Organization of instabilities in multispecies systems, a test of hierarchy theory

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ABSTRACT   The hierarchy theory predicts that system components functioning at lower levels of hierarchy operate or change at higher rates than the components at the level(s) above. If this prediction is correct, then interpretation of stability in complex ecological systems may be in need of revision. We test the prediction using a model of hierarchical structure of habitat and a coral reef fish community. We found that the variability of ecological range and abundance increases exponentially from habitat generalists (high in hierarchy) to specialists (low in hierarchy), as postulated by the hierarchy theory. Our result suggests that community stability is a composite property and should be evaluated by considering the hierarchical structure of that community.

Although the hierarchy theory (HT) provides a framework for examination of (*i*) macropatterns and (*ii*) general structure and mechanisms organizing multispecies assemblages (1–5), almost no empirical tests of the theory are available (6–8). Structure and organization of such systems are intricately linked to the idea of stability. Stability of multispecies communities has been attributed to factors such as environmental constancy, habitat heterogeneity, productivity, or food web attributes. This has become one of the most discussed issues in theoretical and applied ecology (9). Some have recently suggested that whether communities are stable or not is a matter of spatial or temporal scale at which data are collected (10) or aggregated (11).

If communities are organized hierarchically as many have recently suggested (3, 10–12), then we may expect species to respond to the environmental template in accordance with the constraints due to their position in the hierarchy. The measures and interpretation of stability could be further affected depending on the specific behavior of individual levels. Thus, understanding regularities in this complex picture would be of considerable help to conceptualization and measurement of community stability. While the concept of stability itself is rich and many different measures of stability have been developed (e.g., ref. 13), we use one of these measures as example only. We measure stability as constancy in the numbers of individuals (e.g., ref. 14).

HT postulates one important regularity in the form of prediction. The prediction states that components of an ecological entity existing at lower hierarchical levels operate at higher frequencies or change at higher rates than components at hierarchical levels above them (refs. 15 and 16). Our goal is to test this prediction. We conduct the test by applying the habitat-based model (HBM) of community structure (2) to the fish assemblages associated with coral reef patches. This model is based on the following assumptions reflecting the habitat structure and species properties: (*i*) habitat is a nested hierarchy of multidimensional patches, (*ii*) patches become smaller and more fragmented with increased resolution of habitat grain (i.e., when one moves down the hierarchy), (*iii*)

regionally available species display a broad range of specializations relative to this habitat structure, and (*iv*) species from that pool are sorted to various patches of the habitat according to their abiotic requirements, competitiveness, predation pressure, available resources, and facilitating interactions. All these variables are dimensions of the model. In practice the model appears as a nested mosaic of microhabitats, primarily because most variables, even such as patterns of variation in time, can be represented in space. Distribution of species in the mosaic provides an indirect means of assessing their performance in the multidimensional space without actually analyzing individual dimensions of that space. Like any general model, HBM is weaker at addressing specific mechanisms but should be more useful for analyzing aggregated patterns. Expected abundance of species is calculated as the function of ecological range and the size of habitat occupied. The general formula used in an earlier paper has the form (modified from ref. 2): $N_i = F(ER_i/ER_{max})^2$, where N_i is the abundance of species i, F is a site- or taxon-specific coefficient or function (if known and necessary), ER_i is the range of species i, and ER_{max} is the maximum range available to species in the community in question.

Thus a species occupying large and less isolated patches should have a higher mean density than a species occupying small and more isolated microhabitats. This approach has been taken by Hanski (17) to one level of habitat mosaic and it predicts a bimodal distribution of abundances (18). HBM addresses several levels of habitat mosaic and predicts polymodal distribution of abundances. The ecological range can be estimated in a variety of ways depending on the available data. Ideally, all relevant ecological dimensions should be quantified to obtain the niche volume that could then be used in the model as a measure of ecological range, either in its entirety (e.g., ref. 19) or by choosing the most limiting dimension only. More likely, because of the data limitations, the range will be estimated as a portion of a gradient over which a species is present. We take this latter approach on the basis that a species found on a greater number of patches and/or a larger mean patch size is exposed to a broader gradient of microhabitat conditions and biotic interactions (e.g., larger patches tend to have more fish, coral, algal, and invertebrate species; ref. 20). We accept this approach because it captures the general relationship of species to their habitat well (see below). Earlier tests show that the model correctly and uniquely predicts existence of several discontinuities in the ecological ranges of species (2, 18, 21). These discontinuities lead to an emergence of clusters of species with similarly scaled ecological ranges. In consistency with HT, such scaled clusters of ranges are indicative of and interpreted as hierarchical levels of organization. They have been experimentally shown in a stream setting to reflect the nested structure of habitat mosaic (2). While the identification of levels is indirect and relies on distributional patterns (2, 3) and there are logical limits to their independent spec-

Abbreviations: HT, hierarchy theory; HBM, habitat-based model.

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ification (22), such identification makes the test possible. As quantitative data on frequency or rate of change may be difficult to obtain, we use a measure of variability instead. We first established that hypothetical populations changing at lower rates (or with longer periods), when sampled at relatively small temporal scales, reveal less variation than populations changing more quickly (see *Appendix* for details). Furthermore, the simulation indicates that the relationship between frequency of change and estimates of variation is linear (unpublished data). The test is specifically defined then as demonstrating that, on average, species assignable to lower hierarchical levels (= smaller scale of habitat use—i.e., species with narrow ecological ranges) show greater variability than ecologically broad species that "use" higher hierarchical levels (for more explanation, see Fig. 1). The null model (Fig. 1*B*) states that the mean relative variability of species descriptors, abundance and ecological range in this test, does not differ among species classified at different hierarchical levels.

Data and Analyses

We used data on the composition and abundance of 52 fish species associated with coral back reef patches in Discovery Bay, Jamaica, at depths of 3–10 m. Data were collected over two winter seasons (1990, 35 patches and 876 individuals; 1991, 40 patches and 1380 individuals) from the same area. Different numbers of fish in each year are due to the method of model standardization. The standardization requires that the sampled ecological range is greater than that of the most broadly distributed species. Annual changes in regional density and distribution of species create the need for different sample sizes. Each patch has been censused and its diversity and abundance have been recorded. We report details of the field work elsewhere (23). For the purpose of this study, we equate the ecological range of species with the size of the habitat used by a species. The habitat size includes two components: the number of separate patches and the size of these patches.

(*i*) We established that the community structure was hierarchical (multiscaled) with respect to habitat use and revealed
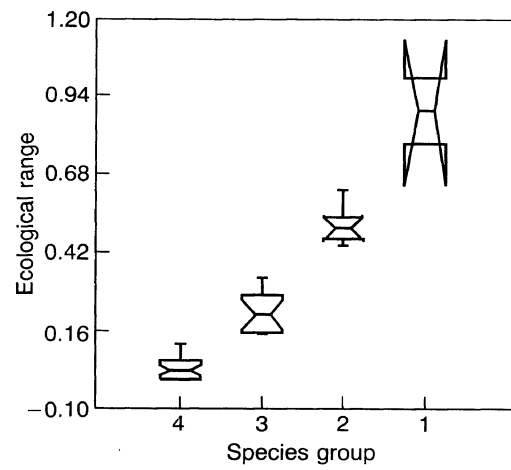
FIG. 2. Ecological ranges of species grouped into four clusters. Boxes show medians and quartiles (SYSTAT cluster analysis: group variance, $P < 0.036$, Bartlet test for homogeneity; ANOVA between groups, $P < 0.001$; Tukey HSD multiple comparisons, all $P < 0.000$). Ranges were calculated using the equation that gave the best prediction of abundances: $ER = a(P_i/P_{tot}) + b(SA_i/SA_{tot})$, where a and b are constants fitted by nonlinear regression to reduce the residuals, SA is the cumulative surface area of all patches occupied by the ith species, and P is number of patches on which the ith species occurred.

discontinuities in the pattern of ecological ranges (Fig. 2) as predicted by HBM (2). Individual ecological ranges used in the cluster identification were obtained by including the number of patches and the sizes of patches and modified by fitting constants. The constants were fitted to improve the power of ecological range in predicting species abundances. (*ii*) We found that the community conforms with other expectations of HBM; i.e., it shows a strong positive correlation between species ecological range and abundance (Fig. 3) and that ecological ranges are nested (Cochran's $Q = 288$). For this test we used an equation without the fitted constants (Fig. 3). While this last finding is not new (24), it affirms the adequacy of the data set and of the model for the test. (*iii*) We
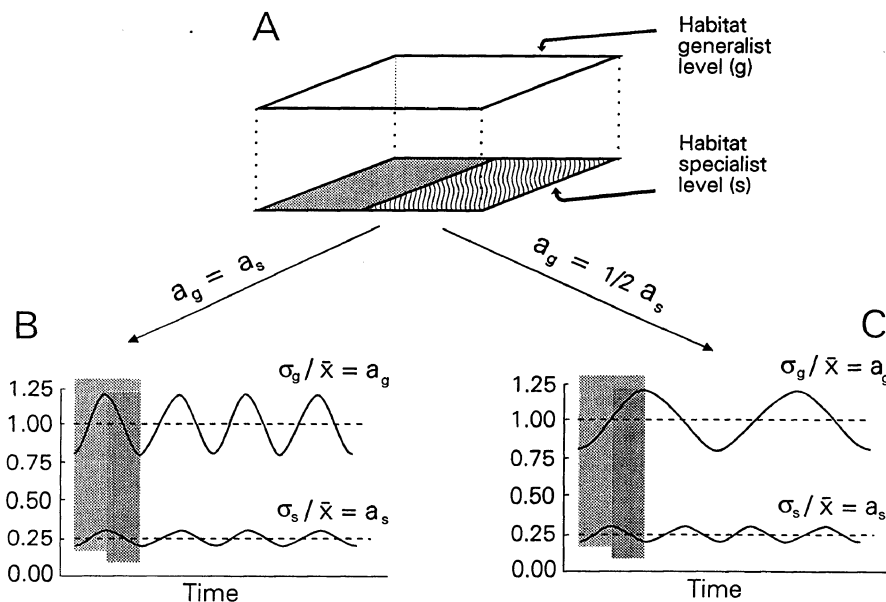
FIG. 1. Model and test—how the postulate of HT about level frequencies translates into variation of parameters measurable in the field. (*A*) Representation of a simple habitat with two levels of resolution and three units; one occupied by a generalist species (g) and two by specialists (s). (*B*) Null model: the relative variability expressed as some measure of variation (e.g., σ) over the mean ($\bar{x}$) is the same for specialists and generalists. (*C*) The prediction of HT: the relative variability of generalists is less than that of specialists. (*B* and *C*) *y* axis shows some observed community or species parameter—e.g., abundance, ecological range, or richness. Note that the qualitative result will not change irrespective of the temporal scale of observation (shaded areas indicate two time intervals for comparison).
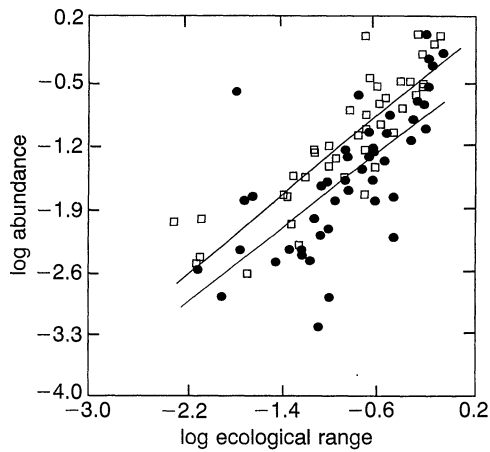
FIG. 3. Predicted and observed relative abundances of 52 fishes in 1990 (□) and 1991 (●) ($r^2 = 0.745$, $P < 0.001$, and $r^2 = 0.503$; regression lines do not differ in slope, $P < 0.01$), respectively. Observed fish abundances were corrected for the unequal times they were present on or near patches (unpublished data). To test the relation between range and abundance, ecological range has been calculated independently of abundance by using: $ER = (SA_iP_i)^{1/2}/(SA_{tot}P_{tot})^{1/2}$, where SA_{tot} and P_{tot} are the cumulative area of all sampled patches and the total number of patches, respectively.

examined the variation within clusters by grouping fish species of similar ecological ranges. The abundance and range values of the clusters are represented on 0–1 scales in Fig. 4. For each fish species we calculated the absolute change of abundance and range values from one year to another. Subsequently, we made the within cluster means of these differences relative to the mean cluster abundance and range, respectively, by dividing them by the respective cluster mean. We plotted this relative variation against the mean ecological range of fish in the cluster. This procedure provided an indirect means for depicting variability of four individual hierarchical levels detected through the cluster analysis.

We also created a second null model to assess the effect of stochastic variation on the results. Such variation alone might produce the observed patterns because the same observational error will result in greater relative variation among rare than common species. The model assumed random variation of fish abundance with 50% turnover rate and 70% increase

in total abundance in year 2 (= actual change from year 1 to year 2). The curves representing the simulated and observed cluster variability (Fig. 4A) differ in slopes and intersects, when log-transformed ($P < 0.001$). This indicates that stochasticity of considerable magnitude cannot explain the observed differences in variability between habitat generalists and specialists. The shape of the simulated curve indicates further that declining variation in clusters containing ecologically broad species is not an artefact of the division by increasingly larger means. Variation in ecological range behaved similarly to that of abundance (Fig. 4B), suggesting that actual ecological range is not fixed by individual species requirements but is codefined by the community condition. Turnover rates of 0% and 100% show no significant difference to the 50% rate plotted. Rates >100% are unrealistic for the species censused because such rates would imply that individuals older than 1 year are all replaced by similar individuals within 12 months.

Discussion

Possible sources of error include statistical artefacts and the effects of heterogeneity. Small standard errors reduce the possibility that the link between the mean and variance (power law) caused the pattern (see ref. 25). Indeed, the mean abundance of narrow species was much smaller than that of broad habitat users but the number of habitat specialists was much greater than the number of generalists (two in cluster representing the highest level of hierarchy). Furthermore, as largely the same patches were sampled in both years, we rule out the effect of spatial heterogeneity as an alternative explanation.

Our results are not isolated. Moths, aphids, and bracken insects reveal the same general pattern [data in Gaston and Lawton (26)]. These authors analyzed absolute variation and concluded that habitat specialists vary less than generalists. Comparing the variation among absolute abundances of habitat generalists and specialists cannot address the question of stability for two reasons. It ignores limits imposed by the habitat grain: A habitat specialist that uses a fraction of the habitat cannot change its ecological range as much as a generalist that uses most of it, and different initial densities and density means define how much species operating at different levels of hierarchy may change in abundance.
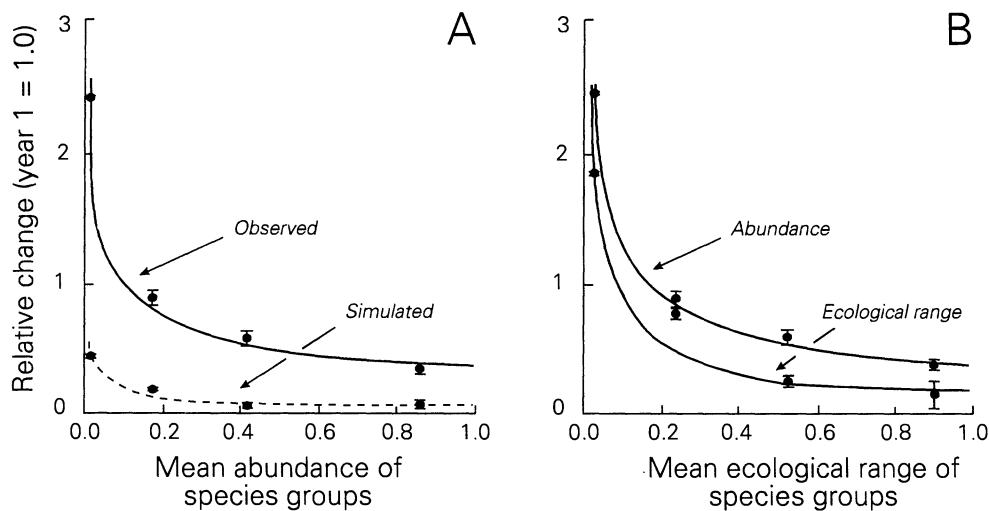

FIG. 4. Group variation as a function of habitat level associated with a group. High mean values of the ecological range correspond to high habitat levels. The trend is highly significant for abundance whether plotted against the group abundance or ecological range means (in A, $r^2 = 0.960$ and in Fig. 3, $r^2 = 0.981$, $P = 0.006$, respectively; for log-transformed values, $P < 0.013$) but not significant for simulated variation ($P < 0.071$). Variation of the ecological ranges behaves similarly to that of abundance (in B, $r^2 = 0.879$ and $P < 0.041$). Bars represent SEMs.

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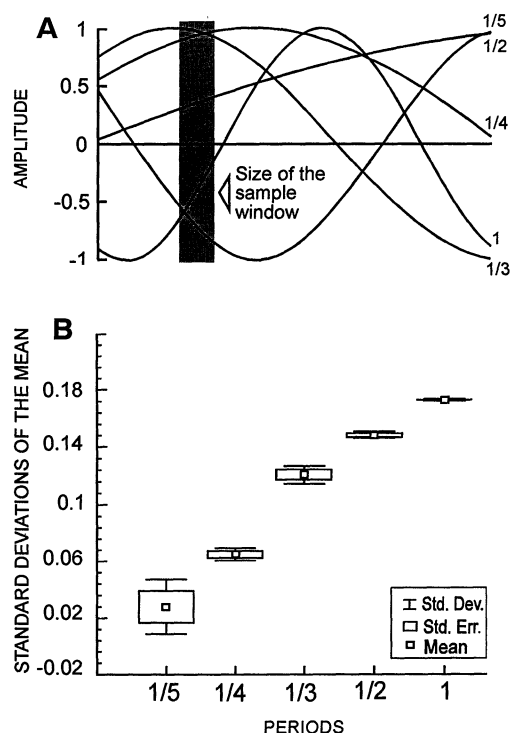
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FIG. 5. Illustration of the link between the frequency of variation in population size and the measured variance at time scales less than one full period, with 1 representing the fastest behavior and 1/5 the slowest. (*A*) One of the three data sets used to calculate standard deviations and the size of the sampling window for data in *B*. Fractions describe the portion of the period of each curve shown in the figure. (*B*) Trend in standard deviations as a function of the frequency or period length.

Our results also suggest that the question of community persistence cannot be resolved by simple field tests or adjustments of scale, whether spatial, temporal, or taxonomic, as recently attempted (23), because communities are organized hierarchically. Different levels in this hierarchy may display different degrees of stability, as measured by the variation in abundance and spatial distribution in this case. We believe that similar regularities will also be discovered at the population and ecosystem levels.

Appendix: The Link Between Frequency of Population Change and Estimate of Variation at Short Time Scales

We represented changes in population size as a sine function of time. This simplified model illustrates steps needed to establish the link between the frequency (or period after which the function returns to the original state) and a measure of variation. A natural population may not undergo cyclic changes, and it may show other periodicities and stochastic variation. These factors have little bearing on the nature of the relationship we need to demonstrate.

We created five functions of increasingly shorter period: $y_1 = x \sin \Pi$, $y_2 = x \sin 2\Pi$, $y_3 = x \sin 3\Pi$, $y_4 = x \sin 4\Pi$, and $y_5 = x \sin 5\Pi$. Values of each function were calculated for 1000 time units for the interval x (0,2) such that the slowest

behaved function $y = x \sin \Pi$ contained values covering one complete period.

The five functions were randomized as to when they began their course on the x axis. Three randomized sets of data were created. A random length of the x axis corresponding to the length of the shortest period ($y = x \sin 5\Pi$, 200 values for each y_i) was used to estimate variation of each "population" (Fig. 5*A*).

The five populations were sampled using a moving window of 20 adjacent values (Fig. 5*A*) to calculate standard deviations for each curve. These standard deviations vary in response to the portion of the curve and the sampling window size. Details of these patterns of variation will be described separately (unpublished data).

We obtained means of standard deviations for three sets of data and then plotted between-set means and respective errors (Fig. 5*B*). Thus, the figure shows variation between replicated simulations and the overall trend in means.

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