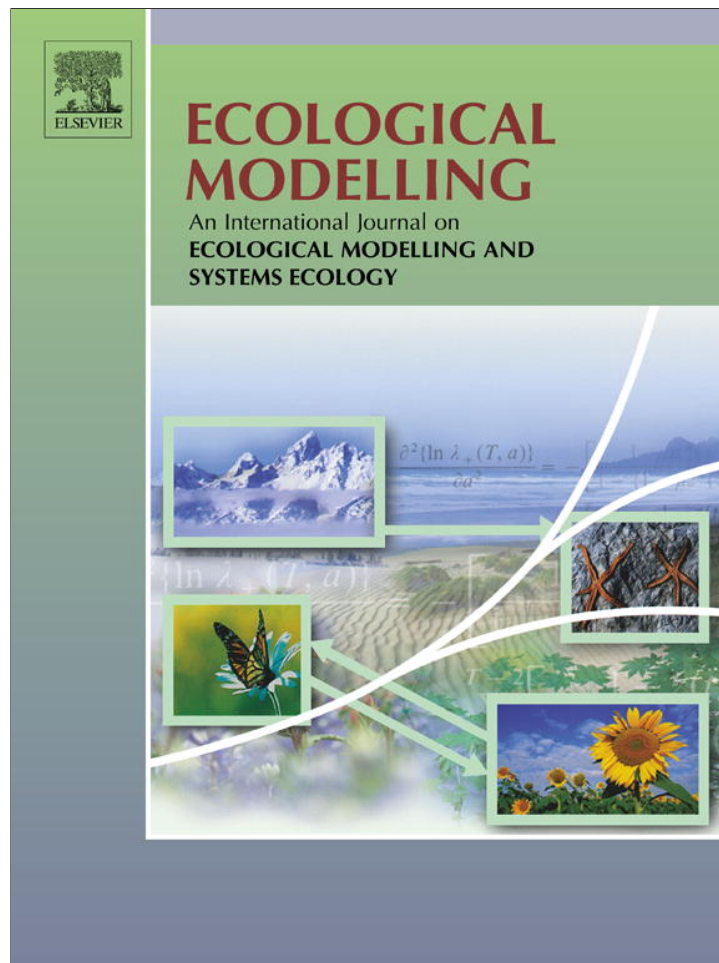


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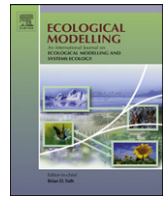
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# Ecological Modelling

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## Varying effects of connectivity and dispersal on interacting species dynamics

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### 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.

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### 1. Introduction

Landscape fragmentation has a major impact on landscape mosaics due to normal fluctuations in climate, species growth, re-growth, 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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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

**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 <sup>a</sup>
$D_{U,x}$	Prey density threshold affecting prey dispersal	Poisson distributed with mean 90 <sup>b</sup>
$D_{L,x}$	Prey density threshold affecting predator dispersal	Poisson distributed with mean 30 <sup>b</sup>
$M_x$	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 <sup>a</sup>
$f$	Predator reproduction rate (after predation)	Poisson distributed with mean 50 <sup>a</sup>
$d$	Predator death rate	Poisson distributed with mean 6 <sup>a</sup>
$D_{U,y}$	Predator density threshold affecting prey dispersal	Poisson distributed with mean 70 <sup>b</sup>
$M_y$	Predator movement capability	Poisson distributed with mean 60

<sup>a</sup>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.

<sup>b</sup>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.

better understanding of system dynamics and improved strategies for landscape management.

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

from a predator–prey modeling experiment by Wilson (1998) and those influencing dispersal are taken from Baggio et al. (2011). It is important to note that Wilson (1998) first uses species birth and death rates to model population dynamics in a deterministic, continuous-time fashion. In order to utilize deterministic rates in the proposed stochastic ABM setup, the continuous-time dynamics must be discretized; the resulting value is in the form of an exponential distribution that can then be used to represent the probabilistic measures of discrete birth and death events. Values taken from Baggio et al. (2011) already determine probabilistic events or are in the form of dimensionless proportions and need no further transformation. The functional form of all probabilities determining discrete, stochastic events will be displayed in the following subsections.

Detailed information on model development and implementation can be found in the Overview, Design concepts, and Detail (ODD) protocol write-up (Grimm et al., 2006), which is included as supplementary content. Furthermore, the ODD outline and the NetLogo code have been uploaded to the model archives of the openabm website ([www.openabm.org](http://www.openabm.org)), a large ABM repository and global forum for promoting rigorous model verification and scientific collaboration<sup>1</sup>.

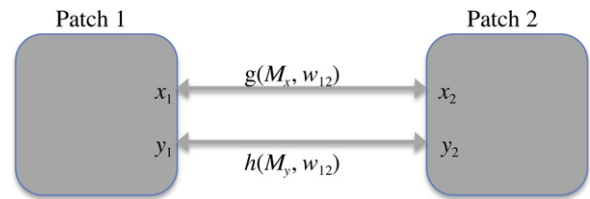
### 2.1. Two-patch landscape

The ABM developed for this study is based on the one developed by Baggio et al. (2011), however the model presented simplifies the landscape (reducing a network to two linked patches) in order to examine the interactions in more detail. The link existing between the two patches represents the theoretical cost of movement of a species (i.e. the difficulty in dispersing from one patch to another). This cost of movement is defined as the weight of the existing link ( $W_{ij}$ ), and serves as a proxy for distance and dispersive capability between the two arbitrary patches  $i$  and  $j$ . The weights mimic the difficulty/ease with which predators and prey are able to move from one patch to another; they can also be described as the cost of movement from one patch to another. Adding weights representative of movement costs to species allows for a more realistic appraisal of the existing relationship between species dispersal and connectivity. Furthermore, including weights allows for the consideration of individual variation within a single species. More precisely, some members of a species may be successful in their attempt to traverse corridors from one habitat patch to another, while others fail, thus highlighting the importance of species management between protected areas (Hilty et al., 2006). Additionally, as will be described in more detail later, the model compares several movement threshold functions in order to evaluate persistence outcomes for species with different dispersal mechanisms. The drawback of adding such intricacies as cost of movement is that it further complicates the model and increases the amount of constraints when considering manager intervention. Therefore, a two-patch, one-link model is developed and analyzed, to compensate for the level of complexity in the system under study (see Fig. 1 for an illustration of the metapopulation model). Focusing on the two-patch system allows for a key assessment of the effects of connectivity on predator–prey dynamics and generalization to metapopulations of larger scale.

### 2.2. The species

#### 2.2.1. Birth and death events

To represent the species, let  $x_i$  and  $y_i$  represent the total predator and prey population, respectively, on patch  $i$ . Individual prey



**Fig. 1.** Metapopulation dynamics. This is an illustration of the metapopulation model with two patches. Successful traversal from one patch to the other is dependent on the relative measure between the movement capability of the species and the weight of the edge (i.e.  $g(M_x, w_{12})$ ). Though there exist only one edge between the patches the two arrows signify that the measure for successful dispersal may differ between predator and prey. See Table 1 for further description of the parameters.

and predators are assigned randomly to each patch, however the initial populations of predator and prey on each patch are fixed. In each time-step, a prey agent on patch  $i$  reproduces if a number drawn from a uniform probability distribution on the unit interval (between  $[0,1]$ ) is less than the prey reproduction probability denoted  $1 - \exp[-r(1 - D_{x,i})]$ ;  $r$  is the deterministic, intrinsic growth rate of prey agents<sup>2</sup>.  $D_{x,i}$  denotes the density of prey agents on patch  $i$ ; this measure is computed as  $D_{x,i} = x_i/C_i$ , where  $C_i$  represents the carrying capacity of agents for patch  $i$ . Note that reproduction by a given prey agent is truncated by increasing prey density on its local patch. An abundant prey population leads to scarcity of resources needed for further growth. Truncation of reproduction in this way relates directly to the widely used model of logistic growth for prey species.

Prey mortality on patch  $i$  occurs as a result of predation, which is determined by the event that the prey agent is detected (proportional to the density of prey,  $D_{x,i}$ ) and the deterministic rate of predation,  $c$ . And so, successful predation occurs on patch  $i$  with predation probability,  $1 - \exp(-cD_{x,i})$ . Note that the predation event will only occur if predator and prey are located on the same patch. In the event that prey availability on patch  $i$  is small, the predation probability also suffers a decrease as the likelihood of detecting prey is reduced; this mechanism is directly comparable to type I functional response of predators in a classic Lotka–Volterra system (Holling, 1959). Predator reproduction depends on the successful capture and consumption of a prey agent and immediately occurs with the probabilistic rate,  $f$ ; this method of directly linking foraging to reproduction is consistent with most widely studied predator–prey formulations (Gotelli, 2008; Holland and Hastings, 2008; Lotka, 1925; Volterra, 1926, 1931). Natural mortality for predators occurs with some probability,  $1 - \exp(-d)$ , where  $d$  is the deterministic predator mortality rate.

#### 2.2.2. Dispersal

Species dispersal can be described using a mixture of partial random movement along with dispersal indicators dictated by some threshold population level (Kun and Scheuring, 2006; Metz and Gyllenberg, 2001; Ruxton and Rohani, 1998; Travis et al., 1999). In this study, the idea of random walks is fused with density-dependent dispersal to model species movement as a biased random walk (Nonaka and Holme, 2007)<sup>3</sup>. Movement is still random, but becomes increasingly biased, and eventually constant, as

<sup>2</sup> All successful stochastic events described from this point on are determined by drawing a random number from a uniform probability distribution on the unit interval  $[0,1]$  and checking to see that this number is indeed less than the specified probabilistic rate for a given event.

<sup>3</sup> Nonaka and Holme (2007) use the form  $\exp(-d(x,y)/\delta)$  to represent a forager's probability of moving to a patch  $(x,y)$  from a given location.  $d(x,y)$  represents the distance from patch  $(x,y)$  to the closest habitable patch with resources and  $\delta$  is a scaling factor that is positively correlated with the level of stochasticity in the forager's random walk.

<sup>1</sup> The code for the model presented and the ODD are available at the openabm site (<http://www.openabm.org/search/luceneapi.node/salau>).

some density threshold is reached. Use of a biased random walk to characterize species movement is also present in other works that incorporate species dispersal and optimal foraging (Focardi et al., 1996; Pyke, 1981; Wiens et al., 1993).

Relevant studies, stemming from analytic models of metapopulation dynamics, characterize density-dependent dispersal as a two-stage process, individual willingness to move and successful dispersal. Ruxton et al. (1997) and Silva et al. (2001) call for the incorporation of dispersal mortality into analytic, density-dependent metapopulation models as a realistic addition that may have a stabilizing effect on model dynamics. Boitani et al. (2007) does an exhaustive review of the literature for ecological network design and construction and also asserts that incorporation of species willingness to move as well as the probability of successful dispersal should be considered in models of species dynamics on fragmented landscape. Furthermore, all mathematical metapopulation models assuming density-dependent species dispersal essentially treat movement as a two-stage process as dispersal rates can often be divided into two proportions; one proportion characterizing the population density of willing dispersers and the other representing dispersal mortality (Amarasekare, 2004; Hudgens and Haddad, 2003; Sanchirico and Wilen, 1999, 2001, 2005)<sup>4</sup>.

Under a probabilistic framework, the two-stage dispersal process becomes the amalgamation of two stochastic events. This formulation, though adding another level of complexity, just converts the two-stage process into a conditional probability where the likelihood of successful dispersal is first based on the probability that an agent is willing to move and then finalized by the agent's ability to traverse the landscape (also probabilistic). This formulation has already been implemented in existing ABM studies of species dynamics and density-dependent dispersal (Bach et al., 2006; Hovestadt et al., 2010; Tang and Bennett, 2010). Since the aim of this study is to assess the joint effects of connectivity and density-dependent dispersal intensity on interacting population dynamics, we also develop and utilize a proxy for the two-stage dispersal process. The functional forms of the probabilities used to characterize the two-stage dispersal process will be presented later in the current subsection.

We assume that species movement is governed by simple rules that mimic intraspecies competition (Bartumeus and Levin, 2008) and antipredatory behavior (Creel, 2005; Fischhoff et al., 2007; Ives and Dobson, 1987; Lima, 2002; Luttbeg and Schmitz, 2000; Nelson et al., 2004) in prey, and foraging strategy (Bartumeus and Levin, 2008; Ioannou et al., 2008; Lima, 2002; Linhares, 1999) in predators. Implicit in this assumption is that both predator and prey are aware of the population immediately surrounding them (i.e. their local patch), but not global population densities. Prey and predator population densities on a patch  $i$ ,  $D_{x,i}$  and  $D_{y,i}$  respectively, are computed based on the carrying capacity,  $C_i$ <sup>5</sup>. At high densities, with respect to intraspecies competition, prey agents are more likely to move and may do so collectively as a subpopulation. At low densities, there is no scarcity of resources and so prey willingness to move becomes less of a factor and is better characterized as an isolated, random event. The same mechanism is adopted for antipredatory behavior. A small number of predators pose little or no risk to the prey population; and so prey movement becomes less biased. At

high predator densities, prey agents are, collectively, more apt to move in search of refuge.

Prey agents on patch  $i$  can determine their willingness to move between patches at each time-step with probability,

$$\begin{aligned} & (D_{x,i}/D_{U,x})^n \quad \text{if } D_{x,i} < D_{U,x} \\ & 1 \quad \quad \quad \text{if } D_{x,i} \geq D_{U,x}, \end{aligned} \tag{1}$$

indicating prey willingness to move due to intraspecies competition, or with probability,

$$\begin{aligned} & (D_{y,i}/D_{U,y})^n \quad \text{if } D_{y,i} < D_{U,y} \\ & 1 \quad \quad \quad \text{if } D_{y,i} \geq D_{U,y}, \end{aligned} \tag{2}$$

indicating prey willingness to move due to excess predation pressure. As displayed in Fig. 2 the probability of dispersing increases to the maximal limit of 1, where every prey agent is willing to move, as prey or predators population densities approach threshold proportions on the current patch  $i$ .  $D_{U,x}$  and  $D_{U,y}$  are proportional measures of intensity in resource competition and antipredatory behavior respectively; these are the two density thresholds influencing prey willingness to disperse with probability (1) and (2) respectively. If prey agents do choose to move, whether or not a maximum density threshold has been exceeded, the probability of successful dispersal to the neighboring patch must be calculated. The assessment of successful prey dispersal from patch  $i$  to patch  $j$  is determined with probability,

$$\begin{aligned} & M_x/W_{i,j} \quad \text{if } M_x < W_{i,j} \\ & 1 \quad \quad \quad \text{if } M_x \geq W_{i,j} \end{aligned} \tag{3}$$

The probabilistic rate of successful dispersal given by (3) is conditional on prey willingness to move and dependent on the weight of the traversable link between patches ( $W_{i,j}$ ) and the innate ability to move in prey ( $M_x$ ); we assume innate movement ability is constant throughout a single simulation run and equal for all agents of the same species. Unsuccessful dispersal can be interpreted as mortality via movement. A dispersing prey agent may die (assumed via movement) when the weights of the links attached to its current patch are all much larger than its innate ability to move (thereby decreasing the likelihood of successful dispersal). Additionally, a moving prey agent may be subject to dispersal mortality if the chosen patch has a prey or predator density that has already reached a density threshold<sup>6</sup>.

Willingness to move in predators is governed by a prey-related density threshold. More precisely, at each time-step a predator agent decides to leave patch  $i$  with probability,

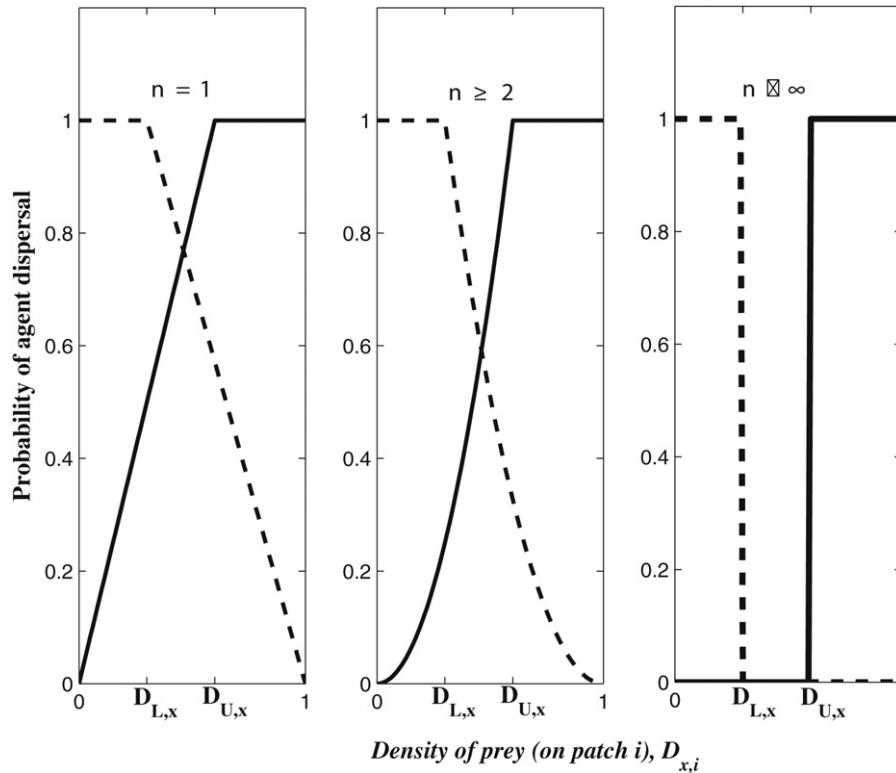
$$\begin{aligned} & [(D_{x,i} - 1)/(D_{L,x} - 1)]^n \quad \text{if } D_{x,i} > D_{L,x} \\ & 1 \quad \quad \quad \text{if } D_{x,i} \leq D_{L,x} \end{aligned} \tag{4}$$

Note, if the prey density on the current patch falls below some predetermined threshold ( $D_{L,x}$ ), predators leave patch  $i$  with proba-

<sup>4</sup> For example, using a continuous-time metapopulation model, Amarasekare (2004) characterizes the successful dispersal rate of a population,  $N_1$ , as,  $\alpha_1(N_1/K_1)^{\delta}$

<sup>5</sup> Predator population density is defined, similar to prey population density, as  $D_{y,i} = y_i/C_i$ . Note that  $C_i$  is an upperbound on the number of agents patch  $i$  can support. In general, predator agents will not attain such high amounts because growth is limited by prey abundance, predation, and the reproduction rate (see Section 2.2.1.).  $D_{y,i}$  is an underestimated proportion but remains a relatively good measure of predator abundance on patch  $i$  relative to prey numbers.

<sup>6</sup> This form of additive mortality for dispersing agents stems from the assumption that individuals willing to disperse due to proposed threats (e.g. intraspecies competition, predation pressure, etc.) are, all else equal, unfit to survive on other patches where the same pressures exist. This assumption is based on the characterization of dispersal as a strategy employed by natural agents in order to fortify their reproductive and survival capacity while escaping threats that increase mortality risk (Giske et al., 2003; McLane et al., 2011; Railsback, 2001). In any case, we have considered the effects of this assumption and verified that its incorporation does not contradict the qualitative aspects of the results to be displayed and discussed in the following sections; results of the ABM experiment with and without additive dispersal mortality can be viewed in the supplementary material.



**Fig. 2.** Threshold dispersal of prey (-) and predator (- -). The plots (from left to right) showcase the suite of dispersal mechanisms used to represent threshold dispersal in this study; spanning from *ramp* (far-left) to *Bang–bang* dispersal (far-right). The plots highlighted with solid black lines (-) represent threshold dispersal in prey agents as a function of interspecies competition (with corresponding threshold density,  $D_{U,x}$ ). The plots highlighted with dashed black lines (- -) represent threshold dispersal in predators as influenced by prey availability (with corresponding threshold density,  $D_{L,x}$ ).

bility 1 (see Fig. 2). Predators survive dispersal from patch  $i$  to some patch  $j$  with probability,

$$\begin{aligned} &M_y/W_{i,j} \quad \text{if } M_y < W_{i,j} \\ &1 \quad \quad \quad \text{if } M_y \geq W_{i,j} \end{aligned} \quad (5)$$

where  $M_y$  denotes the predator’s ability to move (also equal for all predator agents during a single rune). Dispersal mortality for predators is evaluated in the same manner as prey.

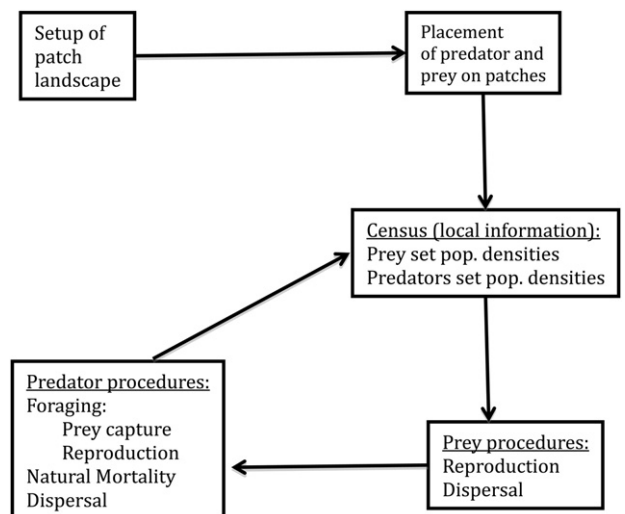
It is expected that the range of functional forms applied in this study will play an important role in gauging the effects of connectivity. We characterize the dispersal mechanism using a piecewise function with comparable shape to the Holling type- $n$  functional of the form. As we vary the parameter,  $n$ , which controls intensity in species’ willingness to move, we are able to capture a suite of dispersive behavior spanning from *ramp* ( $n = 1$ ) to *bang–bang* ( $n \Rightarrow \infty$ ) dispersal (Fig. 2). *Ramp* dispersal characterizes species movement with a high probability of occurrence before or after a threshold density is crossed (weakly biased random movement). *Bang–bang* dispersal can be characterized as strict threshold behavior where every member of a species is willing to move after some threshold density has been crossed (Baggio et al., 2011); this can be thought of as collective movement or herding behavior. The intermediate case ( $1 < n$ ), termed *half-pipe* dispersal, contains strategies that support strongly-biased random movement; this case is of particular importance in this study. The *half-pipe* dispersal mechanism maintains that with relatively low likelihood, individuals and small subpopulations can still move between patches before a threshold density is crossed. After the threshold density is crossed, all members of the species choose to disperse. The *half-pipe* dispersal mechanism captures the idea of biased random movement and, furthermore, its qualitative form may have a significant effect on the relationship

between connectivity, interspecies interaction, and predator–prey population levels.

### 2.3. Simulation

#### 2.3.1. Event scheduling

In this subsection, we give an overview of the model processes undergone during one time-step of the ABM.



**Fig. 3.** Initialization and process diagram. Portrayed is the order of events in the ABM during a simulation; this figure covers events from the initialization of the landscape to the actions of the agents.

Fig. 3 gives a pictorial representation of the processes described below. This outline will also be available under the 'model development' of the ODD protocol in the supplementary material. Process overview and scheduling is as follows:

1. The landscape is initialized first; the number of patches is fixed at two throughout all simulation experiments. A link is placed between the patches and assigned a specific weight, which stays fixed throughout a run. We assume maximum capacity is equal for every patch.
2. The initial population of prey (predators) on each patch is Poisson distributed with mean 250 (100).
3. Each individual prey and predator on patch  $i$  then internalizes local information by counting the number of predators and prey on its patch (including itself) and determining the population density values  $D_{x,i}$  and  $D_{y,i}$ . We assume that agents do not update these values until the beginning of the next time-step so as to create the idea that agents actions, especially events that are density-dependent, occur in some simultaneous fashion and no single agent receives the most current information. Also note that only agents existing at the beginning of a time-step can perform the specified procedures (e.g. reproduction, dispersal, predation) within that time-step. Thus the earliest period in which new offspring can perform a procedure is in the next time-step following birth.
4. All prey events are conducted first. During a time-step, each surviving prey agent from the previous time-step has the ability to reproduce with some density-dependent probability. After all possible prey reproduction events have occurred prey dispersal events are calculated. As discussed in the previous subsection, successful prey dispersal is a two-step process; first the agent's willingness to move from patch  $i$  to target patch  $j$  is calculated with density-dependent probability (1) or (2) and, in the event that the prey agent is willing to disperse, then it moves successfully with probability (3). Prey dispersal mortality occurs if probability (3) is not achieved, if intraspecies competition on target patch  $j$  is too great ( $D_{x,j} > D_{U,x}$ ), or if predation pressure on target patch  $j$  has exceeded prey agent limits ( $D_{y,j} > D_{U,y}$ ) – the latter two inequalities reflect additive dispersal mortality (see footnote vi).
5. Predator events begin with foraging. As long as prey agents remain on the current patch, each predator agent will successfully capture one with some probability. Following successful capture of prey, a predator agent consumes the prey and reproduces with some probability. After foraging and reproduction events, predators die naturally according to some probability. Finally, the event of successful predator dispersal from patch  $i$  to target patch  $j$  is determined using probability (4) and (5); similar to the two-stage movement process of prey. Predator dispersal mortality occurs if probability (5) is not achieved or if prey availability on target patch  $j$  is too low ( $D_{x,j} < D_{L,x}$ ).
6. Procedures 3–5 are repeated each time-step until the specified terminal time of the simulation.

Examples of coexistence and extinction dynamics are provided for two select simulation runs, denoted runs A and B, to provide some idea about the range of dynamics captured in the ABM (Fig. 4). Parameters for run A and B are determined with the same specifications given in Table 1 and differ in the magnitude of the weight between patches ( $w_{12}$  equals 80 and 50 respectively).

For different levels of connectivity, predator–prey dynamics may display high or low amplitude oscillation (see panel 4.1 vs. 4.4). Population patterns across patches (i.e. the level of synchrony) may also differ depending on model parameters. For instance, panel 4.3 of run A suggests no distinct pattern between predator dynamics in patches 1 and 2, whereas panel 4.6 of run B shows a distinct positive

correlation between both predator populations. Note that predator extinction in run B is facilitated by large oscillatory dynamics in the coupled system. Synchrony also plays a major role as a positive correlation in inter-patch dynamics reduces the occurrence of rescue effects to buffer local extinction events. Results from run A and B suggest that more connected systems may also adversely affect predator–prey persistence, but a more formal analysis on the effects of connectivity and dispersal is given in Section 3.

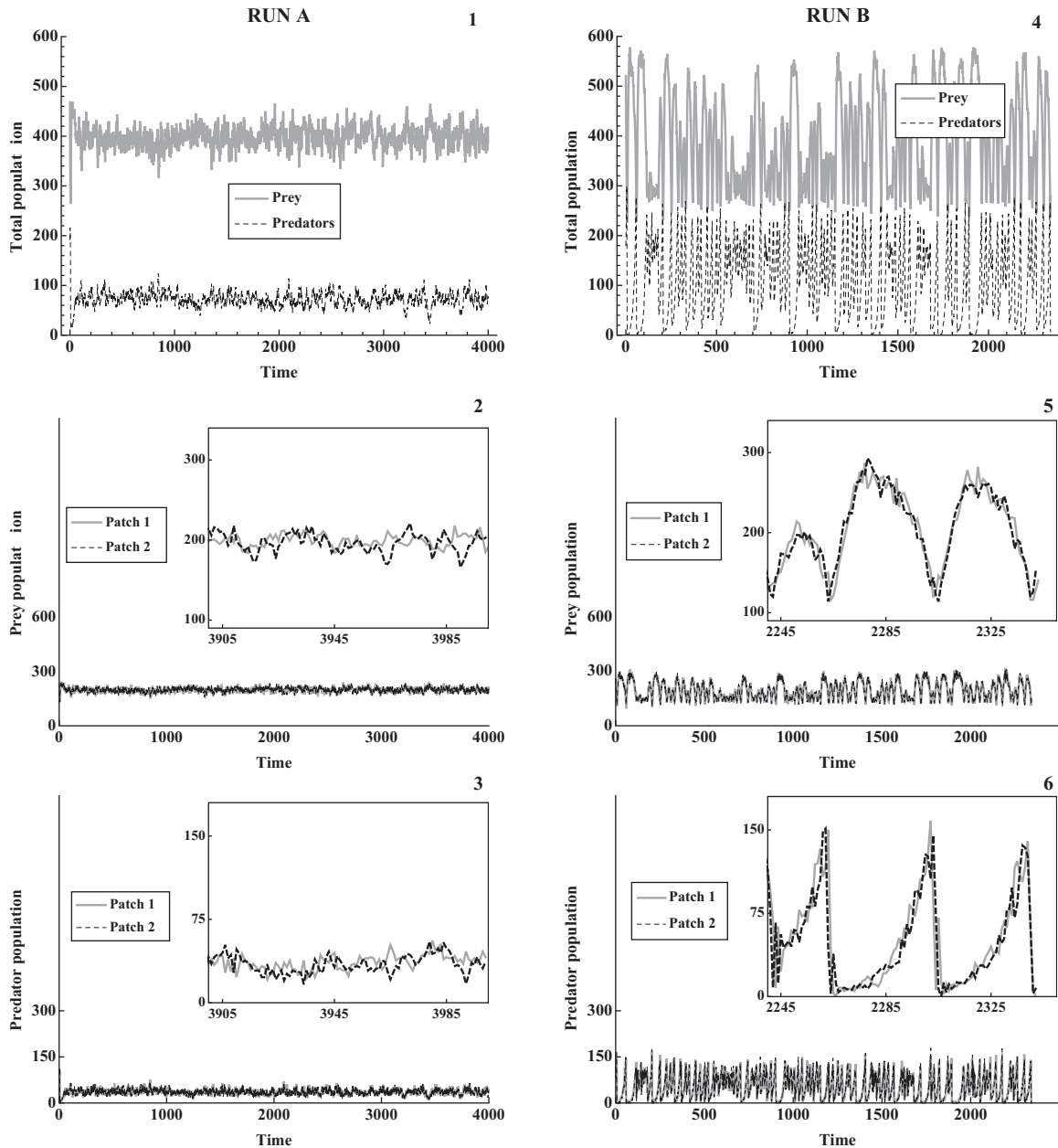
### 2.3.2. Model iteration and data collection

As described in the Section 1, we aim to study the role of connectivity in dictating the possibility of coexistence between a predator and prey population and to gain insight into how the role of connectivity is affected by density-dependent dispersal mechanisms. Both of these objectives can be addressed by varying the level of connectivity between the two patches and the magnitude of  $n$  to simulate differences in the dispersive behavior of both species. To address the issue of parameter sensitivity and ensure that the qualitative results of the ABM experiment are robust to parameter uncertainty, a Monte Carlo scheme is employed. In utilizing the Monte Carlo method, we randomize all predator and prey attributes, as well as the initial population of both species, at the start of every run by drawing values from a Poisson distribution. A specific Poisson distribution determines the value of an attribute for a given species. Refer to Table 1 for the mean values of each attribute. Carrying capacity is the only parameter not randomized during the Monte Carlo sweep as it is strongly suggested that random variation in this parameter has little effect on qualitative results so long as the experimental value is large enough to overcome demographic stochasticity (Hovestadt et al., 2010). During the experiments carrying capacity is fixed at 500 prey agents per patch, which we strongly assert is a value large enough to render demographic stochasticity a nonissue; Hovestadt et al. (2010) make the same claim with a carrying capacity value of 100 agents.

Due to the stochastic nature of the agent attributes, we compute 400 runs for each parameter combination with a fixed level of connectivity and dispersal intensity. In total, 84,000 simulations are computed to reduce the variability in model outcome. The data collected include minimum/maximum number of prey and predators per patch (updated each 100th time-step), the average number of dispersing predator and prey agents per patch, the average rate of predation pressure per patch and, in the event of extinction, the extinction time.

## 3. Results and discussion

Fig. 5 illustrates the relationship between connectivity level, dispersal mechanism, and the likelihood of coexistence for the predator and prey species. The likelihood of coexistence (on the vertical axis of all panels in Fig. 5) is calculated using the total number of runs, out of 400 simulations with a fixed level of connectivity and type  $n$  dispersal, in which the predator and prey population remain extant for over 4000 time-steps. The likelihood is measured as a probability and so it takes value between 0 and 1 with a larger value corresponding to a greater chance of coexistence between predators and prey. The horizontal axis for all panels in Fig. 5 span from 5 to 305 (high–low) and represents the connectivity between the two patches. Each panel in Fig. 5 contain plots for two consecutive values of type  $n$  dispersal ranging from  $n=1$  (panel A) to  $n=40$  (panel E). The panels encompass a wide array of half-pipe functions that approximate the transition from ramp dispersal (weakly-biased random movement) to the bang–bang case (strongly-biased). To represent bang–bang dispersal we set  $n=40$  as we find no substantive changes beyond this value.



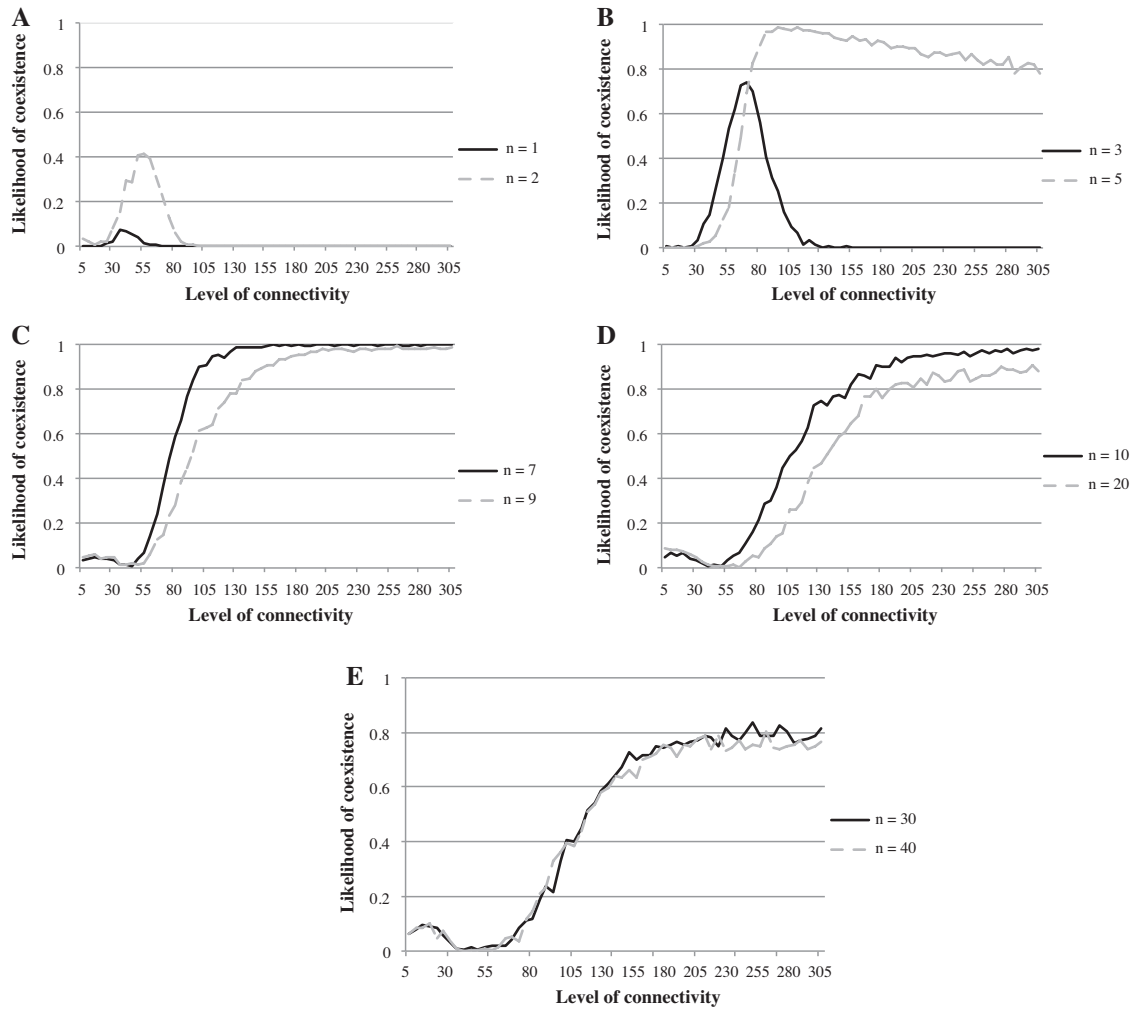
**Fig. 4.** Run A – Coexistence and extinction dynamics (*Left column*) 3 panels from a sample run of the ABM (run A), where predators and prey coexist for 4000 time-steps – the designated benchmark for long-run persistence. The parameters used in run A are in line with specifications given in Table 1, additionally,  $w_{12} = 80$  and  $n = 3$ . Data panels for run A include, (1) time series plot of the total predator and prey population, (2) time series plot of prey population on patches 1 and 2 with an inset (top right corner) of the last 100 time-steps to highlight the level of (a) synchrony in population patterns across patches, and (3) time series plot of predator population with an inset of dynamics in the last 100 time-steps. (*Right column*) 3 panels from a sample run of the ABM (run B), where predators go extinct short of the 4000th time-step, thus ending coexistence and terminating the run. The parameters used in this run are in line with specifications given in Table 1, additionally,  $w_{12} = 50$  and  $n = 3$ . Data panels for run B include, (4) time series plot of the total predator and prey population, (5) time series plot of prey population on patches 1 and 2 with an inset of the last 100 time-steps, and (6) time series plot of predator population with an inset of dynamics in the last 100 time-steps. Note that high amplitude cycling and synchrony in the coupled system are the main drivers of predator extinction in this example.

Fig. 5 displays a result that is not immediately clear from the construct of the model. For each choice of a type  $n$  dispersal mechanism, it is shown that the most favorable choice for survivability of both species on the landscape does not occur at the margins of connectivity. For each panel in Fig. 5 the likelihood of coexistence rises to a peak at a relatively intermediate level of connectivity before decreasing to zero for further increase in connectivity,  $W_{12}$ . Essentially, there are tradeoffs to increasing and/or decreasing the connectivity of a patch. These tradeoffs exist due to the interplay between foraging (resource scarcity) and evasion (prey refuge), two processes that characterize the movements of the predator and

prey. In effect, the landscape must be connected enough to allow for the foraging of both species, but also restrictive enough to allow for prey refuge and to protect against overcrowding. As a result, a landscape configuration promoting coexistence cannot be attained at the margins of connectivity.

The objectives of corridor management associate increased connectivity between patches of viable land with positive responses in the coexistence and maintenance of a larger ecosystem. While there are clear reasons for advocating connectivity (prevention of local extinctions, minimization of genetic drift, allowing for dispersal and colonization, etc.), there are equally arguments against this





**Fig. 5.** The effect of connectivity and dispersal on likelihood of coexistence. A–E represent the effects of landscape connectivity and type of dispersal mechanism on the likelihood of coexistence between predators and prey. Each panel contains two plots for differing dispersal mechanisms ( $n$ ). Panels A and B clearly show an increase and eventual decrease in the likelihood of coexistence (for  $n = 1, 2, 3, 5$ ) as connectivity is decreased. Note for  $n \geq 7$ , the likelihood of coexistence will also reach a peak, but declination is delayed and coexistence is prolonged for lower levels of connectivity.

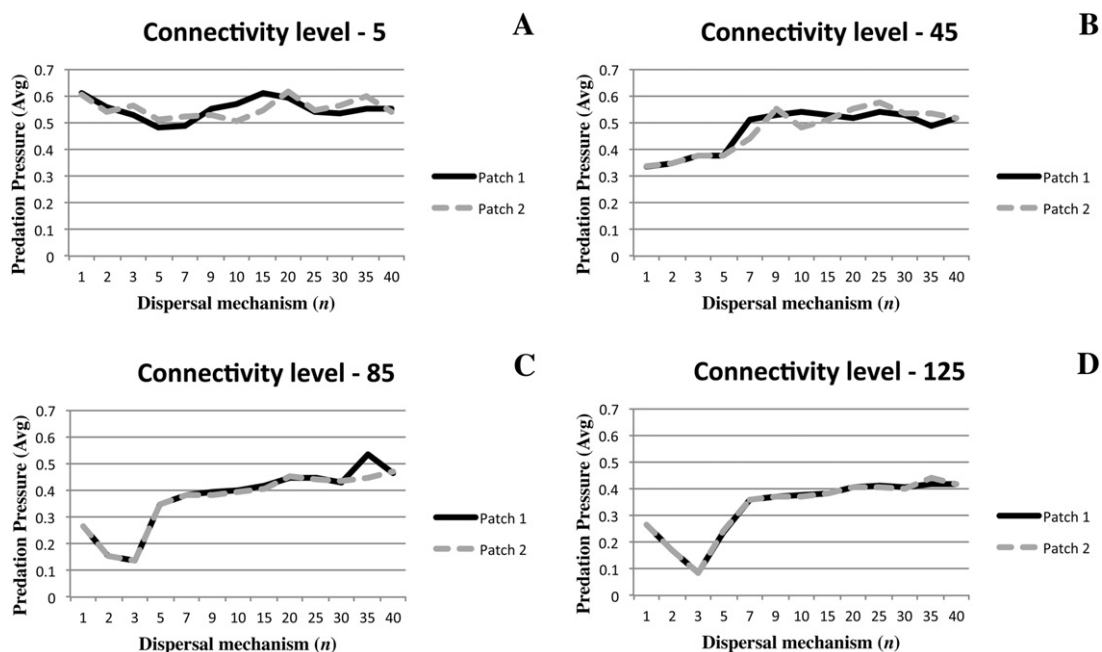
strategy (the swift spread of some invasive species, wildlife disease, and global synchrony whereby the metapopulation becomes effectively a single population, etc.). In this model, we provide another argument against ever-increasing connectivity in the context of natural species interaction. When a predator–prey relationship is explicitly taken into account we show there are definite trade-offs to connectivity at the extremes. This result is interesting because intermediate connectivity signifies different targets for managers and modified goals for conservation groups; targets and goals that vary with species vagility.

For each dispersal mechanism type  $n$ , the relationship between connectivity and the likelihood of coexistence maintain the same qualitative shape. Therefore, the result emphasizing the trade-offs to increased connectivity is a robust finding. However, the intensity of movement, as dictated by increased type  $n$  dispersal functions, plays a big role in determining the effects of connectivity on coexistence levels. Fig. 5 shows that the most favorable levels of connectivity occur at higher values of  $W_{12}$  (a more intermediate level of connectivity) for increasing values of  $n$ .

Transitioning from species characterized by weakly-biased to strongly-biased random movement (increasing  $n$ ), we find intermediate connectivity is optimal and survivability is more probable for systems with even less connectivity. This may be due to the fact

that for populations where movement is, for the most part, collective and motivated by sharp density-dependent feedback (large  $n$ ), a larger subpopulation is more apt to move and escape the various pressures of their current patch only when such threats are forthcoming; thereby avoiding excess dispersal mortality (recall Fig. 2). In effect, these predator and prey are better informed; these agents take advantage of available resources on their native patch and are more likely to disperse only to avoid resource scarcity and welfare threats, as opposed to random will. However, this does not fully explain the reason why greater likelihoods of coexistence occur at increasingly lower, intermediate regions of connectivity for the better-informed, collective dispersers. This result is further elucidated by considering the relationship between dispersal mechanism ( $n$ ), connectivity level, and direct species interaction in the form of predation pressure.

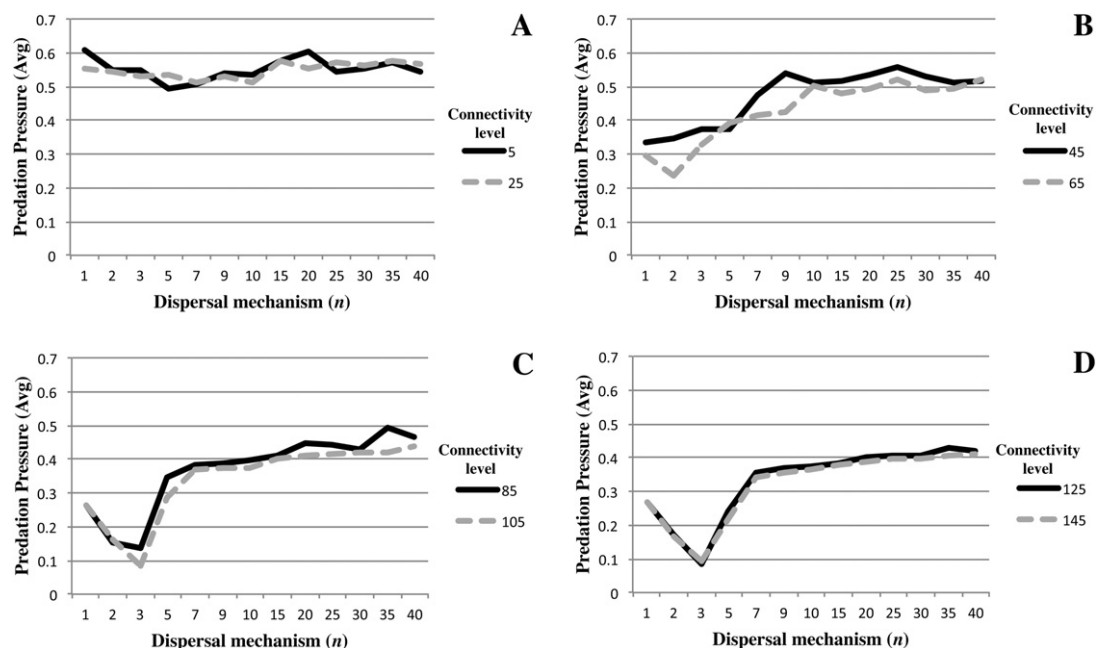
Predation pressure is a key indicator in evaluating the likelihood of coexistence because the measure must remain in a bounded region that ensures predator survival but also restricts overpredation and system collapse. As discussed in Section 2.2.2, an increased number of individual predators disperse when faced with low prey abundance. If all predator agents disperse in this uniform manner, which occurs for values of larger  $n$ , then the same density pressures still exist on both patches. Prey scarcity will persist since large



**Fig. 6.** Predation pressure on patch 1 versus patch 2. This figure displays the average predation pressure on patches 1 and 2 throughout the ABM simulation experiment. Average predation pressure is measured as the ratio of the total number of predator to prey agents in the metapopulation, averaged over the duration of a simulation. The independent variable in this case is dispersal mechanism ( $n$ ), which varies from 1 to 40. The data is further stratified by panels A–D, each one giving an idea of the correlation in measurements of predation pressure between the two patches for a subsequently larger cost of movement value (5–125). The main result stemming from this figure is that there appears to be strong positive correlation between patch 1 and 2 with respect to predation pressure, at all levels of connectivity.

predator subpopulations will deplete resources on both patches; Fig. 6 displays the suggested positive correlation between patches 1 and 2 with respect to predation pressure. To counteract this issue, increased likelihood of coexistence is attained at lower levels of connectivity because the pressure of two subpopulations of collective, dispersing predators is reduced by increased mortality

via movement; Fig. 7 illustrates this point. For relative all levels of connectivity depicted (5–145) in Fig. 7, predation pressure maintains an upward trend suggesting that predators employing stronger biased dispersal mechanisms put more strain on the prey population. However, for increasingly lower levels of connectivity predation pressure is reduced due to increased dispersal mortality



**Fig. 7.** The effect of dispersal and connectivity on average predation pressure. This figure showcases the effects of dispersal intensity and connectivity level on the average predation pressure over the entire metapopulation. Each panel contains two plots for differing levels of connectivity. Panels B–D clearly show an increase in predation pressure for larger values of  $n$  suggesting that overpredation becomes more of an issue for populations of strongly biased dispersers. Although the upward trend still persists for larger  $n$ , increasing the cost of movement between patches (5–145) has the effect of reducing the overall magnitude of predation pressure.

(as a result of the increase in the cost of movement). For example, the maximum predation pressure in a metapopulation with a connectivity level of 25, which is attained for larger values of  $n$ , is approximately 0.6 (panel A) as opposed to peak predation pressure of 0.4 in a metapopulation with connectivity 125; a 33% reduction in pressure.

And so the increase in dispersal mortality as determined by an increase in the cost of movement mitigates predation pressure, which serves to bolster prey abundance and welfare. Reduction in predation pressure is key especially for populations of strongly-biased individual dispersers. This result supports similar findings by Ruxton et al. (1997) and Silva et al. (2001) on the stabilizing role of dispersal mortality. This experiment is a good example that provides interesting insights into the subtle interplay between inter-patch dynamics (connectivity) and intra-patch processes (willingness to move) and the consequences for coexistence.

#### 4. Conclusion

Firstly, we have developed a system that dictates low landscape connectivity is detrimental to the management goal of species coexistence as expected by both theory and practice. The creation of a link between two distinct populations allows for the possibility of local extinction and globally extant populations. If one patch is subject to species extinction, repopulation is very likely if a traversable connection exists to an alternate, viable population. And so, isolation may increase the risk of global extinction because the probability of repopulation is effectively zero. However this conclusion does not necessarily imply that the probability of species survival increases monotonically with higher levels of connectivity. Rather, like most conclusions drawn from actual management practice, tradeoffs exist.

A more connected landscape could reduce the likelihood of global extinction and allow for more efficient foraging; however, at high levels of connectivity we encounter new threats; overcrowding and overpredation, and global synchrony. With high levels of connectivity intraspecific competition becomes an issue on both patches leading to overcrowding. Furthermore, predators are able to traverse the landscape freely and frequently, keeping their population high. The augmented level of predation efficiency causes large boom-bust cycles in the interacting populations (with stochasticity, this outcome may very well lead to extinction). Likewise, a well-connected system can be considered a single habitat, which can be described as global synchrony; this could also be considered a weakness when system shocks are incorporated. And so, large predator-prey boom-bust cycles and global synchrony will tend to destabilize the system and make it susceptible to global extinction.

The model developed in this study reveals that, for species movement characterized by derivatives of the *half-pipe* dispersal mechanism, there exist some intermediate range of connectedness that allows for local repopulation but at the same time protects against high amplitude oscillation and global synchrony. Although collective movement may be a common phenomenon in nature it is not necessarily the case that large populations move as one; it may be the case that smaller subpopulations engage in herd dispersal. Therefore, *Bang-bang* dispersal may be a strong assumption with respect to threshold movement, while the *half-pipe* dispersal function (a stronger reflection of biased random movement) may be a more accurate assumption for the dispersal scheme. The results discussed, using the *half-pipe* dispersal mechanism, suggest that support for greater connectivity may be ill advised. Knowledge of these connectivity trade-offs is pertinent to the management process. For a given landscape and set of species, if the manager assumes that the landscape is not at this optimal connectivity

level, some interesting questions must be addressed to devise an effective strategy (based on landscape alteration) for coexistence, including:

*What sort of feedbacks should the manager employ when deciding to alter the landscape?*

*How does management strategy change when a patch develops multiple linkages?*

The aforementioned questions are all relatively open as this study only serves to develop insight into the drivers that could help better inform corridor managers. To a certain degree, the success of the manager will be determined by identifying the appropriate interval of connectivity at which the likelihood of coexistence is maximized. Existence of such a threshold would signify that it may not be enough for the manager to just act based on feedback, but that it must work to maintain a minimum, significant level of connectivity or higher (based on other conservation goals).

We utilize an agent-based modeling approach to address the issue of landscape alteration and corridor management of a predator-prey metapopulation. The ABM allows us to do away with assumptions of average aggregate behavior (suppositions of a deterministic construct) and model behavior and interaction from the micro-level and see how this bottom-up approach serves to affect interactions, behavior, and population levels. Different degrees of connectivity lead to different population dynamics and persistence outcomes. The effect of connectivity on inter- and intra-patch dynamics depends heavily on the nature of threshold dispersal, which affects species interaction. For species movement that closely resembles the form characterized by the *half-pipe* dispersal function, an intermediate level of connectivity is most desirable. Depending on the nature of the species' dispersal mechanism, differing levels of connectedness between patches may lead to variable results from coexistence to global extinction, it is now the goal of corridor advocates to manage the landscape at a level that balances tradeoffs between the various necessities considered by each species.

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#### Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.ecolmodel.2012.04.028>.

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