.09**	**0.146**	-0.063
Ost6	*Potamocypris* sp.	-0.001	-0.023	-0.006	-0.024
PolyT	Polychaete T	**0.305**	**-0.25**	**0.246**	-0.194
PolyJ	Dorsovilleid polychaete	**0.46**	**-0.36**	**0.348**	**-0.25**
Tany	Tanypodid sp.	0.059	-0.047	0.05	-0.039

Population synchrony tended to decline with increasing distance between pools for the majority (21/24) of the species in the system, but the nature of the relationship did not change along habitat specialization of species irrespective of which method Levin's or the OMI was used. This was the case whether or not the confounding effects of environmental synchrony were removed (Fig. 5-3: C1 and C2 and D1 and D2, Table appendix 5-1).

In addition, a general linear model, GLM, analysis performed on the raw data, (as opposed to one performed on the regression slopes shown in Figures 5-2 and 5-3), with species categorized as either specialist (12 species; niche breath =<10.66) or generalist (12 species; niche breath >10.66) based on Levin's niche values, confirmed these findings (Table 5-3). Specifically, it showed that population synchrony does depend on environmental synchrony ($p = 0.002$) and specialization category ($p = 0.002$). More importantly, it also showed that specialists and generalists significantly differ in their responses to different levels of environmental synchrony (interaction between environmental synchrony and specialization, $p = 0.015$) and for different distances (interaction between distance and specialization, $p = 0.001$), with generalists responding significantly more to distance. Furthermore, GLM analysis showed that environmental synchrony affects population synchrony irrespective of distance (interaction between environmental synchrony and distance, $p=0.41$).

Table 5-3. A factorial regression Analysis of the data set of each of 24 species in 49 rock pools. Abbreviation: ES (Environmental synchrony) = synchrony in the value of salinity between a pairs of pools.

	SS	df	F	p
Intercept	0.338	1	1.748	0.186
ES	1.783	1	**9.225**	**0.002**
Distance	0.556	1	2.878	0.090
Generalist/Specialist	1.936	1	**10.015**	**0.002**
ES × Distance	0.130	1	0.672	0.412
ES × Generalist / Specialist	1.145	1	**5.923**	**0.015**
Distance × Generalists / Specialist	1.285	1	**6.647**	**0.010**
ES ×Distance × Generalist /Specialists	0.078	1	0.404	0.525
Error	865.423	4477		
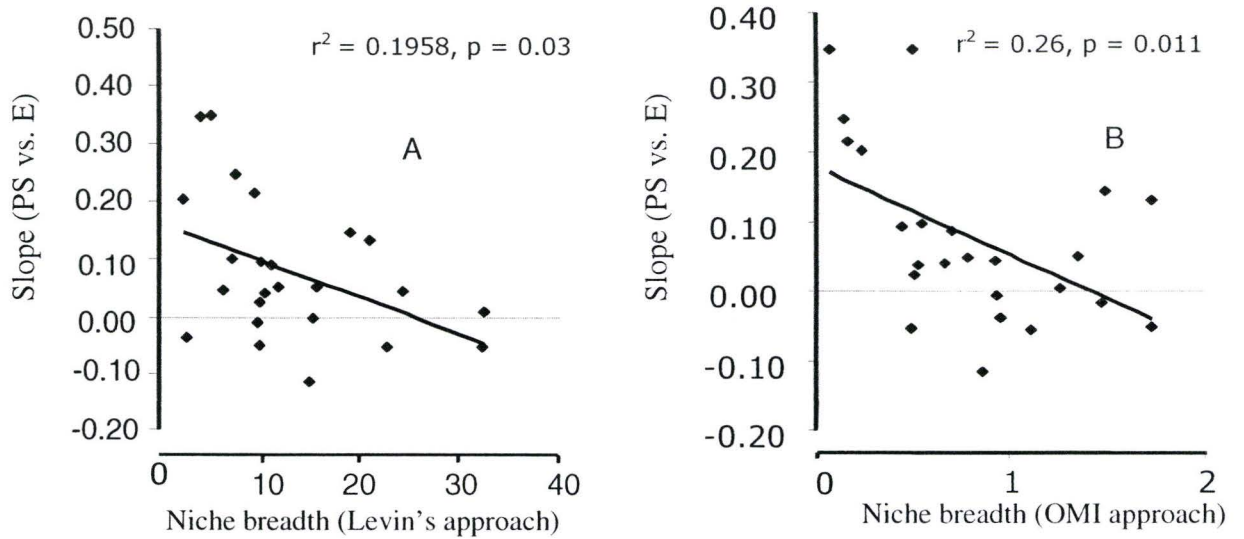
Figure 5-1. Environmental synchrony affects population synchrony depending on habitat specialization of species. A – niche breadth calculated by Levin's approach; B – niche breadth calculated by OMI approach. Data points are slope values of regressions between pure effects of environmental synchrony (removing the confounding effects of distance) and population synchrony for each of 24 species.
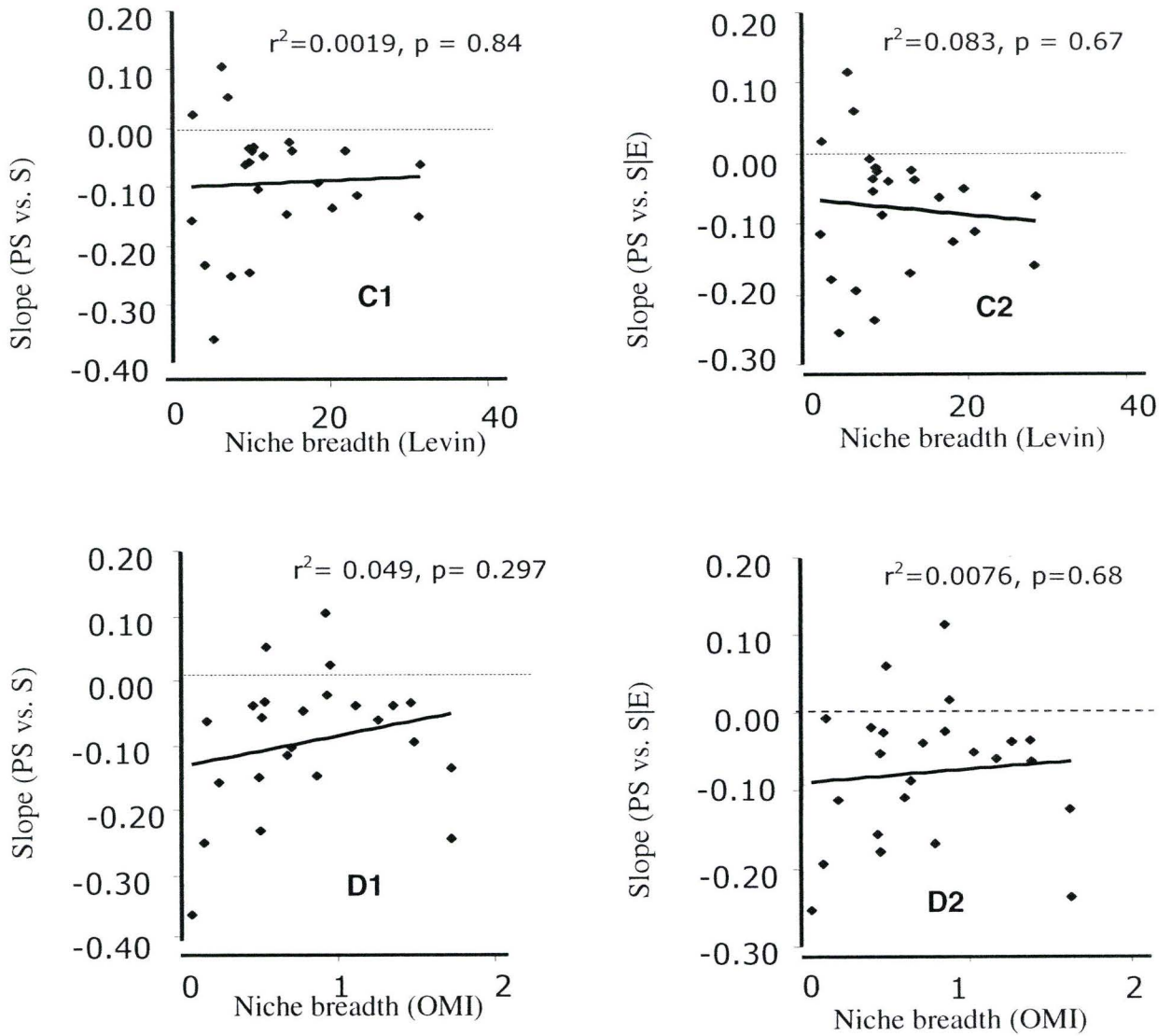
Figure 5-2. The effect of distance between pools on population synchrony does not depend on species specialization. C – Niche breadth calculated by Levin's approach; D – niche breadth calculated by OMI approach. C1 and D1: The effect of synchrony of salinity; C2 and D2: the effect of synchrony of salinity once the confounding effects of

distance has been removed. Data points are slope values of regressions between pure effects of distance between pairs of pools and population synchrony for each of 24 species. Note that the mean slope is significantly less than 0, which indicates a tendency of population synchrony to decline with distance even though such declines are generally neither strong nor significant.

DISCUSSION

In a cluster of 49 rock pools metacommunity both synchrony in environmental conditions (local factor) and distance between pools (regional factor) play a role in determining population synchrony among invertebrate species. As hypothesized, we found that the effect of environmental variability was increasing with the specialization (synchrony among specialists was correlated more with synchrony of physical variables in the same pools). However the effect of distance on population synchrony did not significantly decline with the decline of specialization (although its variance did). This particular combination of results suggests that species of different habitat specialization show systematic differences with respect to local processes involving environmental characteristics but show fewer difference with respect to regional processes involving distance, at least when long-term dynamics is concerned.

Although statistically significant regional synchrony was present in more than half of all species, its values were relatively low. This may be due to the fact that our study system is highly heterogeneous with respect to physical conditions. Such heterogeneity may result in diversity of local population dynamics, which may reduce the overall levels of population synchrony (regional synchrony) in the system. Several studies (e.g., Bjørnstad et al. 1995, Williams and Liebhold 2000) demonstrated that

habitat heterogeneity reduces population synchrony. It seems that environmental heterogeneity has a major impact on the observed synchrony among populations in our system. In this context, the finding that 13 out of 24 species showed synchrony (Table 5-1) indicates an unexpectedly common phenomenon. However, in eight of these species neither environmental synchrony nor increasing distance was able to explain their population synchrony. This implies contributions from other synchronizing factors that were not included in the study (e.g., rainfall, predation pressure) when the synchronization took place and independent population dynamics in different pools when synchrony did not take place, possibly historical effects, reproductive delays, and other population and intra-community factors.

Species at both ends of specialization spectrum, the specialists and the generalists, exhibit synchrony under some circumstances. First, synchronized environmental conditions among pairs of pools induce synchrony among population of specialist species inhabiting those pairs more than they do among populations of generalists, suggesting that the population dynamics of specialists species appear to be more tightly constrained by local conditions that those of generalists species. Second, the degree of population synchrony associated with distance between pools is only weakly related to habitat specialization (synchrony of specialists vary, generalists always decline). Thus, the different response to environmental synchrony and weak differentiation of response to

distance are intriguing because they must arise from conflating of dispersal and environmental control on the overall pattern. The finding appears to be compatible with the hypothesis that generalists respond to spatial factors more than specialists. Under that hypothesis, generalist synchrony should decline with distance while that of specialists should not decline or decline less because their population synchrony would often be overridden by environmental conditions, irrespective of the distance between host patches (pools). Although, a plot of the slopes includes a mixture of responses (cf. Fig. 3) without an apparent trend, it nevertheless is informative. The lack of systematic change in distance-specialization regression slopes may result from the fact that some pools may be distant but similar and thus synchronize specialists but not generalists. In fact, an additional analysis based on the GLM indicates clearly that a difference between specialists and generalists exists. Indeed, the greater scatter of slope values for specialists and negative values for generalists (Fig. 3) is precisely what should occur for the reasons mentioned above.

More importantly, we found that the relative importance of dispersal (space) and correlated value of environmental conditions (environment) contribute to synchronization of different categories of species differently. The implications of this finding are several. First, they may offer an explanation for why others had difficulties in detecting synchrony. This is illustrated by the fact that when we combine specialists and

generalists, we do not see the effect of distance but when we entered these two categories into GLM, the effect is clear.

Implications for metacommunity research

In general, the finding that generalist species synchronize more as the patch proximity increases is consistent with patch dynamics and mass effects models of metacommunities. However, specialist behavior has new implications. Species sorting model relies on the assumption that species presence and abundance is related to local environmental conditions. The timing and nature of that relationship depends on the nature and timing of variation in environmental conditions. When those conditions are synchronized, we find specialist populations responding likewise. When environmental conditions are not synchronized, specialists' synchronization disappears. Thus, in a natural community, a mixture of responses is a likely condition. This mixture represents a complexity that may not avail itself to easy tests of metacommunity models.

As with any analysis, there are a methodological design decisions that could influence some of the results. One of the methodological choices is the measure of habitat specialization. The choice of the method used in determining habitat specialization may affect the results. Therefore, we used two methods; one is dependent on measured

environmental factors and another independent of such factors. We found the results to be similar and without any impact on the conclusions.

We concur with others (e.g., Leibold et al. 2004, Cottenie 2005) that the metacommunity concept represents a more complete approach to dynamics of interacting species in landscapes composed of discrete habitat patches. This inclusive approach faces natural complexity that may be greater than that associated with studies of single species or single communities. General elements of this complexity include heterogeneous environmental template, gradient of species specialization, and temporal variation of the former. We believe that the advancement of metacommunity concept and specific models will be well served but dissecting mutual effects and interactions between these elements of complexity.

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Table Appendix 5-1: The slopes and correlation coefficients (r) for the relationship between population synchrony and environmental (ES), spatial (S), pure environmental (E1|S), and pure spatial (S|E1) aspects of the metacommunity structure.

Common name	Slope$_{PS.E}$				$r_{PS.E}$			
	PS vs. ES	PS vs S	PS vs E1|S	PS vs S|E1	PS vs E	PS vs S	PS vsE|S	PS vs S|E
Alon	0.111	-0.103	0.087	-0.088	0.097	-0.111	0.087	-0.092
CrabL	0.022	**-0.061**	0.005	**-0.060**	0.023	**-0.074**	0.005	**-0.071**
Cyc9	0.232	-0.158	0.202	-0.114	0.177	-0.132	0.202	-0.093
CycL	-0.071	**-0.148**	**-0.114**	**-0.168**	-0.047	**-0.117**	**-0.114**	**-0.130**
CycM	0.093	0.053	0.098	0.060	0.078	0.052	0.098	0.058
CycS	0.064	**-0.115**	0.041	**-0.109**	0.061	**-0.139**	0.041	**-0.131**
Daphn	0.146	**-0.136**	0.132	-0.125	0.149	**-0.156**	0.132	-0.142
Dipter	0.012	0.104	0.044	0.115	0.012	0.115	0.044	0.122
Gyratr	**0.218**	-0.062	**0.215**	-0.008	**0.214**	-0.079	**0.215**	-0.009
Harp	-0.041	-0.039	-0.054	-0.050	-0.037	-0.041	-0.054	-0.051
HarpM	**0.375**	-0.231	**0.346**	-0.178	**0.279**	-0.178	**0.346**	-0.135
Leid	-0.115	-0.245	-0.051	-0.237	-0.124	-0.342	-0.051	-0.323
Mos1	-0.014	**-0.150**	-0.054	**-0.158**	-0.012	**-0.164**	-0.054	**-0.170**
Nema	-0.043	0.024	-0.038	0.017	-0.041	0.028	-0.038	0.019
Oligo	0.041	-0.057	0.023	-0.053	0.039	-0.071	0.023	-0.063
Ost1	0.046	-0.033	0.038	-0.026	0.040	-0.037	0.038	-0.029
Ost2	**0.099**	-0.039	0.094	-0.019	**0.090**	-0.038	0.094	-0.018
Ost4	0.053	-0.039	0.051	-0.037	0.074	-0.064	0.051	-0.061
Ost5	-0.011	-0.033	-0.017	-0.036	-0.013	-0.044	-0.017	-0.046
Os5A	**0.161**	-0.094	**0.146**	-0.063	**0.145**	**-0.090**	0.146	-0.059
Ost6	-0.001	-0.023	-0.006	-0.024	-0.001	-0.024	-0.006	-0.025

CHAPTER 6

Conclusions

CONCLUSION

Main conclusions

The research presented in this dissertation represents a comprehensive analysis of the importance of species traits in determining the appropriate metacommunity model for a particular community. This determination is accomplished by evaluating the relative importance of underlying local and regional processes to the observed community composition and structure. In general, the results presented in my dissertation suggests that both environmental (local) and spatial (regional) processes play roles in structuring species communities in the rock pool metacommunity, although which of these processes is most important depends on the degree of habitat specialization of species.

Habitat specialization and model fitting

My work shows that a metacommunity system can exhibit an internal differentiation of structuring processes, with habitat specialists governed predominantly by environmental factors and habitat generalists governed mainly by spatial factors. Consequently, the dynamics of different groups of species in a metacommunity are explained by different models. However, when an identical analysis is applied to the entire set of species, the relative importance of local and regional processes resembles more the pattern shown by habitat generalists but differs from that observed in specialists. I conclude that this shift in interpretation of which model applies best and, consequently, which processes affect the pattern of species distribution and abundance, indicates that a

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natural metacommunity can exhibit composite dynamics. Ellis et al. (2006) results support my finding indirectly: they found it difficult to satisfactorily fit any single metacommunity model to a natural community. In other words, my study has highlighted that forcing a fit of any one metacommunity model to all species in a metacommunity may lead to flawed inferences about both the characteristics of the metacommunity in question and the validity of the model. Since one of the goals for fitting a metacommunity model is to make predictions regarding the dynamics of species, fitting a model that is inappropriate for a significant number of species is likely to lead to erroneous predictions. Because predictions differ between the models, an error of this type may have negative implications for decision making in biodiversity conservation. For example, the patch dynamics model predicts that regional diversity decreases with increasing rates of dispersal, whereas the neutral model predicts that local and regional diversity is fairly independent of dispersal rates among the localities (Chase et al. 2005). Choosing the patch dynamics model would guide a manager to enhance connectivity among sites whereas a consequence of choosing the neutral model might result in other actions. Thus, further progress in testing and applying the current metacommunity models requires that differences in ecological species traits, particularly those pertaining to habitat specialization, be examined before conclusions are made about model suitability.

Data resolution and population dynamics considerations

Habitat specialists are governed by environmental processes to a greater extent than generalists that utilize a broader range of habitat types and thus are less restricted by local conditions (Pandit et al. 2009). Initially, I drew this conclusion based on snapshot data (where nine years of data were analyzed on a year by year basis, each year representing a replicate). However, the findings may be unreliable if one considers the variation of results among individual years. For example, for specialists, pure environment explained significantly more variance in species abundance for 5 years of data, while both environment and space were significant to explain the variance in specialist abundance for 3 years of data, and in only one year neither environment nor space explained significantly in the variance of species abundance. This variation among the years may be reflecting temporal changes in community composition in a single habitat. This, therefore, reveals that understanding the influence of environmental processes over time (environmental variability) and how they vary between generalists, specialists and intermediate species is an important issue in metacommunity. However, other well established concepts (population synchrony and temporal turnover) that tackle aspects of temporal changes of species and their abundances in multiple habitats provided convenient analytical tools that can be employed in the study of metacommunities. One temporal pattern of abundance of species is population synchrony, which is defined as simultaneous rise and fall in population size in different habitat patches (Paradis et al. 2000). Another is species temporal turnover, which is defined the rate of change in

species composition at a site over time (Oberdorff et al. 2001, La Store and Boecklen 2005, Davies et al. 2005). The analyses involving synchrony and species turnover, in which long term population dynamic patterns are considered, further corroborate my initial findings that specialists were explained better by the characteristics of the rock pool environment than generalists. Specifically, my analysis provided evidence that the effects of environmental forces on temporal population dynamics are different for different group of species. In the case of temporal turnover (Chapter 4), I reach similar conclusions to those I found using species synchrony analysis (Chapter 3). For example, the rate of temporal turnover is different for different groups of species: a group of specialist species has higher turnover than the generalists and the turnover rate of a group of specialist increases when environmental variability increases (see detail in chapter 4).

Furthermore, my study shows that both rate of temporal turnover and degree of population synchrony decreases when species richness increases in the metacommunity. This is supported by the fact that population variability is often relatively higher (i.e., population are unstable) in communities with higher species richness (e.g., Ives 1995; Doak et al. 1998; McCann 2000, Gonzalez and Descamps 2004). Thus these findings (Chapters 3 and 4) show that pattern of synchrony and temporal turnover differ among species depending on two factors: habitat specialization and species richness. Species richness reduced both synchrony of local populations and temporal turnover of community composition, irrespective of specialization. Thus, my research challenges the

current metapopulation paradigm by including two important aspects, each capable of systematic interference with the traditional expectations of metapopulation dynamics.

To sum up the preceding paragraphs, my research draws attention to one more dimension along which metacommunity dynamics can differentiate – an interaction between species richness and species specialization. I present this in greater detail in Chapters 3 and 4. Further, chapter 5 examined joint contribution and interactions between spatial, environmental variables and temporal dynamics of species along the habitat specialisation. It shows evidence that the effect of environmental force (environmental synchrony) was increasing with specialization. Synchrony among specialists was correlated more with synchrony of physical variables in the same pools. However, the effect of distance on population synchrony show fewer difference with respect to regional processes involving distance, at least when long term dynamics is concerned. It seems that environmental factors override the dispersal effect. A general linear model (GLM) analysis performed on population synchrony showed that population synchrony does depend on environmental synchrony and specialization category. More importantly, it also shows that specialists and generalists significantly differ in their responses to different levels of environmental synchrony (interactions between environmental synchrony and specialization) and for different distances (interaction between distance and specialization), with generalists responding significantly more to distance.

I thus conclude with a general statement that community composition or population dynamics of different groups of species within a metacommunity system are governed by different processes. Thus, from the metacommunity perspective, the dynamics of habitat specialists are best explained by a combination of species sorting and mass effects, while that of habitat generalists are best explained by patch dynamics and neutral models. Consequently, we infer that a natural metacommunity can exhibit complicated dynamics, with some groups of species (e.g., habitat specialists) governed according to environmental processes, and other groups (e.g., habitat generalists) governed mainly by dispersal processes.

Summary of main conclusions

The Jamaican rock pool systems and a laboratory experiment confirm the expectations that a system of discrete habitats connected by species dispersal exhibits internal differentiation of structuring processes. These processes are primarily driven by habitat specialization of participating species and by differences in habitat variation. Unless this aspect is explicitly included in deriving metacommunity predictions and designing their tests, habitat specialization may remain an important confounding factor. When, we account for habitation specialization, we may gain substantial new insights into the workings of spatially fragmented habitats and their communities.

Direction for future research

- This research provided evidence that the dynamics of specialist and generalist species are different in metacommunity. Thus, the most obvious direction forward is to expand the role of species' trait in metacommunity theory. Although this research is based on an invertebrate community and rock pool metacommunity, the range of ecosystem properties in the Jamaican pools is narrow compared to the natural range of variation in aquatic systems. Similar analyses in analogous (but larger) systems would be useful to verify the findings and make general conclusions.

- Throughout my papers and this dissertation, I categorized the species of the metacommunity based on niche breadth, which depends on the uniformity of species distribution among the habitats. I defined habitat generalists and specialists to have higher and lower niche breadth values, respectively. In fact, this categorization is a relative as I did not statistically test whether the species with lower niche breadth values are specialists in terms of environmental requirements, diets, or other traits. To verify my inferences, future research should include analyses using species categorized into specialists and generalists by alternative methods, preferably those relying directly on environmental variables to determine species niche breadth.

- One limitation of this research is that it investigates the role of habitat specialization in the metacommunity to the rock pool system at only one scale, the entire test system. However, the relative importance of environmental and spatial processes changes depending on the spatial scale used to collect and analyze data (Buckley et al. 2004) and, therefore, the applicable metacommunity model must change as well (Chase and Leibold 2002, Freestone and Inouye 2006). Therefore, future metacommunity studies in this system should focus on the differences in metacommunity model assignment as a function of spatial scale. I hypothesize that if only a fraction of the pools is studied, the metacommunity model would change. Because at small spatial scale environments are likely to be more homogeneous, either the neutral or patch dynamic model would be more appropriate to explain metacommunity structure. However, as the spatial scale under investigation increases, local environments are likely become more different from each other and therefore species sorting or mass effect models would become more suitable.

Management implication of my research

- The management and conservation of ecological communities depends on our capacity to predict community composition and distribution of species on large spatial scales. The ability to make such predictions is vital because both landscapes and habitats are becoming fragmented at an alarming rate. Metacommunity theory has been developed to aid in understanding of biodiversity patterns in fragmented

landscapes. However, it has not been tested empirically in a wide range of systems. My findings have highlighted the importance of species' traits in a metacommunity. These findings may aid both conservation biologists and environmental planners in making decisions related to the conservation of biodiversity. This research provided evidence that within a metacommunity species dynamics differ along the gradient from habitat generalists to specialists. Consequently, the most obvious direction forward is to expand the role of species' traits in metacommunity theory. The traditional approach of fitting one metacommunity model for all species in a metacommunity seems to be inadequate, and may lead to erroneous conclusions as well as recommendations regarding biodiversity conservation.

- Furthermore, improving the metacommunity theory by incorporating the role of species traits can prove to be useful for environmental remediation efforts. Understanding that different categories of species (generalists vs. specialist) are governed by different factors (spatial, environment.) can provide useful information with regards to how individual species would respond to environmental remediation efforts in fragmented landscapes.

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Appendix

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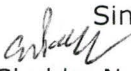Phone: (202) 833-8773, Fax: (202) 833-8775

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