Network Analysis for Species Management in Rivers Networks: Application to the Loire River

A. Chaput-Bardy^{a,b,*†}, N. Alcalá^{c,d†}, J. Secondi^{a,e‡}, S. Vuilleumier^{c,f‡}

^a GECCO, Groupe Ecologie et Conservation des Vertébrés, Université d'Angers, UFR Sciences, 2 Boulevard Lavoisier, F-49045 Angers cedex 1, France

^b La Maison du Lac de Grand-Lieu, rue du Lac, F-44830 Bouaye, France.

^c Department of Ecology and Evolution, University of Lausanne, CH-1015 Lausanne, Switzerland.

^d Department of Biology, Stanford University, Stanford, CA 94305-5020, USA.

^e UMR 5023 Écologie des Hydrosystèmes Naturels et Anthropisés, Université de Lyon 1, ENTPE, CNRS, F-69622 Villeurbanne, France.

^f School of Life Sciences, École Polytechnique Fédérale de Lausanne, CH-1015 Lausanne, Switzerland.

nalcala@stanford.edu

severine.vuilleumier@epfl.ch

jean.secondi@univ-angers.fr

* Corresponding author at: La Maison du Lac de Grand-Lieu, rue du Lac, 44830 Bouaye, France (tel: +33249109002 ; email: chaput_bardy_audrey@hotmail.com or a.cadou@maisondulacdegrandlieu.com)

[†] Both authors contributed equally.

[‡] Both authors supervised the research project.

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 more than 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.

Keywords: connectivity, conservation biology, dispersal, freshwater species, graph theory, river

49 1. Introduction

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

66 Not all freshwater organisms move strictly along the watercourses, though. Many species use
67 two dispersal pathways in river networks: along the river watercourses and overland (between
68 watercourses). Either of these can drastically alter the estimates of connectivity among habitat
69 patches and other critical estimates like habitat occupancy or population persistence. These
70 alternative dispersal behaviors are well documented empirically (Campbell Grant et al., 2010,
71 2007) but are seldom implemented in the design of wildlife management plans.

72 The use of network theory as a means of modeling metapopulation dynamics and connectivity
73 in river networks is promising for the management of freshwater ecosystems (Campbell Grant
74 et al., 2007; Erös et al., 2011a, 2011b; Fagan, 2002). By definition, a network is a set of nodes
75 (points) connected by edges (links). In metapopulation ecology, nodes represent suitable
76 habitat patches and edges potential pathways or corridors for dispersal (e.g. Baguette et al.,
77 2013; Minor and Urban, 2008; Urban and Keitt, 2001). Using conceptualized representations
78 of metapopulations as networks, various measures characterizing critical aspects of
79 population viability can be estimated. For example, the metapopulation capacity of a
80 fragmented landscape has been derived from the network centrality measure (Hanski and
81 Ovaskainen, 2000). Network metrics have also been used to estimate population abundance
82 and persistence (Webb et al., 2013). Among them, connectivity indices can quantify the
83 importance of a habitat patch for dispersal within the network by quantifying how frequently
84 a habitat patch is used as an intermediate step between other habitat patches during dispersal
85 (e.g. the betweenness centrality, Erös et al., 2011a). In addition, the range expansion of a
86 population can be characterized by measuring how large a network is (e.g., using the diameter
87 of the network, Barták et al., 2013; Rayfield et al., 2011). The effect of habitat fragmentation
88 on connectivity can also be quantified using metrics such as the probability of connectivity,
89 *PC* (Saura and Pascual-Hortal, 2007). *PC* quantifies the amount of reachable habitat in the
90 landscape by accounting for the connectivity both within and between groups of connected
91 habitat patches (Saura, et al., 2014; Saura and Pascual-Hortal, 2007). Finally, network
92 analysis algorithms allow for testing both the robustness to fragmentation and the resilience to
93 disturbance of population networks by assessing network properties (summarized by network
94 metrics) as nodes are removed in increasing numbers (Barabasi and Bonabeau, 2003; Fortuna
95 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 discusses 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 *dynamic 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.

2.3 Simulation of colonization

Our aim was to simulate the current focal species' distributions given their introduction site along the river, accounting for both the spatial structure of the habitat and the dispersal abilities of the species. To do so, we simulated colonization along the river using a stochastic patch occupancy model (SPOM; see review in Hanski and Ovaskainen, 2003). Under SPOMs, the habitat is subdivided into a finite number of habitat patches, and only the presence or absence of the focal species is modelled, not its local dynamics. Colonization along the river then occurred as a succession of colonization events from occupied habitat patches. Our model quantified the dynamics of occupied and unoccupied habitat patches, thus following the metapopulation paradigm (Levins, 1969) commonly used in conservation biology (Bascompte and Solé, 1998; Hanski and Ovaskainen, 2000). However, in our model we only simulated the colonization process and did not consider the metapopulation dynamics per se (i.e., extinction-colonization dynamics), because extinction events were not likely to be important in the time scale investigated, and because we were interested in the expansion of the species in the network and the control of this expansion. The colonization process is characterized by a unique parameter that represents the maximal dispersal distance and depends on the presence of unoccupied habitat within this range. One critical advantage of this approach is the limited number of model parameters – which are often difficult to estimate. Such an approach has proven successful in describing large-scale population dynamics and the design of conservation plans (Akçakaya et al., 2007).

Under the SPOM, the state of occupancy of patch i is denoted p_i , where p_i is 1 if patch i is occupied, and 0 otherwise. We considered a colonization process, where empty patches could become occupied, but occupied patches could not become unoccupied, so the number of empty patches decreased through time. Following Hanski (1994), the connectivity of patch i , denoted S_i , followed:

$$S_i = \sum_j m_{ij} p_j A_j. (1)$$

Where m_{ij} is 1 when habitat patches i and j are within the species dispersal distance and 0 otherwise. We assumed that habitat patches have the same sizes and thus $A_j=1$ for all j . We considered time to be continuous, and that the rate at which an empty patch i is colonized was proportional to S_i , with proportionality constant c . The process simulated was thus a continuous-time Markov chain, and the waiting time for a change in habitat patch occupancy was exponentially distributed with rate $\sum_j c S_j (1 - p_j)$, where terms in $(1 - p_j)$ ensured that only empty patches could be colonized. The probability of colonization of habitat patch i was thus

$$C_i = \frac{c S_i (1 - p_i)}{\sum_j c S_j (1 - p_j)} = \frac{S_i (1 - p_i)}{\sum_j S_j (1 - p_j)} (2)$$

Interestingly, the constant c from the numerator and the denominator cancel out in eq. 2; as a result, we can compute the probability of colonization of all habitat patches without knowing the actual colonization rate. This reduces the number of model parameters and makes our model robust to estimation error in the colonization rate.

Simulation of the colonization process was a random process that relied, from eqs. 1 and 2, on the matrix $\mathbf{M} = [m_{ij}]$, representing the network of habitat patches and the occupancy vector $\vec{p} = [p_1, p_2, \dots, p_n]$. To start each simulation, we set $p_i=1$ for the habitat patch i documented to be

the introduction site of the focal species and $p_j=0$ for all other habitat patches $j, j \neq i$. Then, at each step of the simulation, a new empty habitat patch was colonized. This habitat patch was randomly selected among habitats within the dispersal distance of the species according to their colonization probability C_j , where greater C_j values indicate a higher probability of being selected i.e. the colonized habitat patch was selected randomly [0-1] among the normalized distribution of C_j . Therefore, an empty habitat patch could be colonized only when located within the range (dispersal distance) of an occupied patch. Its probability of being colonized increases with the number of occupied patches present in its range (defined by the dispersal distance). Thus, in the model, a unique number, the maximal dispersal distance, characterized colonization. Dispersal was thus uniform within its range and modeled without kernel structure, an assumption that has been shown to be robust when evaluating management scenarios (Chadès et al., 2011). Colonization proceeded as long as the number of occupied patches $\sum_i p_i$ was less than the observed number of occupied patches for the focal species. The algorithm was implemented in R (R Core Team). This simulation was replicated 100 times for each dispersal distance.

2.4. Comparison of simulated and observed ranges

To compare the simulated and observed distributions of the species in the network, and to estimate the species' dispersal distances we calculated *the species range* (Barták et al., 2013). The species range was defined as the length of the union of all the shortest paths between pairwise occupied habitat patches (Barták et al., 2013). We also considered the *size* of the species range, which was defined as the number of habitat patches included in the species range. We further estimated the predictive accuracy of the correspondence between observed and simulated species distributions by computing the true skill statistic (TSS) as proposed by Allouche et al. (2006). The TSS is defined as follows:

$$TSS = sensitivity + specificity - 1, \quad (3)$$

with sensitivity being the proportion of observed presences that are predicted as such and the specificity being the proportion of observed absences that are predicted as such. Sensitivity thus accounts for omission errors, taken as the size of the union of observed and simulated ranges, divided by the size of the observed range. Likewise, specificity includes commission errors. In our case the specificity corresponded to the size of the union of observed and simulated patches outside the species range, divided by the observed number of patches outside of the range.

TSS values range from -1 to +1, where a value of 1 predicts a perfect agreement between observed and simulated species distributions, and a value equal to or less than 0 signals a performance no better than random. As for our investigations, where we evaluated increasing values of dispersal distance, we expected sensitivity to converge to a constant value. The number of occupied habitat patches increased with dispersal distance, as did the proportion of overlap between observed and simulated presences. However, the specificity decreased with increasing dispersal distance, because the proportion of observed absences that were predicted as such decreased. There was thus a maximum value for the TSS, which could be identified by considering the value of the slope of the TSS.

2.5 Measures of connectivity

We quantified the connectivity in the network with two measures: *the betweenness centrality*, as a local measure of connectivity (i.e., contribution of a habitat patch to the network), and *the*

probability of connectivity (*PC*) of habitat patches, as a global measure of connectivity (i.e., whole network). Betweenness centrality measures the number of times a given habitat patch acts as a “bridge” along the shortest path between two other habitat patches, considering all pairs of patch in the network (Freeman, 1978), and is given as:

$$B_i = \sum_{s \neq i, t \neq i} \frac{v_{s,t}^i}{v_{s,t}}, (4)$$

where $v_{s,t}^i$ is the number of paths from patch s to patch t that pass through patch i and $v_{s,t}$ is the total number of paths from patch s to patch t . Betweenness centrality (B_i) has values between 0 and 1, which indicates the importance of a given patch in the transfer of information (here individuals) between other patches of the network (Estrada and Bodin, 2008). This measure has been used to highlight major routes for dispersal (Estrada and Bodin, 2008; Minor and Urban, 2007; Urban et al., 2009). B_i scores were computed between all pairs of habitat patches in each network generated and for each dispersal distance. Because networks associated with the two species have different numbers of edges, we did not compare the absolute scores across networks. Instead, we used the Jenks' Natural Breaks algorithm (Jenks, 1963) to classify each habitat patch as having a high, medium or low value of B_i . The probability of connectivity characterizes how important the surrounding of a habitat patch is in relation to the whole network. It specifically computes the probability that two randomly chosen habitat patches are reachable from one other (Saura and Pascual-Hortal, 2007). *PC* was computed as follows for a network composed of n habitat patches:

$$PC = \frac{\sum_i \sum_j m_{ij}^*}{(n-1)^2}, (5)$$

where $m_{ij}^* = 1$ if there is a path between nodes i and j , and 0 otherwise and $m_{ii}^* = 0$ for all i . *PC* ranges from 0 (when all habitat patches are isolated) to 1 (when no patches are isolated). *PC* can also be interpreted as a prediction of the colonization process, because it corresponds to the proportion of habitat that would be colonized if the colonization simulations were run long enough for the species to occupy its entire reachable habitat.

2.6. Management strategies and their assessment

We assessed four management strategies designed either to promote colonization of a species of conservation interest or to control the expansion of an invasive species. The first two conservation strategies would protect habitat patches of the river network either randomly - **the random protection strategy** - or by targeting habitat patches with the highest betweenness centrality scores - **the targeted protection strategy**. The proportion of protected habitat patches in the network varied between 0.5% and 10%. We then evaluated the performance of both conservation strategies by progressively removing habitat patches from the network at random until 80% of the habitat patches were removed. For the two control strategies, no habitat patch was protected, and habitat patches were progressively removed from the network until 80% were gone. Similar procedures to those described above were used to remove the habitat patch either at random - **the random control strategy**, or according to habitat patch betweenness centrality scores - **the targeted control strategy** - in which patches with the highest scores were removed first.

We evaluated the relative efficiency of the four above-described management strategies to maintain network connectivity by assessing resilience of the network in relation to habitat

removal (Albert et al., 2000). A network was assumed to be robust and resilient if increasing the loss of patches did not decrease the PC value. Finally, we computed the minimum number of habitat patches needing to be removed to reduce by half the initial value of PC , denoted α_{min} :

$$\alpha_{min} = \min \left\{ \alpha \in \{0, 1, \dots, n\} \mid \frac{PC_{\alpha}}{PC_0} \leq 0.5 \right\}, (6)$$

where PC_{α} is the value of PC following the removal of α habitat patches and PC_0 is the initial value of PC , without habitat patch removal. We reported the median value of α_{min} across the 1 000 replicates.

Wilcoxon signed-rank tests were carried out between strategies (random *versus* targeted), across different dispersal distances, and for different proportions of habitat patch protection (0.5% to 10% when applies).

Network analyses and computation of connectivity indices were computed using the package *igraph* (Csardi and Nepusz, 2006) available in R (R Core Team).

2.7 Case study: a protected and an invasive species in a large river network

We retrieved the spatial distribution of waterways (excluding rivulets) of the Loire River (Appendix A, Fig. A1) from the French national hydrographical database (BD CARTHAGE® 2011, <http://www.sandre.eaufrance.fr/>). The river network was then modeled as 18 084 habitat patches distributed along the river network and connected by edges 1km in length. For the beaver, supplementary simulations were conducted restricting colonization processes to the mainstream and its main tributaries with Strahler order greater than 1 (Strahler, 1957); this network was referred as the ‘main network’ and will be compared to the ‘whole network’.

The distributions of the Eurasian beaver and the African clawed frog on the Loire River were provided by the French National Agency for Wildlife (ONCFS). In particular, the presence-absence data from the Loire River watershed was utilized (Appendix A, Fig. A2 and A3). We considered 399 habitat patches that were occupied by the Eurasian beaver and 57 habitat patches for the African clawed frog.

We compared the observed species distributions with simulated ones under different dispersal scenarios. Observed distributions were obtained by assigning the observed species occurrences to habitat patches and edges in the spatial river network (overlap). We explored a wide range of dispersal distances for both species, from 2 to 200 km for beavers along watercourses and from 1 to 20 km overland and along watercourses for African clawed frogs. Chosen distances and dispersal abilities encompass expected dispersal values for both species. Indeed, beavers have been shown to disperse over long distance in rivers, with observed dispersal distances varying from a few kilometers to 170 km (Heidecke, 1984; Saveljev et al., 2002). The longest dispersal distance recorded on the Loire River for the European beavers is 80 km (Fustec et al., 2001; Halley and Rosell, 2002). The African clawed frog was estimated to spread between water bodies at a rate between 3.1 km/year and 5.4 km/year (Lobos and Jaksic, 2005), and the colonization rate of the Loire River watershed is estimated at 1 km/year (Fouquet and Measey, 2006). In the simulations, each species was ‘introduced’ into the patch nearest to their documented introduction site, close to Blois for beavers (47°35'38"N, 1°19'41"E) and Bouillé Saint Paul for frogs (47°1'33.96"N, 0°20'42"W).

3. Results

3.1. Network topology and colonization

For both species, TSS values increased with dispersal distance, reaching a maximum value at a dispersal distance identified by the slope of the TSS values., namely when the TSS values are maximal and the slope is close to zero i.e. within $[-0.003;0.003]$. For the beaver, the maximum TSS value was reached when the dispersal distance was between 80 km to 180 km (Fig. 2a) for the whole network and between 120 and 180 km for the main network (Fig. 2b). For the African clawed frog, this distance was between 4 km and 10 km. The maximal values of TSS are around 0.4 (whole network) and 0.7 (mainstreams) for the beaver, and 0.7 for the frog (Fig. 2). This means that up to 70% of the simulated range corresponded to the observed range, with up to 85% of the habitat patches correctly classified. According to TSS, simulations predicted the observed species distributions when dispersal was greater than 80 km for the Eurasian beaver and greater than 4 km for the African clawed frog.

We computed betweenness centrality scores for the observed occupancy patches for both species considering distances ranging from 80 to 180 km for the beaver and from 4 to 10 km for the frog. For the Eurasian beaver, which disperses in-stream, only 1% of habitat patches showed a high betweenness centrality (range 34 733-79 617), while 7% showed a medium score (range 8 440-34 733). The patches with the highest centrality scores were located on the mainstreams in the center of the network (Fig. 3). For the African clawed frog, which disperses overland, 16% and 23% of patches showed high (range 210-523) and medium (range 63-210) betweenness centrality scores, respectively. Patches with the highest scores were scattered in the eastern part of the colonized area (Fig. 4) and were independent of the dispersal distance (from 4 to 10 km). The patch scores were highly correlated across dispersal distances in both species (Spearman rank correlation test: Eurasian beaver $0.868 < \rho < 0.916$, $p < 2E-16$; African clawed frogs $0.455 < \rho < 0.774$, $p < 1.024E-12$). Consequently, we only present results for an 80-km dispersal distance in the beaver and 4-km dispersal distance in the frog.

3.2. Effect of management strategy on connectivity

We assessed network robustness to fragmentation and resilience (i.e. the capacity to respond to perturbations) under the four management strategies described above: random protection, targeted protection, random control, and targeted control of patches.

Protection strategy – For each species, we observed an abrupt transition between high and low *PC* values (Fig. 5 and 6). The percentage of removed patches required to reach the transition increased with dispersal distance. For the Eurasian beaver (Fig. 5), when considering 1% of protected patches, the transition occurs around 2%, 40% and 60% of removed patches, representing distances of 80 km, 120 km and 160 km, respectively. Thus, network robustness increased with dispersal distance (Table 1). For the African clawed frog a much larger proportion of habitat patches (40-60%) had to be removed to decrease the *PC* value, and the effect of dispersal distance was weaker (Table 1).

The percentage of protected patches did not significantly influence the changes in *PC* values for either species (Fig. 5 and 6, Appendix A: Tables A1 and A2). For the beaver, when considering a 120 km maximum dispersal distance and 1%, 5% and 10% of protected patches, the transition occurred when 40% of the habitat patches were removed. We also found limited evidence of an effect of the protection strategy (random *vs* targeted) on connectivity (Table 2). Although the percentage of removed patches required to halve *PC* median value was always higher in the protection strategy, we only detected a few significant effects in four cases (Table 2). Assuming a dispersal distance of 80 km for the beaver, we found that removing less than 1% of patches was sufficient for halving the *PC* whatever the protection strategy. We also found that targeted protection was better than random protection when the percentage of protected patches reached 10%. For the African clawed frog, halving the *PC* required substantial habitat patch removal (48% to 89%), and a significant difference between random and targeted strategies was observed when 10% of habitat patches were protected (assuming 6-km dispersal distance).

Control strategy – The number of removed patches necessary to halve the *PC* values was lower under the targeted control strategy than under the random control strategy, regardless of species or dispersal distance. The effect was particularly strong in the Eurasian beaver under the targeted strategy (Fig. 7, Table 3). When using a targeted strategy, removing less than 10% of occupied patches for all dispersal distances considered (80 km, 120 km and 160 km) was enough to halve *PC* (Fig. 7). On the contrary, for the African clawed frog, between 17.42% and 51.36% of patches had to be removed to halve *PC* (Fig. 7, Table 3). The dispersal distance determined the transition between high and low *PC* values, but in interaction with the control strategy applied and the species considered. For the beaver, *PC* increased with dispersal distance for the random control strategy but it did not for the targeted control strategy. For the African clawed frog, results were very similar in all dispersal distances considered and in both strategies (Table 1), and robustness was significantly higher for the 8-km dispersal distance than for the 4-km dispersal distance.

4. Discussion

4.1. Forecasting the colonization of river networks

Up to 70% of the distribution ranges of two species that colonized different parts of the same river network could be explained by simulating a simple colonization process. This result suggests that the topology of the river network plays an important role in predicting species distributions in riverine ecosystems (Bertuzzo et al., 2009; Campbell et al., 2007; Fagan, 2002). This result is also important for management issues since the model as described here requires only a restricted number of parameters: network topology, range of dispersal distances, and dispersal behavior. Though many factors are expected to influence connectivity (and ultimately species dispersal and range size) such as environmental gradients, landscape structure, and local habitat quality (Peterson et al., 2013), we found that for both species the networks' geometric configuration seemed to be the major predictor of the colonization process.

It is also noteworthy that the observed and simulated ranges matched more closely for long-dispersal distances (*i.e.*, > 80 km for the beaver and > 3 km for the African clawed frog). For

the Eurasian beaver, this dispersal distance is consistent with maximal empirical estimates of dispersal on the Loire River (Fustec et al., 2001), and is in the higher range of commonly measured dispersal distances in other waterways for this species (Saveljev et al., 2002) or for the Canadian beaver, *Castor canadensis* (Sun et al., 2000). For the African clawed frog, the colonization front has been estimated to shift at a speed of 1km/year (Fouquet and Measey, 2006). Therefore, colonization may have been strongly influenced by (rare) long-dispersal events in both species.

An important feature of our method is its ability to compare species distributions and estimate dispersal distances from a single time-point, and without knowing the actual colonization rate of the species. It might thus allow the study of many invasive species for which data is scarce and colonization dynamics are unknown.

4.2. Assessing the efficiency of alternative strategies

Our second objective was to assess the efficiency of four management strategies that either target or ignore protection or destruction of central habitat patches. Contrasting results were found between strategies, but consistent ones arose across species. We found no effect of the protection strategy (random vs targeted) on network connectivity (*PC* values), even when 10% of habitat patches were protected; this effect was weak in both species except when dispersal distances were short and at least 10% of the habitat patches were protected. Otherwise, we observed a strong overlap of simulation results with observed results. The targeted habitat patch removal strategy had a much greater impact on the reduction of connectivity at the network scale than the random one, regardless of dispersal behavior and species. We observed that the habitat patch network was sensitive to targeted attacks and was relatively robust to the random loss of habitat patches. Removing the patches with the highest betweenness centrality scores rapidly split the network into isolated sub-units. This result suggested that the targeted control strategy may be an efficient management option in river ecosystems for a large number of invasive species with contrasting dispersal characteristics. However, increasing dispersal distances tended to buffer this effect (Cushman et al., 2010). The actual efficiency of the targeted control strategy may thus depend on the frequency of long-distance dispersal events of the focal species.

4.3. Characterizing the importance of habitat patches within a river network

Our results emphasize that habitat spatial arrangement and dispersal behavior are jointly critical in estimating connectivity in river watersheds (Campbell Grant et al., 2007). Indeed, the number and location of patches with the high connectivity (highest betweenness scores) depend directly on dispersal pathways, which are themselves determined by the topology of the network and species dispersal abilities (e.g., in-stream or overland dispersal). We observed that patches were more weakly connected for the beaver (in-stream dispersal) than for the frog (overland dispersal). This discrepancy had consequences on the efficiency of management strategies. For the Eurasian beaver, over 37% of patches did not contribute to network connectivity (had a null betweenness centrality score), and protecting targeted patches with high betweenness centrality scores did not significantly improve robustness of the network, results that held true considering different dispersal abilities. We observed better performance, even if differences were not significant, of the targeted strategy over the random strategy. This result may be worthy of consideration in future conservation strategies. However, the conservation benefit may be marginal with regards to the costs of implementing this strategy, as the constraint of selecting specific patches rather than random patches might carry additional costs (renting/buying land, site restoration, etc.). This slight advantage of the

targeted strategy over the random strategy is thus an important finding for management, as it alleviates constraints on the choice of sites to protect.

Considering the control of expanding African clawed frog populations, network robustness for this species was high and up to 40% of random patches had to be removed before a change in connectivity was observed. In contrast, the network was split much more efficiently when highly connected patches were first removed (target control). The management of the African clawed frog thus seems difficult, as a large number of patches need to be controlled to reduce network connectivity. It is interesting to note that very long-dispersal distances would not necessarily affect management efficiency in this case and that although overland dispersal offers more pathways to connect habitat patches than in-stream dispersal, the topology of the network appears critical for the connectivity between habitat patches.

4.4. A model with limited parameter for the management of populations in river networks and limits

Using a limited set of parameters (dispersal abilities and habitat patch distribution), we did not expect a perfect match between the simulated ranges and the actual distributions of our focal species. Discrepancies were necessarily caused by local, historical, or present-day factors. In order to obtain better fits, information on habitat quality (Carranza et al., 2011; Urban and Keitt, 2001; Van Looy et al., 2013), population dynamics (growth rate, population size and structure, Neeson et al., 2012), dispersal (kernel or rate, Cushman et al., 2013) and landscape structure in the colonized range (Radinger and Wolter, 2015) would be required. However, reaching this level of precision requires a deep knowledge of species' ecology and behavior and high quality environmental data, none of which are consistently available, namely due to time and budget constraints. In contrast, our approach requires limited ecological investigation and may allow rapid implementation of action plans. This feature is particularly desirable for the control of fast spreading invasive populations. More generally, identifying the central patches that maximize population connectivity is crucial for maintaining metapopulation systems, optimizing reintroduction success, or cutting short biological invasions. The management strategies tested here were either targeted or random relative to the central habitat patches. We considered habitat patches with the highest betweenness centrality scores to be central. While such approaches have been shown to poorly perform in small networks, they are recommended for large and complex ones (Chadès et al., 2011). Using other heuristic search methods, such as simulated annealing or genetic algorithms, might have improved the identification of central habitat patches in our network (Ascough et al., 2008) but would have required different functions to be optimized for each of the scenarios investigated (Nicol et al., 2010). River networks generate heterogeneity in suitability (habitat vs non habitat), and their spatial structure can be easily extracted and used to simulate dispersal and colonization processes. Our study shows that spatial network analysis is an effective tool to predict the expansion of a population, to identify highest priority patches, and to select between alternate strategies for conservation planning in river drainages.

Acknowledgements

The authors thank the editor and reviewers whose comments and suggestions greatly improved the manuscript. We also thank Kristen Irwin for a careful reading of the manuscript. This work was funded by the “Plan Loire Grandeur Nature” and the European Regional Development Fund to JS and ACB, and by the Swiss National Science Foundation grants no.PMPDP3158381 to SV.

References

- Akçakaya, H.R., Mills, G., Doncaster, C.P., 2007. The role of metapopulations in conservation, in: Macdonald, D., Service, K. (Eds.), *Key Topics in Conservation Biology*. Blackwell Publishing, Oxford, UK, pp. 64–84. doi:10.1002/jcp.22422
- Albert, R., Jeong, H., Barabasi, A.-L., 2000. Error and attack tolerance of complex networks. *Nature* 406, 378–382. doi:10.1038/35054111
- Allouche, O., Tsoar, A., Kadmon, R., 2006. Assessing the accuracy of species distribution models: Prevalence, kappa and the true skill statistic (TSS). *J. Appl. Ecol.* 43, 1223–1232. doi:10.1111/j.1365-2664.2006.01214.x
- Ascough, J.C., Maier, H.R., Ravalico, J.K., Strudley, M.W., 2008. Future research challenges for incorporation of uncertainty in environmental and ecological decision-making. *Ecol. Model.* 219, 383–399. doi.org/10.1016/j.ecolmodel.2008.07.015
- Baguette, M., Blanchet, S., Legrand, D., Stevens, V.M., Turlure, C., 2013. Individual dispersal, landscape connectivity and ecological networks. *Biol. Rev. Camb. Philos. Soc.* 88, 310–326. doi:10.1111/brv.12000
- Barabasi, A.-L., Bonabeau, E., 2003. Scale-free networks. *Sci. Am.* 288, 60–69.
- Barták, V., Vorel, A., Šimová, P., Puš, V., 2013. Spatial spread of Eurasian beavers in river networks: A comparison of range expansion rates. *J. Anim. Ecol.* 82, 587–597. doi:10.1111/1365-2656.12040
- Bascompte, J., Solé, R.V., 1998. *Modeling spatiotemporal dynamics in ecology*. Springer, New York.
- Bertuzzo, E., Muneeppeerakul, R., Lynch, H.J., Fagan, W.F., Rodriguez-Iturbe, I., Rinaldo, A., 2009. On the geographic range of freshwater fish in river basins. *Water Resour. Res.* 45, 1–11. doi:10.1029/2009WR007997
- Campbell Grant, E.H., Lowe, W.H., Fagan, W.F., 2007. Living in the branches: population dynamics and ecological processes in dendritic networks. *Ecol. Lett.* 10, 165–75. doi:10.1111/j.1461-0248.2006.01007.x
- Campbell Grant, E.H., Nichols, J.D., Lowe, W.H., Fagan, W.F., 2010. Use of multiple dispersal pathways facilitates amphibian persistence in stream networks. *Proc. Natl. Acad. Sci. U. S. A.* 107, 6936–6940. doi:10.1073/pnas.1000266107
- Carranza, M.L., D’Alessandro, E., Saura, S., Loy, A., 2011. Connectivity providers for semi-aquatic vertebrates: the case of the endangered otter in Italy. *Landsc. Ecol.* 27, 281–290. doi:10.1007/s10980-011-9682-3
- Chadès, I., Martin, T.G., Nicol, S., Burgman, M., Possingham, H.P., Buckley, Y., 2011. General rules for managing and surveying networks of pests, diseases and endangered species. *P. Natl Acad. Sci. USA* 108: 8323–8328. doi/10.1073/pnas.1016846108

519 Csardi, G., Nepusz, T., 2006. The igraph software package for complex network research.
520 InterJournal Complex Syst. 1695.

521 Cushman, S.A., Compton, B.W., Mcgarigal, K., 2010. Habitat fragmentation effects depend
522 on complex interactions between population size and dispersal ability: Modeling
523 influences of roads, agriculture and residential development across a range of life-history
524 Characteristics, in: Cushman, S.A., Huettmann, F. (Eds.), Spatial Complexity,
525 Informatics, and Wildlife Conservation. Springer, New York, pp. 367–383.
526 doi:10.1007/978-4-431-87771-4

527 Cushman, S.A., Landguth, E.L., Flather, C.H., 2013. Evaluating population connectivity for
528 species of conservation concern in the American Great Plains. Biodivers. Conserv. 22,
529 2583–2605. doi:10.1007/s10531-013-0541-1

530 Erős, T., Olden, J.D., Schick, R.S., Schmera, D., Fortin, M.-J., 2011a. Characterizing
531 connectivity relationships in freshwaters using patch-based graphs. Landsc. Ecol. 27,
532 303–317. doi:10.1007/s10980-011-9659-2

533 Erős, T., Schmera, D., Schick, R.S., 2011b. Network thinking in riverscape conservation – A
534 graph-based approach. Biol. Conserv. 144, 184–192. doi:10.1016/j.biocon.2010.08.013

535 Estrada, E., Bodin, O., 2008. Using network centrality measures to manage landscape
536 connectivity. Ecol. Appl. 18, 1810–1825. doi:10.1890/07-1419.1

537 Fagan, W., 2002. Connectivity, fragmentation, and extinction risk in dendritic
538 metapopulations. Ecology 83, 3243–3249. doi:10.1890/0012-
539 9658(2002)083[3243:CFAERI]2.0.CO;2

540 Fortuna, M.A., Gomez-Rodriguez, C., Bascompte, J., 2006. Spatial network structure and
541 amphibian persistence in stochastic environments. Proc. R. Soc. B Biol. Sci. 273, 1429–
542 1434. doi:10.1098/rspb.2005.3448

543 Fouquet, A., 2001. Des clandestins aquatiques. Zamenis 6, 10–11.

544 Fouquet, A., Measey, G.J., 2006. Plotting the course of an African clawed frog invasion in
545 Western France. Anim. Biol. 56, 95–102. doi:10.1163/157075606775904722

546 Freeman, L., 1978. Centrality in social networks conceptual clarification. Soc. Networks 1,
547 215–239. doi:10.1016/0378-8733(78)90021-7

548 Fustec, J., Lode, T., Le Jacques, D., Cormier, J.P., 2001. Colonization, riparian habitat
549 selection and home range size in a reintroduced population of European beavers in the
550 Loire. Freshw. Biol. 46, 1361–1371. doi:10.1046/j.1365-2427.2001.00756.x

551 Halley, D., Rosell, F., 2002. The beaver's reconquest of Eurasia: status, population
552 development and management of a conservation success. Mamm. Rev. 32, 153–178.
553 doi:10.1046/j.1365-2907.2002.00106.x

554 Hanski, I. 1994. A practical model of metapopulation dynamics. J. Anim. Ecol. 63, 151–162.
555 doi:10.2307/5591

556 Hanski, I., Ovaskainen, O. 2003. Metapopulation theory for fragmented landscapes. Theo.
557 Popul. Biol. 64, 119–127. doi:10.1016/S0040-5809(03)00022-4

558 Hanski, I., Ovaskainen, O., 2000. The metapopulation capacity of a fragmented landscape.
559 Nature 404, 755–758. doi:10.1038/35008063

560 Heidecke, D., 1984. Untersuchungen zur Ökologie und Populationsentwicklung des
561 Elbebibers *Castor fiber albus* Matschie, 1907, Teil 1. Biologische und

562 populationsökologische Ergebnisse. Zool. Jb. Syst. 111, 1–41.

563 Jenks, G.F., 1963. Generalization in Statistical Mapping. Ann. Assoc. Am. Geogr. 53, 15–26.
564 doi:10.1111/j.1467-8306.1963.tb00429.x

565 Levins, R., 1969. Some demographic and genetic consequences of environmental
566 heterogeneity for biological control. Bull. Entomol. Soc. Am. 15, 237–240.
567 doi:10.1093/besa/15.3.237

568 Lobos, G., Jaksic, F., 2005. The ongoing invasion of African clawed frogs (*Xenopus laevis*) in
569 Chile: causes of concern. Biodivers. Conserv. 14, 429–439. doi:10.1007/s10531-004-
570 6403-0

571 Minor, E.S., Urban, D.L., 2008. A graph-theory framework for evaluating landscape
572 connectivity and conservation planning. Conserv. Biol. 22, 297–307. doi:10.1111/j.1523-
573 1739.2007.00871.x

574 Minor, E.S., Urban, D.L., 2007. Graph theory as a proxy for spatially explicit population
575 models in conservation planning. Ecol. Appl. 17, 1771–1782. doi:10.1890/06-1073.1

576 Moilanen, A., Nieminen, M., 2002. Simple connectivity measures in spatial ecology. Ecology
577 83, 1131–1145. doi:10.2307/3071919

578 Nicol, S.; Chadès, I.; Linke, S.; Possingham, H.P., 2010. Conservation decision-making in
579 large state spaces. Ecol. Model. 221, 2531–2536. doi:10.1016/j.ecolmodel.2010.02.009

580 Neeson, T.M., Wiley, M.J., Adlerstein, S.A., Riolo, R.L., 2012. How river network structure
581 and habitat availability shape the spatial dynamics of larval sea lampreys. Ecol. Model.
582 226, 62–70. doi:10.1016/j.ecolmodel.2011.11.031

583 Peterson, E.E., Ver Hoef, J.M., Isaak, D.J., Falke, J. a, Fortin, M.-J., Jordan, C.E., McNyset,
584 K., Monestiez, P., Ruesch, A.S., Sengupta, A., Som, N., Steel, E.A., Theobald, D.M.,
585 Torgersen, C.E., Wenger, S.J., 2013. Modelling dendritic ecological networks in space:
586 an integrated network perspective. Ecol. Lett. 16, 707–19. doi:10.1111/ele.12084

587 Radinger, J., Wolter, C., 2015. Disentangling the effects of habitat suitability, dispersal and
588 fragmentation on the distribution of river fishes. Ecol. Appl. 25, 914–927.
589 doi:10.1890/14-0422.1

590 Rayfield, B., Fortin, M., Fall, A., 2011. Connectivity for conservation: a framework to
591 classify network measures. Ecology 92, 847–858. doi:10.1890/09-2190.1

592 Samia, Y, Frithjof L., Hastings A. 2015. Connectivity, passability and heterogeneity interact
593 to determine fish population persistence in river networks. J R Soc Interface 12,
594 20150435. doi.org/10.1098/rsif.2015.0435

595 Saura, S., Bodin, Ö., Fortin, M.-J., 2014. Stepping stones are crucial for species' long-distance
596 dispersal and range expansion through habitat networks. J. Appl. Ecol. 51, 171–182.
597 doi:10.1111/1365-2664.12179

598 Saura, S., Pascual-Hortal, L., 2007. A new habitat availability index to integrate connectivity
599 in landscape conservation planning: Comparison with existing indices and application to
600 a case study. Landsc. Urban Plan. 83, 91–103. doi:10.1016/j.landurbplan.2007.03.005

601 Saveljev, A.P., Stubbe, M., Stubbe, A., Unzhakov, V. V, Kononov, S. V, 2002. Natural
602 Movements of Tagged Beavers in Tyva. Russ. J. Ecol. 33, 460–465.
603 doi:10.1023/A:1020911800651

604 Strahler, A.N., 1957. Quantitative analysis of watershed geomorphology. Trans. AUG 38,

605 913–920. doi:10.1029/TR038i006p00913

606 Sun, L., Müller-Schwarze, D., Schulte, B.A., 2000. Dispersal pattern and effective population
607 size of the beaver. *Can. J. Zool.* 78, 393–398. doi:10.1139/z06-029

608 Urban, D., Keitt, T., 2001. Landscape connectivity: a graph-theoretic perspective. *Ecology* 82,
609 1205–1218. doi:10.2307/2679983

610 Urban, D.L., Minor, E.S., Treml, E. a, Schick, R.S., 2009. Graph models of habitat mosaics.
611 *Ecol. Lett.* 12, 260–73. doi:10.1111/j.1461-0248.2008.01271.x

612 Van Looy, K., Cavillon, C., Tormos, T., Piffady, J., Landry, P., Souchon, Y., 2013. A scale-
613 sensitive connectivity analysis to identify ecological networks and conservation value in
614 river networks. *Landsc. Ecol.* 28, 1239–1249. doi:10.1007/s10980-013-9869-x

615 Vuilleumier S., Bolker B.M., Lévêque O., 2010. Effects of colonization asymmetries on
616 metapopulation persistence. *Theor. Popul. Biol.* 78, 225-238.
617 doi:10.1016/j.tpb.2010.06.007

618 Vuilleumier, S., Possingham, H.P., 2006. Does colonization asymmetry matter in
619 metapopulations? *Proc. R. Soc. Biol. Sci. Ser. B* 273, 1637–42.
620 doi:10.1098/rspb.2006.3469

621 Webb, J.A., Padgham.M., 2013. How does network structure and complexity in river systems
622 affect population abundance and persistence? *Limnologia* 43, 399-403.
623 doi:10.1016/j.limno.2013.04.006

624

Table 1. Effect of management strategy and dispersal distance on network robustness for the Eurasian beaver and the African clawed frog. Differences between median values of probability of connectivity were tested using Wilcoxon signed-rank tests. Significant p-values after a Bonferroni correction are in bold (p-value < 0.00005). Note that for protection strategies, results are reported for simulations where 0.5% of patches were protected.

Species	Management strategy	Dispersal distance (km)	W	p-value
Eurasian beaver	Protection	targeted 80 vs 120	50	<2.2E-16
		80 vs 160	36.5	<2.2E-16
		120 vs 160	1093	7.4E-06
		random 80 vs 120	178	<2.2E-16
		80 vs 160	50.5	<2.2E-16
		120 vs 160	1121.5	3.8E-05
	Control	targeted 80 vs 120	2145.5	0.318
		80 vs 160	2184.5	0.405
		120 vs 160	2414	0.888
		random 80 vs 120	242	2.2E-16
		80 vs 160	92.5	2.2E-16
		120 vs 160	1517	9.4E-05
African clawed frog	Protection	targeted 4 vs 6	906.5	0.002
		4 vs 8	743.5	3.7E-06
		6 vs 8	1100.5	0.040
		random 4 vs 6	957.5	0.011
		4 vs 8	735.5	6.7E-06
		6 vs 8	1046	0.020
	Control	targeted 4 vs 6	801	0.0008
		4 vs 8	585	9.4E-07
		6 vs 8	920	0.009
		random 4 vs 6	955.5	0.010
		4 vs 8	732.5	6.0E-06
		6 vs 8	1042	0.018

Table 2. Effect of management strategies (targeted vs. random protections) on the robustness of the network colonized by the Eurasian beaver and the African clawed frog in the Loire River. Robustness was estimated using probability of connectivity (*PC*). The percentage of removed patches for halving *PC* is reported excepted when *PC* did not decrease below 0.5 (in red). Differences between median values of *PC* were tested using Wilcoxon signed-rank tests. Significant p-values after a Bonferroni correction are in bold (p-value < 0.00005).

Species	% protected patches	Protection strategy	Dispersal distance (km)								
			80			120			160		
			% removed patches PC = 0.5	W	p-value	break	W	p-value	% removed patches PC = 0.5	W	p-value
Eurasian beaver	0.5	targeted	<1	861.5	3E-07	47.52	2078	0.251	68.14	2067.5	0.162
		random	<1			37.78			60.05		
	1	targeted	<1	1750	0.007	46.92	2623.5	0.291	69.98	2090	0.111
		random	<1			38.04			58.10		
	2	targeted	<1	1670	0.331	47.07	2191.5	0.079	72.93	2129	0.066
		random	<1			37.34			58.92		
African clawed frog	5	targeted	<1	867.5	1E-10	55.00	2586	0.371	76.25	2764.5	0.047
		random	<1			38.00			58.44		
	10	targeted	63.97	4643.5	<2E-16	62.97	2987.5	0.008	77.58	2739.5	0.063
		random	<1			37.28			58.11		
	0.5	targeted	50.84	1341	0.776	71.83	415	0.332	87.90	1359	0.488
		random	48.37			65.20			80.28		
African clawed frog	1	targeted	50.90	1355.5	0.698	72.01	410	0.354	86.95	1358	0.495
		random	48.22			65.62			80.55		
	2	targeted	58.63	1504	0.141	80.79	540.5	0.031	PC > 0.5	1386	0.248
		random	48.08			64.72			81.07		
	5	targeted	62.34	1526.5	0.098	90.76	579	0.011	PC > 0.5	1453.5	0.012
		random	48.03			65.32			80.78		
African clawed frog	10	targeted	70.01	1708.5	0.002	PC > 0.5	734	8E-06	PC > 0.5	1479	0.007
		random	48.42			65.09			80.28		

Table 3. Effect of management strategies (targeted vs. random control) on the robustness of the network colonized by the Eurasian beaver and the African clawed frog in the Loire River. Robustness was estimated using probability of connectivity (*PC*). The percentage of removed patches for halving the *PC* is reported. Differences between median values of *PC* were tested using Wilcoxon signed-rank tests. Significant p-values after a Bonferroni correction are in bold (p-value < 0.00005).

Species	Dispersal distance (km)	Control strategy	% removed patches <i>PC</i> = 0.5	W	p-value
Eurasian beaver	80	targeted	<1	260.5	2.6E-16
		random	<1		
	120	targeted	5.70	203.5	< 2.2E-16
		random	38.22		
	160	targeted	6.59	207.5	< 2.2e-16
		random	59.09		
African clawed frog	4	targeted	17.42	711	6.0E-06
		random	47.67		
	6	targeted	21.69	646.5	4.1E-06
		random	65.02		
	8	targeted	51.36	837.5	1.2E-04
		random	80.55

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.

Fig. 2. Predictive accuracy of species distribution models according to TSS values (first axis) and corresponding slopes (second axis) across dispersal distances, in the Eurasian beaver (between 2 and 200 km in-stream dispersal) and in the African clawed frog (between 1 and 20 km overland dispersal). Values displayed represent 100 replicates of colonization simulations across the whole river network (a) and across the mainstreams (b) for the beaver and only across the whole network for the frog (c).

Fig. 3. Location of patches occupied by the Eurasian beaver ($n = 399$) according to their betweenness centrality scores. Scores correspond to a 80-km dispersal distance (low = 0-8 440, medium = 8440-34733, high = 34 733-79 617).

Fig. 4. Location of patches occupied by African clawed frog ($n = 57$) according to betweenness centrality scores. Scores correspond to 4-km dispersal distance (low = 0-63, medium = 63-210, high = 210-523).

Fig. 5. Relative efficiency of protection strategies in the Eurasian beaver - Robustness of the network ($n = 399$ patches) to fragmentation for 3 dispersal distances (80, 120, 160 km) and the percentage of protected patches (1, 5, 10%). *PC* as a function of removed patches for two management strategies of patches: random (blue) and targeted (red) protections. Lines represent the median value; areas represent the 95% and 5% quantiles of the distribution as network fragmentation was performed 1 000 times. A purple area corresponds to an overlap between distributions of random (blue) and targeted (red) strategies. The dashed line corresponds to a value of $PC = 0.5$.

Fig. 6. Relative efficiency of protection strategies in the African clawed frog - Robustness of the network ($n = 57$ patches) to fragmentation according to dispersal distances (4, 5 and 6 km) and the rate of protected patches (1, 5 and 10%). *PC* as a function of removed patches for two management strategies of patches: random (blue) and targeted (red) protections. Lines represent the median value; areas represent the 95% and 5% quantiles of the distribution as network fragmentation was performed 1 000 times. A purple area corresponds to an overlap between distributions of random (blue) and targeted (red) strategies. The dashed line corresponds to a value of $PC = 0.5$.

Fig. 7. Relative efficiency of control strategies in the Eurasian beaver and African clawed frog- Robustness of the network to fragmentation according to dispersal distances. *PC* as a function of removed patches for two management strategies of patches: random (blue) and targeted (red) controls. Lines represent the median value; areas represent the 95% and 5% quantiles of the distribution as network fragmentation was performed 1 000 times. A purple area corresponds to an overlap between distributions of random (blue) and targeted (red) strategies. The dashed line corresponds to a value of *PC* = 0.5.