Ecological Modelling 242 (2012) 81–91

Contents lists available at SciVerse ScienceDirect

Ecological Modelling

journal homepage: www.elsevier.com/locate/ecolmodel

Varying effects of connectivity and dispersal on interacting species dynamics

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ARTICLE INFO

Article history:
Received 4 September 2011
Received in revised form 12 April 2012
Accepted 14 April 2012
Available online 6 July 2012

Keywords:
Landscape fragmentation
Habitat connectivity
Predator–prey
Agent-based model
Metapopulation
Density-dependent dispersal

ABSTRACT

Increased landscape fragmentation can have deleterious effects on terrestrial biodiversity. The use of protected areas, as islands of conservation, has limits to the extent of biodiversity conservation due to isolation and scale. As a result, there is a push to transition from solely developing protected areas to policies that also support corridor management. Given the complexities of multi-species interaction on a fragmented landscape, managers need additional tools to aid in decision-making and policy development. We develop an agent-based model (ABM) of a two-patch metapopulation with local predator–prey dynamics and variable, density-dependent species dispersal. The goal is to assess how connectivity between patches, given a variety of dispersal schema for the targeted interacting populations, promotes coexistence among predators and prey. The experiment conducted suggests that connectivity levels at both extremes, representing very little risk and high risk of species mortality, do not augment the likelihood of coexistence while intermediate levels do. Furthermore, the probability of coexistence increases and spans a wide range of connectivity levels when movement is less probabilistic and more dependent on population feedback. Knowledge of these connectivity tradeoffs is essential for assessing the value of habitat corridors, and can be further elucidated under the agent-based framework.

1. Introduction

Landscape fragmentation has a major impact on landscape mosaics due to normal fluctuations in climate, species growth, regrowth, colonization, and the resultant availability of resources. However, the effects of industrialization, urbanization, pollution, and other ramifications of an ever-growing economy have further exacerbated conditions leading to the increasing fragmentation of landscapes (Meyer and Turner, 1992). As a result, when considering the management of wildlife, it is necessary to adopt a systemic view, thus shifting focus from managing a single species on a full landscape to managing fragmented populations of several interacting species across patchy landscapes (Wiens et al., 1997).

Indeed, a change in the nature of the problem regarding restoration and conservation has also brought about a change in the potential management tools and possibilities with which to deal with the problem accordingly. One of the more frequently used management tools involves the designation of certain key habitats for species survival as enclosed, protected areas where species management and surveillance are priority – commonly known as a "fences and fines" or fortress conservation approach (Brown, 2002). However, with the hardships to rural communities that come about from the designation and accumulation of protected areas (Brockington et al., 2008; Brown, 2002), the cost of enforcing rules and protecting the enclosed area against human encroachment (Child, 2004), the limits to the area placed under protection, and global and regional climate change threats faced by species confined to an enclosed area, managers may benefit from exploring more dynamic and holistic forms of management (Walters, 1986). Rather than restricting species to conservation "islands" in an attempt to shelter them from the possible threats that come with a changing landscape, species dispersal should be facilitated by establishing broader, multi-use protected areas and, together with conservation corridors spanning protected areas and other types of land tenure (Beier and Noss, 1998; van Aarde and Jackson, 2007). This alternate form of management takes a broader perspective of species management beyond reserves. Such an approach has taken shape in multiple forms including the transfrontier conservation areas of southern Africa, such as the Kavango-Zambezi Conservation Area or the Great Limpopo Transfrontier Conservation Area (Schoon, 2008), the large-scale Yellowstone to Yukon Conservation Initiative, or corridor connectivity projects of the Wildlands Project (Soulé and Terborgh, 1999).

Motivated by research on metapopulations, many conservation biologists expect that giving species the freedom to move between

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http://dx.doi.org/10.1016/j.ecolmodel.2012.04.028

patches of fragmented landscape increase their chances for survival by dealing with problems of resource scarcity and climatic and other types of heterogeneity. Naturally, this leads many managers to expect species to benefit from increased connectivity. An increase in connectivity, however, besides aiding species dispersal through an otherwise fragmented system, may also favor spread of disease, pests, and/or invasive species through a system. And so, without the inclusion of these diffusive populations and processes, the effects of landscape connectivity on species conservation cannot be fully addressed. Improper modeling of the system, through the absence of key phenomena, often leads to simplistic and misleading conclusions. In addition to the threats of invasive species and disease, we demonstrate that a baseline phenomenon already exists by which the obvious tradeoffs in connectivity are observable. This behavior is interspecies interaction. The modeling of predator and prey interactions using a Lotka–Volterra framework across a patchy landscape, tracking the movement and dispersal mechanism of a mobile resource, provides insight into population dynamics that balance the different necessities of both species.

As described throughout this paper, interspecies interaction tells us that, besides the spread of pests and disease, increased connectivity also favors other mechanisms that can lead to global extinction. As a result, protected areas and corridors between them should be managed in a more adaptive way so as to maintain an intermediate level of connectivity and keep the population levels in a more stable range in the face of stochastic life events. However, adaptively managing for species conservation requires continuous assessment of criteria for landscape alteration based on possible corridor location and construction, as well as effectively utilizing feedback from population dynamics when manipulating connectivity; a difficult and daunting task. This study aims to provide some insight into the latter problem of using feedback from population dynamics to guide alterations in landscape connectivity by adopting the individual or agent-based modeling (IBM/ABM) framework and setting up the natural system as an agglomeration of prey and predator individuals on interlinked habitat patches.

A large number of existing analytical and computational models place emphasis on how a single species is affected by fragmentation (Bodin and Norberg, 2007; Minor and Urban, 2007; Urban and Keitt, 2001). Other works on fragmented landscapes focus on the survivability of interacting populations using rather simplistic dispersal mechanisms (Cuddington and Yodzis, 2000; Droz and Pekalski, 2001). In particular, this paper builds on previous work that utilized a 10-patch ABM framework (Baggio et al., 2011) that showed how increased connectivity does not benefit both predators and prey alike and hints the fact that intermediate levels of connectivity may be more beneficial for conservation purposes. Here the system is downscaled to a more tractable model with two habitat patches connected through a corridor. The modeling exercise has two goals. The first comes from how varying the threshold dispersal functions of the two species affect the optimal level of connectivity represented by the distance separating the two habitat patches. The second main goal of this study is to extend current theory by including active connectivity variation on landscapes and thus helping managers to understand existing tradeoffs regarding connectivity, and species survival. The agent-based system provides a modeling environment conducive to repeated scenario testing and the incorporation and aggregation of individual characteristics and behavior. Furthermore, ABMs can incorporate stochasticity in the form of measurement error, event uncertainty and rare phenomena (Bonabeau, 2002). By using an agent-based framework rather than a typical Lotka–Volterra (or other) deterministic model of species interaction, we gain a better representation of the stochasticity inherent in reality, which may lead to more plausible scenarios, a better understanding of system dynamics and improved strategies for landscape management.

Table 1
Summary of variables, symbols and values used in the ABM.

Symbol	Variable name	Default values for Monte Carlo runs
P	Number of patches	2
C	Carrying capacity of a patch	500
L	Number of links	1
W_{ij}	Weight of link connecting patch i to j	Varies from 5 to 305
N_x	Initial number of prey on each patch	Poisson distributed with mean 250
x_i	Number of prey on patch i at a given time-step	N/A
r	Prey reproduction rate	Poisson distributed with mean 25[a]
$D_{U,x}$	Prey density threshold affecting prey dispersal	Poisson distributed with mean 90[b]
$D_{L,x}$	Prey density threshold affecting predator dispersal	Poisson distributed with mean 30[b]
M_x	Prey movement capability	Poisson distributed with mean 30
N_y	Initial number of predators on each patch	Poisson distributed with mean 100
y_i	Number of predators on patch i at a given time-step	N/A
c	Predation rate	Poisson distributed with mean 90[a]
f	Predator reproduction rate (after predation)	Poisson distributed with mean 50[a]
d	Predator death rate	Poisson distributed with mean 6[a]
$D_{U,y}$	Predator density threshold affecting prey dispersal	Poisson distributed with mean 70[b]
M_y	Predator movement capability	Poisson distributed with mean 60

[a] The original mean values taken from Wilson (1998) are decimals. Values taken from a Poisson distribution are rescaled by a factor of 100 so random outcomes remain comparable to the original values. For example, the mean value for the predator death rate (d) is 0.06, so random values are drawn from a Poisson distributed with mean 6 and then divided by 100. Note, these mean values are rates not proportions and need not be bounded above by 1.

[b] The original mean values are proportions. Values taken from the Poisson distribution are rescaled by a factor of 100. In the event that the rescaled distribution returns a value greater than 1, the value is replaced with 1.

To summarize, this paper has two main objectives and both can be achieved through abstraction of the agents (predators and prey), simulation of the dynamical process, and documentation of the ABM outcomes. First we aim to study the role of connectivity in dictating the likelihood of coexistence among a predator and prey population. Secondly, we aim to gain insight into how the role of connectivity is affected by the suite of sigmoidal functions used to represent density-dependent dispersal in both species. Assessing the effects of inter-patch connectivity using a family of dispersal functions makes the model applicable across a range of mobile species, thus allowing for more informed decision-making when looking at establishing corridors and changing connectivity between protected areas.

2. Materials and methods

As briefly outlined above, we formulate an agent-based representation of interacting predators and prey on a heterogeneous landscape. The model is built so as to assess the role of connectivity given different dispersal functions. In the following subsections, we give a detailed description of the agent-based model implemented in NetLogo 4.1.3 by describing parameters and variables used to characterize individual predator and prey behavior. Table 1 provides a summary of agent attributes. The parameter values characterizing stochastic species birth and death events are taken