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Predictions and retrodictions of the hierarchical representation of habitat in heterogeneous environments

Jurek Kolasa[a,*], Craig R. Allen[b], Jan Sendzimir[c], Craig A. Stow[d]

[a] Department of Biology, McMaster University, Hamilton, Ontario, Hamilton, Canada
[b] U.S. Geological Survey – Nebraska Cooperative Fish & Wildlife Research Unit, School of Natural Resources, 423 Hardin Hall, University of Nebraska, Lincoln, NE 68583, USA
[c] International Institute for Applied Systems Analysis, Laxenburg, Austria
[d] NOAA – Great Lakes Environmental Research Laboratory, Ann Arbor, MI, USA

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ABSTRACT

Interaction between habitat and species is central in ecology. Habitat structure may be conceived as being hierarchical, where larger, more diverse, portions or categories contain smaller, more homogeneous portions. When this conceptualization is combined with the observation that species have different abilities to relate to portions of the habitat that differ in their characteristics, a number of known patterns can be derived and new patterns hypothesized. We propose a quantitative form of this habitat–species relationship by considering species abundance to be a function of habitat specialization, habitat fragmentation, amount of habitat, and adult body mass. The model reproduces and explains patterns such as variation in rank–abundance curves, greater variation and extinction probabilities of habitat specialists, discontinuities in traits (abundance, ecological range, pattern of variation, body size) among species sharing a community or area, and triangular distribution of body sizes, among others. The model has affinities to Holling's textural discontinuity hypothesis and metacommunity theory but differs from both by offering a more general perspective. In support of the model, we illustrate its general potential to capture and explain several empirical observations that historically have been treated independently.

1. Introduction

Recognition that ecological phenomena occur at various scales has informed ecological research for over 20 years. Allen and Starr (1982) made the first comprehensive review of the conceptual and practical issues associated with the multiscale nature of ecology, which they centered on a hierarchical view of ecological systems. Following from this initial work, the scale-dependence of ecological patterns became a major focus in ecology, as well as the interaction of processes at various scales (e.g., Davies et al., 2005; Sandin and Pacala, 2005). The application of this view to research problems of community and ecosystem ecology was particularly successful with respect to interpretation of ecological patterns but less so in formulating testable hypotheses. Instances where such hypotheses have been formulated are limited; Kolasa (1989) postulated the existence of discontinuities in community structure and Holling (1992) proposed a link between landscape texture and body size distributions (textural discontinuity hypothesis). This modest record contributes to a more limited recognition and understanding of the hypotheses and predictions arising from the multiscale perspective than they deserve to have. However, the hierarchical view of ecological systems has significant potential for explaining old and predicting new processes, patterns, and relationships. An approach that has the ability to account for observations that had previously required separate and unconnected models – a case of retrodiction – would be particularly useful.

We attempt to address this need by reviewing the predictions of hierarchy theory as applicable to broadly defined community ecology and by generating further testable hypotheses derived from a single conceptual construct. Specifically, we advance a model linking the structure of the environment to structure and dynamics of communities and to properties of their constituent species. First, we describe the model to accommodate various ecological premises. Then we formalize its quantitative potential. Finally, we apply it to a selection of contemporary problems in ecology.

2. Verbal and graphical model of habitat–species relationship

2.1. Habitat structure

Any habitat, aquatic or terrestrial, is a nested mosaic of smaller habitats such that larger fragments contain smaller subcategories,

* Corresponding author at: Department of Biology, McMaster University, 1280 Main Str W, Hamilton, Ontario L8S 4K1, Canada.
E-mail address: kolasa@mcmaster.ca (J. Kolasa).

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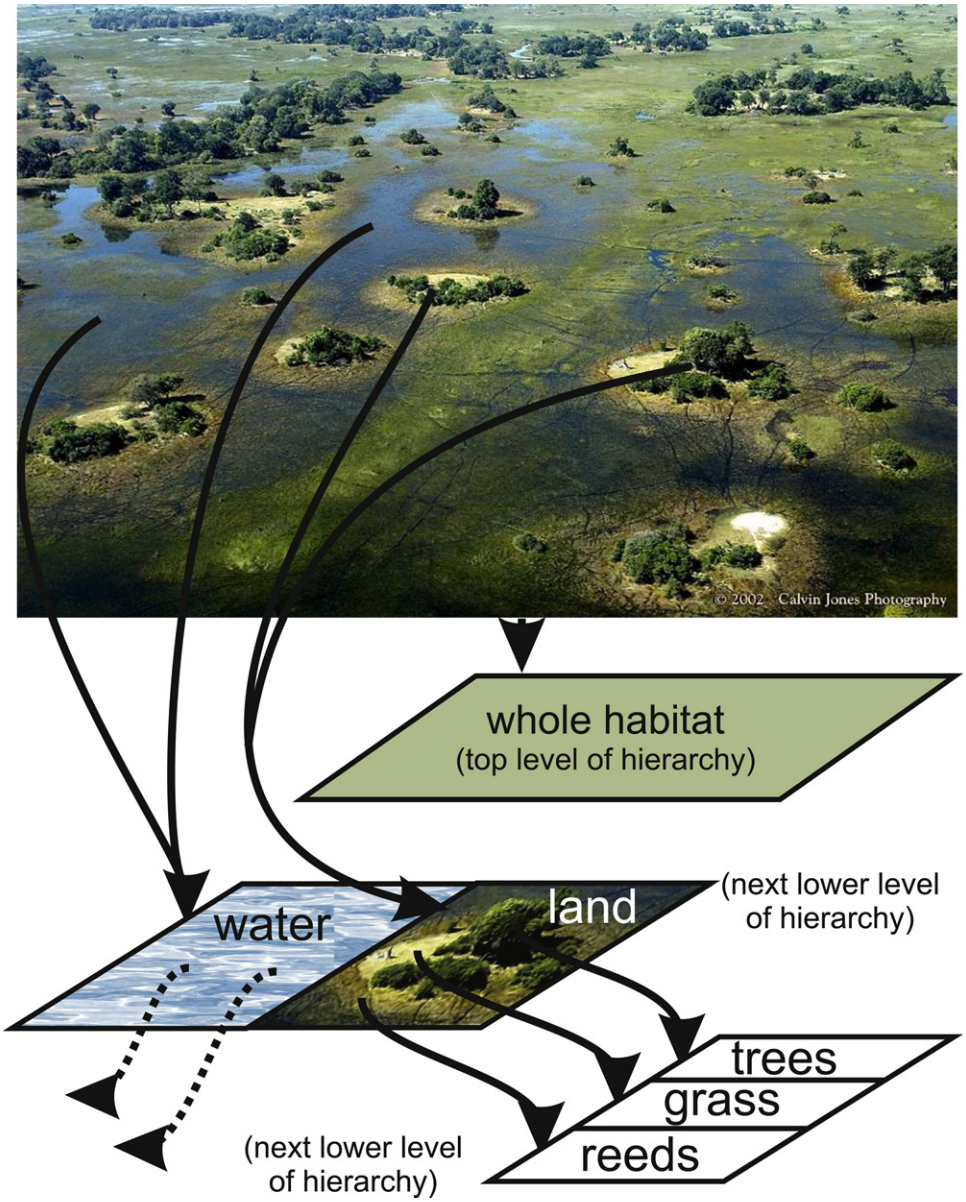

Fig. 1. An example of hierarchical structure of habitat–Okavango delta swamps. Depending on the chosen level of resolution, the swamp can be represented as a homogeneous habitat of one kind, or as two subcategories of aquatic and terrestrial patches, or as a collection of microhabitats within each of the two categories. The process of zooming in can continue as desired.

Photograph by Calvin Jones, with permission.

and those in turn are composed of even finer microhabitat subcategories that are even smaller (Fig. 1). Indeed, the metaphor provided by the pictorial example can be extended to other dimensions. Specifically, we assume that habitat is a nested hierarchy of multidimensional volumes (for detailed discussion see Kolasa and Waltho, 1998). Because any habitat dimension except time can be mapped onto space, we interpret the habitat as (1) a hierarchical mosaic of patches with (2) lower-level patches nested within higher-level patches, and (3) with each level having a distinct set of attributes arising from distinct processes (Fig. 1). It is the interaction of such habitat hierarchy with a subset of species from the regional species pool that determines which of these attributes are meaningful and thus worthy of consideration. Also, while this structure is best conceived as multidimensional, it is likely that one or very few dimensions exert major influence on the performance of any single species (Polechová and Storch, 2008). The commonly accepted notion of a limiting factor provides solid logical support for this assumption. If one factor limits abundance and distribution of a population, whether it is a resource or constraint of some other nature, the other factors, by definition, do not play such a role at the same point in time or play roles too minor to consider.

To examine the model properties we use two dimensions only. Two dimensions provide the model with a spatial attribute, although this considerable simplification does not convey any specific configuration of actual habitats in space. The model identifies the total amount of space a particular habitat occupies on average relative to a higher-level habitat unit. Each unit can take various configurations in space. It can occur as a contiguous patch, or it can differ in size and be split to differing degrees (Fig. 2a–c). Regardless of spatial configuration, two habitat types are represented in the model as two subunits (Fig. 2d) that are members of a single, higher level unit. Extending this approach permits representation of the whole habitat as a nested structure of units emerging at increasing levels of resolution (Fig. 3).