RESEARCH ARTICLE

Combining network theory and reaction–advection–diffusion modelling for predicting animal distribution in dynamic environments

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Abstract

1. Movement is a key process driving animal distributions within heterogeneous landscapes. Graph (network) theory is increasingly used to understand and predict landscape functional connectivity, as network properties can provide crucial information regarding the resilience of a system to landscape disturbances, e.g. removal of habitat patches. The temporal dimension of movement patterns, however, is not generally included in network analysis, which can lead to a discrepancy between observed space use and landscape connectivity. Reaction–advection–diffusion models, when coupled with network analysis, could provide a powerful mechanistic framework based upon spatio-temporal dimensions of animal movement, but this approach remains poorly developed for ecological studies.

2. We developed a mechanistic space use model that considers both residency time in resource patches and movement amongst those patches within a spatial network. The framework involves two main steps: first, the network topology that best reflects functional connectivity for the study system is identified; second, a spatio-temporal flow dynamic is implemented within the network using reaction–advection–diffusion modelling. To illustrate the approach, we used observations of radiocollared plains bison *Bison bison bison* that were travelling in a meadow network within a forest matrix.

3. In the model application, we found that the graph best reflecting the functional connectivity of bison was a complex graph of ultra-small world scale-free network type. The reaction–advection–diffusion model involved the effect of meadow area and inter-meadow distance on bison travels. Simulations showed that a simple graph or distance-based graphs provided less accurate predictions of bison distribution, while also predicting different management actions to effectively impact bison space use.

4. Our study demonstrates how reaction–advection–diffusion modelling, coupled with network theory, can provide a robust mechanistic framework for predicting animal distribution in dynamic environments. The modelling approach can be applied to a large range of systems that are subjected to rapid environmental changes due to habitat management or natural resource extraction, for example.

Furthermore, our study demonstrates that management and conservation planning can strongly depend upon network structure, and that a faulty assessment of network topology can result in poor planning, with potential unexpected impacts on animal distributions.

KEYWORDS

animal space use, distance-based graph, minimum planar graph, reaction–advection–diffusion model, residency time, scale-free, small world, spatial graph

1 | INTRODUCTION

Understanding animal movement is a fundamental and pressing challenge in ecology, notably because this information can help to characterize and anticipate the impact of human-induced altered landscapes on population spatial distributions (Nathan et al., 2008). Graph (or network) theory has been demonstrated to be particularly valuable in describing and predicting animal movements within heterogeneous landscapes (Courbin, Fortin, Dussault, & Courtois, 2014; Fox & Bellwood, 2014; Rhodes, Wardell-Johnson, Rhodes, & Raymond, 2006). Indeed, at some scale that is relevant to a given animal population, most landscapes can be viewed as spatial networks, where nodes are resource patches and links are potential movements between nodes (Fall, Fortin, Manseau, & O'Brien, 2007). These networks can be drawn with different mathematical rules, each one associated with particular properties of landscape functional connectivity reflecting the specific interplay between animal movements and habitat attributes (Courbin et al., 2014). For example, the minimum planar graph (MPG) considers that individuals move in a stepping stone fashion among resource patches, such that links in a MPG never cross (Fall et al., 2007). Another rule is to represent potential movements as a function of Euclidean or functional distance (e.g. least-cost modelling), where only patches closer than a certain threshold are connected (Lookingbill, Gardner, Ferrari, & Keller, 2010; Minor & Urban, 2008; O'Brien, Manseau, Fall, & Fortin, 2006). Those mathematical rules are frequently used to model landscape connectivity for terrestrial mammals (Bunn, Urban, & Keitt, 2000; Courbin et al., 2014; Lookingbill et al., 2010; O'Brien et al., 2006), even without testing the relevance of more complex graphs. This choice might reflect the fact that when movement data are too limited to identify the most relevant network among different network types, the mathematical rules associated with these types of network can still predict landscape connectivity solely based upon patch distribution (i.e. based on structural connectivity). The constraints imposed by such stringent rules, however, could hinder our capacity to understand and predict distribution patterns of animals, and their responses to landscape changes. Indeed, whenever tested, complex network topologies often best reflect the movements that various species make among resource patches (Fox & Bellwood, 2014; Rhodes et al., 2006). This is significant for wildlife conservation and management because network topology informs on the impact that landscape disturbances (e.g. removal of habitat patches) should

have on network resilience and, overall, on animal distributions (Fall et al., 2007). For example, a complex network of scale-free type tends to be resistant to the random removal of nodes, but it is highly sensitive to targeted removal of hubs (Albert, Jeong, & Barabasi, 2000; Minor & Urban, 2008). In contrast, a disturbance would affect a MPG rather similarly, regardless of the nodes removed because of the presence of alternative paths (Reunanen, Fall, & Nikula, 2012). The graphical representation of landscape connectivity that is most faithful to the system under study should thus be identified, which would enable implementation of effective management actions and prediction of how individual movement flows should be reorganized following a disturbance.

Although graph theory can provide crucial information on animal movements within a patch network, inference on population space use dynamics still requires an understanding of the temporal dimension of movement patterns (Jacoby & Freeman, 2016; Nathan et al., 2008). For example, network analysis alone failed to identify preferred sites for a population of broadnose sevengill shark *Notorynchus cepedianus*, because it did not account for residency period in the different sites (Stehfest, Patterson, Barnett, & Semmens, 2015). Integration of the temporal dimension of movement into a network requires the use of dynamic models, such as a reaction–advection–diffusion model (Barrat, Barthelemy, & Vespignani, 2008). Reaction–advection–diffusion models have been coupled with spatial networks to evaluate metapopulation dynamics (Colizza, Pastor-Satorras, & Vespignani, 2007; Sarhad, Carlson, & Anderson, 2013), but their potential application to the study of animal movement remains largely overlooked (Cantrell & Cosner, 2004). A reaction–advection–diffusion model simulates variation in individual density through time at any given point in space (Turing, 1952), and as such, the reaction process that is generally linked to population growth can be readily adapted to model residency time in resource patches of networks. The implementation of both advection–diffusion and reaction processes should then provide a powerful mechanistic framework for describing and anticipating animal spatial distributions in dynamic environments.

We developed a mechanistic space use model that considers both residency time in the resource patches and movement among patches in a spatial network. Our approach integrates reaction–advection–diffusion modelling and spatial network theory to predict animal distributions in heterogeneous landscapes. We then used field observations of plains bison *Bison bison bison* to illustrate the

approach. Specifically, (1) we determined the most relevant type of network; (2) because the relevant type of network was complex for this system, we used a statistical model to predict the spatial graph that was based upon the observed functional connectivity; (3) we then predicted, based upon habitat attributes, residency time in patches and movement mechanisms among patches; (4) we evaluated the effect of network structure on bison space use patterns; (5) and finally, we assessed how the targeted removal of resource patches should affect bison distribution based on network structure.

2 | MATERIALS AND METHODS

First, we developed the modelling framework that involves the reaction–advection–diffusion model and predictions of the network topology that best reflected landscape functional connectivity for our study system. Second, we illustrated and tested the approach with empirical data.

2.1 | Development of reaction–advection–diffusion model

A classic reaction–diffusion model applied to a network with N nodes takes the general form:

$$\frac{dU(t)}{dt} = F(U(t)) + G(U(t))$$

(1)

where $U(t) = (u_1(t), \ldots u_2(t), \ldots u_N(t))^T$ is the vector of animal densities at time t in the N nodes of the network, $\frac{dU(t)}{dt}$ is the vector of instantaneous rate of change in $U(t)$, $F = (f_1(U(t)), f_2(U(t)), \ldots, f_N(U(t))^T$ is the vector of reaction functions in the N nodes of the network and $G = (g_1(U(t)), g_2(U(t)), \ldots g_N(U(t))^T$ is the vector of diffusion functions in the N nodes of the network (Kouvaris, Kori, & Mikhailov, 2012).

While the reaction term usually models population growth (Cantrell & Cosner, 2004), the reaction also can be modelled as the density of individuals leaving node i, based upon residency time in node i:

$$f_i(U(t)) = -\frac{u_i(t)}{T_i}, i \in \{1, \ldots, N\}$$

(2)

where T_i is the average residency time in node i; higher is the residency time in node i, lower is the number of individuals leaving patch i.

Simple diffusion considers that individual flow is the same between connected network patches (i.e. an unweighted network, Kouvaris et al., 2012), and that animal movements have no bias with respect to habitat features. We can relax this assumption by considering directional biases in animal movement, i.e. an advection term. Advection properties can be modelled by assigning weights to the network's links, which then reflects an uneven flow of individuals between connected network patches. The advection process then

can be implemented by modifying the diffusion term in Equation 1 according to:

$$g_i(U(t)) = \sum_{j=1}^{N} a_{ji} \frac{u_j(t)}{T_j}, i \in \{1, \ldots, N\}$$

(3)

where a_{ji} is the weight that is assigned to movement from node j to node i ($a_{ii} = 0$), which is proportional to the number of individuals arriving to patch i. The weights a_{ji} are standardized such that, $\sum_{k=1}^{N} a_{jk} = 1$, which implies that individuals leaving patch j will distribute themselves among all nodes connected to node j.

Equation 1 now takes the following form:

$$\frac{dU(t)}{dt} = (I - A) T^{-1} U(t),$$

(4)

where I is the identity matrix, A is the weighted adjacency matrix of the network containing all weights a_{ij}, $i, j \in \{1, \ldots, N\}^2$, and T is a diagonal matrix of the residency times in the N nodes of the network. Predicted densities at any time of the simulation can be transformed to estimate relative intensity of space use as follows,

$$I_i(t) = \frac{u_i(t)}{\sum_{j=1}^{N} u_j(t)'}$$

(5)

where $I_i(t)$ is the relative intensity of use for node i at time t.

2.2 | Identification of spatial network topology

2.2.1 | Selection of characteristic network metrics

Multiple network metrics are available to describe landscape connectivity and to distinguish between network types (Rayfield, Fortin, & Fall, 2011). In this study, we focused on three metrics to identify the network type that can best predict landscape connectivity of an empirical dataset: the degree distribution (i.e. the distribution of the number of links that each node has), the global clustering coefficient C (or the proportion of triangles, i.e. the number of connected triplets of nodes over the total number of triangles in the graph) and the characteristic path length L (i.e. the number of links in the shortest path between two nodes, averaged over all pairs of nodes; Rayfield et al., 2011). We chose these metrics because they allow to evaluate whether a network topology is complex and similar to classic complex network topologies found in real world, such as scale-free or small-world networks (Newman, 2003).

2.2.2 | Network metrics behaviour for different network types

The degree distribution reflects whether the connectivity is maintained by some hubs, as is the case with scale-free network types (Albert et al., 2000). In such networks, the degrees conform to a power-law distribution whereas in simpler graphs, such as the MPG, the degrees should have a distribution close to the Gaussian, reflecting a more homogeneous pattern of connectivity (Reunanen et al., 2012).

The global clustering coefficient associated with the characteristic path length of a graph allows to evaluate whether the type of the graph is similar to that of a small-world network. Such a graph has shortcuts between nodes that result in a short characteristic path length and a large global clustering coefficient (Watts & Strogatz, 1998). Although MPG does not have shortcuts, its characteristic path length tends to be relatively long (Fall et al., 2007). If a spatial graph has the small-world properties, then we expect two main features: (1) its global clustering coefficient should be much higher than the global clustering coefficient of a random graph C_R constructed with the same number of nodes and the same number of links, and (2) its characteristic path length should be proportional to the characteristic path length of its associated random graph (L_R, Newman, 2003).

Using these metrics, we can evaluate which network, among four classic topologies (i.e. a MPG, a scale-free, a small-world and a distance-based graph, Fox & Bellwood, 2014; O'Brien et al., 2006), best fits the empirical network of a given study system. We can then predict the relevant network based upon the best topology.

2.3 | Predicting links in complex networks

Predicting links based on functional connectivity and the actual structure of the network is generally not implemented for spatial networks. Here, we propose to predict links using a latent space random graph mixed model (ERGMM) and the observed animal movements (Hoff, Raftery, & Handcock, 2002). A latent space random graph mixed model is a social network model that proved to be efficacious in predicting actual linkages in a spatial network (Fletcher, Acevedo, Reichert, Pias, & Kitchens, 2011).

Link prediction is based upon the position of each node in a latent space, meaning that connected nodes would be closer in the latent space than unconnected nodes. Covariates associated with node and link properties also can be added to better define the functional connectivity that is used to predict links. Several models reflecting different hypotheses on link prediction thus can be constructed a priori, and then compared using the Bayesian information criterion (BIC). The best model for predicting links (i.e. lowest BIC) can be selected a posteriori and used to estimate a probability of link presence between each pair of nodes. The probabilities then can be dichotomized to {0, 1} (i.e. absence vs. presence, Figure 1), based upon a threshold that maximizes the Cohen's kappa which assesses the similarity between observed and predicted links (Fletcher et al., 2011).

2.4 | Case study

2.4.1 | Study area

The study was conducted in Prince Albert National Park, Saskatchewan, Canada (53°44′N, 106°39′W). Plains bison occupy *c.* 1,000 km^2 of the park's southwestern corner, which is composed of deciduous and conifer stands (85%), meadows (10%) and water bodies (5%). Because bison strongly select meadows (Fortin, Fryxell,

O'Brodovich, & Frandsen, 2003), which are dispersed throughout the forest matrix, graph theory is highly applicable to study landscape connectivity within this system (Dancose, Fortin, & Guo, 2011).

2.4.2 | Spatial data

Landscape data

We delimited meadows from the rest of the landscape using the supervised classification of a SPOT 5 multispectral image (August 2008, 10-m resolution, Dancose et al., 2011). We also extracted meadow area and Euclidean distance between meadow centroids from this image. Extraction of habitat information was performed using QUANTUM GIS software (QGIS 2016).

Bison data

Movements can be strongly influenced by environmental factors that are likely to change with seasons; thus, we focused our analysis on summer data (weeks 18–33, Merkle, Fortin, & Morales, 2014). We followed 43 adult females (>3 years old) using GPS collars (4400M, Lotek Engineering, Newmarket, ON, Canada; TGW 4780-3, Telonics, Mesa, AZ, USA) between 2005 and 2015 (Laval University, ethical approvals #2011196-1 and #2017001-1). Three to fifteen bison were monitored each summer and 1,410 locations on average (range: 37–1,918) were collected per individual (relocation frequency varying between every 1 or 3 hr for all animals, Table S1). Because hourly relocations provided more detailed information on bison movements, we only retained hourly data to construct individual trajectories. To estimate relative intensity of space use based upon empirical data, we resampled all GPS data to obtain relocations every 3 hr and kept only individuals followed continuously the whole season (N = 22 individuals; 867 locations/individual, on average for the summers of 2005, 2007 and 2010–2015; range: 851–895). In addition, we used bison trail data collected in the field during summer 2008 to validate whether GPS-collar data provided a good assessment of meadow connectivity (Appendix S1).

2.4.3 | Network construction

Empirical graph

We used trajectories of bison produced by GPS relocations at 1-hr interval to build the empirical network of plains bison (N = 75,519 relocations). Specifically, we identified when a move occurs between two meadows, and determined the source (departure) and target (arrival) meadow. When two or more collared bison were travelling together, we considered their collective move from a source to target meadow as a single link use. Using all inter-meadows moves, we constructed the empirical network using the IGRAPH package in R software (R Core Team, 2016).

Network based on complex topology

To predict links in the spatial graph, we fitted the empirical graph to a ERGMM. We selected a priori the key covariates involved in
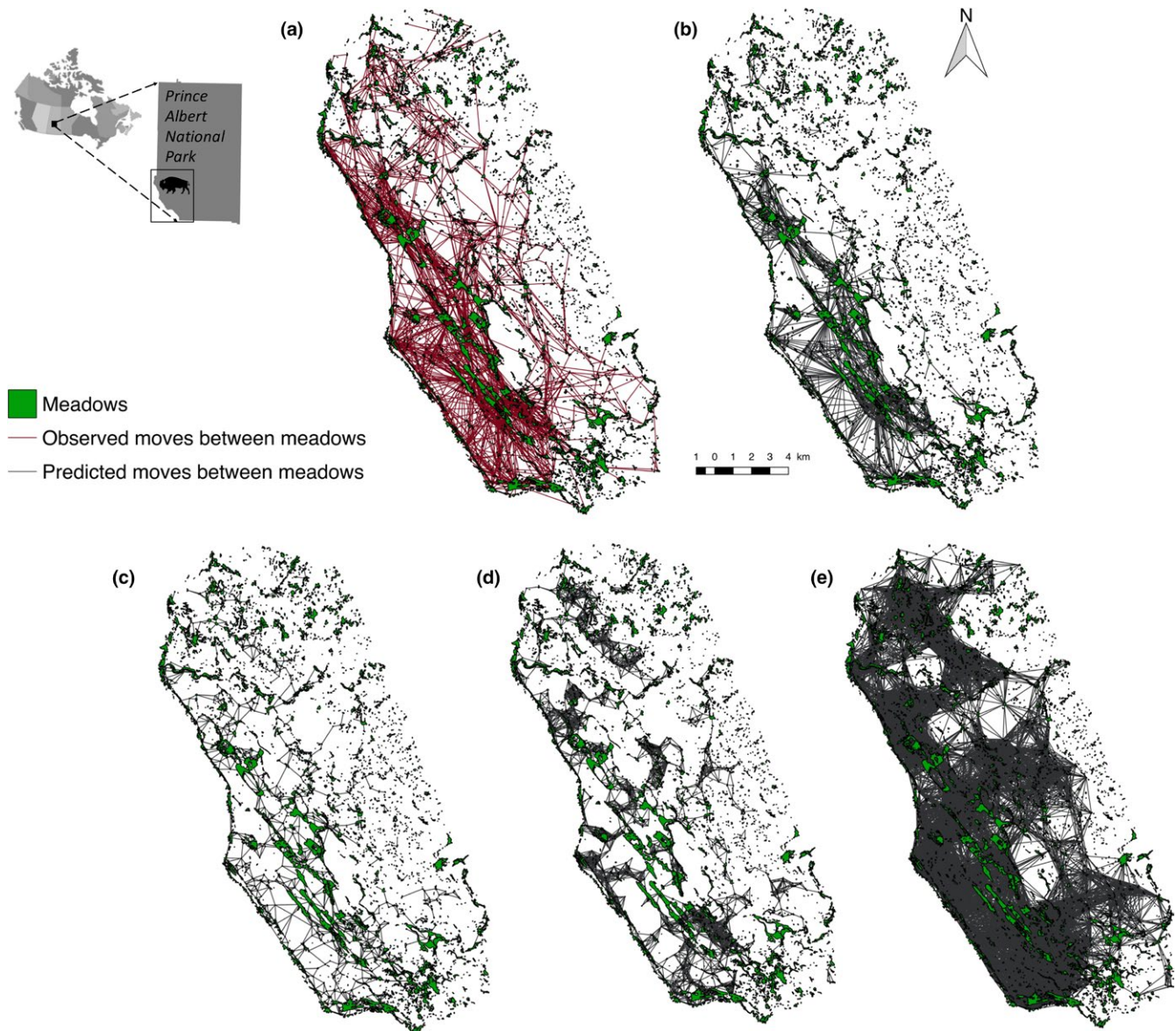
FIGURE 1 Graphical representation of different network structures to model landscape functional connectivity of the population of plains bison in Prince Albert National Park during summer. (a) Empirical graph based on bison GPS trajectories. (b) Ultra-small world scale-free network. (c) Minimum planar graph. (d) 700-m distance threshold network. (e) 1,800-m distance threshold network. Bison occupy the southwestern corner of the park during summer time (black rectangle on the map of the park)

bison functional connectivity (i.e. meadow area and distance between meadows, Dancose et al., 2011; also see Results), and which reflected the empirical network properties (i.e. number of triangles, see Results). In addition, we considered random effects on the source and target meadows to model direction in inter-patch movements (Fletcher et al., 2011). We used the LATENTNET package in R software to fit the model using the Markov Chain Monte Carlo algorithm and predicted the links.

Additional networks

Because the MPG and distance-based graphs are commonly used in the literature, we also considered those two types of network to evaluate the effect of network structure on space use patterns of

bison. We thus built the MPG using the GRAINSCAPE package in R software. We only retained MPG links that connected visited meadows.

Distance-based network requires defining a distance threshold below which movement among patches may occur. The probability that two nodes i and j are connected is usually modelled as $p_{ij} = e^{-\phi d_{ij}}$, where d_{ij} is the distance between nodes i and j and ϕ is the rate of decay of the probability with distance (Ferrari, Preisser, & Fitzpatrick, 2014). By fitting a linear model to the log distribution of link length of the empirical graph, we first estimated the rate of decay ϕ. Then, from the estimated equation (i.e. $p_{ij} = e^{-0.0017 d_{ij}}$, $R^2 = .95$), we calculated the presence probability of each link among all visited meadows. We then dichotomized the probabilities so that all those greater than a given threshold were set to 1 and the others

were set to 0. The threshold value was chosen so as to maximize the Cohen's kappa (Fletcher et al., 2011). Equivalent distance associated to the threshold probability maximizing the Cohen's kappa was 700 m. We also used a tail distance for which $p_{ij} = 0.05$ (Bunn et al., 2000; Ferrari et al., 2014), equivalent to 1800 m. Thus, two threshold distance graphs were built to predict bison movement among meadows, one for which meadows at distance <700 m were connected and one for which meadows at distance <1,800 m were connected.

For all predicted networks, we extracted the degree distribution, the clustering coefficient and the characteristic path using the IGRAPH package in R software. We also identified the links that were predicted by the MPG (MGP links) and those that were not (non-MPG links).

2.4.4 | Prediction of residency time and patch choice

Residency time in meadows

We used the method developed by Bastille-Rousseau, Fortin, Dussault, Courtois, and Ouellet (2011) to calculate individual residency time in each meadow: for a given meadow and a given individual, we considered portions of the movement segments entering and leaving the meadow (assuming constant speed), together with the number of successive locations inside the meadow. Because some radiocollared females travelled together from time to time (i.e. bison form a fusion–fission society, Fortin et al., 2009), we considered only one trajectory for a group of bison. The residency time for each meadow was then predicted from the fit of a linear model linking log-residency time in meadows to two habitat attributes (i.e. meadow area and relative risk of wolf predation in meadow, Appendices S2 and S3). Statistical analyses for residency time were performed using the linear mixed model implemented in package LMERTEST in R software.

Patch choice implemented with link weights

Link weight was estimated from the fit of a conditional logistic regression linking some habitat attributes (i.e. meadow area, Euclidean distance between meadows and relative risk of wolf predation in meadow, Appendices S2 and S4) with empirical patch choices (Fortin et al., 2005). Following Merkle et al. (2014), we identified, for each inter-meadow move, all available meadows within a radius of 3.2 km from the source meadow (95% of all observed inter-meadows movements). We then selected 20 random meadows within that radius based upon their distance to the source meadow (see Merkle et al., 2014 for more details on random meadow selection). Finally, we compared attributes of the target meadow with the attributes of the random meadows using a conditional logistic regression (Appendices S2 and S4). We ran the model for MPG and non-MPG links separately, to evaluate whether different mechanisms were implied in the two movement types. Statistical analysis for patch choice was performed using package survival in R software.

Link weights were then calculated using the estimated coefficients from conditional logistic regression (Appendix S4) as follows,

1. Considering a meadow i connected to m meadows with MPG links, the weight for a MPG link from meadow i to meadow j, $j \in \{1, ..., m\}$, is:

$$a_{ij}^{\text{MPG}} = \frac{\exp\left(\sum_{p=1}^{p} \hat{\beta}_p^{\text{MPG}} X_p^j\right)}{\sum_{j=1}^{m} \exp\left(\sum_{p=1}^{p} \hat{\beta}_p^{\text{MPG}} X_p^j\right)}, \quad (6)$$

where $\hat{\beta}_p^{\text{MPG}}$, $p \in \{1, ..., P\}$ are the P estimates of the regression coefficients for MPG links and X_p^j, $p \in \{1, ..., P\}$ are the values of the P covariates for meadow j.

2. Considering the same meadow i connected to s meadows with non-MPG links, the weight for a non-MPG link from meadow i to meadow j, $j \in \{1, ..., s\}$ is:

$$a_{ij}^{\text{non-MPG}} = \frac{\exp\left(\sum_{p=1}^{p} \hat{\beta}_p^{\text{non-MPG}} X_p^j\right)}{\sum_{j=1}^{m} \exp\left(\sum_{p=1}^{p} \hat{\beta}_p^{\text{non-MPG}} X_p^j\right)}, \quad (7)$$

where $\hat{\beta}_p^{\text{shortcut}}$, $p \in \{1, ..., P\}$, are the P estimates of the regression coefficients for non-MPG links and X_p^j, $p \in \{1, ..., P\}$ are the values of the P covariates for meadow j.

3. Finally, we corrected the weight with the intensity of use of each link type (MPG links had twice the use of non-MPG links, Table S4), with standardization that depended upon link type:

$$a_{ij} = \frac{2.0}{3} a_{ij}^{\text{MPG}}, \text{if } i \rightarrow j \text{ is a MPG link}$$
$$a_{ij} = \frac{1.0}{3} a_{ij}^{\text{non-MPG}}, \text{if } i \rightarrow j \text{ is a non-MPG link} \quad (8)$$

2.5 | Model simulations

In each network, we simulated 300 individuals moving among the connected meadows. Initially, all meadows were used uniformly meaning that all meadows had the same initial conditions (i.e. 300/number of connected meadows in the network). We then used the fourth order Runge–Kutta method to solve the system of ordinary differential equations (Equation 4, Dahlquist & Björck, 2008). We first validated the model (Appendix S5), then evaluated the effect of network structure on bison space use pattern. In our case, the most relevant network was an ultra-small world scale-free network (see Results); without loss of generality, we have thus exemplified our approach using this complex network. Specifically, we ran the model using the ultra-small world scale-free network, the MPG and the two distance-based networks for defining landscape connectivity.

To evaluate the similarity between predicted space use at the end of the season, i.e. after 112 simulated days, and space use obtained empirically, we used the pseudo-R^2 of a linear model including an exponential spatial correlation (Box, Jenkins, Reinsel, & Ljung,

2015). The empirical space use index consisted of the proportion of 3 hr relocations in each meadow. Statistical analyses were performed using package NLME in R software.

Finally, to demonstrate the utility of our model and the advantages of using the best network, we evaluated the impact of potential management actions (e.g. fence erection) on bison distribution. We used the ultra-small world scale-free network, the MPG and the two distance-based networks to identify the 10 most connected meadows in each network (yellow stars, Figure 4). We then changed the accessibility of these nodes in the network by setting the weights of the existing links arriving and leaving those meadows to zero. For example, this could be implemented in the field using fences (Fortin et al., 2010). We ran the model with the modified networks and compared predicted space use before and after the intervention for all network structures.

3 | RESULTS

GPS-collar data provided a good assessment of meadow connectivity. Indeed, the observed connectivity from trail data was relatively similar to the observed connectivity from GPS data (Figure S1).

3.1 | Properties of the empirical network

The degree distribution of the empirical network of plains bison in the study area decayed as a power function, meaning that few meadows were highly connected (i.e. hubs), while most meadows had few links (Figure 2). Also, the empirical network had a much higher clustering coefficient than its associated random graph, meaning that the proportion of triangles in the graph was greater than would be expected by chance alone (Table S2). Further, the characteristic path length of the empirical graph was equivalent to the characteristic path length of its associated random graph (Table S2). The properties of the empirical graph were thus more closely related to an ultra-small world scale-free network, a complex network (Figure 1).
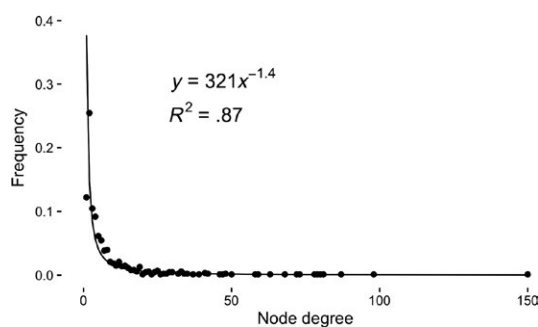

FIGURE 2 Degree distribution (black dots) of the empirical spatial network of plains bison in Prince Albert National Park based upon the movements of 43 GPS-collared individuals in the summers 2005–2015. The distribution decays as a power function, that is, $y \propto x^{-\alpha}$, with $\alpha(\pm S.E) = 1.4$ (± 0.073) (solid line), as expected for scale-free networks

3.2 | Network based on complex topology

The best model for predicting links in the spatial network of plains bison during summer included meadow area, Euclidean distance between meadows and the number of triangles in the network (Table S2, Model 1). The spatial network predicted using the best model was based upon 539 connected nodes including 3,418 links. The predicted graph had the same properties as the empirical graph, that is ultra-small world scale-free network (Figure 1).

3.3 | Effect of habitat attributes on residency time and patch choice

Residency time in meadows could be explained by their areas, with bison staying longer in larger meadows ($\hat{\beta}_{log(area)}(\pm S.E) = 0.32 \pm 0.013$ $p < .001$, Table S4). Patch choice was mainly explained by the area of the target meadow and the distance between the source and target meadows for both MPG and non-MPG links (Table S5). Most observed inter-patch movements were not predicted by the MPG, but those MPG links were used twice as much as non-MPG links (Table S5).

3.4 | Effect of network structure on space use pattern

Space use patterns predicted by the reaction–advection–diffusion model strongly differed, depending upon the structure of the spatial network used to model functional connectivity (Figure 3). The minimum planar graph and both networks based on distance predicted much more uniform use of meadows than did the ultra-small world scale-free network. Hubs were more intensely used in the complex network compared to the other types of network, more closely reflecting the observed space use of bison (Figure 3).

3.5 | Effect of an intervention on space use pattern

The 10 most connected meadows were different, depending upon network structure (Figure 4) and, as a result, removing nodes yielded different changes in the intensity of meadow use. The removal of hubs in the ultra-small world scale-free network increased the use of specific areas in the summer bison range and decreased the use of some meadows close to affected ones (Figure 4). In contrast, the removal of hubs from the MPG or from the two networks based on distance slightly and uniformly increased the use of all remaining meadows (Figure 4).

4 | DISCUSSION

We developed a model of animal distribution by combining reaction–advection–diffusion modelling and network theory. The mechanistic approach relies upon three main components: (1) the structural properties of the underlying spatial network; (2) the residency
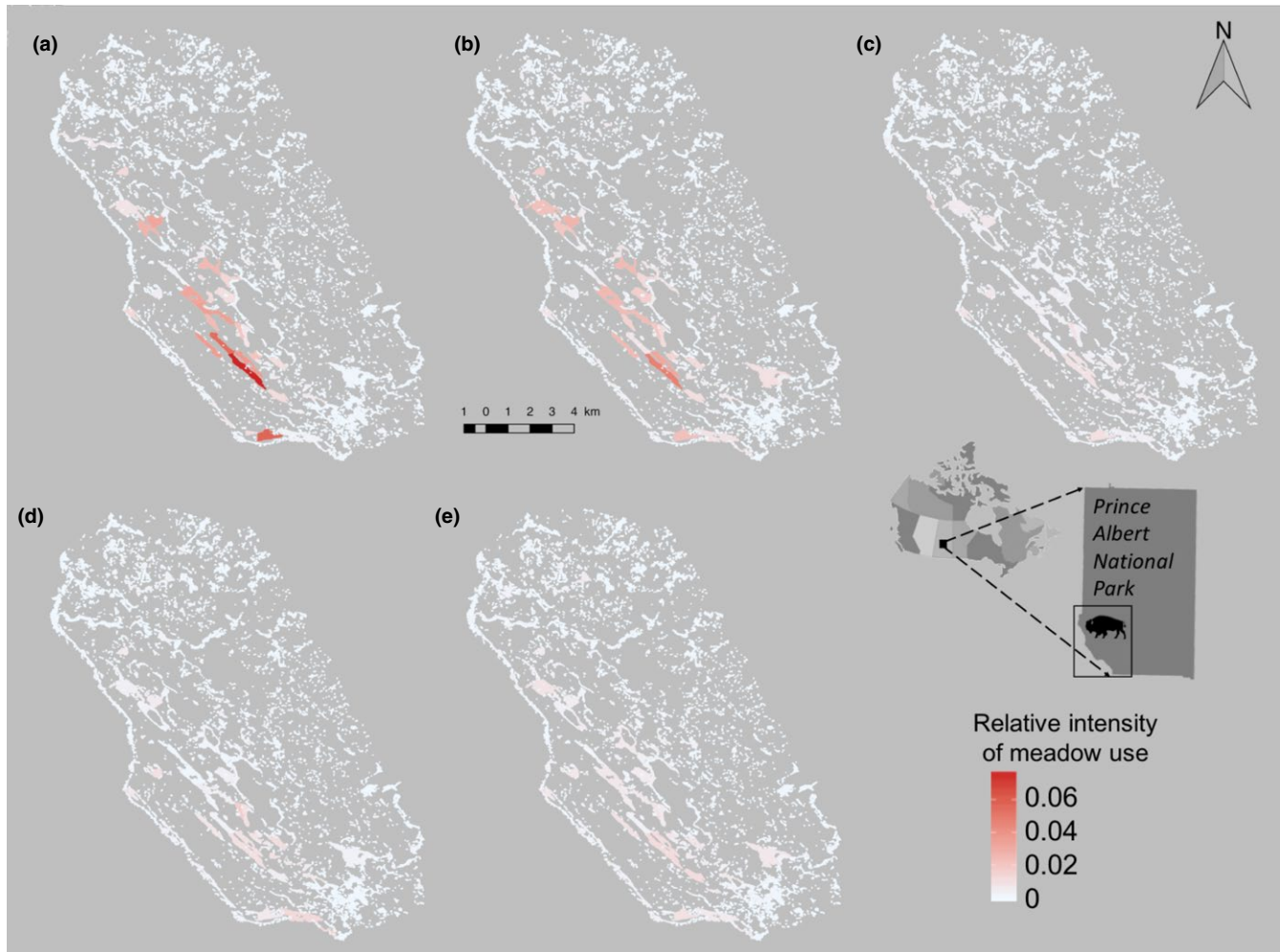
FIGURE 3 Relative intensity of meadow use estimates for plains bison in Prince Albert National Park: (a) based upon geolocations of 22 bison during summer over 8 years of monitoring (2005, 2007, 2010–2015); predicted by the reaction–advection–diffusion model while considering different network structures (b) ultra-small world scale-free network, (c) mininum planar graph, (d) 700-m distance threshold network and (e) 1800-m distance threshold network. Goodness-of-fit of (b), (c), (d) and (e–a) are respectively pseudo-$R_B^2 = .74$, pseudo-$R_C^2 = .21$, pseudo-$R_D^2 = .21$ and pseudo-$R_E^2 = .37$

time in resource patches; and (3) the functional connectivity of resource patches. Part of our contribution rests in the integration of two ecological fields that have been largely developed in parallel: theories of spatial network and of reaction–advection–diffusion. We demonstrate that this combination provides a robust mechanistic framework based upon spatial and temporal dimensions of animal movement to describe and anticipate animal distributions. The framework can disentangle the relationships between observed space use and the underlying characteristics of movement patterns and, as a result, it improves our ability to predict change in animal distributions following a disturbance. Such an ability to anticipate animal distribution dynamics is becoming increasingly relevant for animal conservation and management because human activities create resource networks that can rapidly change over space and time. An increasing number of species and populations are becoming established in such highly dynamic resource networks (Fischer & Lindenmayer, 2007), because of industrial activity such as resource extraction (O'Brien et al., 2006).

The accuracy with which the model was able to predict the spatial distribution of plains bison in Prince Albert National Park strongly depended upon the accuracy of the underlying network used to make inferences. While a MPG or a distance-based graph are generally used to predict links in spatial networks of terrestrial species (Bunn et al., 2000; Courbin et al., 2014; Minor & Urban, 2008; O'Brien et al., 2006), the spatial network for plains bison in the park corresponded more closely to an ultra-small world scale-free network, a complex network having structural properties that differ from a MPG or a distance-based graph. In a MPG, there are no shortcuts among nodes and individuals simply traverse the landscape using stepping stone paths (Fall et al., 2007), resulting in a relatively homogeneous pattern of connectivity and space use within the graph (Figure 3). Although, MPG fit could probably be improved using least-cost path instead of Euclidean distance (O'Brien et al., 2006), all patches would still be stepping stones. In distance-based graphs, shortcuts may arise when the distance threshold is large enough (Figure 1). However, the degree distribution of the graph
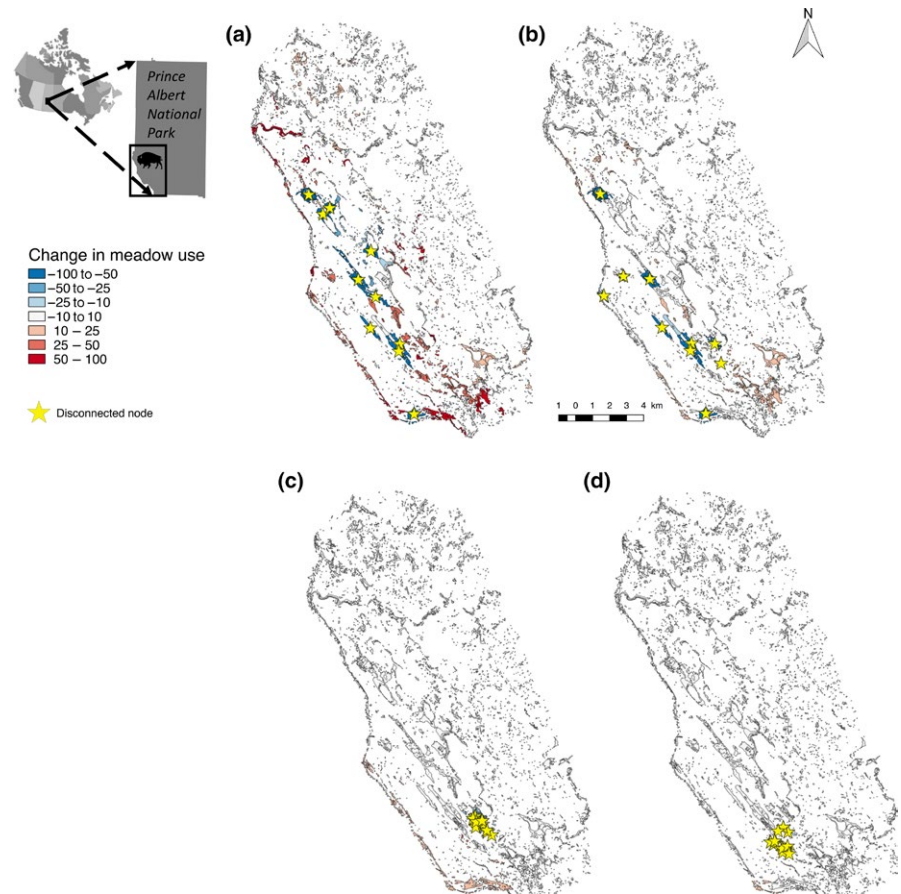
FIGURE 4 Change in relative intensity of meadow use estimates for plains bison in Prince Albert National Park: predicted by the reaction–advection–diffusion model while considering different network structures for implementing the removal of the 10 most connected meadows (yellow stars) (a) ultra-small world scale-free network, (b) mininum planar graph, (c) 700-m distance threshold network and (d) 1,800-m distance threshold network. The value represents the change in the relative intensity of meadow use in comparison to model prediction before meadow removal (Figure 3)

stays relatively homogeneous independently to the distance threshold, as it was the case with both thresholds we used (700 m and 1,800 m, also see Minor & Urban, 2008). Thus, this relatively homogeneous pattern of connectivity is also reflected in space use within the graph (Figure 3). In contrast, an ultra-small world scale-free network has both hubs and shortcuts that reflect the highly heterogeneous pattern of connectivity within the graph (Fox & Bellwood, 2014). Space use therefore was also largely heterogeneous with the occurrence of some heavily used hubs relative to the other nodes. This pattern is more consistent with bison distribution that is observed in the park (Figure 3). These findings reveal that landscape connectivity can be strongly organized over space, and overlooking such organization can induce spurious inference regarding space use.

Complex spatial networks have been identified in other empirical studies, such as in the inter-patch movements network of white-striped freetail bats *Tadarida australis* and various herbivorous fish species (Fox & Bellwood, 2014; Rhodes et al., 2006). The spatial network of bat roosting sites had the property of a scale-free graph, with one hub maintaining connectivity for the whole group of trees (Rhodes et al., 2006). Complex networks likely occur more frequently than has been currently described in the ecological literature. Network properties can provide us crucial information on how the system can withstand landscape disturbance, such as resource extraction, as long as network topology is accurately identified (Newman, 2003). Indeed, since

network structural properties have an effect on network robustness, a perturbation would have different consequences on landscape connectivity, depending upon the topology of the graph and the specific nodes that are disturbed (Figure 4). For example, Fox and Bellwood (2014) showed that coral reef fishes had spatial networks with small world properties, such that the concentration of fishing effort at known aggregation sites could increase the risk of extinction of coral reef fish species. The potential effect that a disturbance could exert on the coral reef fish community remains an assumption that cannot be fully evaluated using only network analysis, because the temporal dynamic of movement is then ignored (Stehfest et al., 2015). Ferrari et al. (2014) showed the utility of using dynamic network models for studying dynamical processes. Indeed, they modelled the temporal changes in the occurrence of links within a patch network to identify habitat patches that contributed the most to pathogen range expansion. Our study demonstrates the advantages of dynamic network models for wildlife conservation and management. We used reaction–advection–diffusion modelling to provide an effective tool to anticipate variation in space use following, for example, management-induced changes in landscape connectivity (Figure 4).

Accurate modelling of landscape connectivity using spatial network requires an understanding of the interplay between animal movement and habitat attributes (Nathan et al., 2008). Here, we offer guidance on how to predict links in a spatial network while considering structural and functional connectivity. Indeed,

meadow area and distance between meadows were two key co-variates to predict the links in the spatial network of plains bison, using the ERGMM. The resulting network had similar properties than the empirical graph of bison constructed directly from GPS data. The adjustment was not as good for the distance-based and minimum planar graphs, which only consider inter-meadow distances in our case. Thus, the ERGMM can provide an accurate and superior model of landscape connectivity without being limited by the number of landscape attributes (i.e. a large variety of parameters can be implemented at a relatively low computational cost). Besides, considering the fast development of telemetry tools (e.g. GPS-collars are now available for a broad range of species, Cagnacci, Boitani, Powell, & Boyce, 2010) and geographic information systems, movement among patches and residency time can then be estimated for an increasing number of species in various landscapes. Our modelling approach should thus be increasingly used in ecological studies.

In conclusion, our work has demonstrated how reaction–advection–diffusion modelling coupled to network theory can provide a robust mechanistic framework to predict animal distributions in dynamic environments. Our modelling framework could be applied to a large range of systems that experience rapid environmental changes due to habitat management, for example. Finally, complex networks can be relevant for modelling landscape connectivity in ecological studies, and identifying appropriate conservation or management targets.

AUTHOR'S CONTRIBUTIONS

M.-C.P. and D.F. conceived the ideas and designed the methodology; M.-C.P. extracted the GIS information and conducted statistical analysis; M.-C.P. and A.F. constructed the reaction–advection–diffusion model; T.D., L.-P.R. and D.F. were in charge of fund raising for the project; M.-C.P., T.D., A.F., L.-P.R. and D.F. wrote the manuscript; all authors contributed critically to the drafts and gave final approval for publication.

DATA ACCESSIBILITY

Matlab code and the data supporting this article are available on Open Science Framework (https://osf.io/uzwfv/; https://doi.org/10.17605/osf.io/uzwfv).

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