Modeling Decision-making across Habitat Patches: Insights on Large-Scale Conservation Management

Michael Schoon[1], Jacopo Baggio[2], Kehinde Salau[3], Marco Janssen[2]

[1]School of Sustainability, Arizona State University

michael.schoon@asu.edu

[2]Center for the Study of Institutional Diversity, School of Human Evolution and Social Change, Arizona State University

jbaggio@asu.edu and Marco.Janssen@asu.edu

[3]Mathematical, Computational and Modeling Science Center, School of Human Evolution and Social Change, Arizona State University

ksalau@asu.edu

Abstract. In recent years there has been a shift in biodiversity conservation efforts from the confines of enclosed protected areas to a more expansive view of interlinked habitat patches across multiple land tenure types and land uses. However, much work remains on how conservation managers can intervene in such a system to achieve the sustainability of basic conservation goals. Building off of an existing agent-based model (ABM) of a two-patch metapopulation with local predator-prey dynamics and variable, density-dependent species migration, this model examines the capacity of a manager to interact with and modify the ecosystem to achieve biodiversity conservation goals. In this paper, we explore managers' strategies aimed at maintaining one of two goals – local coexistence of both predators and prey (sustained coexistence on one patch) or global coexistence of predators and prey (sustained coexistence on both patches). To achieve management's goal, the manager varies the level of connectivity between two habitat patches (i.e. a manager is thus able to facilitate or restrict movement of species between habitat patches) based on one of three monitoring strategies – the monitoring of predator population levels, the monitoring of prey population levels, or the monitoring of the vegetation carrying capacity of the habitat patches. Our goal is to help facilitate management decisions and monitoring choices in conservation projects that move beyond the confines of a protected area and into mosaics of multiple land tenure types typical of many of today's large-scale conservation projects.

Keywords: Conservation, Biodiversity, population dynamics, management, adaptive management

1 Introduction

Patchy mosaic landscapes have always occurred in nature due to disturbances caused from fluctuations in climate, the ebb and flow of species populations, and other stochastic events. However, the effects of industrialization, urbanization, pollution, and other indicators of a growing economy play an ever-growing role in the increasing fragmentation of landscapes [1,2]. In truth, these anthropogenic forces have been the main drivers of fragmentation in recent times. As a result, when considering the optimal management of wildlife, conservation biologists and environmental managers must look away from simple heuristics for managing single species in a specific place to the complex challenge of managing several fragmented populations across a patchy landscape [3]. Indeed, a change in the nature of the problem regarding restoration and conservation has also brought about a change in the possible management tools and possibilities with which to deal with the problem accordingly. In the past, one of the more common approaches in species conservation relied upon the designation of certain key habitats for species welfare as enclosed, protected areas where species management and surveillance took precedence. However, with the hardships often imposed on local communities that came from the designation and accumulation of protected areas [4], the need for protecting the enclosed area against human encroachment [5], and both global and regional climate change threatening isolated, local species populations, most conservationist have begun to explore more dynamic forms of management. Rather than restricting species in an attempt to shelter them from the possible threats that come with a changing landscape, managers now work to aid species dispersal within protected areas as well as, more expansively, along corridors spanning land tenure types with varying levels of management and different types of goals [1,6-7]. This alternate form of management is known as corridor management [8].

Corridors to link previously separated habitat patches and create large-scale reserve networks have become increasingly popular with implementation projects ranging from explicitly linked and coordinated management in transboundary protected areas [9], large landscape conservation networks like Yellowstone to Yukon [10], and collaborative management programs and modeling experiments with emphasis on connecting multiple land tenure arrangements [11]. These projects partner governmental agencies, NGOs, and private citizens and attempt to better match the scale of management to the scale of the ecological dilemmas being confronted, such as firescapes [12], species dynamics [13], and biodiversity loss [14-15].

Conservationists believe that giving species the freedom to move between patches of fragmented landscape increases their chances of dealing with problems of resource scarcity and climate heterogeneity. Naturally, this initially led managers to believe that increased connectivity would always benefit species' quest for survival. An increase in connectivity, besides aiding species dispersal through an otherwise disconnected system, however, may also provide conduits for the spread of disease or pest species through a system. Clearly, most conservationists and land managers understand this threat. What is not intuitively obvious is that there is a more fundamental reason for the eventual deleterious effects of increased connectivity that has to do with multiple species interaction. For example, in models of predator-prey interaction on simple networks, coexistence initially increases with increased ease of movement between habitat patches [16]. However, as connectivity continues to increase, there are decreasing improvements to coexistence until a maximum level of likely coexistence is reached (Fig.1). Beyond this point, increasing connectivity between patches reduces the likelihood of coexistence.

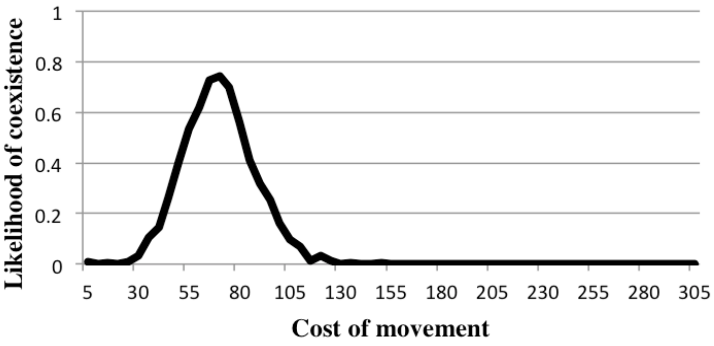

Fig. 1. The effect of connectivity on likelihood of species coexistence. On the x-axis, 5 corresponds to a low cost of movement (thus high connectedness between patches), while 305 denotes a high cost of movement (i.e. minimal connectivity between patches). Adapted from [16]

The challenge lies in converting these findings from a simple model into useful information for managers confronting the complexities of reality. What these models do is rephrase the questions that we ask and the types of decisions confronting managers. Managers are not confronted with simple all-or-nothing, binary decisions. Instead, managers must try to maintain intermediate levels of connectivity between habitat patches by means of improving habitat, securing water and food sources, and coordinating across tenure boundaries to open pathways between patches. This article unpacks this complex decision-making process and attempts to do four things. First, it makes sense of the ecological results and what it means to switch from binary decision-making to thinking about a continuum of landscape connectivity. Second, it helps the manager understand the type of information that can help guide this decision-making. Third, it compares management decisions made locally (from the perspective of a single land tenure patch) with decisions made at a larger scale. Finally, it shifts the nature of the decision-making from a single point in time on a near-equilibrium static landscape to a mindset of adaptive management in a dynamic, non-equilibrium environment [17]. In other words, the goal of this paper is to start bridging the gap between theory and practice with respect to the effect of corridors and corridor management on species coexistence. Managers need to be aware of scale effects (i.e. local vs. global objectives) and what species (or trophic levels) to monitor so as to reduce monitoring costs.

This study aims to provide some insight into these tasks by adopting the agent-based modeling (ABM) framework to better understand the natural system based on the interactions of prey and predator individuals on interlinked habitat patches. A manager can increase or decrease the ease of movement between habitat patches based on feedback received from the system with a goal to maintain biodiversity (the coexistence of species) at either a patch-level or a network-level. The article will proceed with the methodology that will explain how theoretical scenarios were converted into a model. The results from the model help to explain the interesting phenomenon of intermediate connectivity and how managers can improve decision-making based upon monitoring different types of information. The discussion compares decision-making at two different scales, which support current efforts to move to more collaborative, larger-scale landscape management. The conclusion revisits the concept of shifting from static viewpoints to the need for adaptive management in a dynamic world.

2 Methods

A large number of existing analytical and agent-based models (ABM) place emphasis on how a single species is affected by fragmentation [18-20]. Other work on fragmented landscapes focus on the well-being of interacting populations using random diffusion (i.e. at every timestep and individual of a species has a certain probability to move to a neighboring patch) as a dispersal mechanism [21-23]. We believe that in the context of socio-ecological systems, the ABM framework allows for a more plausible representation of reality and may very well lead to a better understanding of corridor ecology, allowing the building of plausible scenarios, and consequently improved strategies for landscape management. ABMs can incorporate stochasticity in the form of measurement error, event uncertainty and rare phenomena that conservationists and managers are sure to encounter [24]. Additionally, ABMs enable the modeling and tracking of management decisions over long time periods and facilitate decision-making experimentation across various scenarios of species interaction, feedback loops, diverse landscapes, and adjusting for various types of perturbation.

The ABM builds upon parameters and rules from previous models [16, 25]. A simplified landscape portrayed as two connected patches forms the environment. The connection between the two patches represents the ease of movement on the landscape between habitats. Predators and prey reproduce, die, and move across the landscape according to predetermined rules. Predators hunt and kill prey prior to consumption. The carrying capacity of the patches is dynamic and based on the abundance of residing prey and their associated impact on vegetation. A manager is able to alter the connection between patches in order to hinder or facilitate movement. In this study, the management objective is always to maximize the time of coexistence between predator and prey. Fig.2 provides a flow diagram of the model described.

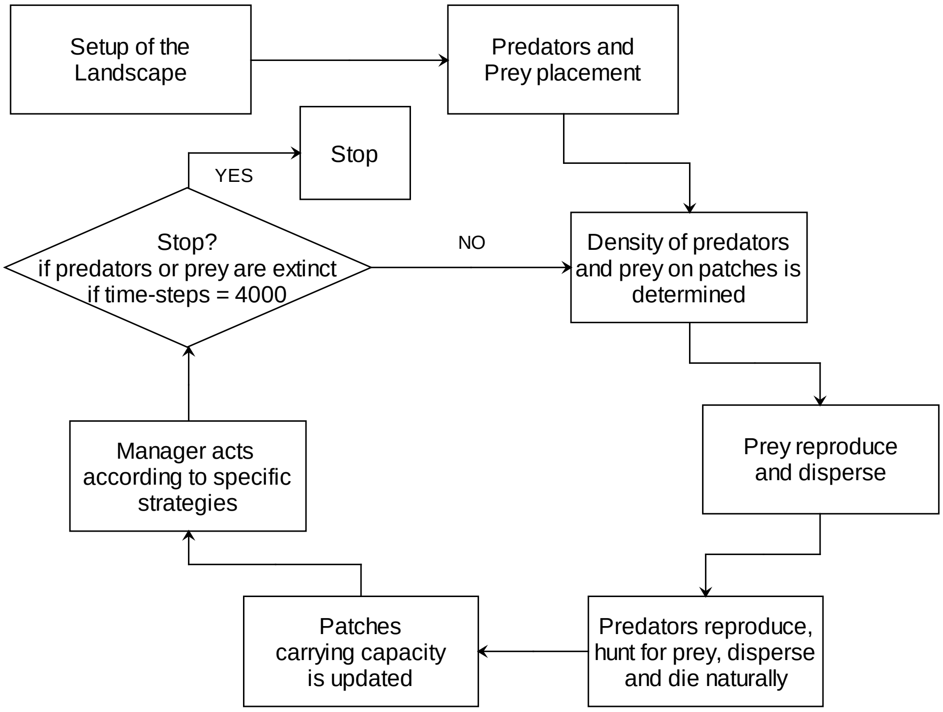

Fig. 2. Flow diagram of the model

2.1 2-Patch Landscape

The landscape is portrayed as two distinct, but connected, habitat patches (shown in Fig.3). Each habitat patch is characterized by a given level of vegetation, that represent its ability to sustain prey population. The connection between the two patches is characterized by an attribute that represents the difficulty/ease with which predators and prey are able to move from one patch to another as portrayed in Fig.3.

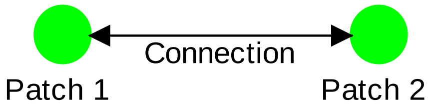

Fig. 3. Graphical representation of the landscape

2.2 The Species

Individual prey and predators are assigned randomly to each patch, however their initial population count on each patch is fixed. Each prey agent has the ability to reproduce or die via predation at every time-step (with some probability). Note that the predation event will only occur if predators and preys are located on the same patch. Prey natural mortality also occurs with some fixed probability. Predators have a fixed probability of reproduction at every time-step, which depends on the successful capture and consumption of prey. Natural mortality for predators also occurs with some fixed probability.

Individual prey determine their willingness to move between habitat patches at each time step with some probability. This probability increases to the maximal limit (where every prey agent is willing to move) as prey or predators approach their maximum density thresholds. This increasing willingness stems from two mechanisms that spur prey movement – resource competition from excessive prey populations [26] and anti-predatory behavior from increasing predator populations on the current patch [27-29]. If individual prey choose to migrate to a target patch, regardless of whether a maximum density threshold has been exceeded on its current patch, successful migration is probabilistic. The stochastic assessment of successful migration depends on the current ease of movement between patches and the prey agent's innate ability to move, which is an individual attribute in the ABM. Unsuccessful migration can be interpreted as mortality via migration. A prey agent dies, most likely, if its current habitat patch has no connections, if the ease of movement between its current patch and the target patch is much larger than its innate ability to move (thus the likelihood of reaching a neighboring patch is miniscule), or if the target patch has a prey or predator density that has already reached a density threshold.

Individual predators make similar calculations for each time step and move between habitat patches according to a prey-related density threshold [30-31]. More precisely, if the prey density on the current patch is too low, predators are more likely to migrate and successfully reach the target patch with some probability. Predators die if their current patch is isolated, the ease of movement between their current patch and others is higher than the predator's ability to move (thus not reachable), or the prey density on the target patch is too low. Values used in the model, as well as symbols and variables are reported in table 1 of the supplementary material.

2.3 Management Strategies

This paper focuses on possible management strategies adopted to maintain coexistence of species (i.e. biodiversity). The main assumptions underlying management action is the ability to influence the system through decision-making and action. In this model, a manager is able to alter connectivity between the two patches by increasing or decreasing the weight of the connection (i.e. restrict/ease movement) between them. Costs and multiple managers with multiple objectives are, at this stage, not taken into account. Further, in order to focus on management strategies, the ecological part of the model does not vary beyond the initial model parameters as depicted in the model overview, design and detail protocol (see ODD in the supplementary material) [32]. The exploration of the ecological model is detailed in [25] and [16].

In this model, a manager has six different possible strategies that guide his/her actions. Strategies always maintain the same objective: to maximize the time of coexistence. Managers make decisions based on the type of coexistence (local vs. global) they manage for and based on which trophic level (vegetation vs. prey vs. predator) they monitor. Six different strategies are devised as portrayed and explained in table 1 and depicted in Fig.4.

Table 1. Management feedback controls

		Monitoring		
		Vegetation	**Prey**	**Predators**
Scale	**Local** **(Single Patch)**	**Strategy name**: *locveg*. **Description**: Manager concerned with coexistence on a specific patch and acts based on vegetation levels (or carrying capacity), thereby reducing or increasing the cost of moving to/from the specific patch.	**Strategy name**: *locprey*. **Description**: Manager concerned with coexistence on a specific patch and acts based on the density of local prey, thereby reducing or increasing the cost of moving to/from the specific patch.	**Strategy name**: *locpred*. **Description**: Manager concerned with the coexistence on a specific patch and acts based on the density of the local predators, thereby reducing or increasing the cost of moving to/from the specific patch.
	Global **(All Patches)**	**Strategy name**: *globveg*. **Description**: Manager concerned with coexistence on the entire landscape and acts based on vegetation levels (or carrying capacity), thereby reducing or increasing the cost of moving between patches.	**Strategy name**: *globprey*. **Description**: Manager concerned with coexistence on the entire landscape and acts based on the density of global prey, thereby reducing or increasing the cost of moving between patches.	**Strategy name**: *globpred*. **Description**: Manager concerned with coexistence on the entire landscape and acts based on the density of the global predators, thereby reducing or increasing the cost of moving between patches.

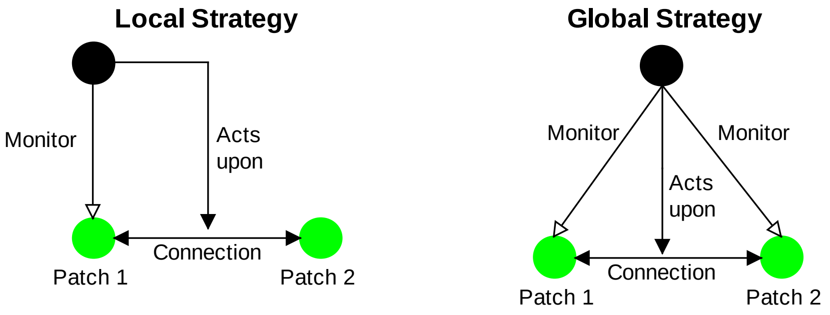

Fig. 4. Difference between global and local strategies.

A manager may monitor the level of vegetation, prey or predators on one or both patches. This may be viewed as the differences between separately managing a national unit of a transboundary protected area as opposed to managing at the transboundary park level [33]. Management action involves hindering or facilitating the movement of species (prey and predators) by increasing or decreasing the cost of movement between patches. A manager is assigned different population-density threshold levels (i.e. high/low observed population levels) below or above which he is forced to act. Different threshold levels are explored; the only constraint being that lower thresholds must be smaller than upper thresholds.

3 RESULTS

This model builds on previous work regarding predator-prey interactions on a networked landscape or set of connected habitat patches [25,16]. In the current version of the model, it examines management decision-making and how managers can better accomplish specific goals based on diverse monitoring protocols by increasing/decreasing the ease of movement to and from habitat patches. In what follows, we examine the results of 400 simulation runs for each parameter combination of upper and lower density thresholds, monitoring scale, and initial movement ease, as shown in the supplementary material, and share insights into 1) the meaning of intermediate levels of patch connectivity for managers' decision-making, 2) the ramifications of monitoring different types of data, and 3) the varying levels of success of different strategies for maintaining the coexistence of species, a proxy for biodiversity conservation.

3.1 Insights into the meaning of intermediate connectivity

As alluded to in Fig.1 and discussed briefly in the introduction, conservation biologists and environmental managers clearly understand that increasing connectivity, while often desired, carries its own set of risks – from disease propagation to the spread of pests and invasive species. By modeling the interactions of predator and prey across a networked landscape, we can begin to assess these potential trade-offs from increasing connectivity. The current model demonstrates that connectivity brings with it threats beyond potentially facilitating the propagation of perturbations throughout a system [34-36]. These threats include the combination of increased connectivity and interspecies interaction favors synchrony of predator and prey populations (versus asynchrony) and boom-bust cycles (versus limit cycles), two mechanism that can lead to global extinction. By synchrony, we refer to the possibility for metapopulations to revert to the dynamics of a single patch population under conditions of high connectivity. Therefore, managers confront dangerous system dynamics in which boom-bust cycles and synchronous populations emerge at high levels of connectivity, while low levels of connectivity likewise result in excessive species extinctions due to overly restricted movements and local population extinction events. As a result, we need a 'dynamic manager' to keep the population levels in the stable range amidst stochastic life events.

3.2 Insights from monitoring different types of data

In order to assess which strategy is likely to lead to a higher level of coexistence we test the different strategies described in the previous section – monitoring vegetation levels, prey population, or predator population at either the local or global scale. Looking first at the ramifications of monitoring strategies, our results suggest that, if resources are limited, monitoring the meso-level species (i.e. prey) may lead to more favorable outcomes overall as opposed to monitoring top (predator) or basal (vegetation) species. Fig.5 displays our results independent of initial conditions and internal species parameters described in the supplementary material. The depth of color reflects the average time of coexistence (how many time-step, on average, prey, predator and vegetation have coexisted). The axes of the panels represent density thresholds, which act as a kind of warning signal, indicating when a manager should utilize a given strategy.

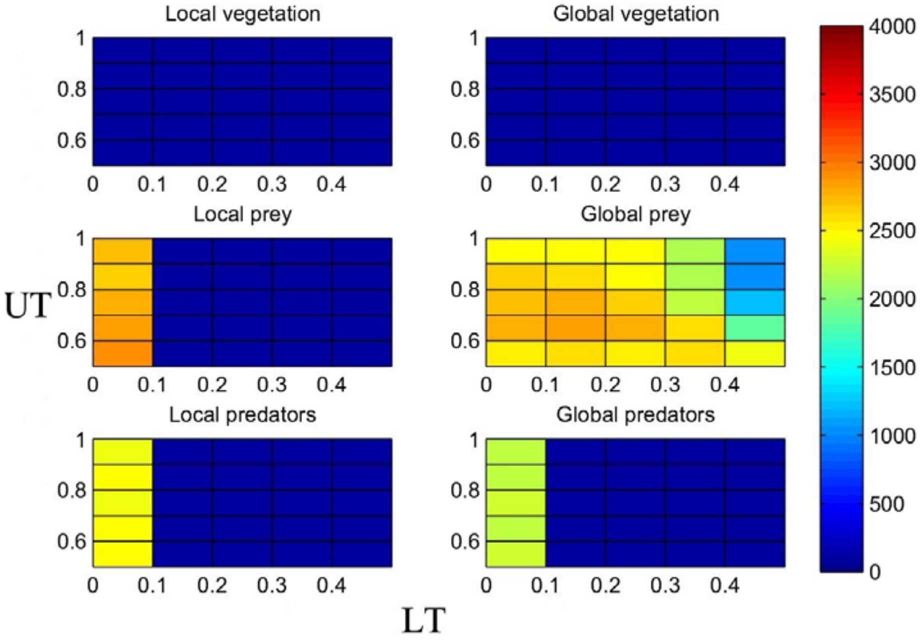

Fig. 5. Coexistence results for specific threshold parameters and monitoring strategies. The colors represent average time of coexistence and are coded with respect to the color-bar on the right side of the figure. The *x*-axis for each panel graph, denoted LT (lower density threshold), assumes values between 0 and 0.5. For vegetation density below the corresponding LT, the manager acts to hinder species movement; while for predator (or prey) densities below the corresponding LT, the manager acts to facilitate movement of species. The *y*-axis for each panel graph, denoted UT (upper density threshold), assumes values between 0.5 and 1. For vegetation density exceeding the corresponding UT, the manager acts to facilitate species movement; while, for predators (or prey) densities exceeding their corresponding UT, the manager acts to hinder movement of species.

Fig.5 suggests that management based on monitoring prey population density levels leads to a longer period of predator-prey coexistence. This increased coexistence period at the "meso"-monitoring level stems from the manager's improved responsiveness to changes emerging from shifting vegetation levels, which affect prey populations and desire to migrate as well as shifting predator populations, which also impact prey populations and their propensity to move. At either other monitoring level, changing densities that impact species populations are often one step removed from the species reaching problematic density levels that take time to propagate to the other levels.

3.3 Insights from strategies on species coexistence

Fig.5 furthers suggests that biodiversity outcomes improve by managing at the global scale. Scale mismatches in management may lead the system to an undesired state. As conservation biology theory suggests, bigger is often better [8, 37-38]. In this case, managing at the global scale often improves managerial responses and facilitates improved decision-making. More in detail, we can divide the strategies proposed into three main categories – 1: strategies that always lead to poor coexistence (i.e. local and global vegetation), 2: strategies that lead to high coexistence when the landscape does not require actively decreasing connectivity (local prey, local predators, and global predators), 3: strategies that lead to longer coexistence time and that are robust to errors of managers in defining and acting upon specific density thresholds (global prey).

The first category comprises local and global vegetation. Monitoring vegetation is the worst possible choice. According to our model, if a biodiversity manager monitors only vegetation (or basal species), results would, on average, be catastrophic. The second category comprises three different strategies: local prey, local and global predator. These strategies may lead to high levels of coexistence time.

However, in order to reach high coexistence time levels, a manager needs to know the system very well. As portrayed in Fig.5, all strategies belonging to these categories are very sensitive to low density thresholds. A small mistake may lead to results that are the opposite of what the manager expected. Global prey belongs to the third category. It is the only strategy that allows for high levels of coexistence time under a wide variety of choice of density thresholds (thus allowing more likely positive results even in case of errors and misunderstanding of the system). Monitoring meso-species (prey in the case of the model presented) and managing at the appropriate scale (global) will greatly increase chances of longer coexistence time.

4 Discussion

The model presented here compares monitoring at multiple trophic levels and decision-making at two different scales with results that support current efforts to move to more collaborative, larger-scale landscape management. The discussion focuses on four key take-aways – the need to take a more progressive and dynamic view of connectivity, clear support for conservation theory regarding connectivity through the use of new techniques, the importance of selecting appropriate monitoring plans, and insight into why the landscape perspective performs superior to patch-level management. Altering connectivity has a definite effect on local and global population dynamics. Past ecological models, as discussed earlier, show the effect of connectivity on inter- and intra-patch dynamics and inter-species populations. As expected from theory, low landscape connectivity is counterproductive to the management effort. This is because the creation of a traversable link between two distinct populations allows for the possibility of local extinction and globally extant populations via rescue effects. If one patch is subject to species extinction, repopulation is very likely if a connection exists to an alternate, viable population. Therefore, isolation may increase the risk of global extinction because the probability of repopulation is effectively zero. However, this conclusion does not imply that increased connectivity is an unequivocal positive and is positively correlated with species coexistence. Rather, like most conclusions drawn from actual management practice, tradeoffs exist [1]. We instead argue for a more progressive view of connectivity.

The dynamics of the ecological model imply that there exists some intermediate range of connectedness that allows for local repopulation but at the same time protects against high amplitude oscillation and global synchrony. However, the dynamics of the model also suggest that managers must take a more dynamic view of connectivity. A manager's job is not about setting a level of connectivity in perpetuity, but rather that it may require regular change and needs to be assessed routinely. As a result, manager's, in an adaptive management mindset, need to keep these types of questions in mind:

- What sort of feedbacks should the manager employ when deciding to alter the landscape?
- How frequently must the manager act to ensure relative stability of the system?
- Can the manager locate the intermediate range of connectedness that fosters coexistence? Or will periodic alterations continue throughout time?
- Can corridor management, based on intra- and inter-patch population feedbacks, be considered successful?

Moreover, the success of the manager will be determined by selecting a monitoring strategy that facilitates quick and accurate system assessment. As the model results indicate, some monitoring strategies, such as monitoring of vegetation levels, suggest coexistence is wholly improbably and make it nearly impossible to understand system dynamics in a way that enables an accurate setting of connectivity levels for long-term conservation goals. Alternate monitoring strategies may provide this understanding under some circumstances but not others, such as the monitoring of predator levels or local prey populations. Fortunately, other strategies – monitoring prey population densities at a global scale – provide much more robustness in finding the appropriate level of connectivity regardless of initial conditions or temporary changes due to external perturbations. One may say that it is better to monitor everything or at least multiple indicators, but this may prove too costly, intractable from a time-perspective, and an inefficient use of managerial focus.

Finally, taking a landscape perspective, similar to that in transboundary protected areas, large landscape conservation programs like Yellowstone to Yukon or the Northern Jaguar Project, and collaborative management programs with emphasis on connecting multiple land tenure arrangements, clearly leads to superior results than through management at the individual patch level. The global strategy of monitoring at a landscape level and acting upon the connection between patches, as expected from both theory and practice, leads to more desirable outcomes. While this may also be seen as common sense, it still seems to be an elusive phenomenon in reality. Initiatives such as the collaborative projects mentioned above have moved in this direction, but the vast majority of conservation programs continue to manage on a patch-by-patch basis.

This research program utilizes 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. In so doing, we also use a new methodological approach to help triangulate in and confirm theories of conservation biology regarding connectivity as well as current thoughts on the appropriateness of adaptive management in practice [17]. Our goal has been to take a first step toward providing managers with both insights from the modeling efforts and support for those taking a critical perspective of current management practices, as well as providing a tool that managers can use to incorporate their own data and move towards more complex understandings of reality.

5 Conclusion

Both theoretically and methodologically, this research revisits the concept of shifting from static viewpoints to the need for adaptive management in a dynamic world. It takes a first pass at modeling efforts on how managers many influence biodiversity outcomes through the management of connectivity and how choices of scale of management and monitoring systems lead to differential results. However, this initial pass at a simple network with a single manager raises a number of additional questions.

The next phase of research needs to increase the complexity of the network and begin to address the question: How well do we expect the results of the 2-patch system to translate to systems with more fragmented habitat patches? Although recognizing the consequences of habitat fragmentation on the resilience of simple ecological system is important, understanding the consequences of simple management strategies is crucial in order to assess possible outcomes that may enhance or reduce the resilience of a simple ecological system. From this perspective, we can begin to assess more complex, and more realistic, patch landscapes.

Extensions of the model from an ecological perspective are also possible, but may come at the expense of methodological problems (i.e. the risk that the ABM becomes too complicated) while providing few additional meaningful insights. However, other extensions clearly make sense from a managerial perspective. We outline four of these opportunities below. First, given the diverse range of sensitivities to starting conditions and levels of knowledge about the system, it is important that future work incorporates perturbations or disturbances to the system. System shocks may lead to very different outcomes than those presented here; however, these are the types of events that practitioners confront daily – large, infrequent disturbances like floods and fires, pest outbreaks, and invasive species. Second, we focus in the initial model on management goals of coexistence, but managers often look at different types of inter-species dynamics such as between a species of concern and an invasive species [39]. The current modeling efforts could likewise provide guidance on a new suite of management goals with appropriate tweaks to the model. Third, as suggested above, future models will provide benefit to managers and practitioners by moving from a two-patch system to more of a network/graph-theoretic perspective [3]. This could include the analysis of multiple types of network configurations. Finally, and most importantly, future work needs to expand from the simple decision-making of a single manager to the complex interactions of two managers. There we can have various types of patch dynamics such as source/sink versus source/source, differences in management goals or monitoring strategies, and differences in ordering decisions.

To conclude, this is a first step in our understanding management impacts on a landscape by altering the connectedness between patches. Simple management decisions have important consequences on predator-prey dynamics. Simple management decisions and, most of all, simple management tools are able to make a difference. By monitoring the right species and managing at the right scale we may be able to increase the efficiency of biodiversity management with beneficial effects for the peaceful coexistence of biodiversity conservation and human beings. Although this may be only the first step, it still gives important indication as to where management effort should be focused.

6 References

1. Hobbs, R.J., Hussey, B.M.J., Saunders, D.A.: Nature conservation: the Role of corridors. J. Environ. Manage. 31, 93-4 (1990)

2. Meyer WB, Turner II BL. Human population growth and global land-use/cover change. Annu. Rev. Ecol. Syst. 23, 39-61 (1992)

3. Bunn, A.G., Urban, D.L., Keitt, T.H.: Landscape connectivity: A conservation application of graph theory. J. Environ. Manage. 59, 265-78 (2000)

4. Brockington D, Duffy R, Igoe J.: Nature unbound: Conservation, capitalism, and the future of protected areas. Earthscan, London (2008)

5. Child, B.: Parks in transition: Biodiversity, rural development, and the bottom line. Earthscan, London; (2004)

6. Beier, P., Noss, R.F.: Do habitat corridors provide connectivity? Conserv. Biol. 12, 1241-1252 (1998)

7. van Aarde, R.J., Jackson, T.P..:Megaparks for metapopulations: Addressing the causes of locally high elephant numbers in southern Africa. Biol. Conserv. 134, 289-97 (2007)

8. Hilty, J.A., Lidicker, W.Z., Merenlender, A.M.: Corridor ecology: the science and practice of linking landscapes for biodiversity conservation. Island Press, Washington, DC (2006)

9. Schoon, M.L.: Building robustness to disturbance: Governance in southern african peace parks. Dissertation. Indiana University (2008).

10. Soulé, M.E., Terborgh, J. (eds): Continental Conservation: Scientific Foundations of Regional Reserve Networks. Island Press, Washington, DC (1999)

11. Groeneveld, R., Weikard, H.: Terrestrial metapopulation dynamics: a nonlinear bioeconomic model analysis. J. Environ. Manage. 78, 275-85 (2006).

12. York, A., and Schoon, M.L.: Collective action on the Western range: Coping with external and internal threats. Int. J. Comm. 5, 388-409 (2011)

13. Soulé, M.E., Terborgh, J.: Protecting nature at regional and continental scales: a conservation biology program for the new millennium. Bioscience. 49, 809-817 (1999)

14. Lewis, D.J., Plantinga, A.J., Nelson, E., Polasky, S.: The efficiency of voluntary incentive policies for preventing biodiversity loss. Resour. Energy Econ. 33, 192-21 (2011)

15. Langpap, C., Kerkvliet, J.: Endangered species conservation on private land: Assessing the effectiveness of habitat conservation plans. J. Environ. Econ. Manag. 64, 1-15 (2012).

16. Salau, K., Schoon, M.L., Baggio, J. A., Janssen, M.A.: Varying effects of connectivity and dispersal on interacting species dynamics. Ecol. Model. 242, 81-91 (2012)

17. Fontaine, J.J.: Improving our legacy: Incorporation of adaptive management into state wildlife action plans. J. Environ. Manage. 92, 1403-1408 (2011)

18. Urban, D.L., Keitt, T.: Landscape connectivity: A graph-theoretic perspective. Ecology. 82:1205-1218 (2001)

19. Fahrig, L., Nuttle, W.K.: Population ecology in spatially heterogeneous environments. In: Lovett, G.M., Turner, M.G., Jones, C.G., Weathers, K.C. (eds) Ecosystem function in heterogeneous landscapes. Springer, New York (2005)

20. Bodin, Ö., Norberg, J.: A network approach for analyzing spatially structured populations in fragmented landscape. Landscape. Ecol. 22, 31-44 (2007)

21. Cuddington, K.M., Yodzis, P.: Diffusion-limited predator–prey dynamics in Euclidean environments: An allometric individual-based model. Theor. Popul. Biol., 58:259-78 (2000)

22. Droz, M., Pekalski, A.: Coexistence in a predator-prey system. Phys. Rev. E. 63, 051909.051901-6 (2001)

23. Hovel, K.A., Regan, H.M. Using an individual-based model to examine the roles of habitat fragmentation and behavior on predator–prey relationships in seagrass landscapes. Landscape Ecol. 23(Suppl 1),75–89 (2008)

24. Holling, C.S.: Two cultures of ecology. Conserv. Ecol. 2, 4 (1998)

25. Baggio, J.A., Salau, K., Janssen, M.A., Schoon, M.L., Bodin, Ö.: Landscape connectivity and predator-prey population dynamics. Landscape Ecol. 26, 33-45 (2011)

26. Bartumeus, F., Levin, S.A.: Fractal reorientation clocks: Linking animal behavior to statistical patterns of search. PNAS, 105, 19072-19077 (2008)

27. Ives, A.R., Dobson, A.P.: Antipredator behavior and the population dynamics of simple predator-prey systems. Am. Nat. 130, 431-47 (1987)

28. Nelson, E.H., Matthews, C.E., Rosenheim, J.A.: Predators reduce prey population growth by inducing changes in prey behavior. Ecology 85,1853-1858 (2004)

29. Fischhoff IR, Sundaresan SR, Cordingley J, Rubenstein DI. Habitat use and movements of plains zebra (Equus burchelli) in response to predation danger from lions. Behav Ecol 2007; 18:725-9.

30. Lima, S.L.: Putting predators back into behavioral predator–prey interactions. Trends Ecol. Evol. 17, 70-75 (2002)

31. Ioannou, C.C., Ruxton, G.D., Krause, J.: Search rate, attack probability, and the relationship between prey density and prey encounter rate. Behav. Ecol. 19,842-846 (2008)

32. Grimm, V., Berger, U., Bastiansen, F., Eliassen, S., Ginot, V., et al.: A standard protocol for describing individual-based and agent-based models. Ecol. Modell. 198, 115–126 (2006)

33. Schoon, M.L.: Governance Structures in Transboundary Conservation: How Institutional Evolution Influences Cross-Border Cooperation. Conserv. Soc. (forthcoming)

34. Pastor-Satorras, R. ,Vespignani, A.: Epidemic spreading in scale-free networks. Phys. Rev. Lett. 86, 3200–3203 (2001)

35. Boccaletti, S., Latora, V., Moreno, Y., Chavez, M., Hwang, D.-H.: Complex networks: Structure and dynamics. Phys. Rep., 424, 175-308 (2006)

36. Buldyrev, S. V., Parshani, R., Paul, G., Stanley, H. E., Havlin, S.:Catastrophic cascade of failures in interdependent networks. Nature, 464, 1025-1028 (2010).

37. MacArthur, R. H., Wilson, E. O.: The Theory of Island Biogeography. Princeton University Press, Princeton (1967)

38. Hanks, J.: Transfrontier Conservation Areas (TFCAs) in Southern Africa. J. Sustain. Forest. 17, 127-148 (2003)

39. Fenichel, E.P., Horan, R.D., Bence, J.R.: Indirect management of invasive species with bio-control: a bioeconomic model of salmon and alewife in Lake Michigan. Resour. Energy Econ. 32, 500-518 (2010)

ODD Protocol: Managing Connectivity

Purpose:

Exploring the management choice set to uncover which subsets of strategies are most effective at maximizing species coexistence on a fragmented landscape.

State Variables and Scales:

The model includes subpopulations of predator and prey, habitat patches, links, and a manager capable of altering landscape connectivity. Variables differ for the main groups as follows.

Individual predator-prey variables

- Prey:
    - Location (which patch they feed on)
    - Density on a patch
    - Reproduction rate
    - Natural death rate
    - Movement capability

- Predators:
    - Location (which patch they search for prey)
    - Density on a patch
    - Natural death rate
    - Predation (probability of attacking and killing a prey that is located on the same patch)
    - Reproduction rate (a consequence of predation)
    - Movement capability

Landscape variables:

- Patches:
    - Number of patches
    - Size of patches (maximum carrying capacity)
- Links
    - Number of links in the metapopulation
    - Weight of links represent movement cost and the survival likelihood for both species

Manager variables:

- Different type of strategy used to manage the landscape
    - Local vegetation

    - A manager is concerned with the carrying capacity on a specific patch and acts based on vegetation (or carrying capacity), thereby reducing or increasing the ability of species to move to the specific patch.
  - Global vegetation
    - A manager is concerned with the carrying capacity on all patches and acts based on vegetation (or carrying capacity), thereby reducing or increasing the ability of species to move to one of the patches.
  - Local prey
    - A manager is concerned with the number of prey on a specific patch and acts based on the density of the prey species, thereby reducing or increasing the ability of species to move to the specific patch.
  - Global prey
    - A manager is concerned with the number of prey on the whole landscape and acts based on the density of the prey species, thereby reducing or increasing the ability of species to move to one of the patches.
  - Local predator
    - A manager is concerned with the number of predators on a specific patch and acts based on the density of the predator species, thereby reducing or increasing the ability of species to move to the specific patch.
  - Global predator
    - A manager is concerned with the number of predators on the whole landscape and acts based on the density of the predator species, thereby reducing or increasing the ability of species to move to one of the patches.

Process Overview and Scheduling:

The model comprises two connected patches. The link that connects the two patches represents the cost of movement between habitats. Predators and prey move across the landscape according to predetermined rules. Prey and predators reproduce, predators are able to hunt and kill prey and die of natural causes. The carrying capacity of the patches is dynamic, based on the presence of prey. A manager is able to alter the connection between patches in order to hinder or facilitate movement of species. The management objective is always the maximization of the coexistence time.

Figure 1 gives a graphical representation of the process above:

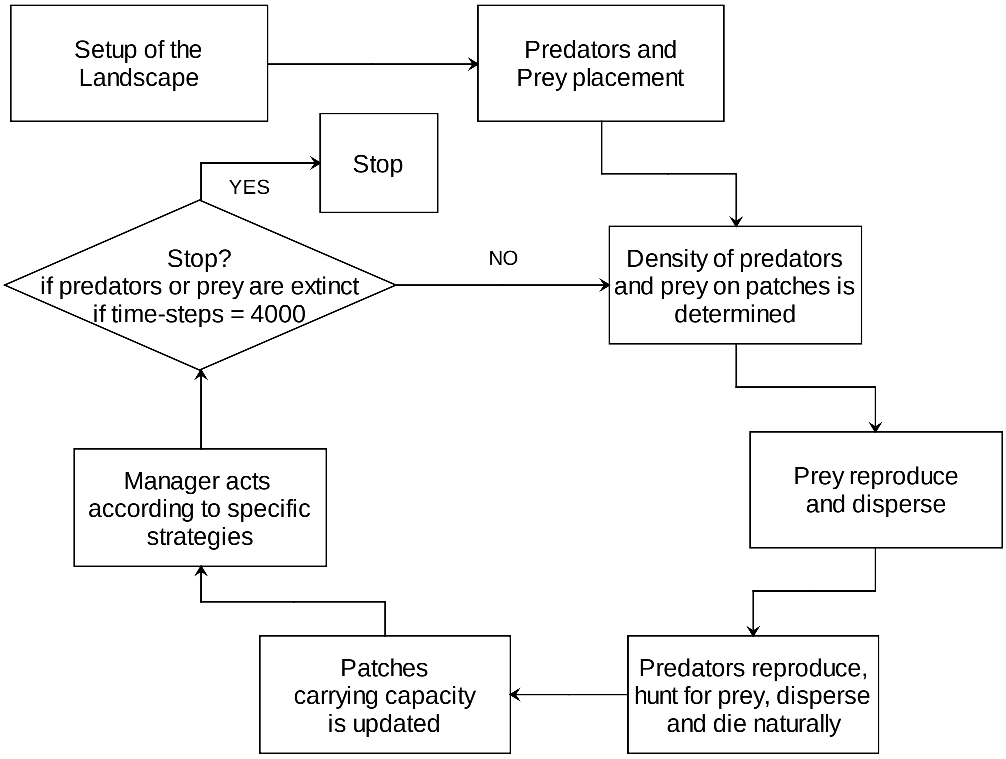

Fig. 6 Initialization and Process diagram

Design Concepts:

Emergence. Population cycles and size dependent on landscape (network).

Interaction. Prey and predators interact through predation and density thresholds (depending on the maximum capacity of their residing patch) that affect their willingness to move. The manager interacts with the ecological system by altering species' ability to move across the landscape.

Stochasticity. The model assumes probabilistic events (initial placement of predators and prey, predation, reproduction, death, dispersal).

Output. The focus is on determining which strategies maximize extinction time (as determined by the absence of both species on the landscape), while minimizing variability in the number of actions undertaken by a manager, using a given strategy.

Initialization:

Patches are fixed and placed randomly. Links are formed between all patches to give the representation of a fully connected network. The weights of these links are chosen in a systematic manner. Maximum carrying capacity is equal for every patch. Predators and prey are randomly assigned with equal populations on each patch. Reproduction, death, and dispersal rates are equal for each prey (predator) agent (i.e. every prey (predator) has the same likelihood of demographic event occurrence). Predation rate, the probability that a predator will catch and consume a prey agent at every given time-step, is also equal for each predator agent.

Upper and lower density thresholds are assigned for prey, while an upper density threshold is assigned for predators. Density thresholds do not vary across patches. These thresholds are used to determine species dispersal once the simulation begins.

A specific strategy is given to a manager. According to the strategy the manager acts by increasing or decreasing the weights connecting the patches, thus altering the rate of successful species dispersal.

Variables are initialized as shown in the table below. In order to correct for the high stochasticity of the model, repeated runs with the Poisson distributed parameters are performed (The mean values for the Poisson distributions are given in the table below). During the simulations the weight of a link will vary according to the actions taken by the manager, which involve facilitating or hindering movement between patches.

Input:

Symbol	**Variable Name**	**Values from distributions used in Monte Carlo simulations**
P	Number of patches	2
C_i	Carrying capacity of a patch	500
DC_i	Limit of prey before deterioration	$0.4 * C_i$
RC_i	Limit of prey before restoration	$0.9 * C_i$
E	Number of links	1
w_{ij}	Weight of link connecting patch *i* to *j*	Takes the initial following values: 30, 60, 100, 250, 500, and 1000. It varies according to manager 'action, but it never falls below 1.
N_x	Initial number of prey on each patch	Poisson with mean 250
x_i	Number of prey on patch *i* at a given point in time	N/A
r	Prey reproduction rate	Poisson with mean 0.25 (25%)
$D_{U,x}$	Prey density threshold affecting prey dispersal	Poisson with mean 0.9 (bounded above by 1)
$D_{L,x}$	Prey density threshold affecting predator dispersal	Poisson with mean 0.3
M_x	Prey movement capability	Poisson with mean 30
N_y	Initial number of predators on each patch	Poisson with mean 100
y_i	Number of predators on patch *i* at a given point in time	N/A
c	Predation rate	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 0.06 (6%)
$D_{U,y}$	Predator density threshold affecting prey dispersal	Poisson with mean 0.7

M_y	Predator movement capability	Poisson with mean 60
Sm	Strategy used by the manager	None, local-veg, global-veg, local-prey, global-prey, local-predator, global-predator
$DM_{U,c}$	Upper threshold of carrying capacity used to determine manager action	Varies between 0.5 and 1 with 0.1 increments
$DM_{L,c}$	Lower threshold of carrying capacity used to determine manager action	Varies between 0 and 0.5 with 0.1 increments
$DM_{U,x}$	Prey upper density threshold used to determine manager action	Varies between 0.5 and 1 with 0.1 increments
$DM_{L,x}$	Prey lower density threshold used to determine manager action	Varies between 0 and 0.5 with 0.1 increments
$DM_{U,y}$	Predator upper density threshold used to determine manager action	Varies between 0.5 and 1 with 0.1 increments
$DM_{L,y}$	Predator lower density threshold used to determine manager action	Varies between 0 and 0.5 with 0.1 increments
iw_{ij}	Weight increase when manager takes action	10
dw_{ij}	Weight decrease when manager takes action	10

Submodels:

Model Setup:

- Network
  - Landscape is represented by a fully connected, weighted, undirected network
  - Multiple links between two patches and loops are not allowed
  - N number of patches is chosen
  - Links are placed between patches
  - Links have some weight assigned
  - Capacity C is assigned to every patch: $C = 500$

- Prey and Predators
  - Initial number of prey, N_x is Poisson distributed with mean 250
  - Initial number of predators, N_y is Poisson distributed with mean 100
  - Random assignment of predators and prey to a patch i
  - Let x_i be a prey assigned to patch i, then the density of prey on patch i $D_{x,i} = \frac{\sum x_i}{C}$
  - Let y_i be a predator assigned to patch i, then the density of predators on patch i, $D_{y,i} = \frac{\sum y_i}{C}$

Model Development:

- Patch, Prey, Predator (consecutively)
    - Calculate population density on their patch (local information)
- Prey
    - Prey on patch *i* reproduce with probability $1-e^{-r(1-D_{x,j})}$, where *r* is Poisson distributed with mean 0.25
    - Prey dispersal (3 scenarios)
        - **1.** When no population density thresholds are exceeded ($[D_{x,i} < D_{U,x}]$ and $[D_{y,i} < D_{U,y}]$)
            - Each prey picks two numbers at random between 0 and 1, call it *rand* and *sand*
            - If *rand* $< (D_{y,i} / D_{U,y})^n$ *or sand* $< (D_{x,i} / D_{U,x})^n$
                - Prey agent wants to move to some neighboring patch.
                - Prey picks another random number, denoted *band.* Let *K* be the set of all neighboring patches *k* s.t *band* $< (M_x / W_{ik})$ {Note $W_{ik} = W_{ki}$},
                    - **If** *K* nonempty
                        - Prey randomly chooses an element (patch) *j* from *K*
                        - Prey agent moves successfully to patch *j*
                        - Prey agent calculates population density on new patch *j*
                        - If $(D_{x,i} > D_{U,x})$ then the prey agent dies (overpopulation)
                    - **Else**
                        - Prey agent dies (death via dispersal)
        - **2.** Intraspecific competition for space/food ($[D_{x,i} > D_{U,x}]$)
            - Prey agent wants to move to the nearest neighboring patch *j*.
            - Prey picks a random number, call it *band*
                - **If** *band* $< (M_x / W_{ij})$
                    - Prey agent moves successfully
                    - Prey agent calculates prey density on new patch *j*
                    - If $(D_{x,j} > D_{U,x})$ then the prey agent dies (overpopulation)
                - **Else**
                    - Prey agent dies (death via dispersal)

        - **3.** Anti-predator behavior ($[D_{y,i} > D_{U,y}]$)
            - Same procedure as **2.**
- Predators
    - Predation
        - If there any prey on the predator's resident patch *i*
            - Pick one prey agent at random
            - With probability $1-e^{-cD_{x,j}}$, where *c* is Poisson distributed with mean 0.9, successfully eat the prey

- With corresponding probability f, which is Poisson distributed with mean 0.5, predator agent gives birth
- Predators die of natural causes with probability d, which is Poisson distributed with mean 0.06
- Predator dispersal (2 scenarios)
  - **1.** When no population density thresholds are exceeded ([$D_{x,i} > D_{L,x}$]
    - Each predator picks one number at random between 0 and 1, call it *rand*
    - If $rand < ([D_{x,i} - 1]/[D_{L,x} - 1])^n$
      - Predator picks another random number, denoted *band.* Let K be the set of all neighboring patches k s.t $band < (M_y / W_{ik})$ {Note $W_{ik} = W_{ki}$},
        - **If** K nonempty
          - Predator randomly chooses an element (patch) j from K
          - Predator moves successfully to patch j
          - Predator calculates population density on new patch j
          - If $(D_{x.j} < D_{L,x})$ then the predator agent dies (food scarcity)
        - **Else**
          - Predator agent dies (death via dispersal)
  - **2.** Predator foraging behavior ([$D_{x,i} < D_{L,x}$])
    - Predator picks another random number, denoted *band.* Let K be the set of all neighboring patches k s.t $band < (M_y / W_{ik})$ {Note $W_{ik} = W_{ki}$},
      - **If** K nonempty
        - Predator randomly chooses an element (patch) j from K
        - Predator moves successfully to patch j
        - Predator calculates population density on new patch j
        - If $(D_{x,i} < D_{L,x})$ then the predator agent dies (food scarcity)
      - **Else**
        - Predator agent dies (death via dispersal)

Carrying capacity update

On each patch:

- **If** $x_i => DC_i$ (if there are too many prey on patch i)
  - **Set** $C_i = C_i - 1$ (capacity of patch i is reduced)
- **If** $x_i < RC_i$ (if there are few prey on patch i)
  - **Set** $C_i = C_i + 1$ (capacity of patch i is increased)

Manager strategies

A manager acts upon a given strategy. A strategy *Sm* is given at the beginning of each simulation run and remains constant throughout the simulation run. It is worth mentioning that strategies containing the term ‘local’ reflect management of only one specific patch, while ‘global’ strategies pertain to management of the whole landscape.

- None: Manager does not act
- Local-veg: Manager actions depend on the carrying capacity of a specific patch *i*. His objective is local maximization of species coexistence.
  - If the carrying capacity of patch *i* (C_i) is below a specific threshold, the manager will hinder species movement towards that patch so as to allow patch recovery.
    - **If** $C_i \leq C_i * DM_{U,c}$
      - **Set** $wij = wij + iw_{ij}$
  - If carrying capacity of patch *i* (C_i) is above a certain threshold, the manager will facilitate species movement towards that patch so as to promote species propagation.
    - **If** $C_i \geq C_i * DM_{L,c}$
      - **Set** $wij = wij - dw_{ij}$
- Global-veg: Manager actions depend on the carrying capacity of all patches. The objective is global maximization of species coexistence.
  - If the carrying capacity of patch *i* (C_i) or patch *j* (C_j) is below a specific threshold, while neither patch *i* or *j* have carrying capacity above $C_{i(j)}*DM_{L,c}$, the manager will hinder species movement towards that patch so as to allow patch recovery.
    - **If** $C_i \leq C_i * DM_{U,c}$ OR $C_j \leq C_j * DM_{U,c}$
      AND
      $C_i \geq C_i * DM_{L,c}$ OR $C_j \geq C_j * DM_{L,c}$
      - **Set** $wij = wij + iw_{ij}$
  - If the carrying capacity of patch *i* (C_i) or patch *j* (C_j) is above a specific threshold, while neither patch *i* or *j* have carrying capacity below $C_{i(j)}*DM_{U,c}$, the manager will facilitate species movement towards that patch so as to allow repopulation.
    - **If** $C_i \geq C_i * DM_{L,c}$ OR $C_j \geq C_j * DM_{L,c}$
      AND
      $C_i \leq C_i * DM_{U,c}$ OR $C_j \leq C_j * DM_{U,c}$
      - **Set** $wij = wij - dw_{ij}$
- Local-prey: Manager actions depend on the number of prey living on a specific patch *i*. The objective is local maximization of species coexistence.
  - If prey density on patch *i* is below a specific threshold $DM_{L,x}$ the manager will facilitate species movement to repopulate patch *i*.
    - **If** $D_{x,i} \leq DM_{L,x}$
      - **Set** $wij = wij - dw_{ij}$
  - If prey density on patch *i* is above a specific threshold $DM_{U,x}$, the manager will hinder species movement to avoid endangering the carrying capacity.
    - **If** $D_{x,i} \geq DM_{U,x}$
      - **Set** $wij = wij + iw_{ij}$
- Global-prey: Manager actions depend on the number of prey living throughout the landscape. The objective is global maximization of species coexistence.

    - If prey density on patch *i* or *j* ($D_{x,i}$ and $D_{x,j}$) falls below $DM_{L,x}$, while density of prey is not above $DM_{U,x}$ in any other patch, the manager will facilitate species movement.
        - **If** $D_{x,i} \leq DM_{L,x}$ OR $D_{x,j} \leq DM_{L,x}$
          AND
          $D_{x,i} \geq DM_{U,x}$ OR $D_{x,j} \geq DM_{U,x}$
            - **Set** $wij = wij - dw_{ij}$
    - If prey density on patch *i* or *j* ($D_{x,i}$ and $D_{x,j}$) is above a $DM_{U,x}$, while density of prey is not below $DM_{L,x}$ in any other patch, the manager will hinder species movement.
        - **If** $D_{x,i} \geq DM_{U,x}$ OR $D_{x,j} \geq DM_{U,x}$
          AND
          $D_{x,i} \leq DM_{L,x}$ OR $D_{x,j} \leq DM_{L,x}$
            - **Set** $wij = wij + iw_{ij}$
- Local-pred: Manager actions depend on the number of predators living on a specific patch *i*. His objective is local maximization of species coexistence.
    - If predator density on patch *i* is below a specific threshold $DM_{L,y}$ the manager will facilitate species movement to repopulate patch *i*.
        - **If** $D_{y,i} \leq DM_{L,y}$
            - **Set** $wij = wij - dw_{ij}$
    - If predator density on patch *i* is above a specific threshold $DM_{U,y}$, the manager will hinder species movement to avoid endangering the carrying capacity.
        - **If** $D_{y,i} \geq DM_{U,y}$
            - **Set** $wij = wij + iw_{ij}$
- Global-pred: Manager actions depend on the number of predators living throughout the landscape. The objective is global maximization of species coexistence.
    - If predators density on patch *i* or *j* ($D_{y,i}$ and $D_{y,j}$) falls below $DM_{L,y}$, while density of predators is not above $DM_{U,x}$ in any other patch, the manager will facilitate species movement.
        - **If** $D_{y,i} \leq DM_{L,y}$ OR $D_{y,j} \leq DM_{L,y}$
          AND
          $D_{y,i} \geq DM_{U,y}$ OR $D_{y,i} \geq DM_{U,y}$
            - **Set** $wij = wij - dw_{ij}$
    - If prey density on patch *i* or *j* ($D_{y,i}$ and $D_{y,j}$) is above a $DM_{U,y}$, while density of prey is not below $DM_{L,y}$ in any other patch, the manager will hinder species movement.
        - **If** $D_{y,i} \geq DM_{U,y}$ OR $D_{y,j} \geq DM_{U,y}$
          AND
          $D_{y,i} \leq DM_{L,y}$ OR $D_{y,j} \leq DM_{L,y}$
            - **Set** $wij = wij + iw_{ij}$

Implementation:

Netlogo 4.1.3