

# Merging Spatial and Temporal Structure within a Metapopulation Model

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**ABSTRACT:** Current research recognizes that both the spatial and temporal structure of the landscape influence species persistence. Patch models that incorporate the spatial structure of the landscape have been used to investigate static habitat destruction by comparing persistence results within nested landscapes. Other researchers have incorporated temporal structure into their models by making habitat suitability a dynamic feature of the landscape. In this article, we present a spatially realistic patch model that allows patches to be in one of three states: uninhabitable, habitable, or occupied. The model is analytically tractable and allows us to explore the interactions between the spatial and temporal structure of the landscape as perceived by the target species. Extinction thresholds are derived that depend on habitat suitability, mean lifetime of a patch, and metapopulation capacity. We find that a species is able to tolerate more ephemeral destruction, provided that the rate of the destruction does not exceed the scale of its own metapopulation dynamics, which is dictated by natural history characteristics and the spatial structure of the landscape. This model allows for an expansion of the classic definition of a patch and should prove useful when considering species inhabiting complex dynamic landscapes, for example, agricultural landscapes.

*Keywords:* metapopulation models, patch dynamics, spatially realistic models, dynamic landscape, persistence, fragmentation.

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Within the metapopulation framework, two structures have emerged as critical in the study of species persistence within patchy landscapes. The importance of spatial struc-

ture (i.e., heterogeneity) has been supported by many studies (Durrett and Levin 1994; Moilanen and Hanski 1995; With and Crist 1995; Bascompte and Solé 1996; Hanski 1998; Bevers and Flather 1999; Hill and Caswell 1999; With and King 1999; Hanski and Ovaskainen 2000) that show that spatial features such as patch connectivity, patch size, and the assumption of local dispersal are essential to understanding the dynamics of a population. In addition to the spatial structure of the landscape, recent research also has touted the importance of the temporal structure of the landscape (Merriam et al. 1991; Gyllenberg and Hanski 1997; Marquet and Velasco-Hernández 1997; Brachet et al. 1999; Hanski 1999; Keymer et al. 2000; Crone et al. 2001; Johst et al. 2002; Marquet et al. 2003). The general consensus is that temporal components interact with the spatial components to determine metapopulation persistence (Fahrig 1992; Hanski 1999; Keymer et al. 2000; Johst et al. 2002).

Many natural landscapes are dynamic (e.g., prairie pot-holes subjected to periodic drought, canopy gaps in forests), and landscapes dominated by humans often exhibit temporal changes in structure as well (e.g., crop rotations in agricultural ecosystems, schedules of timber harvest in managed forests). The prevalence of dynamic landscapes requires a closer consideration of patch dynamics in the persistence of metapopulations. In this article, we develop a metapopulation model that integrates both the spatial heterogeneity and temporal dynamics of patches within the landscape.

## Models

Our model is an analytically tractable patch model that incorporates both the spatial and temporal structure of the landscape by blending two previous models. We chose to capture the spatial structure of the landscape by following a spatially realistic Levins model (SRLM; Moilanen and Hanski 1995). Temporal structure was added by emulating a dynamic landscape model (DLM; Keymer et al. 2000). In this section, we provide a brief review of each of these previous models, followed by an overview of our

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