RESEARCH ARTICLE

A comprehensive framework to assess multi-species landscape connectivity

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Abstract

1. Due to the central role of landscape connectivity in many ecological processes, evaluating and accounting for it has gained attention in both theoretical and applied ecological sciences. To address this challenge, researchers often use generic species to simplify multi-species connectivity assessments. Yet, this approach tends to oversimplify movement behaviour, likely reducing realism and precision of connectivity model outputs. Also, the most widely used methods and theories for assessing landscape connectivity, namely circuit and network theories, have strong limitations. Finally, uncertainty or robustness estimates are rarely integrated in connectivity assessments.

2. Here, we propose a versatile framework, which, instead of using arbitrary defined generic species, first identifies species groups based on species' environmental niches and morphological, biological, and ecological traits. Second, it combines circuit and network theories to take the best of the two methods to assess landscape connectivity for those groups, while integrating uncertainties in modelling choices. Specifically, ecological continuities (i.e. landscape elements contributing to connectivity) are calculated for these groups and used together with group dispersal capacities to derive network-based connectivity metrics for conservation areas. We detailed our framework through a case study where we assess the connectivity of 1619 protected areas in metropolitan France for 193 vertebrate species.

3. Our study revealed that both the protection of ecological continuities and the connectivity of protected areas for 11 mammal and 19 bird groups, respectively, were quite low, with variations among groups. Different protection types (i.e. national parks, reserves or prefectural orders) contributed unequally to the overall connectivity of group-specific suitable habitats. Considering uncertainty propagation was crucial, as many connectivity metrics varied among repetitions.

4. The proposed framework combines different connectivity tools to provide a more relevant and comprehensive assessment of landscape connectivity. It can be used to inform the decision-making process for spatial planning, particularly in the context of connectivity conservation and management, or support theoretical studies to better understand the ecological role of landscape connectivity. Its flexibility allows easy application under various environmental conditions, including future scenarios.

KEYWORDS

circuit theory, dispersal, ecological continuity, generic group, network theory, protected areas, uncertainty, vertebrates

1 | INTRODUCTION

While landscape connectivity is inherently species-specific, there is a growing trend towards evaluating landscape connectivity for multiple species to meet the rising demand for comprehensive multispecies conservation assessments (Santini et al., 2016a; Wood et al., 2022). Connectivity assessments generally involve estimating the degree to which landscapes hampers organism movements, that is landscape resistance (Zeller et al., 2012). Best practices involve deriving resistance maps by inferring landcover-specific friction coefficients from observed movement pathways (Brennan et al., 2020; Keeley et al., 2016). However, these analyses are often resource-intensive (i.e. from collecting and processing fine-scale movement data) and limited to single (or few) species evaluations based on research or spatial planner interests, reducing consequently the representativity of connectivity assessment (Brennan et al., 2020). Surrogate or generic focal species (sensu Wood et al., 2022), assumed to be representative of biodiversity, are often used to simplify landscape connectivity evaluation, notably in terms of computational time and model output interpretation and management (Albert et al., 2017; Meurant et al., 2018). However, on one hand, the surrogate (i.e. umbrella) species approach can still require a high number of species to be evaluated to embrace the diverse responses to landscape fragmentation observed in nature (Cuervo & Møller, 2020; Spinozzi et al., 2012; Vetter et al., 2011). For example, Dutta et al. (2023) showed that, for large European mammals, up to nine species out of 24 (i.e. 38%) had to be selected as surrogates to fully capture connectivity goals. On the other hand, the generic species approach often relies on local expert-opinion, leaving empirical inputs out and resulting in species with coarse characteristics (e.g. forest-dwelling species with long dispersal range), hence likely reducing precision and realism of connectivity model outputs (Foster et al., 2017; Watts et al., 2010; Williamson et al., 2020; but see Brennan et al., 2022). To address these challenges, a more flexible approach could empirically cluster species based on habitat requirements and sensitivity to fragmentation-related traits. This approach would have the potential of reducing dimensionality, consequently calculation time and interpretation complexity, while preserving realism (Lechner et al., 2017). Despite its theoretical promise, it has not been fully explored.

One of the possible approaches for estimating connectivity is based on network theory (Santini et al., 2016a; Saura et al., 2017; Ward et al., 2020), a widely adopted approach offering multi-scale connectivity indicators (Keeley et al., 2021; Saura & Pascual-Hortal, 2007). In this approach, the landscape is represented as nodes (e.g. protected areas) interconnected by edges reflecting potential movement among nodes (Fall et al., 2007). These edges can represent either Euclidean or functional distances (i.e. through least cost paths), but they have been criticized for unrealistic assumptions, such as species having perfect knowledge of the landscape and optimizing their movement paths—conditions that are rarely met, especially when species enter unfamiliar environments (Coulon et al., 2015; Etherington, 2016). Randomized shortest paths provide a more realistic estimate of movement path by incorporating a stochasticity parameter allowing to digress from the optimal pathway hypothesis (Panzacchi et al., 2016; Saerens et al., 2009; Van Moorter et al., 2023). Yet, network theory alone may not fully capture the potential role of the matrix in connecting important habitat patches. For example, when applied to protected area connectivity, network-centric perspective assumes that movements occur exclusively among reserves, restricting the identification of potential important areas for ecological connectivity.

To address these limitations, circuit theory offers an alternative by assuming individuals move as biased random walkers in heterogeneous environments (McRae et al., 2008). In circuit theory, each pixel of the landscape can be modelled as a node connected to neighbouring pixels through resistors, allowing for continuous connectivity estimation and the identification of multiple—omnidirectional—movement pathways (e.g. as implemented within the Omniscape algorithm, McRae et al., 2016). Specifically, the omnidirectional approach calculates the cumulative current from all pairwise connections between source and target pixels (e.g. pixels of suitable habitat) within a defined radius, without constraining movement among pre-defined zones like, for instance, protected areas (de Rivera et al., 2022; McRae et al., 2016). Cumulative current maps are then used to quantify the potential contribution of landscape elements to the overall connectivity (Pither et al., 2023), referred here as ecological continuities. While

this omnidirectional approach in circuit theory provides a continuous, more comprehensive and realistic evaluation of landscape connectivity compared to network theory, it does not provide the commonly used connectivity indices in theoretical or applied studies that can be obtained from network theory (Courbin et al., 2014; Keeley et al., 2021; Laliberté & St-Laurent, 2020; Pither et al., 2023; Wade et al., 2023).

Another issue with landscape connectivity analyses, is that it frequently involves arbitrary decisions, including assigning resistance value to landcover types or delineating important patches (Liang et al., 2023; Wade et al., 2023). These decisions often rely on debatable assumptions, leading to uncertainty in connectivity estimates (Belote et al., 2022; Zeller et al., 2017). Yet, uncertainty estimates are generally overlooked in connectivity studies, with only 19% of 181 studies conducting sensitivity or uncertainty analyses (Riordan-Short et al., 2023; Zeller et al., 2012). Incorporating uncertainty in connectivity estimates has many advantages including for example, strengthening decision making in spatial planning, or accounting for the dynamic aspects of movement behaviour and its variations to provide more biologically meaningful connectivity estimates and maps.

In this study, we present a framework to assess landscape connectivity for multiple species with diverse requirements building on the generic species approach and combining the advantages of both circuit and network theories, while accounting for uncertainty in model parameters (Figure 1). Our approach involves (1) optimizing the construction of robust generic groups, homogeneous in terms of environmental niches, and morphological, ecological and biological traits; (2) estimating ecological continuities, along with their uncertainties, using the omnidirectional approach of the circuit theory for each of the generic groups; and (3) calculating multi-scale network-based connectivity metrics, along with their uncertainty, derived from group-specific ecological continuities and dispersal capacity (Figure 1). We showcase the framework along with a case study where we evaluate the current connectivity of protected areas in France for a diverse range of mammal and bird species.

2 | MATERIALS AND METHODS

2.1 | Species list

We considered the current connectivity (i.e. considering the 2010–2020 period) of 1619 protected areas in metropolitan France for 193 vertebrate species, including 52 mammals and 141 birds (Table S1). The species were selected for their conservation importance including endemic species, species of the Birds and Habitats directives (annexes I, II and IV) and threatened species (Critically endangered, Endangered and Vulnerable categories) according to the European or national international union for conservation of
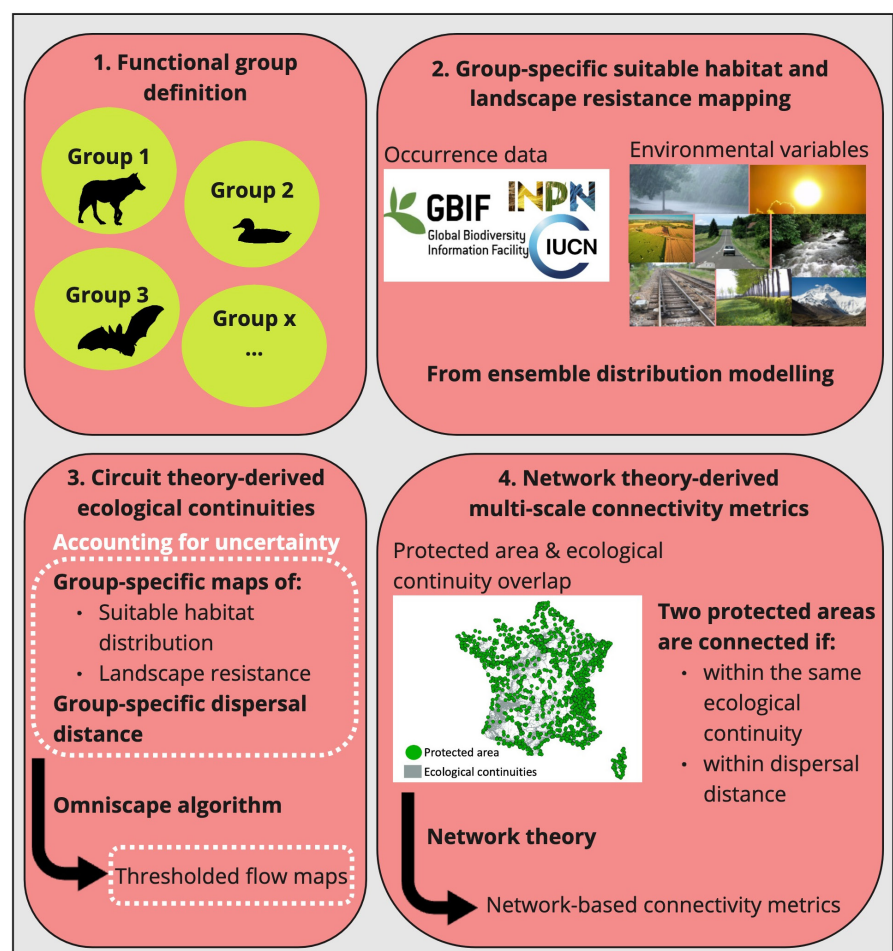

FIGURE 1 Summary of the framework workflow.

nature (IUCN) red lists (Council of the European Communities, 1992; IUCN, 2022; Léonard et al., 2020).

2.2 | Distribution data

We collected species-specific presence data in metropolitan France from the global biodiversity information facility (GBIF, https://www.gbif.org/, see Appendix S1 for download DOIs) and the French database of the national inventory of natural heritage (INPN, https://inpn.mnhn.fr). We selected occurrences observed between 2010 and 2020 with location uncertainty below 1km. We considered only occurrences that were within the species-specific native range according to the IUCN distribution maps (https://www.iucnredlist.org/resources/spatial-data-download). Then, we re-projected occurrences over a gridded map of $1km^2$ to identify pixels where species were observed at least once (i.e. presence) and pixels where species had not been observed (i.e. pseudo-absence). On average, 1215 (range: [5–11,443]) pixels of presence were detected per species (Table S2).

2.3 | Environmental data

We selected 13 environmental variables classically used in species distribution and connectivity modelling (Bogdanović et al., 2023; Karger et al., 2023; Leoncini et al., 2023), including climatic conditions (annual mean temperature, mean daily precipitations, temperature seasonality, precipitation seasonality), topography (average slope, elevation coefficient of variation), land systems and densities of water bodies and linear elements (i.e. road density, railway density, large stream density, large lake density and hedge density). Climatic variables were computed as averages over the 2010–2020 period over a $1km^2$ gridded map using the CHELSA climate data (Karger et al., 2017). Topological variables were obtained from the French numerical terrain model (BD Alti, https://geoservices.ign.fr/bdalti) at $25 \times 25m$ resolution resampled over a $1km^2$ gridded map. We used the European land system map at $1km^2$ (Dou et al., 2021), to extract land systems in France. Density of water bodies per $1km^2$ pixel were calculated using the Copernicus layer of water and wetness (https://land.copernicus.eu/en/products/high-resolution-layer-water-and-wetness) estimated for the 2009 to 2018 period. Road, railway, hedge, large stream and large lake densities were calculated per $1km^2$ pixel using the BD TOPO of the French national institute of geographical and forestry information (https://geoservices.ign.fr/documentation/donnees/vecteur/bdtopo). All pairwise correlations between the selected variables were below 0.7.

2.4 | Protected areas

Protected areas included national parks, national and regional natural reserves, biological reserves, prefectural biotope protection order, prefectural geotope protection order and prefectural order for natural habitat protection. These protections encompass strict protections having reglementary land management that excludes or reduces human activities within sites. Spatial delineations of PAs were downloaded from the French database of the national inventory of natural heritage in September 2023 (https://inpn.mnhn.fr/telechargement/cartes-et-information-geographique/).

2.5 | Building robust and relevant generic groups

To be as representative as possible, generic groups should cover the observed variation in ecological attributes, life history traits and tolerance to environmental conditions across species. We thus chose to follow the efforts made in functional ecology to define emergent or functional groups. More specifically, we followed the classification procedure proposed in Boulangeat et al. (2012) to define emergent groups for dynamic vegetation modelling. The overall idea is to group species based on their shared environmental niche and morphological, ecological and biological traits (Boulangeat et al., 2012).

Here, considering landscape connectivity evaluation, we chose to concentrate on the environmental niche (i.e. considering climatic and topographical variables) and eight traits for connectivity: *life history*: number of offsprings per year; *foraging behaviour*: trophic level and diet; *movement behaviour*: mean dispersal distance and activity time; *habitat requirements*: habitat use and nesting habitat use and *morphology*: body mass (see Table S3 for trait compilation). These selected traits here are assumed to be relevant for landscape connectivity analyses (see Table S4), but users can easily modify or adapt the trait selection depending on study goal.

We calculated one dissimilarity matrix for each trait based on the Sokal and Michener metric for binary variables and the Euclidean distance for quantitative variables (Pavoine et al., 2009). We also computed a dissimilarity matrix for the environmental niche by calculating species niche distances in a multivariate principal component analysis (Broennimann et al., 2012). Distance matrices showing a skewed distribution were a priori normalized. We then calculated a weighted average of the nine dissimilarity matrices considering 50% of the weight on environmental niche, mean dispersal distance, habitat and nesting habitat use (i.e. each matrix has a 1/8 weight), and 50% of the weight on the other traits (i.e. each matrix has a 1/10 weight). This weighting scheme was the one providing the most relevant and meaningful group compositions (i.e. this might vary in other regions or for other species sets). Finally, we optimized the final number of generic groups based on a hierarchical clustering algorithms along with evaluation metrics (e.g. Dunn index, Halkidi et al., 2001). We performed the procedure separately for birds and mammals.

2.6 | Estimation of ecological continuities

2.6.1 | Omnidirectional approach

The Omniscape algorithm requires three key inputs: a source distribution raster (i.e. sources are pixels among which the flow is

modelled), a resistance distribution raster (i.e. low resistance reflects high permeability) and a radius defining the moving window over which all pairwise connections are calculated among source pixels (Landau et al., 2021; McRae et al., 2016, see Appendix S2 for detailed algorithm steps). The algorithm produces a raster of cumulative current flow, which is then normalized to reflect landscape connectivity adequately (and to be comparable between different situations or context). This normalization involves first estimating the potential flow from the landscape's resistance-free scenario (i.e. the amount of flow if the landscape would not impede movement) and then dividing the cumulative current flow by the potential flow (McRae et al., 2016). As a result, a normalized flow below 1 indicates less flow than expected if the landscape was not resistant to movements such that the pixels can be categorized based on their normalized flow regarding their level of movement impedance (Cameron et al., 2022; McRae et al., 2016). Complementarily, the potential flow allows to identify the level of source pixel aggregation across the landscape (McRae et al., 2016).

In our framework, we defined group-specific ecological continuities as groups of pixels located in areas showing source pixel aggregation (i.e. potential flow higher than the 5% quantile of potential flow distribution excluding null values) with few or no impedance to movement flow (i.e. normalized flow $\geq f_{norm}$, where f_{norm} was set to 0.7, 0.8 or 0.9 see Cameron et al., 2022). We tested different values of f_{norm} to account for the uncertainty in landscape permeability where there was less flow than expected when the landscape had no resistance to movements (i.e. when $0.7 \leq f_{norm} < 0.9$). For each tested f_{norm} value, we filtered our $1\,km^2$ grid to only retain pixels above both thresholds and aggregated adjacent pixels to delineate group-specific ecological continuities.

2.6.2 | Primary parameter estimation

Source raster

Source pixels were defined as suitable habitats for a generic group. We calibrated a group-specific suitable habitat map using species distribution models (Guisan & Thuiller, 2005). We first merged species-specific binary gridded maps into group-specific binary gridded maps. To do so, we overlaid species-specific binary gridded maps so that all pixels with at least a given species was allocated to presence. Then, we ran four machine-learning algorithms (i.e. artificial neural network, XGboost, random forest and MaxEnt) to produce a committee averaging ensemble model to predict the potential habitat suitability of each $1\,km^2$ pixel as a function of the 13 environmental variables for each group (implemented into the *biomod2* Rpackage, Thuiller et al., 2019). Details on pseudo-absence sampling and model validation are provided in Appendix S3. The probability of habitat suitability of each pixel can then be used to classify each pixel as suitable (i.e. a source) or unsuitable (i.e, not a source) according to a specific threshold ($p_{threshold}$). We chose $p_{threshold} = \{0.5, 0.6, 0.7\}$ to select source pixels resulting in three estimates of source raster for each group.

Resistance raster

Resistance maps were built from the group-specific habitat suitability map following a non-linear relationship (see figure 1 in Keeley et al., 2016):

$$R_i = 100 - 99 \frac{(1 - e^{-cH_i})}{(1 - e^{-c})}, \tag{1}$$

where R_i is the resistance value of pixel i ranging between 1 and 100, H_i is the habitat suitability of pixel i [0–1], and c is a factor determining the shape of the curve. When $c = 0.25$, resistance increases almost linearly with a decreasing suitability, while when c increases, resistance becomes an increasingly nonlinear negative exponential function of suitability (Keeley et al., 2016). This relationship allows to model the tolerance for lower-suitable habitat during movement as demonstrated in several taxa in particular during dispersal events (Keeley et al., 2016, 2017; Mateo-Sánchez et al., 2015; Trainor et al., 2013). It also allows the researcher to integrate parameter uncertainty by simulating landscape connectivity with estimated resistance maps extracted with different c values. Notably, we chose $c = \{2, 4, 8, 16\}$ resulting in four resistance rasters per group.

Radius of the moving window

We sampled between 2 and 10 radiuses within the group distribution of species-specific mean dispersal distance according to the intra-group dispersal distance variability. Notably, two, three or six radiuses were sampled if the difference between minimum and maximum intra-group dispersal distances was lower than 10, 30 or 60 km, respectively, and 10 radiuses were sampled otherwise.

2.6.3 | Omniscape run

We ran the Omniscape algorithm for each of all possible combinations per group of source rasters, resistance rasters and radiuses of the moving window resulting in 32 runs on average per group (range: 12–120). We defined block size as $b = 1/10$th of the radius of the moving window (truncated to 1 if $b < 1$) as it reduces time processing of the algorithm without much impact on the results (McRae et al., 2016; Phillips et al., 2021). We then derived ecological continuities accounting for different values of f_{norm}, resulting in 97 estimates on average per group (range: 36–360) and 2916 in total. By comparison, if species were treated individually, 6948 ecological continuities would have been estimated. We then calculated the percentage of overlap between protected areas and each estimate of ecological continuities. Finally, we produced a map of ecological continuity probability for each group by summing all binary-maps of a group and dividing it by the number of estimates for the group. We also calculated a probability map for all mammals or all birds by calculating an average of all mammal- or bird-group maps weighted by the species number in each group. This weighting procedure can be adjusted to account for other criteria (e.g. conservation status).

2.7 | Calculation of multi-scale network metrics

The probability of connectivity (PC) is a network metric used to assess landscape connectivity accounting for both landscape connections and composition (Saura et al., 2018; Saura & Pascual-Hortal, 2007; Ward et al., 2020). PC is defined as follow:

$$PC = \frac{\sum_{i=1}^{N} \sum_{j=1}^{N} a_i a_j p_{ij}^*}{A^2}. \tag{2}$$

We used here the PC metric as the probability that two points randomly sampled in group-specific suitable habitat fall into reachable protected areas. Consequently, we defined N as the total number of protected areas in the landscape, a_i and a_j are the area of connected group-specific suitable habitat in protected area i and j, respectively, A the total area of group-specific suitable habitat in the landscape and p_{ij}^* the maximum product probability for patches i and j to be connected.

More precisely, p_{ij}^* considers both direct and indirect connections among patches i and j, and selects the one with the highest probability of connections. Additionally, PC can be partitioned in two fractions (Ward et al., 2020):

$$PC = PC_{intra} + PC_{inter}, \tag{3}$$

where PC_{intra} reflects the intrapatch network connectivity (i.e. when $i = j$), and PC_{inter} the interpatch connectivity from either direct or indirect flux (i.e. when $i \neq j$). Based on the landscape-scale PC metric, metrics at the patch level can also be derived (Bodin & Saura, 2010; Saura & Rubio, 2010). Notably, for patch k,

$$PC_{intra}^k = \frac{a_k^2}{A^2}, \tag{4}$$

$$PC_{flux}^k = \frac{\sum_{\substack{j=1 \\ j \neq k}}^{N-1} a_k a_j p_{kj}^* + \sum_{\substack{i=1 \\ i \neq k}}^{N-1} a_i a_k p_{ik}^*}{A^2}, \tag{5}$$

where PC_{intra}^k is the intrapatch connectivity for patch k and PC_{flux}^k is the total area-weighted dispersal flux through the connections of patch k to or from all of the other patches in the landscape (i.e. when k is either at the starting or the end of the pathway). We also calculated the normalized betweenness for each patch k, B_{norm}^k to assess the total contribution of patch k to the connectivity among other network patches (i.e. when k is an intermediate patch along the shortest pathway connecting two other patches, thereafter named a stepping stone) (Rayfield et al., 2011).

To generate the network of connections, we considered two PAs as potentially connected for a given group only if they both belonged to the same ecological continuity within a specific run and were reachable from each other based on the group's dispersal capacity. We only retained portion of PAs that intersected an ecological continuity. Connections exceeding the selected dispersal distance for the specific run were excluded, and only those within the defined dispersal range were retained. The length of each connection was calculated as the edge-to-edge minimum distance within the ecological continuity. We subsequently calculated the connectivity metrics locally (i.e. for each PA) and globally (i.e. for all PAs) using the Rpackages *gdistance*, *igraph*, *sf*, *terra* and *raster* (R Core Team, 2023).

2.8 | Sensitivity analysis of connectivity metrics to uncertainty of input parameters

We evaluated which parameters had a strong effect on the uncertainty of connectivity metrics by assessing their influence on connectivity estimates. Notably, we ran mixed linear models including the log-transformed PC, PC_{intra} or PC_{inter} as response variable, and scaled dispersal distance, suitability to resistance c coefficient, thresholds for source selection $p_{threshold}$ and ecological continuity delineation f_{norm} as explanatory variables. We included group identification as a random variable to account for the non-independence between simulations within a group. We ran the models using the *lmerTest* R package (Kuznetsova et al., 2017).

3 | RESULTS

3.1 | Building robust and relevant generic groups

The 193 species were clustered into 11 groups of mammals and 19 of birds (Appendix S4). Groups were made of 1 to 45 species with shared environmental and trait characteristics and were controlled by experts (Appendix S4).
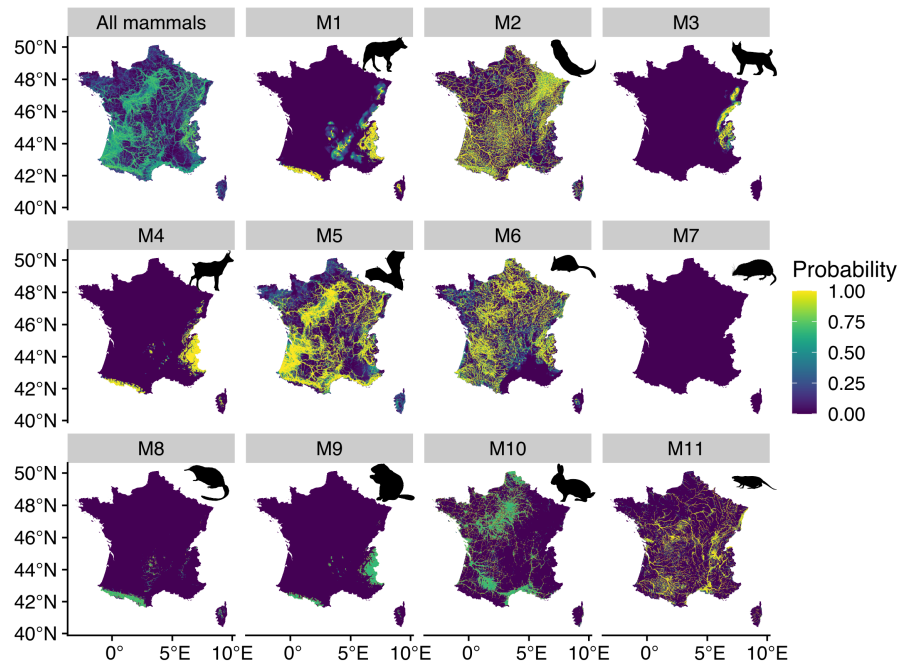
3.2 | Estimation of ecological continuities

The maps of ecological continuities varied considerably across the 30 vertebrate groups (Figure 2; Appendix S5). For example, the beaver (*Castor fiber*) and southern water vole (*Arvicola sapidus*) showcased continuous ecological continuities dependent on water stream distributions (M11 group, Figure 2) whereas the Alpine marmot (*Marmota marmota*) and mountain hare (*Lepus timidus*) had ecological continuities mostly restricted to Alpine and Pyrenean mountains (M9 group, Figure 2). In contrast, we found no ecological continuity for shrew species (i.e. *Crocidura leucodon*, *Crocidura suaveolens* and *Sorex alpinus*, M7 group) as a result of their very short dispersal distances (i.e. less than 1 km), indicating that a finer spatial resolution should be used to properly estimate the ecological continuities for this group. Different patterns were also observed for birds (Appendix S5); for example, the ecological continuities for the rock dove (*Columba livia*) and turtle dove (*Streptopelia turtur*) were mostly uninterrupted, albeit restricted to the western and southeastern part of the territory (A10 group). Conversely, the ecological continuities for the greater flamingo (*Phoenicopterus roseus*, A17) were scarce and restricted to the Mediterranean coast.

Considering uncertainty in parameter estimation highlighted important and critical areas for spatial planning. For instance, ecological continuities for the common swift (i.e. *Apus apus*, A8) remained largely unsensitive to parameter variation (i.e. ecological continuity probability ~1), such that a protection of these areas would be likely highly beneficial for the species (Appendix S5). Similarly, ecological continuities for Eurasian lynx (i.e. *Lynx lynx*, M3), revealed bottleneck areas connecting the Vosges, the Jura and the Alpes regions, emphasizing the need for either nature restoration of these areas or protection to maintain these critical remnant elements connecting the landscape (Figure 2).

In general, the ecological continuities were poorly covered by the current distribution of protected areas (average 3.1%), with notable variation among groups (Figure 3). Yet, protected areas effectively covered ecological continuities for mountainous species (e.g. M4,

FIGURE 2 Estimates of ecological continuities for 52 mammal species clustered into 11 groups (M1 to M11) for the 2010–2020 period in metropolitan France.
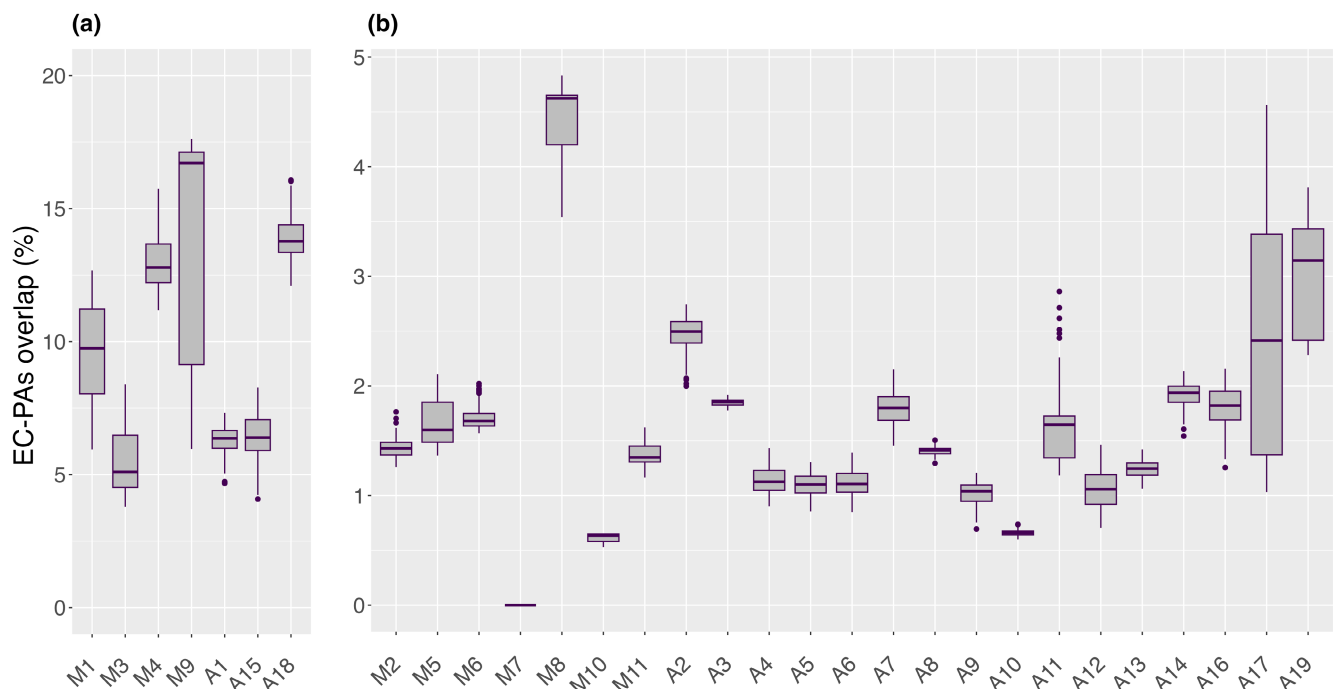
FIGURE 3 Strict protection of ecological continuities (EC) for 193 vertebrate species clustered into 11 groups of mammals and 19 groups of birds for the 2010–2020 period in metropolitan France. The percentages reflect the proportion of the surface of ecological continuities that are covered by protected areas (PAs) based on several combinations of model parameters for each group. M1 to M11: Mammal groups and A1 to A19: Bird groups. Groups have been split into two panels based on their percentage values for variations of small values to be readable: (a) large values, (b) small values.

M9 or A18 groups) with up to 16.1% of overlap (range: 13.9%–16.1%, A18 group) but minimally for the European rabbit (*Oryctolagus cuniculus*, M10) and the rock dove and turtle dove (A10 group, Figure 3). Overall, intra-group variability was observed across all groups, with certain groups displaying greater variability than others, due to their stronger sensitivity to input parameters. For example, ecological continuity delineation for the M9 group was strongly sensitive to the normalized flow threshold such that ecological continuities of this group were highly reduced when the threshold was set to 0.9 while ecological continuities for the Eurasian eagle-owl (*Bubo bubo*, A19 group) were more strongly impacted by habitat suitability threshold.

3.3 | Multi-scale network metrics

Connectivity of group-specific suitable habitat through protected areas was generally low, with global PC metrics never exceeding 3.0%, and extreme groups having a probability of 0 (Figure 4). Access to protected suitable habitat relied on intra-patch or inter-patch connectivity alternatively among groups (i.e. $PC_{intra} > PC_{inter}$, or inversely). Accounting for uncertainty in model parameters underscored the variability in PC metric estimates for some groups, with certain groups also displaying greater variability than others, due to their stronger sensitivity to input parameters (Figure 4). For example, bat species (M5 group) had dispersal distances ranging from 1 to 340 km, resulting in substantial variation in the PC metric across the different sampled distances.

Local connectivity metrics identified the contribution of different types of protections to overall landscape connectivity for the 193 evaluated vertebrate species. Intra-site connectivity was mainly

driven by national parks (likely due to their large size), although natural or biological reserves influenced some groups (Figure 5; Appendix S6). Connectivity of protected suitable habitat through direct or indirect connections of PAs involved both the national parks and natural or biological reserves (Figure 6; Appendix S7). Natural or biological reserves and prefectural protection orders acted as stepping stones to connect protected suitable habitat for most evaluated mammals and birds (Figure 7; Appendix S8).

3.4 | Sensitivity analyses

Connectivity estimates were strongly sensitive to dispersal distance, the tolerance to unsuitable habitat (i.e. c coefficient), the distribution of suitable habitat (i.e. $p_{threshold}$) and the normalized flow threshold (i.e. f_{norm}) (Table 1). All four parameters significantly impacted PC and PC_{inter} metrics, with dispersal distance having the most influential effect, followed by the normalized flow threshold, the tolerance to unsuitable habitat, and then the distribution of suitable habitat (Table 1). PC_{intra} was however not sensitive to the dispersal distance as expected by definition.

4 | DISCUSSION

We presented a versatile framework for evaluating multi-species landscape connectivity based on three innovative components: (1) the empirical grouping of species based on environmental niche overlap and shared morphological, ecological and biological traits for dimension reduction; (2) the use of circuit theory to delineate
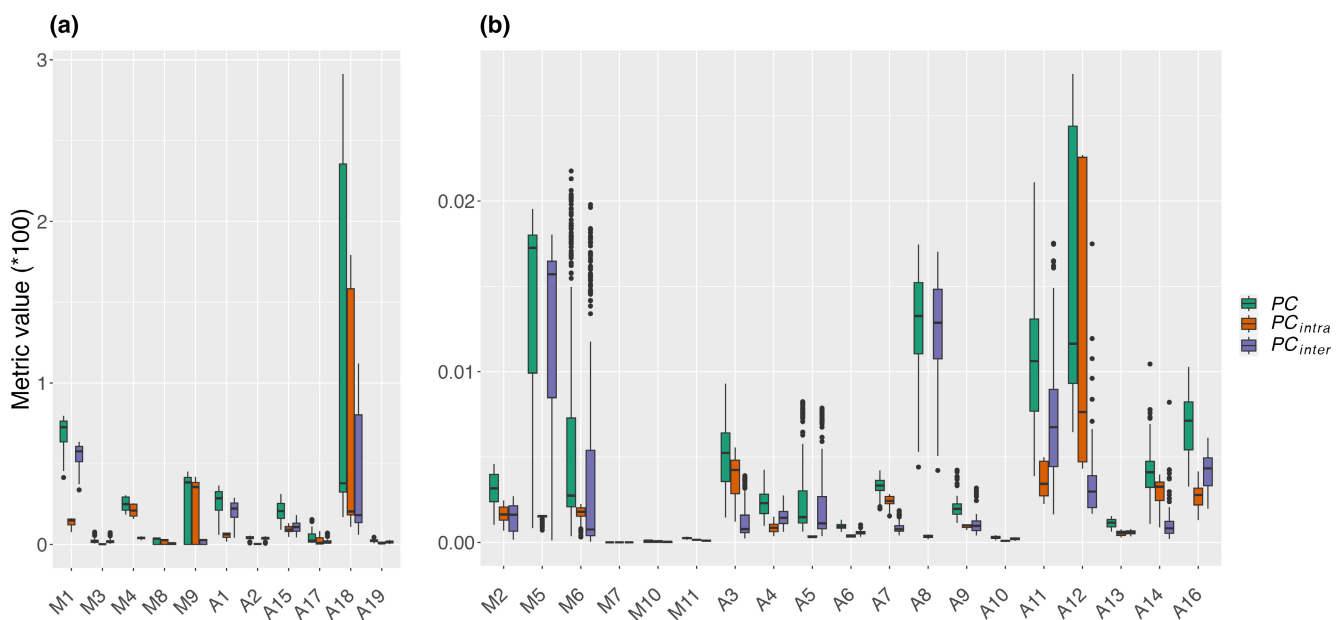

FIGURE 4 Estimates of suitable habitat connectivity through strictly-protected areas for 193 vertebrate species clustered into 11 groups of mammals and 19 groups of birds for the 2010–2020 period in metropolitan France. M1 to M11: Mammal groups and A1 to A19: Bird groups. Groups have been split into two panels based on their metric values for variations of small values to be readable: (a) large values, (b) small values.
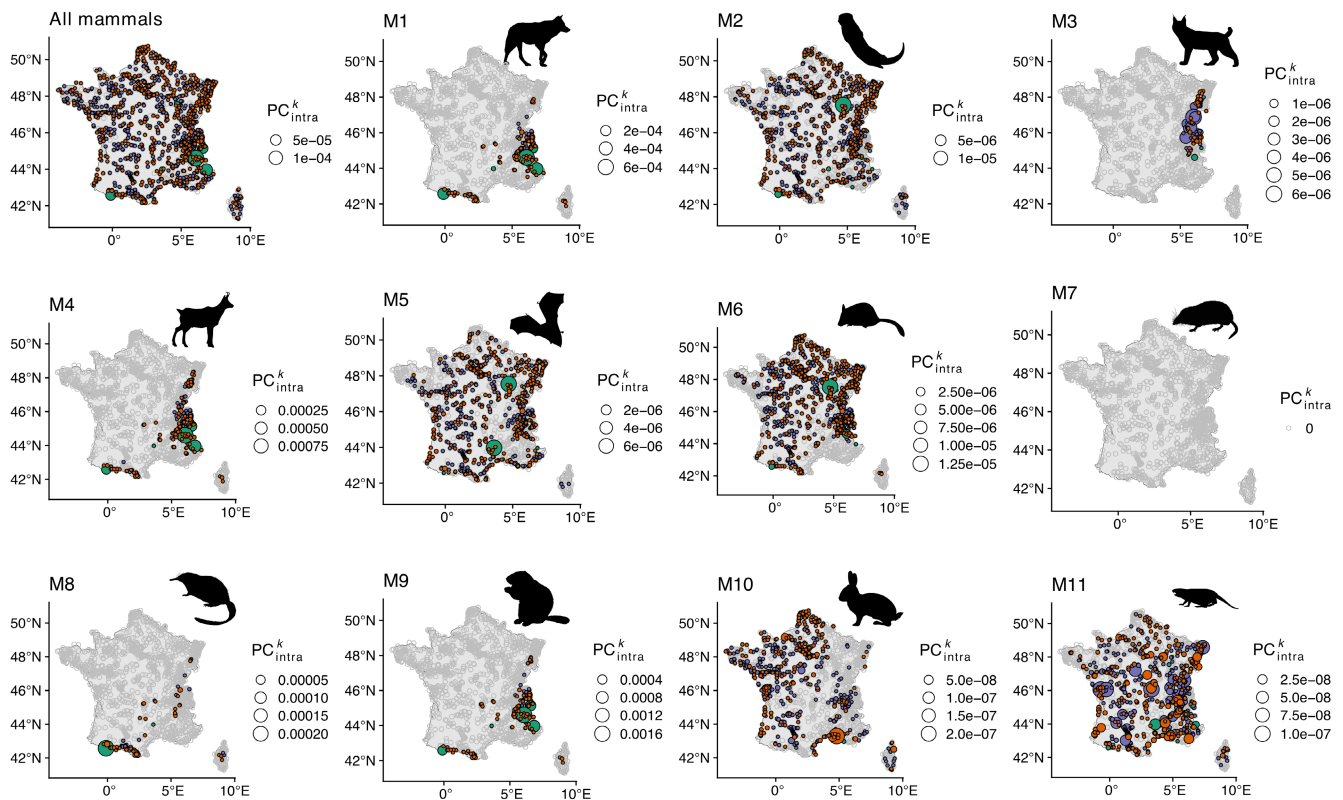
FIGURE 5 Average contribution of different types of protections (i.e. green: Core of national park, orange: Natural or biological reserve, purple: Prefectural protection order) to the amount of reachable strictly protected suitable habitat inside individual site (i.e. median of PC_{intra}^{k} for site k, over all combinations of model parameters for a group) for 52 mammal species clustered into 11 groups (M1 to M11) for the 2010–2020 period in metropolitan France.

continuously, comprehensively and more reasonably ecological continuities then used together with group dispersal capacity to derive multi-scale network-based connectivity metrics; and (3) the incorporation of parameter uncertainty in the estimation of ecological continuities and connectivity metrics. We believe it might prove useful in many different situations and areas.

Applying our framework to 193 vertebrate species in metropolitan France, we found heterogeneous distributions of ecological continuities among groups, low levels of both protection of ecological continuities and connectivity of protected areas for mammals and birds, with variations among groups. Furthermore, our analysis highlighted distinct contributions of each protection type to the overall connectivity of group-specific suitable habitat.

An effective evaluation of multi-species landscape connectivity must consider biodiversity representativeness, and thereby might become prohibitive in terms of computational time and output management when a high number of species is at stake. Different strategies have been used to reduce species dimension in connectivity analysis (reviewed in Wood et al., 2022) which are generally efficient to reduce calculation time but at the cost of degraded realism and precision (Dutta et al., 2023). By integrating species' environmental niches and traits, our method builds ecologically relevant generic focal species, providing a more informative landscape connectivity assessment and offering a less challenging and reproducible

approach. Typically, we ran the framework for 193 species clustered into 30 groups, thereby reducing by 85% the dimension of the study while still being representative of our species pool. Future attempts to assess how our approach outperforms other strategies to reduce species dimension in connectivity analysis will be needed though to evaluate and consolidate its accuracy.

Network theory, a fundamental tool in landscape connectivity assessment, offers informative and multi-scale connectivity indexes (Jacoby & Freeman, 2016). However, determining potential connections among network nodes is a critical step (i.e. network link presence) (Urban et al., 2009). While many graph models can be used to define network links (e.g. minimum planar graph, distance-based network), they have several shortfalls: (1) links are restricted to neighbourhood nodes in commonly-applied planar graphs, which is unrealistic for many taxa, (2) links only reflect the structural properties of the landscape when they are calculated in Euclidean space, (3) multiple pathways are not accounted for when calculated from least-cost paths (although randomized shortest paths have overcome this limitation, Saerens et al., 2009), and (4) least-cost paths are likely unrealistic (Etherington, 2016; Prima et al., 2018; Saura et al., 2018). Additionally, network theory assumes that movements are constrained among network nodes, although it can be realistic when nodes reflect preferred habitat patches (Courbin et al., 2014), it is likely not the case when nodes are protected areas. Here, we tried
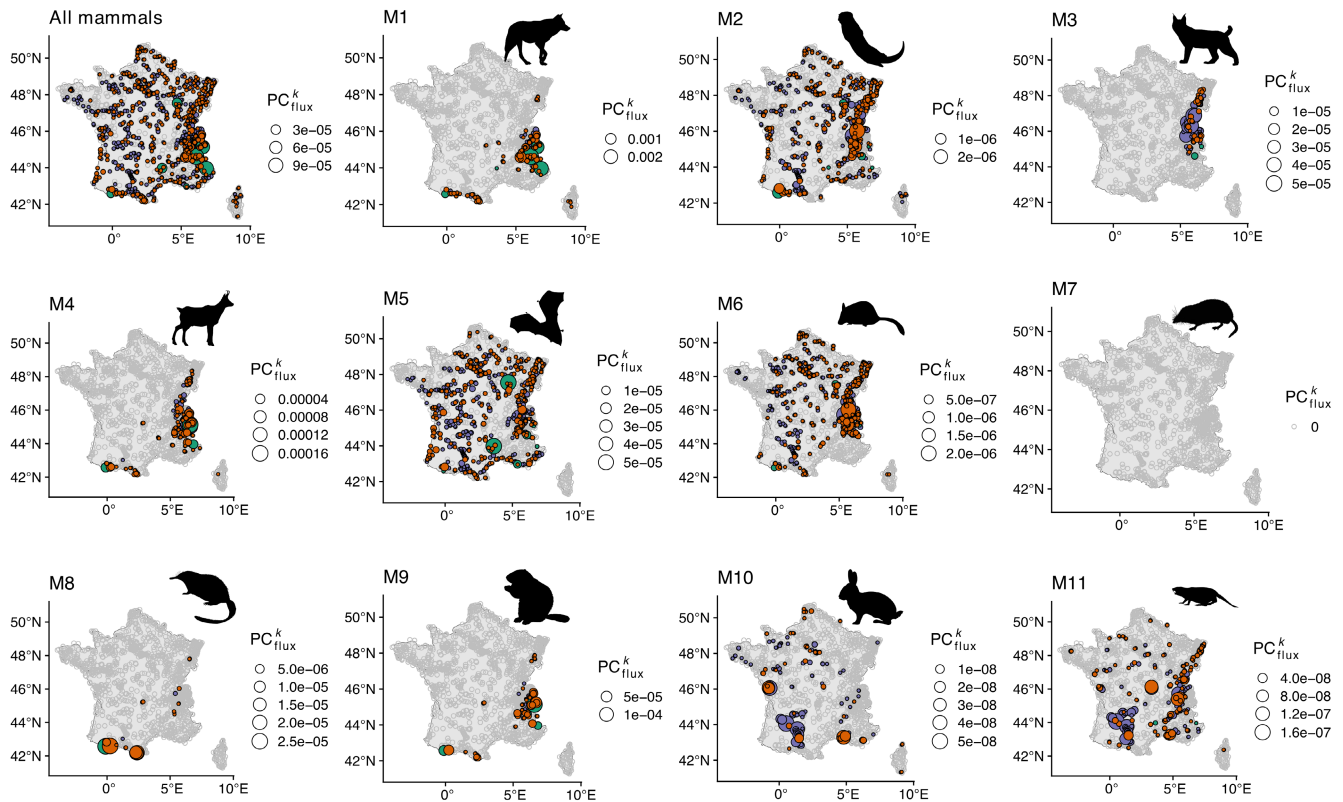
FIGURE 6 Average contribution of different types of protections (i.e. green: Core of national park, orange: Natural or biological reserve, purple: Prefectural protection order) to the amount of reachable strictly protected suitable habitat through direct or indirect connections among sites (i.e. median of PC_{flux}^{k} for site k, over all combinations of model parameters for a group) for 52 mammal species clustered into 11 groups (M1 to M11) for the 2010–2020 period in metropolitan France.

to bypass these limitations by using circuit theory as a first step to delineate ecological continuities, viewed as landscape areas in which species movement flow among suitable pixels is possible. These ecological continuities were then used to refine potential connections among network nodes (i.e. protected areas in our case study) to generate connectivity patterns based on more biologically meaningful assumptions than common practices (Brennan et al., 2022; Santini et al., 2016b; Saura et al., 2017).

Like in any scenario-based prediction (Thuiller et al., 2019), considering uncertainty in parameter estimates in landscape connectivity assessment is crucial. While most analyses of landscape connectivity do not propagate uncertainty of unknown parameters (Riordan-Short et al., 2023), our study demonstrates that connectivity estimates are highly sensitive to parameters (i.e. group dispersal distance, habitat suitability distribution, landscape resistance, delineation of ecological continuities), emphasizing the need to account for parameter uncertainty systematically. These results align with the growing consensus in the field that landscape connectivity should not be viewed as a deterministic process (Keeley et al., 2017; Riordan-Short et al., 2023; Zeller et al., 2012, 2017). More generally, accounting for different parameter values allows to consider varying intra-group or species movement responses to internal or external factors such as landscape composition and configuration, as observed in the field (Bowler & Benton, 2005; Herrero et al., 2020). To our knowledge, our framework is the first to account extensively

for uncertainty in landscape connectivity assessment. Yet, additional uncertainty including the one on species traits (e.g. body mass, number of offsprings per year, etc.) could be incorporated into our framework as species can demonstrate strong individual and temporal variations for those attributes.

Our framework can be used for both theoretical and applied studies. Notably, we selected the PC metric, known for its efficacy in assessing landscape connectivity for spatial planning and change analysis (Saura & Pascual-Hortal, 2007; Saura & Rubio, 2010). In that context, the PC-based metrics offer consistent indicators for comparing different landscapes over time or space, facilitating for example, the evaluation of reserve selection scenarios or the impact of global changes on protected areas' connectivity (Pascual-Hortal & Saura, 2006). Other network metrics (e.g. degree distribution) could however easily be applied for more theoretical studies such as on how ecological processes link to network topology and resilience (Kininmonth et al., 2009; Prima et al., 2019). Finally, maps of ecological continuities show great promise to support connectivity conservation and planning and could become a key layer to inform meta-population and community models.

In light of the EU Biodiversity Strategy 2030, aiming to protect at least 30% of the territory by 2030, with 10% under strict protection (Cazzolla Gatti et al., 2023; Spiliopoulou et al., 2023), we found that strictly protected areas in metropolitan France are inadequately
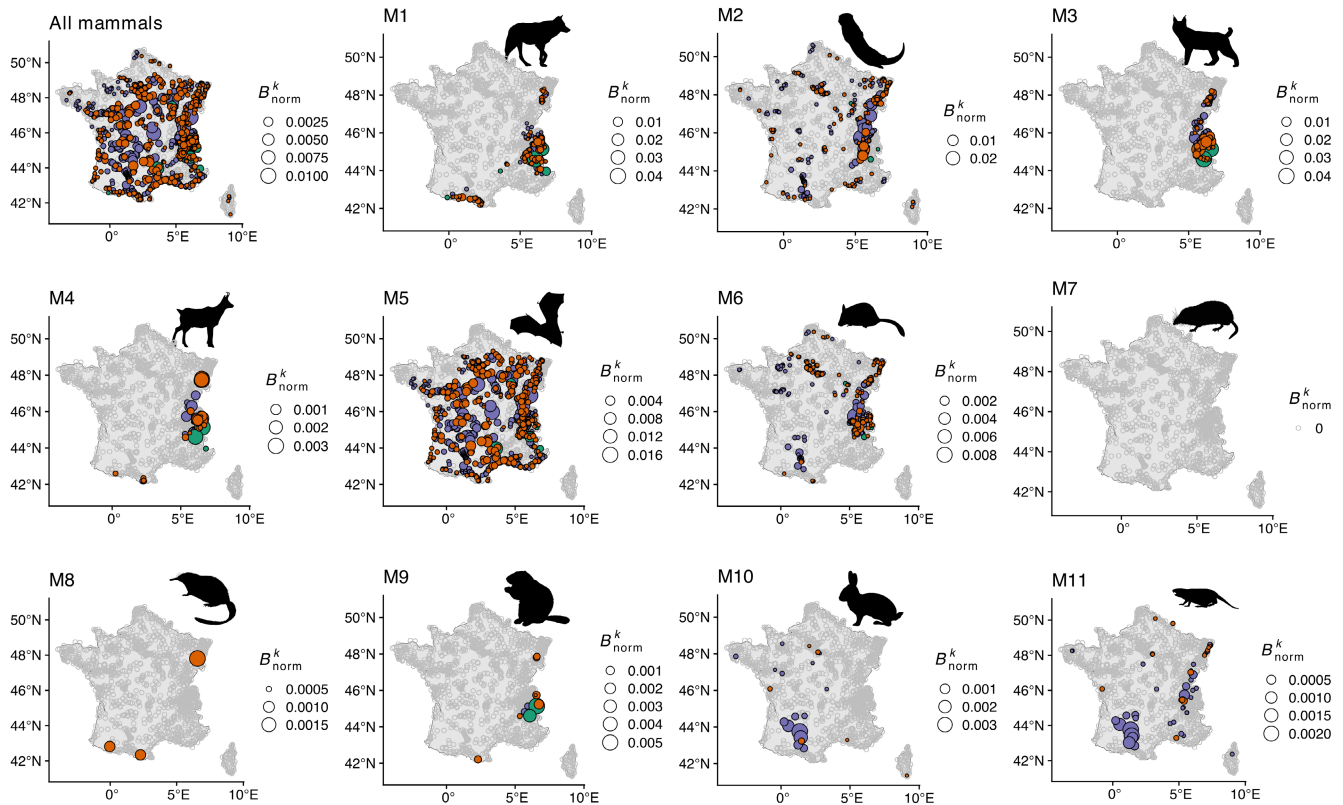
FIGURE 7 Average contribution of different types of protections (i.e. green: Core of national park, orange: Natural or biological reserve, purple: Prefectural protection order) as stepping stones (i.e. median of B_{norm}^k for site k, over all combinations of model parameters for a group) for 52 mammal species clustered into 11 groups (M1 to M11) for the 2010–2020 period in metropolitan France.

TABLE 1 Effects of group dispersal distance, habitat suitability distribution (Suitability threshold, $p_{threshold}$), tolerance to unsuitable habitat during group movement (c parameter) and normalized flow threshold (f_{norm}) on PC metrics estimated for 11 mammal and 19 bird groups in metropolitan France for the 2010–2020 period.

Metric	Variable	Beta	95% CI	*p*-Value
PC	Dispersal distance	0.378	0.333, 0.423	<0.001
	Suitability threshold	0.094	0.065, 0.124	<0.001
	Tolerance to unsuitable habitat	0.133	0.103, 0.162	<0.001
	Normalized flow threshold	−0.269	−0.298, −0.239	<0.001
PC_{intra}	Dispersal distance	0.012	−0.029, 0.053	0.6
	Suitability threshold	0.132	0.105, 0.159	<0.001
	Tolerance to unsuitable habitat	0.093	0.066, 0.120	<0.001
	Normalized flow threshold	−0.197	−0.225, −0.170	<0.001
PC_{inter}	Dispersal distance	0.590	0.536, 0.644	<0.001
	Suitability threshold	0.044	0.008, 0.079	0.015
	Tolerance to unsuitable habitat	0.167	0.132, 0.203	<0.001
	Normalized flow threshold	−0.328	−0.363, −0.293	<0.001

Note: All PC metrics were log-transformed. All explanatory variables were scaled before running the linear mixed models. M7 group was excluded from the analysis as all PC metrics equaled 0. Abbreviations: CI, confidence interval; PC, probability of connectivity.

protective of vertebrate ecological continuities and poorly connected. Protected area connectivity could notably be enhanced based on a strategic expansion of protected areas and via the restoration of ecological corridors among disrupted ecological continuities. Our maps of ecological continuities provide notably valuable information for selecting potential areas to protect and restore.

5 | CONCLUSIONS

Our flexible framework to evaluate multi-species landscape connectivity in heterogeneous environments should contribute to both theoretical and applied ecological studies. Accounting for biodiversity representativeness, functional landscape use, and uncertainty

in model parameters, our approach is adaptable to various environmental conditions, including future global changes. Finally, we urge that the strategic expansion of protected areas and the restoration of key ecological corridors emerge as a priority to enhance landscape connectivity and support biodiversity conservation efforts in metropolitan France.

6 | PERSPECTIVES

Although our framework provides a step forward to more practical and comprehensive assessment of landscape connectivity for multiple species, there is room for further improvements. Connectivity analysis are largely biased towards vertebrate species (Brennan et al., 2022; Clauzel et al., 2023; Liang et al., 2023), and a more balanced evaluation of landscape connectivity including a broader taxonomical range (e.g. invertebrate species) would be beneficial for a thorough representativeness of biodiversity in conservation planning (Chowdhury et al., 2023). This would require improving theoretical knowledge on the movement behaviour for those taxa (e.g. tolerance to unsuitable habitat) and the development, evaluation and consolidation of trait databases on these groups. In addition, due to the paucity of freely available movement datasets, landscape connectivity model predictions are still deeply lacking systematic validation procedures (Riordan-Short et al., 2023). Initiatives such as the MoveBank platform have the potential to contribute to both theoretical knowledge and model evaluation in movement ecology (Kays et al., 2022). Finally, accounting for species interactions in multi-species landscape connectivity models remains a challenge (Unnithan Kumar et al., 2022; Wood et al., 2022), that should be addressed in the near future based on the growing availability of models and global knowledge database on this topic (Poggiato et al., under review, GLOBI database https://www.globalbioticinteractions.org/about). Such development will open avenues for bringing together community, landscape and movement ecology and promote more realistic, efficient and optimized actions for biodiversity conservation.

CONFLICT OF INTEREST STATEMENT

The authors declare that they have no conflict 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.14444.

DATA AVAILABILITY STATEMENT

The data and codes are archived on Zenodo at https://zenodo.org/records/13934759 (Prima, 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.

Table S1. Species list.

Table S2. Number of $1\,km^2$ presence pixels per species and per group.

Table S3. Species-trait compilation (see Appendix S4 for level description of categorical variables).

Table S4. Trait selection for landscape connectivity analysis.

Appendix S1. Download DOIs of GBIF occurrence data.

Appendix S2. Omniscape algorithm steps.

Appendix S3. Group distribution modelling.

Appendix S4. Generic group composition and characteristics for 52 mammal and 141 bird species of metropolitan France.

Appendix S5. Estimates of ecological continuities for 141 bird species clustered into 19 groups (A1 to A19) for the 2010–2020 period in metropolitan France.

Appendix S6. Average contribution of different types of protections (i.e., green: core of national park, orange: natural or biological reserve, purple: prefectural protection order) to the amount of reachable strictly-protected suitable habitat inside individual site (i.e., median of PC_{intra}^k for site k, over all simulation for a group) for 141 birds species clustered into 19 groups (A1 to A19) for the 2010–2020 period in metropolitan France.

Appendix S7. Average contribution of different types of protections (i.e., green: core of national park, orange: natural or biological reserve, purple: prefectural protection order) to the amount of reachable strictly-protected suitable habitat through direct or indirect connections among sites (i.e., median of PC_{flux}^k for site k, over all simulations for a group) for 141 bird species clustered into 19 groups (A1 to A19) for the 2010–2020 period in metropolitan France.

Appendix S8. Average contribution of different types of protections (i.e., green: core of national park, orange: natural or biological reserve, purple: prefectural protection order) as stepping stones (i.e., median of B_{norm}^k for site k, over all simulations for a group) for 141 bird species clustered into 19 groups (A1 to A19) for the 2010–2020 period in metropolitan France.