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► To cite this version:

Simon Tarabon, Calvet Coralie, Vincent Delbar, Thierry Dutoit, Francis Isselin-Nondedeu. Integrating a landscape connectivity approach into mitigation hierarchy planning by anticipating urban dynamics. *Landscape and Urban Planning*, 2020, 202, pp.103871. 10.1016/j.landurbplan.2020.103871 . hal-02877287

HAL Id: hal-02877287

<https://hal.science/hal-02877287>

Submitted on 19 Nov 2020

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Integrating a landscape connectivity approach into mitigation hierarchy planning by anticipating urban dynamics

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ABSTRACT

Urbanization leads to land-use changes and landscape fragmentation, impacting natural habitats and their connectivity. In principle, many local decision-makers are obliged to adopt a mitigation hierarchy whereby development projects must be designed to avoid impacts on biodiversity, reduce, and ultimately compensate for the remaining impacts to reach the goal of *no net loss* (NNL) of biodiversity. In practice, however, both developers and regulators lack relevant practical tools to support their strategies to better anticipate and plan this mitigation hierarchy. More importantly, the available tools generally ignore connectivity issues and ecological constraints. Here, we propose an original methodology that anticipates future urban needs under different development scenarios and selects the most relevant strategies for biodiversity offsets (BO). We used a spatialized digital simulator (called *SimUrba*) to model fine-scale urban dynamics, combining it with ecological networks modelling based on graph theory to assess the environmental impacts of urbanization on a habitat connectivity index for focal species. We test the different outcomes produced by adopting two offset ratios (1:1 and 2:1) using this approach. The methodology is applied to empirical data on the future urban sprawl of a large French city up to 2040 under two realistic development scenarios currently discussed by policy-makers, and on 20 species that we grouped by type of habitat. Our results reveal that the most highly impacted species are those associated with open and semi-open areas, and cultivated plots. Then, we identify the most promising cells for BO implementation to compensate for negative effects on habitat area, according to gains in habitat connectivity. We further show that using both private and public land can maximize habitat connectivity by including larger plots and reducing the number of plots needing long-term monitoring. Finally, we demonstrate that using standard offset ratios that ignore connectivity issues is very risky and can compromise any BO objective. Overall, we show that this framework provides decision-makers with a valuable and precise strategic tool that articulates land-use planning with ecological constraints to identify whether, how and where NNL objectives can be achieved.

1. Introduction

In developed countries, fragmentation and habitat loss, mainly due to urban growth, are major causes of biodiversity decline (Maxwell, Fuller, Brooks, & Watson, 2016). Urban sprawl and the resulting artificialization of semi-natural areas affect landscape connectivity and biodiversity conservation (Haverland & Veech, 2017). Landscape connectivity means “the degree to which the landscape facilitates or impedes species movement among resource patches” (Taylor, Fahrig, Henein, & Merriam, 1993). It depends on the quantity and spatial arrangement of the landscape, including the landscape matrix, core habitat areas (i.e. where individuals perform their life cycle functions like feeding, breeding or daily dispersing), the corridors between habitat patches, as well as the species’ dispersal ability (Forman, 1995; Saura, Bodin, & Fortin, 2014). Recent studies have highlighted the need to conserve ecological networks at a large scale, because their integrity

allows individuals to move and exchange genes, thereby ensuring populations’ survival (Boitani, Falcucci, Maiorano, & Rondinini, 2007; Kiesecker, Copeland, Pocewicz, & McKenney, 2010).

To date, few effective tools have been developed to properly assess landscape connectivity (Kool, Moilanen, & Treml, 2013). Among the most common models are cost-distance analysis (Adriaensen et al., 2003), circuit theory (McRae, 2006; McRae, Dickson, Keitt, & Shah, 2008), stochastic simulation models (Allen, Parrott, & Kyle, 2016; Tracey, 2006) and graph-theory-based models (Minor & Urban, 2008; Urban, Minor, Treml, & Schick, 2009). Graph theory is a relevant mathematical framework for the analysis of functional connectivity and for ecological conservation issues (Correa Ayram, Mendoza, Etter, & Salicrup, 2016; Foltête, 2019) requiring connectivity metrics (Rayfield, Fortin, & Fall, 2011; Saura & Rubio, 2010). Landscape graphs are simplified representations of ecological networks where habitat patches appear as nodes. The potential movements of individuals or fluxes

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between patches appear as links that connect pairs of nodes (Urban et al., 2009). They have recently grown in popularity as a way to easily identify ecological networks (see for instance Clauzel & Bonneville, 2019; Mechai et al., 2018; Niculae, Nita, Vanau, & Patroescu, 2016), to assess the effects of fragmentation and loss of landscape connectivity (Clauzel, 2017; Liu, Peng, Zhang, & Zhao, 2016; Tournant, Afonso, Roué, Giraudoux, & Foltête, 2013), and to wholly or partially implement the mitigation hierarchy (for instance Bergès et al., 2020; Clauzel, Bannwarth, & Foltête, 2015; Tarabon, Bergès, Dutoit, & Isselin-Nondedeu, 2019a, b). Moreover, graph-theory-based models can be combined with species distribution models (SDMs) to identify habitat patches (see Tarabon et al., 2019a). SDMs relate species distribution records to environmental data and can be used to produce maps of habitat suitability (Elith et al., 2006). Nevertheless, SDMs require large-scale databases of species occurrences, making this type of modeling challenging (Bigard, Thiriet, Pioch, & Thompson, 2020).

In response to biodiversity losses mainly caused by urban development (Haddad et al., 2015), national regulations in many countries require developers to implement a three-step mitigation hierarchy aimed at first avoiding, and failing this, reducing impacts on biodiversity and then compensating for them (Maron et al., 2018). The mitigation hierarchy has been part of environmental policies since the 1970s in many countries, but only applied since the 2000s following recent regulatory developments. It aims to reach the goal of *no net loss* (NNL) or *net gain* of biodiversity (Gibbons & Lindenmayer, 2007; Maron et al., 2016). In the last compensation step, developers have to implement biodiversity offsets (BO) providing ecological gains elsewhere through restoration or habitat creation actions on public or private land, in a quantity at least equal to what was impacted. Depending on the environmental policy, they generally have to comply with offset ratios (between the amount of area negatively impacted and the compensation area) to reduce the effects of delays and uncertainties (Bull, Hardy, Moilanen, & Gordon, 2015; Moilanen & Kotiaho, 2018). However, neither France nor Europe imposes any standard equivalence assessment method (EAM) of calculating the offset ratios, which can lead to extensive requirements for land (Bezombes, Gaucherand, Kerbiriou, Reinert, & Spiegelberger, 2017). In other countries, such as in the United States, there is a standard calculation method such as Florida's Uniform Mitigation Assessment Method (UMAM) (Reiss & Hernandez, 2018). Yet there is a lack of clear guidelines and methods that could help developers and regulators properly anticipate and assess the actual impacts of development on biodiversity, and the relevance of the proposed BO (Gardner et al., 2013; Maron, Dunn, McAlpine, & Apan, 2010a; Moreno-Mateos, Maris, Béchet, & Curran, 2015; Thorn, Hobbs, & Valentine, 2018).

In addition, despite recent European regulatory requirements (e.g. the Green Infrastructure Strategy in Europe, the green and blue corridors recommended by the “*Grenelle de l'Environnement*” in France), little attention is paid to the territorial organization of BO. Anticipating, organizing and pooling offsets are key to reaping BO benefits (Bigard et al., 2020), particularly in territories where the pressure of urbanization is relatively strong and where the landscape suffers from fragmentation (Haverland & Veech, 2017). The mitigation hierarchy is also only applied to certain components of biodiversity, when it should apply to the whole range (Bezombes, Gaucherand, Spiegelberger, Gouraud, & Kerbiriou, 2018; Carreras Gamarra, Lassoie, & Milder, 2018). For example, landscape connectivity is not a primary criterion within the mitigation hierarchy, nor for land-use and urban planning, as pointed out by different authors (Bergsten & Zetterberg, 2013; Bigard, Pioch, & Thompson, 2017; Kujala, Whitehead, Morris, & Wintle, 2015). In practice, BO implementation has so far taken little account of issues related to the spatial configuration of ecosystems in the landscape. Yet this should be a major component of BO, since connectivity appears to be a key factor in BO successes (May, Hobbs, & Valentine, 2017; Scolozzi & Geneletti, 2012; van Teeffelen et al., 2014). Adopting a landscape approach also appears essential to implement the three steps of the mitigation hierarchy; this should be based on scientific

methodology and tools that can properly anticipate future negative impacts of urban development and to implement their avoidance (Bigard et al., 2020). Although a growing literature addresses BO from an ecological perspective (Calvet, Ollivier, & Napoleone, 2015), as well as the use of spatial tools in conservation planning (Almenar et al., 2019), no work so far has linked these two issues.

We propose to fill this gap by addressing the following question: how can we better anticipate and plan mitigation hierarchy implementation at territorial scales in relation to future urban development? We developed a methodological framework to implement mitigation hierarchy planning within a landscape connectivity approach. We considered both ecological connectivity and urban dynamics, seeking to (1) minimize the ecological impacts of land development, and (2) enhance the application of the mitigation hierarchy.

We first simulated future urbanization needs under two different development scenarios using a bespoke urban model called *SimUrba* developed by Calvet et al. (2020) and described here. We then assessed their impact on ecological networks using the spatial ecology tool *Graphab* (Foltête, Clauzel, & Vuidel, 2012). Then, we implemented the mitigation hierarchy, first by avoiding ecological impacts from urbanization and, when necessary, by identifying the most appropriate locations for BO (corresponding to new habitat patches) from two different sets of potential sites (public and private land) and using two different offset ratios (2:1 and 1:1).

We empirically tested this approach with a case study located in the French Occitanie region: the Toulouse conurbation, closely concerned by these planning issues. Indeed, its territorial cohesion program (SCoT) is currently undergoing revision aimed at reconciling spatially balanced economic growth with environmental objectives, especially under recent French regulatory changes (e.g. Council Directive 85/337/EEC, Directive 2014/52/EU, French laws n°2015-991 and n°2016-1087; Wende, Bezombes, & Reinert, 2018). In this context, local authorities have been given greater responsibility for urban and environmental planning.

This paper is organized in three sections. First, we present the overall methodological approach. Then we apply it to the Toulouse conurbation case study. Lastly, we conclude on the lessons learned in the context of BO, offering further research and policy recommendations.

2. Methods

2.1. The overall methodological approach

We propose a four-step method aimed at: 1) mapping the ecological value of a study area and its ecological networks based on several representative species and a global connectivity index (Equivalent Connectivity; Saura, Estreguil, Mouton, & Rodríguez-Freire, 2011), 2) simulating future urban sprawl according to two development scenarios (a past-trend scenario and an urban sprawl reduction scenario called “factor 4”), 3) assessing the ecological impacts of these two scenarios, and 4) implementing the mitigation hierarchy including appropriate and ecologically relevant biodiversity offsets based on landscape networks. Fig. 1 summarizes this overall approach.

2.2. Study area

We selected a study area where our approach could be tested as part of the review process for a land-use planning scheme (SCoT), and for which data was accessible: the Toulouse conurbation, in the Occitanie region of Southern France, (Fig. 2a). The Toulouse conurbation's SCoT covers an area of 1,181 km² and encompasses 964,000 inhabitants spread over 114 municipalities and 5 municipal communities. The Metropolis of Toulouse is very attractive, and the SCoT predicts 250,000 to 300,000 additional inhabitants and 140,000 new jobs by 2030. Nearly 10,000 additional inhabitants yearly should settle in the

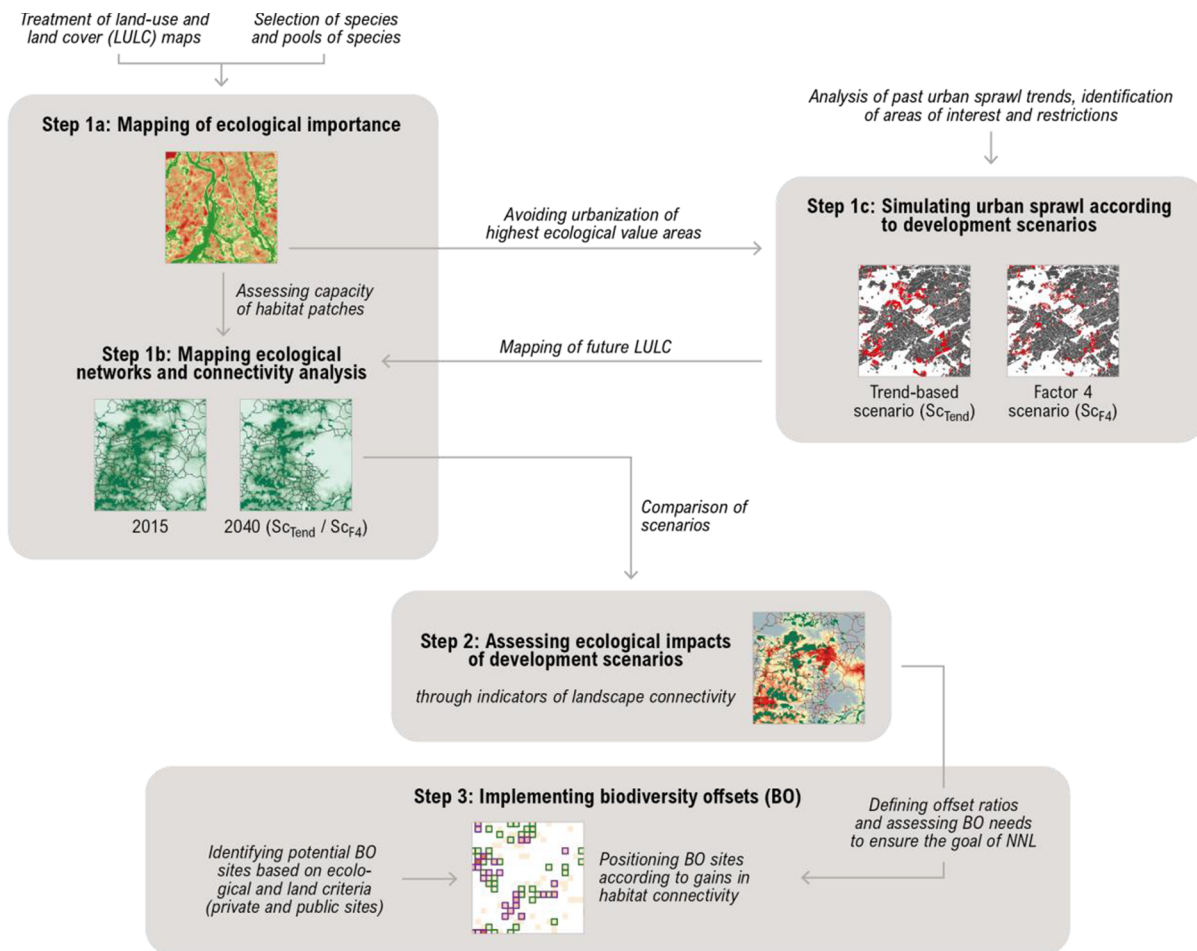


Fig. 1. Summary of the overall method proposed. The first steps of the mitigation hierarchy are applied from 1c by avoiding urbanization of areas of highest ecological value, before implementing BO if necessary (step 3). Note that steps 1a, 1b and 1c are concurrent, numbering of the steps is not chronological.

suburban area and along the main lines of transportation. Therefore, meeting current needs and those of future generations requires real control of space consumption. Given the diversity and spatial proximity

of land uses, and the high stakes regarding biodiversity conservation and the maintenance of a still-thriving agriculture, this is a particularly great challenge. To avoid the edge effect in urban and connectivity

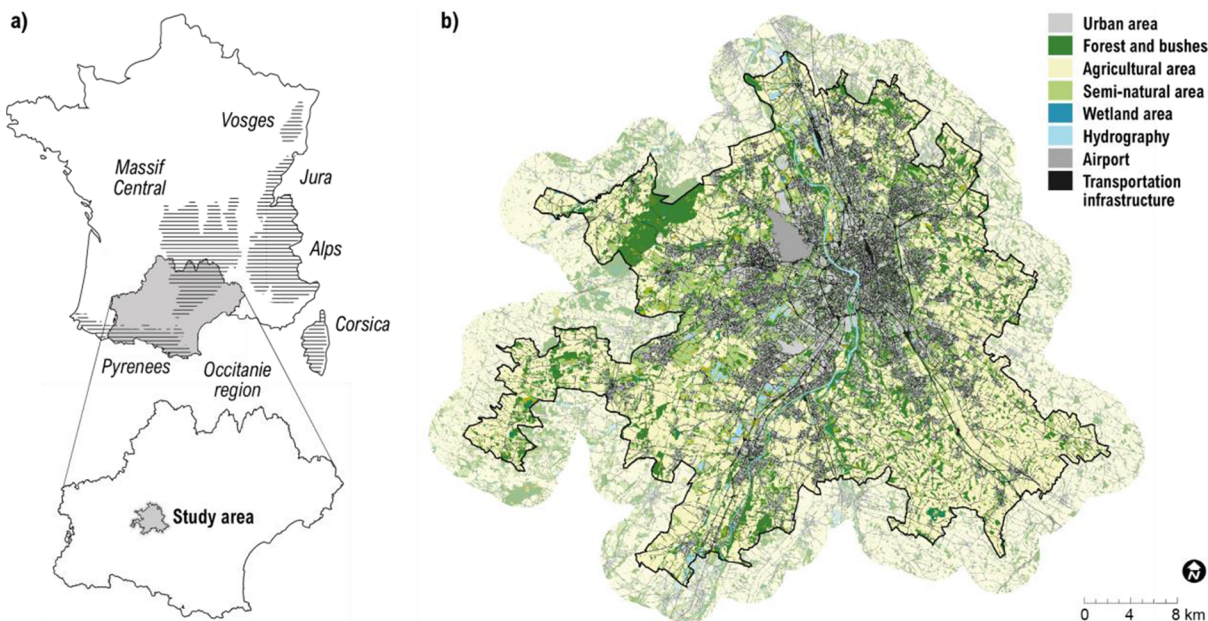


Fig. 2. Location (a) and land-use map (b) of the study area of Toulouse conurbation.

analysis, we applied a buffer zone of 5 km around the administrative boundary of the Toulouse conurbation (Fig. 2b). We defined this distance according to the availability of land-use and environmental geo-data, the computation times of models, and the dispersal distance of the focal species.

2.3. Species data

Landscape graphs are intended for modeling the ecological networks of single species by focusing on well-identified habitat. However, the development of efficient mitigation hierarchy strategies requires measures of benefit to overall biodiversity, including both rare and more common species with various habitat preferences. Thus, a large set of representative species needed to be used to model ecological networks and cover all the issues related to offsetting in this study area with multispecific conservation goals (Sahraoui, Foltête, & Clauzel, 2017).

We selected species of conservation interest in the context of the mitigation hierarchy for the Toulouse region, identifying 20 species, 16 vertebrate and 4 invertebrate, particularly affected by development projects there (Biotope, 2018). Of these, 15 are protected under the EU Habitats and Birds Directives, and 14 are included in the French list for national consistency of the green and blue corridor (*cohérence nationale de la Trame Verte et Bleue*) defined by the French National Museum of Natural History (Sordello, Conruyt-Rogeeon, Merlet, Houard, & Touroult, 2013). Two of these species, the roe deer and fire salamander, are not protected outside France but are highly affected by human activities and road development (Jiang, Ma, Zhang, & Stott, 2009; Vincenz & Reyer, 2005).

Based on their habitat preferences, we then grouped them under 5 types of area: open and semi-open, cultivated, forest, watercourses and ponds (Table 1). See Appendix 1 for more details on the species' habitat preferences and dispersal capacities.

2.4. Mapping of ecological value of landscape and ecological networks

The first step in implementing a planned and strategic mitigation hierarchy is to identify areas with high ecological value. Habitat quality will be used to assess the capacity of habitat patches other than surface area (see below in this Section), and then to begin the mitigation hierarchy process by avoiding urbanization of those areas of highest

ecological value (see Section 2.7).

Here, we mapped the ecological value of landscape based on landscape ecology indicators, as proposed by Bigard et al. (2020). We selected eight relevant indicators in the landscape ecology framework related to landscape structure, nature of land cover and use, and species occurrence. Indeed, the ecological value of landscape relies not only on LULC characteristics (including different biodiversity indicators such as type of LULC, form, inventory and protection areas, and ecological functionality level) but also on the composition and configuration of the landscape (such as density, rarity or shape of habitats) (see Table 2 and related literature). We produced a map of landscape ecological values that is not species-specific, although we are aware that the set of indicators is not always appropriate for all species. However, various considerations make this approach relevant. First, the values of the different indicators are weighted together (see below) and the average value within a habitat patch then enables the area of this patch to be weighted. Thus, if nuances according to species appear for some indicators, they will have very little impact on the analysis of connectivity and the calculation of the global connectivity index. Moreover, this approach is more easily reproducible for stakeholders than species-by-species mapping, which is tedious. In addition, weighting the surface area of habitat patches with the average value of overall ecological importance within them renders connectivity analyses more likely to be performed.

Data used to map the ecological value of landscape are presented in Table 3. As the initial typology included many different land covers, we classified them into 23 land cover categories to model ecological networks (see Appendix 2 for details).

We used *Land Facet Corridor Designer* (Beier & Brost, 2010) to calculate the Local Shannon Index (Shannon, 1948), and the *SDMtoolbox* (Brown, Bennett, & French, 2017) for species richness. The Fractal Dimension Index (FRAC; Eq. (1)) for a landscape element i (according to LULC) is given by the following formula (Crossman, Bryan, Ostendorf, & Collins, 2007):

$$FRAC = \frac{2 \ln(0.25 \times p_i)}{\ln a_i} \quad (1)$$

where a_i is the area and p_i the perimeter of the landscape element.

We first tested collinearity and estimated the effect of multicollinearity among variables with the variance inflation factor (VIF), taking a stepwise approach where a VIF is calculated with the *usdm*

Table 1

List of targeted species used in the study. Some are included in the French list for national consistency of the green and blue corridor (*cohérence nationale de la Trame Verte et Bleue*: TVB) and/or protected under the EU Habitats and Birds Directives.

Habitat group	Taxonomic group	Species		TVB	European protection
		Scientific name	Vernacular name		
Open and semi-open areas	Bird	<i>Cisticola juncidis</i>	Zitting cisticola	×	×
	Reptile	<i>Lacerta bilineata</i>	Western green lizard	×	×
	Butterfly	<i>Phengaris arion</i>	Large blue	×	×
	Orthopteran	<i>Stethophyma grossum</i>	Large marsh grasshopper	×	×
	Mammal	<i>Oryctolagus cuniculus</i>	European rabbit	×	
Cultivated areas	Bird	<i>Burhinus oedicnemus</i>	Stone-curlew		×
		<i>Emberiza calandra</i>	Corn bunting		×
	Amphibian	<i>Epidalea calamita</i>	Natterjack	×	×
Forest areas	Bird	<i>Muscicapa striata</i>	Spotted flycatcher	×	×
	Mammal	<i>Sciurus vulgaris</i>	Red squirrel		×
		<i>Capreolus capreolus</i>	Roe deer		
	Chiropteran	<i>Nyctalus leisleri</i>	Lesser noctule	×	×
	Amphibian	<i>Salamandra salamandra</i>	Fire salamander		
Watercourses	Coleopteran	<i>Cerambyx cerdo</i>	Great Capricorn beetle		×
		Bird	<i>Alcedo atthis</i>	European kingfisher	×
	Mammal	<i>Lutra lutra</i>	European otter	×	×
	Reptile	<i>Natrix natrix</i>	Grass Snake	×	
	Dragonfly	<i>Coenagrion mercuriale</i>	Southern damselfly	×	×
Ponds	Amphibian	<i>Pelodytes punctatus</i>	Parsley frog	×	
		<i>Triturus marmoratus</i>	Marbled newt	×	×

Table 2

Indicators related to landscape structure, land-use and land-cover (LULC), land form and species occurrence selected and used to assess the ecological value of each cell at 20-m resolution.

Indicators	Justification	Categories	Value
LULC rarity	A rare environment considered important and requiring special attention (CRENAM, 2011). We considered the proportion of each land cover (except urban areas) relative to the total area of natural and semi-natural areas.	High: < 1%	1
		Medium: 1–5%	0.6
		Low: > 5%	0.3
LULC diversity	A high diversity or local richness of habitats considered beneficial for biodiversity. Particularly favorable habitats are homogeneous in size (CRENAM, 2011; McGarigal & Cushman, 2005). The richness and homogeneity of areas are summarized by the Local Shannon Index (Shannon, 1948).	Not affected: water bodies and courses	0
		High to low	0 to 1
Biodiversity potential	Different LULC offer differing potential for the development or maintenance of biodiversity (Kujala et al., 2015; Letourneau & Thompson, 2014). We ranked all types of land cover based on scoring by experts according to their biodiversity potential.	High: natural grasslands, broad-leaved and mixed forests, trees outside forests, moors and heathlands, wetland areas	1
		Medium to high: coniferous forests, temporary pastures, hedges and bushes	0.75
		Medium: tree plantations, urban parks	0.50
		Low: crop areas, other agricultural areas, water bodies, watercourses	0.25
Wetland area	Wetland areas offer high levels of biodiversity (Kujala et al., 2015).	Very low: artificial areas	0
		High: identified wetland area	1
		Medium: potential wetland area (buffer zone of 50 m on each side of watercourses and water bodies)	0.50
Inventory and protection areas	The ecological value of natural environments is reflected in protection, inventory and management measures (Gray et al., 2016; Le Saout et al., 2013).	Very low: no wetland area	0
		Major contribution: ZNIEFF I, APPB, sites d'intérêt communautaire, zones de protection spéciale Natura 2000	1
		Major contribution: ZNIEFF II	0.75
		Significant contribution: sites classés, sites inscrits, ZICO	0.50
Ecological functionality level	Biological corridors play an important role in the preservation of biodiversity (Hüse, Szabó, Deák, & Tóthmérész, 2016). This study used corridors identified in the territorial cohesion program.	Others	0
		Major ecological corridors	0.5
		Secondary ecological corridors	0.25
Form complexity	Ecotones are also very important in biological processes. We used the Fractal Dimension Index (FRAC) as a measure of complexity derived from the perimeter/area ratio (Crossman et al., 2007).	Low to very low	0
		High to low	1 to 0
Species richness	Species richness is an indicator of the number of species recorded in a cell (Gotelli & Colwell, 2011).	High to low	1 to 0

package for each variable and the variable is selected if values are below the threshold ($VIF < 10$; Naimi, Hamm, Groen, Skidmore, & Toxopeus, 2014).

Then, we produced a 20-m resolution raster map by combining variables. The value of each cell is the average of each indicator value using a uniform weighting.

Next, we used *Graphab* (version 2.4; Foltête et al., 2012; see <http://thema.univ-fcomte.fr/productions/graphab/>) to model the ecological networks and conduct the connectivity analysis from landscape graphs and an associated connectivity metric, the Equivalent Connectivity (*EC*) index proposed by Saura et al. (2011).

We prepared a 20 m-resolution raster map by combining different vector data. Areas showing transport infrastructure (roads, railways and associated land) were dilated by 10 m to avoid any breaks due to the rasterizing of the initial vector data. We based the analysis on several vertebrate and invertebrate species from the study area (see Section 2.3). The nodes of landscape graphs were defined according to the land-cover categories favored as habitat by each species. These were derived from the biological literature, as were the minimum areas of nodes (Appendix 2). Species distribution models (SDMs) could not be used here due to a lack of species occurrence data at the scale of the study area. Then, the different land-cover categories defined during data compilation were assigned to six resistance classes based on the species' ability to move within them: highly suitable, suitable, neutral, unfavorable, highly unfavorable or barrier to animal movement (Mimet, Clauzel, & Foltête, 2016).

Habitat connectivity was assessed from the Equivalent Connectivity index (*EC*; Saura et al., 2011), an ecologically relevant metric appropriate to this mitigation hierarchy context. Indeed, the *EC* index uses the concept of 'amount of reachable habitat' for a species at the landscape scale (Saura et al., 2011; Saura & Rubio, 2010). The index is

derived from the Probability of Connectivity index (*PC*; Saura & Pascual-Hortal, 2007), defined as "the probability that two animals randomly placed within the landscape move to habitat areas that are reachable from each other." Thus, the *EC* index fulfils all the requirements of a connectivity metric, meeting conservation objectives linked to habitat loss and landscape fragmentation (Bergès et al., 2020). *EC* is a combined measure of habitat amount and habitat connectivity, and the index is based on node attributes (here, on quality-weighted habitat area) and link attributes transformed into probability of dispersal p_{ij} between nodes i and j . p_{ij} values are calculated with a decreasing exponential function of the distance d_{ij} between patch i and j , taking into account the dispersal capacity of the focal species (Eq. (2)):

$$p_{ij} = e^{-\alpha d_{ij}} \quad (2)$$

where α is a cost distance-decay coefficient: α is usually set so that $p_{ij} = 0.5$ when d is the median dispersal distance, or $p_{ij} = 0.05$ when d is the maximum dispersal distance (Saura & Pascual-Hortal, 2007).

Here, we took into account a cumulative dispersal distance (cost distance) at the metapopulation level. These metapopulation dynamics are key factors in population viability (Saunders, Hobbs, & Margules, 1991). Dispersal distances were extracted from existing literature reviews; however, no literature review gave maximum dispersal distances for birds. Therefore, we used an allometric relationship from Sutherland, Harestad, Price, and Lertzman (2000), as proposed in Sahraoui et al. (2017), which links diet types and species body mass, as well as dispersal capacity, given by the following formula: $13.1 \times M^{0.63}$. Bird body size (M , in kg) was extracted from the data set of Lislevand, Figuerola, and Székely (2007) containing 3,769 bird species. Then, dispersal distance values in metric units ($Dist_M$) were converted into cost units ($Dist$) using a linear regression between link topological distance and link cost distance for all the links of the graph, as given in

Table 3
Sources of data used to map the ecological value of landscape and to simulate ecological networks and urban dynamics.

Step	Detail	Data	Period	Source	Description
Ecological value and habitat connectivity mapping	Preparation of the land-cover map	BD TOPO®	2015	The French National Geographical Institute (IGN)	Hedges and bushes
		European Urban Atlas		The European Environment Agency	Urbanized areas
	Calculation of species richness	BD FORET®	2015	The French National Geographical Institute (IGN)	Forest types
		Agricultural areas	2016	The French Record of Agricultural Plots (RPG)	Grasslands and other agricultural areas
		Wetland inventory	2017	The <i>Conseil Général de la Haute-Garonne</i>	Wetlands
Simulation of urbanization process	Measuring demography	Occurrences of species	2005–2015	The French SINP (<i>Système d'Information sur la Nature et les Paysages</i>) of the National Institute of Natural Heritage (INPN)	Recorded species occurrences
		Sub-communal base IRIS (<i>Ilots Regroupés pour l'Information Statistique</i>)	2009–2015	The French <i>Institut national de la statistique et des études économiques</i> (INSEE)	Housing and demographical census
	Measuring artificialization	BDALTI® 5m	2009–2016	The French National Geographical Institute (IGN)	National topographical database
		–MAJIC (<i>Mise À Jour des Informations Cadastreles</i>)	2015	The French National Geographical Institute (IGN)	Digital Elevation Model
		Local Urban Plan	2017	The French <i>Direction générale des Finances Publiques</i> (DGFIP)	Land register and associated housing data
Hierarchization of biodiversity offsetting targets	Fitting to local planning	Local Urban Plan	2017	Metropolis of Toulouse	Local urban planning scheme
		Measuring land-cover change	2017	The French <i>Centre d'Études Spatiales de la Biosphère</i> (CESBIO)	Land cover from Sentinel 2 satellite data
	Preserving important ecological areas	Ecological value of landscape	2017	See Section 2.4 of the paper	Computed ecological values
		Building restrictions	2018	The National Institute of Natural Heritage (INPN)	Heavily protected natural areas
	Locating shops and services	Existing biodiversity offsets	2018	The French <i>Ministère de la Transition Écologique et Solidaire</i>	Biodiversity offset areas
		SIRENE database	2018	The French <i>Institut national de la statistique et des études économiques</i> (INSEE)	All public or private establishments
	Locating public transport	OSM Public Transport	2018	OpenStreetMap Contributors	Bus stops, missing from BDTOPO® database
		Building restrictions	2018	<i>Direction Départementale des Territoires</i> (31)	Flood-risk areas, a main component of the French <i>plan de prévention du risque inondation</i> (PPRI)
		Identifying plots for compensation	2018	SAFER (<i>Société d'aménagement foncier et d'établissement rural</i>)	Regulatory pressures linked to agricultural activities
		MAJIC (<i>Mise À Jour des Informations Cadastreles</i>)		2017	The French <i>Direction Générale des Finances Publiques</i>

the following formula (Eq. (3)):

$$Dist = e^{\text{intercept} + \text{slope}(Dist_M)} \quad (3)$$

See Appendix 3 for further details on data used and calculations of EC index.

2.5. Simulation of dynamics with SimUrba

We used an *ad hoc* model, *SimUrba*, developed by Calvet et al. (2020) and presented here, which simulates urban dynamics based on the consumption of space related to future needs (including housing, commercial and industrial areas, roads and parking) per inhabitant under different development scenarios. *SimUrba* is an open source model available at: <https://gitlab.com/vidlb/simurbapy>. Data used in this section are presented in Table 3.

The simulation approach of *SimUrba* combines a cellular automaton and a geographic information system. The literature contains other models that model urban systems (e.g. Mup-City, UrbanSim, SLEUTH as well as GeOpenSim, etc.). These were used as a starting point, but we decided to create our own model to better respond to our research problem and available data (more detail in Appendix 4). Our model differs in the way we estimate housing needs from census data, so we can also focus our analysis of the results on comparing scenarios with different degrees of urban sprawl. We also added fine building data, to estimate population density at the individual building level, to our diachronic analysis of the trend in per capita space consumption. Thus, we were able to choose the type of results we wanted to obtain from the simulation output. For example, we were able to separate the numerical results on the consumption of built versus floor space, the average height of buildings in a cell, and many other indicators that we wanted to include in the sensitivity analysis.

The model estimates the probability of a cell (spatial unit) becoming urbanized in the future. The urbanization process is modeled according to estimated future needs in terms of built space. To do so, the model first assesses past trends in space consumption per inhabitant, and subsequently evaluates the future urban needs of the selected area based on its estimated population growth. Future projections of population growth are based on INSEE data (*Institut national de la statistique et des études économiques*). The time period chosen depends on the data available for the selected area. Here, we used data from 2009 to 2015 to assess past trends (see Section 2.3).

The probability of a cell becoming urbanized, in our case by 2040, depends on several “restriction” and “urbanization potential” parameters. For instance, our “urbanization potential” parameters included location indicators such as “being in areas that will be urbanized” according to the local development plans. Moreover, a cell close to amenities and services (such as roads, shops, schools and healthcare services) is more likely to be urbanized in the future. *SimUrba* also identifies areas where urbanization is restricted or not allowed (such as regulatory zones, existing biodiversity offsetting areas, floodplains and areas with slopes greater than 30%), called the “restriction” parameters.

To implement the first steps of the mitigation hierarchy (i.e. avoidance and reduction of ecological impacts), we added two further indicators to the simulations of urban dynamics: the ecological value of the study area (provided by the previous step of the method), and agricultural dynamics and land pressure estimated locally from existing studies or databases (Biotope, 2018). Our objective was to identify areas of potential conflict between agriculture, urbanization, and biodiversity conservation. Thus, we favored particularly intense urbanization for cells of less ecological or agricultural importance.

Lastly, two different development scenarios were simulated: (1) a trend-based scenario (hereafter Sc_{Trend}) based on a diachronic analysis (2009–2015), where the past trend in per capita space consumption is maintained up to 2040, and which can be described as “business as usual”, and (2) a scenario where space consumption reduces in

accordance with regulatory targets (e.g. *Plan Biodiversité* 2018 in France), the “factor 4 scenario” (hereafter Sc_{F4}), the per capita space consumption calculated in the trend-based scenario being divided by 4 by 2040.

2.6. Assessment of ecological impacts

We calculated the ecological impacts of the urban development scenarios on habitat connectivity with the following formula (Eq. (4)):

$$\Delta X = \frac{X_{2040} - X_{2015}}{X_{2015}} \times 100 \quad (4)$$

where X_{2015} and X_{2040} are the metric values of habitat connectivity (amount of reachable habitat on EC index with habitat area weighted by ecological value) assessed for each species before (in 2015) and after (in 2040) the simulated future urbanization. ΔX provides information on the habitat patches and ecological connectivity that will be lost or reduced due to urbanization.

2.7. Implementation of planned and relevant biodiversity offsets

To address the mitigation hierarchy, we first considered whether the plots were public or private, assuming that public plots would be more readily available for BO. This yielded a first set of all-public potential plots, called “ P_{BO1} ”. Then, we added plots of private land located near major ecological corridors identified in the territorial cohesion program (SCoT), with the objective of increasing the number of plots available, including the most ecologically relevant sites, and supporting ecological networks like the “green and blue corridors” (Chaurand, Bigard, Vanpeene-Bruhier, & Thompson, 2019). We called this mixed public and private set of potential plots “ P_{BO2} ”. In addition, farming was taken into account when selecting BO sites to avoid possible conflicts with agricultural activities (we excluded irrigated areas and major agricultural interests like famous wine-producing areas) thanks to a collaboration with SAFER (*French land development and rural establishment agencies*), the agency responsible for rural land development.

Certain landscape and area criteria were also considered in BO site selection. We restricted to areas of 0.5 ha or more located outside future urban areas, wetlands and existing BO sites. Since our approach was species-centered, we were also able to exclude habitats unsuitable for the species considered (e.g. we excluded forest patches for species from open/semi-open and cultivated areas). After identifying areas for BO, we addressed ecological connectivity using *Graphab*’s “patch addition process” as described by Foltête, Girardet, and Clauzel (2014). This enabled us to identify where BO would maximize species’ connectivity, by iteratively adding a virtual node (corresponding to a new habitat patch) in the centroid of each pre-targeted plot and adding new links from this node to the other nodes. This stepwise procedure is currently applied in studies aimed at identifying the most strategic habitats to prioritize for biodiversity preservation or restoration, as well to propose landscape management actions to protect terrestrial mammals, amphibians and birds (Clauzel et al., 2015; Clauzel, Jeliaskov, & Mimet, 2018; Mimet et al., 2016). It results in a map of favorable habitat patches for the species classified under a habitat type, created by overlaying the prioritization maps of individual species.

Then, we identified plots from both P_{BO1} and P_{BO2} (see above) as candidates for BO to compensate for negative impacts on habitat area, using two standard offset ratios from current BO practice: 1:1 and 2:1 (called “ $R_{1:1}$ ” and “ $R_{2:1}$ ”, respectively) (Curran, Hellweg, & Beck, 2014). Landscape graphs being species-specific, ecological impacts are different for each species, even within the same group. Therefore, we used the highest habitat area loss value among species belonging to the same group to define BO objectives in terms of area, according to the offset ratio applied.

Lastly, we assessed residual impacts on habitat connectivity from BO sites identified using the $R_{2:1}$ offset ratio, assuming this to be more

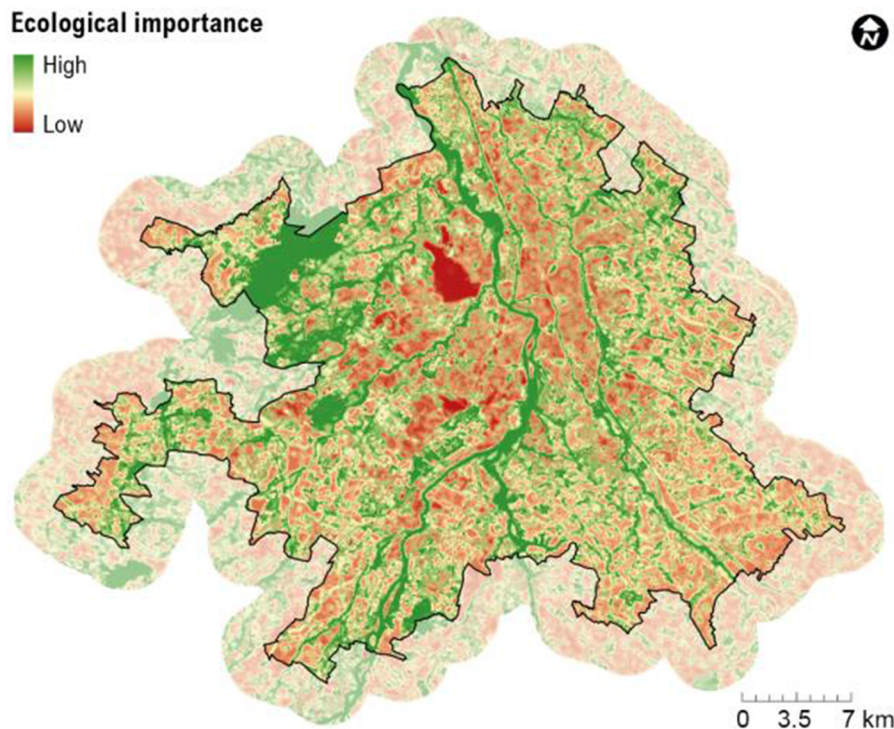


Fig. 3. Ecological value map according to the multi-criteria analysis detailed in Section 2.4. The denser the green, the higher the ecological value. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

likely to reach the NNL objective. When the ratio was not met, we attempted to identify the appropriate minimum ratio to ensure NNL in habitat connectivity (Bergès et al., 2020).

3. Results

3.1. Mapping of ecological value

We calculated a VIF for each indicator selected to map the ecological value of landscape. All values were below the threshold (VIF < 10). Therefore, there were no further exclusions among the variables presented in Table 2.

The ecological value map of the Toulouse region used to assess habitat connectivity is presented in Fig. 3. The gradient represents the cells' ecological importance, ranging from very high to low or zero.

In this study case, urban areas are generally the least valuable in terms of biodiversity. Ecological value is mainly derived from natural or semi-natural areas preserved from urbanization, inventory and protection areas, and green and blue infrastructures.

3.2. Simulation of urban dynamics

Future projections of urban sprawl are based on an increase of + 1.464% in inhabitants each year, generating supplementary urbanization in 2040 of 6,108 ha for Sc_{Trend} and 4,286 ha for Sc_{F4} (Fig. 4). New urbanization is mainly distributed around urban centers offering the widest urbanization potential. The greatly reduced urban sprawl obtained in Sc_{F4} (−30%) is due to the densification of existing buildings (via a fitting method which takes into account height rules for surrounding buildings) to meet estimated needs.

3.3. Assessment of ecological impacts

This result reveals the potential areas of conflict between future development and biodiversity conservation issues. Both urban development scenarios led to a decrease in total patch surface area (S) and in habitat

connectivity (EC index). The average decreases in S and EC values for Sc_{Trend} were −5.6% and −6.3%, respectively, and for Sc_{F4} , −4.1% and −4.8%, respectively. The most impacted species were those from open/semi-open and cultivated areas, particularly *Cisticola juncidis* and *Burhinus oedicnemus*: on average, these groups lost more than 8% and 10% of surface area and habitat connectivity, respectively, under the worst-case urbanization scenario (Sc_{Trend}). Others were very little affected, such as species linked to watercourses (for details, see Table 4).

3.4. Implementation of appropriate biodiversity offsets

Considering P_{BO1} (exclusively public plots), appropriate sites for BO were identified on 1,164 ha of public land distributed over 452 cells of 50 ha for species associated with forest areas, watercourses and ponds. For species from open/semi-open and cultivated areas, 577.3 ha were identified, distributed over 391 cells. Considering P_{BO2} (including private plots), we added another 3,788.8 ha for species associated with forest areas, watercourses and ponds, and 2,918.0 ha for the other species, together distributed over 1,159 and 1,238 cells, respectively. The position of the plots is illustrated in Appendix 6.

For easier readability, we focus our results on the more optimistic “factor 4” scenario (Sc_{F4}). It can be assumed that the Sc_{Trend} scenario will show more alarming results, since dense urbanization generates more impacts on habitat networks (Calvet, Napoléone, & Salles, 2015; Tannier, Bourgeois, Houot, & Foltête, 2016). Thus, for each species pool and sets of plots P_{BO1} and P_{BO2} , we identified the most promising cells for BO implementation, i.e. where habitat creation (to compensate for negative effects on habitat area) generated the highest gain in habitat connectivity (based on EC index). Fig. 5 shows the most promising areas in red, while those generating lower gains in connectivity tend towards white. From the areas maximizing habitat connectivity, we selected the BO sites required to meet the NNL objective for each habitat group under both P_{BO1} and P_{BO2} (for each habitat group, the highest impact value among species belonging to the group was used). BO site requirements are illustrated in Fig. 5 by green and purple squares corresponding to offset ratios of 1:1 and 2:1, respectively.

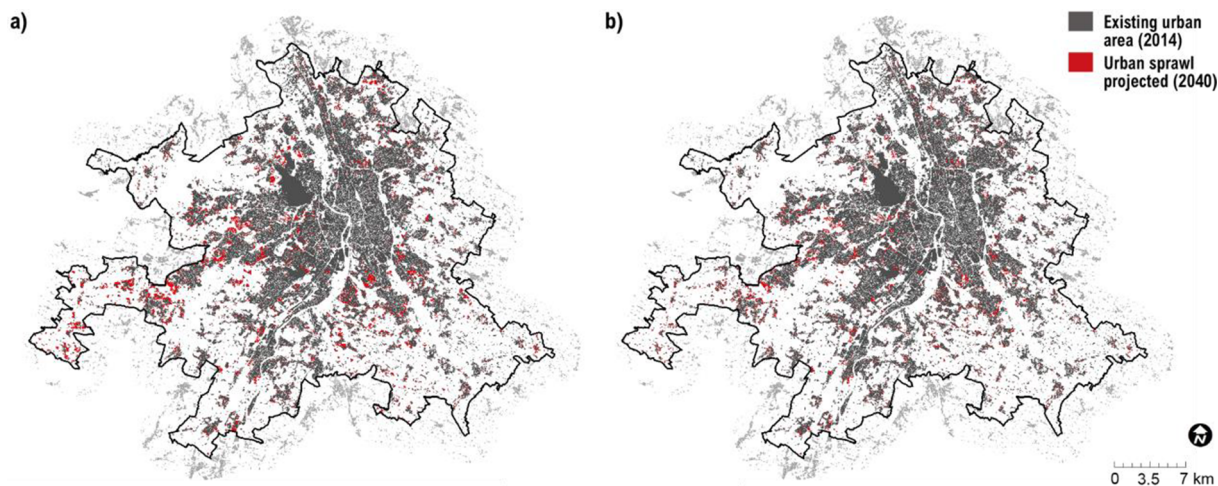


Fig. 4. Simulation of urban sprawl (in red) modeled with *SimUrba* for a) the trend-based scenario (Sc_{Trend}) and b) the “factor 4” scenario (Sc_{F4}). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

3.5. Assessment of residual impacts on habitat connectivity

Habitat connectivity (regarding *EC* index) was maintained for most species, with the exception of 4 (in bold font in Table 5). The residual impacts vary between -0.3% and -1.9% . For these species, we thus estimated the minimum offset ratio that would ensure compliance with the NNL objective in terms of connectivity at from 217% to 338% (Table 5).

4. Discussion

Our paper provides a combined methodological framework to anticipate and plan the mitigation hierarchy. Future urban dynamics are modeled and a landscape connectivity standpoint is taken to assess ecological impacts. We use complementary indicators to precisely quantify and spatialize the ecological impacts of urban sprawl, and to locate their most relevant areas for biodiversity offsetting. Our analyses emphasize the role of development scenarios in space consumption and thus in biodiversity conservation.

Table 4

Assessment of ecological impacts for the trend-based (Sc_{Trend}) and “factor 4” (Sc_{F4}) scenarios based on variation in habitat area (ΔS) and *EC* index (ΔEC). ΔS_{moy} and ΔEC_{moy} indicate the average value for each species group (see Appendix 5 for area values in ha.). The orange boxes represent maximum values of losses within habitat groups or between them.

Habitat group	Species	Sc_{Trend}				Sc_{F4}			
		ΔS	ΔS_{moy}	ΔEC	ΔEC_{moy}	ΔS	ΔS_{moy}	ΔEC	ΔEC_{moy}
Open and semi-open areas	<i>Cisticola juncidis</i>	-11.8%		-25.3%		-9.5%		-19.4%	
	<i>Lacerta bilineata</i>	-13.0%		-11.0%		-11.5%		-9.2%	
	<i>Phengaris arion</i>	-2.3%	-8.0%	-3.9%	-11.2%	-1.7%	-6.6%	-2.6%	-8.6%
	<i>Stethophyma grossum</i>	-1.4%		-0.2%		-1.0%		-0.1%	
	<i>Oryctolagus cuniculus</i>	-11.6%		-15.7%		-9.1%		-11.7%	
Cultivated areas	<i>Burhinus oediconemus</i>	-15.9%		-20.9%		-12.8%		-16.4%	
	<i>Epidalea calamita</i>	-6.9%	-9.2%	-4.2%	-10.5%	-5.1%	-7.0%	-3.2%	-8.0%
	<i>Emberiza calandra</i>	-4.9%		-6.4%		-3.1%		-4.5%	
	<i>Muscicapa striata</i>	-9.6%		-13.1%		-8.0%		-11.5%	
Forest areas	<i>Sciurus vulgaris</i>	-4.8%		-6.3%		-2.7%		-3.8%	
	<i>Capreolus capreolus</i>	-3.6%	-5.1%	-2.7%	-5.5%	-1.6%	-3.1%	-1.3%	-4.0%
	<i>Nyctalus leisleri</i>	-4.6%		-7.8%		-2.5%		-5.2%	
	<i>Salamandra salamandra</i>	-4.3%		-2.6%		-2.2%		-1.9%	
	<i>Cerambyx cerdo</i>	-3.9%		-0.7%		-1.6%		-0.4%	
	<i>Alcedo atthis</i>	-0.4%		-0.3%		-0.2%		-0.3%	
Watercourses	<i>Lutra lutra</i>	-0.4%	-1.4%	-0.7%	-0.5%	-0.2%	-0.8%	-0.4%	-0.4%
	<i>Natrix natrix</i>	-4.4%		-0.8%		-2.7%		-0.6%	
	<i>Coenagrion mercuriale</i>	-0.4%		-0.2%		-0.2%		-0.2%	
Ponds	<i>Pelodytes punctatus</i>	-1.4%	-4.1%	-0.2%	-1.9%	-1.0%	-3.0%	-0.2%	-1.6%
	<i>Triturus marmoratus</i>	-6.9%		-3.6%		-5.1%		-2.9%	

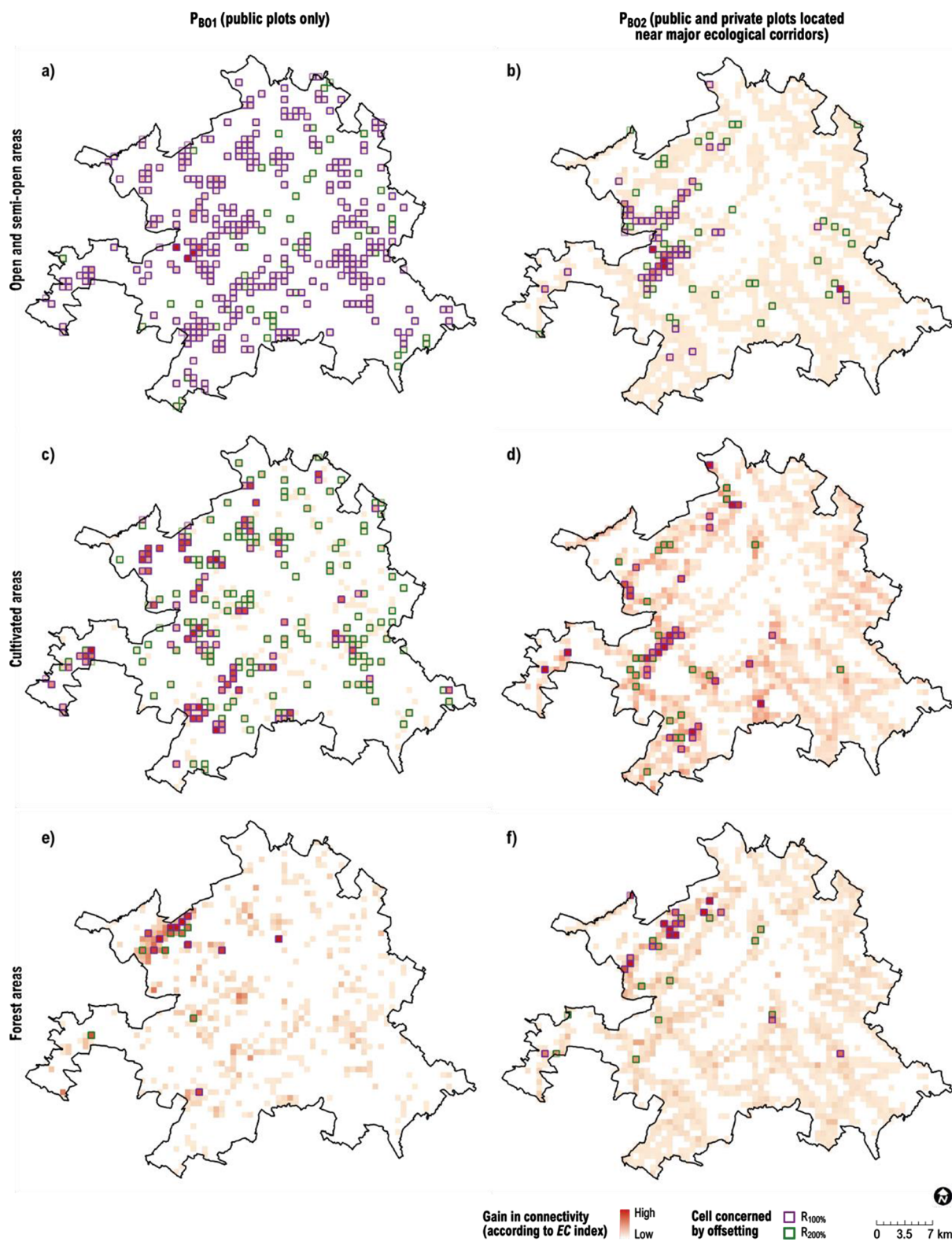


Fig. 5. Potential gains in habitat connectivity (*EC* index) for three habitat groups (a and b: open and semi-open areas; c and d: cultivated areas; e and f: forest areas; watercourses and ponds are not illustrated here for readability issues) under the Sc_{P4} scenario for two sets of available areas P_{B01} (a, c and e) and P_{B02} (b, d and f), the first consisting exclusively of public plots and the second including both public and private plots located near major ecological corridors (see Section 2.6). Purple squares represent priority cells for BO, i.e. plots where gains in connectivity are maximized, with an offset ratio of 1:1 (of impacts on habitat area); green squares represent cells added to reach 2:1. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

supply of potential sites (for instance here, open, semi-open, and cultivated areas; Fig. 5a, b).

However, since this was done here in parallel for each species group, it generated several conflict areas involving different BO needs

within the same plot (for instance BO linked to forest areas and open areas), especially where the offset ratio used was high. This issue, previously raised by many authors (see for instance Maron, Dunn, McAlpine, & Apan, 2010b; Weissgerber, Roturier, Julliard, & Guillet,

Table 5

Assessment of residual impacts based on variation in EC index (ΔEC) and on the minimum offset ratio (R_{min} ; expressed as a percentage) required to meet the NNL objective for habitat connectivity. We applied the analysis from urbanization scenario SC_{F4} and offset ratio $R_{2.1}$.

Habitat group	Species	ΔEC $R_{2.1}$	R_{min}
Open and semi-open areas	<i>Cisticola juncidis</i>	+13.4%	217%
	<i>Lacerta bilineata</i>	+8.3%	
	<i>Phengaris arion</i>	-0.3%	
	<i>Stethophyma grossum</i>	+6.1%	
Cultivated areas	<i>Oryctolagus cuniculus</i>	-1.0%	338%
	<i>Burhinus oedicnemus</i>	-1.9%	246%
	<i>Epidalea calanita</i>	+9.2%	
Forest areas	<i>Emberiza calandra</i>	+5.9%	283%
	<i>Muscicapa striata</i>	+11.3%	
	<i>Sciurus vulgaris</i>	+5.3%	
	<i>Capreolus capreolus</i>	+10.2%	
	<i>Nyctalus leisleri</i>	-0.8%	
	<i>Salamandra salamandra</i>	+1.7%	
Water courses	<i>Cerambyx cerdo</i>	+1.4%	
	<i>Alcedo atthis</i>	+1.0%	
	<i>Lutra lutra</i>	+0.4%	
	<i>Natrix natrix</i>	+1.4%	
	<i>Coenagrion mercuriale</i>	+0.3%	
Ponds	<i>Pelodytes punctatus</i>	3.0%	
	<i>Triturus marmoratus</i>	+7.1%	

2019), affects the feasibility of BO, making it impossible to implement all the offsets. Here, including under potential BO sites the private plots of land located near the main corridors of the SCOT proved to be one solution to this problem. In our study case, it significantly reduced the areas in conflict (Table 6).

Moreover, where private plots of land were used for BO (P_{BO2}), fewer were needed (for instance, Fig. 5b, d) because they were on average much larger than the public plots (+21.6%). Using fewer plots means fewer long-term constraints, like monitoring and management of compensatory plots (i.e. fewer sites to manage, fewer actors to coordinate, etc.). But it should be noted that multiple offset sites can limit the risk of larger-scale ecological failure (Moilanen, Van Teeffelen, Ben-Haim, & Ferrier, 2009), and may thus be more successful in promoting specific types of biodiversity (Herrera, Alagador, Salgueiro, & Mira, 2018; Wintle et al., 2019).

While we are aware that land-use conflicts cannot be reduced solely by using private plots, it should be remembered that the public plots commonly used by developers to implement BO are often subject to criticism concerning their ecological relevance. However, environmental and urban planners have little control over private land, which in practice limits access to relevant potential BO sites. Stakeholders would thus find it advantageous to adopt a mixed approach, for example considering private-public partnerships.

Adopting a landscape perspective to pursue the NNL objective has implications for ecological equivalence assessment (Quétier & Lavorel, 2011). Here, we proposed to estimate the minimum offset ratio that would ensure NNL of biodiversity for several species in terms of habitat

Table 6

Assessment of the proportion of areas where conflict arises over the differing offsets required. A value of 1 means there is no conflict while values from 2 to 5 represent the number of species pools in conflict situations. This analysis covers both offset ratios applied ($R_{1.1}$ and $R_{2.1}$) and highlights differences in conflict area between the two sets of potential BO offsetting sites (ΔS_{BO}).

Value	$R_{1.1}$			$R_{2.1}$		
	P_{BO1}	P_{BO2}	ΔS_{BO}	P_{BO1}	P_{BO2}	ΔS_{BO}
5	0 (0.0%)	0 (0.0%)	0 (0.0%)	0 (0.0%)	0 (0.0%)	0 (0.0%)
4	6.15 (0.9%)	0.11 (0.0%)	-6.04 (-0.9%)	44.01 (6.1%)	25.45 (2.9%)	-18.56 (-3.2%)
3	107.43 (16.3%)	37.23 (6.4%)	-70.20 (-9.9%)	96.40 (13.4%)	74.84 (8.6%)	-21.56 (-4.8%)
2	281.56 (42.8%)	205.81 (35.5%)	-75.75 (-7.3%)	426.93 (59.2%)	310.12 (35.4%)	-116.81 (-23.8%)
1	263.19 (40.0%)	336.54 (58.1%)	+73.35 (+18.1%)	153.37 (21.3%)	464.40 (53.1%)	+311.06 (+31.8%)

connectivity, consistent with the warnings of Bergès et al. (2020) on the riskiness of using a standard offset ratio.

4.2. Implications and opportunities for biodiversity conservation

Our methodological framework provides a relevant and comprehensive tool at the territorial scale, meeting two needs. First, identifying urban dynamics is a challenge because there is no standard simulation model for urban sprawl, despite the many developed to meet different research objectives. *SimUrba* was developed to address biodiversity conservation in the context of land-use planning scenarios and the application of the mitigation hierarchy. Second, the precise identification of local conservation issues requires specific ecological indicators and methods. Here, a habitat network connectivity model based on landscape graphs was used to estimate the impacts of projected urban dynamics on species' habitats in an ecologically relevant way (Foltête, 2019; Gamarra, Lassoie, & Milder, 2018).

Applying the mitigation hierarchy highlights areas of tension between future urbanization and conservation issues that can be taken into account in planning the best sites for biodiversity offsets. Bunton, Ernst, Hanson, Beyer, Hammill, Runge, Venter, Possingham, and Rhodes (2015) showed the usefulness of coordination between linear infrastructure planning and conservation offset planning. In our case, this approach helps to identify the most appropriate locations for biodiversity offsets in terms of functional ecology. The hierarchization of BO sites enables relevant conservation sites to be selected, so as to reconnect existing ecological corridors and to integrate BO into broader conservation actions that make sense locally. This is consistent with Dupont (2017), who pointed out the many advantages of pooling BO and green and blue infrastructure, provided that the principle of additionality is respected: i.e., measures are taken (or planned) in addition to existing public or private commitments for the protection of the environment (Dupont & Lucas, 2017). This form of BO organization strengthens local biodiversity conservation and helps ensure BO success through natural recolonization during site restoration, a major factor in meeting the NNL of biodiversity objective (Resasco, 2019). Our method is similar in its anticipation of offsets to the mitigation bank model (Bekessy et al., 2010), which was shown to outperform *project-by-project* BO (Scemama & Levrel, 2013). Our projections should therefore make offsetting sites more ecologically relevant.

4.3. Improving the methodological framework

The main limitations of the proposed methodology are related to the data used, particularly to prepare the LULC map. Although landscape graphs are a good compromise between the information yielded and the data requirements of landscape connectivity analysis (Foltête, 2019; Saura & de la Fuente, 2017), combined models require a lot of data, and there is a risk of over-simplification or inconsistent results depending on the sources (Simpkins, Dennis, Etherington, & Perry, 2018). Here, our modeling approaches involve closely-related results; variations can stem both from the mapping of landscape's ecological value and from

the estimation of urban sprawl. For instance, we combined several relatively precise and reliable sources of data (European Urban Atlas provided by the European Environment Agency, BD TOPO by the French National Geographical Institute, the French Record of Agricultural Plots, etc.; see Table 3). However, data availability is a frequent challenge in this kind of study, and stakeholders may, depending on study areas (for example, the Urban Atlas only covers large urban zones with more than 100,000 inhabitants), have to use less detailed databases (e.g. Corine Land Cover in Europe). Photointerpretation could be an alternative way to produce LULC maps, but this requires significant technical and human resources (Hay & Castilla, 2008). Regarding the indicators in ecological value mapping, stakeholders must avoid using oversimplified indicators derived only from land cover maps (rarity, diversity, potential, wetland). Some used here are examples of relevant indicators (e.g. inventory and protection areas, species richness, ecological functionality). Moreover, if sufficient species occurrence data are available (for instance from regional NGOs), species distribution models (SDMs) can be used to determine suitable habitats according to Bigard et al. (2020). Note that this study used an indicator related to species richness. However, if collaborative databases are not available or if they contain observations from different sources using inconsistent sampling strategies, we suggest that stakeholders use this indicator with caution, and only if it is consistent with their other data.

In this paper, we defined resistance surface values by transforming a qualitative classification of resistance according to the well-documented preferences of each species. However, (Simpkins et al., 2018) acknowledge that the performance of resistance surfaces is context-specific. Different populations of the same species in different landscape matrices could differ in their tolerance to unsuitable land use and land covers, which could affect the resistance surfaces. Here, we did not generate values through expert knowledge (Le Roux et al., 2017) nor based on context-specific empirical values (Reed et al., 2017). Therefore, the values of the resistance surfaces may not be reliable enough to be used in a detailed study in the same part of France. But they are good enough for the purposes of this paper, which does not aim for the most accurate resistance surfaces available nor apply state-of-the-art methods to obtain them. Alternatives could be used in similar studies. For instance, some authors proposed using SDM-derived maps to calculate a species-specific landscape resistance surface (Dufлот, Avon, Roche, & Bergès, 2018; Rödder, Nekum, Cord, & Engler, 2016). However, SDMs require the acquisition of species occurrence data. At this spatial scale, databases like the French SINP nature and landscape system (*Système d'Information sur la Nature et les Paysages*; <http://inventaire.naturefrance.fr/>) can be used, but information is still too incomplete and inaccurate (only 28% of SINP data is considered to be spatially and temporally accurate; ONB, 2018) to make SDM results robust, as discussed by Bigard et al. (2020).

In the same way, Moilanen (2011) noted that habitat patches are not always mapped explicitly in landscape graphs. Here, for technical feasibility reasons (quantity of data), we defined habitat patches according to the land-cover map, which does not take into account possible ecological constraints that may limit species' presence (neighboring roads, topography, etc.). Using a SDM could provide a practical and relevant solution (see Tarabon et al., 2019a), especially in a changing global context, since we are studying the impacts of urbanization by 2040. Will species still occupy the same habitats in areas vulnerable to climate change, like the Mediterranean basin (Allen, Antwi-Agyei, Aragon-Durand, Babiker, Bertoldi, Bind, Brown, Buckeridge, Camilloni, & Cartwright, 2019)? Although most of the species distribution remains adapted to all the climate scenarios considered, some species may well disappear from some regions (Ofori, Stow, Baumgartner, & Beaumont, 2017). Where the use of SDM is feasible, adding climate variables to models would be relevant (Dilts et al., 2016), as the question of species' vulnerability to climate change represents a real challenge in terms of the dimensioning of BO (Quétiér & Lavorel, 2011).

Another possible limitation is that the offsetting step in our approach using landscape graphs is based on only two offset ratios. Depending on the ecological issues involved, this may not be enough to represent local or regional environmental policies, thus possibly leading to underestimations. Moreover, this methodological framework is based solely on the creation of habitats (adding habitat patches). We did not include (except in the avoiding steps) assessment and management of existing natural areas to enhance population viability (Hodgson, Moilanen, Wintle, & Thomas, 2011). Evaluating the potential for ecological gain at this spatial scale of analysis is difficult, and would require a detailed study of the ecological quality of the offset sites (Weissgerber et al., 2019). Demonstrating the positive impact of BO on habitat connectivity would involve numerous non-measurable values and components of biodiversity (Calvet et al., 2015; Moreno-Mateos et al., 2015). Research perspectives raised here include improving the accuracy and reliability of our simulation models. Some authors have shown that improving overall and local connectivity can be effective as offsetting measures, and an alternative to creating new habitats (Dalang & Hersperger, 2012). A wider approach could balance mitigation efforts between restoring habitat areas and reducing patch isolation (Fahrig, 2017). Thus, our models could be improved by incorporating more qualitative developments, such as wildlife crossings. Wildlife crossings lead to landscape defragmentation and reconnect environments with each other, thereby enhancing the overall connectivity of ecological networks (Bergès et al., 2020; Mimet et al., 2016; Tarabon, Bergès, Dutoit, & Isselin-Nondedeu, 2019b).

Finally, a wider territorial scale (from towns or municipalities to provinces or regions) could be relevant in the context of spatial BO planning (Bigard et al., 2017). For instance, in France, the regional sustainable development plan, called "SRADDET" (*Schéma Régional d'Aménagement, de Développement Durable et d'Égalité des Territoires*), uses the regional scale, promoting the principles of sustainable development within broader territorial and ecosystem dynamics. This provides an overall view of the main organizational processes at work in the area, but not at such a fine and accurate scale. Analysis such as that performed in this study would be difficult on a wider scale: data acquisition would be too complex and calculations too lengthy or unfeasible. In this study, we applied a buffer zone of several kilometers around the administrative boundary of the Toulouse conurbation, a compromise that took into account the availability of land-use and environmental geo-data, the computation times of models, and the dispersal distance of the focal species. The buffer zone we considered here was not always, i.e. for four species, at least equal to their maximal dispersal distance, as suggested by Bergès et al. (2020) and Fletcher, Reichert and Holmes (2018). Data acquisition and computation time permitting, this rule should be respected as far as possible in similar studies.

5. Conclusion

To meet the need for spatial tools in applying BO policies, we propose a methodological framework that can be used to implement a planning strategy respecting the mitigation hierarchy. Its originality lies in combining a simulation of projected urbanization up to 2040 with a simulation of the impacts on ecological networks within landscape ecology. We show through the case study of the Metropolis of Toulouse that simulations of projected urban development and mapping can be used to enhance land-use and offset planning.

This approach can improve the application of the mitigation hierarchy, especially by anticipating future land and conservation conflict areas, and by proposing appropriate biodiversity offsets. Moreover, this framework should support public decision-makers by taking into account relevant local factors, with several advantages as highlighted by Regnery and Siblet (2017). First, the assessment of the residual impacts of future urbanization could give local stakeholders a better understanding of the limits of BO. Second, its territorial organization offers a

comprehensive overview of the plans, policies and instruments related to the offsetting, so as to develop a framework of clear biodiversity objectives. Third, planning biodiversity offsets upstream could foster forward-looking territorial management, developing social dialogue and promoting the integration of ecological, social and economic issues.

CRedit authorship contribution statement

Simon Tarabon: Conceptualization, Methodology, Validation, Formal analysis, Writing - original draft, Visualization. **Coralie Calvet:** Methodology, Validation, Investigation, Software, Writing - original draft. **Vincent Delbar:** Formal analysis, Software. **Thierry Dutoit:** Supervision. **Francis Isselin-Nondedeu:** Supervision, Writing - original draft.

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.

Acknowledgements

Simon Tarabon thank the Association for Research and Technology (ANRT) funded by the Ministry for Higher Education and Research, and Fabrice Vullion and Fabienne Theuriau (Soberco Environnement) for funding and involvement under the CIFRE agreements (n° 2016/1378). Coralie Calvet thank the Labex CeMeb for funding, and Paul Chapron, Mickaël Brasebin and Julien Perret (from the IGN research lab) for their participation in the development of SimUrba. Lastly, authors thank Marjorie Sweetko for revising the English manuscript.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.landurbplan.2020.103871>.

References

- Adriaansen, F., Chardon, J., De Blust, G., Swinnen, E., Villalba, S., Gulinck, H., & Matthysen, E. (2003). The application of 'least-cost' modelling as a functional landscape model. *Landscape and Urban Planning*, 64(4), 233–247.
- Allen, C. H., Parrott, L., & Kyle, C. (2016). An individual-based modelling approach to estimate landscape connectivity for bighorn sheep (*Ovis canadensis*). *PeerJ*, 4, e2001.
- Allen, M., Antwi-Agyei, P., Aragon-Durand, F., Babiker, M., Bertoldi, P., Bind, M., ..., Cartwright, A., 2019, Technical Summary: Global warming of 1.5 °C. An IPCC Special Report on the impacts of global warming of 1.5° C above pre-industrial levels and related global greenhouse gas emission pathways, in the context of strengthening the global response to the threat of climate change, sustainable development, and efforts to eradicate poverty.
- Almenar, J. B., Bolowich, A., Elliot, T., Geneletti, D., Sonnemann, G., & Rugani, B. (2019). Assessing habitat loss, fragmentation and ecological connectivity in Luxembourg to support spatial planning. *Landscape and Urban Planning*, 189, 335–351.
- Beier, P., & Brost, B. (2010). Use of land facets to plan for climate change: Conserving the arenas, not the actors. *Conservation biology*, 24(3), 701–710.
- Bekessy, S. A., Wintle, B. A., Lindenmayer, D. B., McCarthy, M. A., Colyvan, M., Burgman, M. A., & Possingham, H. P. (2010). The biodiversity bank cannot be a lending bank. *Conservation Letters*, 3(3), 151–158.
- Bergès, L., Avon, C., Bezombes, L., Clauzel, C., Duflot, R., Foltête, J.-C., ... Spiegelberger, T. (2020). Environmental mitigation hierarchy and biodiversity offsets revisited through habitat connectivity modelling. *Journal of Environmental Management*, 256, 109950.
- Bergsten, A., & Zetterberg, A. (2013). To model the landscape as a network: A practitioner's perspective. *Landscape and Urban Planning*, 119, 35–43.
- Bezombes, L., Gaucherand, S., Kerbirou, C., Reinert, M.-E., & Spiegelberger, T. (2017). Ecological equivalence assessment methods: What trade-offs between operationality, scientific basis and comprehensiveness? *Environmental management*, 60(2), 216–230.
- Bezombes, L., Gaucherand, S., Spiegelberger, T., Gouraud, V., & Kerbirou, C. (2018). A set of organized indicators to conciliate scientific knowledge, offset policies requirements and operational constraints in the context of biodiversity offsets. *Ecological Indicators*, 93, 1244–1252.
- Bigard, C., Pioch, S., & Thompson, J. D. (2017). The inclusion of biodiversity in environmental impact assessment: Policy-related progress limited by gaps and semantic confusion. *Journal of environmental management*, 200, 35–45.
- Bigard, C., Thiriet, P., Pioch, S., & Thompson, J. D. (2020). Strategic landscape-scale planning to improve mitigation hierarchy implementation: An empirical case study in Mediterranean France. *Land Use Policy*, 90, 104286.
- Biotope, 2018, Decision support study for implementing an mitigation hierarchy strategy at the regional scale: Report 2, pp. 145.
- Boitani, L., Falcucci, A., Maiorano, L., & Rondinini, C. (2007). Ecological networks as conceptual frameworks or operational tools in conservation. *Conservation biology*, 21(6), 1414–1422.
- Brown, J. L., Bennett, J. R., & French, C. M. (2017). SDMtoolbox 2.0: The next generation Python-based GIS toolkit for landscape genetic, biogeographic and species distribution model analyses. *PeerJ*, 5, e4095.
- Bull, J., Hardy, M., Moilanen, A., & Gordon, A. (2015). Categories of flexibility in biodiversity offsetting, and their implications for conservation. *Biological Conservation*, 192, 522–532.
- Bunton, J., Ernst, A., Hanson, J., Beyer, H., Hammill, E., Runge, C., & Rhodes, J. (2015). Integrated planning of linear infrastructure and conservation offsets. *International Congress on Modelling and Simulation 2015: Partnering with industry and the community for innovation and impact through modelling* (pp. 1427–1433). Modelling and Simulation Society of Australia and New Zealand.
- Calvet, C., Delbar, V., Chapron, P., Brasebin, M., Perret, J., & Moulherat, S. (2020). Biodiversity facing development choices: A modeling approach applied to the Occitanie region. *Sciences, Eaux et Territoires*, 31, 24–31.
- Calvet, C., Napoléone, C., & Salles, J. (2015). The biodiversity offsetting dilemma: Between economic rationales and ecological dynamics. *Sustainability*, 7(6), 7357–7378.
- Calvet, C., Ollivier, G., & Napoleone, C. (2015). Tracking the origins and development of biodiversity offsetting in academic research and its implications for conservation: A review. *Biological Conservation*, 192, 492–503.
- Carreras Gamarra, M. J., Lassoie, J. P., & Milder, J. (2018). Accounting for no net loss: A critical assessment of biodiversity offsetting metrics and methods. *Journal of Environmental Management*, 220, 36–43.
- Chaurand, J., Bigard, C., Vanpeene-Bruhier, S., & Thompson, J. D. (2019). Articulating the green and blue corridor policy and the mitigation hierarchy: Complementarities and limits for an effective biodiversity conservation in France. *VertigO-la revue électronique en sciences de l'environnement*, 19(1).
- Clauzel, C. (2017). Evaluating and mitigating the impact of a high-speed railway on connectivity: A case study with an amphibian species in France. *Railway Ecology*:215..
- Clauzel, C., Bannwarth, C., & Foltête, J.-C. (2015). Integrating regional-scale connectivity in habitat restoration: An application for amphibian conservation in eastern France. *Journal for Nature Conservation*, 23, 98–107.
- Clauzel, C., & Bonnevalle, C. (2019). Apports de la modélisation spatiale pour la gestion de la trame verte et bleue. *Cybergeo: European Journal of Geography*.
- Clauzel, C., Jeliakov, A., & Mimet, A. (2018). Coupling a landscape-based approach and graph theory to maximize multispecific connectivity in bird communities. *Landscape and Urban Planning*, 179, 1–16.
- Correa Ayram, C. A., Mendoza, M. E., Etter, A., & Salicrup, D. R. P. (2016). Habitat connectivity in biodiversity conservation: A review of recent studies and applications. *Progress in Physical Geography*, 40(1), 7–37.
- CRENAM (2011). *Identifying potential biodiversity reservoirs*. Ecological networks of the Massif Central project: IPAMAC project., France55.
- Crossman, N. D., Bryan, B. A., Ostendorf, B., & Collins, S. (2007). Systematic landscape restoration in the rural-urban fringe: Meeting conservation planning and policy goals. *Biodiversity and Conservation*, 16(13), 3781–3802.
- Curran, M., Hellweg, S., & Beck, J. (2014). Is there any empirical support for biodiversity offset policy? *Ecological Applications*, 24(4), 617–632.
- Dalang, T., & Herspenger, A. M. (2012). Trading connectivity improvement for area loss in patch-based biodiversity reserve networks. *Biological conservation*, 148(1), 116–125.
- Dilts, T. E., Weisberg, P. J., Leitner, P., Matocq, M. D., Inman, R. D., Nussear, K. E., & Esque, T. C. (2016). Multiscale connectivity and graph theory highlight critical areas for conservation under climate change. *Ecological Applications*, 26(4), 1223–1237.
- Duflot, R., Avon, C., Roche, P., & Bergès, L. (2018). Combining habitat suitability models and spatial graphs for more effective landscape conservation planning: An applied methodological framework and a species case study. *Journal for nature conservation*, 46, 38–47.
- Dupont, L. (2017). Biodiversity offset and green and blue corridor: A combination to explore for biodiversity. *Revue juridique de l'environnement*, 42(4), 649–658.
- Dupont, V., & Lucas, M. (2017). The law for the reconquest of biodiversity: Towards a strengthening of the legal regime of biodiversity offsetting? *Cahiers Droit, Sciences & Technologies*, 7, 143–165.
- Eliith, J., Graham, C. H., Anderson, R. P., Dudík, M., Ferrier, S., Guisan, A., & Lehmann, A. (2006). Novel methods improve prediction of species' distributions from occurrence data. *Ecography*, 29(2), 129–151.
- Fahrig, L. (2017). Ecological responses to habitat fragmentation per se. *Annual Review of Ecology, Evolution, and Systematics*, 48, 1–23.
- Fletcher, R. J., Jr, Reichert, B. E., & Holmes, K. (2018). The negative effects of habitat fragmentation operate at the scale of dispersal. *Ecology*, 99(10), 2176–2186.
- Foltête, J.-C. (2019). How ecological networks could benefit from landscape graphs: A response to the paper by Spartaco Gippoliti and Corrado Battisti. *Land Use Policy*, 80, 391–394.
- Foltête, J.-C., Clauzel, C., & Vuidel, G. (2012). A software tool dedicated to the modelling of landscape networks. *Environmental Modelling & Software*, 38, 316–327.
- Foltête, J.-C., Girardet, X., & Clauzel, C. (2014). A methodological framework for the use of landscape graphs in land-use planning. *Landscape and Urban Planning*, 124, 140–150.

- Forman, R. T. (1995). Some general principles of landscape and regional ecology. *Landscape ecology*, 10(3), 133–142.
- Gamarra, M. J. C., Lassoie, J. P., & Milder, J. (2018). Accounting for no net loss: A critical assessment of biodiversity offsetting metrics and methods. *Journal of environmental management*, 220, 36–43.
- Gardner, T. A., Hase, A., Brownlie, S., Ekstrom, J. M., Pilgrim, J. D., Savy, C. E., ... Ward, G. (2013). Biodiversity offsets and the challenge of achieving no net loss. *Conservation Biology*, 27(6), 1254–1264.
- Gibbons, P., & Lindenmayer, D. B. (2007). Offsets for land clearing: No net loss or the tail wagging the dog? *Ecological Management & Restoration*, 8(1), 26–31.
- Gotelli, N. J., & Colwell, R. K. (2011). Estimating species richness. *Biological diversity: frontiers in measurement and assessment*, 12, 39–54.
- Gray, C. L., Hill, S. L., Newbold, T., Hudson, L. N., Börger, L., Contu, S., ... Scharlemann, J. P. (2016). Local biodiversity is higher inside than outside terrestrial protected areas worldwide. *Nature Communications*, 7(1), 1–7.
- Guillet, F., & Semal, L. (2018). Policy flaws of biodiversity offsetting as a conservation strategy. *Biological conservation*, 221, 86–90.
- Haddad, N. M., Brudvig, L. A., Clobert, J., Davies, K. F., Gonzalez, A., Holt, R. D., ... Collins, C. D. (2015). Habitat fragmentation and its lasting impact on Earth's ecosystems. *Science advances*, 1(2), e1500052.
- Haverland, M. B., & Veech, J. A. (2017). Examining the occurrence of mammal species in natural areas within a rapidly urbanizing region of Texas. *USA, Landscape and Urban Planning*, 157, 221–230.
- Hay, G. J., & Castilla, G. (2008). Geographic Object-Based Image Analysis (GEOBIA): A new name for a new discipline. *Object-based image analysis* (pp. 75–89). Springer.
- Herrera, J. M., Alagador, D., Salgueiro, P., & Mira, A. (2018). A distribution-oriented approach to support landscape connectivity for ecologically distinct bird species. *PLoS one*, 13(4), e0194848.
- Hodgson, J. A., Moilanen, A., Wintle, B. A., & Thomas, C. D. (2011). Habitat area, quality and connectivity: Striking the balance for efficient conservation. *Journal of Applied Ecology*, 48(1), 148–152.
- Hüse, B., Szabó, S., Deák, B., & Tóthmérész, B. (2016). Mapping an ecological network of green habitat patches and their role in maintaining urban biodiversity in and around Debrecen city (Eastern Hungary). *Land Use Policy*, 57, 574–581.
- Jiang, G., Ma, J., Zhang, M., & Stott, P. (2009). Effects of human activities on the spatial distribution of eastern roe deer *Capreolus pygargus bedfordi* in the Lesser Khingan Mountains, northeastern China. *Mammal Research*, 54(1), 61–76.
- Kiesecker, J. M., Copeland, H., Pocewicz, A., & McKenney, B. (2010). Development by design: Blending landscape-level planning with the mitigation hierarchy. *Frontiers in Ecology and the Environment*, 8(5), 261–266.
- Kool, J. T., Moilanen, A., & Tremel, E. A. (2013). Population connectivity: Recent advances and new perspectives. *Landscape Ecology*, 28(2), 165–185.
- Kujala, H., Whitehead, A. L., Morris, W. K., & Wintle, B. A. (2015). Towards strategic offsetting of biodiversity loss using spatial prioritization concepts and tools: A case study on mining impacts in Australia. *Biological Conservation*, 192, 513–521.
- Le Roux, M., Redon, M., Archaux, F., Long, J., Vincent, S., & Luque, S. (2017). Conservation planning with spatially explicit models: A case for horseshoe bats in complex mountain landscapes. *Landscape ecology*, 32(5), 1005–1021.
- Le Saout, S., Hoffmann, M., Shi, Y., Hughes, A., Bernard, C., Brooks, T. M., ... Badman, T. (2013). Protected areas and effective biodiversity conservation. *Science*, 342(6160), 803–805.
- Letourneau, A., & Thompson, J. (2014). *Methodological note for identifying areas important for the biodiversity and ecological continuities conservation in Languedoc region, Annexe au SRCE Languedoc-Roussillon*. Montpellier: DREAL-Région LR.
- Lislevand, T., Figuerola, J., & Székely, T. (2007). Avian body sizes in relation to fecundity, mating system, display behavior, and resource sharing. *Ecology*, 88(6), 1605–1605.
- Liu, Y., Peng, J., Zhang, T., & Zhao, M. (2016). Assessing landscape eco-risk associated with hilly construction land exploitation in the southwest of China: Trade-off and adaptation. *Ecological indicators*, 62, 289–297.
- Maron, M., Brownlie, S., Bull, J. W., Evans, M. C., von Hase, A., Quétier, F., ... Gordon, A. (2018). The many meanings of no net loss in environmental policy. *Nature Sustainability*, 1(1), 19.
- Maron, M., Dunn, P. K., McAlpine, C. A., & Apan, A. (2010a). Can offsets really compensate for habitat removal? The case of the endangered red-tailed black-cockatoo. *Journal of Applied Ecology* (Print), 47(2), 348–355.
- Maron, M., Dunn, P. K., McAlpine, C. A., & Apan, A. (2010b). Can offsets really compensate for habitat removal? The case of the endangered red-tailed black-cockatoo. *Journal of Applied Ecology* (Print), 47(2), 348–355.
- Maron, M., Ives, C. D., Kujala, H., Bull, J. W., Maseyk, F. J., Bekessy, S., ... Gibbons, P. (2016). Taming a wicked problem: Resolving controversies in biodiversity offsetting. *BioScience*, 66(6), 489–498.
- Maxwell, S. L., Fuller, R. A., Brooks, T. M., & Watson, J. E. (2016). Biodiversity: The ravages of guns, nets and bulldozers. *Nature*, 536(7615), 143–145.
- May, J., Hobbs, R. J., & Valentine, L. E. (2017). Are offsets effective? An evaluation of recent environmental offsets in Western Australia. *Biological Conservation*, 206, 249–257.
- McGarigal, K., & Cushman, S. (2005). The gradient concept of landscape structure [Chapter 12]. In John A. Wiens, & Michael R. Moss (Eds.). *Issues and Perspectives in Landscape Ecology* (pp. 112–119). Cambridge University Press.
- McRae, B. H. (2006). Isolation by resistance. *Evolution*, 60(8), 1551–1561.
- McRae, B. H., Dickson, B. G., Keitt, T. H., & Shah, V. B. (2008). Using circuit theory to model connectivity in ecology, evolution, and conservation. *Ecology*, 89(10), 2712–2724.
- Mechai, S., Margos, G., Feil, E. J., Lindsay, L. R., Michel, P., Kotchi, S. O., & Ogden, N. H. (2018). Evidence for an effect of landscape connectivity on *Borrelia burgdorferi* sensu stricto dispersion in a zone of range expansion. *Ticks and Tick-borne Diseases*, 9(6), 1407–1415.
- Mimet, A., Clauzel, C., & Foltête, J.-C. (2016). Locating wildlife crossings for multispecies connectivity across linear infrastructures. *Landscape Ecology*, 31(9), 1955–1973.
- Minor, E. S., & Urban, D. L. (2008). A graph-theory framework for evaluating landscape connectivity and conservation planning. *Conservation biology*, 22(2), 297–307.
- Moilanen, A. (2011). On the limitations of graph-theoretic connectivity in spatial ecology and conservation. *Journal of Applied Ecology*, 48(6), 1543–1547.
- Moilanen, A., & Kotiaho, J. S. (2018). Fifteen operationally important decisions in the planning of biodiversity offsets. *Biological conservation*, 227, 112–120.
- Moilanen, A., Van Teeffelen, A. J., Ben-Haim, Y., & Ferrier, S. (2009). How much compensation is enough? A framework for incorporating uncertainty and time discounting when calculating offset ratios for impacted habitat. *Restoration Ecology*, 17(4), 470–478.
- Moreno-Mateos, D., Maris, V., Béchet, A., & Curran, M. (2015). The true loss caused by biodiversity offsets. *Biological Conservation*, 192, 552–559.
- Naimi, B., Hamm, N. A., Groen, T. A., Skidmore, A. K., & Toxopeus, A. G. (2014). Where is positional uncertainty a problem for species distribution modelling? *Ecography*, 37(2), 191–203.
- Niculae, M.-I., Nita, M. R., Vanau, G. O., & Patroescu, M. (2016). Evaluating the functional connectivity of Natura 2000 forest patch for mammals in Romania. *Procedia Environmental Sciences*, 32, 28–37.
- Ofori, B. Y., Stow, A. J., Baumgartner, J. B., & Beaumont, L. J. (2017). Influence of adaptive capacity on the outcome of climate change vulnerability assessment. *Scientific reports*, 7(1), 12979.
- ONB (2018). *Gaps in naturalist knowledge produced and shared in France*. Paris: Observatoire National de la Biodiversité.
- Quétier, F., & Lavorel, S. (2011). Assessing ecological equivalence in biodiversity offset schemes: Key issues and solutions. *Biological conservation*, 144(12), 2991–2999.
- Rayfield, B., Fortin, M.-J., & Fall, A. (2011). Connectivity for conservation: A framework to classify network measures. *Ecology*, 92(4), 847–858.
- Reed, G., Litvaitis, J., Callahan, C., Carroll, R., Litvaitis, M., & Broman, D. (2017). Modeling landscape connectivity for bobcats using expert-opinion and empirically derived models: How well do they work? *Animal Conservation*, 20(4), 308–320.
- Regnery, B., & Sibley, J.-P. (2017). *Biodiversity offset: Concepts and limits for conserving biodiversity*. Scientist publication of the French Museum.
- Reiss, K. C., & Hernandez, E. (2018). Florida Uniform Mitigation Assessment Method. *Wetland and Stream Rapid Assessments* (pp. 371–379). Elsevier.
- Resasco, J. (2019). Meta-analysis on a Decade of Testing Corridor Efficacy: What Have We Learned? *Current Landscape Ecology Reports*, 1–9.
- Rödger, D., Nekum, S., Cord, A. F., & Engler, J. O. (2016). Coupling satellite data with species distribution and connectivity models as a tool for environmental management and planning in matrix-sensitive species. *Environmental management*, 58(1), 130–143.
- Sahraoui, Y., Foltête, J.-C., & Clauzel, C. (2017). A multi-species approach for assessing the impact of land-cover changes on landscape connectivity. *Landscape ecology*, 32(9), 1819–1835.
- Saunders, D. A., Hobbs, R. J., & Margules, C. R. (1991). Biological consequences of ecosystem fragmentation: A review. *Conservation biology*, 5(1), 18–32.
- Saura, S., Bodin, O., & Fortin, M. J. (2014). Stepping stones are crucial for species' long-distance dispersal and range expansion through habitat networks. *Journal of Applied Ecology*, 51(1), 171–182.
- Saura, S., & de la Fuente, B. (2017). Connectivity as the amount of reachable habitat: conservation priorities and the roles of habitat patches in landscape networks. *Learning Landscape Ecology* (pp. 229–254). Springer.
- Saura, S., Estreguil, C., Mouton, C., & Rodriguez-Freire, M. (2011). Network analysis to assess landscape connectivity trends: Application to European forests (1990–2000). *Ecological Indicators*, 11(2), 407–416.
- Saura, S., & Pascual-Hortal, L. (2007). A new habitat availability index to integrate connectivity in landscape conservation planning: Comparison with existing indices and application to a case study. *Landscape and Urban Planning*, 83(2–3), 91–103.
- Saura, S., & Rubio, L. (2010). A common currency for the different ways in which patches and links can contribute to habitat availability and connectivity in the landscape. *Ecography*, 33(3), 523–537.
- Scemama, P., & Levrel, H. (2013). The emergence of the US wetland compensation market: Impacts on organizational patterns and transaction characteristics. *Revue d'économie politique*, 123(6), 893–924.
- Scolozzi, R., & Geneletti, D. (2012). A multi-scale qualitative approach to assess the impact of urbanization on natural habitats and their connectivity. *Environmental Impact Assessment Review*, 36, 9–22.
- Shannon, C. (1948). A Mathematical Theory of Communication. *Bell System Technical Journal*, 27 379-423 & 623-656.
- Simpkins, C. E., Dennis, T. E., Etherington, T. R., & Perry, G. L. (2018). Assessing the performance of common landscape connectivity metrics using a virtual ecologist approach. *Ecological modelling*, 367, 13–23.
- Sordello, R., Conruyt-Rogeeon, G., Merlet, F., Houard, X., & Touroult, J. (2013). *Review on needs relating to movements and ecological functionality of 39 species proposed for the French list for national consistency of the green and blue corridor Muséum national d'histoire naturelle (MNHN)-Service du Patrimoine naturel et Office pour les insectes et leur environnement*. Opie, 20.
- Sutherland, G. D., Harestad, A. S., Price, K., & Lertzman, K. P. (2000). Scaling of natal dispersal distances in terrestrial birds and mammals. *Conservation ecology*, 4(1).
- Tannier, C., Bourgeois, M., Houot, H., & Foltête, J.-C. (2016). Impact of urban developments on the functional connectivity of forested habitats: A joint contribution of advanced urban models and landscape graphs. *Land Use Policy*, 52, 76–91.
- Tarabon, S., Bergès, L., Dutoit, T., & Isselin-Nondedeu, F. (2019a). Environmental impact assessment of development projects improved by merging species distribution and habitat connectivity modelling. *Journal of environmental management*, 241, 439–449.
- Tarabon, S., Bergès, L., Dutoit, T., & Isselin-Nondedeu, F. (2019b). Maximizing habitat

- connectivity in the mitigation hierarchy. A case study on three terrestrial mammals in an urban environment. *Journal of Environmental Management*, 243, 340–349.
- Taylor, P. D., Fahrig, L., Henein, K., & Merriam, G. (1993). Connectivity is a vital element of landscape structure. *Oikos*, 571–573.
- Thorn, S., Hobbs, R. J., & Valentine, L. E. (2018). Effectiveness of biodiversity offsets: An assessment of a controversial offset in Perth. *Western Australia, Biological Conservation*, 228, 291–300.
- Tournant, P., Afonso, E., Roué, S., Giraudoux, P., & Foltête, J.-C. (2013). Evaluating the effect of habitat connectivity on the distribution of lesser horseshoe bat maternity roosts using landscape graphs. *Biological Conservation*, 164, 39–49.
- Tracey, J. (2006). Individual-based modeling as a tool for conserving connectivity. *Conservation Biology Series-Cambridge*, 14, 343.
- Urban, D. L., Minor, E. S., Tremblay, E. A., & Schick, R. S. (2009). Graph models of habitat mosaics. *Ecology letters*, 12(3), 260–273.
- van Teeffelen, A. J., Opdam, P., Wätzold, F., Hartig, F., Johst, K., Drechsler, M., ... Quétier, F. (2014). Ecological and economic conditions and associated institutional challenges for conservation banking in dynamic landscapes. *Landscape and Urban Planning*, 130, 64–72.
- Vincenz, B., & Reyer, H.-U. (2005). *Road Effects on a Fire Salamander Population (Salamandra salamandra terrestris)*. Universität Zürich.
- Weissgerber, M., Roturier, S., Julliard, R., & Guillet, F. (2019). Biodiversity offsetting: Certainty of the net loss but uncertainty of the net gain. *Biological Conservation*, 237, 200–208.
- Wende, W., Bezombes, L., & Reinert, M.-E. (2018). Introduction of a European Strategy on No Net Loss of Biodiversity. *Biodiversity Offsets* (pp. 5–15). Springer.
- Wintle, B. A., Kujala, H., Whitehead, A., Cameron, A., Veloz, S., Kukkala, A., ... Cadenhead, N. C. (2019). Global synthesis of conservation studies reveals the importance of small habitat patches for biodiversity. *Proceedings of the National Academy of Sciences*, 116(3), 909–914.