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Research article

Are human-induced changes good or bad to dynamic landscape connectivity?

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ABSTRACT

Land managers must find a compromise between rapidly changing landscapes and biodiversity conservation through ecological networks. Estimating ecological networks is a key approach to enhance or maintain functional connectivity by identifying the nodes and links of a graph, which represent habitats and their corresponding functional corridors, respectively. To understand the current state of biodiversity, it is necessary to consider dynamic landscape connectivity while relying on relevant land cover maps. Although a current land cover map is relatively easy to produce using existing data, this is challenging for past landscapes. Here we investigated the impact of changes in landscape connectivity in an urban landscape at a fine scale on the habitat availability of two bird species: the tree pipit *Anthus trivialis* and the short-toed treecreeper *Certhia brachydactyla*. These species, exhibiting different niche ecologies, have shown contrasting population trends at a medium-term scale. The occurrences of *C. brachydactyla* were better correlated with resistance values that maximise the use of corridors, whereas the occurrences of *A. trivialis* better fitted with intermediate resistance values. The statistical approach indirectly highlighted relevant information about the ecology the capacity of both species to use urban habitats. Landscape connectivity increased for both species over the 24-year study period and may have implications for local abundances, which could explain, at the national scale, the increase in populations of *C. brachydactyla*, but not the decrease in populations of *A. trivialis*. Thus, more attention must be paid on rural habitats and their associated species that are more impacted by human activities, but efforts could also be achieved in urban areas especially for highly corridor-dependent species. Studying dynamic landscape connectivity at a fine scale is essential for estimating past and future land cover changes and their associated impacts on ecological networks, to better reconcile human and biodiversity concerns in land management.

1. Introduction

Human-induced land cover changes (LCC) are causing major disruptions to ecosystems worldwide and threatening biodiversity and associated ecosystem services (Benítez-López et al., 2010; Leclère et al., 2020; Maxwell et al., 2016). Over the last few decades, LCC have manifested mainly through habitat loss and degradation, thus reducing suitable habitats into several isolated patches (i.e., biogeographic islands). The remaining patches serve as the last refuges for biodiversity (Fahrig, 2003; Wilcove et al., 1987). Surrounded by unsuitable habitats, organisms living in these isolated patches may encounter difficulties

moving between them, thus increasing the risk of inbreeding and entering into a vortex of extinction (Frankham, 2005; Keyghobadi, 2007). Landscape connectivity, defined as the extent to which the landscape facilitates or impedes movement between suitable patches (Taylor et al., 1993, 2006), plays a crucial role in ensuring the persistence and resilience of wildlife populations. Therefore, researchers have used landscape modelling approaches to describe both *structural connectivity* (i.e., physical relationships of landscape features) and *functional connectivity* (i.e., the organism's behavioural response to both the landscape structure and the landscape matrix) (Taylor et al., 1993, 2006).

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The concept of landscape resistance has become widely accepted for simulating how organisms perceive the landscape (Adriaensen et al., 2003; McRae et al., 2008; Spear et al., 2010). This involves assigning ecological cost values to various landscape features, which represent obstacles to movement. Among the various modelling approaches, graph theory is frequently used due to the limited amount of input data required as well as its ability to characterise ecological processes (Calabrese and Fagan, 2004; Foltête et al., 2014; Zeller et al., 2018). In accordance, graph theory is often used combined with the resistance-based approach to analyse functional connections (links) between biodiversity reservoirs (nodes) as key elements of graphs (Foltête et al., 2014, 2020; Pascual-Hortal and Saura, 2008; Saura and Rubio, 2010). Indeed, resistance-based models have been extensively used during the past two decades, showing strong correlations with real or measured connectivity from telemetry or gene flows (Balbi et al., 2018; Zeller et al., 2018).

The challenge of landscape connectivity is to understand and predict the current biological flux for each landscape element of the study area. This is commonly achieved by analysing a land cover map of the current landscape with the assumption that this landscape explains the structure, gene flow or abundance of the studied populations (Zeller et al., 2020). However, the current landscape structure and its connectivity can also result from past land cover (Lira et al., 2019; Uroy et al., 2021). Therefore, to understand an ecological process, it may be more relevant to consider both past and current landscapes and investigate the potential time-lag effects on (meta)-populations or communities (Epps and Keyghobadi, 2015; Lira et al., 2019; Uroy et al., 2021). Landscape connectivity modelling should be not limited to a 'time-static' landscape when considering its temporal dynamics (Zeller et al., 2020). For example, sedentary populations do not move across the landscape in the same way in autumn or winter as they do in spring, as patch resources and their availability change with the seasons (Martin et al., 2018; Mui et al., 2017). It is thus crucial to have at least two relevant snapshots of the studied landscape to understand and explain its ecological processes (Balkenhol et al., 2015; Uroy et al., 2021; Zeller et al., 2020). In this context, studying landscape connectivity along with the associated populations raises several challenges. The first challenge is to obtain a reliable land cover map that describes complex environments like urban areas. Even though remote sensing, which is increasingly accessible due to recent technological advances, can acquire the height of elements such as LiDAR (Neyns and Canters, 2022; Shahtahmassebi et al., 2021), this type of technology remains expensive and difficult to obtain or process. However, there is substantial evidence that high map accuracy, notably with a high spatial resolution, is important to predict species richness or organism movements (App et al., 2022; Barr et al., 2021; Balbi et al., 2019; Salgueiro et al., 2021). The second challenge is to reconstruct past landscapes from archive images, although this lacks information about the height of elements. Nevertheless, some remote sensing studies have shown that vegetation strata can be extracted from very high resolution images (Merciol et al., 2019; Morin et al., 2022; Puissant et al., 2014). Thus, for some species, it is not easy to accurately characterise and model habitats and their associated corridors in terms of their current or past landscapes. Several questions thus arise. What is the role played by urban habitats in landscape connectivity dynamics? Are LCC always detrimental? Are two habitats located on different sides of a city truly isolated? Were they connected 20 years ago? Without telemetry and genetic data, these questions cannot be accurately answered without reliable maps of current and past landscapes.

Among the different taxa impacted by human activities, birds are a good taxon to understand the positive and negative consequences of land management (Fahrig et al., 2015; Guetté et al., 2017; McKinney, 2008). A long-term population monitoring of birds in France (Suivi Temporel des Oiseaux Communs), initiated by the French National Museum of Natural History, observed that population trends vary according to their global ecology (Fontaine et al., 2020). Generalist and forest species tend to exhibit more stability over time, in contrast to

open-field and urban species, which clearly show population declines. In this context, investigations are needed to determine whether changes in land cover at a fine scale could explain both positive and negative population trends.

In this study, we used both a current and a past land cover map of the city of Poitiers, France, to investigate changes in landscape connectivity of two birds at a fine scale (i.e., 1m of spatial resolution) over a 24-year period. We obtained the current and past land cover maps using remote sensing approaches. The very high resolution of these maps allowed us to describe small elements such as hedgerows or isolated trees. We assess changes in landscape connectivity for two bird species showing different ecological requirements: the short-toed treecreeper *Certhia brachydactyla*, a specialist of forest landscapes with low dispersal capacity found in urban canopies and rural areas, and the tree pipit *Anthus trivialis*, a specialist of shrubby and bocage landscapes with medium dispersal capacity found in rural areas. Here, the occurrences of these two birds, recorded between 2015 and 2021, allowed us to validate our resistance-based maps and to add robustness to our connectivity models. Regarding the results of Fontaine et al. (2020), we expected that the landscape connectivity of *C. brachydactyla* increased between 1993 and 2017 whereas the landscape connectivity of *A. trivialis* decreased over this period.

2. Material and methods

2.1. Study area

The study area is the city of Poitiers, France (46.34° N, 0.20° E), and its surrounding area (extending over 225 km²). Located in the west of France, this area has an oceanic climate. The elevation ranges from 50 m to 160 m, the average temperature is 11.5 °C and the average annual precipitation is 687 mm. With a population of 131,499 inhabitants (census in 2017, INSEE), Poitiers is an important historical metropolis of western France. Its urban areas have mostly expanded since 1950, with a highway built around 1970 and a high-speed railway (HSR) in 2012. This urban landscape contains semi-natural areas such as wetlands along the Le Clain River, forests, open fields and an urban natural park. These semi-natural areas promote the presence of biodiversity, including protected species. Hence, this is a region of particular interest for understanding spatiotemporal landscape changes and their impact on biodiversity.

2.2. Land cover map of 2017

We built a land cover map of 2017 using the available public French databases and remote sensing products as described in Morin et al. (2022) (Fig. 1). Considering the high complexity and heterogeneity in the urban ecosystem, the approach using geographic object-based image analysis (GEOBIA) allowed us to enhance the land cover map by identifying and extracting the urban green areas (Neyns and Canters, 2022; Shahtahmassebi et al., 2021).

Among the existing databases, the BD Topo (2017) of the French National Geographic Institute (IGN) vector database was downloaded and used to identify watercourses and water bodies, buildings, transport infrastructure and wooded areas. In addition, the Registre Parcellaire Graphique vector database of 2017 was used to identify the agricultural plot boundaries, while the French land cover maps (OSO) (Inglada et al., 2017) from 2016, 2017, 2018 and 2019 were used to extract annual croplands and permanent grassland. The urban extent was extracted from the OSO of 2017.

To enhance this map, we used GEOBIA, including a learning step to characterise and distinguish wooded and herbaceous vegetation in urban areas. For this purpose, we used a false-colour image from 2017 with a 0.5m spatial resolution provided by the IGN. This GEOBIA method contains four main steps: (1) pre-processing step, including the extraction of spectral and textural information, (2) segmentation, (3)

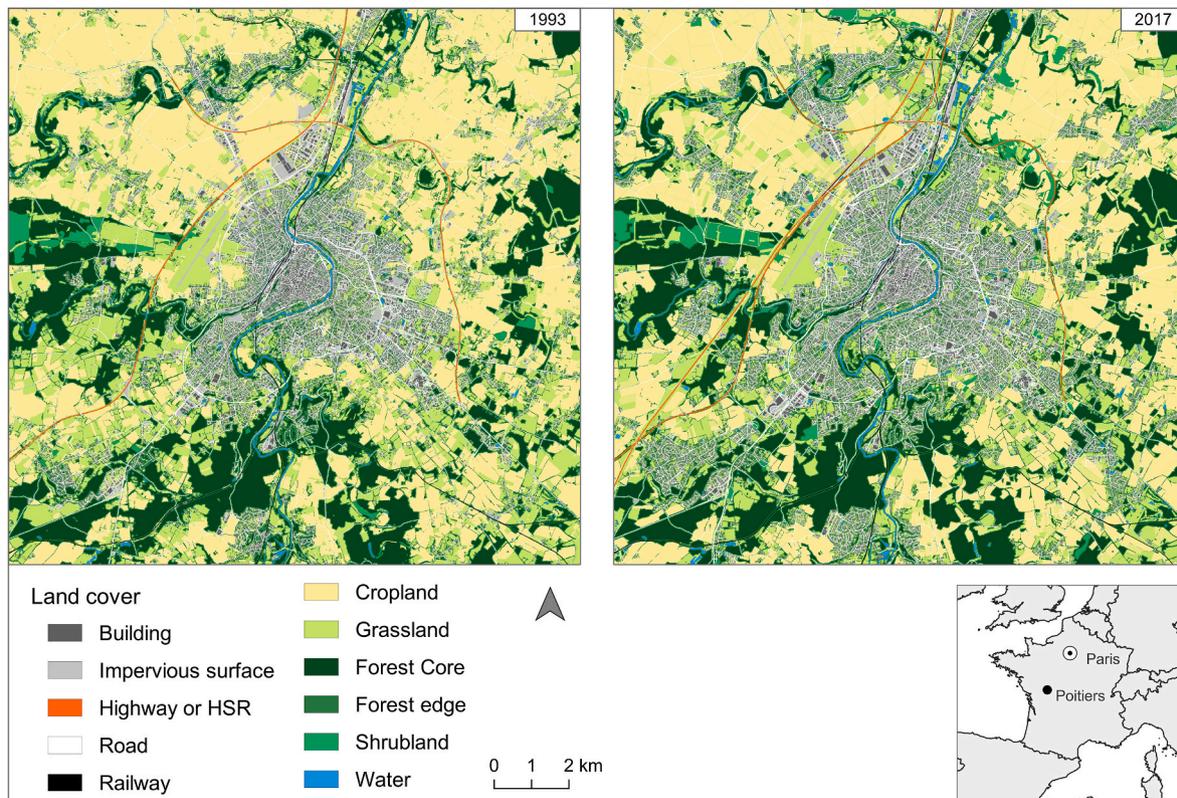


Fig. 1. Land cover maps of Poitiers from 1993 to 2017.

classification and (4) evaluation of classification accuracy (Blaschke et al., 2014; Chen et al., 2018). We used the *LargeScaleMeanShift* algorithm with a spatial radius of 5 pixels, a range radius of 28 pixels and a minimum segment size of 60 pixels. The normalised difference vegetation index (NDVI) was calculated. Four Haralick textures were calculated from the brightness (i.e., mean of NIR, Red and Green spectral bands) with a window size of 7×7 pixels: *Energy*, *Entropy*, *Contrast*, *Correlation*. The average within segments was extracted for all spectral bands and textures and the standard deviation was extracted from textures and the green band. The classification step included a random forest classification (i.e., machine learning algorithm) to create decision rules and identify three classes: artificial areas, herbaceous and wooded vegetation (see Morin et al., 2022 for more details). We chose a value of 250 for the number of trees in the forest and 4 for the depth of the trees corresponding to a third of the number of the predictor variables (Rodríguez-Galiano et al., 2012). A stratified subsampling was used followed by a cross-validation process as suggested by Dupuy et al. (2020) to improve the classification accuracy. Training data were divided into five roughly equal subset to produce five different classifications. Finally, these classifications were merged by majority voting. Training dataset included 1860 polygons: 1134 for artificial areas, 350 for grass and 376 for trees. Polygons were selected by photointerpretation across all the study area to avoid spatial autocorrelation, which can bias the evaluation of the classification performance (Mannel et al., 2011). The classification showed high global accuracy with an overall accuracy of 95.20% and a Cohen's kappa of 0.90. At the category level, artificial areas, grass and trees showed F-Scores of 94.6%, 95.8% and 85.52% respectively. Vegetation strata were well detected and differentiated from artificial areas (i.e., buildings, roads, parking areas, bare soil), which strongly improved the amount of urban vegetation identified and the precision of its detection (Morin et al., 2022).

2.3. Land cover map of 1993

We used the land cover map of 1993 described in Morin et al. (2023) (Fig. 1). The methodology used aerial images from the IGN and Landsat-5 TM scenes to reconstruct the past landscape using GEOBIA. This land cover map has a spatial resolution of 0.5 m and contains the same land cover categories as the land cover map of 2017.

The Orfeo Toolbox (OTB) open-source project (Grizonnet et al., 2017) was used to conduct the remote sensing analysis, while the QGIS project (Quantum GIS Development Team, 2019) was used for the remote sensing and GIS analysis. The two land cover maps of 1993 and 2017 were resampled to a spatial resolution of 5 m to facilitate landscape analysis.

2.4. Analysis of landscape changes

We investigated the landscape structure and the functional connectivity in the two land cover maps.

2.4.1. Landscape composition and configuration analysis

We compared the LCC between 1993 and 2017 using several landscape metrics that describe the landscape structure. These metrics were calculated using the QGIS project (Quantum GIS Development Team, 2019) and LecoS (Jung, 2016). To characterise the landscape composition, we computed the percentage of impervious surface (i.e., buildings, roads, railways, other impervious surfaces), cropland, grassland (i.e., meadows, lawns, herbaceous vegetation) and wooded vegetation (i.e., forests, hedgerows, shrublands, isolated trees). Concerning the landscape configuration, we computed the number and the mean surface of patches for these four categories. These metrics were calculated at the landscape level (i.e., whole study area) as well as at the local level using choropleth maps with grids of 500×500 m.

2.4.2. Functional connectivity: building and validating ecological networks

2.4.2.1. Landscape connectivity metrics in 2017. We assessed functional connectivity using graph theory. We used Graphab software (Foltête et al., 2012a) to model landscape graphs for two bird species: the short-toed treecreeper *Certhia brachydatyla*, a forest core species, and the tree pipit *Anthus trivialis*, an edge forest species. In this study, we tested three different resistance scenarios ranging from 1 to 100: linear, logarithmic and exponential resistance values (RV) (Table 1) (Balbi et al., 2018; Balkenhol et al., 2015). Testing several resistance value scenarios allow to create more or less differences between categories and so to ensure stable results and limiting misclassifications. Five categories were created to classify the land cover categories: (1) habitat, (2) favourable elements, (3) neutral elements, (4) unfavourable elements and (5) ecological barrier. The minimum size of habitat (i.e., nodes) was set to 0.3 ha for both species. Choices in these steps have been made according to literature and expert opinion (see Appendix 1).

The landscape graph can be pruned using a maximum dispersal distance to identify the functional corridors between habitat patches. Moreover, this parameter is integrated when computing the connectivity metrics to estimate the habitat availability at different spatial scales.

Even though these two species are well known, it is not easy to identify their dispersal capacity. We determined this distance using the approach described by Sahraoui et al. (2017, 2021a) based on an allometric relationship. Sutherland et al. (2000) showed that diet type and body mass were correlated with the dispersal distance for mammals and birds. We thus used the allometric conversion for birds ($13.1 M^{0.63}$) as well as the dataset of Lislevand et al. (2007) to extract the body mass of the two species. Therefore, the median dispersal distance of *C. brachydactyla* and *A. trivialis* was 760 m and 1280 m, respectively. The dispersal distance was converted into a cost distance (conversion distance function) in the landscape graphs for each resistance scenario (Appendix 1) (Foltête et al., 2012a).

Thus, we computed (1) the equivalent connectivity characterising the habitat availability at the global level (i.e., the whole study area) and (2) the number of patches divided by the number of components to describe the fragmentation level. A component is a region in which habitat patches are functionally connected. The equivalent connectivity (Sahraoui et al., 2021b; Saura et al., 2011) is calculated based on the habitat quantity and the probability of interaction between habitat patches using a dispersal distance:

$$\sqrt{\sum_{i=1}^n \sum_{j=1}^n a_i a_j p_{ij}^*}$$

where a_i and a_j are the area of patches i and j , and p_{ij}^* is the maximum probability of movement between these patches following the formula:

$$p_{ij} = e^{-\alpha d_{ij}}$$

where α determines the decreasing intensity of the probability of dispersion, d is the dispersal distance and p describes the dispersion set to 0.05 for a maximum dispersal distance (used in this study for all connectivity metrics) and set to 0.5 for a median dispersal distance.

In addition, the flux (Foltête et al., 2012b; Saura and Torné, 2009; Urban and Keitt, 2001) was calculated at the local level (i.e., patch level)

that characterises habitat availability by summing the area of the adjacent accessible habitats weighted by the dispersal distance:

$$\sum_{j=1}^n a_j^\beta e^{-\alpha d_{ij}}$$

where a_j is the area of patch j , β allows the weighting of the carrying capacity of patches (its value is set to 1 when the carrying capacity is weighted by the area of patches and 0 if the patches have an equal carrying capacity) and $e^{-\alpha d_{ij}}$ characterises the probability of movement between patches i and j as described above. Here, the term ‘carrying capacity’ refers to the ability of a habitat patch to support a specific number of individuals (Appendix 2). The flux metric was then interpolated (i.e., gFlux) using the dispersal distance value. This method gives a value that characterises the habitat availability for each pixel. This spatial generalisation of a local metric was proposed by Foltête et al. (2012b) to increase the accuracy of species distribution models.

2.4.2.2. Bird occurrences. Bird occurrences come from the dataset of the Ligue de Protection des Oiseaux, a national bird association. This dataset, validated by experts, contains protocolled and opportunistic data. The opportunistic data refer to information collected by a non-standardised method. Even though professional surveys contain more detailed information (e.g., presence and absence information), they have fewer data points. Conversely, opportunistic data include more occurrences and cover a larger area, although they are only composed of occurrences of presence and have a biased spatial distribution (e.g., close to cities). These complementary data are increasingly used in species distribution models or for the prediction of species abundance (Coron et al., 2018; Giraud et al., 2016; Préau et al., 2020; Wood et al., 2022). This dataset is composed of around 96,000 records of 50 different species. It was filtered while keeping the data between 2015 and 2021 to obtain sufficient information and fit with our study period. A broader time window could influence the temporal variation of the distribution of the impacted species, for example, by LCC due to urbanisation. The two selected species were chosen as they are both specialist species, well distributed and not too rare with occurrences of 2730 and 1022 for *C. brachydatyla* and *A. trivialis*, respectively (Appendix 2).

2.4.2.3. Statistical validation of the connectivity models. Point process models (PPM) (Baddeley et al., 2015) were used in this study to explain the distribution of each species according to the best model of functional connectivity and the sampling variables. This method aims to model the number of occurrences (N) and their spatial location (s) in an inhomogeneous Poisson process with an intensity $\mu(s)$ describing the expected number of presence records per unit area for a given location. The inhomogeneous Poisson process is a generalisation of the MaxEnt model (Phillips et al., 2006; Renner and Warton, 2013) and pseudo-absence logistic regression (Warton and Shepherd, 2010). One advantage of this method is its use of presence occurrences to explain the spatial distribution of a phenomenon. We used the same approach as in De Solan et al. (2019) to study the spatial distribution of both species. Dummy points were added to the presence points to increase the accuracy of the models using a quadrature scheme of 100×100 m to allow the likelihood convergence in PPMs. Geyer (1999) saturation point process models were used to manage

Table 1

Resistance values of categories. The classes were: a) buildings, b) impervious surfaces, c) highways & highspeed railways, d) main roads, e) railways, f) croplands, g) grasslands, lawns and others herbaceous elements, h) forests cores, i) Forest edges, shrublands and isolated trees, j) water bodies and courses.

Categories	Certhia brachydatyla	Anthus trivialis	Resistance values		
			Linear	Logarithmic	Exponential
Habitat	h, i	i	1	1	1
Favourable	g	f, g	25	68.4	3.2
Neutral	b, f	b, h	50	90	10
Unfavourable	d, e, j	d, e, j	75	96.8	31.6
Ecological barrier	a, c	a, c	100	100	100

the residual spatial aggregation detected in the initial PPM and avoid bias parameter estimates and standard errors (De Solan et al., 2019; Dormann et al., 2007). The Geyer process model is similar to the PPM, although it also considers that intensity ($\mu(s)$) is influenced by the adjacent records. The spatial interaction between points is managed by a saturation parameter that influences the strength of the interaction and the maximum distance radius of the interaction. Both parameters were maximised by pseudo-likelihood to identify a distance value of 101 m and a saturation value of 14 for *C. brachydactyla* and a distance value of 401 m and a saturation value of 9 for *A. trivialis*.

2.4.2.4. Predicted variables. When using opportunistic data, the challenge resides in estimating the sampling effort, because the data are not protocolled. Thus, we used the entire dataset of birds (i.e., 96,000 occurrences of 50 species) to approximate the sampling effort and create a grid of 500×500 m to count the number of unique dates within each cell. Then, the centroids of these cells were extracted to conduct ordinary kriging to interpolate the number of dates for each pixel in the study area (Appendix 3). This measure was used as a proxy of the sampling effort. Accessibility was characterised by quantifying the percentage of transport infrastructures (roads, railways) for each pixel via a moving window analysis with a 250 m radius (Appendix 3). This metric was calculated to consider a likely stronger sampling effort by citizens around this infrastructure, thus reflecting its greater reachability (De Solan et al., 2019). The interpolated connectivity metric (i.e., linear, logarithmic or exponential RV) was included in each model to test its influence on the occurrence of the species (Appendix 3). All variables were normalised. For *C. brachydactyla*, the connectivity metrics were tested using a second-order polynomial function to better predict the presence of the species. For *A. trivialis*, the connectivity metrics were log-transformed before the PPM. As suggested in other studies, it is important to validate the form of covariates by exploring the smoothed partial residuals (Baddeley et al., 2015; Chang et al., 2013; Renner et al., 2015). As highlighted by Renner et al. (2015), PPM can integrate individual information such as behaviour to understand ecological processes. Hence, the use of this connectivity metric should be relevant to explain the species distribution, because the interpolated flux is calculated from the perception of the landscape (i.e., landscape structure and species behaviour) and the probability of dispersion (i.e., dispersal capacity). The variables used were not correlated.

GIS analysis was conducted using QGIS v.3.10 (Quantum GIS Development Team, 2019) and statistical analysis using R v.3.6.1 (R Core Team, 2022) and the spatstat package (Baddeley et al., 2015).

2.4.2.5. Comparing functional connectivity changes. Once the best model was identified, global metrics can be calculated to quantify the habitat availability at the whole study area which is directly linked to the carrying capacity of the number of individuals. Then, the habitat availability can also be calculated, with a population-based approach: $\beta = 1$. The interpolation of the connectivity metric (here the Flux) is more likely to reflect the abundance of individuals (or the species richness of a specific guild of species) than the presence of individuals.

Functional connectivity analysis was performed on the cartography of 1993. The functional connectivity metrics as described above were calculated (i.e., equivalent connectivity at the global level, the number of patches divided by the number of components). The flux metric was computed using the best RV (i.e., linear, logarithmic or exponential) and the identical cost-distance values of the 2017 map in order to interpolate this metric to obtain its generalisation (i.e., $gFlux$). To compare the two dates, the generalised flux was normalised (Sahraoui et al., 2017):

$$gFlux_{norm} = \frac{(gFlux - \overline{gFlux})}{\sigma(gFlux)}$$

where $gFlux$ is the generalised flux, \overline{gFlux} is the mean value of all pixels and $\sigma(gFlux)$ is the standard deviation.

To identify any gains and losses in functional connectivity since 1993 at the local scale, we computed the difference between the $gFlux_{norm}$ values of 2017 and the $gFlux_{norm}$ values of 1993 (Sahraoui et al., 2017). Then, the variation of the flux metric was calculated using both an equal carrying capacity ($\beta = 0$) of habitat patches and an area weighted-based carrying capacity ($\beta = 1$) (Appendix 6).

3. Results

3.1. Landscape composition and configuration analysis

LCC were measured for impervious surfaces, croplands, grasslands and forests using the composition and configuration landscape indices based on the two land cover maps (Fig. 2). At the global level, urban areas increased from 3555.11 ha (15.8% of the study area) in 1993 to 4299.57 ha (19.10%) in 2017, representing a 21% increase in urban areas. The number of patches also increased from 13,525 to 16,516, although the mean patch area was constant between the two dates (Fig. 2). Regarding croplands, their area decreased from 7724.69 ha (34.3% of the study area) to 7039.49 ha (31.2%), representing a decrease of 8.88%. A consolidation of their patches was also observed, with a loss of 2521 patches between 1993 and 2017 and an increase of 68,223.72 ha for the mean area of the patches. Grasslands were more fragmented in 2017 than in 1993, with their area decreasing from 4833.26 ha (21.8% of the study area) to 3941.42 ha (17.5%) in 2017, representing a decrease of 18.45%. Grassland patches were more numerous and smaller in 2017, with 68,281 patches and a mean area of 575.76 ha compared with 39,531 patches and a mean area of 1219.52 ha in 1993. Wooded areas were larger in 2017 than in 1993, increasing from 6469.32 ha (28.75% of the study area) to 7208.73 ha (32%), thus representing an increase of 11.43%. In addition, there were 3789 more patches of wooded areas in 2017, while their mean area remained constant.

To better understand these temporal variations, choropleths maps were created to identify the main changing areas (Appendix 4). Urban areas largely sprawled around the centre of Poitiers in residential areas but also in small towns located in proximity and following the creation of the high-speed railway. These areas became denser, showing a greater number of patches and lower values of the fragmentation index (i.e., landscape division index) (Appendix 4). Interestingly, the size and number of wooded vegetation areas increased with the urban areas (e.g., residential areas) in some forests and shrublands. Croplands and grasslands showed antagonistic behaviour in terms of their surface areas.

3.2. Functional connectivity analysis

3.2.1. Results and comparison of point process models

To compare the functional connectivity between 1993 and 2017, the connectivity models were tested based on the occurrences of both studied species and the land cover in 2017.

For the two species, the connectivity models were correlated with their distribution (Table 2). Accessibility had no effect on the occurrences of *C. brachydactyla* but had a negative effect on *A. trivialis* whose records were dispersed on account of transport infrastructure. The number of unique dates had a positive influence in terms of the records for both species. The Geyer spatial interaction matrix suggested that the occurrences of both species were aggregated with an estimate = 0.2893 \pm 0.0409 SE, $Z_{val} = 7.0597$, $p < 0.0001$ for *C. brachydactyla* and an estimate = 0.2974 \pm 0.0117 SE, $Z_{val} = 25.3689$, $p < 0.0001$ for *A. trivialis*.

The Akaike information criterion (AIC) values used to rank the three connectivity scenarios indicated a lower value for the logarithmic RV scenario for *C. brachydactyla* and the linear RV scenario for *A. trivialis* (Table 2). The connectivity metric tends to slightly overestimate the intensity, but overall, the agreement between partial residuals and fitted parametric effects indicates that the models are adequate (Appendix 5).

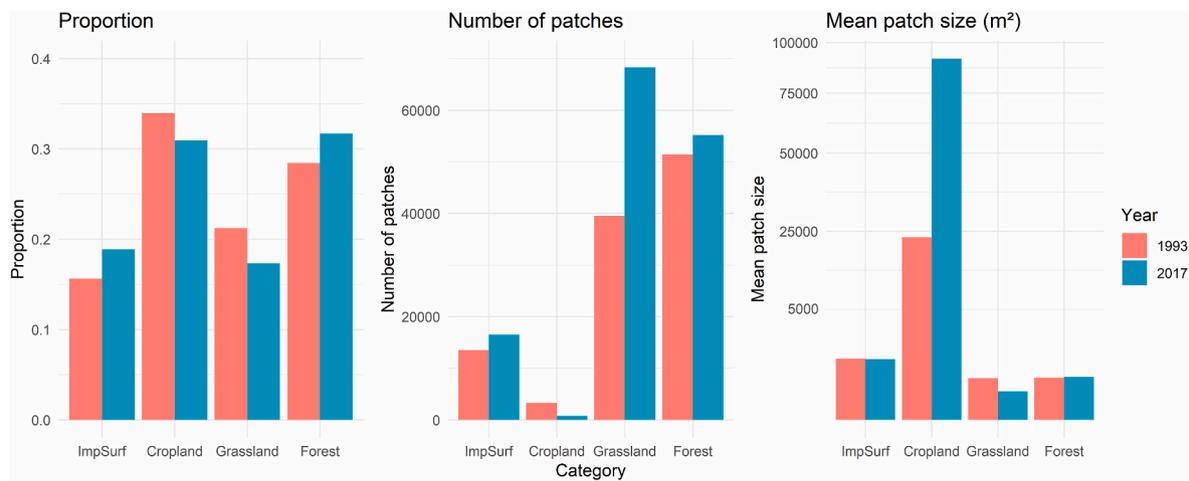


Fig. 2. Structural connectivity metrics calculated for 1993 and 2017.

Table 2
Results of the point process models for each landscape connectivity model.

<i>Certhia brachydactyla</i>	Variable	Estimate	Standard error	CI95.lo	CI95.hi	Z value	Z test	AIC	ΔAIC
Linear VR	Intercept	-13.3520	0.0792	-13.5074	-13.1966	-168.4101	***	64,688.62	47.22
	gFlux	1.4660	0.1466	1.1785	1.7534	9.9964	***		
	gFlux ²	-0.5530	0.1150	-0.7786	-0.3274	-4.8050	***		
	Nb date	0.1485	0.0641	0.0228	0.2741	2.3171	*		
	Access	0.1115	0.1094	-0.1030	0.3260	1.0184			
	Interaction Geyer matrix	0.2871	0.0405	0.2077	0.3665	7.0888	***		
Logarithmic VR	Intercept	-13.3534	0.0955	-13.5406	-13.1661	-139.7875	***	64,641.40	0
	gFlux	1.4660	0.1357	1.1999	1.7321	10.7986	***		
	gFlux ²	-0.5583	0.1278	-0.8089	-0.3077	-4.3674	***		
	Nb date	0.1686	0.0661	0.0389	0.2983	2.5485	*		
	Access	0.1027	0.1138	-0.1204	0.3258	0.9022			
	Interaction Geyer matrix	0.2893	0.0409	0.2089	0.3696	7.0606	***		
Exponential VR	Intercept	-13.2347	0.0883	-13.4079	-13.0615	-149.7541	***	65,079.92	438.52
	gFlux	1.2985	0.0917	1.1187	1.4783	14.1570	***		
	gFlux ²	-0.5776	0.0722	-0.7193	-0.4359	-7.990	***		
	Nb date	0.1030	0.0628	-0.0200	0.2261	1.6403			
	Access	0.0711	0.1205	-0.1650	0.3073	0.5901			
	Interaction Geyer matrix	0.2926	0.0417	0.2109	0.3743	7.0178	***		
<i>Anthus trivialis</i>	Variable	Estimate	Standard error	CI95.lo	CI95.hi	Z value	Z test	AIC	ΔAIC
Linear VR	Intercept	-14.9747	0.0734	-15.1186	-14.8308	-203.9516	***	25,806.86	0
	gFlux	0.6750	0.0382	0.6001	0.7499	17.6586	***		
	Nb date	0.2294	0.0097	0.2102	0.2486	23.4534	***		
	Access	-0.1408	0.0260	-0.1918	-0.0897	-5.4025	***		
	Interaction Geyer matrix	0.2974	0.0117	0.2744	0.3204	25.3689	***		
Logarithmic VR	Intercept	-14.9693	0.0733	-15.1130	-14.8256	-204.2194	***	25,819.33	12.47
	gFlux	0.6728	0.0387	0.5968	0.7487	17.3543	***		
	Nb date	0.2359	0.0096	0.2170	0.2549	24.4590	***		
	Access	-0.1462	0.0262	-0.1975	-0.0948	-5.5806	***		
	Interaction Geyer matrix	0.2932	0.0116	0.2703	0.3161	25.0664	***		
Exponential VR	Intercept	-14.9626	0.0731	-15.1059	-14.8193	-204.6817	***	25,836.91	30.05
	gFlux	0.5899	0.0339	0.5234	0.6563	17.3956	***		
	Nb date	0.2175	0.0101	0.1977	0.2374	21.4748	***		

Interestingly, the occurrences showed different response behaviours with the connectivity models. For *A. trivialis*, the intensity followed a linear relationship with the log-transformed connectivity values, whereas the intensity of *C. brachydactyla* seemed to follow a plateau for which an increase in the connectivity value did not increase this intensity (Appendix 5). It is important to note that, for *A. trivialis*, the intensity also follows a quadratic relationship with the untransformed connectivity values, but that the log-transformation linearises this relationship.

3.2.2. At the global level

The functional connectivity results were similar with higher connectivity indices for 2017 at the global level for both species. Equivalent

connectivity increased from 1.39×10^7 to 1.42×10^7 for *C. brachydactyla*, an increase of 2.16%, and from 5.83×10^6 to 6.27×10^6 for *A. trivialis*, an increase of 7.55% (Fig. 3). In other words, habitat availability was higher for *A. trivialis* compared with *C. brachydactyla*. Habitats were more fragmented in 1993 than in 2017. Concerning the forest habitat patches, 1248 patches (>0.3 ha) were identified in 1993 regrouped into 11 components (ratio of 113.45), while 1603 patches were found in 10 components (ratio of 160.3) in 2017. The forest edge patches were also more numerous and better connected in 2017 with 1593 patches and 16 components (ratio of 99.56) compared with 1216 patches and 25 components (ratio of 48.64) in 1993 (Fig. 3).

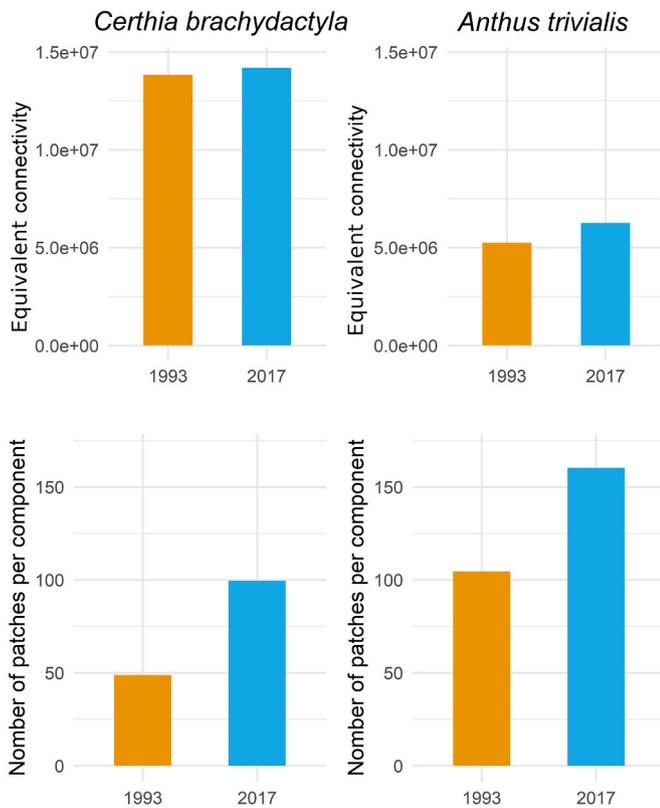


Fig. 3. Functional connectivity at the global scale.

3.2.3. At the local level

At the local scale, LCC had negative and positive impacts on the functional connectivity of the two species (Fig. 4). An increase in local functional connectivity was found for protected areas.

The habitat availability of *C. brachydactyla* was negatively impacted by the high-speed railway to the west of Poitiers. Urban sprawl induced positive changes on habitat availability by adding wooded vegetation instead of crops. However, this was accompanied by an increase in road density (e.g., small town south-west of Poitiers). Positive changes mainly came from shrublands, which increased between 1993 and 2017. When the generalised connectivity metric was weighted by the area of habitat patches (reflecting more the biological flux), different results were produced, showing the more negative impact of high-speed railway and urban sprawl, while a more attenuated or positive impact was observed in the southern part of the study area.

Concerning *A. trivialis*, temporal variations were quite similar around the forest patches. Due to a higher dispersal distance, positive values were more concentrated around wooded urban areas. The rise in shrublands also substantially increased the habitat areas. However, losses in functional connectivity were also slightly higher in some areas, for example, to the north of Poitiers. Considering the generalised connectivity metric weighted by the area of habitat patches, connectivity was globally higher around Poitiers (the main city), while HSR also had a greater impact on potential biological flux. Considering these weighted-area metrics, LCC seemed to have a more positive impact on *A. trivialis* (except for HSR) than on *C. brachydactyla* (Appendix 6).

4. Discussion

In this study, we investigated the impact of LCC on the habitat availability of two bird species at a fine scale. Current landscape connectivity models were validated using occurrences to find the best

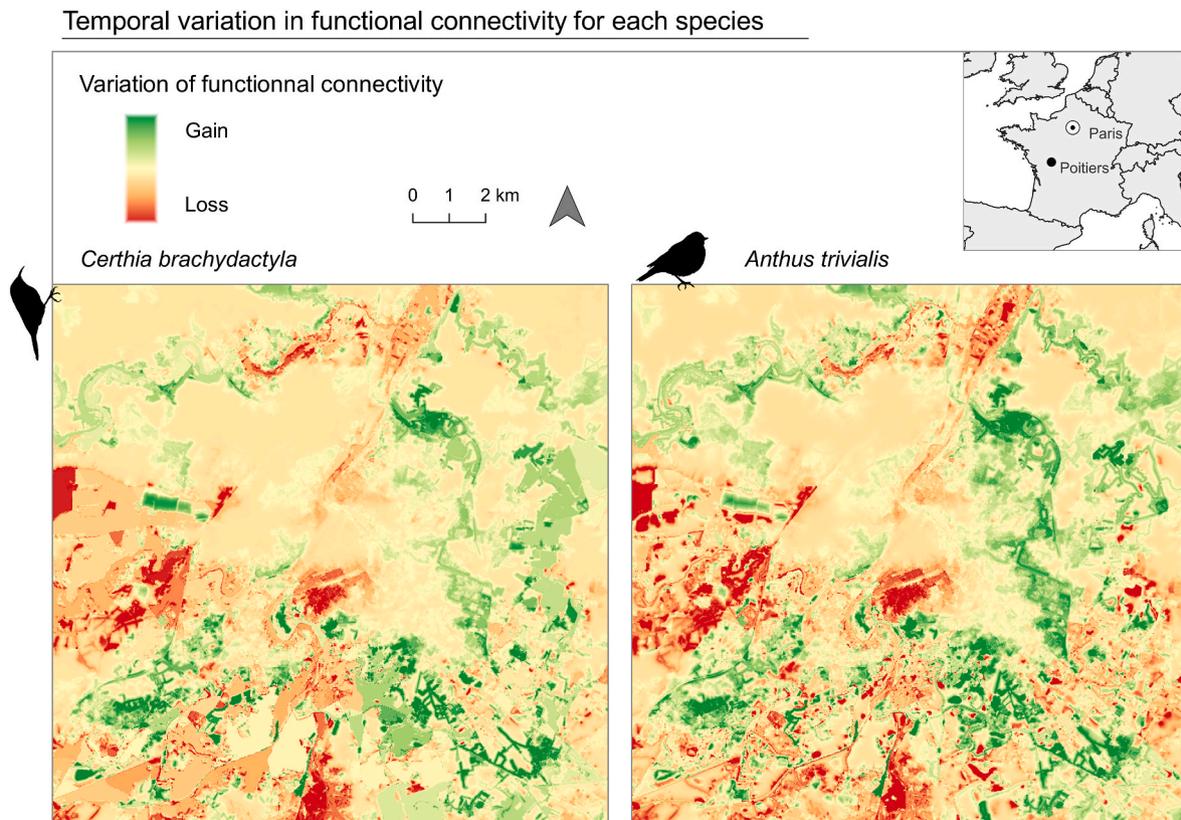


Fig. 4. Functional connectivity at the local scale, with the generalisation of the Flux metric calculated based on the equal carrying capacity of all habitat patches ($\beta = 0$).

parameters which were then applied to determine the connectivity of the past landscape. We then compare landscape connectivity between 1993 and 2017. Results indicated both positive and negative impacts at the local level, contributing to improved ecological connectivity at the global level for both species.

4.1. Dispersal behaviour and resistance values

The spatial distributions of *C. brachydactyla* and *A. trivialis* align with the connectivity modeling due to their respective ecologies. This was expected as we used allometric approach to determine dispersal distance (Sahraoui et al., 2017, 2021a) and to test several RV. The occurrences of *C. brachydactyla*, which is a sedentary species and specialist of wooded habitats and has a low dispersal capacity, were more correlated with logarithmic RV. These RV described a more resistant landscape matrix, suggesting that the suitable habitat elements (i.e., trees) are strongly used to disperse. This is in accordance with the literature, which confirms that this species is more prone to using trees to disperse (Balbi et al., 2021; Clergeau and Burel, 1997; Gianpasquale, 2017; Snell et al., 2020). By contrast, the records of *A. trivialis* are better fitted with the linear RV, which is rather congruent with its ecology because it is a migratory species whose dispersion depends less on suitable landscape elements. Previous studies indicate that transforming resistance values can be more effective depending on the use of corridors by individuals to move and potentially helping to understand their behaviour (Balbi et al., 2018; Balkenhol et al., 2015; Keeley et al., 2016; Zeller et al., 2018). Although our results are relevant to the ecology of both species, no scientific consensus has been found and does not apply universally to all species regarding this approach. The results depend on how the resistance map was constructed and the method used to model the ecological networks (e.g., graph theory, circuit theory).

4.2. Have land cover changes been good or bad for the two bird species?

At the global level, habitat availability was higher in 2017 than in 1993 on account of the more abundant wooded vegetation in the studied zone. Indeed, croplands as well as grassland have been replaced by wooded and new residential areas with vegetation including numerous trees as revealed by the structural connectivity results. The greater dispersal capacity of *A. trivialis* explained the higher equivalent connectivity value and the lower fragmentation degree at the global level compared with *C. brachydactyla*. It should be noted that the landscape matrix is also less permeable for *A. trivialis* compared with *C. brachydactyla* that could also explain the higher equivalent connectivity value. Unsurprisingly, the habitat availability was negatively impacted at the local level by the high-speed railway and positively impacted by the large habitat areas created since 1993. As expected, the high-speed railway and main roads prevent the movement of organisms because of their high RV. The increase in wooded vegetation in residential areas promoted functional connectivity when such environments replaced croplands. Concurrently, regenerative forests and conservation projects had a favourable impact by increasing shrubland or forest areas. Moreover, the potential biological flux (weighted-area-based metric) showed that LCC had more positive impacts for *A. trivialis*, probably due to its higher dispersal capacity compared with *C. brachydactyla*.

4.3. Biological flux modelling and population trends

Interestingly, the long-term population monitoring of birds in France (Suivi Temporel des Oiseaux Communs) initiated by the French National Museum of Natural History showed that *C. brachydactyla* populations increased by up to 12.6% between 2001 and 2019 (Fontaine et al., 2020). This observation is consistent with the positive connectivity changes for this species related to urbanisation and the increase in forest areas, validating our first hypothesis. Indeed, *C. brachydactyla* can be found in both urban and rural areas, as suggested by our results and the

literature (Balbi et al., 2021; Guetté et al., 2017; Snell et al., 2020), and even though populations are more prone to live in rural environments, they are not negatively impacted by urban areas (Guetté et al., 2017). Conversely, this monitoring showed that *A. trivialis* populations decreased by 19.3% between 2001 and 2019. Fontaine et al. (2020) observed that species that are specialists of agricultural land dramatically decreased between these two dates, rejecting our second hypothesis. This timeframe corresponds to more intensive agricultural practices with the use of neonicotinoids, among others, which probably had a negative impact on biodiversity. Even if *A. trivialis* is a specialist of bocage landscapes and an “urban avoider” as highlighted by our results and other studies (Guetté et al., 2017), which could explain their population decrease, this is not consistent with the increase in functional connectivity. In this context, it will be interesting to include habitat quality in the landscape connectivity model by quantifying the agricultural practices (e.g., pesticides use, mechanisation). For instance, dynamic connectivity models could integrate changes in croplands (i.e., presence or absence of crop consolidation) to serve as a proxy of changes in land farming management. Since the scale of comparison between population trends (i.e., national) and connectivity analysis (i.e., local) is not the same, it is possible that local populations have been increasing over the last few decades despite their decline on a national scale.

Our findings suggested that wooded elements in (new) urban and forest areas can be favourable for forest species such as *C. brachydactyla*. In this way, future green urban areas will be able to shelter some forest species (Balbi et al., 2021; Mimet et al., 2020; Snell et al., 2020; Tremblay and St Clair, 2009). However, efforts could be made to protect birds near urban areas, especially against cats, which are arguably the most significant threat to birds (Loss et al., 2013). Because urban vegetation and its biodiversity is crucial for human well-being (Cox et al., 2017; Luck et al., 2011), urban ecological networks must be studied using reliable data (e.g., fine scale land cover maps) to be more functional. On the other hand, more attention should be given to the northern forest species and urban avoiders, as climate change and human activities tend to favour more generalist species (Callaghan et al., 2019; Le Viol et al., 2012; Morelli et al., 2020). As highlighted above, the decline in *A. trivialis* populations and other open-field specialist populations at the national scale is probably due to recent changes in farming systems (Fontaine et al., 2020). Our results also suggest, in our studied zone, a land consolidation of croplands along with their decrease between 1993 and 2017 combined with a decrease in grasslands, which is consistent with international trends (van Vliet et al., 2017). Therefore, this species, which is favoured by agricultural landscapes displaying wooded vegetation and well-developed hedges, potentially suffers from the intensive practices found in large agricultural areas resulting from land consolidation. Alternatives to conventional farming have to be applied to enhance habitat quality and create more agroecological infrastructure and protected areas (e.g., Natura 2000 areas) (Duru et al., 2015; Kerbiriou et al., 2018). Urban parks and wastelands could also be beneficial for these populations (Meffert et al., 2012). Increasing the quality and quantity of habitat and landscape connectivity is crucial to supporting open-field populations.

4.4. Broader implications for conservation planning

The strengths of the statistical approach (PPM) used in this study are its use of opportunistic data to (i) consider the spatial autocorrelation of occurrences, (ii) evaluate the impact of the sampling effort on species distribution, (iii) identify the most likely connectivity model and (iv) integrate different behaviour responses into the landscape structure and matrix (De Solan et al., 2019; Renner et al., 2015). Moreover, this method, based on graph theory, needs a relatively limited amount of input data (Calabrese and Fagan, 2004; Foltête et al., 2014). The precision of the fine-scale land cover maps was also a key element in the model habitat availability and was probably more important for *C. brachydactyla* because of its dispersal behaviour. To go further, it will

be interesting to compare the results of this statistical approach with those based on telemetry or genetic data, which rely more on movements (Balbi et al., 2018, 2019; Zeller et al., 2018). Our approach tends to be more accessible (compared with telemetry or genetic data), because occurrences are increasingly available through citizen science projects, thus making them useful in ecology research (Coron et al., 2018; Giraud et al., 2016; Wood et al., 2022). Thus, we suggest using both opportunistic and protocolled data to validate ecological networks for robust predictions whenever more robust data (telemetry or genetic) are not available. Additional data such as mark-release-recapture methods or playback recalls for birds can also be used to better understand the dispersal behaviour of organisms and their willingness to move in response to different elements (Balbi et al., 2021).

Validating past functional connectivity remains a challenge, because the associated biological data are not usually available. However, it is possible to use current evidence of (meta-)populations or communities using occurrences, telemetry or genetic information to disentangle the effect (and the time-lag effect) of spatiotemporal land cover and connectivity changes (Epps and Keyghobadi, 2015; Lecoq et al., 2021; Lira et al., 2019; Uroy et al., 2021). Our methodology was interesting to estimate habitat availability over time and could be completed by testing the correlation between local connectivity metrics and species richness or abundance (Foltête et al., 2012b; Ribeiro et al., 2011). Indeed, landscape connectivity relies on the dispersal capacity of organisms, which shapes the distribution and persistence of populations (Hanski and Ovaskainen, 2000; Keyghobadi, 2007; Perry and Lee, 2019; Reigada et al., 2015). The dispersion of organisms also depends on their perception of the landscape (App et al., 2022; Baguette and Van Dyck, 2007; Balbi et al., 2021; Bélisle, 2005). For example, small landscape elements like isolated trees can trigger an individual's willingness to move. Regarding these facts, very high resolution land cover maps based on remote sensing methods can help to understand current biodiversity through the prism of time. Such maps have been shown to be essential for studying landscape dynamics, as their descriptions play an important role in both landscape connectivity and biodiversity assessments in urban and rural landscapes (App et al., 2022; Balbi et al., 2021; Barr et al., 2021; Morin et al., 2022; Salgueiro et al., 2021; Tiang et al., 2021). As a consequence, the use of reliable fine-scale maps is precious in terms of conservation planning and should help to better understand current biodiversity and its spatiotemporal dynamics as well as to test land management scenarios (Sahraoui et al., 2021b; Tarabon et al., 2020; Wellmann et al., 2020).

CRedit authorship contribution statement

Elie Morin: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Software, Validation, Visualization. **Ny Tolotra Razafimbelo:** Formal analysis, Software. **Jean-Louis Yengué:** Funding acquisition, Project administration. **Yvonnick Guinard:** Funding acquisition, Project administration, Supervision. **Frédéric Grandjean:** Funding acquisition, Project administration, Supervision, Writing – review & editing. **Nicolas Bech:** Conceptualization, Funding acquisition, Methodology, Project administration, Supervision, Validation, Writing – review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.jenvman.2023.120009>.

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