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Habitat degradation and loss as key drivers of regional population extinction

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ABSTRACT

Habitat quality is a fundamental driver of species distributions and population outcomes but is often difficult to measure and compare alongside measures of habitat amount and fragmentation. Consequently, habitat quality is often omitted from many landscape-level habitat analyses or more indirectly or subjectively represented in resulting habitat management or conservation planning. Yet, the implications of this conceptual and planning omission are poorly understood. We lack general theory that identifies the conditions under which habitat quality is expected to play a vital role in characterizing local and regional population responses. Using a factorial simulation design, we examined the independent contributions of habitat quality, amount, and fragmentation to population persistence to identify the conditions under which habitat quality might be expected to play a more important role than those of habitat amount or fragmentation. We generated a wide range of fractal landscapes, independently varying in habitat amount, fragmentation, and quality in QRule. We simulated interactive animal movement, habitat selection, and persistence for r and K strategist species with short and long dispersal abilities using spatially explicit individual-based models developed in HexSim. Population abundance and extinction risk were recorded through time for each landscape-species combination and used to quantify the relative influence of habitat amount, fragmentation, and landscape quality on population outcomes. We found that habitat degradation influenced extinction risk through a wide range of landscape conditions and species attributes. The most severe extinction responses were observed in scenarios of combined habitat loss and degradation, suggesting that the interactive effects of these variables may greatly affect persistence. Landscape quality modified extinction risks associated with habitat amount-fragmentation thresholds, and we found evidence for quality-based extinction thresholds as habitat was degraded. The strength of landscape-level quality on extinction risk outcomes suggests that habitat degradation should be further investigated as a major driver of population responses to landscape change. A more inclusive paradigm may be required to elucidate the general influences landscape change on population extinction. Habitat degradation, along with habitat loss and fragmentation, should be explicitly considered when assessing the implications of landscape change on population extinction.

1. Introduction

Habitat loss, fragmentation, and habitat degradation threaten population persistence and biodiversity (Fischer and Lindenmayer, 2007), yet we know little about the relative influences of these three processes. Habitat loss and fragmentation are often cited as the primary threats to population persistence (e.g., Fahrig, 1997) and much research has sought to determine the relative importance of these processes on population size or extinction risk (e.g., Andrén, 1994; Fahrig, 1997; Flather and Bevers, 2002; With and King, 1999). The role of habitat quality has been largely neglected in landscape-level studies (Mortelliti et al., 2012). Yet, if habitat quality is defined by habitat properties (i.e., resources or conditions) that have an effect on individual or population survival and fecundity (e.g., Hall et al., 1997), it should be expected that quality plays a role in population distributions and outcomes (Mortelliti et al., 2010), particularly when quality is spatially autocorrelated (Schooley and Branch, 2007). Indeed, when patch-level quality has

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been explicitly examined against patch size or isolation, habitat quality is often found to be a key driver of population responses (Jaquiery et al., 2008; Mortelliti et al., 2014; Ovaskainen and Hanski, 2001; Prugh et al., 2008; Wiegand et al., 2004; Wilson et al., 2009; With, 2004).

The exclusion of habitat quality from many landscape-level habitat analyses likely results from the difficulty in measuring habitat characteristics and reliably associating those conditions with demographic outcomes. Habitat quality is often multi-faceted, affecting multiple population outcomes (e.g., survival and reproduction), difficult to directly describe with remotely sensed imagery and evaluate alongside measures of habitat amount and fragmentation (Johnson, 2007). Consequently, habitat quality is often omitted or more subjectively represented in habitat management or conservation planning. As the implications of excluding habitat quality from landscape-level responses of species to habitat change are poorly understood, a more complete understanding of the relative influence of habitat quality has value for landscape ecology and the management of landscapes for species conservation (Mortelliti et al., 2010).

Habitat quality is likely to be important under some conditions; however, we know little about the circumstances under which the influences of quality supersede those of habitat quantity and configuration habitat (Mortelliti et al., 2010). Patch-level studies are increasingly examining the role of habitat quality; however, but we lack general theory and hypotheses describing the influences of habitat quality on landscape-level population responses to landscape conditions. Disentangling the general influences of habitat quality, amount, and fragmentation on population outcomes such as persistence will help in prioritizing data collection and implementing effective actions that are targeted at the most threatening processes (Mortelliti et al., 2012).

1.1. Habitat influence expectations

Landscape-level studies that have separated out the effects of habitat amount and fragmentation generally conclude that habitat amount is the key factor driving distribution patterns (Mortelliti et al., 2010; Radford and Bennett, 2007; Trzcinski et al., 1999; Villard et al., 1999). Despite variation in results due to modeling approaches and population viability measures, it is also generally agreed that habitat amount better predicts population persistence (Fahrig, 1997; Fahrig, 2003; With, 2004). Habitat loss reduces the total amount of suitable habitat, and if all else is equal, decreases the population size by limiting the capacity of the landscape to support individuals. As smaller populations are subject to greater risk of extinction via stochastic events (Gaggiotti and Hanski, 2004), regional populations are expected to persist longer in landscapes with more habitat.

The effects of fragmentation per se (which involve the breaking apart of habitats) are generally characterized as being secondary to habitat amount on population outcomes (Mortelliti et al., 2010; Radford and Bennett, 2007; Trzcinski et al., 1999). Yet the level of habitat fragmentation is expected to substantively influence population outcomes in landscapes composed of low habitat amounts (Fahrig, 1998, 1997; Flather and Bevers, 2002; Villard and Metzger, 2014). Where habitat is limiting, habitat loss and fragmentation interact to produce smaller more isolated patches, resulting in greater rates of local extinction (Fahrig, 2002; Fahrig, 2003). Habitat fragmentation can also affect the capacity of the landscape if habitat fragments become too small to support individual or group ranges and may also affect population size if the configuration of habitats (independent of habitat loss) limits the distribution of the population.

While less of a prominent concern, habitat degradation may be a more serious conservation issue for some species and systems (Doak, 1995). Habitat degradation is often a slow transformation from optimal to sub-optimal habitat, wherein habitat quality is reduced and habitats are less able to provide the appropriate conditions (i.e., resources) for individual survival and population persistence (Hall et al., 1997). All else being equal, lower quality landscapes have fewer or less valuable resources (e.g., food, shelter, cover) than higher quality landscapes and should have increased risks of extinction. In lower quality habitats, range sizes may need to increase to meet individual resource needs and the larger movement distances required to find unoccupied habitat may be too great to avoid fitness consequences. Hence, coarse-grained differences in the density or value of resources among landscapes could be expected to translate into differences in capacity and ultimately, extinction risk. As habitat quality affects the potential capacity of the landscape to support individuals, we expect habitat degradation influences to be evident over a wide range of habitat amounts and levels of fragmentation, in contrast to isolation effects which are primarily of interest at low amounts of habitat (Fahrig, 1997). Landscape-level studies that have included habitat quality support this variable's importance in predicting regional population size (Wiegand et al., 2005) and extinction risk (Klok and De Roos, 1998). However, we still know little about the relative influence of habitat degradation and the circumstances under which quality is important to explicitly consider. Further, the potential influences of habitat degradation have yet to be studied from a spatially-explicit perspective over a range of habitat qualities, and examined across a broad range of organisms.

Habitat loss, degradation, and fragmentation often co-occur in landscapes and may interact under specific conditions to produce disproportionately large risks of extinction. Threshold population responses may arise from mechanisms that result in the under-occupancy or reduced productivity of habitat patches. For example, habitat loss results in larger inter-patch distances and reduced dispersal success. When combined with degradation which can limit resources, trigger density-dependent emigration, or reduce vital rates, smaller and more geographically limited populations may result in disproportionately large risk of extinction. Extinction thresholds have been observed in studies of habitat loss and fragmentation (Swift and Hannon, 2010). Here, we extend this parameter state-space to include habitat quality and examine population outcomes for indications of quality-related extinction thresholds and quality-induced shifts in previously observed amount-fragmentation thresholds.

1.2. Approach

To aid in extending general landscape-level hypotheses to include the influences of habitat quality, we constructed a spatially explicit individual-based model system to simulate regional population responses to a range of landscape attributes. We examined extinction risk responses to factorial combinations of a broad range of habitat amounts, fragmentation, landscape quality, organism life history strategies (r vs. K selected), and dispersal distances. In doing so, we sought to provide insights into the (1) relative influences of habitat amount, degradation, and fragmentation in model systems, (2) range of conditions under which landscape-level quality may be influential and important to explicitly consider, and (3) identification of extinction thresholds influenced by habitat degradation. We expected habitat quality to exert a substantive influence on extinction risk and to outweigh the effect of fragmentation in many circumstances. Further, we expected degradation to influence extinction risk through much of the parameter space and the influences of habitat quality and quantity to be somewhat substitutable (as in Griffen and Drake, 2008).