Assessing the role of connectivity and dispersal in 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 of a two-patch metapopulation with local predator-prey dynamics and variable, density-dependent species migration. 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.

KEYWORDS: Landscape fragmentation, habitat connectivity, Predator-prey, Agent-based model, Metapopulation, Density-dependent dispersal, corridor

1 Introduction

Landscape fragmentation has always had a major impact on landscape mosaics due to normal fluctuations in climate, species growth, re-growth, and 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 [17]. As a result, when considering the management of wildlife, conservation biologists and land managers must now take a more systemic view and look away from managing a single species on a full landscape to managing the fragmented populations of several species across patchy landscapes [25].

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 welfare as enclosed, protected areas where species management and surveillance are priority – commonly known as a "fences and fines" or fortress conservation approach. However, with the hardships to rural communities that come about from the designation and accumulation of protected areas [5], the cost of enforcing rules and protecting the enclosed area against human encroachment [7], and global and regional climate change threats faced by species confined to an enclosed area, most conservationist have begun to explore more dynamic and holistic forms of management. Rather than restricting species to conservation "islands" in an attempt to shelter them from the possible threats that come with a changing landscape, managers now work to aid species dispersal within broader, multi-use protected areas and, more expansively, along larger conservation corridors spanning protected and unmanaged areas [3, 24]. This alternate form of management is known as corridor management. 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 [21], the large-scale Yellowstone to Yukon Conservation Initiative, or corridor connectivity projects of the Wildlands Project [22].

In line with research on metapopulations, conservation biologists believe that giving species the freedom to move between patches of fragmented landscape increases their chances for survival by dealing with problems of resource scarcity and climate heterogeneity. Naturally, this leads managers to believe that increased connectivity is always beneficial for species survival. 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 will be described in more detail later, 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, we need a 'dynamic manager' to help maintain an intermediate level of connectivity and keep the population levels in a more stable range amidst stochastic life events.

In order to cope with the ensuing tradeoffs in connectivity previously described, long-enduring corridor conservation efforts rely on a dynamic management scheme that can alter the existing patchy landscape and influence connectivity in favor of conservation and coexistence (the long-term maintenance of both predator and prey species). However, assessing criteria for landscape alteration based on possible corridor location and construction, as well as effectively utilizing feedback from population dynamics when manipulating connectivity, can be 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 agent-based modeling (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 theoretical and agent-based models place emphasis on how a single species is affected by fragmentation [4, 23]. Other analytic works on fragmented landscapes focus on the well being of interacting populations using rather simplistic dispersal mechanisms [8, 9, 10, 14]. In particular, this paper builds off of work first elaborated in a 10-node ABM framework [1]. Using a two-node ABM where the nodes represent habitat patches and the edge between them represents a corridor connecting them. The focus in this model comes from how varying the threshold migration functions of the two species affect the optimal level of connectivity. By using an agent-based framework rather than a typical Lotka-Volterra (or other) deterministic model of species interaction, we lose the general, qualitative results of the aggregate system. However, 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. 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 that conservationists and managers are sure to encounter [13]. This paper utilizes an agent-based representation of an interacting metapopulation of two species on a fragmented landscape to shed light on the importance of intermediate levels of connectivity for conservation of interacting populations.

2 Methods

2.1 2-Patch Landscape

The ABM developed for this study is based on the one developed by Baggio et al. (2011) in a similar study on the effects of connectivity on an unweighted network representation of a fragmented habitat for predators and prey. Baggio et al. utilize a 10-node network system where the existence of an edge directly translates to successful migration of predators and prey from one patch to another. While the Baggio et al. paper formally takes a network approach to understanding interspecies interactions in metapopulations, this research simplifies the landscape (minimizes the network to two nodes) in order to examine the interactions in more detail.

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

Symbol	**Variable Name**	**Values from distributions used in Monte Carlo simulations**
P	Number of nodes	2
C	Carrying capacity of a node	500
E	Number of edges	1

W_{ij}	Weight of edge linking node *i* to *j*	Varies from 5 to 105
N_x	Initial number of prey on each node	Poisson with mean 250
x_i	Number of prey on node *i* at a given point in time	N/A
r	Prey reproduction rate	Poisson with mean 0.25 (25%)
m	Prey natural mortality rate	Poisson with mean 0 (0%)
$D_{U,x}$	Prey density upper limit	Poisson with mean 0.9 (bounded above by 1)
$D_{L,x}$	Prey density lower limit	Poisson with mean 0.3
M_x	Prey movement capability	Poisson with mean 30
N_y	Initial number of predators on each node	Poisson with mean 100
y_i	Number of predators on node *i* at a given point in time	N/A
c	Predation probability	Poisson with mean 0.2 (20%)
f	Predator reproduction rate (after predation)	Poisson with mean 0.5 (50%)
d	Predator death rate	Poisson with mean 0.03 (3%)
$D_{U,y}$	Predator density upper limit	Poisson with mean 0.7
T_h	Predator handling time	0
M_y	Predator movement capability	Poisson with mean 60

The model presented in this study deviates from the creation of Baggio et al. in that it not only considers the existence of an edge as an indicator of successful migration but also the corresponding weight assigned to the edge. The weight (W_{ij}) of an edge serves as a proxy for distance between the two arbitrary nodes *i* and *j*. Essentially, 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 node 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 protected area to another, while others fail. Additionally, as will be described in more detail later, the model compares several movement threshold functions in order to facilitate changing the model dynamics across different types of species. The drawback of adding such complexities as cost of movement is that it further complicates the model and increases the amount of constraints when considering manager intervention. Therefore, a two-node, one-edge model is developed and analyzed, to compensate for the level of complexity in the system under study. In any case, the analysis of the two-node system will allow for a key assessment of the effects of connectivity on predator-prey dynamics and generalization to metapopulations of larger scale.

2.2 The Species

Birth and Death Events. Let x_i and y_i represent the predator and prey population on some node i at a given point in time. Individual prey and predators are assigned randomly to each node, however their initial population count on each node is fixed. Each time-step, prey agents have the ability to reproduce, with some probability determined by growth rate r, or die via predation with some probability jointly determined by the event that the prey agent is detected (proportional to the density of prey) and the act of predation, c. Note that the predation event will only occur if predators and prey are located on the same node. Moreover, prey natural mortality also occurs with some fixed probability determined by prey mortality rate, m. Predators have a fixed probability of reproduction at every time-step, f, which depends on the successful capture and consumption of a prey agent. Natural mortality for predators also occurs with some fixed probability determined by predator death rate, d.

Migration. As discussed in earlier sections, species migratory behavior (solely characterized in this study as movement from one node to another), or willingness to move, has been given different treatments in the literature. Baggio et al. (2011) used a switching function (i.e. *bang-bang* dispersal), where species migration is null until some population density threshold is crossed, at which point every member of the population is willing to move. Species dispersal can also be described using a mixture of partial random movement with migration indicators dictated by some threshold population level. In this study, the idea of random walks/migration is fused with density-dependent dispersal to model species movement as a biased random walk [19]. Migration is still random, but becomes increasingly biased, and eventually constant, as 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 [12, 20, 26].

We assume that species willingness to move is governed by rules that mimic intraspecies competition [2] and anti-predatory behavior [6, 11, 16] in prey, and foraging strategy [2, 15] in predators. Implicit in this assumption is that both predator and prey are knowledgeable of local patch, but not global, population densities. Prey and predator population densities on some node i, $D_{x,i}$ and $D_{y,i}$ respectively, are computed based on the carrying capacity, C_i. At high densities, with respect to intraspecies competition, prey agents are more likely to move and may migrate 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 a random event. The same mechanism is adopted for anti-predatory behavior. A small number of predators pose little or no risk to the prey population; and so prey migration becomes less biased. At high predator densities, prey agents are, collectively, more apt to move.

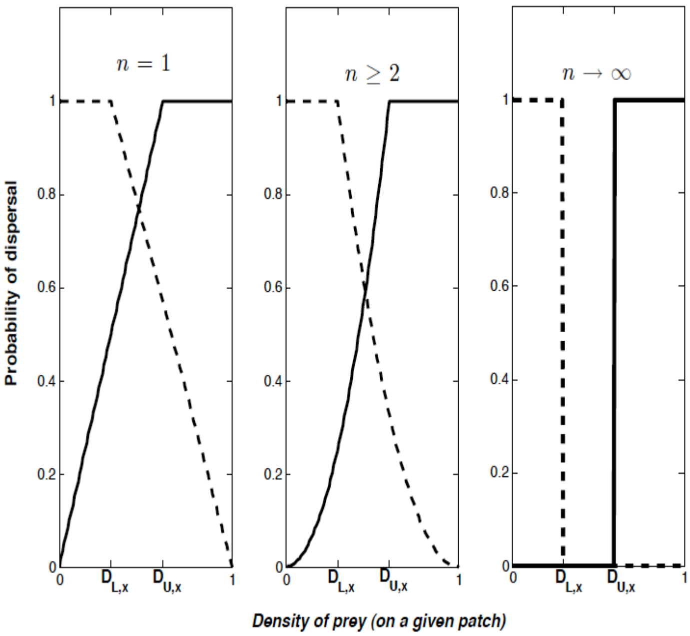

Fig 1. Threshold dispersal of prey (*straight line*) and predator (*dashed line*). The plots (from left to right) showcase the suite of dispersal mechanisms used to represent threshold migration in this study; spanning from *ramp* (far-left) to *bang-bang* dispersal (far-right). The plots highlighted in black represent threshold migration in prey as a function of interspecies competition (with corresponding threshold density, $D_{U,x}$). The plots in blue represent threshold migration in predators as influenced by foraging (with corresponding threshold density, $D_{L,x}$).

Prey agents can determine their willingness to move between nodes at each time-step with some probability. As displayed in figure 1, the probability of migration increases to the maximal limit (where every prey agent is willing to move) as prey or predators approach their maximum density thresholds on the current patch. $D_{U,x}$ and $D_{U,y}$, measures of intensity in resource competition and anti-predatory behavior respectively, are the two maximum density thresholds that affect prey dispersal. The maximum density threshold related to interspecies competition is denoted in figure 1. Whether or not a maximum density threshold has been exceeded, if prey agents do choose to migrate, then the probability of successful migration to the neighboring patch must be calculated. The assessment of successful migration is determined probabilistically and depends on the weight of the traversable edge and the prey agent's innate ability to move (M_x), which is an individual attribute in the ABM. The notion of a migratory success probability relaxes the constraint put on species dispersal under the framework of Nathan et al. (2008), which assumes that movement between nodes is only possible if the weight of an existing edge is lower than the movement capability of the dispersing prey or predator agent.

Unsuccessful migration can be interpreted as mortality via migration. A dispersing prey agent dies (assumed via migration), the weights of the edges attached to its current node are all much larger than its innate ability to move (thereby decreasing the likelihood of successful migration), or if the chosen node has a prey or predator density that has already reached a density threshold.

Predators move between nodes according to a prey-related density threshold. More precisely, if the prey density of the current node falls below some predetermined threshold ($D_{L,x}$), predators move to the other node with some distance-related likelihood; this is also showcased in figure 1. Predators die (via migration) if the current node is isolated, with some probability when the weight of the edge attached to their current node exceeds their ability to move (M_y), or when the prey density of the chosen node is too low. Throughout this study we always assume that predators can move over a larger distance than 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 migratory behavior spanning from *ramp* ($n = 1$) to *bang-bang* ($n \Rightarrow \infty$) dispersal; this is also showcased in figure 1. *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 migration 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 migration 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 migrate before a threshold density is crossed. After the threshold density is crossed, all members of the species choose to migrate. 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.

3 Results

This paper has two main objectives and both can be studied through generalization, simulation, and documentation. First we aim to study the role of connectivity in dictating the possibility of coexistence among a predator and prey population. The second is 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. Both these objectives can be addressed by varying the level of connectivity between the two nodes and the magnitude of n to simulate differences in the migratory behavior of both species.

In utilizing the Monte Carlo scheme, we randomize all predator and prey attributes at the start of every run using a random poisson generator. The mean values for each of the parameters in this modeling experiment, noted in table 1, are taken from similar individual based studies by Wilson (1998) and Baggio et al. (2011). Due to the stochastic nature of the model, we compute 400 identical runs for each combination describing level of connectivity and migratory behavior 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 timestep) and time to extinction (if applicable).

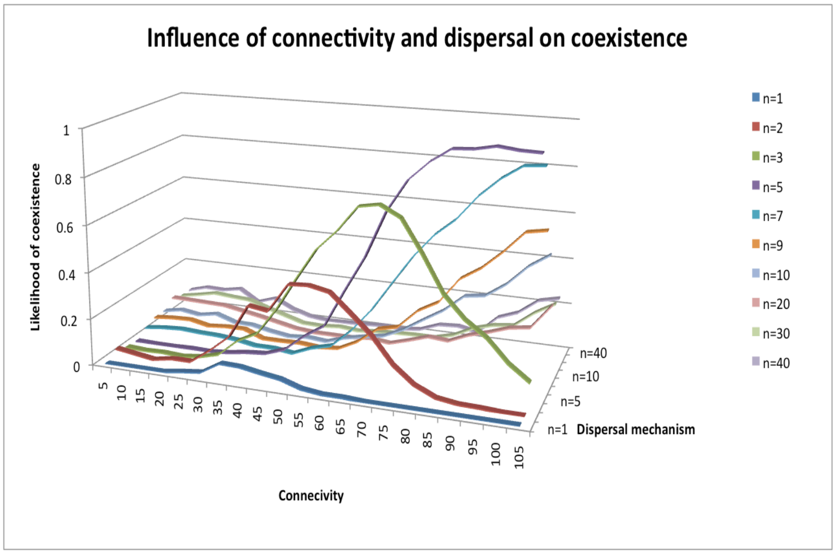

Fig. 2. Displays the effects of landscape connectivity and choice of dispersal mechanism on the likelihood of coexistence between predators and prey. Note, although not shown, for *n* = 10 and beyond, likelihood will also reach a peak and decline.

Figure 2 shows 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 fig. 2) 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 a proportion 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 in figure 2 spans from 5-105 (high - low) and represents the connectivity between the two patches. The depth axis spans *n* = 1…40, using a wide range of *half-pipe* functions to approximate the transition from *ramp* dispersal (weakly-biased random movement) to the *bang-bang* (strongly-biased). To represent the bang-bang dispersal we set $n = 40$ as we find no substantive changes beyond this value.

Interesting enough, figure 2 displays an intuitive result, but not one that is immediately clear from the construct of the model. For each choice of a type n dispersal mechanism, it is clear that the most favorable choice for survivability of both species on the landscape does not occur at the margins of connectivity. For each graph in figure 2 the likelihood of coexistence rises to a peak at a relatively intermediate level of connectivity before decreasing to zero for further perturbations of 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 refugia), 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 extremes of connectivity.

Corridor management views increased connectivity between patches of viable land as a positive for the coexistence and maintenance for a larger ecosystem. While there are clear reasons for assuming this (prevention of local extinctions, minimization of genetic drift, allowing for dispersal and colonization, etc.), there are equally clear reasons against this assumption (the swift spread of some invasive species, wildlife disease, 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 definitely trade-offs to connectivity at the margins. This result is most interesting because intermediate connectivity signifies different targets for managers and modified goals for conservation groups.

For each dispersal mechanism type n, the relationship between connectivity and the likelihood of survivability maintain the same qualitative shape. Therefore, the result emphasizing the tradeoffs to increased connectivity is a robust finding. However, the intensity of migratory behavior, as dictated by increased type n dispersal, plays a big role in determining the effects of connectivity on coexistence levels. Figure 2 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, 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 migration is, for the most part, collective and motivated by density-dependent feedback, a larger subpopulation is more apt to move and escape the various pressures of their current patch. In effect, these predators and prey are better informed and migrate using feedbacks that help them avoid resource scarcity and threats to their safety.

But why do the optimal levels of connectivity occur at lower, intermediate regions for the better-informed, collective migrants? Large populations of prey migrate when faced with food scarcity and/or predation pressure; similarly, predators migrate from patches with low prey count. If all the agents act and migrate in this way, then the same pressures still exist. Food scarcity will still be an issue since large prey populations will deplete resources on both patches and so will a large predator population (which subsequently leads to the problem of refugia loss). To counteract this issue increased likelihood of survivability is attained at lower levels of connectivity as the pressures of two populous species of collective migrants is reduced by increased mortality via migration. This is a good example about the subtle interplay between inter-patch dynamics (connectivity) and intra-patch processes (willingness to move) and the consequences for coexistence.

4 Discussion

Firstly, we have developed a system that dictates low landscape connectivity is detrimental to the management effort. The creation of a link between two distinct populations allows for the possibility of local extinction and globally extant populations. If one node 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 note necessarily imply that increased connectivity is essential and positively correlated with species coexistence. 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, overpredation, and global synchrony. With high levels of connectivity intra-species competition becomes an issue on both patches leading to overcrowding. Furthermore, predators are able to traverse the landscape freely and frequently, keeping their population vitalized. 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 one population, 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 migration characterized by derivates 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 migration may be a common phenomenon in nature it is not necessarily the case that large populations move as one, this may occur on the subpopulation scale. Therefore, *bang-bang* dispersal may be a strong assumption with respect to threshold migration, while the *half-pipe* migration 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, 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 multi-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. Altering connectivity has a definite effect on local and global population dynamics. The effect of connectivity on inter- and intra-patch dynamics depends heavily on the nature of threshold migration, which affects species interaction. For migration that closely resembles that 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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