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Population Ecology in Spatially Heterogeneous Environments

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Abstract

Historically, population ecologists have equated environmental spatial heterogeneity with habitat spatial structure. Early models represented habitat spatial structure simply as population subdivision into habitat patches. Later models included at first partially and then fully explicit representation of the spatial relationships among habitat patches. More recently, landscape population ecologists have broadened the view of spatial heterogeneity to include the composition and configuration of the whole landscape. A change in landscape composition refers to a change in the cover types in the landscape, the proportions of each, or both. A change in landscape configuration refers to a change in the spatial pattern of cover types, independent of any change in landscape composition. We hypothesize that changes in landscape composition generally have much larger effects on population persistence than changes in landscape configuration. Landscape configuration should have a large effect on population persistence when both (i) configuration has a large effect on among-patch movement of the organism and (ii) among-patch movement has a large effect on population persistence. The first condition should hold for species whose movement direction is constrained, and the second condition should hold either (i) when colonization of empty habitat is important for persistence or (ii) for species that require more than one type of habitat. We discuss extensions of these ideas to the effects of landscape configuration on ecosystem processes.

Introduction

The potential effects of environmental spatial heterogeneity on population dynamics and interactions have been of concern to population ecologists for decades. In this chapter, we review the ways in which spatial heterogeneity of the environment has been incorporated in models of population dynamics and interactions. We then discuss the current view of spatial heterogeneity

in landscape population ecology, and we review the evidence for effects of *compositional heterogeneity* and *configurational heterogeneity* on population ecology. Finally, we present a hypothesis that predicts the circumstances in which a change in landscape configuration should have a large effect on population ecology, and we discuss possible extensions of the hypothesis to effects of landscape configuration on ecosystem processes.

History of Environmental Spatial Heterogeneity in Population Ecology

The ways in which population ecologists incorporate environmental heterogeneity into population models have changed markedly over time. In this section, we review the implicit and explicit representation of environmental spatial heterogeneity in models of population dynamics and population interactions. Our review is limited to models in which the underlying environment is spatially heterogeneous in some way. We do not include the many spatially explicit population models in which the underlying environment is assumed to be homogeneous, such as reaction-diffusion models of population spread in a homogeneous environment (e.g., Lewis 1997), cellular automata models of disease spread in a homogeneous environment (e.g., Holmes 1997), or models exploring the generation of population spatial pattern in a homogeneous environment (e.g., Pacala and Levin 1997). Note that this review is not exhaustive; we have selected representative examples for each method of incorporating environmental spatial heterogeneity into models. In each case, we focus on the earliest examples that we know of, even though all the views of spatial heterogeneity persist simultaneously in the current literature.

Population Subdivision

The first theories of population ecology assumed spatial homogeneity of the environment (e.g., Verhulst 1838; Lotka 1925; Volterra 1926; Nicholson and Bailey 1935). However, with Gause's classic experiments in 1934, population biologists began to understand that population theories based on spatial homogeneity are likely to fail in the real world. Gause showed that a predator-prey relationship was "inherently self-annihilative"; it could persist only when a portion of the prey population was protected by a "privileged sanctuary," or when reintroductions of prey occurred at intervals. This implied that persistence of natural populations depends on environmental patchiness or spatial heterogeneity. Laboratory experiments by Huffaker (1958) and Pimentel (1963) supported this conclusion.

Theoretical examination of the influence of environmental spatial heterogeneity on populations began with models that represented spatial heterogeneity as habitat subdivision, resulting in separation of the population