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Effects of landscape and patch-level attributes on regional population persistence

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Species responses are influenced by processes operating at multiple scales, yet many conservation studies and management actions are focused on a single scale. Although landscape-level habitat conditions (i.e., habitat amount, fragmentation and landscape quality) are likely to drive the regional persistence of spatially structured populations, patch-level factors (i.e., patch size, isolation, and quality) may also be important. To determine the spatial scales at which habitat factors influence the regional persistence of endangered Ord's kangaroo rats (*Dipodomys ordii*) in Alberta, Canada, we simulated population dynamics under a range of habitat conditions. Using a spatially-explicit population model, we removed groups of habitat patches based on their characteristics and measured the resulting time to extinction. We used proportional hazards models to rank the influence of landscape and interacting patch-level variables. Landscape quality was the most influential variable followed by patch quality, with both outweighing landscape- and patch-level measures of habitat quantity and fragmentation/proximity. Although habitat conservation and restoration priorities for this population should be in maximizing the overall quality of the landscape, population persistence depends on how this goal is achieved. Patch quality exerted a significant influence on regional persistence, with the removal of low quality road margin patches (sinks) reducing the risk of regional extinction. Strategies for maximizing overall landscape quality that omit patch-level considerations may produce suboptimal or detrimental results for regional population persistence, particularly where complex local population dynamics (e.g., source-sink dynamics) exist. This study contributes to a growing body literature that suggests that the prediction of species responses and future conservation actions may best be assessed with a multi-scale approach that considers habitat quality and that the success of conservation actions may depend on assessing the influences of habitat factors at multiple scales.

Introduction

Many imperiled species occupy complex human-modified landscapes that are subject to habitat changes at multiple spatial scales. Physical habitat alterations affect both the conditions of patches as well as the broader landscape context, and associated impacts may influence the persistence of regional populations. To better understand scale-dependent ecological processes, habitat factors are increasingly measured at both local and regional scales, and multi-scale data are associated with observed population outcomes (Thornton, Branch, & Sunquist, 2011). The importance of cross-scale analyses and planning is increasingly recognized (Graf, Bollmann, Suter, & Bugmann, 2005; Razgour, Hanmer, & Jones, 2011), and a number of studies report significant influences from multiple spatial scales (i.e., landscape, patch, within-patch). Cross-scale interactions are likely to be common across a range of taxa, including invertebrates, herpetofauna, birds (e.g., Betts, Forbes, & Diamond, 2006; Renfrew & Ribic, 2007), and particularly important in mammals (e.g., Schooley & Branch, 2007; Thornton et al., 2011). Yet, tracking the influences of habitat variables at multiple spatial scales can be an onerous task (e.g., Fedy et al., 2014), and the selection of a single spatial scale at which to experiment, conduct further analyses, or make management policy is an attractive alternative. Species conservation and management plans often

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focus on a single spatial scale, and rarely address multiple or interacting scales (Du Toit, 2010; Razgour et al., 2011). The results of multi-scale analyses are often simply used to identify the level (i.e., patch vs. landscape) or spatial scale (e.g., distance) at which habitat attributes most strongly influence population responses (Cushman & Mcgarigal, 2004), rather than simultaneously considering the influences arising at multiple scales (Denoel & Lehmann, 2006). Further, multi-scale analyses are often focused on assessing local population outcomes (e.g., site occupancy, occurrence) rather than regional population outcomes (Thornton et al., 2011), such as metapopulation persistence, that may be more relevant to species conservation and habitat protection goals.

Landscape-level variables are expected to be associated with regional extinction risk to a greater extent than patch-level variables (e.g., patch size, quality, and isolation; Wilson et al., 2002) because they summarize habitat characteristics, rather than describe their variation or individual states. Yet the patch-level details of landscapes can exert meaningful influences on local and regional population persistence (Brito & Fernandez, 2002). Broad-scale habitat conditions may be insufficient to describe population dynamics that emerge from differences among habitat patches and their local populations. For example, landscapes comprised of the same average quality could contain patches of similar qualities or very disparate qualities. The latter condition may incite source-sink dynamics, altering local productivity and movements, and ultimately influencing regional stability and risk of extinction. Although landscape-level habitat attributes may influence regional persistence to a greater extent, patch-level attributes may be instrumental in explaining regional extinction risk and valuable in informing conservation and management actions.

At the landscape-level, few studies have directly contrasted the influence of habitat amount, level of fragmentation, as well as overall landscape quality on regional population outcomes. Yet landscape quality can significantly influence regional population persistence and even outweigh the effects of other habitat variables (Heinrichs, Bender, Gummer, & Schumaker, 2010; Klok & De Roos, 1998; Wiegand, Revilla, & Moloney, 2005). Regional landscape quality can influence the functional capacity of the landscape to support individuals, and those with higher overall capacity may support larger populations that are less prone to stochastic extinction (Gaggiotti & Hanski, 2004).

Similarly, metapopulation analyses that focus on habitat conditions within and among patches have emphasized the roles of patch size and isolation in determining local population dynamics and persistence (Jaquiery et al., 2008; Mortelliti, Amori, & Boitani, 2010; Ovaskainen & Hanski, 2001; Prugh, Hodges, Sinclair, & Brashares, 2008; Wiegand, Revilla, & Knauer, 2004; Wilson, Johnson, & Bissonette, 2009; With, 2004). Classical patch-based analyses have generalized variation in resource quality to achieve conceptual simplicity and overcome analytical constraints (Hokit & Branch, 2003). Although the inclusion of patch habitat quality does not always improve model fit (Moilanen & Hanski, 1998; Vögeli, Serrano, Pacios, & Tella, 2010), an increasing number of studies are recognizing the potential inadequacy of the area-isolation paradigm and are examining the role of habitat quality, or the variation in the value or density of resources and environmental conditions (Hall, Krausman, & Morrison, 1997) in influencing population dynamics and persistence (Dennis & Eales, 1997; Fleishman, Ray, Sjorgren-Gulve, Boggs, & Murphy, 2002; Franken & Hik, 2004; Franzén & Nilsson, 2010; Mortelliti et al., 2010; Ozgul, Armitage, Blumstein, Vanvuren, & Oli, 2006; Pellet, Fleishman, Dobkin, Gander, & Murphy, 2007; Prugh et al., 2008; Schooley & Branch, 2009; Thomas et al., 2001).

To examine the importance of conservation planning based on multi-scale habitat conditions, we used a case study to assess the relative influence of landscape- and patch-level variables, including habitat quality, on regional population persistence. We constructed a spatially-explicit, individual-based population model for an endangered Ord's kangaroo rat (*Dipodomys ordii*) population in Alberta, Canada, and used habitat removal scenarios and resulting extinction risks to rank the influences of patch and landscape habitat variables on regional population persistence. Previous research identified the types of habitat that are likely to contribute long-term persistence and population recovery (e.g., active dunes vs. road-side habitats; Heinrichs et al., 2010) but did not characterize the relative effects of habitat quantity, quality, and configuration or their scale of influence on regional population persistence.

Materials and methods

Overview

We developed a spatially-explicit, individual-based population model (described in Heinrichs et al., 2010) based on 15 years of field data from a population of the Ord's kangaroo rat in southeastern Alberta, Canada. Patch sizes, qualities, and locations were mapped, and groups of habitat patches were iteratively removed based on a factorial combination of attributes. The resulting changes in landscape characteristics were measured and the risk of regional population extinction was quantified. Landscape- and patch-level habitat variables were ranked using Cox proportional hazards models.

Study system

The Ord's kangaroo rat is the only species of kangaroo rat that occurs in Canada, and it is endangered by its small population size and dramatic fluctuations, geographic isolation, and rapid loss and degradation of natural habitat (COSEWIC, 2006). The distribution of this northern population of kangaroo rats is limited to one small region (cluster of active sand dune complexes) in south-eastern Alberta and south-western Saskatchewan (COSEWIC, 2006; Fig. 1).

Natural habitat for this species consists of actively eroding sand dunes, as well as partially-stabilized sand dunes where encroaching vegetation limit the amount of open sand. Kangaroo rats also inhabit sandy soils exposed by human activities (Gummer, 1997; Bender, Gummer, Dzenkiw, & Heinrichs, 2010; Kaufman & Kaufman, 1982; Nero & Fyfe, 1956; Smith & Hampson, 1969; Stangl, Schafer, Goetze, & Pinchak, 1992), including the margins of sandy roads and graded fireguards (i.e., firebreaks COSEWIC, 2006). Road margin habitats have more densely compacted soils, colder soil temperatures, and lower overwinter survival rates among kangaroo rats, compared to natural sand dune habitats (Teucher, 2007). Road margins and fireguards are also subject to frequent disturbance from human activities (e.g., vehicle traffic, grading), are often dominated by invasive plant species that may influence diet composition of kangaroo rats, and impose greater risk of predation and parasitism of kangaroo rats than natural habitats (Teucher, 2007). Although roads may facilitate movement along a linear corridor (COSEWIC, 2006), they may also direct movement away from natural habitats including sand dunes (Heinrichs et al., 2010). To a lesser extent, kangaroo rats also inhabit other natural, exposed sandy soils (such as steep valley slopes). Kangaroo rats do not typically occupy stabilized sand dunes (Kenny, 1989).

Discrete patches of natural and anthropogenic habitats (and associated roads) are embedded in a largely homogeneous unsuitable matrix; therefore, we did not map matrix heterogeneity or explicitly model movement responses to matrix elements.

Habitat removals

We identified individual patches of habitat for kangaroo rats based on a habitat-occurrence model (Bender et al., 2010; see