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Bringing circuit theory into spatial occupancy models to assess landscape connectivity

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Abstract

1. Occupancy models were originally developed to better understand species distribution while accounting for imperfect detection. Because species distribution is not only shaped by habitat quality but also by the ability of individuals to reach suitable habitats, spatial dynamic occupancy models have been proposed to extend the original framework by defining that site colonisation was a function of the Euclidean distance to occupied sites. However, not all sites in the landscape are equally accessible due to the presence of barriers, that of corridors, etc. To account for connectivity between sites, the Euclidean distance has recently been replaced by a least-cost path distance, which explicitly accounts for landscape resistance, but assumes that individuals will follow the optimal route.
2. To relax this assumption, we first developed a new spatial occupancy model that incorporates commute-time distance derived from circuit theory to model accessibility across sites. This distance has the advantage of modelling movement as a random walk and accounting for the fact that colonisation could be achieved from multiple paths. Our approach allows for the explicit estimation of landscape connectivity from detection/non-detection data and a direct measure of connectivity uncertainty.
3. We implemented the model in the Bayesian framework using the *nimble* R package, which allows useful R connectivity functions to be called from within the model. Second, we carried out a simulation study to assess the performance of our model by considering four scenarios depicting an increasing level of landscape resistance. Third, to illustrate our new approach, we studied the recolonisation of two carnivores in France.
4. We quantified the degree to which rivers facilitate Eurasian otter (*Lutra lutra*) colonisation and highways impede Eurasian lynx (*Lynx lynx*) colonisation. Overall, spatial occupancy models provide a flexible framework to accommodate any distance metric designed to align with species dispersal ecology.

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KEYWORDS

commute-time distance, dynamic occupancy models, hierarchical models, *Lutra lutra*, *Lynx lynx*, nimble, non-invasive monitoring, resistance surface

1 | INTRODUCTION

The distribution of a population is not only the result of current conditions, but is also influenced by the historical variations it has experienced (Guisan et al., 2017). Initially, species distribution models (SDM) have overlooked this dynamic component, assuming that a population at a given location and time is at equilibrium with its environment (Guisan & Zimmermann, 2000).

With the emergence of large-scale and long-term monitoring, researchers have extended SDM to model species distribution over time. Among others, dynamic occupancy models explicitly estimate the probabilities of colonisation and extinction, acknowledging that favourable sites are more likely to be colonised (MacKenzie et al., 2017). While these probabilities can be a function of site characteristics, their spatial arrangement in the landscape is, however, commonly ignored in the standard dynamic occupancy model. When applying this model, researchers are often confronted with spatial autocorrelation, where locations close to each other have correlated values (Dormann et al., 2007). This autocorrelation can come from an unaccounted variable that is itself autocorrelated or from unmodelled biological processes (e.g. dispersal, source/sink dynamics, competition, etc.) (Guélat & Kéry, 2018). In practice, researchers might be interested in modelling the mechanisms and not just controlling for spatial autocorrelation (see Dormann et al., 2007; Guélat & Kéry, 2018). Therefore, researchers who want to study the underlying process need methods to explicitly model it.

The standard dynamic occupancy model was extended by explicitly defining that the colonisation of unoccupied sites was a function of the Euclidean distance to occupied sites, also referred to as the isolation by distance concept in the metapopulation theory (Chandler et al., 2015; Risk et al., 2011; Sutherland et al., 2014). Therefore, these models acknowledge that sites close to occupied sites are more likely to be colonised and unravel spatial autocorrelation arising from species ability to reach suitable habitat.

However, the way the landscape is structured (e.g. presence of barriers, corridors) also affects site accessibility, this is usually referred to as landscape connectivity. Developments in spatial capture-recapture (SCR) models have overcome this issue by replacing the Euclidean distance with a least-cost path distance (LCP) (Royle et al., 2013; Sutherland et al., 2015), which is often used in landscape ecology (Coulon et al., 2015; Zeller et al., 2012). Therefore, the proximity between locations in the landscape is not only a function of isolation by distance but it also integrates resistance of the matrix. Howell et al. (2018) built on this idea and replaced the Euclidean distance in the dynamic occupancy model formulation proposed by Chandler et al. (2015) by the LCP distance. This model allows for an explicit estimation of cost values and connectivity. An important assumption of the LCP approach is that all individuals are omniscient

and will follow the optimal route. However, in situations where dispersers do not have previous knowledge of the landscape, assuming that individuals will only follow one optimal path is strong (Diniz et al., 2020).

To relax this assumption, circuit theory has been introduced as a conceptual framework that applies principles from electrical circuit theory to model the movement of individuals across the landscape, like electrons in a circuit (McRae et al., 2008). In circuit theory, the landscape is considered a network of interconnected nodes linked by resistors that form the resistance surface. By assigning resistance values to each landscape feature, circuit theory quantifies the potential flow of individuals between sites. This formulation implies that an individual moving through the landscape is unaware of the optimal route between patches and makes decisions at each step. In circuit theory, the commute-time distance is used to compute the distances between sites. This distance is defined as the expected number of steps a random walker would take to move between patches and return. The commute-time distance has the advantage of being able to account for path redundancy; in other words, the commute-time distance between patches decreases when there are multiple ways to join these patches (McRae et al., 2008).

In summary, the two most commonly used connectivity algorithms make different assumptions about how movement occurs between occasions. This ultimately leads to different representations of which sites may be accessible on the following occasion (McRae & Beier, 2007). The LCP distance assumes that there is a single optimal path, which will favour long circuitous routes that traverse the least resistant habitats. In contrast, the commute-time distance accounts for paths redundancy by assuming a random walk, which highlights stepping stones surrounded by resistant habitats if multiple paths lead to them (McClure et al., 2016). These discrepancies have also demonstrated the value of the circuit algorithm in modelling population recolonisation. Circuit algorithms are less sensitive to input data used to construct the resistance surface than cost-distance algorithms, resulting in more accurate movement predictions when input data are of a lower quality (Zeller et al., 2018). In particular, two studies have demonstrated that circuit algorithms outperform the cost-distance algorithm in modelling dispersal in carnivore populations with estimated resistance from habitat suitability models (see Jackson et al., 2016; McClure et al., 2016). Despite many applications of circuit theory in landscape ecology and the demonstrated value of the metric in the context of modelling carnivore recolonisation from occurrence data, the commute-time distance has yet to be brought into the occupancy framework.

In this paper, we integrate the commute-time distance in the colonisation process of dynamic occupancy models to model species recolonisation in structured landscapes. We adopt a hierarchical representation of occupancy models (MacKenzie et al., 2017)

which we implement in the Bayesian framework using Markov chain Monte Carlo (MCMC) methods in the *nimble* R package (de Valpine et al., 2017). To investigate how our model performed, we simulated occupancy data across four scenarios where colonisation was increasingly associated with landscape structure. We quantified the consequence of misspecifying the movement model by comparing the accuracy of the LCP distance occupancy model to that of the commute-time distance occupancy model. Then, to illustrate our approach, we used two contrasted case studies on carnivore recolonisation in France: The Eurasian otter (*Lutra lutra*) in the Massif Central and the Eurasian lynx (*Lynx lynx*) in the Jura mountains. Using our model and long-term detection/non-detection data, we aimed to quantify the degree to which rivers facilitate otter recolonisation and highways impede lynx recolonisation.

2 | MATERIALS AND METHODS

2.1 | Spatial dynamic occupancy model with commute-time distance

Dynamic occupancy models rely on detections and non-detections, denoted $y_{ij,t}$, of a species at site i on a secondary occasion j during a primary occasion t (Figure 1). Because the true presence-absence $z_{i,t}$ of a species at site i during primary occasion t is only partially observed, we accommodate the imperfect species detection with probability $p_{ij,t}$, which we estimate from repeated secondary occasions j :

$$y_{ij,t} \sim \text{Bernoulli}(p_{ij,t} z_{i,t}), \quad (1)$$

$$z_{i,t} \sim \text{Bernoulli}(\Psi_{i,t}), \quad (2)$$

where $\Psi_{i,t}$ is the occupancy probability at site i during primary occasion t . Probabilities of colonisation and persistence are denoted γ and ϕ . A site is occupied in a given primary occasion if it was unoccupied at the previous primary occasion and is colonised, or if it was occupied in the previous primary occasion and persisted:

$$\Psi_{i,t} = \gamma_{i,t-1} (1 - z_{i,t-1}) + \phi_{i,t-1} z_{i,t-1}. \quad (3)$$

The probability $\gamma_{i,t-1}$ of a site i to be colonised between primary occasion $t - 1$ and t , is a function of its accessibility to occupied sites at the previous primary occasion and a site colonisation probability γ_0 . The site colonisation probability γ_0 and the persistence probability ϕ can be modelled as a function of covariates using standard logistic regression, thus accounting for the impact of local variables on site occupancy dynamics. The accessibility probability is defined as the complementary of the product of the probabilities of not being accessible over all occupied sites m in the landscape, where M is the total number of sites:

$$\gamma_{i,t-1} = \left(1 - \prod_{m=1}^M (1 - \rho_{i,m,t-1} z_{m,t-1}) \right) \times \gamma_0. \quad (4)$$

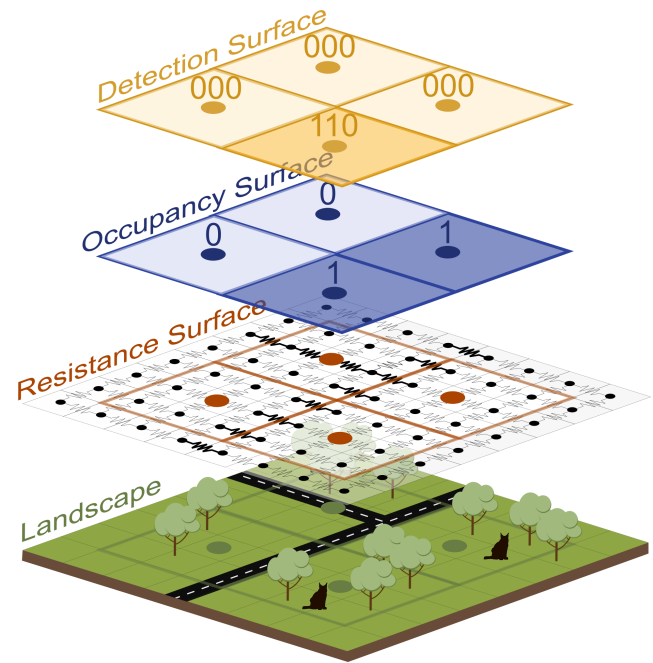


FIGURE 1 Graphical description of the spatial occupancy framework accommodating commute-time distance. The landscape is discretised into a spatial graph where nodes (black and orange points) are linked to the four neighbouring nodes by resistors to form the resistance surface. Resistance values between nodes are function of a resistance value (α) estimated by the model and a spatial covariate, here the presence of the road. The proximity between the four occupancy sites (blue points) is defined according to the commute-time distance. This distance is computed between all pairs of orange nodes that match the centre of the occupancy sites. Note that the resistance surface has a larger extent and a finest resolution than the occupancy surface to allow multiple routes between sites. The focal species can be present (denoted 1) or not (denoted 0) at each occupancy site (in blue). Occupancy state at each site in the following primary occasions arises from a site colonisation probability (γ_0) and the commute-time distance to occupied sites in the previous primary occasion. At each site, we conducted in this example three repeated secondary occasions where the focal species can be detected (1) or not (0) and is presented here on the detection surface (in yellow).

The probability $\rho_{i,m,t-1}$ that site i is accessible by site m between primary occasion $t - 1$ and t is called pairwise accessibility probability, and is modelled with a Gaussian kernel with a fixed intercept. This formulation allows us to have a probability that decreased with increasing distance between sites $d_{i,m}$ and equals to 1 when $d_{i,m} = 0$:

$$\rho_{i,m,t-1} = \exp\left(-d_{i,m}^2 / 2\sigma^2\right), \quad (5)$$

where σ is the scale parameter that describes the colonisation distance. This formulation slightly differs from previous formulation of the model with Euclidean or LCP distance, which also estimates the intercept of the Gaussian kernel but does not estimate site colonisation probability (Appendix S2; Chandler et al., 2015; Howell et al., 2018).

The originality of our model lies in the use of a commute-time distance $d_{i,m}$ instead of a Euclidean distance (Chandler et al., 2015)

or a LCP distance (Howell et al., 2018). In circuit theory, distances are computed on a resistance surface, which is obtained using a spatial resistance variable in raster format (McRae et al., 2008). From this raster, we arbitrarily defined a graph where each pixel is a node connected to the eight adjacent nodes with resistors. We decided on the number of adjacent nodes as a trade-off between ecological realism and computational burden (Figure 1). The resistance or cost between two adjacent nodes x and x' is a function of the value of the resistance variable c_1 at these nodes and an estimated resistance parameter $\alpha \in \mathbb{R}$:

$$\text{cost}(x, x') = \frac{\exp(\alpha \times c_1(x)) + \exp(\alpha \times c_1(x'))}{2}. \quad (6)$$

When $\alpha > 0$, the landscape impedes movement, whereas the more α is negative, the more the landscape facilitates movement. Overall, when $\alpha = 0$, the resistance between all adjacent nodes is the same and the landscape structure does not influence movement.

Given a source and a destination in the graph, the commute-time is defined as the average number of steps needed to join the two nodes and back during a random walk. This connectivity measure between nodes in an undirected graph has the properties of distances measures and verifies the non-negativity, the definiteness, the symmetry and the triangle inequality (Fouss et al., 2007). As in an electrical circuit, the interesting property is that commute-time distance between two nodes decreases when the number of paths that connect them increases and when the length of paths decreases (Fouss et al., 2007). The commute-time distance is computed as twice the number of edges in the graph times the effective resistance between the two nodes and is therefore proportional to the effective resistance between two nodes (Chandra et al., 1997). To compute commute-time distances, we use the `commuteDistance()` function of the *gdistance* R package (version 1.6.4, van Etten, 2017). To improve computation times in our case studies, we precalculated distances between patches for a set of resistance values rounded to one decimal, which saved us the need to compute distances between sites at each MCMC iteration. All analyses were conducted in R (version 4.3.1, R Core Team, 2023). We implemented the spatial occupancy model with commute-time distances in the Bayesian framework using *nimble* (version 1.0.1, de Valpine et al., 2017). *Nimble* allows the user to call any R functions like `commuteDistance()` from within a model, which made the implementation of our model possible. We provide the *nimble* code for dynamic occupancy models, models accommodating Euclidean distance, LCP distance and our model with commute-time distance (Appendix S1). Although the LCP distance occupancy model and the commute-time distance occupancy model differ only in their practical implementation of distance, they diverge by their underlying ecological assumptions. The LCP distance assumes that only one optimal path exists between two sites, whereas the commute-time distance does not assume omniscience of individuals moving through the landscape. Furthermore, the commute-time distance acknowledges that sites linked by multiple paths are more accessible. These differences result in distinct representation of landscape structure.

2.2 | Simulation study

We conducted a simulation study to assess the performance of our model at different levels of landscape resistance to movement. This simulation study was designed to match the monitoring of a colonising carnivore (see the next section). We simulated detection data across $T = 3$ years (i.e. primary occasions), $K = 6$ sampling occasions (i.e. secondary occasions) and $M = 16 \times 16$ occupancy sites with a spacing of 1 du (du for distance unit) (Figure 2). We set the detection probability constant across the study area with $p = 0.3$. As we simulated a colonising species, we assumed that the persistence probability was high, $\Phi = 0.9$, and the site colonisation probability was also constant across the study area and high, $\gamma_0 = 0.8$.

We defined a resistance surface with a resolution of $0.25 \times 0.25 \text{ du}$ with a 2 du buffer around sites to allow colonisation

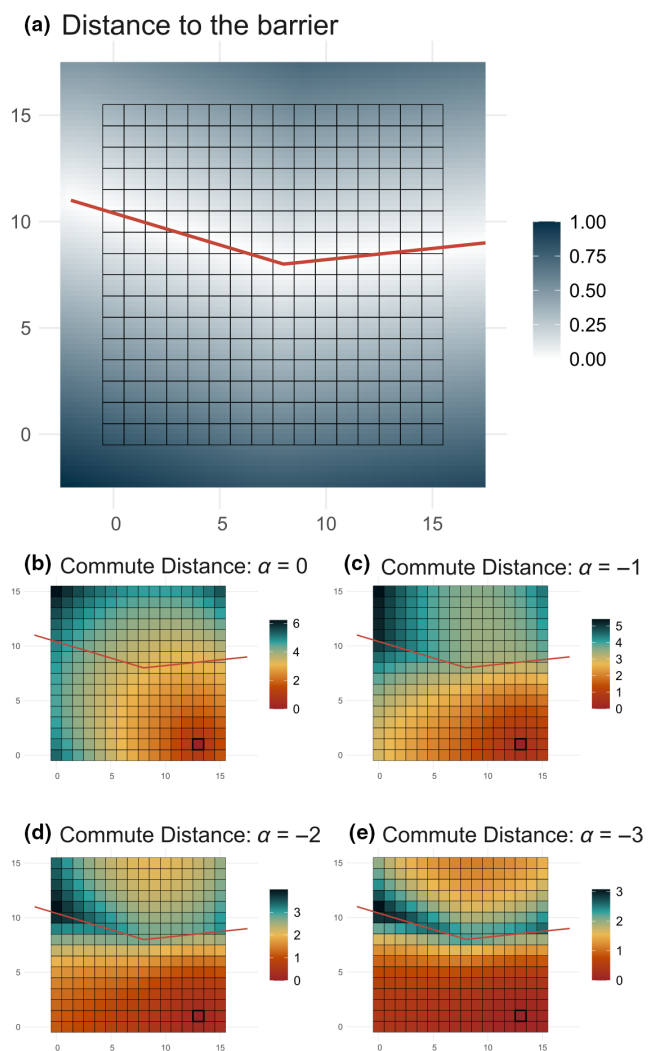


FIGURE 2 (a) Map of the distance to the barrier (in red), which is the resistance covariate used in the simulation study scaled between 0 and 1 and the 256 occupancy sites represented by black squares. Below map (a), the four other maps represent the commute-time distance from each site to cell 19 in bold with decreasing resistance parameter to the distance to the barrier. The four scenarios are respectively (b) $\alpha = 0$, (c) $\alpha = -1$, (d) $\alpha = -2$ and (e) $\alpha = -3$.

routes outside the occupancy surface. The resolution of the resistance covariate was more precise than the occupancy surface. The resistance covariate represented the Euclidean distance to a barrier and was scaled between 0 and 1 (Figure 2).

To compare how the model performed, we defined four scenarios with increasing levels of landscape resistance to site accessibility. At the first primary occasion, we considered that the 22 sites in the bottom right of the study area were occupied to simulate a colonisation from one side of the barrier (Appendix S2 Figures A2–A5). This corresponded to an occupancy probability at the first primary occasion of $\Psi_1 = 0.086$.

We assumed that increasing the distance to the barrier facilitated accessibility; hence, we considered negative resistance parameters. The first scenario accounted for no resistance $\alpha = 0$ while the three other scenarios increased landscape facilitation to colonisation (i.e. $\alpha = -1, -2$ and -3) (Figure 2). However, to control for the effect of resistance-related variation in colonisation distance, we decreased σ for each scenario (Morin et al., 2017). When decreasing resistance, the extent of movement increased for a given σ and more sites are colonised which can reduce bias. We calculated the number of sites occupied on the second primary occasion across 20 simulated datasets for each scenario and a range of σ values (Appendix S2 Figure A1). We set the mean number of sites occupied on the second primary occasion to be approximately 60 sites, which gave us $\sigma = 0.6, 0.55, 0.4$ and 0.3 respectively for $\alpha = 0, -1, -2$ and -3 . For each scenario, we generated 100 datasets. We calculated the relative bias, coefficient of variation and coverage of the 95% credible intervals for all model parameters, with the commute-time distance dynamic occupancy model. Moreover, in order to assess the consequences of misspecifying the non-Euclidean distance in the model, that is, using a LCP distance when the movement model is better approximated by the commute-time distance, we also fitted the LCP distance occupancy model to the 400 datasets and computed the root mean square error (RMSE) for each model.

We used non-informative priors on all parameters (see Appendix S2 Table A1). To avoid the computational burden of computing commute-time distances at each MCMC iteration, we pre-calculated distances between all sites for resistance values between -5 and 5 every 0.1 values, or between -8 and 2 for scenario 4 with LCP distance occupancy model and stored these values in a three-dimensional matrix. This object was stored in the R global environment to avoid compiling it. The values are retrieved at each MCMC iteration using a *nimble* function that finds the distance value given the minimum of the range of resistance values (here -5) and the rounding value (here 0.1). This trick avoids the need to create a *nimble* function that calls the *gdistance* functions (*commuteDistance()* and *costDistance()*) written in R language and slows down the *nimble* model compiled in C++. This was done at the cost of a slight loss in the precision of α to one decimal. For each model, we ran three chains and discarded the first 2000 iterations as burn-in. For scenarios 1 and 2, each chain had a length of 8000 iterations, while we used 12,000 iterations for scenarios 3 and 4. Convergence was assessed using the Gelman–Rubin statistic, $\hat{R} < 1.1$, effective sample size > 100 and visual inspection of trace plots (Brooks & Gelman, 1998).

2.3 | Applications

2.3.1 | European otter population in the Massif Central

We studied an Eurasian otter population distributed in the Massif Central in France (Figure 5a,b). We used detection/non-detection data from 158 sites in the Massif Central that were previously analysed by Couturier et al. (2023). The sites were 300m transects along rivers where the centre was placed at potential marking locations (e.g. bridges, water mills, confluences). These centres are the spatial units where occupancy was estimated. The monitoring was composed of two primary occasions, with the first lasting two consecutive winters to maximise the number of sites monitored, from November to April in 2003–2004 and in 2004–2005 (primary occasion 1) and from October 2011 to April 2012 (primary occasion 2). Otters in the Massif Central are genetically similar (Pigneur et al., 2019), suggesting that the new colonised sites were likely to be from individuals already present in the area. Therefore, we did not include other sites that was not monitored. Otter recolonisation is a slow process, making the assumption of closure within a primary occasion most likely valid. Each site was visited between one and four times on the first primary occasion and between two and threetimes on the second primary occasion.

We considered the initial occupancy probability as a function of elevation (BD ALTI® Version 2.0, 01/2023) because otters are assumed to colonise lower elevation from the mountains (Appendix S3 Figure A1A). The detection probability was assumed to be primary occasion-specific (Couturier et al., 2023). Because otters mainly use rivers to colonise new habitats, we computed the distance to the closest river (BD TOPO® Version 3.3, 12/2022) to create the resistance surface with a resolution of 0.04 km^2 . This surface encompasses all sampling sites with a 30km buffer around them to account for all possible alternative routes between sites, because the propagation speed was estimated at 10 km year^{-1} in France (Van Looy et al., 2014).

We ran three chains each of length 50,000 and we discarded the first 1000 iterations as burn-in. We used non-informative priors on all parameters (Appendix S3 Table A1). For the resistance parameter, we used a uniform distribution between -2 and 7 , because otters are semi-aquatic and do not go far away from rivers, and therefore the larger distances to rivers are assumed to strongly impede their movements (Couturier et al., 2023).

2.3.2 | Eurasian lynx population in the Jura mountains

As a second case study, we considered the lynx population present in the French Jura mountains (Figure 5c,d). We used a 100 km^2 grid with 644 cells in the French Jura where sampling occurred at least once during the study period. Because lynx recolonisation is a slow process, we defined three primary occasions at 10-year intervals in 1999–2000, 2009–2010, and 2019–2020. We considered months from November to April as secondary occasions. A detection occurred

on a secondary occasion if a sign of lynx presence (e.g. tracks, hair, camera trap picture) was detected in a cell of the grid. Then the detection was assigned to the site defined as the centre of the grid cell. The monitoring was carried out by a network of observers trained by the French Biodiversity Agency. We assumed that the detection probability varied according to the sampling effort, calculated as the number of observers present in a cell on a given primary occasion and secondary occasion (Louvrier et al., 2018). The lynx is an elusive species living in forested areas where its main prey, ungulate species, occur (Molinari-Jobin et al., 2007). Therefore, we assumed that the initial occupancy probability was a function of forest cover which we retrieved from CORINE land cover data (Appendix S4 Figure A1). We considered the distance from the centre of the pixel to the nearest highway computed from Open Street Map data (OpenStreetMap Contributors, 2023) as the resistance covariate with a resolution of 6.25 km². This surface encompassed the sampling grid with a 50km buffer.

We ran three chains each of length 10,000 and we discarded the first 1000 iterations as burn in. We used non-informative priors on all parameters (Appendix S4 Table A1).

3 | RESULTS

3.1 | Simulation study

Parameters $\gamma_0, p, \phi, \Psi_1$ were unbiased in all scenarios (Figure 3a). Parameter α was more and more positively biased as the absolute value of α increased up to 0.11 for scenario 4 and conversely σ was

negatively biased up to -0.07 for scenario 4. The coefficient of variation was under 25% for all parameters (Figure 3b). Between 100% and 90.6% of the 95% credible intervals covered the actual parameter values (Appendix S2 Table A2).

The commute-time occupancy models and the LCP occupancy models have a small RMSE <0.2 for the predicted colonisation probability. The estimated resistance parameter α was more negative for the LCP occupancy models for scenarios 2, 3 and 4, with a mean estimated value of $-0.01, -1.02, -2.14$ and -3.32 , respectively for scenarios 1 to 4 for the commute-time occupancy models and $0.97, -1.83, -3.80, -5.32$ for the LCP occupancy models. The commute-time models had a smaller RMSE, with respective mean values of 0.03, 0.04, 0.04 and 0.04 for each scenario, compared to the LCP models with respective mean values of 0.11, 0.12, 0.09 and 0.07 (Figure 4).

3.2 | Applications

We detected otter presence at 122 out of the 158 sites over the two primary occasions and lynx presence at 128 out of the 644 sites surveyed over the three primary occasions (Appendices S3 and S4 Figure A1). Hereafter, we provide the mean of parameter posterior distributions along with 95% credible intervals. The two models converged according to visual inspection of trace plots and Gelman–Rubin statistics ($\hat{R} \leq 1.07$; Appendix S3 & S4; Brooks & Gelman, 1998). The detection probability of otters was high throughout the study area, respectively 0.57 [0.49; 0.65] and 0.80 [0.74; 0.85] in the first and second primary occasions (Appendix S3

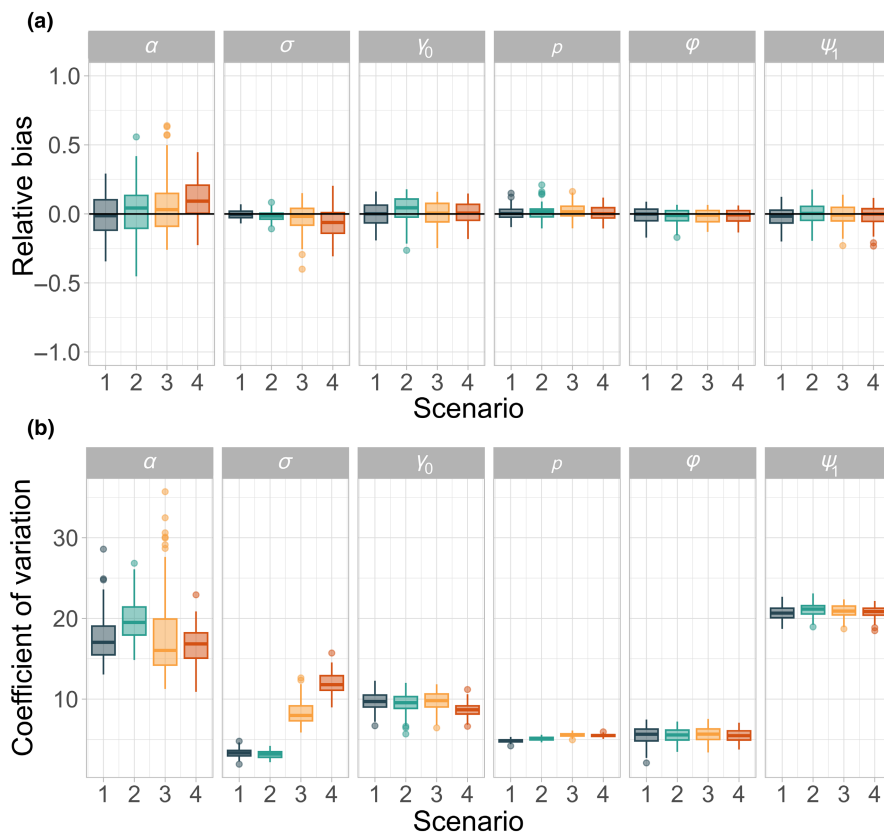


FIGURE 3 Model parameters (a) relative bias ($\frac{\hat{\alpha} - \alpha_{true}}{\alpha_{true}}$) and (b) coefficient of variation ($\frac{\hat{\sigma}}{\alpha_{true}} \times 100$) according to the four scenarios. The panels represent model parameters which are the resistance parameter α , the scale parameter σ , the site colonisation probability γ_0 , the detection probability p , the persistence probability ϕ and the occupancy probability at the first primary occasion Ψ_1 , in that order. Boxplots represent the median, the 50% quantiles and the 95% quantiles. For each scenario, we simulated 100 datasets. We discarded the simulations for which the models did not converge, that is four for scenario 3 and seven for scenario 4.

FIGURE 4 Distribution of root mean square error ($\sqrt{\frac{\sum_{i=1}^M (\gamma_{i,1} - \hat{\gamma}_{i,1})^2}{M}}$) of predicted colonisation probabilities $\gamma_{i,1}$ at each site between the first and the second primary occasion. Results from the 100 datasets of each scenario with the commute-time distance occupancy model and the least-cost path distance occupancy model.

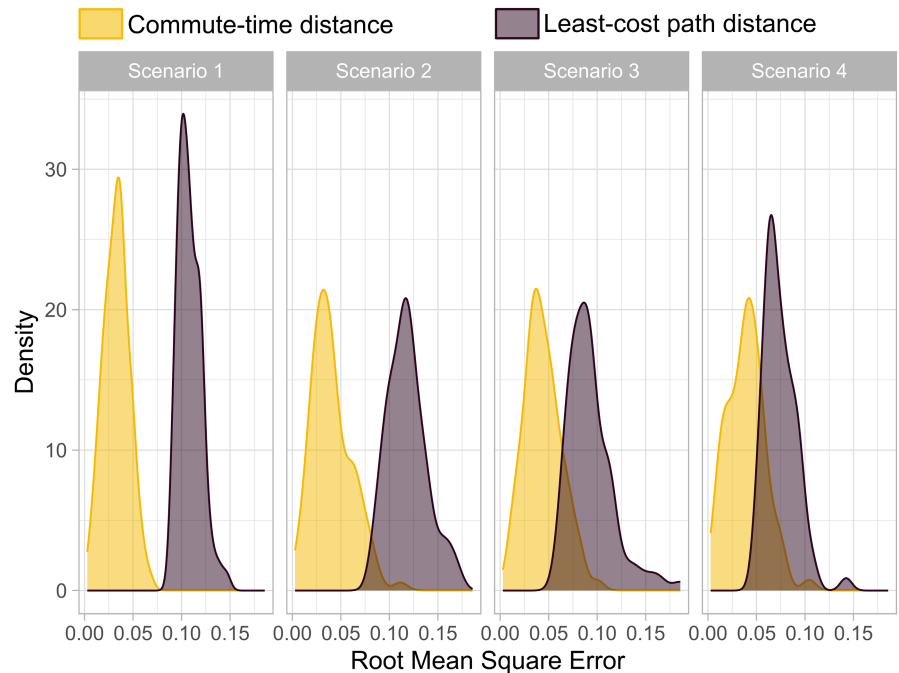


Figure A3A). The initial occupancy probability of otters increased with increasing elevation from 0.29 [0.17; 0.42] at 75 m to 0.88 [0.69; 0.98] at 1280 m (Appendix S3 Figure A3B). The detection probability of lynx increased with increasing sampling effort from 0.27 [0.23; 0.32] to 0.36 [0.23; 0.51] (Appendix S4 Figure A3A). The initial occupancy probability of lynx increased sharply with increasing forest cover, ranging from 0.01 [0.00; 0.02] without forest cover to 0.59 [0.43; 0.73] at 81% of forest cover (Appendix S4 Figure A3B).

Both species had high persistence probabilities, 0.95 [0.87; 0.99] and 0.68 [0.58; 0.79], respectively for the otter and lynx. The site colonisation probability for the otter and the lynx was also high and respectively equal to 0.66 [0.50; 0.87] and 0.94 [0.78; 1] for a given site. Colonisation of both species was linked to habitat structure. For otter, the posterior distribution of the resistance parameter α showed two modes at 0.4 and 5 [−0.8, 5.2] (Appendix S3 Figure A2). The highest mode at 5, which is the one supported by the data, confirmed that the rivers were facilitating otter accessibility to sampling sites. The resistance surface showed areas with a cost too high to allow any path to use this node for given scale parameter. In contrast, for the lynx, the resistance parameter was estimated at −0.72 [−0.34; −1.12], meaning that the higher distance from the roads was facilitating connectivity between sites (Figure 5a,c). On both resistance surfaces, the further the site was from the rivers or highways, the greater was the cost uncertainty (Figure 5b,d).

We also mapped the occupancy probability for otter and lynx (Figures 6 and 7) along with associated uncertainty (posterior standard deviation). In both case studies, the area occupied increased during the study period. In the Massif Central, almost all sites were occupied by otters in 2011, and only a few sites in the western part of the study area remained unoccupied (Figure 6). In the Jura mountains, lynx occupancy was bounded by highways. As the distance

from the core of the population increased, the uncertainty decreased (Figure 7).

4 | DISCUSSION

Dynamic occupancy models offer a comprehensive understanding of species distribution over time while accounting for imperfect detection (MacKenzie et al., 2017). We extended existing models to map and quantify landscape resistance to population recolonisation from occupancy data by integrating commute-time distance from circuit theory, therefore relaxing the assumption of omniscience and accounting for multiple routes (McRae et al., 2008). We showed that commute-time distance is more accurate to model the colonisation in space compared to LCP distance when the underlying movement model follows rules from circuit-theory (Figure 4). Our spatial occupancy model provides valuable insights into potential barriers to species recolonisation and the identification of ecological corridors. Unlike traditional approaches that rely on expert opinion to define resistance costs (Compton et al., 2007; Zeller et al., 2012), our spatial occupancy model estimates resistance and connectivity based on empirical data and provides a direct measure of uncertainty.

In the two case studies, we found differences in the strength and sign of landscape resistance to accessibility. The estimated resistance was positive for the otters regarding the distance to rivers, which is consistent with the semi-aquatic nature of this species (Van Looy et al., 2014). The presence of fewer rivers in the western part of the study area resulted in slower colonisation. In contrast, the resistance parameter was negative for the lynx population regarding the distance to highways, and the population range on the third primary occasion was clearly shaped by these linear features (Figure 7). Further away from the population core, the standard deviation of

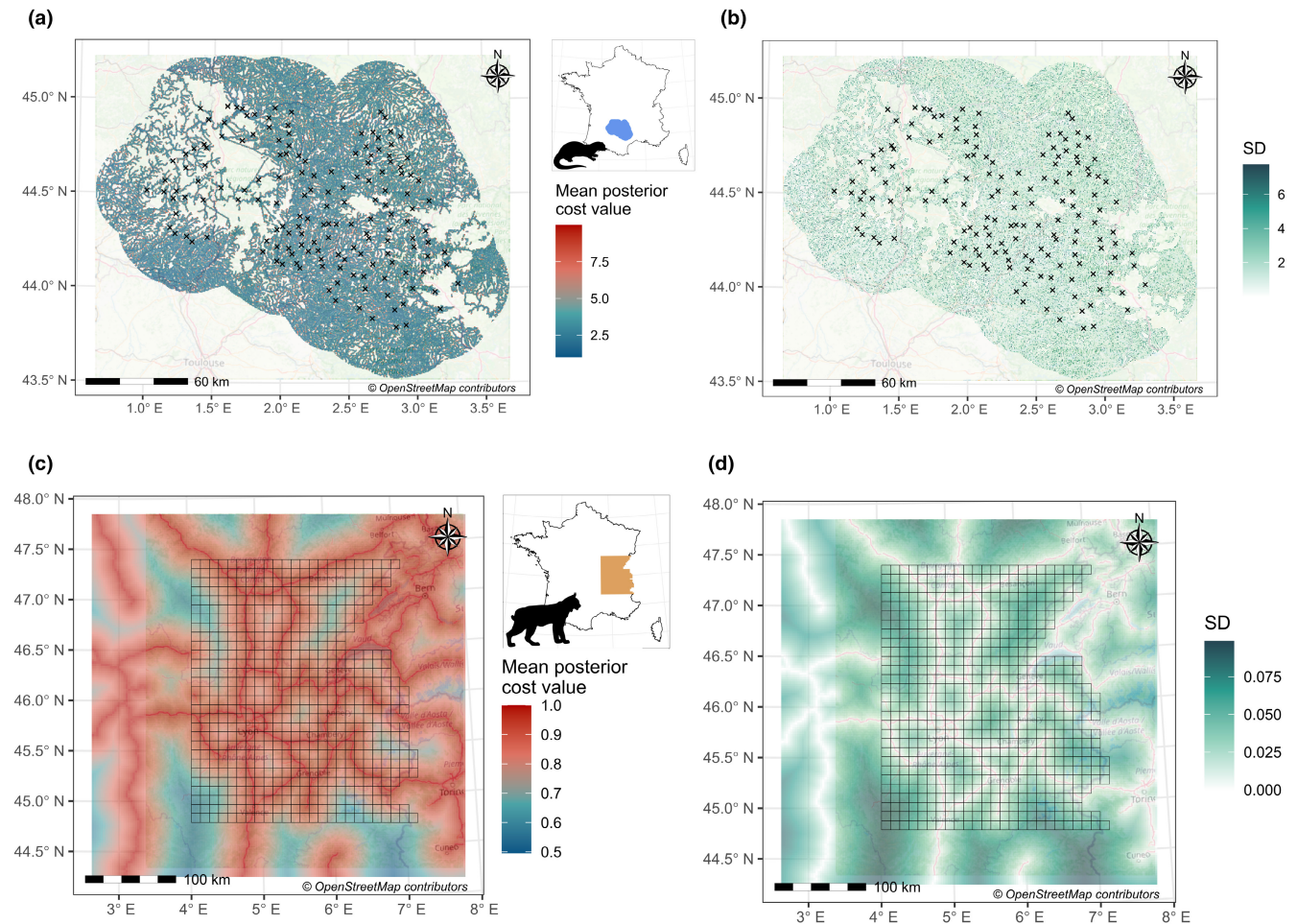


FIGURE 5 Distribution of sampling sites for the two case studies in France. On the top panels, black crosses symbolise the centre of 300m transects monitoring otter spraint in the Massif Central, background raster represents the mean posterior cost value estimated from the distance to rivers where pixels with cost higher than 10 were removed as the estimated scale parameter was 0.67 [0.39, 2.08] to highlight areas with lower cost (a) and corresponding standard deviation (b). On the bottom panels, 100km² squares delineate sampling sites of lynx presence in the Jura mountains, background raster represents the mean posterior cost value estimated from the distance to highways (c) and corresponding standard deviation (d). The Open Street Map background map shows the primary roads (red), the major rivers (blue), the country borders (bold grey) and French department borders (grey).

occupancy probability is close to 0. This means a high degree of confidence that these sites are not accessible and, therefore, not occupied. Yet, the habitat on the western side of the highways does not seem favourable for lynx establishment and other factors (e.g. forest cover, elevation) could be included to model site colonisation or accessibility. However, we could not include more than one resistance covariate in the model due to the computational burden. Other landscape covariates correlated with the highway distribution might also limit the accessibility of the lynx to the west.

While our model can be used to inform strategies for preserving or enhancing landscape connectivity, multiplying approaches would allow to assess the sensitivity of the results to the modelling assumptions. In particular, the choice of connectivity algorithm should be based on the specific research question, ecological assumptions about species movement, and the available data (Finerty et al., 2023). Choosing between LCP distance or commute-time distance should not be done statistically and would require an external

validation dataset to properly evaluate the performance of each connectivity algorithm, as has been done in other comparative studies (Riordan-Short et al., 2023; Zeller et al., 2018). Moreover, our approach only focuses on the effect of landscape structure on site accessibility and does not account for gene flow or road mortality (Bauduin et al., 2021). If we were to evaluate the long-term viability of lynx and otter populations, these issues should be addressed and would require genetic and mortality data.

The simulations show a positive bias in α and a negative bias in σ when the true resistance is at its lowest (Scenario 4). These two parameters are correlated, resulting in compensatory heterogeneity as described by Efford and Mowat (2014) in SCR models. Despite this, the predicted colonisation remains accurate, with an RMSE of 0.04 for Scenario 4 with commute-time distance (Figure 4). It is important to note that compensatory heterogeneity does not pose a problem as long as we avoid applying a group effect solely to α or σ . As an illustration, if we include a primary occasion-specific resistance

FIGURE 6 Maps of estimated mean posterior occupancy probabilities for otter in the Massif Central at the first primary occasion in 2003–2005 (a) and second primary occasion in 2011–2012 (b) with respective standard deviation (c, d).

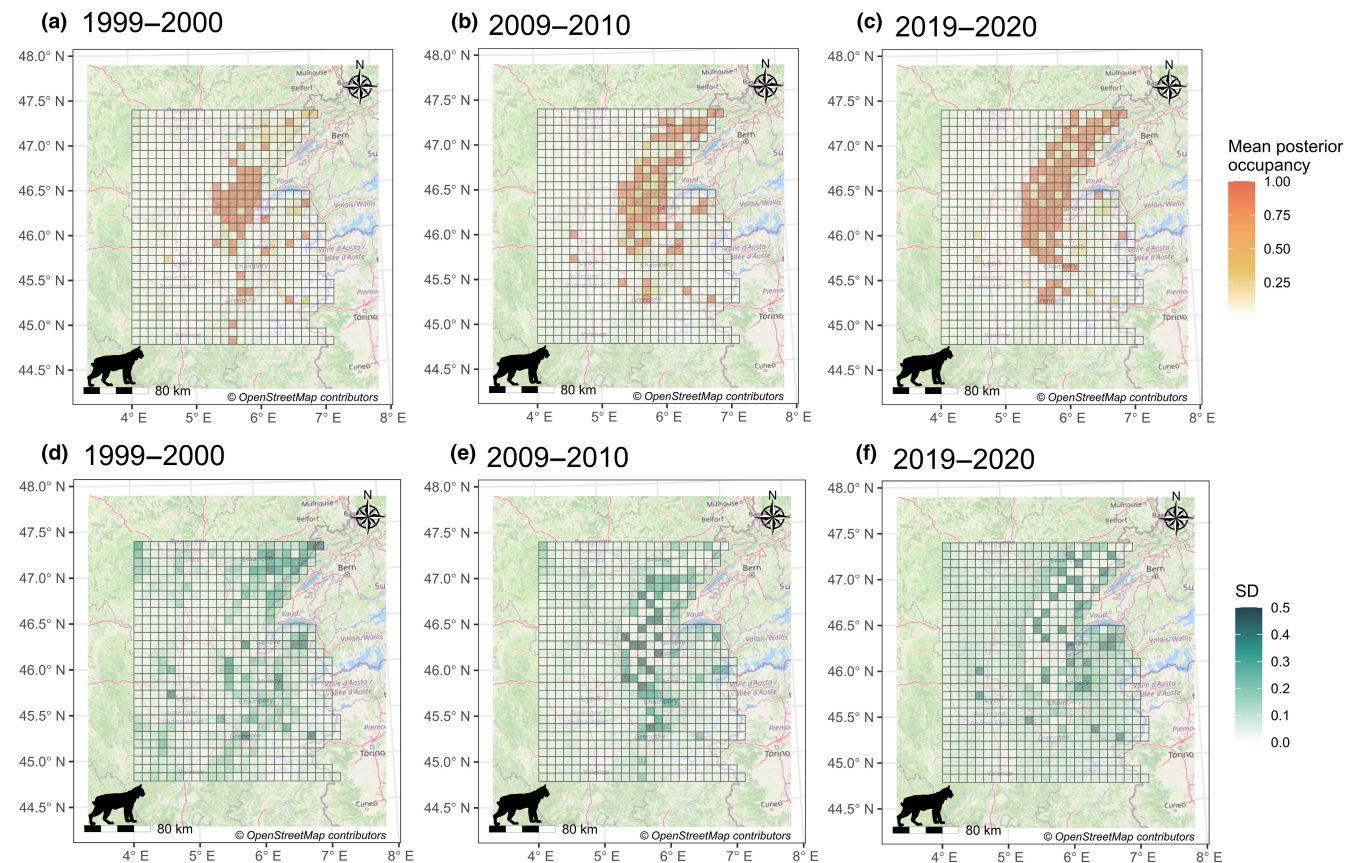
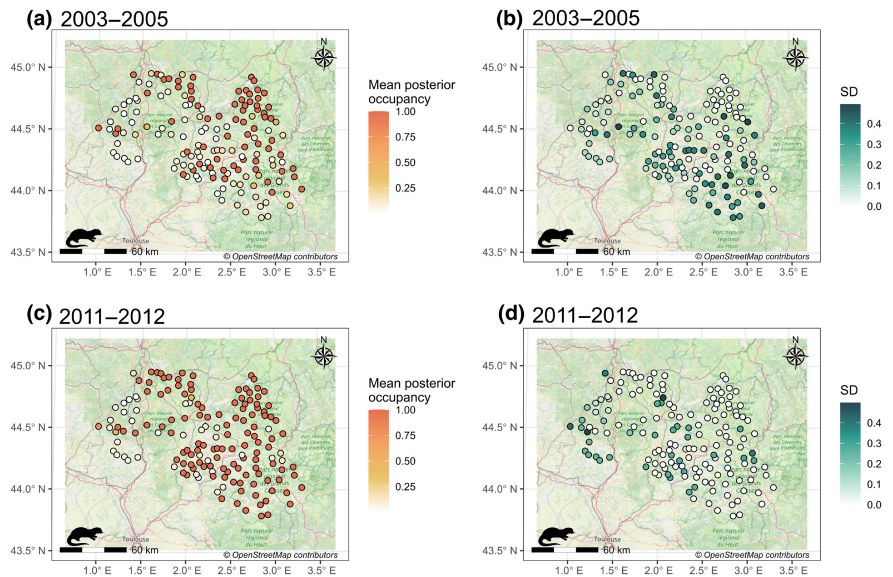


FIGURE 7 Maps of estimated mean posterior occupancy probabilities for the lynx in the Jura mountains in the first primary occasion from November 1999 to April 2000 (a), the second primary occasion from November 2009 to April 2010 (b) and the third primary occasion from November 2019 to April 2020 (c) with respective standard deviation (d–f).

parameter (α_i) in order to investigate whether the effect of a barrier diminishes during the recolonisation process, it would be prudent to apply this temporal effect to σ too.

Defining the extent and resolution of the occupancy surface and the resistance surface is a challenging point to consider when applying our model. For territorial species such as carnivores, the

resolution of the occupancy surface is defined according to home-range size (MacKenzie et al., 2017). However, animal distribution and animal movements are two processes that occur at different spatial scales and are affected by various variables, which explains why we used two distinct surfaces: the occupancy surface and the resistance surface. To model the movement process between

primary occasions, the resolution of the resistance surface has to be the most refined possible to provide a better approximation of continuous space to identify potential dispersal routes (Dupont et al., 2021; Howell et al., 2018; Zeller et al., 2012). In this study, we selected the centre of each occupancy cell as the starting and end points of movement, which may result in underestimating the landscape resistance and overestimating colonisation distances. Alternative parameterisations could be explored, such as taking all resistant nodes within each occupancy cell as starting and end locations or a set of randomly chosen nodes and average commute-time distances among them to define non-Euclidean distances. Similarly, the method avoids the necessity of defining discrete areas to connect, in a similar manner to the wall-to-wall or omnidirectional approaches used in circuit theory (Dickson et al., 2019). Moreover, two key points must be taken into account when defining the resistance and occupancy surfaces. First, the resistance surface should include a buffer large enough to cover all possible paths between sites (Howell et al., 2018). Second, the occupancy surface should contain all sites that can be a source of individuals, including those that are not monitored. In spatial occupancy models, colonisation is a function of pairwise accessibility probability, meaning that the population is closed, and sites can be colonised only by individuals from sites present in the model (Chandler et al., 2015; Risk et al., 2011; Sutherland et al., 2014). Future work will focus on providing rules of thumb, based on simulation studies, to help to choose the distance between sites, the extent of the study area, the resolution of the resistance surface, etc. Such approaches have already been used in the context of SCR models to define the resolution and the extent of the state space (see Efford & Boulanger, 2019).

In the context of landscape connectivity, both LCP distance and commute-time distance offer distinct advantages and limitations. The LCP distance assumes that individuals have perfect knowledge of the landscape and will follow the optimal route, making it a valuable metric for understanding the most efficient paths (Adriaensen et al., 2003). On the other hand, commute-time distance links animal movement via a random walk where a decision is made step by step. By accounting for multiple paths, the commute-time distance approach highlights pinch points in the landscape that most influence connectivity, which may not be on the optimal path (Coulon et al., 2015; McRae et al., 2008). The model implementation is facilitated by *nimble* (de Valpine et al., 2017) which allows users to call R functions from within the model, making it possible to compute Euclidean distance, LCP distance, and commute-time distance (Appendix S2). In reality, accurate modelling of connecting paths likely falls in the continuum between perfect knowledge (LCP) and complete ignorance (commute-time distance) of the landscape structure. The randomised shortest path solves this trade-off at the cost of an additional parameter, $\theta \in \mathbb{R}^+$, to estimate. When $\theta = \infty$, this distance is equivalent to LCP distance and when $\theta = 0$, the distance is equivalent to commute-time distance (Panzacchi et al., 2016). We note that any distances could be included in the model, like spatial absorbing Markov chains (Fletcher et al., 2023) or individual-based dispersal models (Coulon et al., 2015).

The flexibility of our framework makes it easy to introduce additional complexity. We recommend selecting the movement model and landscape variables that best align with the ecology of the focal species, the quality of the data used, and the research question (Diniz et al., 2020; McClure et al., 2016). Besides, with higher complexity comes a higher computational burden and the need for more data. Regarding data requirements, occupancy models rely on detection/non-detection data that are not as informative on movements as GPS or telemetry data. Therefore, having enough variability in the studied process helps the model to converge. For instance, the delay between two primary occasions should be defined according to the colonisation speed of the focal species, to allow for dynamics in colonisation and extinction. We encountered convergence issues when the barrier was impermeable to movement (i.e. no individual is detected on the other side of a barrier). As landscape resistance increases, dispersal events become more difficult to detect. To deal with this issue, the secondary occasions and primary occasions should be defined to maximise detection of these rare dispersal events. We recommend building the sampling design so that the sampling effort is allocated on both sides of a barrier. The sampling effort should not only be limited to the actual population distribution, but should encompass the future areas that will be colonised.

Overall, our modelling framework offers a straightforward approach to efficiently assess connectivity. First, spatial occupancy models provide a data-driven evaluation of connectivity, based on detection/non-detection data, which are readily available. Second, the Bayesian approach with MCMC explicitly propagates uncertainty, which provides reliable and robust inference on connectivity, compared to a maximum likelihood approach that could also be used (see Royle et al., 2013). Last, using R and especially *nimble* ensures reproducibility of our approach (Riordan-Short et al., 2023). By providing a better understanding of population occurrence dynamics over space and time in fragmented landscapes, spatial occupancy models have become a valuable tool for species conservation and management.

AUTHOR CONTRIBUTIONS

Maëlis Kervellec and Olivier Gimenez conceived the ideas and designed methodology; Delphine Chenesseau, Pierre Defos du Rau, Nolwenn Drouet-Hoguet, Christophe Duchamp, Julien Steinmetz and Jean-Michel Vandel collected the data; Maëlis Kervellec, Thibaut Couturier, Olivier Gimenez and Sarah Bauduin analysed the data; Maëlis Kervellec led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

PEER REVIEW

The peer review history for this article is available at <https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/2041-210X.14418>.

DATA AVAILABILITY STATEMENT

Data and scripts available via Zenodo <https://doi.org/10.5281/zenodo.13354571> (Kervellec, 2024).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix S1. Dynamic occupancy models code.

Appendix S2. Simulation study.

Appendix S3. Case study on the otter population.

Appendix S4. Case study on the lynx population.

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