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RESEARCH ARTICLE

A multi-species approach for assessing the impact of land-cover changes on landscape connectivity

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Abstract

Context Land-cover changes (LCCs) could impact wildlife populations through gains or losses of natural habitats and changes in the landscape mosaic. To assess such impacts, we need to focus on landscape connectivity from a diachronic perspective.

Objectives We propose a method for assessing the impact of LCCs on landscape connectivity through a multi-species approach based on graph theory. To do this, we combine two approaches devised to spatialize the variation of multi-species connectivity and to quantify the importance of types of LCCs for single-species connectivity by highlighting the possible contradictory effects.

Methods We begin with a list of landscape species and create virtual species with similar ecological requirements. We model the ecological network of these virtual species at two dates and compute the variation of a local and global connectivity metric to assess the impacts of the LCCs on their dispersal capacities.

Results The spatial variation of multi-species connectivity showed that local impacts range from −6.4% to +3.2%. The assessment of the impacts of types of LCCs showed a variation in global connectivity ranging from −45.1% for open-area reptiles to +170.2% for natural open-area birds with low-dispersion capacities.

Conclusions This generic approach can be reproduced in a large variety of spatial contexts by adapting the selection of the initial species. The proposed method could inform and guide conservation actions and landscape management strategies so as to enhance or maintain connectivity for species at a landscape scale.

Keywords Connectivity · Dispersion · Multi-species · Landscape graphs · Land-cover changes · Impact assessment

Introduction

Changes in land use and land cover and their impact on biodiversity have attracted much political interest in recent decades, as evidenced by the Millennium Ecosystem Assessment (Millennium Ecosystem Assessment 2003) and the recent Rio+20 Summit (UN General Assembly 2012). Such changes are

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currently the main threat to biodiversity worldwide (Baillie et al. 2004) and are likely to remain so well into the twenty-first century (Sala et al. 2000).

It is the loss and fragmentation of habitat arising from land-use/land-cover changes that threaten biodiversity (Fahrig 2003; Solé and Bascompte 2006). The major causes of these mostly anthropogenic disturbances include agricultural practices (Chamberlain et al. 2000; Foley et al. 2005), urban development (Forman 1995; Fahrig 1997), and the construction of transportation infrastructures (Forman and Alexander 1998; Coffin 2007). Studies have shown that the loss of natural habitats directly affects biodiversity (Fahrig 2003; Ewers and Didham 2006), reducing the proportion of patches large enough to sustain a population over time. Habitat fragmentation forces species to organize as metapopulations (Hanski and Ovaskainen 2000) or patchy populations (Giplin and Hanski 1991), making fluxes highly dependent on connections between habitat patches. Consequently, the quality of the landscape mosaic may greatly affect biodiversity (Dunford and Freemark 2005), isolating habitat patches and reducing species richness and abundance. In this context, the assessment of the impacts of land-use and land-cover changes is an important issue. The effects of habitat fragmentation are more difficult to assess than the effects of direct loss of habitat (Geneletti 2006), and approaches based on habitat patches alone are inadequate if species' capacities to move between habitats are ignored. Accordingly, functional connectivity has to be incorporated into ecological impact assessments (Taylor et al. 2006).

Several methods are used to assess the functional connectivity of landscapes, based either on field observations or on modeling approaches. Field observations are extremely labor intensive and fail to provide a complete understanding of functional connections at a large scale. These drawbacks make landscape network modeling a suitable alternative (Calabrese and Fagan 2004). Many studies carried out in the 15 years since the initial work by Bunn et al. (2000) and Urban and Keitt (2001) have shown the relevance of landscape (or patch-based) graphs for modeling ecological networks and assessing landscape connectivity by means of connectivity metrics (Rayfield et al. 2011). In landscape graphs, the nodes are the habitat patches of a given species and the links represent the potential flux between them. This method offers a useful compromise between its ability to estimate potential functional connectivity at a large spatial scale and the amount of input data required (Calabrese and Fagan 2004).

Operationally, landscape graphs have proved their effectiveness in providing decision support in land-use planning (Zetterberg et al. 2010; Galpern et al. 2011; Pereira et al. 2011). Foltête et al. (2014) reported three main possible applications in land-use planning: (1) to support prioritization within ecological networks from the perspective of conservation (2) to increase the connectivity of a network from the perspective of ecological restoration, (3) to assess the potential impact of a given development on the network through reduced or increased connectivity. In the latter case, applications usually concern a specific change, especially anthropogenic developments with negative impacts such as the construction of transport infrastructures (Vasas et al. 2009; Fu et al. 2010; Gurrutxaga et al. 2011; Clauzel et al. 2013; Girardet et al. 2013) or urban development (Goetz et al. 2009; Tannier et al. 2016).

A significant number of studies address the observation and the monitoring of land-use and land-cover changes and their environmental impacts. Turner et al. (2007) even evoke the existence of a land-change science, but also note that land-change assessments are increasingly targeted at specific problems such as the consequences for water and food supplies or for landscape fragmentation. In studying the impacts of land cover changes on ecosystems, several approaches are used to define groups of species representative of their ecosystems, including focal species (Lambeck 1997), landscape species (Sanderson et al. 2002), and ecological profiles (Vos et al. 2001; Opdam et al. 2008). A number of graph-based studies have used the ecological-profile approach to assess connectivity for mammals between protected areas (Minor and Lookingbill 2010) or forested habitats (Mimet et al. 2016; Tannier et al. 2016). Moreover, studies may be based not just on real species but also virtual species, as in Hirzel et al. (2001), Girardet et al. (2013) and Mimet et al. (2016). All these studies respond to particular issues and focus on a single group of species, a particular habitat, and specific land-cover changes. There is currently a lack of research synthesizing all the impacts of land-cover changes on species that are representative of different ecosystems at the landscape scale.

Given these elements, the aim of this study is to propose a methodological framework based on landscape graphs to assess the potential impacts of all types of land-cover changes (LCCs) on connectivity for species that are representative of various ecosystems. We address two methodological issues:

(1) How to locate LCC impacts on multi-species landscape connectivity in the overall space? This involves spatializing LCC impacts at any point in space by taking into account the functional connectivity between habitats.
(2) How to measure (positive or negative) LCC impacts on species with different ecological requirements so as to provide a global impact assessment? To this end, a multi-species approach is essential to avoid focusing exclusively on the specific impacts for a single species. Whereas some LCCs are expected to have a general negative impact (e.g. artificialization of natural areas), other changes may have contradictory effects. For example, it can be predicted that the expansion of forests into former grassland areas will impact forest species positively while adversely affecting species living in open habitats.

We argue that answering these issues will provide operational outcomes in terms of ecological conservation and landscape management. Indeed, the proposed method provides an overview of the ecological impacts of LCCs for different species at the landscape scale. This involves modeling the ecological network of a set of species with different ecological requirements (1) to quantify the global connectivity of these networks and (2) to spatialize the potential connectivity associated with any point of the study area for each species. In a diachronic approach, such modeling can be used to quantify and spatialize the loss or gain in connectivity brought about by LCCs at the landscape scale. This methodological framework is applied to the eastern part of the metropolitan area of Paris (France).

Methods

Study area

The study area (2025 km^2) is located at the urban/rural interface of the eastern part of the metropolitan area of Paris (Fig. 1). Farmland covers 48% of this area, forest 19%, and urbanized areas 19%, especially in the western part. Two valleys (the Marne and the Grand Morin) cross the area from East to West and it is also fragmented by many transportation infrastructures. Its location near a major conurbation means the area has been affected by anthropogenic pressure, such as urban sprawl since the 1970s, the development of transportation infrastructures, and the intensification of agriculture. This area is therefore of particular interest because it is a major challenge to conserve biodiversity there. Biodiversity conservation is a major challenge in this area composed of 18.9% of protected areas (Natura 2000) and Natural Areas of Ecological, Wildlife, and Floristic Interest (ZNIEFF).

Spatial data

Land cover data for the years 1982 (t) and 2012 ($t + 1$) were provided by the Institute for Urban Planning and Development of the Ile-de-France Region (IAU-IDF). This vectorial database containing 81 land-use/land-cover categories was simplified into eight categories for both dates: forests, water bodies, water courses, artificialized areas, and main transportation infrastructures, croplands, grasslands and other herbaceous areas. This information was supplemented by the BD Topo (2012) provided by the French National Geographical Institute (IGN) for mapping buildings and transportation infrastructures. The main transport infrastructures (highways and high-speed railway lines), which are likely to have a barrier effect on the movement of certain species, were distinguished from secondary roads. All these data were combined for each date using GIS software and grouped into 10 land-cover categories, and then converted into 5 m-resolution raster layers. These 10 categories were classified according to the habitat preferences of the studied species reported by the literature. Furthermore, this classification was used to investigate landscape changes such as urbanization, agricultural development, or conversion of natural areas.

Two additional analyses were conducted from the raster layers, given the specific ecological requirements of species living in forest areas and grasslands. A morphological spatial pattern analysis (MSPA) (Vogt et al. 2007) was applied to the forest category to dissociate forest cores from groves, hedgerows and forest edges (named exclusively forest edges in the text), on the base of 2 pixels (i.e. 10 m). Given the

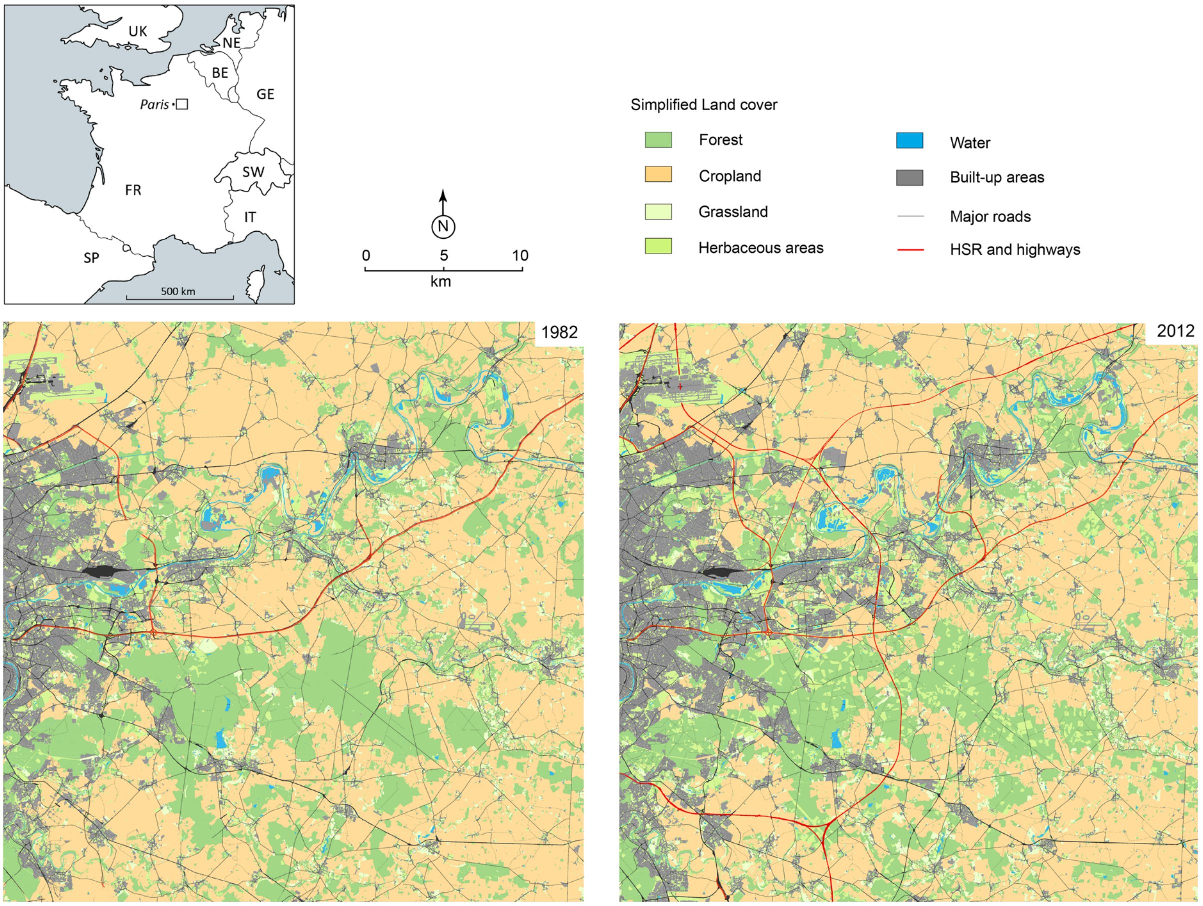

Fig. 1 Location of the study area in the eastern part of the metropolitan area of Paris. Land cover in 1982 and 2012 simplified into eight classes to make the map easier to read

ecological requirements of species living in grasslands, the sunniest grasslands were distinguished from others. To do this, a solar radiation analysis was performed using ArcGis 10 (ESRI 2011) from a DEM surface raster provided by the IGN. This analysis identifies the sunniest polygons, i.e. grassland polygons with above average overall solar radiation. We finally obtained two land-cover maps classified into 12 categories. Online Appendix 1 summarizes the sources of each category and details their content and the GIS processes required for their construction. Table 1 shows land cover transitions between 1982 and 2012.

Construction of virtual species

The objective was to identify a limited number of species representative of the existing landscape types present in the study area. This required three steps, (1) selecting landscape species, (2) defining their ecological requirements, and (3) constructing virtual species.

Selection of landscape species

We refer to the concept of landscape species described by Sanderson et al. (2002) as species whose requirements in terms of habitat size and habitat connectivity make them particularly sensitive to LCCs, especially the alteration of natural landscapes by human activities. When selecting landscape species, other species dependent on the landscapes concerned were also included in the analysis.

We chose to focus on the national list of species defined by the French National Museum of Natural History (MNHN 2011), following a method consistent with the priorities defined by the French

Table 1 Transition matrix of land cover between 1982 and 2012. This matrix was obtained by combining land-cover maps for both dates

1982	1	2	3	4	5	6	7	8	9	10	11	12	Total 1982	Loss
1. Forest cores	**313.39**	**13.35**	**40.3**	**1.2**	**0.53**	**0.86**	**0.67**	**0**	**3.38**	**0.62**	**1.12**	**1.13**	**376.56**	**63.17**
	15.48	*0.66*	*1.99*	*0.06*	*0.03*	*0.04*	*0.03*	*0*	*0.17*	*0.03*	*0.06*	*0.06*	*18.6*	*3.12*
2. Forest edges	**4.34**	**47.52**	**5.25**	**1.31**	**0.31**	**0.49**	**0.14**	**0**	**2.96**	**0.33**	**0.77**	**0.14**	**63.56**	**16.04**
	0.21	*2.35*	*0.26*	*0.06*	*0.02*	*0.02*	*0.01*	*0*	*0.15*	*0.02*	*0.04*	*0.01*	*3.14*	*0.79*
3. Herbaceous areas	**10.36**	**5.79**	**94.92**	**5.74**	**2.23**	**2.95**	**0.92**	**0**	**24.16**	**3.25**	**1.56**	**0.18**	**152.07**	**57.15**
	0.51	*0.29*	*4.69*	*0.28*	*0.11*	*0.15*	*0.05*	*0*	*1.19*	*0.16*	*0.08*	*0.01*	*7.51*	*2.82*
4. Croplands	**2.63**	**1.53**	**56.24**	**868.93**	**19.44**	**26.28**	**3.36**	**0**	**51.59**	**11.55**	**8.37**	**4.16**	**1054.08**	**185.15**
	0.13	*0.08*	*2.78*	*42.91*	*0.96*	*1.3*	*0.17*	*0*	*2.55*	*0.57*	*0.41*	*0.21*	*52.05*	*9.14*
5. Grasslands	**0.6**	**0.4**	**3.77**	**6.88**	**12.03**	**1.32**	**0.06**	**0**	**2.25**	**0.42**	**0.22**	**0.03**	**27.97**	**15.94**
	0.03	*0.02*	*0.19*	*0.34*	*0.59*	*0.07*	*0*	*0*	*0.11*	*0.02*	*0.01*	*0*	*1.38*	*0.79*
6. Sunniest Grasslands	**0.96**	**0.59**	**6.84**	**10.01**	**1.64**	**16.14**	**0.3**	**0**	**3.24**	**0.46**	**0.21**	**0.01**	**40.4**	**24.26**
	0.05	*0.03*	*0.34*	*0.49*	*0.08*	*0.8*	*0.01*	*0*	*0.16*	*0.02*	*0.01*	*0*	*2*	*1.2*
7. Water bodies	**0.03**	**0.02**	**1.12**	**0.16**	**0.01**	**0.01**	**9.5**	**0.01**	**0.27**	**0**	**0.01**	**0.02**	**11.17**	**1.67**
	0	*0*	*0.06*	*0.01*	*0*	*0*	*0.47*	*0*	*0.01*	*0*	*0*	*0*	*0.55*	*0.080*
8. Water courses	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**10.75**	**0**	**0**	**0.04**	**0.01**	**10.79**	**0.04**
	0	*0*	*0*	*0*	*0*	*0*	*0*	*0.53*	*0*	*0*	*0*	*0*	*0.53*	*0*
9. Artificialized areas	**0.53**	**0.34**	**9.9**	**1.37**	**0.58**	**0.42**	**1.07**	**0**	**165.98**	**1.89**	**3.05**	**0.03**	**185.15**	**19.17**
	0.03	*0.02*	*0.49*	*0.07*	*0.03*	*0.02*	*0.05*	*0*	*8.2*	*0.09*	*0.15*	*0*	*9.14*	*0.94*
10. Buildings	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**46.71**	**0.03**	**0**	**46.75**	**0.04**
	0	*0*	*0*	*0*	*0*	*0*	*0*	*0*	*0*	*2.31*	*0*	*0*	*2.31*	*0*
11. Secondary roads	**0.02**	**0.04**	**0.54**	**0.04**	**0**	**0.01**	**0.01**	**0**	**0.52**	**0.12**	**52.64**	**0.3**	**54.23**	**1.59**
	0	*0*	*0.03*	*0*	*0*	*0*	*0*	*0*	*0.03*	*0.01*	*2.6*	*0.01*	*2.68*	*0.08*
12. Main transportation infrastructures	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**2.27**	**2.27**	**0**
	0	*0*	*0*	*0*	*0*	*0*	*0*	*0*	*0*	*0*	*0*	*0.11*	*0.11*	*0*
Total 2012	**332.86**	**69.59**	**218.89**	**895.64**	**36.76**	**48.48**	**16.03**	**10.76**	**254.34**	**65.37**	**68.01**	**8.27**		
	16.44	*3.44*	*10.81*	*44.23*	*1.82*	*2.39*	*0.79*	*0.53*	*12.56*	*3.23*	*3.36*	*0.41*		
Gain	**19.47**	**22.07**	**123.97**	**26.71**	**24.73**	**32.34**	**6.53**	**0.01**	**88.36**	**18.66**	**15.37**	**6**		
	0.96	*1.09*	*6.12*	*1.32*	*1.23*	*1.59*	*0.32*	*0*	*4.36*	*0.92*	*0.76*	*0.3*		

Values in bold correspond to surfaces (in km^2) and values in italic correspond to actual percent of the landscape, as in Pontius et al. (2004)

Ministry of Ecology for the conservation of ecological networks. The initial list was composed of 118 vertebrates and 106 invertebrates, and was not reduced to endangered or flagship species. In this study, we focused exclusively on vertebrate species, whose habitat and movement capacities can be modeled from the maps defined at a certain spatial grain. Habitat patches of invertebrates are often smaller and their movement capabilities slightly greater than the spatial resolution grain. Among vertebrate species, only those present in the study area were selected thanks to the database of the National Institute of Natural Heritage (http://inpn.mnhn.fr), listing species found in each French municipality. Of the 118 vertebrates on the initial list, 43 were selected: 8 amphibians, 6 reptiles, 5 mammals, and 24 birds.

Definition of ecological requirements

To model ecological networks in the most realistic way, we used least-cost distances rather than Euclidean distances (Bunn et al. 2000). From this perspective, each land-cover category was characterized by its capacity to facilitate or impede species movements using the ecological knowledge from the IUCN Red List and regional or national atlas of species. Habitat preferences of each selected species were identified using the same sources. The values of resistance to movement were defined using a logarithmic scale as in Clauzel et al. (2015): habitat or very suitable areas (1), suitable (10), neutral (100), unfavorable (1000), and barrier (10,000).

Modeling ecological networks based on landscape graphs requires a distance to be defined that characterizes the movement capacity of each species. As the dispersal process is a key factor for population viability, each species was characterized by its dispersal distance. For amphibians and reptiles, maximum dispersal distances were extracted from the literature reviews by Smith and Green (2005) and Sordello et al. (2013) respectively. For mammals and birds, there is no literature review for maximum dispersal distances. Therefore median dispersal distances were computed using allometric relationships as in Mimet et al. (2016), linking diet types and species body mass on the one hand, and dispersion capacity on the other. Mammal body size was extracted from the data set of Smith et al. (2003) that compiles this information for all mammals on Earth. Bird body size was extracted from the data set of Lislevand et al. (2007) containing 3769 bird species. Then, the equations of allometric relationships given by Sutherland et al. (2000) were used to convert the body mass M (in kg) of each species to median natal dispersal distances (in km) for carnivorous mammals ($3.45\ M^{0.89}$), herbivorous and omnivorous mammals ($1.45\ M^{0.54}$), and birds ($13.1\ M^{0.63}$). Complete information about movement costs, habitat, and dispersion capacities for each of the 43 species is in Online Appendix 2.

Construction of virtual species

The 43 selected species were arranged into 16 generic groups with identical profiles according to three criteria (Online Appendix 2): (1) their class (amphibian, reptile, mammal, or bird), (2) their main habitat type (forest core, forest edge, open, or aquatic area), (3) their dispersal capacity classified as low (i.e. <4 km) or medium (i.e. >4 km). These 16 generic groups were defined as virtual species representing the real species that composed them. In several cases, a group was represented by a single species. For groups containing several real species, values for dispersal capacities and movement costs were aggregated, by averaging dispersal distances and by keeping the most frequent movement cost attributed to each land-cover category.

Landscape graph analysis

Landscape graphs analyses were performed with Graphab 2.0 software (Foltete et al. 2012a) (see http://thema.univ-fcomte.fr/productions/graphab/).

A landscape graph was generated for each virtual species for 1982 and another for 2012. The nodes of these graphs were defined from the land-cover categories corresponding to the favorable habitat for each virtual species. The linkage thresholds were defined by the dispersal distance of each species, corresponding to the least-cost paths between habitat patches taking into account the values defined for resistance to movement. Dispersal distances expressed in metric units were converted into cost units by applying a linear equation to the links in which the logarithm of Euclidean distance was considered to be a linear function of the logarithm of their cost distance. A specific conversion was performed for each species but not for each date (see above).

Several connectivity metrics have been developed to quantify functional connectivity at different levels of the graph structure: global, by component, and local (Rayfield et al. 2011). In this study, the baseline global connectivity metric was the probability of connectivity index (*PC*) (Saura and Pascual-Hortal 2007):

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

where n is the total number of patches, a_i and a_j are the areas of patches i and j, $p*_{ij}$ is the maximum probability of potential paths between i and j, and A is the total surface area of the study area. p_{ij} was calculated with an exponential function such that:

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

where d_{ij} is the least-cost distance between i and j, and α expresses the intensity of decreasing probability of dispersion p resulting from the exponential function. The value of α was determined such that $p_{ij} = 0.05$ when d corresponds to the maximum dispersal distance (for amphibians and reptiles) and such that $p_{ij} = 0.5$ when d corresponds to the median dispersal distance (for birds and mammals).

The *PC* index is commonly used to compute the functional efficiency of an ecological network, particularly because it is based on a spatial interaction concept (product of the masses of the patches), incorporating both the quantity of habitat and the probability of dispersion (p_{ij}).

To quantify connectivity at the patch scale, we chose the local metric *PCflux* (Foltête et al. 2014), which is the local contribution of each patch to global connectivity. For a given patch *i*, *PCflux* (*i*) is given by:

$$PCflux_i = \frac{\sum_{j=1}^{n} a_i a_j p^*_{ij}}{A^2}$$

where n is the total number of patches, a_i and a_j are the areas of patches i and j, $p*_{ij}$ is the maximum probability of potential paths between i and j, and A is the total surface area of the study area.

Transition decomposition process

We defined a transition decomposition process to evaluate the influence of each LCC on connectivity for each virtual species. The first step was to identify all LCC polygons between 1982 and 2012 and to classify them by type (e.g. forest core to urban, grassland to cropland). In all 112 types of LCCs were identified. Then, each transition type was successively added to the land cover of 1982. The impact of a given transition k on each virtual species was assessed by computing the *PC* variation between 1982 and 2012 such that:

$$I_k = \frac{(PC_k - PC) \times 100}{PC}$$

where *PC* is the initial global connectivity level and PC_k is the global connectivity level taking into account the transition k.

A principal component analysis (PCA) was then performed on the table containing the impact of each of the 112 LCCs for the 16 virtual species. The species were the variables and the LCCs the individuals in this PCA. This analysis provided a synthetic view of the impacts and made it easier to identify relationships between the LCC types and the virtual species. All the impacts being in the same unit, we applied a raw PCA (i.e. based on the variance–covariance matrix) attributing more weight to the more influential LCC types.

Mapping the variation of landscape connectivity

The ecological impact of LCC was assessed from the 16 landscape graphs, one for each virtual species. Since each graph involved a specific definition of patches and links, the local connectivity values could not be combined directly to make a multi-species synthesis. For example, a forest core species and an aquatic species would not have the same habitat patches (and so not the same nodes in the graph) nor the same links. Consequently, we had to shift from a discrete to a continuous representation of the impact in space. This was done by a spatial generalization of the local connectivity values computed for each patch ("Spatial generalization of the local connectivity values" section). Such processing allowed us to define a multi-species connectivity potential suitable for a diachronic analysis ("Spatial variation of landscape connectivity" section).

Spatial generalization of the local connectivity values

This spatial generalization was based on the method proposed by Foltête et al. (2012b) consisting in integrating connectivity criteria into species distribution models by assigning patch-based connectivity metrics to points of species presence located outside these patches. In our case and for a given virtual species, the patch-level connectivity values (*PCflux)* were used to evaluate the potential accessibility of any point (i.e. pixel) to the overall study area. This extrapolation relies on the assumption that individuals may be found outside habitat patches although with a lower probability than of their being found within habitat patches (Hirzel and Le Lay 2008). On this assumption, (1) a given point located outside patches was considered as potentially connected to the habitat network by inheriting the connectivity levels from the surrounding patches and (2) the influence of a patch towards a point should decrease with distance, so that the farther the point from the ecological network, the lower its potential connectivity. The weighting function designed to represent this distance effect was the same as was used to compute the *PC* index, i.e. the negative exponential function such that $w = e^{-\alpha d}$, where w is the weight of a patch with respect to a point located at a least-cost distance d. For a given point, connectivity levels from several patches were attributed by summing the weighted values of *PCflux* as follows, by taking into account least-cost distances:

$$gPCflux(i)_i = \sum_{j=1}^{n} PC_{flux}(j) * w_{ij}$$

where $gPCflux(i)$ is the generalized value of *PCflux* for the point i, and w_{ij} is the weighting of the patch j for the point i.

As a result, we obtained for each virtual species a 5-m spatial resolution map at *t* and *t + 1* on which each pixel took on a value corresponding to its potential of connectivity to the overall network.

Spatial variation of landscape connectivity

The maps of single-species connectivity can be overlaid to spatialize multi-species connectivity (Cushman et al. 2013). First, we normalized single-species potential connectivity maps $P_{l,t}$ to make them comparable by calculating the standardized map $P'_{l,t}$, where $\overline{P_{l,0}}$ is the mean and $\sigma(P_{l,0})$ is the standard deviation of all the raw values of $P_{l,0}$ for species *l* at the intial date as:

$$P'_{l,t} = \frac{P_{l,t} - \overline{P_{l,0}}}{\sigma(P_{l,0})}$$

Then, we combined the 16 single-species maps by averaging connectivity values for all points of the study area at the initial date *t* to obtain a multi-species connectivity potential at *t*, as:

$$P_t = \frac{1}{n}\sum_{l=1}^{n} P'_{l,t}$$

The same process was applied to the subsequent date to obtain a multi-species connectivity potential P_{t+1}. So as not to eliminate the effect of change over time in the normalization process, the conversion procedure from metric dispersal distances to cost-distances for $t + 1$ had to be identical to that used for the initial date, as did values of $\overline{P_{l,0}}$ and $\sigma(P_{l,0})$ of the standardization. The conversion values at $t + 1$ were therefore those used at *t*. This dispensed with, for example, minimizing the effect of a landscape matrix that had become more constraining for the movements of individuals. The local variation of the ecological potential *P* was then computed as the rate of change of all cell values between *t* and $t + 1$:

$$\Delta P = \frac{P_{t+1} - P_t}{P_t}$$

with P_t the connectivity map for all virtual species *l*.

Results

Multivariate analysis of LCC impacts on single-species connectivity

Table 2 sets out the descriptive statistics of the impact of LCCs on the ecological network of each virtual species. Extreme values range from −45.07% for

Table 2 Descriptive statistics of the PC variation (%) for each virtual species

Virtual species	Descriptive statistics of the *PC* variations after decomposed LCCs				Global *PC* variation after all LCCs
	Min	Max	SD	Sum	
Forest core amphibians	−16.87	37	5.156	−96.12	103.24
Open-area amphibians	−11.38	89.7	8.9	1853.28	167.39
Open-area reptiles	−45.07	83.92	9.63	−79.92	25.08
(Semi-)aquatic area reptiles	−7.73	31.09	3.21	616.68	38.32
Forest core mammals with high dispersion capacities	−21.13	4.74	2.2	−17.28	−40.76
Forest core mammals with low dispersion capacities	−18.09	7.84	2.23	299.16	−62.55
Aquatic-area mammals	−11.93	28.1	3.39	48.6	0.69
Forest edge mammals	−35.19	116.14	12.1	250.56	−4.2
Open-area mammals	−28.16	130.86	15.19	519.48	47.99
Varied open-area birds with high dispersion capacities	−11.53	4.7	1.87	116.64	−20.95
Varied open-area birds with low dispersion capacities	−14.05	4.73	2.07	51.84	−26.92
Natural open-area birds with low dispersion capacities	−15.41	170.25	17.04	2649.24	163.53
Forest core birds with high dispersion capacities	−17.7	5.86	1.88	−6.48	−17.05
Forest core birds with low dispersion capacities	−17.17	9.55	2.17	201.96	−26.03
Aquatic-area birds	−10.75	27.27	3.13	82.08	8.86
Forest edge birds	−22.26	60.2	6.97	183.6	−2.13

open-area reptiles to +170.25% for natural open-area birds with low dispersion capacities. In order to test for the existence of a relationship between the LCC surface areas and corresponding *PC* variations for the virtual species, we computed the Pearson's correlations between them. Only varied open-area birds with high dispersion capacities have a correlation coefficient up to 0.5. The LCC impacts taking all LCCs into account simultaneously range from −62.55% for forest-core mammals with low dispersion capacities to +167.39% for open-area amphibians. They are negative for varied open-area birds and for the species depending on forest-core or wooded habitats (apart from forest-core amphibians) and positive for the other species. It should be noted that these values do not systematically have the same sign as the sum of the *PC* variations computed from decomposed LCCs.

From the raw PCA performed on *PC* variations for each LCC and for virtual species, four factors are found to be significant, given the decline in the eigenvalues, with a cumulative variance of 94.9%. Table 3 shows the correlation coefficients between variables (virtual species) and these five factors. F1 refers to the forest-edge birds and mammals. F2 concerns open-area mammals and natural open-area birds whereas F3 refers to open-area reptiles and mammals. F4 refers to species living in aquatic habitats, i.e. amphibians, (semi-)aquatic reptiles, and aquatic-area mammals and birds.

Table 4 synthesizes the contributions of each LCC to factors, giving information about which of them most affect landscape connectivity for virtual species with similar ecological traits. The "forest cores to forest edges" and "croplands to herbaceous areas" LCCs contribute mainly to F1, with a positive effect on connectivity for forest-edge-area birds and mammals. Conversely, "forest edges to forest cores" and "forest edges to herbaceous areas" LCCs have a negative effect on the same virtual species. F2 is largely dominated by changes from croplands to herbaceous areas and grasslands, with a positive effect for open-area mammals and natural open-area birds. LCCs from forest cores to herbaceous areas also favor these species whereas changes from forest cores to forest edges have a negative effect on their connectivity. For F3, the LCCs contributing most are "croplands to grasslands", which favors open-area reptiles and mammals, and the reverse LCC ("sunniest grasslands to croplands") as well as changes from croplands to herbaceous areas, which adversely affect these species. Finally for F4, the biggest contribution is for the change from croplands to water bodies,

Table 3 Pearson's correlations between variables (virtual species) and factors. Given the decline in the eigenvalues, four factors were found to be significant for synthetizing the LCC impacts

Taxonomic groups	Virtual species	F1	F2	F3	F4
Amphibians	Forest core amphibians	0.016	0.033	−0.146	0.976*
	Open-area amphibians	0.078	0.18	−0.219	0.954*
Reptiles	Open-area reptiles	0.193	0.437	0.78*	0.1
	(Semi-)aquatic reptiles	0.016	0.032	−0.144	0.977*
Mammals	Forest core mammals with high dispersion capacities	−0.375	−0.133	0.198	0.069
	Forest core mammals with low dispersion capacities	0.059	−0.122	0.143	0.047
	Aquatic-area mammals	0.004	0.056	−0.157	0.981*
	Forest edge mammals	0.915*	−0.395	0.013	0.004
	Open-area mammals	0.243	0.539*	0.765*	0.084
Birds	Varied open-area birds wih high dispersion capacities	−0.109	−0.242	0.2	0.054
	Varied open-area birds wih low dispersion capacities	−0.118	−0.252	0.196	0.055
	Natural open-area birds	0.427	0.857*	−0.275	−0.082
	Forest core birds with high dispersion capacities	0.018	−0.336	0.206	0.056
	Forest core birds with low dispersion capacities	0.133	0.056	−0.078	−0.006
	Aquatic-area birds	0.07	−0.002	−0.136	0.974*
	Forest edge birds	0.947*	−0.303	0.002	−0.001

* Correlation coefficient > 0.5

Table 4 Factorial coordinates of individuals (LCC)

Transitions	F1	F2	F3	F4
Forest cores to forest edges	186.04***	−75.004*	0.185	−1.25
Forest cores to herbaceous-areas	24.885	58.199*	−29.639	−8.212
Forest edges to forest cores	−55.366*	15.189	2.287	−1.365
Forest edges to herbaceous-areas	−64.823*	40.944	−6.833	−3.63
Croplands to herbaceous-areas	75.093*	136.185**	−65.096*	−12.356
Croplands to grasslands	27.819	51.592*	33.47*	1.549
Croplands to water bodies	1.618	4.925	−15.507	92.135***
Croplands to sunniest grasslands	40.76	83.067*	99.536***	9.661
Water bodies to herbaceous-areas	−1.635	−3.107	6.27	−39.11*
Artificial areas to water bodies	0.453	2.124	−9.605	59.749*
Sunniest grasslands to croplands	−15.603	−32.352	−37.099*	−5.298

Contributions of transition types on selected factors* > 5%, ** > 25%, *** > 50%. Transition types for which all contributions for factors are less than 5% were excluded. Transitions are sorted by increasing surface area

which favors amphibians, (semi-)aquatic reptiles, and aquatic mammals and birds. Changes from artificialized areas to water bodies have the same effect whereas changes from water bodies to herbaceous areas have a negative effect on these species. So although certain specific changes such as "croplands to grasslands" invariably display a positive effect on landscape connectivity for the virtual species, other changes such as "forest cores to forest edges" have a contradictory effect.

Spatial variation of multi-species landscape connectivity

Figure 2 shows examples of connectivity potential for three virtual species at the initial state t and the final state $t + 1$. For open-area amphibians, the potential is distributed along the main river. The negative impact of the construction of transportation infrastructure is visible, as is the positive impact of the creation of water bodies to the northeast. For forest-core mammals with high dispersion capacities, the potential is distributed around the forest clusters. As with open-area amphibians, it too seems to be affected by transportation infrastructures, even if this impact is combined with other changes. The potential of varied open-area birds with high dispersion capacities is mainly distributed over agricultural areas for each date and declines in the center of the study area, where urbanization was most intensive between the two dates.

Figure 3 shows how the combination of the connectivity potential of the 16 virtual species is distributed in space at t and $t + 1$. High potential areas are located principally in the south, dominated by forests and less affected by anthropic developments such as transport infrastructures and artificialized areas. In the north, high values also outline the aquatic areas along the Marne River. Conversely, at each date, the lowest values are to be found mostly in the western part of the area, which is the most artificialized, and close to the high speed railway (HSR) and highways.

From this multi-species connectivity potential at times t and $t + 1$, the variation was calculated at a fine-scale, i.e. for each cell of the map (Fig. 4). The local spatial variation values range from −6.4% to +3% with a mean of −0.4% for the entire study area. Overall, the greatest connectivity losses concern (1) the large forest areas in the south of the study area, which was largely impacted by fragmentation, and (2) the northern area, which was isolated by the construction of major transportation infrastructures. Conversely, connectivity gains are visible in two main zones along the Marne River in the NE and West due to the creation of new water bodies.

Discussion

The graph-based approach was used to model the ecological networks of several species solely from information about their ecological requirements and from land-cover data. The need for so few input data facilitates the diachronic analysis of connectivity. However, it is necessary to obtain information about the dispersal capacities of species, which display significant variations, to model their ecological networks. The lack of such information presents a serious

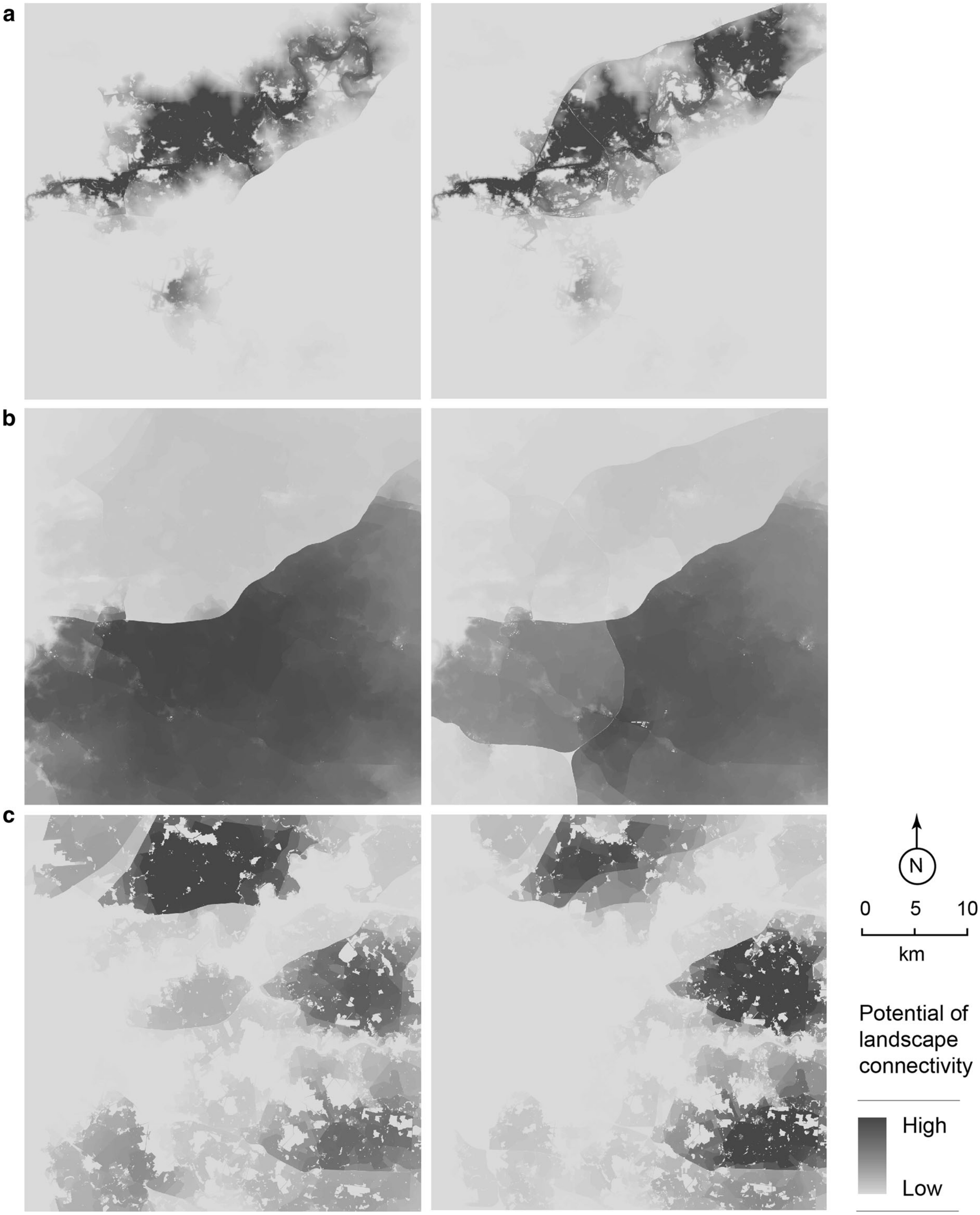

Fig. 2 Examples of connectivity potentials for three virtual species in 1982 (*right*) and 2012 (*left*): **a** for open-area amphibians, **b** for forest core mammals with high dispersion capacities, **c** for varied open-area birds with high dispersion capacities

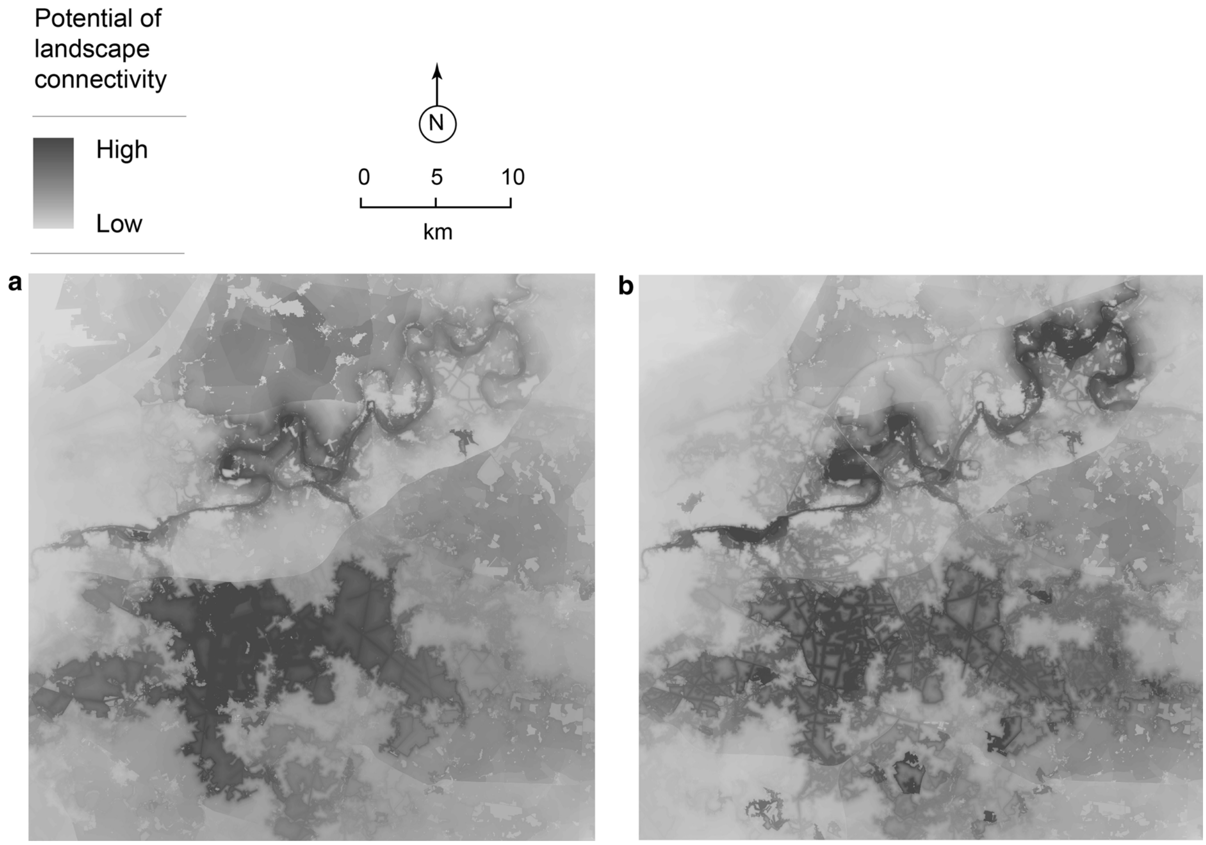

Fig. 3 Combined connectivity potentials of the 16 virtual species for 1982 (**a**) and 2012 (**b**)

difficulty for a multi-species approach. From a literature review and the allometric relationships proposed by Sutherland et al. (2000), we have been able to estimate these distances from specific functional traits (diet type and body mass). Although these allometric relationships are based on empirical studies and may include bias or uncertainties (Nathan 2001; Paradis et al. 2002), they remain relevant for a multi-species analysis and improve the protocol's reproducibility.

The methodology produces two types of results about the impacts of LCCs on connectivity, (1) a spatial assessment and (2) a multivariate statistical analysis.

First, the analysis provided a fine-scale spatial assessment of the impacts of LCCs on functional connectivity for multiple species. For this, it was necessary to map the potential of connectivity at each date. Our approach was based on a spatial generalization of a graph-based metric (*PCflux*) to evaluate the potential accessibility of any point of space (i.e. pixel) to the overall network for each virtual species. This is an effective way to predict the potential of connectivity across a vast study area and for a broad range of species with different dispersal capacities. Such multiple species mapping in a static dimension is similar to the methodological framework proposed by Cushman and Landguth (2012) including the use of resistant kernel connectivity modeling. However, our approach is more realistic in that the potential of connectivity of a point in space takes into account the connectivity at the level of the overall ecological network. It therefore offers the advantage of characterizing local impacts from land changes that have occurred elsewhere in the ecological network of species.

An important point is that the final result depends on how the single-species maps are combined. As the extrapolated patch-based metric takes into account the area of habitat patches, the standardization lends importance to the scarcity of the species habitat. We believe that this approach is consistent with an objective of conserving biodiversity. In order to test

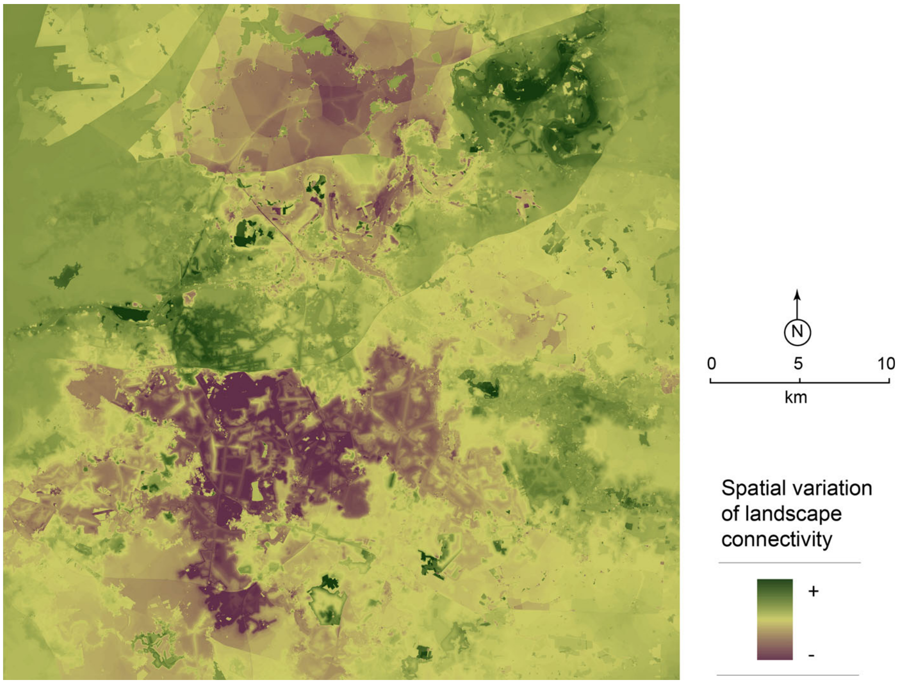

Fig. 4 Spatial variation of connectivity between 1982 and 2012. Areas in *green* have positive variations, areas in *purple* negative variations, and intermediate values are in *yellow*

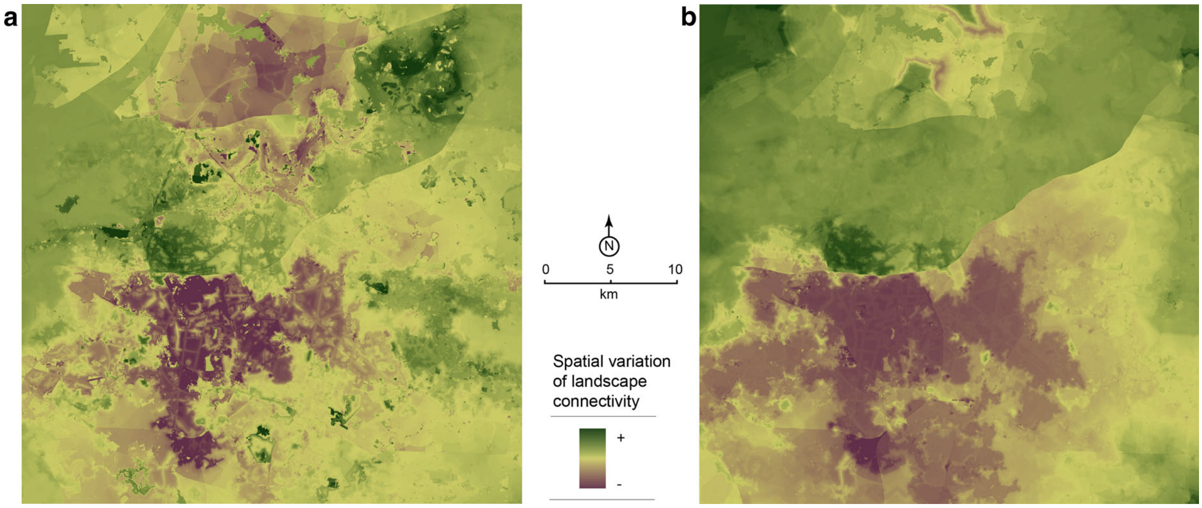

Fig. 5 Comparison of the spatial variation of connectivity based on two ways for combining single-species results. The connectivity potential values for the 16 virtual species have been standardized in the first map (**a**), and are raw values in the second map (**b**)

whether the standardization visually affects the results, we computed a spatial variation map by summing non-standardized single-species maps (Fig. 5). The result is slightly different but still contrasts a main area, which was impacted negatively, made up of forest clusters and the rest of the study area dominated by agricultural areas. In the south, the same area has been impacted negatively, but the non-standardized mapping exhibited a broader but more attenuated impact than the standardized mapping. The main difference between the two maps was the absence of the positive impact area along the main river, which corresponds to aquatic species whose habitat is smaller than for other species. The approach initially adopted seemed more relevant by revealing local impacts on all types of ecosystems (e.g. aquatic areas or forest edges) but the non-standardized mapping exhibits a broader but more attenuated impact compared to the standardized mapping. However, the proposed process could also easily integrate a weighting based on expert knowledge depending on the importance attributed to each species (Martin et al. 2012). The use of relative comparisons could also be a good way to give weight to species according to their importance compared to others, as proposed by Yager (1977) in a pairwise comparison method.

Secondly, the multivariate analysis of LCC impacts on global connectivity provided an overview of the most positive or negative impacts on each virtual species. For some species, we observe a change in the sign of the sum of the *PC* variations computed from decomposed LCCs and the global PC variation taking into account all the LCCs. This change in sign is mainly due to the fact that we are comparing LCC impacts that are considered artificially isolated and a more realistic global PC in which some LCC impacts can be offset by others. Globally, species are impacted to varying degrees by decomposed LCCs, with a variation in global connectivity ranging from −45.07 to +170.25%. These results confirm the initial hypothesis that LCCs could have contradictory effects on connectivity for different species. This is the case for example for the "forest cores to forest edges" transition, which is confirmed to have a positive impact on birds and mammals of forest edge areas and a negative impact on birds of natural open areas and mammals of open areas. Our method has the advantage of highlighting such contradictions. Moreover, a given change does not modify just the composition of the land-cover but also its configuration. The LCC effects on landscape connectivity may therefore differ depending on their form or spatial location. For example, the conversion of croplands to grasslands may have different impacts depending on whether this LCC is completely aggregated or scattered in space, or on whether it occurs in an environment dominated by grassland or dominated by cropland. Likewise, we identified a counterintuitive result, that of the negative influence of croplands becoming herbaceous areas for open-area reptiles and mammals. This result may be explained by the fact that many herbaceous areas have emerged with urbanization and are enclosed within urban areas. A desegregated LCC decomposition process based on each LCC polygon and not on LCC aggregated by types would improve this analysis. This would enable closer investigation of the causes of the PC variation both on the basis of the spatial effects related to the shape of these changes (surface area, configuration, etc.) and on their spatial context. For example, we should not treat the impact of all croplands becoming herbaceous spaces, but instead treat each of the corresponding entities independently. We assume here that the LCC from croplands to herbaceous areas may have a negative effect in some places and a positive effect in others.

Contrary to expectations, the effect of the development of artificialized areas and linear infrastructures on landscape connectivity is absent compared to other LCCs. Indeed, these infrastructures (roads or HSR) have mainly been designated as barriers to the movements of individuals (resistances often between 1000 and 10,000). This result can be explained by the very low spatial footprint of these LCCs in the decomposition process. When adjusting the *PC* index using a (mean or maximum) dispersal distance, we assume that the separating effect of transport infrastructures is lower than when using a larger distance for network traversability as for example in Saura et al. (2011) and Foltête et al. (2014). This contributes to assigning a heavy weight to the terms a_i and a_j in the computation of the *PC* index, and so to emphasizing the impacts due to the LCCs of larger areas. However, we observe that their fragmenting effect is clearly identified by the spatial variations in multi-species connectivity. However, by checking the results of the LCCs impacts by species, it is notable, for example, that varied open-area birds (not correlated to any PCA factors) were invariably negatively impacted (between −14 and −30%) by transitions from natural or agricultural areas to HSR and artificialized areas. In general, the transition decomposition process implemented, consisting in assessing the impact of each LCC individually, does not correspond to the real world where all changes occur simultaneously. Even so, it is one way to supplement the mapping of impacts and it provides clues as to what causes spatial variations in connectivity.

From our generic approach, we began with several assumptions, especially about the definition of cost values and habitat, which have to be considered when interpreting the results. For the cost values attributed to land-cover categories, we used a logarithmic scale ranging from 1 (very favorable) to 10,000 (barrier), which discriminates sufficiently among the elements of the landscape mosaic. Little information was available about the resistance of the landscape mosaic to the movement of selected species. Such modeling could be improved by using observational techniques or landscape genetic methods to validate such costs (Zeller et al. 2012). For habitat, we assumed that the species dispersed from patches under optimal conditions. Faced with the absence of ecological data about species presence or abundance within habitat patches, this assumption implies that patch area is the only quality criterion. To improve our approach, habitat quality could be defined by integrating environmental conditions favorable to species presence. Similarly, our land cover classification remained deliberately simplified to satisfy a generic approach but could be further refined, particularly by taking into account not only land cover but also land use. For example, certain types of croplands may not meet the requirements of species living in agricultural areas. However, as noted by Cushman and Landguth (2012), it is important to keep in mind that real species populations are often distributed idiosyncratically with regard to habitat quality, given historical population factors. To answer this question, we suggest that further research should integrate a species life-cycle based approach into ecological network modeling, as introduced by Zetterberg et al. (2010) in order to integrate the spatial and temporal scales of ecological processes into graph-based connectivity studies. Finally, a validation of our results by diachronic presence/absence and abundance data of species would be an interesting perspective.

Conclusion

In this paper, we have used a graph-based approach to explore the relationship between LCCs and landscape connectivity for a set of virtual species. Landscape graphs have already proven their usefulness for guiding decisions in conservation planning and landscape management (Galpern et al. 2011; Foltête et al. 2014). Specifically, our study provides a relevant example of how to spatialize and synthesize the impacts of LCCs on multi-species landscape connectivity. It provides an assessment of the more or less generalized impact of each transition. It could therefore inform and guide conservation actions and land-use strategies so as to enhance landscape connectivity for species of conservation concern, or maintain connectivity in a context of pressure from human activities.

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