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Intermediate disturbance in experimental landscapes improves persistence of beetle metapopulations

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Abstract. Human-dominated landscapes often feature patches that fluctuate in suitability through space and time, but there is little experimental evidence relating the consequences of dynamic patches for species persistence. We used a spatially and temporally dynamic metapopulation model to assess and compare metapopulation capacity and persistence for red flour beetles (*Tribolium castaneum*) in experimental landscapes differentiated by resource structure, patch dynamics (destruction and restoration), and connectivity. High connectivity increased the colonization rate of beetles, but this effect was less pronounced in heterogeneous relative to homogeneous landscapes. Higher connectivity and faster patch dynamics increased extinction rates in landscapes. Lower connectivity promoted density-dependent emigration. Heterogeneous landscapes containing patches of different carrying capacity enhanced landscape-level occupancy probability. The highest metapopulation capacity and persistence was observed in landscapes with heterogeneous patches, low connectivity, and slow patch dynamics. Control landscapes with no patch dynamics exhibited rapid declines in abundance and approached extinction due to increased adult mortality in the matrix, higher pupal cannibalism by adults, and extremely low rates of exchange between remaining habitable patches. Our results highlight the role of intermediate patch dynamics, intermediate connectivity, and the nature of density dependence of emigration for persistence of species in heterogeneous landscapes. Our results also demonstrate the importance of incorporating local dynamics into the estimation of metapopulation capacity for conservation planning.

Key words: dispersal range; metapopulation capacity; occupancy; patch connectivity; patch dynamics; red flour beetle; resource heterogeneity; Tribolium castaneum.

INTRODUCTION

The concept of a metapopulation (Levins 1969), a set of local populations residing in spatially isolated resource patches connected by dispersal and undergoing local extinction and recolonization, is a popular theoretical framework to understand the dynamics of species in fragmented landscapes (Hanski 1994, Hanski and Gilpin 1997). Early metapopulation models were spatially implicit and ignored many real-world features of landscapes (Harding and McNamara 2002). Subsequently, spatially realistic versions of the Levins model (SRM) were developed (Moilanen and Hanski 1995, Ovaskainen and Hanski 2001). Temporally dynamic models (TDM) were then developed by allowing patches to change in quality over time (Keymer et al. 2000). The characteristic features of SRM and TDM were then merged (DeWoody et al. 2005) to capture in an analytically tractable system the spatiotemporal complexities associated with dynamic, patchy landscapes.

The model of DeWoody et al. (2005), hereafter called the temporally dynamic spatially realistic metapopulation model (TDSRM), allows a patch at a given spatial location in the landscape to exist in three possible states: uninhabitable (0), habitable yet empty (1), and habitable and occupied (2). Each patch i can transition between habitable and uninhabitable states, determined by the area-dependent rates of patch creation (λ_i) and patch destruction (β_i), with λ and β serving as the background creation and destruction rates, respectively, as:

$$\lambda_i = \lambda / A_i$$

$$\beta_i = \beta / A_i.$$

The long-term expected amount of suitable habitat patches in a landscape is given by $s = \lambda/\lambda + \beta)$. The patch transition rate between states is defined by the mean lifetime of a habitat patch ($\tau = 1/\beta$). Thus, smaller values of τ signify higher patch turnover rate. Altering the patch turnover rates allows patch transitions to occur at substantially different time scales, even for landscapes with equal long-term habitat suitability (s). Metapopula-

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