# ABUNDANCE AND RANGE RELATIONSHIP IN A FRAGMENTED LANDSCAPE: CONNECTIONS AND CONTRASTS BETWEEN COMPETING MODELS

## J. Kolasa[1] & J. A. Drake[2]

1 Department of Biology, McMaster University, Hamilton, Ontario, Canada, L8S4K1
Tel: (905) 525-9140 ex. 23100; Fax: (905) 522-6066 E-mail: Kolasa@mcmaster.ca
2 Department of Zoology and Graduate Program in Ecology, University of Tennessee, Knoxville, TN 37996
Tel. (615) 974-7195; Fax: (615) 974-3067; E-mail: Drake@utk.edu

Abstract. The specialization and metapopulation dynamics hypotheses are the most prominent alternative explanations of the oft-reported correlation between the distribution and abundance of species. We suggest that mechanisms underlying the two explanations are interacting to produce the correlation. We aim to quantify the relative contribution of the mechanisms underlying the two proposed explanations, should both have some validity. An analysis of 40 species of invertebrates inhabiting 49 miniature erosional rock pools allowed us to explicitly address the relationship between distribution, specialization, and abundance. The analysis involved regressing species abundances against several measures of specialization and distribution. Compound measures of species specialization (niche volumes) correlated less with the observed densities than when the constituent variables were used separately, especially in combination with the distribution data. The latter group of statistical models increased the amount of variance explained compared to the best niche volume derived estimates (53% vs 79%). The comparisons further suggest that specialization is a much stronger determinant of species abundance than is metapopulation dynamics. This appears to be particularly true in our system of discrete habitats. To put these results in a broader context, we propose a conceptual model to explain the relative importance of stochastic processes and specialization constraints in predicting patterns of species abundance. While this model focuses on site-patch isolation and on ecological differences among sites-patches, it permits other dimensions such as habitat resolution differences among species.

## Introduction

Broadly distributed species have often been shown to have higher density than narrowly distributed species (Hanski 1982, Bock & Ricklefs 1983, Brown 1984, Maurer 1990, Kolasa 1989, Waltho & Kolasa 1994, Collins & Glenn 1991, Bock 1987, Gaston 1990, Lewin 1989, Lawton 1993, Lawton et al. 1994, Mehlman 1994). Several explanations are available, but the question of what factors **are** responsible for the correlation between species local abundance and regional distribution remains largely open (Maurer 1990, Tokeshi 1992). Generally, posited explanations focus on one of two mechanisms. The first mechanism focuses on species tolerance, while the second invokes metapopulation dynamics.

The first mechanism, termed 'environmental control' (Burgman 1989) or 'ecological specialization' (Hanski et al. 1993), was first proposed by Brown (1984). According to Brown, some species have low densities because their ecological ranges are more restricted by a number of independent variables, each limiting individual survival and access to resources, than other species. This ecological range restriction is assumed to be at its weakest in the center of the geographical range and to increase, on average, towards its periphery. By contrast, species with broad geographical ran-

ges experience more favorable ecological conditions over a relatively wider area than species with small geographical ranges. Under such a scenario, broadly distributed species would be more abundant in most cases, and particularly abundant in the center of their distribution. The link between the ecological range and geographical distribution is thus an explanation for the correlation between local abundance and distribution of species, although Hanski et al. (1993) argue that the linkage between local abundance and specialization is not theoretically defensible. According to Lawton (1993), this hypothesis eluded rigorous testing because niche breadths are difficult to measure and interpret in an objective way.

The second mechanism is best represented by a family of patch occupancy models (Levins 1969, Hanski 1982, Gotelli 1991, Maurer 1990, Tokeshi 1992, Hanski & Gyllenberg 1993). In these models, local abundance is a function of the number of patches occupied, modulated by changing probabilities of immigration and extinction. For example, probabilistic processes may be responsible for lower occupancy levels *of* locally rare species when one deals with highly isolated, island-like habitats (Gaston 1994). These models assume that all patches are equal in quality and accessibility (Gaston 1994), and that species in an assemblage

**Table 1. Summary of models.**

| Assumptions and consequences | Specialization model<br>Brown (1984) | Core-satellite model<br>Hanski (1982) | Habitat-based model<br>Kolasa (1989) |
|---|---|---|---|
| Abundance (density) determined by: | increasing number of independently limiting factors (many dimensions) | patch occupancy (extinction and immigration probabilities; one dimension) | - habitat availability (many dimensions)<br><br>- cost of living in a fragmented landscape (metapopulation aspect included indirectly) |
| **Predicted patterns** | | | |
| • distribution vs abundance correlation* | Yes | yes | yes |
| • geographical distribution | central density peak | ? | ? |
| • patch occupancy | relatively constant (environmentally forced) | variable | relatively constant (determined by habitat structure) |
| • abundance frequency patterns | uimodal ** | mostly bimodal, sometimes unimodal | polymodal (?) |
| • number of generalists in a community | no prediction | variable | always low relative to the number of specialists |

\* Gaston (1994) lists the pattern as an assumption but Hanski (1982) identifies it as something to explain. Generally, a model should predict the pattern in order to explain it and so we interpret it accordingly; ** Assuming a random set of species ranges and a bell-shaped distribution of densities over the species ranges.

exhibit comparable metapopulation dynamics (Gotelli & Graves 1996). Patterns predicted by these models reflect spatial dynamics. These models, with some exceptions, indicate that species that are broadly distributed over the system of patches will be more abundant locally (Table 1).

No one has postulated that these general models are mutually exclusive; it is quite possible that both mechanisms operate in a single system. If this is the case, quantification of respective contributions may be more informative than a test for the effects of one or another mechanism. Thus, the question is about the explanatory value of the models rather an their 'correctness'. We evaluate this power using data on invertebrate communities inhabiting erosional rock pools. While both the specialization and metapopulation mechanisms can produce similar patterns, they differ in some respects. For example, the specialization model predicts a correlation between species abundance and some measures of specialization. Because species specialization restricts distribution, the model also predicts a correlation between species abundance and distribution. This poses a problem for differentiating it from the metapopulation model, which also predicts a correlation between species abundance and distribution. One difference between these models is that the metapopulation model does not predict an inverse link between specialization and abundance. We use this difference in the subsequent evaluation of the models by formulating the following specific hypothesis: ***if the specialization model of species abundances is correct, then measures of specialization should correlate well with local abundance*** (i.e., measures of specialization will not correlate well with local abundance),

In order to evaluate the possible effect of metapopulation dynamics, we rely on a third approach that also predicts a positive correlation between range and abundance. This ap-

corrections would bring some size outliers in line with other species (crab larvae, mosquitoes; see Results). Ecological ranges of species were measured as:

- ecological range hyper-volume, or niche volume, calculated as the geometrical mean of maximum ranges over six physical variables

$$ER_{vol} = \left[ (Max_1 - Min_1) * \ldots * (Max_i - Min_i) \right]^{1/i}$$

  where i represents six variables: oxygen, pH, salinity, temperature, light at the pool surface, light at the pool bottom;

- ecological range hyper-volume (or niche volume), calculated as the product of maximum ranges over five PCA factor scores (Burgman 1989) in the same way as $ER_{vol}$ above.

For the ecological hypervolume calculations, each physical variable was considered to be a separate dimension or axis in habitat space even though 'they may covary to different degrees. We did not weight the dimensions as suggested by some (e.g. Hanski 1978) because it was not clear how the physico-chemical parameters relate to resources. To obtain the respective ecological ranges, species were 'projected' onto individual physical parameter axes. This was done by replacing values in the species presence matrix with range values (max - min) observed in a respective pool for a given physical variable. Specifically, whenever a matrix cell had a non-zero entry, that entry was replaced by a range value obtained for each physical parameter in the respective pool. For example, if species *i* was recorded in pool 21 as having density of 50 individuals, the value of 50 would be replaced by a range of observed temperature values, say 7°C (31 °C - 24 °C). Global minimum and maximum values over the whole pool system were then found for each species in each dimension. Differences between these global maximum and minimum values were treated as species ranges defined on each dimension. The resulting ranges were multiplied to obtain the habitat range volume for individual species.

Ecological ranges based on the PCA analysis were obtained following steps similar to those used earlier. The two differences were that factor scores characterizing individual pools were used instead of physical variable values, and scores were standardized to give each axis equal importance (cf. Burgman 1989). The scores were obtained by extracting five factors using orthogonal principal component analysis on the pool parameter matrix (46 variables: multiple measurements of physical variables mentioned earlier, total variance explained by five PCA factors: 88%). The advantage of using PCA scores for characterizing pools, and eventually species, instead of direct field measurements is that the extracted factors can be viewed as statistically independent axes of habitat space (Gauch 1982) and thus provide the most objective description of pool differences.

A potential problem with these two direct ways of measuring ecological range is that the original data on the range of physical variables experienced by a species may also be affected by distribution (Hanski 1978). One might argue that broadly distributed species may experience somewhat greater variation by chance, since they are potentially exposed to greater environmental variability. We assumed that such a possible bias did not significantly affect our analyses. Indeed, one could reverse the argument: a species is more successful in a variety of habitats when it is tolerant of a broad range of environmental parameters (Brown 1984, 1995). This assumption is supported by the fact that highly variable pools tend to be inhabited by species with the broadest ecological ranges (Kolasa et al., submitted). This observation indicates that the measures of ecological range based on physical parameters reflect actual species attributes.

We used three categories of predictors of local species abundance. The first category includes measures of ecological range based on physical parameters (variables a-e, h-i below). The second category consists of the distribution measure (variable $f$). The third category (variable g) includes a predictor that emphasizes effects of fragmentation. We assume that differences in the performance of these predictors will help evaluate the relative importance of mechanisms involved in determining abundance and its relationship with ecological range and species distributions. The specific predictors are:

a) niche volume, based on mean ranges of physical variables experienced by species;

b) niche volume (ecological range), based on maximum ranges of physical variables experienced by species;

c) niche volume (ecological range), based on maximum ranges of 5 PCA factors treated as if they were physical variables experienced by species;

d) a set of maximum ranges of six physical variables (multiple regression);

e) a set of maximum ranges obtained from values of 5 PCA factors (multiple regression), treated in the same way as if they were physical variable ranges experienced by species;

f) distribution alone (occupancy scores = the number of pools a species occurred);

g) abundance values predicted by the habitat-based model:

$$N_i = [p_i / p_{max}]^2$$

where $N_i$ is mean predicted abundance of species *i* expressed in arbitrary units, $p_i$ is the number of pools occupied by species i and $p_{max}$ is the number of pools occupied by the most widely distributed species (i.e. maximum observed for any one species). Note that the exponent serves to introduce 'fragmentation penalty' differentially for habitat generalists and specialists (see Kolasa & Strayer 1988 for details);

h) maximum oxygen ranges observed in pools occupied by each species;

i) maximum ranges based on PCA factor5 calculated for pools occupied by each species.

Each of the variables or variable combinations (d-e), except for (g) which is derived from the distribution, was also analyzed in conjunction with the pool occupancy data. The purpose was to find out if the information on species distribution resulted in an improvement of fit between one of the measures and indicators of ecological range and species abundance. An improved fit would suggest that distribution has an effect on abundance independent of the specialization. We included the two last variables (h-i) because oxygen range and PCA factor5 were the most significant predictors of abundance in the category of single predictors and can also be viewed as ecological range indicators or correlates, if not measures. Whenever necessary, the variables were linearized by log transformations prior to performing the regression analyses. Thus, we obtain a set of exploratory models with different degrees of complexity and different assumptions.

### Results and Discussion

The patterns exhibited by species inhabiting rock pools agreed in the main with those observed in other communities. There are many rare and few abundant species, irrespective of whether the density per sample or per pool is considered (Fig. 1 A,B). Distribution, as measured by the number of sites occupied, was clearly correlated with abundance ($r^2=0.54$, $p < 0.001$. This correlation is similar to values found by others (e.g. Gaston & Lawton 1990, Mehlman, 1994, Bock 1987, Brown 1984, Kolasa 1989).

The compound measures of ecological range, commonly termed niche volume, were the three poorest predictors of abundance (Fig. 2A, blank bars). Similarly, Burgman (1989) and Hanski et al. (1993) found that such measures bore little relationship between the abundance and specialization (plants and butterflies), although Hanski (1978) was satisfied with a 'product' (compound) measure as an approximation of multidimensional resource states. It is possible that the method fails to capture the relationship between specialization and abundance of plants and butterflies. The compound measures we used may be inadequate for analyzing factors influencing species abundances, since they include all non-limiting variable states as well as the limiting ones. By including both categories, such measures may confound the importance of one or a few limiting factors. However, they might be adequate if different resources are limiting at different sites (cf. Hanski 1978).

Most ecological range measures explained about 50-70% of variance (Fig. 2A). Occupancy alone explains almost as high a percentage of variance in species abundance as the specialization measures (Fig. 2B, leftmost bar). Not surprisingly, in most cases this measure improves predictions based on niche volumes or multiple variables (Fig. 2, filled bars). When combined with multiple physical range scores, occupancy explains the largest amount of variance of all the predictor variables and their combinations ($R^2=0.7893$, $p< 0.001$). The habitat-based model (HBM) prediction is best in
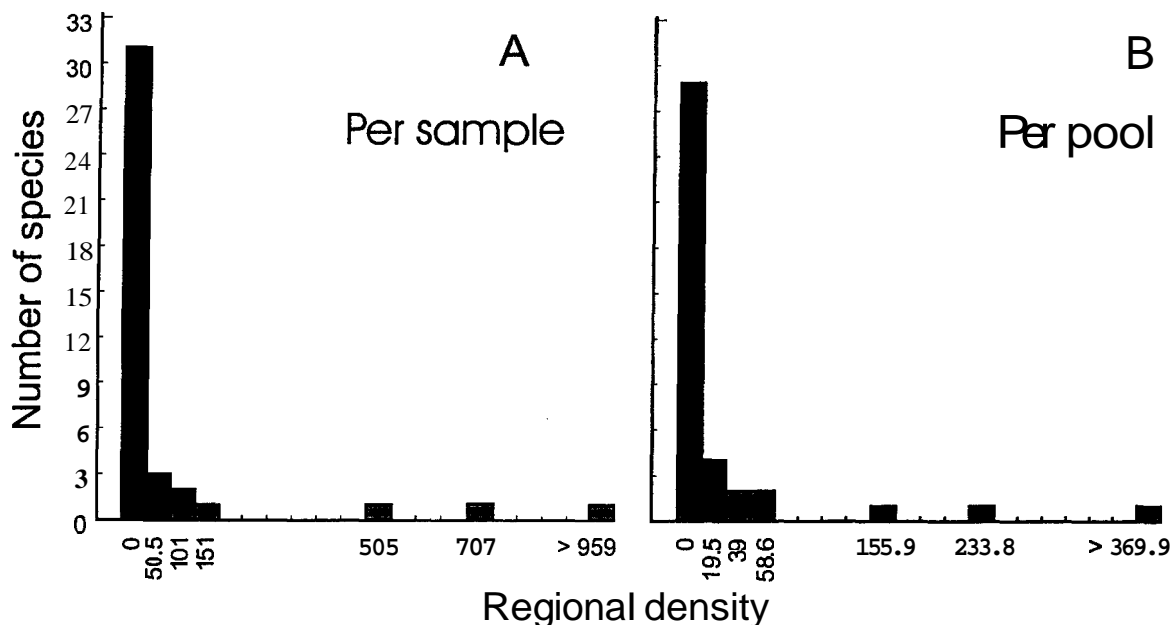


**Figure 1. Frequency distribution of species abundances: (A) based on mean sample density when present; (B) based on mean density in all occupied pools. Numbers on abscissa show beginnings of intervals (intervals are 50.5 and 19.53, respectively).**

proach rests on the assumption of a hierarchical structure of the habitat (Kolasa & Strayer 1988, Kolasa 1989). In the associated model, the habitat-based model, abundance is a function of the habitat range in which a species can operate, with ranges of habitat specialists often being nested within the ranges of habitat generalists. Species with limited distributions or narrow ecological ranges are assumed to live in a more fragmented (or isolated) environment than species not so limited. Species abundance is influenced equally by the degree of fragmentation, which increases both the physiological and population costs, and by the degree of specialization (Table 1). The model differs from the metapopulation approach in more ways. It does impose boundaries on the number of occupied sites (hierarchical constraints: the number of sites is limited by the ecological range of a species), and involves multidimensional habitat space as opposed to the two-dimensional (spatial) view of the core and satellite model. Hanski (1982) hinted at the possibility of an alternative hypothesis that core species may be better adapted to their environment than satellite species, and called it an 'adaptation' hypothesis. This potential inequality of species is the focus of the habitat-based model, where the specialization constrains the permitted patch configurations. Each species may be thus constrained differently, depending on its specialization type and degree. This will result in a 'pattern of usage permissions'. The main feature of this pattern is that a system of landscape patches is seen by some species as much smaller and more fragmented than by others, differentiating among metapopulation dynamics of individual species.

While the habitat-based model shares multidimensional perspective with Brown's model, it differs in that it includes fragmentation costs. In the simplest form, fragmentation cost can be calculated as the ratio of the habitat space available to the top level generalist to the habitat space of $i^{th}$ species (Table 1, Kolasa 1989). Predictions of this model are later used to contrast results obtained for the specialization model alone. Note that we do not test the habitat-based model as such: instead, we use it as a tool that provides reference predictions for the other two models.

Gaston (1994) points out that the metapopulation dynamics and ecological specialization explanations are distinct logical alternatives to be tested. We concur with this view, and add that both kinds of mechanisms may be acting synergistically in producing observed patterns (habitat-based model above). Given that both mechanisms may contribute simultaneously within one community, or even one species, to the correlation between distribution and local abundance, interpretation of results will have to involve the assessment of the relative importance of respective mechanisms, even if one may be mediated by another. We do not favor accepting one mechanism to the exclusion of another (Brown 1995). While some interpretations of this complex picture and anticipated results have to be circumstantial, they may aid in illuminating the applicability of the models. We summarize this picture in Table 2.

The question of whether the specialization model adequately explains species abundances is, despite appearances, difficult to address. Gaston & Lawton (1990; and references

**Table 2. Suggested interpretation of possible outcomes.**

| Relationship | Specialization Model | Metapopulation Model | Habitat-based Model | Comment |
|---|---|---|---|---|
| Negative correlation between specialization measures and density | Supporting the model | Neither supporting nor rejecting the model | Supporting the model | Suggest that metapopulation effects are nil in the test system |
| Positive correlation between distribution and density | Neutral to supporting the model | Supporting the model | Supporting the model | Not surprisingly, models aiming at explaining this relationship also predict it |
| Negative correlation between distribution and specialization combined together and abundance | Neutral (should not improve the model as distribution as already a function of specialization) | Supporting the model only by the degree of improvement over specialization alone | Supporting the model | Gives a quantitative insight into the metapopulation effects |

therein) provide indirect support for the model by showing that rare cases of negative correlation between distribution and abundance may be due to features of broadly occurring habitats, especially due to low availability of suitable patches. Burgman **(1989)** attempted to test Brown's model for plant species. A lack of significant correlation between the niche volume was found, which he assumed to characterize species specialization and frequency of species occurrence. We conducted a similar test in which two areas of Burgman's approach were strengthened: (i) we use data on species local abundances, which were not available to Burgman; (ii) we use discrete and closely situated habitats. The proximity of habitat patches presumably permits effective metapopulation processes to occur. If inter-patch exchanges occur, they will most likely be expressed in patches closely situated to one another. Additionally, at the time scale available to a single project, abundances of small invertebrates are more likely to track and respond to environmental parameters than plants (used by Burgman), where historical effects may be more pronounced. As pool communities occasionally suffer major perturbations, they may represent different stages of recovery and community assembly. This may introduce considerable 'noise' into the relationships of interest. Given the noise and uncertainty as to the successional stages of individual communities, we deemed a correlational approach as the best available method to test the hypothesis.

Our approach is to apply different measures of the ecological range and test them separately or in combinations (also with distribution) as predictors of species abundance. This procedure should help assess performance of individual statistical models, which can then be interpreted as indicative of the importance of the processes underlying a particular model.

## Data and Methods

### Setting

We studied communities inhabiting a system of rock pools. These rock pools are formed primarily by rain erosion on a fossil reef on the northern coast of Jamaica, West Indies, at the Discovery Bay Marine Laboratory grounds. The pools are small in size, ranging from 20-60 cm in width and length and varying in depth from a few centimeters to no more than 50 cm. On average, the pools are located within 1-2 meters of the nearest neighbor and none is separated by more than **5** m from the next nearest pool. Their elevation above the sea level varies from 0-300 cm at high tide, with the tide itself rarely exceeding 30 cm. Some pools are true tide pools, but most are maintained by atmospheric precipitation and occasional wave splash water. We sampled forty-nine pools arbitrarily selected within a radius of less than fifty meters (Kolasa et al. 1996). The pools exhibit strong gradients in physical parameter values and gradients in variability of those values (Schuh & Diesel 1993, which makes them particularly suitable for differentiating among and characterizing species ecological ranges. While the pools sampled are

likely to represent a wide range of ecological conditions, they are but a small fraction of the area. Similar habitats extend for tens of kilometers both east and west of the study site. Our study covers a very small area, which is unlikely to encompass edges of geographical ranges for any significant number of species nor to underestimate species distributions. Thus, the possibly confounding effect of correlation between the geographical distribution and ecological range, a common problem in many other studies, does not arise. Under other data collection protocols (particularly large scale surveys), inclusion of range edges could give rise to a spurious correlation (cf. Bock & Ricklefs **1983).** The study system offers another advantage from the point of view of our specific test. Some, for example Wright **(1991),** suggest that the correlation between distribution and abundance can arise if individuals are distributed randomly and independently among patches. The possibility of random distribution and its consequences can also be ruled out, since individuals of most species are highly clumped (Index of Dispersion, $p < 0.001$).

### Sampling and Community Composition

Physical measurements (oxygen, pH, salinity, conductivity, temperature, and light intensity at the pool edge, water level, and bottom of the pool; Yellow Springs Instruments Oxygen Meter 5 1B and HANNA portable pH meters) were taken on several occasions between December **1989** and June 1994. The number of replicate measurements varied from two (pH) to nine (temperature) depending on instrument availability. Most individual variable measurements were completed within an hour. Samples of fauna were collected on three occasions (Dec 1989, Jan 1990, and Jan 1991). All faunal samplings were completed within a single day. Each sample consisted of one liter volume of water and sediments from a pool slightly stirred to dislodge organisms from the pool sides and from sediments and to homogenize their distribution. Organisms were caught in **a 63** $\mu$m net with a collecting container and immediately preserved in 50% ethanol. Overall 146 samples were analyzed from 49 pools; one sample was lost.

Forty invertebrate species were identified and counted. These species belong to a variety of freshwater and marine taxa, including: Anthozoa (1 species), Hydrozoa (1), Turbellaria (2), Nematoda (1), Polychaeta (2), Oligochaeta (1), Ostracoda (17), Copepoda (5), Cladocera (2), Decapoda (2), and Insecta (6). We extracted a total of over 93,000 individuals from samples and used them for the analysis. One species, a harpacticoid copepod, constituted almost half of all individuals collected.

### Analysis

Species distributions were measured in terms of site occupancy. In the rock pool system, occupancy can be expressed as the number of pools in which the species has been found on at least one occasion. Mean density of a species was calculated by dividing its total abundance by the number of pools it occupied on a given sampling date. No allometric corrections were used to adjust abundance, even though such
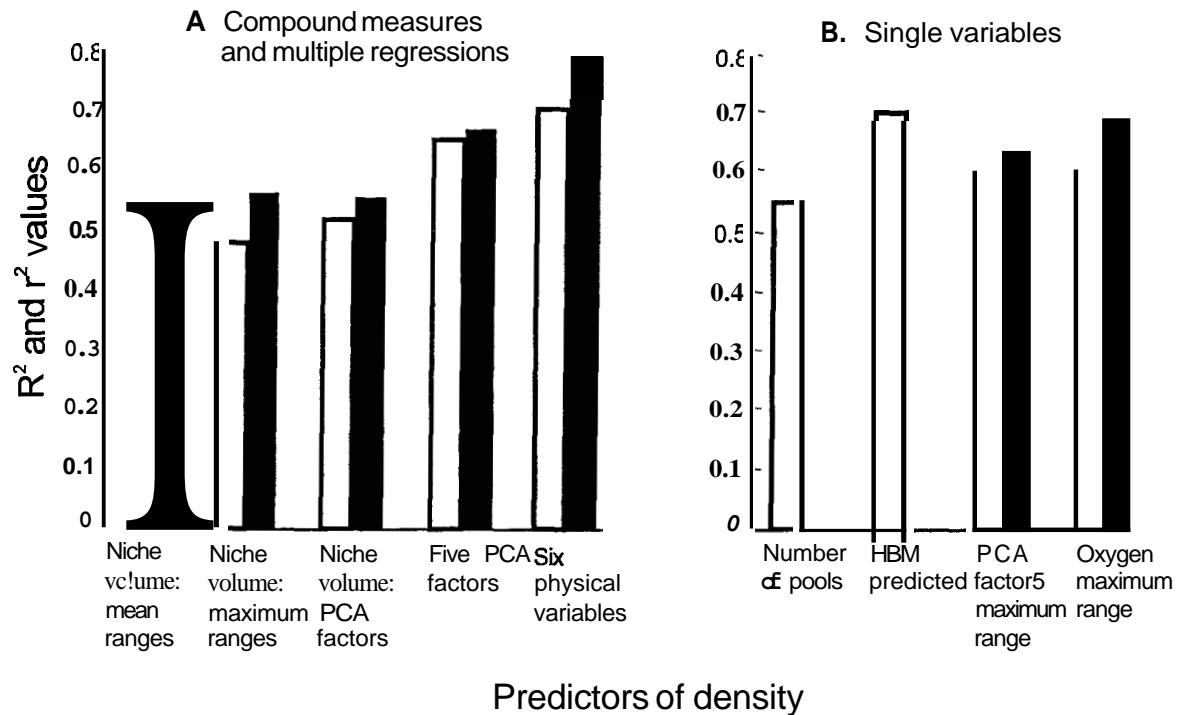
**Figure 2.** Variance of species abundance explained by various measures of ecological range and various models (blank bars); the same regression models explain more variance when combined with the occupancy data (shaded bars): (A) compound measures such as niche volumes and multiple regression models; (B) single variables or measures derived from one observed variable (HBM). All $r^2$ and $R^2$ (multiple regressions) were significant at $p < 0.001$ except the niche volume based on the mean ranges of 6 physical variables.

the 'singles' (unshaded bars) and second best of all measures (Fig. 2B, $r^2$=0.7034). The fact that the HBM turns out to be somewhat better predictor of species abundance than the distribution is significant, since it suggests that metapopulation processes are indeed active. Recall that the HBM increases the costs of dispersal and decreases the success of arrival and establishment in proportion to the degree of fragmentation. Thus, any improvements in prediction over the 'plain' distribution model can tentatively be thought of as being attributable to these components of the metapopulation processes. Conversely, the model gives relative advantage to species occupying many sites, although it does not rely explicitly on extinction and colonization probabilities to compute abundance.

Differences between predictions based on specialization alone (6 physical variables, 5 PCA factors; Fig. 2AB) and those based an specialization combined with occupancy are fairly small and not significant on an individual basis. On average, these differences amount to a 6.6% increase in variance explained (t-test for dependent samples: p<0.015, N=7) for models incorporating habitat fragmentation or occupancy data (indeed, we exclude the comparison to predictions obtained for the niche volume based on mean variable range, as they appear to have little relationship with local abundance). This result is not a consequence of adding an additional variable to the multiple regression models: adding

a random set of numbers produced no improvement in the amount of variance explained. Furthermore, it suggests that only up to **17%** of the abundance variation is determined by factors other than physical parameters of the pools. We interpret this remaining variance as being attributable to metapopulation dynamics played out over a landscape of isolated patches. However, even this last figure is uncertain. Two problems may contribute to the uncertainty. Biotic interactions were not incorporated into the regression models with physical variables and PCA factors. These interactions might, hypothetically, account for the remaining variance leaving no need for additional explanations. However, because there is no obvious way in which biotic interaction effects should correlate with distributions but not with pool properties, we do not think this is serious alternative. The second problem that our results point to is a degree of overlap between the amount of variance explained by the occupancy model alone and the specialization related models (niche volumes, physical variables, PCA factor ranges). In the rock pools studied, it is almost certain that the occupancy is related to specialization (Table 3). Furthermore, we know of no field or laboratory studies showing that, occupancy is not determined by specialization (this applies to studies where occupancy is not defined as presence in potential sites only). The existence of such a relationship has been questioned recently by Hanski et al. (1993), on the grounds that no ex-

**Table 3.** Summary of correlations between the measures of specialization, expressed as ranges of physical variables tolerated by a species across the whole set of pools (i.e., differences between the highest and lower values observed over that range), and the measure of distribution (site occupancy).

| Maximum range (N = 40) of: | $r^2$ or $R^2$ | t | probability |
|---|---|---|---|
| Light at the pool bottom | 0.442 | 1.682 | 0.000003 |
| Light at the pool surface | 0.209 | 3.172 | 0.002994 |
| nH | 0.242 | 3.480 | 0.001274 |
| Temperature | 0.516 | 6.361 | < 0.000001 |
| Salinity | 0.7977 | 12.240 | < 0.000001 |
| Oxygen | 0.452 | 5.596 | 0.000002 |
| 'Niche' volume (all the above multiplied) df = 1,40; F = 61.83 | 0.682 | 9.018 | $c$ 0.000001 |
| All variables (multiple regression) df = 6,33; F = 42.45 | 0.885 | | < 0.000001 |

amples were available to support it. However, if this relationship is as common elsewhere as it is strong in our system, then the metapopulation model needs to be superimposed onto the specialization model. Gotelli & Simberloff (1987) also pointed out the difficulty of testing the core and satellite model by correlational analysis due to the requirement that the species be able to change their distribution through time. To the extent that specialization within the examined community is correlated with distribution, it is unlikely that species will meet this requirement in any significant way. On the other hand, the requirement may not be as important as once thought. Hanski & Gyllenberg (1993) found that a model related to the core and satellite model reproduces some of the same patterns, even when species are fixed in their core or satellite status. However, field testing of the last proposition have yet to be undertaken.

## Conclusions

The study leads to two types of conclusions, methodological and factual. First; compound measures of species habitat space such as 'niche' volume may be inadequate compared to other approaches in addressing range and abundance relationship, at least when physico-chemical variables are used to characterize species. The second and main conclusion is that the specialization hypothesis has strong support in our data (i.e. amount of variance explained, correlation between specialization and distribution). However, it may be difficult to separate from the metapopulation-grounded explanation, since the factors underlyin the two are strongly interrelated. The existence of a strong relationship among specialization, distribution, and abundance is important because the assumption of this relationship underlies Brown's explanation of the correlation between distribu-

tion and abundance. Statistical models with and without habitat fragmentation separate effects of specialization from those attributable to the combination of specialization, spatial habitat structure and occupancy. We tentatively conclude that metapopulation dynamics plays a minor (although detectable) role in a highly differentiated landscape mosaic of miniature rock pool communities. Inter-patch exchanges of individuals of most species are limited in the rock pool system by a high degree of isolation (hot dry rock, no water flow between pools, high pool walls, large differences in physical parameters among adjacent pools). However, we hypothesize that the explanatory role of the metapopulation dynamics will increase in communities in which the dispersability and mobility of organisms is less restrictive (e.g. in many bird and insect assemblages).

Thus, we propose the following relationship among the metapopulation-oriented and specialization-oriented explanations. We view these explanations as extreme points on a gradient defined by low and high patch isolation. On this gradient, the importance of metapopulation dynamics and specialization change gradually (Fig. 3). Furthermore, the interactions among the two should change along the gradient of patch differences. In a low isolation system, one would expect that re-supply (dispersal and colonization) of individuals from other occupied patches would be a major factor in maintaining high levels of patch abundance, as reflected in the core and satellite model (Hanski 1982). As patch-site isolation increases, factors specific to the patch will increasingly determine abundance of its inhabitants. Similarly, increasing differences among patches implies that, while the re-supply process ('rescue effect') may still operate, its effectiveness will decline as target patches become increasingly hostile and arriving propagules fail to sur-

vive or reproduce. Indeed, patch size may also affect the magnitude of the 'rescue effect': it makes a patch more isolated by making it more difficult to find (e.g. Hanski & Gyllenberg 1993). The two dimensions shown in Figure 3 capture the majority of situations discussed in the literature. There is, however, another dimension that should be considered in a more complete model. This dimension recognizes differences in species specialization. Highly specialized species should be affected more by what happens along the habitat difference axis because, in addition to the

probabilistic effects, they will experience lower colonization rates (i.e. lower survival rates after reaching a new and less suitable patch). Points along all the three dimensions, or model axes, represent specific hypotheses. These hypotheses are directly testable by comparing them to data from a diversity of natural systems.
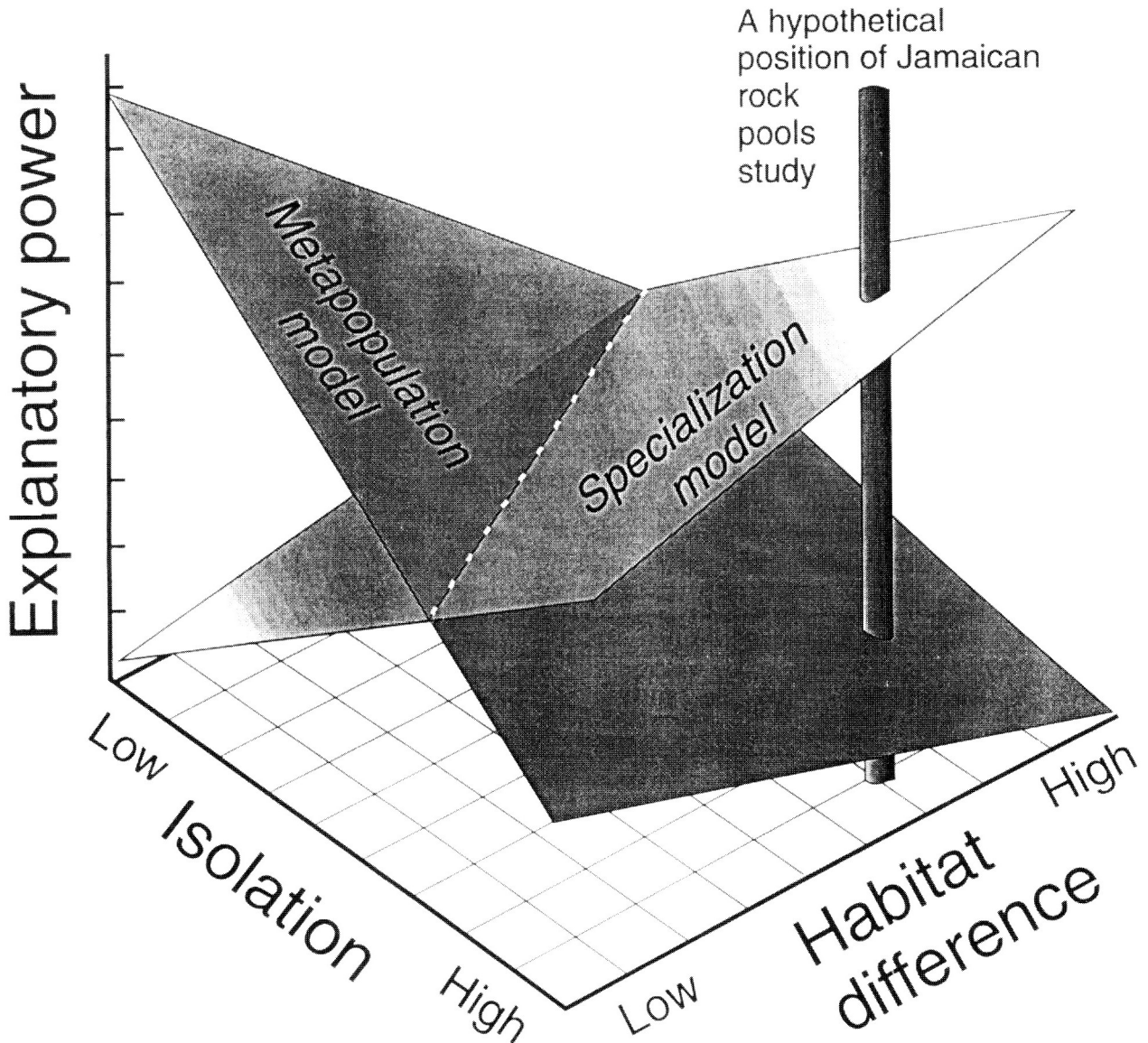
Figure 3. Relative importance of two classes of explanations applicable to the range and abundance correlation. Each plane represents landscapes with different configurations of isolation and habitat differences among patches. As isolation increases and the persistence in a patch increasingly depends on performance of the local subpopulation and less on exchange of individuals with neighboring subpopulations, the metapopulation model should provide a progressively weaker account of the population density. Thus, specialization-focused models are expected to perform better in situations described by upper right portion of the lighter shaded plane, while metapopulation focused models are expected to perform better in situations described by the upper portion of the darker plane. Habitat differences are expected to magnify the effect of isolation and to have greater impact at low isolation levels.

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