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Network analysis for species management in rivers networks: Application to the Loire River

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ABSTRACT

Forecasting the colonization process is important for wildlife managers who supervise the reintroduction of endangered species or control the spread of invasive species. Patch connectivity is thus critical to predicting the fates of expanding populations. Connectivity in river networks results from river dendritic structure and dispersal modality of organisms. Both factors may strongly affect the colonization process and the efficiency of conservation action plans. Based on empirical data, we simulated, using a simplified model with limited number of parameters, the colonization of a large river network, the Loire River, by the native Eurasian beaver and the invasive African clawed frog. For each species, we inferred model parameters (dispersal behavior and distances) by comparing the simulated and the observed distributions. Using network theory, we evaluated the efficiency of alternative conservation strategies to prevent or promote colonization of the river network. Network robustness to fragmentation and disturbance was also assessed. The model accurately predicted > 70% of the observed species ranges. Conservation strategies that selectively protect habitat patches with the highest connectivity values provide a weak advantage at preventing connectivity loss compared to random protection strategies. In contrast, the targeted destruction of highly connected patches had a much stronger effect on the fragmentation of the network than the random removal of habitat patches. Spatial network topology strongly contributes to determining colonization patterns of large river watersheds. Network theory allows tests for robustness of rivers to fragmentation and disturbance, and identification of strategies for conservation planning.

1. Introduction

A major challenge in conservation biology is to predict population persistence. Such predictions are often difficult as they rely on the spatial divisions of populations, dispersal patterns, and the interaction between species of interest and landscape structure. These issues can be addressed by modeling populations into a network of habitat patches that are connected through edges (i.e. connectivity links) depending on the dispersal pathways of individuals (Baguette et al., 2013; Calabrese and Fagan, 2004; Crooks and Sanjayan, 2006; Moilanen and Nieminen, 2002). River networks are particularly challenging to model as a network of habitat patches. Their dendritic and hierarchical structures, as well as the directionality of water flow, bias the movements of individuals so that spatially close watercourses can be isolated from each other (Campbell Grant et al., 2007; Fagan, 2002; Samia et al., 2015). Furthermore, upstream disturbances can affect distant downstream populations because of asymmetric movements of individuals from headwaters to mainstreams (Vuilleumier and Possingham, 2006) but bias can also occur in other directions (Vuilleumier et al., 2010). Consequently, the effects of local environmental changes can propagate along the river network and have a greater impact on the overall connectivity than in most terrestrial environments (Fagan, 2002).

Not all freshwater organisms move strictly along the watercourses, though. Many species use two dispersal pathways in river networks: along the river watercourses and overland (between watercourses). Either of these can drastically alter the estimates of connectivity among

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habitat patches and other critical estimates like habitat occupancy or population persistence. These alternative dispersal behaviors are well documented empirically (Campbell Grant et al., 2010, 2007) but are seldom implemented in the design of wildlife management plans.

The use of network theory as a means of modeling metapopulation dynamics and connectivity in river networks is promising for the management of freshwater ecosystems (Campbell Grant et al., 2007; Erős et al., 2011a, 2011b; Fagan, 2002). By definition, a network is a set of nodes (points) connected by edges (links). In metapopulation ecology, nodes represent suitable habitat patches and edges potential pathways or corridors for dispersal (e.g. Baguette et al., 2013; Minor and Urban, 2008; Urban and Keitt, 2001). Using conceptualized representations of metapopulations as networks, various measures characterizing critical aspects of population viability can be estimated. For example, the metapopulation capacity of a fragmented landscape has been derived from the network centrality measure (Hanski and Ovaskainen, 2000). Network metrics have also been used to estimate population abundance and persistence (Webb and Padgham, 2013). Among them, connectivity indices can quantify the importance of a habitat patch for dispersal within the network by quantifying how frequently a habitat patch is used as an intermediate step between other habitat patches during dispersal (e.g. the betweenness centrality, Erős et al., 2011a). In addition, the range expansion of a population can be characterized by measuring how large a network is (e.g., using the diameter of the network, Barták et al., 2013; Rayfield et al., 2011). The effect of habitat fragmentation on connectivity can also be quantified using metrics such as the probability of connectivity, *PC* (Saura and Pascual-Hortal, 2007). *PC* quantifies the amount of reachable habitat in the landscape by accounting for the connectivity both within and between groups of connected habitat patches (Saura et al., 2014; Saura and Pascual-Hortal, 2007). Finally, network analysis algorithms allow for testing both the robustness to fragmentation and the resilience to disturbance of population networks by assessing network properties (summarized by network metrics) as nodes are removed in increasing numbers (Barabási and Bonabeau, 2003; Fortuna et al., 2006; Minor and Urban, 2008).

Here, we present a method to select management strategies for conservation in river networks. Our method generates spatial networks that account for different dispersal behaviors (along watercourses and/or overland). Firstly, we investigated how dispersal behavior associated with the dendritic structure of river network influences connectivity between habitat patches and colonization in a river network. To do so, we simulated the colonization of the Loire River drainage by a reintroduced species, the Eurasian beaver *Castor fiber* (Linnaeus 1758) and an invasive species, the African clawed frog *Xenopus laevis* (Daudin 1802). The former species disperses along watercourses (Fustec et al., 2001; Halley and Rosell, 2002; Heidecke, 1984; Saveljev et al., 2002), while the latter disperses along watercourses and overland (Fouquet and Measey, 2006; Lobos and Jaksic, 2005). We simulated the expected distribution of both species along the river network for various dispersal distances. Simulation results were then compared to the observed distributions, and value of dispersal distances were estimated for each species based on the true skill statistic (Allouche et al., 2006). Secondly, using inferred dispersal distances for each species, we quantified the effectiveness of management strategies in either promoting (relevant for species of conservation interest) or limiting (relevant for invasive species) colonization of the network. Finally, we provide guidelines as to what may promote or impede colonization of large river networks and discuss general interest in the use of network theory to design conservation and management action plans at the scale of the river network.

2. Materials and methods

2.1. Modeling approaches

Our goal was to simulate the invasion processes that have led to the observed species distributions in the Loire River for the Eurasian beaver and the African clawed frog. Available data included (1) the introduction points and (2) the current distribution. To simulate the species' extension through the network, we used a model that considered successive colonization events generating occupied habitat patches in the river network. From this model, we inferred dispersal distance for the two species in an effort to reproduce the observed distribution. Then, to evaluate different management actions, we considered the currently observed distributions and the inferred dispersal distances. We thus consider first a dynamic model that uses historical range expansion to estimate dispersal and second a (stationary) equilibrium model that utilizes current distributions to evaluate management actions.

2.2. Model of the river network

The river network was modeled as a set of habitat patches (nodes) regularly distributed along the river and a set of edges (corridors) that connect habitat patches (Fig. 1a). The number and distributions of edges within the network depended on the river topology and the dispersal behavior of each species: dispersal occurs along the watercourse (in-stream dispersal, Fig. 1b) for the Eurasian beaver and along the watercourse but also overland for the African clawed frog (in-stream and overland dispersal Fig. 1b). We thus obtained two networks differing in connectivity patterns. These networks were used first to simulate species colonization and second to compare those simulations with the observed distribution of each species in the network. For the latter, habitat patches were considered occupied or unoccupied according to the observed species distribution in the river watershed.

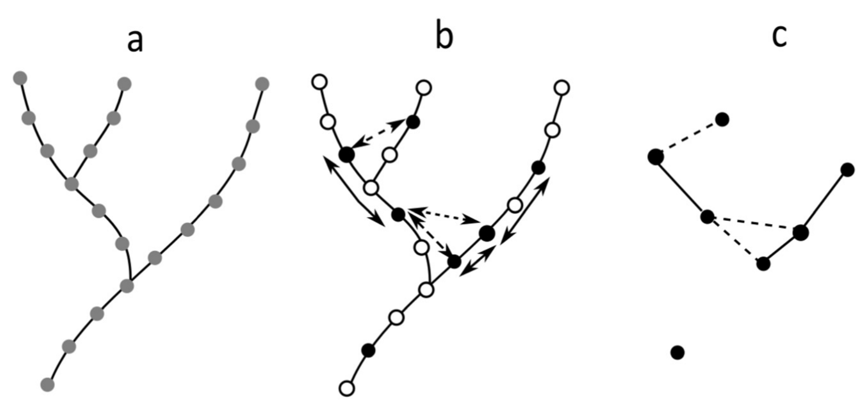

Fig. 1. The river network (a) was modeled as a set of connected spatial habitat patches (grey nodes). This network is converted into a presence-absence map (b) and into a graph according to the dispersal behavior of the species (c). The graph connectivity between occupied patches (black nodes) depended on dispersal behavior – in-stream (b, solid arrows) and overland (b, dotted arrows) - and dispersal distance. The graph (c) shows connections in-stream (solid lines) and overland (dotted lines) between occupied patches.