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

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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 (nine-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 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 generalists; habitat specialists; habitat specialization; Jamaica; mass effects; metacommunity models; neutral models; patch dynamics; species sorting; 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, Cottenie 2005, Holyoak et al. 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, Cottenie 2005, Kolasa and Romanuk 2005, Miller and Kneitel 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 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 in which 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 in which 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 (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, Cadotte et al. 2006, Cadotte 2007). Other metacommunity studies have examined the role of connectivity and dispersal between patches (Gonzalez et al. 1998, Forbes and Chase 2002, Gonzalez and Chaneton 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).

These 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 that 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 dramat-

ically, its effect should be higher on abundance of habitat specialists (Vazquez and Simberloff 2002), as observed in communities of birds (Julliard et al. 2004), mammals and amphibians (Swihart et al. 2003), butterflies (Cleary and Genner 2004), and coral reef gobies (Munday 2004). Habitat specialists are more susceptible to extinction than 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 vs. 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 of 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°28′ N, 77°25′ W; Fig. 1). For the study, we selected 49 rock pools (see Plate 1) 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 from 1 to 37 cm in depth (depth = 12.8 ± 8.3 cm [mean ± SD]). Volumes ranged from 0.5 L to 115 L (12 ± 21 L). On average, the rock pools were located within 1 m of the nearest rock pool, and none were separated by more than 5 m from the nearest pool. Their elevation above sea level ranged from 1 to 235 cm (76.6 ± 80.1 cm) 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.
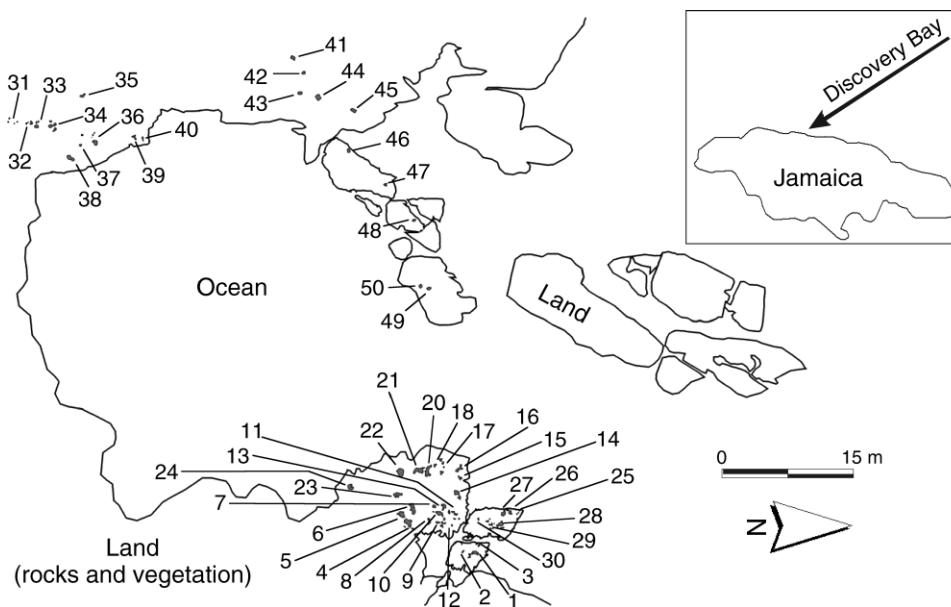
Fig. 1. Location of the study area and 49 rock pools (numbered) at the Discovery Bay Marine Laboratory (DBML), University of West Indies, Jamaica. The arrow indicates the approximate location of the study site in Jamaica.

Sampling design

Annual surveys were carried out between 28 December and 11 January 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, Yellow Springs Instruments, Yellow Springs, Ohio, USA, or Hydrolab, Austin, Texas, USA). Biotic samples were collected by taking 500 mL of water from each pool after stirring the pool to dislodge organisms from the sides and bottom and to homogenize their distribution. Each pool water sample was then filtered through a 63-μm 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 nine 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 (five species), worms (15 species, including oligochaetes, polychaetes, and turbellarians), aquatic insects (18 species), and other crustaceans (six 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 nine 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

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

where B_j is the niche breadth and P_{ij} is 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 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 the Appendix.

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

(Table A1). 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 five species with the greatest niche breadths (as generalists) and five 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 species and a harpacticoid species), 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 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.

Species data.—We created species abundance matrices for the selected habitat generalists, habitat specialists, and all 24 species for each of nine 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).

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. Mean values were used whenever multiple measurements were taken in a given year.

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 (Ripley 1981, Borcard et al. 1992).

Statistical analysis

We used redundancy analysis (RDA) (Borcard et al. 1992, Cottenie 2005, Vanschoenwinkel 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], [$E \mid S$], and [$S \mid E$]; see Table 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) vs. 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 d (Romanuk et al. 2006) and the average time between sampling periods is 10.5 months, temporal autocorrelation between species abundances at these timescales 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 1, Fig. 2). For all 24 species, the variation in species abundance was better explained by the pure spatial (~24%

TABLE 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 Discovery Bay Marine Laboratory (DBML), University of West Indies, Jamaica.

Sample date	Variance explained (%)			
	E	S	$E \mid S$	$S \mid E$
All species				
1989 December	**31.1**	**41.9**	14.7	**25.5**
1990 January	**30.1**	**45.1**	14.1	**29.1**
1991 January	**28.2**	**37.7**	15.7	**25.2**
1992 January	**30.1**	**45.1**	14.1	**29.2**
1993 January	**30.1**	**32.0**	**16.6**	18.5
1994 January	19.1	**30.8**	13.6	**25.3**
1997 January	**38.2**	**38.5**	**17.4**	17.8
1997 June	**31.1**	**46.9**	10.5	**26.2**
1998 January	**32.5**	**43.4**	10.8	**21.8**
Mean	30.1	40.2	14.2	24.3
Habitat generalists				
1989 December	**30.7**	**47.0**	12.5	**28.3**
1990 January	**27.3**	**46.6**	7.9	**27.1**
1991 January	**32.1**	**44.5**	10.7	**20.1**
1992 January	**32.4**	**55.2**	14.3	**37.1**
1993 January	**31.5**	**30.9**	**20.0**	**29.3**
1994 January	18.7	**35.4**	14.7	**33.9**
1997 January	**42.9**	**49.9**	10.2	17.2
1997 June	**29.1**	**50.1**	8.6	**29.5**
1998 January	**36.3**	**44.5**	11.4	19.6
Mean	31.2	44.9	12.3	26.9
Habitat specialists				
1989 December	**44.5**	23.1	**35.2**	14.4
1990 January	**45.1**	23.6	**35.0**	13.4
1991 January	**26.3**	24.1	**22.0**	19.8
1992 January	**40.1**	22.1	**31.7**	13.7
1993 January	**37.8**	21.6	**36.9**	19.7
1994 January	**30.5**	**32.7**	12.8	10.6
1997 January	**65.9**	**29.3**	**44.9**	**24.1**
1997 June	**71.9**	**30.9**	**48.4**	**27.5**
1998 January	**64.0**	23.7	**48.6**	8.3
Mean	47.3	25.7	35.1	16.8

Notes: Boldface indicates the value is significant at $P \le 0.05$. (Actual P values are given in the Appendix.) Abbreviations are: E, variation explained by environmental variables; S, variation explained by spatial variables; $E \mid S$, variation explained by pure environmental variables (contribution of S removed); and $S \mid E$, variation explained by pure spatial variables (contribution of E removed).

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 ~12% of the variation, while the pure spatial component explained ~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 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 (Fig. 2). 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
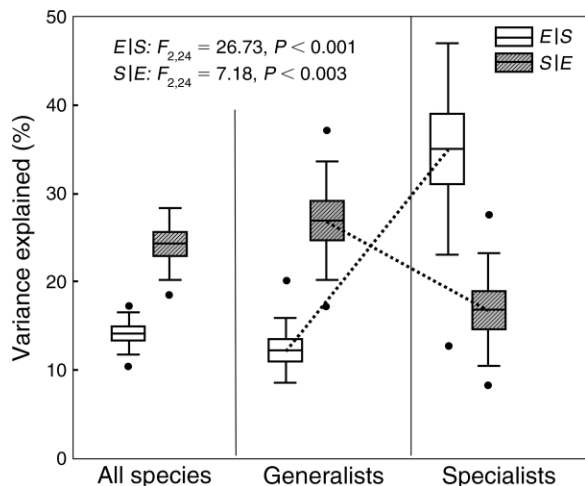
FIG. 2. The relative contribution of pure environment $(E\,|\,S)$ and pure spatial $(S\,|\,E)$ components in explaining the variation in abundance of three species groups for the different sampling periods. Boxes represent the interquartile range, the central bar represents the mean, the whiskers represent the standard error, and the points are outliers outside 1.5 times the distance of the interquartile 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 $S\,|\,E$).

each sampling year. Overall, there was a significant effect of both elevation and salinity on invertebrate community structure in most years (Table 2). 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.

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 upon 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

TABLE 2. Relative contribution (percentage of total variation, Var.) of each of six environmental variables for the community structure of three species groups: all species, habitat generalists, and habitat specialists.

Sample date	Temperature Var. (%)	P	Salinity Var. (%)	P	Oxygen Var. (%)	P	pH Var. (%)	P	Volume Var. (%)	P	Elevation Var. (%)	P
All species												
1989 December	1.0		3.0		8.0	0.00	2.0		3.0		14.0	0.00
1990 January	1.0		3.0		7.0	0.00	3.0		2.0		14.0	0.00
1991 January	4.0		15.0	0.00	1.0		1.0		2.0		5.0	0.04
1992 January	2.0		5.0	0.04	3.0		5.0	0.04	2.0		13.0	0.00
1993 January	3.0		6.0	0.03	3.0		2.0		1.0		15.0	0.00
1994 January	5.0	0.03	2.0		1.0		1.0		2.0		8.0	0.01
1997 January	8.0	0.00	5.0	0.04	4.0	0.05	5.0	0.04	2.0		14.0	0.00
1997 June	2.0		9.0	0.00	1.0		1.0		1.0		17.0	0.00
1998 January	5.0	0.01	2.0		2.0		2.0		5.0	0.03	16.0	0.00
Habitat generalists												
1989 December	0.0		1.0		4.0		4.0		2.0		20.0	0.00
1990 January	0.0		3.0		4.0		5.0	0.05	1.0		14.0	0.00
1991 January	3.0		5.0	0.05	2.0		0.0		2.0		20.0	0.00
1992 January	1.0		3.0		2.0		6.0	0.03	2.0		18.0	0.00
1993 January	5.0	0.03	1.0		7.0	0.00	4.0		1.0		13.0	0.00
1994 January	3.0		1.0		3.0		0.0		2.0		9.0	0.00
1997 January	5.0	0.05	3.0		0.0		7.0	0.01	6.0	0.03	21.0	0.00
1997 June	3.0		4.0		3.0		3.0		1.0		15.0	0.00
1998 January	2.0		3.0		6.0	0.03	5.0	0.04	1.0		19.0	0.00
Habitat specialists												
1989 December	5.0	0.04	23.0	0.00	6.0	0.03	1.0		0.0		9.0	0.01
1990 January	5.0	0.04	24.0	0.00	5.0	0.04	1.0		1.0		9.0	0.01
1991 January	19.0	0.00	2.0		1.0		2.0		0.0		2.0	
1992 January	0.0		12.0	0.00	10.0	0.00	6.0	0.04	1.0		11.0	0.00
1993 January	2.0		14.0	0.00	9.0	0.00	7.0	0.01	0.0		6.0	0.04
1994 January	8.0	0.00	8.0	0.01	6.0	0.05	6.0	0.05	1.0		1.0	
1997 January	31.0	0.00	7.0	0.01	14.0	0.00	1.0		1.0		12.0	0.00
1997 June	32.0	0.00	6.0	0.02	21.0	0.00	1.0		1.0		10.0	0.00
1998 January	34.0	0.00	8.0	0.01	9.0	0.00	2.0		1.0		10.0	0.00

Note: Only P values ≤ 0.05 are reported.

PLATE 1. 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 Fig. 1. Photo: J. Kolasa.

(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., a few data sets of 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 and Kolasa 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 (~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 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 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 or noise 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, in which 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 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. The authors demonstrated that urbanization stressors affect the richness of bird groups differently depending on their life-history traits (cavity vs. 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.

Literature Cited

Amarasekare, P. 2003. Competitive coexistence in spatially structured environments: a synthesis. Ecology Letters 6: 1109–1122.

Amarasekare, P., M. F. Hoopes, N. Mouquet, and M. Holyoak. 2004. Mechanisms of coexistence in competitive metacommunities. American Naturalist 164:310–326.

Bean, K., G. P. Jones, and M. J. Caley. 2002. Relationships among distribution, abundance and microhabitat specialization in a guild of coral reef triggerfish (family Balistidae). Marine Ecology Progress Series 233:263–272.

Bell, G. 2001. Ecology—neutral macroecology. Science 293: 2413–2418.

Borcard, D., P. Legendre, and P. Drapeau. 1992. Partialling out the spatial component of ecological variation. Ecology 73: 1045–1055.

Cadotte, M. W. 2006. Metacommunity influences on community richness at multiple spatial scales: a microcosm experiment. Ecology 87:1008–1016.

Cadotte, M. W. 2007. Concurrent niche and neutral processes in the competition–colonization model of species coexistence. Proceedings of the Royal Society B 274:2739–2744.

Cadotte, M. W., D. V. Mai, S. Jantz, M. D. Collins, M. Keele, and J. A. Drake. 2006. On testing the competition–colonization tradeoff in a multispecies assemblage. American Naturalist 168:704–709.

Chase, J. M., and M. A. Leibold. 2002. Spatial scale dictates the productivity–biodiversity relationship. Nature 416:427–430.

Chave, J. 2004. Neutral theory and community ecology. Ecology Letters 7:241–253.

Chesson, P. 2000. General theory of competitive coexistence in spatially-varying environments. Theoretical Population Biology 58:211–237.

Cleary, D. F. R., and M. J. Genner. 2004. Changes in rain forest butterfly diversity following major ENSO-induced fires in Borneo. Global Ecology and Biogeography 13:129–140.

Colwell, R. K., and D. J. Futuyma. 1971. On the measurement of niche breadth and overlap. Ecology 52:567–576.

Cottenie, K. 2005. Integrating environmental and spatial processes in ecological community dynamics. Ecology Letters 8:1175–1182.

Cottenie, K., E. Michels, N. Nuytten, and L. De Meester. 2003. Zooplankton metacommunity structure: regional vs. local processes in highly interconnected ponds. Ecology 84:991–1000.

Ellis, A. M., L. P. Lounibos, and M. Holyoak. 2006. Evaluating the long-term metacommunity dynamics of tree hole mosquitoes. Ecology 87:2582–2590.

Forbes, A. E., and J. N. Chase. 2002. The role of habitat connectivity and landscape geometry in experimental zooplankton metacommunities. Oikos 96:433–440.

Gilbert, B., and M. J. Lechowicz. 2004. Neutrality, niches, and dispersal in a temperate forest understory. Proceedings of the National Academy of Sciences (USA) 101:7651–7656.

Gonzalez, A., and E. J. Chaneton. 2002. Heterotroph species extinction, abundance and biomass dynamics in an experimentally fragmented microecosystem. Journal of Animal Ecology 71:594–602.

Gonzalez, A., J. H. Lawton, F. S. Gilbert, T. M. Blackburn, and I. Evans-Freke. 1998. Metapopulation dynamics, abundance, and distribution in a microecosystem. Science 281: 2045–2047.

Holt, R. D. 1993. Ecology at the mesoscale: the influence of regional processes on local communities. Pages 77–88 in R. Ricklefs and D. Schlute, editors. Species diversity in ecological communities. University of Chicago Press, Chicago, Illinois, USA.

Holyoak, M., M. A. Leibold, and R. D. Holt. 2005. Metacommunities: spatial dynamics and ecological communities. The University of Chicago Press, Chicago, Illinois, USA.

Hubbell, S. P. 2001. The unified neutral theory of biodiversity and biogeography. Princeton University Press, Princeton, New Jersey, USA.

Jorcin, A. 1999. Temporal and spatial variability in the macrozoobenthic community along a salinity gradient in the Castillos Lagoon (Uruguay). Archiv für Hydrobiologie 146:369–384.

Julliard, R., F. Jiguet, and D. Couvet. 2004. Evidence for the impact of global warming on the long-term population dynamics of common birds. Proceedings of the Royal Society B 271:S490–S492.

Kneitel, J. M., and T. E. Miller. 2003. Dispersal rates affect species composition in metacommunities of Sarracenia purpurea inquilines. American Naturalist 162:165–171.

Kolasa, J., and B. L. Li. 2003. Removing the confounding effect of habitat specialization reveals the stabilizing contribution of diversity to species variability. Proceedings of the Royal Society B 270:S198–S201.

Kolasa, J., and S. T. A. Pickett. 1989. Ecological systems and the concept of biological organization. Proceedings of the National Academy of Sciences (USA) 86:8837–8841.

Kolasa, J., and T. N. Romanuk. 2005. Assembly of unequals in the unequal world of a rock pool metacommunity. Pages 212–232 in M. Holyoak, M. A. Leibold, and R. D. Holt, editors. Metacommunities: spatial dynamics and ecological communities. University of Chicago Press, Chicago, Illinois, USA.

Legendre, P., and E. Gallagher. 2001. Ecologically meaningful transformations for ordination of species data. Oecologia 129:271–280.

Leibold, M. A., M. Holyoak, N. Mouquet, P. Amarasekare, J. M. Chase, M. F. Hoopes, R. D. Holt, J. B. Shurin, R. Law, D. Tilman, M. Loreau, and A. Gonzalez. 2004. The metacommunity concept: a framework for multi-scale community ecology. Ecology Letters 7:601—613.

Leibold, M. A., and T. E. Miller. 2004. From metapopuation to metacommunities. Pages 133–150 in I. A. Hanski and O. E. Gaggiotti, editors. Ecology, genetics and evolution of metapopulations. Elsevier, Burlington, Massachusetts, USA.

Levine, J. M., and M. Rees. 2002. Coexistence and relative abundance in annual plant assemblages: the roles of competition and colonization. American Naturalist 160: 452–467.

Levins, R. 1968. Evolution in changing environments. Princeton University Press, Princeton, New Jersey, USA.

McCauley, S. J. 2007. The role of local and regional processes in structuring larval dragonfly distributions across habitat gradients. Oikos 116:121–133.

McGill, B. J., B. A. Maurer, and M. D. Weiser. 2006. Empirical evaluation of the neutral theory. Ecology 87:1411–1423.

Miller, T. E., and J. M. Kneitel. 2005. Inquiline communities in pitcher plants as a prototypical metacommunity. Pages 122–145 in M. Holyoak, M. A. Leibold, and R. D. Holt, editors. Metacommunities: spatial dynamics and ecological communities. University of Chicago Press, Chicago, Illinois, USA.

Mouquet, N., M. F. Hoopes, and P. Amarasekare. 2005. The world is patchy and heterogeneous! Trade-off and source sink dynamics in competitive metacommunities. Pages 237–262 in M. Holyoak, M. A. Leibold, and R. D. Holt, editors. Metacommunities: spatial dynamics and ecological communities. University of Chicago Press, Chicago, Illinois, USA.

Mouquet, N., P. Leadley, J. Meriguet, and M. Loreau. 2004. Immigration and local competition in herbaceous plant communities: a three-year seed-sowing experiment. Oikos 104:77–90.

Mouquet, N., and M. Loreau. 2002. Coexistence in metacommunities: the regional similarity hypothesis. American Naturalist 159:420–426.

Munday, P. L. 2004. Habitat loss, resource specialization and extinction on coral reefs. Global Change Biology 10:1642–1647.

Munday, P. L., G. P. Jones, and M. J. Caley. 1997. Habitat specialisation and the distribution and abundance of coral-dwelling gobies. Marine Ecology Progress Series 152:227–239.

Peres-Neto, P. R., P. Legendre, S. Dray, and D. Borcard. 2006. Variation partitioning of species data matrices: estimation and comparison of fractions. Ecology 87:2614–2625.

Pinel-Alloul, B., T. Niyonsenga, and P. Legendre. 1995. Spatial and environmental components of fresh-water zooplankton structure. Ecoscience 2:1–19.

Rautio, M. 1998. Community structure of crustacean zooplankton in subarctic ponds—effects of altitude and physical heterogeneity. Ecography 21:327–335.

Ripley, B. D. 1981. Spatial statistics. Wiley, New York, New York, USA.

Romanuk, T. N., and J. Kolasa. 2002. Environmental variability alters the relationship between richness and variability of community abundances in aquatic rock pool microcosms. Ecoscience 9:55–62.

Romanuk, T. N., R. J. Vogt, and J. Kolasa. 2006. Nutrient enrichment weakens the stabilizing effect of species richness. Oikos 114:291–302.

Schlesinger, M. D., P. N. Manly, and M. Holyoak. 2008. Distinguishing stressors acting on land bird communities in an urbanizing environment. Ecology 89:2302–2314.

Shurin, J. B., P. Amarasekare, J. M. Chase, R. D. Holt, M. F. Hoopes, and M. A. Leibold. 2004. Alternative stable states and regional community structure. Journal of Theoretical Biology 227:359–368.

Swihart, R. K., T. M. Gehring, M. B. Kolozsvary, and T. E. Nupp. 2003. Responses of 'resistant' vertebrates to habitat loss and fragmentation: the importance of niche breadth and range boundaries. Diversity and Distributions 9:1–18.

ter Braak, C. J. F., and P. Šmilauer. 1998. CANOCO reference manual and CanoDraw for Windows user's guide: software for canonical community ordination. Version 4. Microcomputer Power, Ithaca, New York, USA.

ter Braak, C. J. F., and P. Šmilauer. 2002. Program CANOCO for Windows. Version 4.5. Biometris, Plant Research International, Wageningen University and Research Centre, Wageningen, The Netherlands.

Therriault, T. W., and J. Kolasa. 2001. Desiccation frequency reduces species diversity and predictability of community structure in coastal rock pools. Israel Journal of Zoology 47: 477–489.

Tilman, D., S. S. Kilham, and P. Kilham. 1982. Phytoplankton community ecology—the role of limiting nutrients. Annual Review of Ecology and Systematics 13:349–372.

Tilman, D., R. M. May, C. L. Lehman, and M. A. Nowak. 1994. Habitat destruction and the extinction debt. Nature 371:65–66.

Travis, J. M. J. 2003. Climate change and habitat destruction: a deadly anthropogenic cocktail. Proceedings of the Royal Society B 270:467–473.

Vanschoenwinkel, B., C. De Vries, M. Seaman, and L. Brendonck. 2007. The role of metacommunity processes in shaping invertebrate rock pool communities along a dispersal gradient. Oikos 116:1255–1266.

Vazquez, D. P., and D. Simberloff. 2002. Ecological specialization and susceptibility to disturbance: conjectures and refutations. American Naturalist 159:606–623.

Yu, D. W., H. B. Wilson, M. E. Frederickson, W. Palomino, R. De la Colina, D. P. Edwards, and A. A. Balareso. 2004. Experimental demonstration of species coexistence enabled by dispersal limitation. Journal of Animal Ecology 73:1102–1114.

APPENDIX

Niche breadth calculations and properties (*Ecological Archives* E090-157-A1).