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Modeling the effect of habitat selection mechanisms on population responses to landscape structure

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ABSTRACT

Novel habitats can become ecological traps for mobile animals if individuals consistently select them over habitats with better fitness consequences. Due to challenges with the measurement of habitat selection and quality, ecological traps are difficult to study in the field. Previous modeling approaches have overlooked the importance of selection cues as a key component in the mechanisms giving rise to ecological traps. We created a spatially explicit, individual-based simulation model to evaluate the effects of landscape structure on population dynamics of a hypothetical species under two mechanisms of habitat selection. In *habitat-based* selection, individuals preferred high-quality patches (leading to adaptive outcomes), selected patches at random (equal-preference) or preferred lower-quality patches (severe ecological traps). In *cue-based* selection they chose based on a structural attribute that was not directly related to fitness (canopy cover). We applied the model to the case of resident birds in landscapes composed of remnant forests and shade coffee agriculture. We designed simulation experiments with scenarios varying in landscape composition, configuration, search area and criteria for habitat preference. While all factors affected population size and individual fitness, the most important variables were proportion of high-quality habitat in the landscape, criteria for habitat preference and their interaction. The specific arrangement of habitat patches and search area had weaker and sometimes unexpected effects, mainly through increasing outcome variance. There was more variation among scenarios when selection was *habitat-based* than *cue-based*, with outcomes of the latter being intermediate between those of adaptive and equal-preference choices. Because the effects of ecological traps could be buffered by increasing the amount of high-quality habitat in the landscape, our results suggest that to truly understand species adaptation to habitat transformation we must always include landscape context in our analyses, and make an effort to find the appropriate scales and cues that organisms use for habitat selection.

1. Introduction

Habitat selection is one of the most important biological processes linking individual behavior with species distribution (Jones, 2001; Lima and Zollner, 1996). Early models of habitat selection made the simplifying assumption that organisms possessed perfect information about habitat quality (Fretwell and Lucas, 1969; Pulliam, 1988). However, mobile animals living in landscapes that have gone through widespread, rapid environmental change, may have less reliable information than those remaining in their original habitats (Battin, 2004; Schlaepfer et al., 2002). Ecological traps arise when individuals indirectly assess habitat quality through cues that become uncoupled from the ultimate fitness consequences they experience after choosing that particular habitat (Remes, 2000; Stamps and Krishnan, 2005). The mismatch between cues and quality leads animals to consistently select unfavorable habitats (ecological traps), and/or to avoid favorable ones (undervalued resources or perceptual traps) (Gilroy and Sutherland, 2007; Patten and Kelly, 2010). The population consequences of these processes differ substantially from those of classic source and sink systems; where unfavorable habitats are only occupied when favorable habitat is either not available or not cost-efficient for a particular individual (Loehle, 2012; Pulliam, 1988; Robertson and Hutto, 2006). While there is general agreement on the potential evolutionary and conservation relevance of this phenomena, knowledge of what makes species vulnerable to traps is constrained by the difficulty in estimating true measures of habitat preference and quality at the appropriate spatial and temporal scales (Battin, 2004; Robertson and Hutto, 2006; Shustack and Rodewald, 2010).

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With ecological modeling, researchers are able to create scenarios where landscape structure is varied systematically while directly testing hypotheses about the interactions between habitat availability, selection, occupancy, and quality (Battin, 2004; Dunning et al., 1995; Pulliam and Danielson, 1991). Modeling has been increasingly used to evaluate the role that habitat selection plays in species adaptation to heterogeneous landscapes, and recently emphasis has been placed on: (1) modeling habitat attractiveness and quality separately to allow for the existence of ecological and perceptual traps (Delibes et al., 2001; Donovan and Thompson, 2001; Fletcher et al., 2012; Kokko and Sutherland, 2001; Kristan, 2003; Shustack and Rodewald, 2010), or (2) incorporating more realistic behavioral assumptions, movement rules and selection constraints to population models (Aarts et al., 2013; DeCesare et al., 2014; Loehle, 2012). Models of ecological traps have matured from comparing population responses to the proportion of sink habitat under different types of preference (Delibes et al., 2001), to incorporating details in their parameterization of habitat quality (Donovan and Thompson, 2001; Kristan, 2003), including life history characteristics and evolution (Kokko and Sutherland, 2001), taking into account differences in individual quality (Shustack and Rodewald, 2010), and differentiating ecological traps according to their origin (Fletcher et al., 2012). None of the models directly assessing ecological traps have been spatially explicit and, therefore, they do not incorporate movement rules or behaviors which may be important to generate realistic patterns (Matthiopoulos et al., 2005; Nakayama et al., 2011; Stephens et al., 2002).

Habitat selection functions in previous models vary according to their specific research aim, but habitat choice has predominately been modeled as individuals selecting among habitat categories. This overly simplistic mechanism may not be readily applicable to populations existing in mosaics or landscapes with habitat gradients (Kristan, 2003). For habitat selection to become maladaptive either selection cues have to make a lower quality habitat more attractive, habitat suitability has to decrease while cues stay the same, or both processes can happen simultaneously (Robertson and Hutto, 2006). By a combination of these mechanisms, novel, man-made habitats can become two different types of ecological traps for highly mobile habitat generalists: equal-preference traps arise when the animal is equally likely to settle in the higher and lower quality habitats whereas severe traps arise when animals favor the lower quality sites (Robertson and Hutto, 2006; Robertson et al., 2013). Given these mechanisms for the appearance of ecological and perceptual traps, we propose that model realism will improve by allowing individuals to use structural attributes that are distributed continuously throughout the landscape as selection cues. Further, we suggest that shifting the focus of model results from long-term effects on population persistence to trends in habitat-specific demography will better match known empirical cases of ecological traps (Battin, 2004; Fletcher et al., 2012).

We created a spatially explicit and individual-based model to explore the effect of habitat and cue-based selection mechanisms on population responses to landscape structure. To explore the consequences that proposed mechanisms for the appearance of ecological traps have in a wide range of ecological contexts, it was necessary to assess the importance of interactions between variables occurring at two very distinct scales: the individual and the landscape level (Lima and Zollner, 1996). Therefore, our model system is one where a mobile animal is present in two habitat types of which one is better quality (source) than the other (sink), but where individuals have innate habitat choice behaviors that cannot be modified after landscape change. We designed two types of choice algorithms: (1) selection based on the habitat type of the cell, from now on called *habitat-based selection*, allowed individuals to either prefer sources over sinks (adaptive selection), show no habitat preference (equal-preference traps), or constantly prefer sinks over sources (severe ecological and perceptual traps); and (2) selection based on an internal characteristic of the cell, from now on called *cue-based selection*, allowed individuals to prefer sites having values for a structural attribute that were equal to or larger than a predetermined threshold, assuming that higher threshold values would result in better differentiation of the habitat types and therefore on more adaptive outcomes.

We chose resident forest birds using shade coffee as the system to parameterize the model because despite the fact that these tropical agroforestry systems stand out for retaining important elements of native biodiversity (Moguel and Toledo, 1999; Perfecto et al., 1996; Philpott et al., 2007), the possibility remains that they function as ecological traps for species with broad habitat requirements (Komar, 2006; Sekercioglu et al., 2007). Whether traps exist or not in the system, and what consequences they could have for the apparent balance between agricultural profit and biodiversity conservation, remains unanswered because with a few exceptions (Cohen and Lindell, 2004; Graham, 2001; Lindell and Smith, 2003; Sekercioglu et al., 2007), studies have either focused on migrants and/or species presence and detection rates as indicators of habitat suitability (Komar, 2006; Sánchez-Clavijo et al., 2008). While this model complements, and is partly based on, ongoing field research trying to address some of these issues (Sierra Nevada de Santa Marta, Colombia); it is still a highly simplified representation of a bird population in our study system, so parameter values were a mix of field and theoretical data. The structure was designed so that it can also be easily adapted to further explore this and other systems.

We designed simulation experiments where we varied landscape structure (composition and configuration) and behavioral rules (habitat preference and search area) to: (1) address which of these four factors (and their interactions) had a larger effect on fitness (measured as population and mean individual size); (2) compare the patterns produced by different levels of *habitat-based* and *cue-based* selection; and (3) compare emerging patterns of population size between simulations with local and global dispersal. We anticipated that all else being equal, more high-quality habitat, less complex landscapes with larger habitat patches, greater search areas, and adaptive or strict *cue-based* selection criteria would lead to faster occupancy of forest, larger individuals, and larger population sizes.

2. Methods

2.1. Model description

We describe here only the general behavior of the model (for a detailed description following the ODD protocol for agent-based models (Grimm et al., 2006; Grimm et al., 2010) see Appendix A). The modeling sequence consisted of three initialization procedures (landscape generator, initial population, and colonization) followed by a yearly cycle of breeding, survival, census, and dispersal (Fig. A.1). Habitat preference criteria were fixed throughout each simulation and for all individuals, while the outcomes from occupying a particular patch changed yearly through habitat-dependent functions. We assumed that forest, being the original habitat, would represent the source for our hypothetical species, while shade coffee, being the novel one, would represent the sink. Percent canopy cover was the shared structural characteristic that individuals used for cue-based selection. All code was written and executed in MATLAB version R2013b (The MathWorks, Inc. 1984–2013).

Landscape generator – the simulation environment was a bounded square grid, made of cells of equal area that represented individual breeding territories. Landscape size was specified as 400 cells, all of which started out as forest. At the beginning of each