



Insights for managers from modeling species interactions across multiple scales in an idealized landscape



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ABSTRACT

In recent years there has been a shift in biodiversity efforts from protected areas to one of interlinked habitat patches across multiple land tenure types. Much work remains on how managers can intervene in such systems to achieve basic goals. We use an agent-based model of a metapopulation with predator–prey dynamics and density-dependent migration to examine theoretically the capacity of a manager to modify the ecosystem to achieve conservation goals. We explore management strategies aimed at maintaining one of two goals – local or global coexistence of species. To achieve their goal, the manager varies the connectivity between patches based on one of three strategies – the monitoring of predator, prey, or the vegetation carrying capacity of the patches. We find that strategies that lead to highest coexistence monitor mid-tier populations globally. Our goal is to use our model results to advance decision-making in conservation beyond protected areas, typical in today's conservation.

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1. Introduction

The effects of industrialization, urbanization, agriculture, and other indicators of a growing economy play an ever-growing role in the increasing fragmentation of landscapes (Hobbs et al., 1990; Meyer and Turner, 1992). In truth, these anthropogenic forces have been the main drivers of fragmentation in recent times. As a result, when considering the optimal management of wildlife, conservation biologists and environmental managers know they must look away from simple heuristics for managing single species in a specific place to the complex challenge of managing several fragmented populations across a patchy landscape (Bunn et al., 2000; Fuller and Sarkar, 2006; Foltête et al., 2012). Indeed, a change in the nature of the problem regarding restoration and conservation has also brought about a change in the possible management tools and possibilities with which to deal with the problem accordingly. In the past, one of the more common approaches in species conservation relied upon the designation of

certain key habitats for species welfare as enclosed, protected areas where species management and surveillance took precedence. However, with the hardships often imposed on local communities that came from the designation and accumulation of protected areas (Brockington et al., 2008), the need for protecting the enclosed area against human encroachment (Child, 2004), and both global and regional climate change threatening isolated, local species populations, most conservationists have begun to explore more dynamic forms of management across a broader, multiple use landscape. Rather than restricting species in an attempt to shelter them from the possible threats that come with a changing landscape, managers now work to aid species dispersal within protected areas as well as, more expansively, along corridors spanning land tenure types with varying levels of management and different types of goals (Hobbs et al., 1990; Beier and Noss, 1998; van Aarde and Jackson, 2007). This alternate form of management comes in many forms and names including corridor management, large-scale conservation, or transboundary conservation (Hilty et al., 2006; Schoon, 2008; Soulé and Terborgh, 1999a,b).

Corridors to link previously separated habitat patches and create large-scale reserve networks have become increasingly popular with implementation projects ranging from explicitly linked and coordinated management in transboundary protected areas (Schoon, 2008), large landscape conservation networks like

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Yellowstone to Yukon (Soulé and Terborgh, 1999a,b), and collaborative management programs and modeling experiments with emphasis on connecting multiple land tenure arrangements (Letourneau et al., 2012; Zerger et al., 2011). These projects partner governmental agencies, NGOs, and private citizens and attempt to better match the scale of management to the scale of the ecological dilemmas being confronted, such as firescapes (York and Schoon, 2011), species dynamics (Soulé and Terborgh, 1999a,b), and biodiversity loss (Lewis et al., 2011; Langpap and Kerkvliet, 2012).

Conservationists believe that giving species the freedom to move between patches of fragmented landscape increases their chances of dealing with problems of resource scarcity and climate heterogeneity—initially leading managers to believe that increased connectivity was essential for species persistence. An increase in connectivity, besides aiding species dispersal through an otherwise disconnected system, however, may also provide conduits for the spread of disease or pest species through a system (Hess, 1994). Clearly, most conservationists and land managers understand this threat. What is not intuitively obvious is that there is a more fundamental reason for the eventual deleterious effects of increased connectivity that has to do with multiple species interaction. For example, in models of tri-trophic species interactions on simple networks, coexistence initially increases with increased ease of movement between habitat patches (Salau et al., 2012). However, as connectivity continues to increase, there are decreasing improvements to coexistence until a maximum level of likely coexistence is reached. Beyond this point, increasing connectivity between patches reduces the likelihood of coexistence.

The challenge lies in converting these findings from a simple model into useful information for managers confronting the complexities of reality. What these models do is rephrase the questions that we ask and the types of decisions confronting managers. Managers are not confronted with simple all-or-nothing, binary decisions. Instead, managers must try to maintain intermediate levels of connectivity between habitat patches by means of improving habitat, securing water and food sources, and coordinating across tenure boundaries to open pathways between patches and, in the process, expand available habitat. However, empirical data availability is often null or very scarce for multiple trophic systems and even then is often for only single snapshots in time. The scarcity or nonexistence of data renders validation and calibration of models aimed at aiding management of complex predator–prey interaction on fragmented landscapes deserving of extensive future research (as explained in Perez and Dragicevic, 2010). This work is a first step in that direction. The work we propose abstracts from specific species and landscapes and attempts to do four things. First, it makes sense of the ecological results and what it means to switch from binary decision-making to thinking about a continuum of landscape connectivity. Second, it helps the manager understand the type of information that can help guide this decision-making. Third, it compares management decisions made locally (from the perspective of a single land tenure patch) with decisions made at a larger-scale. Finally, it shifts the nature of the decision-making from a single point in time on a near-equilibrium static landscape to a mindset of adaptive management in a dynamic, non-equilibrium environment (Fontaine, 2011). In other words, the goal of this paper is to start bridging the gap between theory and practice with respect to the complexity of corridors and corridor management on species coexistence. It tries to provide examples of models and tools that can begin to augment the simplified heuristics currently employed. Managers need to be aware of scale effects (i.e. local vs. global objectives) and what species (or trophic levels) to monitor so as to reduce monitoring costs.

This study aims to provide some theoretical insight into these tasks by adopting an agent-based models (ABM) framework to

better understand the natural system based on the interactions of prey and predator individuals on interlinked habitat patches. In the model, a manager can increase or decrease the ease of movement between habitat patches based on feedback received from the system with a goal to maintain biodiversity (the coexistence of the two species modeled) at either a patch-level or a network-level. The current version of the model focuses on a system of two nodes. While this is a simpler landscape than that faced by most managers in reality, we start with this model as a means to understand how management decisions on monitoring and strategy selection affect outcomes in a simplified world. We revisit this simplification in the discussion and conclusion. The article proceeds with the methodology that will explain how theoretical scenarios were converted into a model (see also the accompanying modeling protocol). The results from the model help to explain the interesting phenomenon of intermediate connectivity and how managers can improve decision-making based upon monitoring different types of information. The discussion compares decision-making at two different scales, which support current efforts to move to more collaborative, larger-scale landscape management. The conclusion revisits the concept of shifting from static viewpoints to the need for adaptive management in a dynamic world as well as the desire to move from a theoretical, modeled landscape to real-world decision-making with real-world data.

2. Methods

A large number of existing analytical and agent-based models (ABM) place emphasis on how a single species is affected by fragmentation (Urban and Keitt, 2001; Fahrig and Nuttle, 2005; Bodin and Norberg, 2007). Other work on fragmented landscapes focus on the persistence of interacting populations using random diffusion (i.e. at every time-step each individual of a species has a certain probability to move to a neighboring patch) as a dispersal mechanism (Cuddington and Yodzis, 2000; Droz and Pekalski, 2001; Hovel and Regan, 2008; Wilson, 1998). The literature does not sufficiently address some fundamental components of the relationship between species and landscape such as the interaction of multiple agents and the corresponding density-dependent effects on dispersal, differing propensities for action across multiple interacting populations, and individual-level diversity. We believe that in the context of social–ecological systems, the ABM framework allows for a more plausible representation of reality and may very well lead to a better understanding of corridor ecology, allowing the building of plausible scenarios, and consequently improved strategies for landscape management. ABMs can incorporate stochasticity in the form of measurement error, event uncertainty and rare phenomena that conservationists and managers are sure to encounter (Holling, 1998). Additionally, ABMs enable the modeling and tracking of management decisions over long time periods and facilitate decision-making experimentation across various scenarios of species interaction, feedback loops, diverse landscapes, and adjusting for various types of perturbation. In effect, ABMs allow for experimentation in the early stages of adoption of an adaptive management regime.

This study draws upon a compilation of work in which we developed an ecological model of predator–prey dynamics on a patchy landscape (Salau et al., 2012; Baggio et al., 2011). The model portrays a tri-trophic (vegetation, prey and predator) two-patch metapopulation model. The connection between the two patches represents the ease of movement for two species (a predator and prey) on the landscape between habitats. Predators and prey reproduce, die, and move across the landscape according to predetermined rules. Predators hunt and kill prey prior to consumption. The carrying capacity of the patches is dynamic and based on the abundance of residing prey and their associated impact on vegetation. A manager is able to alter the connection between patches in order to hinder or facilitate movement. In this study, the management objective is always to maximize the time that predator and prey coexist. Fig. 1 provides a flow diagram of the model described. Detailed explanation of the model, variables used, parameterization and specific functions are reported in the Supplementary material. Detailed explanation of the model and the code outline are archived on <http://www.openabm.org/model/3241/version/2/view>. The following sections will thus attempt to explain the model for a more general audience. Appropriate referrals to the Supplementary material are made throughout the section for the interested reader.

2.1. 2-Patch landscape

The landscape is portrayed as two distinct, but connected, habitat patches (shown in Fig. 2). Each habitat patch is characterized by a given level of vegetation that represents its ability to sustain prey population. The connection between the two patches is characterized by an attribute that represents the difficulty/ease with

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