

CHAPTER 9

Assembly of Unequals in the Unequal World of a Rock Pool Metacommunity

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Introduction

Scale is an important component of an integrated metacommunity theory (Leibold et al. 2004; Holyoak et al., chapter 1), and incorporating various elements of scale is likely to continue to be a major force shaping the metacommunity framework. A number of specific insights have proved useful. Mouquet and Loreau (2002) considered two spatial scales—local and regional—and demonstrated potential interactions between these scales. Hanski and Gyllenberg (1997) showed that local abundance, geographical range, and species-area relationships could have a common conceptual core and represent differently scaled aspects of metapopulations. Some aspects of scale, particularly spatial ones, are formalized in metacommunity theory, such as patch size and distance among patches (Holyoak et al., chapter 1). By contrast, theoretical or experimental investigations of multiple spatial scales are rare (cf. Cadotte and Fukami 2004), and scales other than those discussed above may be important in developing an integrated metacommunity perspective. For example, scale may include dimensions such as gradients in species specialization or gradients in habitat heterogeneity and habitat structure.

In this chapter we consider the importance of different spatial and organizational scales on ecological processes in a metacommunity of rock pools inhabited by a diverse assembly of aquatic invertebrates using a hierarchical view of habitat structure. We also attempt to relate the empirical patterns seen in the rock pool metacommunity to the four metacommunity models articulated by Leibold et al. (2004) and Holyoak et al. (chapter 1). The primary structural feature of the rock pool metacommunity is the nested hierarchy of spatial habitat units, from individual pools to the entire regional array of pools. This structural hierarchy suggests that there is no simple local-regional scale dichotomy in the metacommunity (*sensu* Mouquet and Loreau 2002; Mouquet et al., chapter 10). Instead, habitat is portrayed as a nested hierarchy of habitat units, with each unit reflecting a fraction of multidimensional habitat space and with the whole structure potentially acting as a species sorting mechanism (Kolasa 1989).

First, we will outline and explain a hierarchical model of habitat, its predictions, and relationship to species and metacommunities. Subsequently, we will introduce the study system and illustrate the hierarchical nature of its spatial con-

figuration and the possible constraints the hierarchy may impose on the movement and interactions among species. After describing the system in which metacommunity processes take place, we proceed to identify patterns in support of the hierarchical perspective and patterns that relate our empirical observations to various metacommunity models. In that section we highlight the existence of discontinuities in the observed metacommunity descriptors, positive links between density of individual species, occupancy of sites and degree of habitat specialization, the relationship between local and regional density, and the dependence of local species richness on scale of habitat variability.

A Hierarchical Model of Metacommunities

The habitat-based model (HBM) uses assumptions about (1) species attributes, (2) habitat attributes, and (3) the relation between species and habitat. The model is scale independent and can be applied at any scale of habitat structure.

Species Attributes

With respect to species we assume that: (1) they differ in their ecological needs such that there is a specialization gradient from species with narrow habitat requirements (habitat specialists) to species with broad habitat requirements (habitat generalists), and (2) any habitat may host a set of species representing the full range of habitat specializations. We contrast habitat generalists and specialists, but when referring to these two categories we recognize a gradient of habitat specialization. The differences potentially go far beyond core and satellite dynamics (Hanski 1982) because species interact with multiscale habitat heterogeneity. Different habitat requirements include tolerance limits, resource needs, and conditions for successful reproduction and dispersal such as nursery needs or presence of dispersal conduits. The terms specialist and generalist have a variety of meanings in ecology. The meaning here is general but precise: a specialist is a species restricted to a small volume of the multidimensional habitat space. In contrast, a generalist is a species that is not as restricted (Kolasa and Waltho 1998). Note that a species is evaluated by its relation to the habitat, and it is defined as a specialist or generalist relative to other species in the community, which jointly define the multidimensional habitat space.

Habitat Assumptions

We assume that habitat is a nested hierarchy of multidimensional volumes (for detailed discussion see Kolasa and Waltho 1998). Because any dimension except time can be mapped onto space, we interpret the habitat as (1) a hierarchical mosaic of patches with (2) lower level patches nesting within higher level patches, and (3) with each level and patch at any level involving a distinct set of attributes. For the sake of illustration, we use two dimensions only, which give the model a

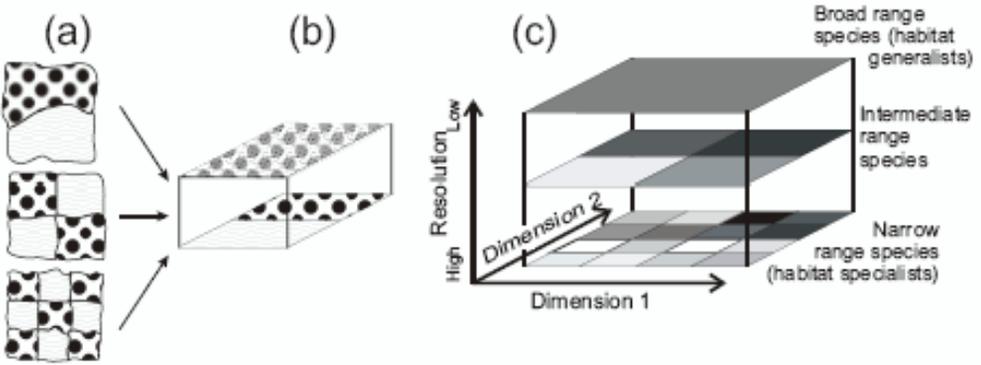


Figure 9.1 A simplified view of habitat hierarchy showing species categories defined by their use of various levels of resolution: (a) each of two types of habitat can take continuous or fragmented forms as illustrated by three combinations; (b) these types are represented in the model as a single two-level habitat hierarchy that can be used by two specialists at the lower level and one generalist at the higher level; (c) a hypothetical habitat structure able to accommodate twenty-one species. Note that habitat grain, size, and diversity changes with resolution. From species' perspective, the habitat becomes more fragmented at higher levels of resolution (i.e., lower levels of structure). While types of habitat patch are shown here as regular subdivisions of the total habitat unit, real structures are much more variable (figure 9.2; for further explanation see Kolasa 1989).

spatial appearance even though this appearance represents a considerable simplification because it does not purport to convey any specific configuration of actual habitats in space. The model only identifies the total amount of space a particular habitat unit occupies on average relative to a higher level unit. Each unit can take various configurations in space as a patch that is either contiguous or **fragmented** to varying degrees (figure 9.1a). Regardless of spatial configuration, two habitat types are represented in the model as two subunits (figure 9.1b). Extending this approach permits representation of the whole habitat as a nested structure of units emerging at increasing levels of resolution (figure 9.1c).

Relationship between Species and Habitat Structure

The relationship between the species and the habitat assumes the following: (1) habitat generalists use the largest habitat units, thus increasing habitat specialization results in the use of progressively smaller habitat units nested within the larger ones; and (2) the density of a species varies positively with the habitat unit size and negatively with the degree of unit isolation from other similar units. Thus, according to the model, the generalists' density will be proportional to the continuous area of the top habitat defined by the two dimensions in figure 9.1c. The situation is different for the specialists at the two lower levels. Although their densities are proportional to the area of the squares used, the expected density is different because their habitats appear as single patches in the generalist's habitat.

In a habitat unit even larger than one shown in figure 9.1c, these habitats would multiply but remain separated from each other by other, unusable, patches. The more specialized the species, the greater the geometrical and ecological distance (e.g., barriers of hostile habitats) between suitable units of the environment. Fragmentation of a habitat unit itself (cf. figures 9.1a and 9.2) can exacerbate this barrier effect. In a sense, resources available to a specialist can be viewed as being diluted in the patchwork of other habitat units. It is not unreasonable to assume that a specialist species faces higher energy and population costs when it uses patchily distributed habitats. By contrast, generalists in the model experience a more continuous distribution of habitat. Theoretically there may be several components to the costs experienced by specialists, such as energetic costs of travel, mortality during dispersal, decreased efficiency through failure to find patchily-distributed resources, or finding and settling in low-quality, sink patches. From now on, the sum of these costs will be assumed to reduce a species' density in proportion to the degree that the habitat is fragmented at the specialist level.

Predictions of the HBM

Consequences of the HBM are that (a) there are few species of habitat generalists and many specialists in species rich communities, (b) specialists have lower local density and habitat fragmentation plays a progressively larger role in determina-

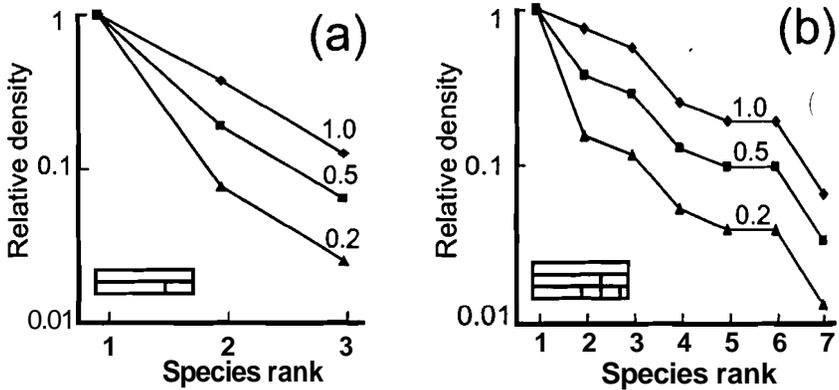


Figure 9.2 Effect of spatial fragmentation on relative density of species predicted by the HBM model: (a) the relative density of species using habitat unit in figure 9.1b as a function of fragmentation depicted in figure 9.1a; (b) the relative density of species using a habitat unit with one more level of resolution (inset shows a habitat able to accommodate 7 species: 1 + 2 + 4), with spatial fragmentation introduced for habitats units at the intermediate level of resolution only. Fragmentation in both panels is similar to that shown in figure 9.1a, that is, each habitat type is split into 1, 2, or 4–5 patches, with corresponding labels of 1, 0.5, and 0.2 to reflect the resulting patch size. Note that the fragmentation of the intermediate level (figure 9.2b) affects habitat specialists at the lower level of structure (ranks 4–7) even though no specific fragmentation was assumed for this level.

tion of their density relative to other factors, (c) community structure is discontinuous, with groups of species having similar degrees of habitat specialization and local density, and (d) local and regional density should converge for generalists.

Furthermore, the model implies that most local communities may transition gradually into metacommunities as spatial scale is increased. A thought experiment illustrates this observation. If the graphical representation of habitat structure in figure 9.1c grew in space by copying itself by 25%, it would mean no change for the top generalist because its habitat would remain continuous. However, two of the four intermediate species and four of the specialists would acquire additional subunits and thus enter the realm of metacommunity dynamics. A further expansion in the same direction by 5% would replicate patches suitable for four more habitat specialists. However, neither the top generalist nor additional intermediate species would experience a different habitat structure in the second step. A complete duplication of the structure would create a complete two-patch metacommunity, except for the top species (unless the duplication was discontinuous in space). Consequently, depending on the actual structure of the habitat, or the structure included in the study, a community of interest would require different degrees of metacommunity level insights.

This model is general in that it does not rely on physical properties, competition, predation or any other specific mechanism acting among the many dimensions that define habitat. Instead, it captures and summarizes the final outcomes of many processes, stochastic and deterministic, external and internal, individualistic and interactive. This hierarchical view of habitat structure guides our exploration into the ecology of the rock pool metacommunity and the parameters that may be important in the development of metacommunity models. It also highlights the importance of a metacommunity paradigm that explicitly considers the metacommunity as a set of interacting continua of properties and processes staged on an uneven playing field.

In general, however, the species in the rock pool metacommunity display a full range of habitat specialization that is positively correlated with their distribution (Kolasa and Li 2003). One can thus formulate the problem of metacommunity as the interaction of a set of species attributes with a set of environmental attributes. Existing metacommunity models do not explicitly recognize multiple scales and species' responses to them. The hierarchical model not only recognizes multiple scales, but also makes predictions about the patterns of densities and degrees of habitat specialization that should result from them.

Habitat-based Model and Other Metacommunity Models

Both the species sorting and mass effects models include a habitat gradient along which species sort. The hierarchical model (HBM) is most like the species sorting model but it explicitly recognizes the hierarchical structure of habitat and species

responses to the habitat. Unlike the mass effects model the hierarchical model assumes that a species will be present in habitats that meet two conditions: they do have required resources (a niche based explanation) and are not excluded from it via biotic interactions such as direct or indirect effects of competition, parasitism, or predation, or by intolerable physical conditions. The HBM does not assume or include explicit mass effects or source-sink dynamics (e.g., Pulliam 2000). However, in empirical tests of the model (e.g., Kolasa 1989) expected density was calculated from the occupancy patterns. Because such patterns do not differentiate between values of the finite rate of increase λ , smaller or larger than 1, both effects may have been subsumed in the relationship between the distribution and density. Indeed, mass effects could promote species occupying habitats that are unsuitable for them and so affect occupancy and distribution patterns. Unlike the neutral and patch dynamics models, in the hierarchical model species are assumed to be found in particular kinds of habitat that are suitable for them, although the model is not restrictive as to how suitable habitats must be. At small spatial and temporal scales, a suitable habitat may simply mean habitat sufficient for survival of immigrants ($\lambda < 1$), while at a larger scale this implies a persistent population ($h \geq 1$). Hence, in the neutral and patch dynamics models, species compositions of particular patches are expected to drift randomly through time and to show no particular habitat associations (see "Differences between Habitat Specialists and Generalists" for a test).

Fitchie and Olff (1999) have proposed an approach to regional diversity that also relies on differences among species in their perception of habitat patches. This model has an advanced formal structure built on a set of specific assumptions concerning body size, habitat fractal structure, and home range of individuals that do not apply to the rock pool metacommunity. The major difference between the HBM and Ritchie and Olff's model is that species' perceptions are analyzed at the individual level in the latter while they are a trait of populations in HBM. Consequently, home range of an individual and its effect on access to the amount and quality of resources forms the foundation of the Ritchie and Olff's model. In HBM, though, the perceptions of a single copepod or midge do not matter. What matters is the ability of a copepod subpopulation to persist in a habitat. Consequently, the home range does not matter in the HBM; the access to resources is determined by the ability of a population to use the habitat. Finally, while in both models habitat is seen as a nested mosaic of patches (which can be more than three-dimensional in the HBM), the HBM does not require the patch shape and arrangement to approach fractal characteristics. Nestedness is a universal habitat feature and thus it is always present. However no evidence exists that the self-affinity of habitat structure assumed by Fitchie and Olff (1999) is a common condition for most species assemblages. Finally, for aquatic invertebrates the body size does not seem to offer any biological insights to their ability to move among patches such as natural pools. Adaptations such as airborne

stages, eggs or ephippia, or ability to withstand transport by water and wind are known to play crucial role (Bohonak and Jenkins 2003).

The Rock Pool Metacommunity

Site

The rock pool metacommunity is located around a small cove near the grounds of the Discovery Bay Marine Laboratory along the northern coast of Jamaica. The system involves a set of 49 coastal rock pools that are formed primarily by rain erosion of fossil reefs (Kolasa, Drake, et al. 1996; Kolasa, Hewitt, et al. 1998; Romanuk and Kolasa 2002). Within the study area shown in figure 9.3a, an additional 180 pools have been identified and analyzed for their community structure. The pools are on average 60×30 cm, have a mean depth of 13 cm and mean volume of 15 liters. On average the rock pools are located within 1 m of the nearest neighbor and none is separated by more than 5m from the next nearest rock pool. Their elevation above sea level is 1–235 cm (mean = 80 cm) at high tide, with the tide rarely exceeding a 30 cm range. Seven of the 49 rock pools are tidal, although tidal flooding is not daily. Most pools are maintained by atmospheric precipitation and occasional wave splash water.

The strengths of the analyses stem from the nature of the study system. The rock pool metacommunity is highly diverse, both biotically and abiotically. The pools have similar history, climate, greatly reduced seasonality, and the system is small enough to allow any species to reach any habitat. The rock pool system shares several general advantages with other aquatic habitat landscapes listed by Resetarits et al. (chapter 16). Furthermore, it can be sampled for community composition and abundance within hours of measuring physical attributes. The main weakness of the approach to date stems from the fact that we infer the community and metacommunity dynamics from temporal snapshots instead of population trajectories. Nevertheless, we believe that such snapshots are informative, especially because they often cover tens or hundreds of generations.

Biotic Composition

We have collected invertebrate rock pool fauna and made physical measurements of the rock pools at least once a year, since the winter of 1989–90 (Kolasa et al. 1998; Therriault and Kolasa 1999, 2000; Romanuk and Kolasa 2001; Therriault 2002). Over seventy species have been identified and counted totaling more than 300,000 individuals from all samples. The majority of species are small benthic animals ranging from 60 μm to 0.5 mm but some are plankton-like (*Orthocyclops modestus*, *Ceriodaphnia* sp.) and swim in the water column. The metacommunity has unusual origin and composition. It is a mix of marine, brackish water, and freshwater organisms, some with poor dispersal abilities and some with non-aquatic dispersive stages (e.g., insects, crabs). The full list of the taxa identified to

date includes: Turbellaria (7 species), Nematoda (1), Polychaeta (5), Oligochaeta (2), Ostracoda (21), Copepoda (8), Cladocera (4), Decapoda (crab) larvae (1), Decapoda (shrimps) (3), Amphipoda (1), Isopoda (1), and Insecta (18). The pool communities experience high desiccation, especially through the summer months when most of the shallow pools may become completely dry (Therriault and Kolasa 2001).

Coupled with the short generation times of the organisms (between less than a week and three months) the annual samples are relatively independent, that is, the current community structure is only partially determined by the community state a year prior to the sampling due to partial reassembly from a species-pool of short-lived organisms and cumulative stochastic effects of environmental and biotic variability (Romanuk and Kolasa 2002). Thus, the sampling regime misses detailed population dynamics but provides a long-term data set consisting of statistically independent snapshots, each separated by many generations from the previous one. Metacommunity patterns are therefore expected to be either at or approaching equilibrium with the environmental template.

The system of rock pool communities exhibits at least five distinct spatial scales (figure 9.3) although additional intermediate but less defined scales may also exist. This multiscale aspect appears to be an inherent feature of natural metacommunities (cf. Miller and Kneitel, chapter 5). Dispersal is likely to be modified by all of the five scales: regional (figure 9.3a), groups of rock terraces (figure 9.3b), pools on a single rock (figure 9.3c), pools lying in a single watershed (figure 9.3d), and individual pools (figure 9.3e). Rock pool species, which include taxa with diverse life histories such as turbellarians and mosquitoes, vary strongly in their dispersal abilities, and perceive individual patches on a gradient from either totally isolated to fully accessible or connected (Kolasa and Drake 1998). This does not differ from the general patterns established for inland aquatic invertebrates (Bohonak and Jenkins 2003). Consequently, a local pool community is likely to result from a blend of variably scaled immigration rates and the interaction of processes that are akin to population dynamics, metapopulation dynamics, and island biogeography, depending on which of the five or more scales one chooses to look at (figure 9.3).

As spatial scale changes, we would expect different biotic and abiotic dispersal processes to become relevant. The intermediate scales include subregions of the regional scale that share similar patterns of wind and precipitation or portions of a rock terrace where large invertebrate territories may affect several but not all watersheds. In particular, crabs that move actively in and out of pools on a daily basis can act as vectors for dispersal of rock pool invertebrates by carrying propagules in their digestive system or gill chambers. A different set of dispersal mechanisms operates at each scale (cf. Bohonak and Jenkins 2003). For example, adjacent pools that remain unconnected by water channels may exchange propagules or organisms via rain drop splash and overland transport by am-

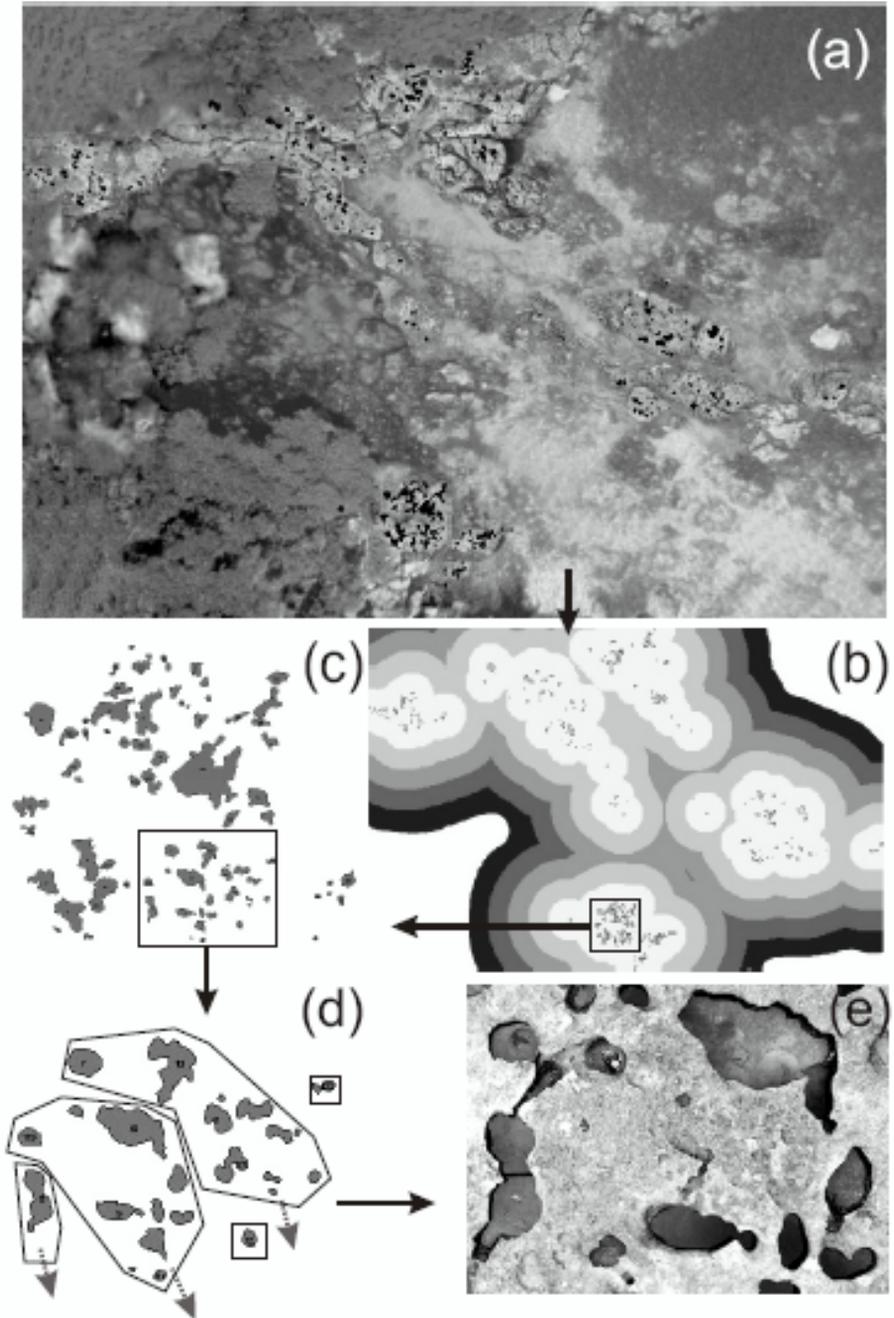


Figure 9.3 Physical layout of the rock pool system in Discovery Bay, Jamaica: (a) aerial view of the inlet with rock terraces and outlines of rock pools, ~ 60 m across; (b) distance based groups of pools; each group may encompass several rock terraces; (c) pools of one rock terrace; (d) five natural watersheds (bounded by polygons) on one rock terrace (courtesy of D. G. Jenkins, University of Central Florida); (e) individual pools in one of the watersheds. Shaded arrows indicate watershed outflow.

prohibited animals as evidenced by specimens caught after rain in beaker traps set nearby. Pools in a watershed experienced directional transfer of animals in addition to the previous mechanisms (Jenkins, pers. comm.). Pools of different watersheds receive animals as a cumulative function of pool-to-pool exchanges and a directional transfer within a watershed. As the spatial scale increases, the role of wind, storm, and large animal mediated dispersal increases; the relative contribution of these factors changes depending on the rock terrace elevation and relative position on a land-ocean gradient. The pools, watersheds, rock terraces, groups of rocks, and the region form a distinct spatial nested hierarchy, with a number of important consequences for modeling organism exchanges and their dynamics.

Recolonization experiments have shown that dispersal is high enough to allow reconstitution of local communities within six to twelve months, irrespective of their degree of isolation (A. Biggers, pers. comm.). However, the hierarchical structure of the habitat and habitat specialization of species mediates colonization patterns (Kotliar and Wiens 1990; Kolasa and Rollo 1991). If habitats of similar qualities are within the same spatial subunit (such as on a rock terrace), then predictions based on regional (entire metacommunity) dispersal rates will fail quantitatively because they assume a mean degree of interpatch isolation greater than the effective isolation of patches within the rock terrace.

Background Analyses and Review of Results

Specialization and Occupancy

Rock pool species show a strong link between distribution measured as occupancy, p , and habitat specialization. This is true for a variety of measures of habitat specialization but one method illustrates the point. Numerous other measures of specialization can be used and most produce similar results (unpublished). We have used a method of calculating ecological range that is largely immune to occasional occurrence of individuals outside conditions preferred and tolerated by a species. This immunity is achieved by weighing exposure to environmental variables by local density. We obtained tolerance ranges for each species using CANOCO's (software package) Canonical Correspondence Analysis module from four significant CCA axes. These were averaged and regressed on the occupancy (used in this chapter) expressed as the cumulative number of pools a species occupied over nine years ($r = 0.818$, $p < 0.0001$, $F = 145$; or $r = 0.896$, $F = 292$; if $y = ax^h$ is fitted). The regression indicates that distribution (occupancy) and specialization to physical conditions have a significant degree of equivalency in the system of interest.

Because occupancy reflects both the habitat suitability and the stochastic effects of immigration and extinction, the unexplained variance could represent a coarse indicator of the importance of patch dynamics. At the same time, occu-

pancy can be used as an empirical substitute for specialization but not, indeed, in direct tests of models involving occupancy independently of specialization. This need for caution is supported by the fact that dispersal and hence distribution does affect measures of habitat specialization (Pulliam 2000), with more mobile species sampling a greater range of habitat conditions. We believe, however, that the methods employed here to evaluate the ecological specialization of species reduces any potential bias to an acceptable minimum.

Hierarchical Nature of the Rock Pool Metacommunity

Space is the most obvious dimension in the habitat hierarchy, however the spatial map is not a strict organizational tool in the hierarchy, nor do the habitat attributes necessarily match the spatial map. In fact, for the rock pool metacommunity the match is very weak because pools that cluster according to their physicochemical properties may be scattered in different locations of the spatial hierarchy. To add to this complexity, the degree of match is scale-dependent, with the two hierarchies — one spatial and one of habitat properties — intersecting at some scales but not at others. For example, groups of rock terraces at higher elevations share pools that are more similar to each other due to the dominant effect of rain and leaf litter on their water quality. A GIS (Geographic Information Systems) analysis of the rock pool metacommunity linking species patterns and physicochemical properties (Romanuk 1999) showed that all physical variables exhibited some spatial autocorrelation. However, the clustering scale differed among variables. The net result is that clusters of physicochemical properties may be scattered in different locations of the spatial hierarchy. For example, elevation and salinity showed subregional clustering while depth, temperature, oxygen, and pH all showed smaller scales of clustering.

The hierarchical structure of the metacommunity can also be seen in patterns of species habitat use. Species view the habitat at different levels in the habitat hierarchy ranging along a gradient from habitat specialists to generalists. However, this gradient is not necessarily continuous, since scale breaks or discontinuities are expected consequences of the hierarchical structure of habitat (cf. Kolasa 1989; Allen and Holling 2002). Such discontinuities are registered in assemblage attributes. Data from the rock pool metacommunity provide a good example of this phenomenon (figure 9.4) and can be seen in the graph combining degree of specialization and local density for ostracod species. Ostracods group into three distinct scales of habitat use; a group of highly specialized species with low local densities, a group of generalists with high local densities, and an intermediate group (figure 9.4). In addition to discontinuities ostracods illustrate a trend in the distribution-density relationship. The scale discontinuities in how species perceive their habitat can be used to guide decisions regarding the number of scales that would be important for modeling. For ostracods, any model using three scales might do a satisfactory job.

Assembly of Unequals

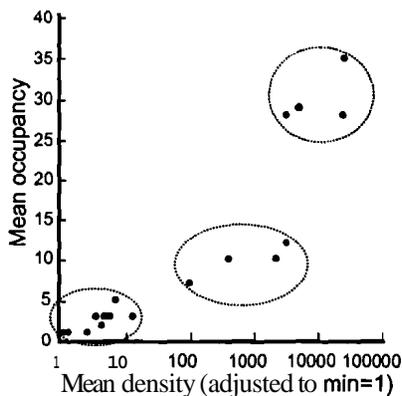


Figure 9.4 Groups of ostracod species identified by similarity of occupancy and mean local density based on one 0.5 liter water samples taken over twelve annual snapshot censuses of forty-nine rock pool communities. Density is scaled up to the minimum of one and has no relationship to observed values per liter. Arbitrary ellipses help to delineate the groups.

Habitat Specialization

Two primary observations on the ecology of metacommunities are integral to an understanding of rock pool metacommunity processes. We have already discussed the importance of viewing the habitat as a nested hierarchy of patches that exist in multidimensional space. In this section we present the results of analyses that suggest that species perceive habitat fragments differently, depending on their dispersal abilities and habitat tolerances.

Differences between Habitat Specialists and Generalists

Several observations are relevant to applying the HBM to the rock pool metacommunity system. Species vary in their local density over both space and time. In metacommunities, relative variability in density will have strong effects on the probability of whether a species will be present or not in a patch. This occurs because species with low population numbers are more likely to become locally extinct than species with high population numbers. In rock pools, specialists vary more than generalists in their relative variability (coefficients of variation) but tend to vary less in absolute terms (Kolasa and Li 2003). Mean local densities of species (represented as ranks) also relate strongly to occupancy (figure 9.5a), which can be interpreted in favor of the link between local presence (and thus regional occupancy) and habitat suitability. The density and occupancy relationship could also arise under special circumstances of uniform habitat space and random distribution of individuals, with the relationship being described by the Poisson probability distribution (Wright 1991). These circumstances do not

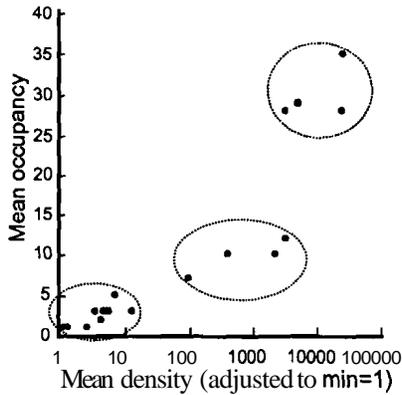


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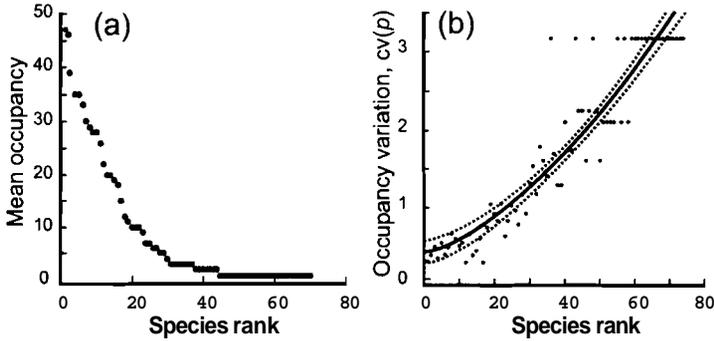


Figure 9.5 Species occupancy (a) and (b) its variability (coefficient of variation, cv) as a function of mean species rank in abundance. Occupancy and cv of occupancy are based on ten annual censuses.

appear to apply to the rock pool metacommunity for which abundant evidence of nonrandom, environmentally determined distribution (Therriault and Kolasa 1999) exists. Wright (1991) proposed that a set of species conforms to the Poisson null model if the slope of a regression (b) between mean abundance and $\ln(1 - p)$ is -1.0 . For the rock pool metacommunity this slope is markedly different ($b = -0.126$, $r^2 = 0.289$).

The density-occupancy relationship however results in a triple-edged sword for specialists in the rock pool community where specialists are locally and regionally rare, and their local population densities as well their occupancy are relatively more variable (figure 9.5b). These species' attributes suggest that the population dynamics of specialists are fundamentally different than the dynamics of generalists in the metacommunity. The importance however of specialists to the dynamics of the local communities in the metacommunity is unknown. Statistical analyses of the rock pool metacommunity described earlier indicate that the population dynamics of generalists dominate the dynamics of local communities (Therriault and Kolasa 2000). These effects were positive or negative depending on the identity of the generalist and specifically affected long-term changes in evenness. In this system, generalists may represent large-scale integrators of the metacommunity (like in Figure 9.1c), a role analogous to hyperparasitoids in butterfly metacommunities (Van Nouhuys and Hanski, chapter 4), or common coral reef species (Waltho and Kolasa 1994). If habitat generalists vary over time, then rare species should also vary in response to habitat generalists, thus increasing community variability (Therriault and Kolasa 2000).

The hierarchical model (HBM) postulates a general abundance pattern as an outcome of the interaction between the habitat structure and a gradient of species attributes. Unlike the regional similarity model (Mouquet and Loreau 2002), the HBM implies poor regional performers will also be, on average, poor local performers in terms of their density. This further implies that mean and regional

density of individual species should be strongly correlated, which is the case in the rock pool metacommunity (figure 9.6). This relationship captures that regionally rare species fail to attain high densities at sites where they manage to persist; without exception, local rarity implied regional rarity (figure 9.6). Furthermore, there is an accelerated convergence between local and regional densities as predicted by the HBM for abundant and thus broadly distributed species.

One other consequence of the assumptions of the HBM is a relative constancy of local composition. This consequence is shared with the species sorting model as the HBM relies on species sorting at multiple levels of resolution. The patch dynamics model and the neutral model imply a continuous drift of community composition. In the HBM, however, as long as the environment retains its attributes over time, local communities should retain not only its composition but also the density structure. Furthermore, habitat specialists should show less site tenacity than habitat generalists. Various analyses support this postulate. The community similarity to itself declined dramatically with the number of desiccation events and the pattern was evident whether just composition (Jaccard's index), rank structure (Kendall's W), or composition and density were considered (Therriault and Kolasa 2001). Where the mean richness was reduced, its decline was predominantly due to the differential loss of habitat specialists (Kolasa et al. 1998).

Habitat generalists and specialists also differ in variation of their distribution measured by occupancy (p), with specialists showing greater variability in the number of pools occupied (figure 9.5a, b). Recall that we define occupancy as the number of sites a species is found in and specialization as a species position in the multidimensional hierarchy of habitat attributes. However, this hierarchy imposes only a partial relationship between occupancy and specialization due to

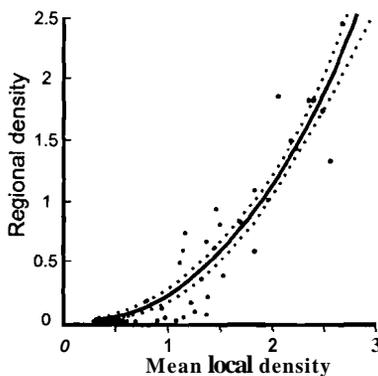


Figure 9.6 Regional density and local density (\log_{10} -transformed) of species are strongly related ($y = 0.215x^{2.368}$, $r^2 = 0.902$, $p = 0.0000$). Local density of a species is the mean of that species of all the pools it was present on a single day, averaged over ten annual censuses. The regional density of a species is the total population of the species in a region divided by the volume of waters sampled (region is treated here as a single large pool) and averaged over ten censuses.

differences in habitat attributes. Furthermore, rock pool species with high local densities have the greatest occupancy and the lowest temporal variability in density. These descriptive trends may both result from and affect metacommunity dynamics.

Other Effects of Scale

We postulated earlier that the metacommunity patterns appear to differ qualitatively depending on scale. The effect of environmental variability on species richness and abundance is clearly scale dependent (figure 9.7; Romanuk and Kolasa 2002). We found that species richness is lower in pools with higher temporal variability in abiotic conditions, while species richness is higher in pools with greater

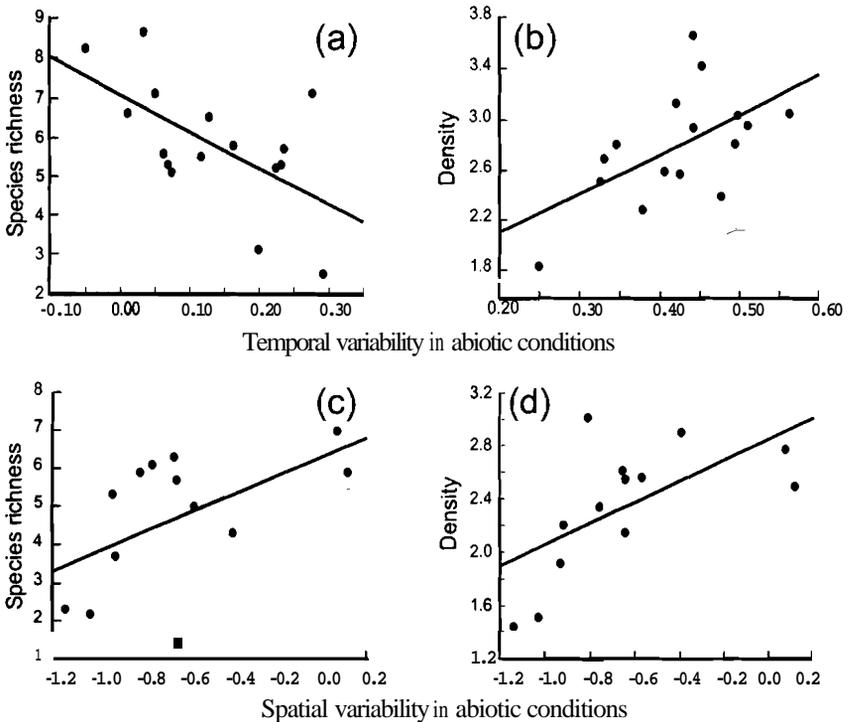


Figure 9.7 Effect of heterogeneity at different scales on species richness and combined pool density for different groups of rock pools (Reid 2003). Temporal variability of the whole pool among dates represents a larger scale (a and b) while spatial variability at 5 cm lag distances and 10 cm depth increments (c and d) represents a smaller scale. Panel (a) shows richness declines in freshwater pools that vary more in time; (b) density increases in saline pools; (c) richness increases in brackish water pools that are internally more heterogeneous; and (d) density also increases in such pools. The variability at either scale is a geometric mean of the standard deviations (SD) of the four abiotic variables (temperature, oxygen, pH, and salinity).

spatial variability in abiotic conditions (figure 9.7). In contrast, mean community density is higher in pools with greater spatial and greater temporal variability in abiotic conditions. The scale-dependent effect of environmental variability is most likely due to different processes arising at different scales. Spatial variability in abiotic conditions may increase species coexistence through increases in the number of suitable habitats (cf. Holyoak 2000), while temporal variability in environmental conditions may decrease species coexistence through intermittent reductions of suitable habitat that may drive some populations to local extinction. Frequent desiccation is an extreme example of such a process.

Applicability of the Four Metacommunity Perspectives to the Rock Pool System

Neutral Model

Fuller et al. (2004) have calibrated and tested the neutral model (Hubbell 2001) of community assembly using data from the rock pool metacommunity. On the whole the model performed fairly well, however it underestimated the density of species that are rare as defined by their rank. This was likely due to high predator density in some pools where predators improved the survival of rare species thus elevating the representation of rare species in the metacommunity. This result underscores the potential of cross-trophic interactions to influence community structure and the proportional abundance of species in the metacommunity (Holt 2002). These results also affirm the importance of habitat structure, inclusive of its biotic component, argued throughout this chapter. In addition, the hierarchical structure of the habitat and the species attributes might also contribute to the departure from predictions of the neutral model (Kotliar and Wiens 1990; Kolasa and Rollo 1991). If habitats of similar qualities occur within the same spatial subunit, then predictions based on mean regional dispersal rates (cf. Resetarits et al., chapter 16) will fail quantitatively. This is because predictions based on mean dispersal rates assume a mean degree of interpatch isolation that is greater than the effective isolation. Consequently, habitat specialists should perform somewhat better when the habitat patches they need are clustered. A GIS analysis supports this argument by revealing a nontrivial degree of spatial autocorrelation among physical properties of rock pools (Romanuk 1999).

Furthermore, using the hierarchical framework produces an intriguing pattern that may be relevant to testing the neutral model. When relative density predicted by the HBM is plotted against species ranks, an S-shaped curve emerges (figure 9.2b). This S-shaped curve is also predicted by the neutral model and is reminiscent of those seen in natural communities.

Species Sorting

Various aspects of this model of local community assembly and regional persistence gain support in the analyses to date. Experiments in which we emptied and

cleaned rock pools and allowed their recolonization showed that dispersal was effective enough to allow most if not all the species in the pool to reach any rock pool within days or weeks. Furthermore, we found that habitat specialists were differentially absent from physically variable pools, which led to impoverished and yet more predictable composition (Kolasa et al. 1998). Ample evidence exists for linking individual species, species richness, and community metrics to individual physical variables, composite gradients expressed as principal components, or their variability in rock pools (Therriault and Kolasa 2000, 2001; Romanuk and Kolasa 2002; Kolasa and Li 2003). All of these links are strongly consistent with the idea that most species are restricted to specific subsets of pools defined by the interaction between the physical attributes of the pools and the tolerance ranges of species.

Species sorting processes have important but previously unrecognized consequences for metacommunities. One is the asymmetry of interactions that arise from nested distributions. Habitat generalists interact with more species than habitat specialists, have larger populations, and are regionally buffered against abiotic and biotic variability. This results in different population dynamics at all scales. Furthermore, habitat generalists are members of both species-rich and species-poor local communities where they influence local dynamics differently as a result of their different contribution to the local abundance structure. Finally, habitat generalists are likely to dominate community patterns of variability without being themselves affected by local competitors or predators. Habitat generalists also dominate the community patterns of specialists (Therriault and Kolasa 2000).

These general constraints are likely to interact with species' life histories, the presence of predators, and the availability of resources. Such effects have been demonstrated to have strong effects in other aquatic microcosms (Miller et al. 2002), but have yet to be examined in the rock pool system.

Mass Effect Model

Preliminary work on the rock pool communities (D. G. Jenkins, pers. comm.) shows that dispersal may occur in large pulses and may be directional. However, the intensive dispersal that takes place after major rain events is uneven and largely restricted to the watersheds that encompass several pools. The frequency of dispersal reflects the stochastic external forcing (storms) and exhibits strong directionality due to downstream movement of water. Upstream flow and dispersal can also occur when ocean waves and high tides combine to flood some rock terraces, which was observed twice between 1989 and 2003. The two kinds of flow have different consequences. The rain-generated flows move only a fraction, albeit substantial, of a local community to pools downstream from the focal pool, thus adding species and individuals to an already established community. The ocean influence has an entirely different impact—it removes most individuals of

the original community and homogenizes species composition across all affected patches. In sum, given the frequency of rains relative to the pace of population dynamics of constituent populations, the mass dynamics model is likely to apply at the watershed level in the rock pool system while other models may be more appropriate at different scales.

Patch Dynamics Model

The examination of the natural rock pool metacommunity has provided strong evidence that both habitat, at multiple scales, and species are highly differentiated. This evidence appears to violate the basic assumptions of the patch dynamics model. We do not see how it could apply to the complex, hierarchical structure of the rock pool metacommunity. Earlier, we suggested (Kolasa and Drake 1998) that the explanatory power of the patch dynamics model as applied to metapopulations declines with the increasing differences among quality of habitat patches and their isolation. We believe that this conclusion applies to metacommunities as well.

All Four Models

Some observations pertain to all models. For example, the fact that regional and mean local densities of all species are strongly correlated does not flow directly from any of the four perspectives on metacommunity. According to the Mouquet and Loreau (2002) model, a species should compensate for poor regional performance in at least some patches (regional similarity; the mass effect paradigm). The species sorting model (Leibold 1998) appears more likely to accommodate this pattern because it explicitly allows for a gradient of performance along a gradient of environmental constraints (e.g., resources). Our data suggest that such constraints are indeed very strong. A further analysis of perturbation and physical variability patterns, which also differ substantially among individual rock pools, might lead to tightening of this line of inference. The increasing variability of occupancy along the gradient of species specialization has a biologically relevant consequence. As species diversity increases during assembly or in reflection of rich habitat structure, the number of specialists in a community also increases but the predictability of their density declines. Thus, the determinacy of community composition declines with increasing species diversity. It is unclear if any of the models are able to reproduce this effect; however a promising approach taken by Holt (2002) yields results that converge with the above idea.

The most recent extension of the source-sink model (Mouquet and Loreau 2003) led those authors to quantitative predictions concerning the abundance structure of local communities and the whole metacommunity. Some of these predictions appear to converge with the hierarchical model. For instance, high dispersal homogenizes species distribution (cf. habitat generalists in the HBM). Other predictions, such as emergence of the logarithmic series distribution of rela-

tive densities in highly isolated or highly invulnerable communities do not. Future empirical tests and field experiments could discriminate between such alternatives.

Desirable Additions to Theory

The hierarchical view of habitat structure implies a more complex approach to calculation of the dispersal rates. Dispersal is a function of both organism vagility and spatial resistance imposed by an emergence of dispersal boundaries within habitat hierarchy. Thus, an average (mean field) dispersal rate would not take care of the problem, even though it might sometimes provide a reasonable approximation or serve as a useful theoretical tool (e.g., Holt 2002). An appropriate model should make dispersal rate dependent on the availability of *accessible* patches. Formally, this could be obtained by weighting the dispersal success (cf. Mouquet and Loreau 2002) or dispersal distance (Hanski 1998) by the number of hierarchical levels separating suitable patches (cf. figure 9.1, where the lowest-level specialist would have to cross, on average, three hostile patches and two other [potentially hostile] habitats to reach another suitable patch). Such weighting could employ one of the hierarchical tree distance algorithms already used in phylogenetic studies (cf. Mitchell 1996). Furthermore, differential performance of species in different patches translates into different effective patch density and spatial configuration for each species. The dispersal should thus be further modified to reflect this differential effect.

A similar challenge emerges with respect to incorporation of scale discontinuities into the conceptualization of the relationship between species and their habitat. Hierarchy of structure, whether spatial, temporal, or organizational, implies discontinuities in response variables such as occupancy, densities, or patterns of their variability (Kolasa 1989). Empirical work on this and other systems shows strong discontinuities in various attributes. A question emerges as to what additional components or modifiers of metacommunity models could reproduce such discontinuities.

Conclusions

In this paper we review the ecology of a rock pool metacommunity using a hierarchical view of habitat structure and present several aspects of the ecology of metacommunities that may prove valuable in the construction of metacommunity models. We suggest that three observations are integral to an understanding of rock pool metacommunity processes: (1) the habitat is arrayed in a nested hierarchy of discrete patches that exist in a multidimensional habitat space; (2) species perceive habitat fragments differently, depending on their dispersal abilities and habitat tolerances, along a specialist to generalist gradient; and (3) interactions between the hierarchical structure of habitat and species attributes produces discontinuities in species' response patterns that may be a common feature

of multispecies systems. The hierarchical model views the metacommunity in multidimensional space as a set of interacting continua of properties and processes staged on an unequal hierarchical playingfield. Species at different levels of the hierarchy exist and interact asymmetrically with their environment and each other. Of the four metacommunity models, we found a stronger correspondence between patterns and processes in the rock pool system and the species sorting model than the patch dynamic, mass effect, or neutral metacommunity models.

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