INTRODUCTION

The role of habitat selection in landscape ecology

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Landscape ecology – whether it is defined as the fragmentation of habitats into insular or weakly coupled subpopulations or by the interaction of scale-dependent processes among ecological communities (or species, or populations) – involves forms of spatial analysis. Habitat selection analyses how organisms become distributed in response to spatial heterogeneity. Thus, processes associated with habitat selection should be central to landscape ecology. Insofar as the individual-level activity of habitat selection has predictable population and community level consequences, habitat selection can form a mechanistic basis for understanding landscape ecology.

A survey of any major ecological journal reveals considerable confusion and disagreement on the roles of spatially-dependent processes in the evolution, structure and function of natural systems. Part of the confusion is due, no doubt, to the complexity of spatial interactions. Processes responsible for spatial patterns may themselves be dependent upon spatial, temporal and even organizational scales. Some processes such as density-dependence (dependence on population size) operate across a spectrum of spatial and temporal scales.

Assumptions of density-dependence are central to our views of natural selection, to our understanding of population dynamics and community structure and to our management of natural resources. Once again, habitat selection provides a natural forum for considering this central role of density-dependent and scale-interdependent processes. Within the conceptual framework of habitat selection, we feel it is possible to develop a set of inter-related theories that explain observed patterns of distribution and abundance at several ecological scales. (A similar claim can be made for a central role of habitat selection in evolutionary processes; see *Evolutionary Ecology*, 1987, Vol. 1, No. 4).

The papers that follow come from a colloquium on 'Habitat selection: theoretical and empirical links to landscape ecology' at the 1991 World Congress of Landscape Ecology in Ottawa, Canada. They reflect our belief in a central role for the theory of density-dependent habitat selection in understanding many issues in evolutionary ecology. Support for our belief can be found in single-species models that predict patterns of habitat use in response to changes in population size. These models have been confirmed by observation and field experiments (Krebs, 1971; Milinski, 1979; Whitham, 1979; Morris, 1989). Multi-species models, which are also being rapidly confirmed, have revealed the dramatic density-dependent effects that competitors and predators have on habitat choice (Rosenzweig, 1991).

Most of the models, and their associated tests, have either explicitly, or implicitly, dealt with

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course-grained environments coupled with cost-free habitat selection (Brown and Rosenzweig, 1986). Brent Danielson notes that these models apply whenever patterns of abundance in a landscape can be described using only the weighted averages of each of the constituent habitat types. However, it is clear that evolutionary games of habitat selection are played in arenas that encompass many different scales and configurations of heterogeneity. Under these conditions, patterns of abundance may frequently interact with the frequency, dispersion, spatial scale, configuration and relative qualities, of habitat patches. This, Danielson notes, is the purview of landscape ecology. Our authors have begun to weld the chain of logic and observation that links it to evolutionary ecology.

In the first paper, Brown and Pavlovic examine the evolution of habitat specialization in response to passive habitat selection along a continuum of spatial scales between fine and coarse-grained habitats. The interaction between population density and the scale of heterogeneity determines the exposure of alternative evolutionary strategies to selection. While the ecological context of the population's members may be a subset of habitat patches, their evolutionary context can be the entire landscape. Even under passive movement of individuals among habitats, habitat specialization and exposure to habitats combine to form a positive evolutionary feedback. Brown and Pavlovic conclude that habitat specialization is evolutionarily stable even in the absence of active habitat selection and in the presence of high migration rates.

Next, Tarja and Laurie Oksanen consider the interaction between habitat selection and scale of habitat patchiness to re-evaluate classic theories on the role of consumers in the population dynamics of their prey. They model a small scale source-sink phenomenon where patches of productive habitat are embedded within a matrix of 'barren' habitat. Differences among landscapes are quantified by the predator's travel time between productive patches. In accord with models of patch use, increased travel time devalues the overall quality of the landscape to the predator, increases patch resident times and increases the mean standing crop of prey within both the high and low quality habitats. The small-scale of heterogeneity promotes strong apparent competition between prey residing in the productive patches and prey occupying the barren areas. Increasing the amount of productive habitat may actually drive the prey extinct in the barrens. Some of these predictions are scale dependent and clearly demonstrate the necessity of considering habitat selection when understanding trophic dynamics in heterogeneous landscapes.

The Brown–Pavlovic and Oksanen models assume landscapes composed of only two habitats (often defined as high and low quality), each of which can be exploited. The proportion of the two habitats has profound effects on the dynamics and evolutionary strategies of their occupants. Danielson generalizes that approach to include a third class of entirely unusable habitat. In this case, patches of source and sink habitat exist within a sea of unusable habitat. If the proportion of sink habitat is reduced through substitution with the unusable one, the average patch quality of the entire landscape will be reduced. However, the average population density may actually increase because individuals have a higher probability of finding patches of source habitat. When applied to two species that compete within patches, habitat selection may result in landscape-wide interactions that are more intensely competitive or that are even mutualistic.

The paper by Morris capitalizes on differential costs of habitat selection at different spatial scales to test landscape theories using real data. At the fine-grained scale, habitat selection obeys the rules of patch use model from foraging theory and is influenced by costs of travelling through or around unprofitable patches. At the coarse-grained scale, habitat selection obeys the rules of dispersal models where cost is represented by lost opportunities for reproduction while the individual attempts to relocate its home range. The two forms of cost can be differentiated in the slopes and intercepts of isodars. Isodars plot the density of individuals in two habitats such that an individual's expected reproductive success is the same in both. The analysis of deer mice

living in prairie landscapes yields a remarkable result. In terms of population dynamics, the size of their landscape may be on the order of only 100 m.

The final and highly innovative paper by Holt and Gaines returns to mechanisms of source and sink dynamics to address the essence of evolutionary adaptations. They wish to know how habitat selection influences the evolution of a species' fundamental niche. An important result, foreshadowed by Brown and Pavlovic's work on passive habitat selection, is that whenever the majority of a population is found in the source habitat, natural selection will bias evolution towards increased specialization on that habitat. Habitat selection followed by the evolution of habitat specialization may reduce and constrain the fundamental niché to those habitats where fitness is already high. Perversely, the very adaptations that make an organism successful in a complex landscape may place the population in an evolutionary straitjacket that increases its vulnerability to environmental changes and decreases its evolutionary flexibility. Density-dependent habitat selection exacerbates this process by which fundamental nichés become highly conservative evolutionary characters.

Skeptics might accuse us of overzealously promoting density-dependent habitat selection as a framework for understanding processes and patterns in ecology. We acknowledge this criticism. Perhaps the analogy is inappropriate. Habitat selection may be more like a scaffold whose parts can be forever reassembled to help build, and thereafter modify or restore, the structure of ecology.

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