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Research Paper

Assessing habitat loss, fragmentation and ecological connectivity in Luxembourg to support spatial planning

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ABSTRACT

The increasing global population requires new infrastructure and urban development, and these land use changes have an impact on habitats and their ecological connectivity. To anticipate and minimise these impacts, environmental and urban planners require tools and methods that they can use at early planning stages. This paper investigates and selects landscape ecology techniques that can be used by planners to assess the effects in terms of changes in habitat loss, fragmentation and ecological connectivity due to expected land use changes. The selected techniques were tested in Luxembourg. Twelve landscape metrics, four connectivity indices, and one connectivity model were selected based on their straightforwardness, widespread application, and accessibility. Land cover maps and proposed areas of urban development up to 2030 were used as input data, together with adapted resistance surfaces from previous studies and a matrix of presence/absence for six target species. The combined analysis reveals a trend of increasing habitat fragmentation and loss of habitats, as well as a reduction of ecological connectivity with regard to all the targeted species, and suggests that this trend will likely continue in the near future. The selected landscape metrics, connectivity indices, the connectivity model and the software used to run them makes the abovementioned techniques easy to use by non-experts, and their combination helps to reduce some of the limitations of each individual technique. Both aspects might be useful in order to mainstream the use of landscape ecology techniques in spatial planning processes.

1. Introduction

The current, global population growth, which is estimated to be 81 million people per year (United Nations. (2018), 2018), will require increased urban development and productive land uses that could have negative ecological consequences. Among these, habitat loss and fragmentation (i.e. increase in the subdivision of habitats) as a result of land use conversion are already widely recognised as a major threat to biodiversity conservation, especially for industrialised regions such as Europe (Adriaensen et al., 2003; Jaeger, 2000; Madadi et al., 2017; Scolozzi & Geneletti, 2012a). Habitat loss, fragmentation and the creation of new barriers resulting from land use changes (e.g. increase of unsuitable land covers or linear infrastructures impeding species movement) affect the ecological connectivity for different species (Januchowski-Hartley et al., 2013; Mimet, Clauzel, & Foltête, 2016). For example, if the distance between suitable patches surpasses a species-specific threshold (e.g. maximum distance the species could move over a certain land cover), a reduction of the ecological connectivity for that species will occur (Edelsparre, Shahid, & Fitzpatrick, 2018). For this reason, land use conversions should consider the potential negative ecological impacts and avoid or mitigate them. Hence, in order to minimise habitat loss, fragmentation, and a reduction of ecological connectivity, spatial planners should take advantage of accessible, easy to use, and robust tools to evaluate spatial planning alternatives at early stages.

In the past two decades, landscape metrics have been used to analyse changes in landscape patterns to provide information on the potential impacts on abiotic and biotic functions (Lausch & Herzog, 2002) where the assessment of habitat loss and fragmentation has been a major topic (e.g. McAlpine & Eyre, 2002; Braaker et al., 2014). Landscape metrics can be defined as indicators that measure the spatial composition and configuration of patches, classes of patches (e.g. land-cover classes), or an entire landscape mosaic (e.g. groups of land cover classes in an area of study) at a specific scale (McGarigal, 2013). By characterising changes in the composition and configuration of landscape patterns (e.g. inter-patch distance, patch density) at different

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levels (patch, class, and landscape), landscape metrics can be used to measure habitat loss, fragmentation, and changes in structural connectivity, i.e. the degree to which a landscape mosaic does or does not facilitate the movement of a species among patches (Taylor, Fahrig, Henein, & Merriam, 1993). The use of graph theory is also considered useful in representing landscapes as a set of nodes (patches) and links (connection between two nodes, at first based on distance), from which metrics known as connectivity indices have been developed in order to measure changes in structural connectivity (Loro, Ortega, Arce, & Geneletti, 2015; Saura & Pascual-Hortal, 2007; Zemanova et al., 2017).

More recently, connectivity models have been developed for measuring functional connectivity, i.e. responses of individuals to landscape elements and their spatial configuration in the landscape mosaic (Kindlmann & Burel, 2008; Tischendorf & Fahrig, 2000). Examples of these model types include least-cost path analysis, circuit theory (both based on graph theory), matrix theory, and agent or individual-based modelling (see Kool, Moilanen, and Treml (2013) for a detailed explanation on connectivity models). Connectivity indices can also be used in combination with least-cost path modelling approaches when aspects such as the landscape resistance to the movement of specific species in a study area is taken into account for the definition of links (Scolozzi & Geneletti, 2012b).

Landscape metrics, connectivity indices, and connectivity models provide many valuable alternatives for characterizing land fragmentation and connectivity. However, this plethora of tools makes it difficult for spatial planners to identify appropriate metrics, indices or models to use, especially when in some cases there is still no agreement among experts (Calabrese & Fagan, 2004). Additionally, scientific studies often only take into account one representative species when assessing the potential effects of land use changes or adequacy of ecological corridors (e.g. Benedek, Nagy, Rácz, Jordán, & Varga, 2011; Gray, Wilmers, Reed, & Merenlender, 2016), although recent multi-species studies are emerging (e.g. Pereira, Saura, & Jordán, 2017; Pereira, 2018). If single-species studies are used to guide environmental or urban plans, this could generate a bias towards the better conservation of certain groups of species and make plans for broader biological conservation ineffective. It then becomes relevant for environmental planners to draft planning alternatives making use of a larger set of representative species, while balancing the amount of data required to ensure the feasibility (in time and cost) of the assessments.

The aim of this paper is two-fold. The first objective is to select appropriate landscape metrics, connectivity indices, and the tools/software to analyse functional connectivity that are accessible to planners for the assessment of landscape fragmentation and changes in structural and functional connectivity from non-urban to urban contexts. The second objective is to apply the selected metrics, indices, and models to a specific national landscape currently faced with the challenges of land fragmentation and connectivity, simulating a scenario similar to the ones planners might face in practice. Luxembourg was selected as a case study since it is already one of the most (habitat) fragmented countries in the EU (Agency, 2011), and its population is expected to almost double between 2015 and 2060, reaching one million people by 2062 (Eurostat, 2015). This application helps identify the strengths and weaknesses of the proposed methodology, suggests refinements required to facilitate its applicability in planning processes, and informs spatial planners about the impact of future land-use conversions.

2. Materials & methods

Fig. 1 summarises the methodological steps from the selection of metrics, connectivity indices and models to the mapping and interpretation of results. The following sub-sections describe each step in detail.

2.1. Selection of landscape metrics, connectivity indices and ecological connectivity models

An initial literature review of case studies, comparative studies, and critical reviews was performed on Scopus including the terms fragmentation, landscape metrics, and connectivity (see specific search string in Table S0, Supplementary Material). The search was limited to the last 10 years to ensure the selection of up-to-date applications of landscape metrics, connectivity indices and models. This search returned 158 papers. From those, only 57 (Table S1, Supplementary Material) ultimately assessed fragmentation (25 papers), connectivity (25 papers), or both (7 papers) using landscape metrics or ecological connectivity indices or connectivity models. The latter were classified by modelling approaches based on the classification of Kool et al. (2013).

Supported on the discussions in the papers and key references (e.g. Kindlmann & Burel, 2008; Uuemaa, Mander, & Marja, 2013) about adequacy and limitations, 20 landscape metrics (landscape, class, and patch level), 9 connectivity indices, and 17 ecological connectivity tools/software were pre-selected for the assessment of habitat loss and fragmentation, and ecological connectivity. As a condition, the pre-selected metrics and indices should be able to be calculated making use of Fragstats v 4.4 (McGarigal, Cushman, & Ene, 2012) or Conefor v 2.4 (S. Saura & Torné, 2012). Both software are open-source and widely used by scientists for an automatised calculation of metrics and connectivity indices, compatible with GIS outputs, facilitating the integration of results into spatial outputs. The preselected metrics were also mentioned at least three times in the literature review in habitat fragmentation studies (Table S2a, Supplementary Material).

Next, the metrics were narrowed down to a smaller set of 12 landscape metrics (Table 1) according to three criteria: simplicity, lack of redundancy, and history of application. If landscape metrics presented no difference in terms of adequacy, the most simple ones (i.e. fewer geometrical attributes and less mathematical operations) were prioritised. The history of application shows that the adequacy of the metrics have already been demonstrated, reinforcing their robustness.

From the nine connectivity indices, four were selected (Table 1), the only ones mentioned at least three times in the papers (Table S2b, Supplementary Material). Also, a review by Baranyi, Saura, Podani, and Jordán (2011) showed that three out of these four connectivity indices (i.e. the ones that can be run at node level) stood out for their capacity to capture most of the variability in the connectivity changes of patches. In other words, these indices are non-redundant and complementary indicators that will ensure time-effectiveness in terms of analysis and posterior interpretation of the assessments.

With respect to the 17 ecological connectivity tools/software, 11 were identified in the literature, and the other six were already known by the authors (see the list of tools and short description in Table S3, Supplementary Material). Only eight were freely available and not dependent on commercial software (i.e. UNICOR, Guidos, Connectivity Analysis Toolkit, Maxent, Circuitscape, Condatis, Graphab, and LSCorridors), which was an essential criterion to ensure accessibility to tools for planners. From these, UNICOR and Guidos were excluded because of their lack of accessibility in terms of technical knowledge required. UNICOR was excluded because it requires additional software (ZonationX), python packages and needs to be run through a python editor, making it less user-friendly. Guidos toolbox includes many tools, but it is a software more tailored to experts with a strong technical background in image analysis for ecological purposes. Later, taking into account the redundancy of modelling approaches, the Connectivity Analysis toolkit was excluded because it is based on the assessment of centrality connectivity indices, which would include the connectivity indices calculated through Conefor. Outputs from Maxent in the form of a species distribution grid at 1 km resolution, already developed by Titeux, Mestdagh, and Cantú-Salazar (2013) in a previous work, are used as inputs in the case study to give information on the presence/

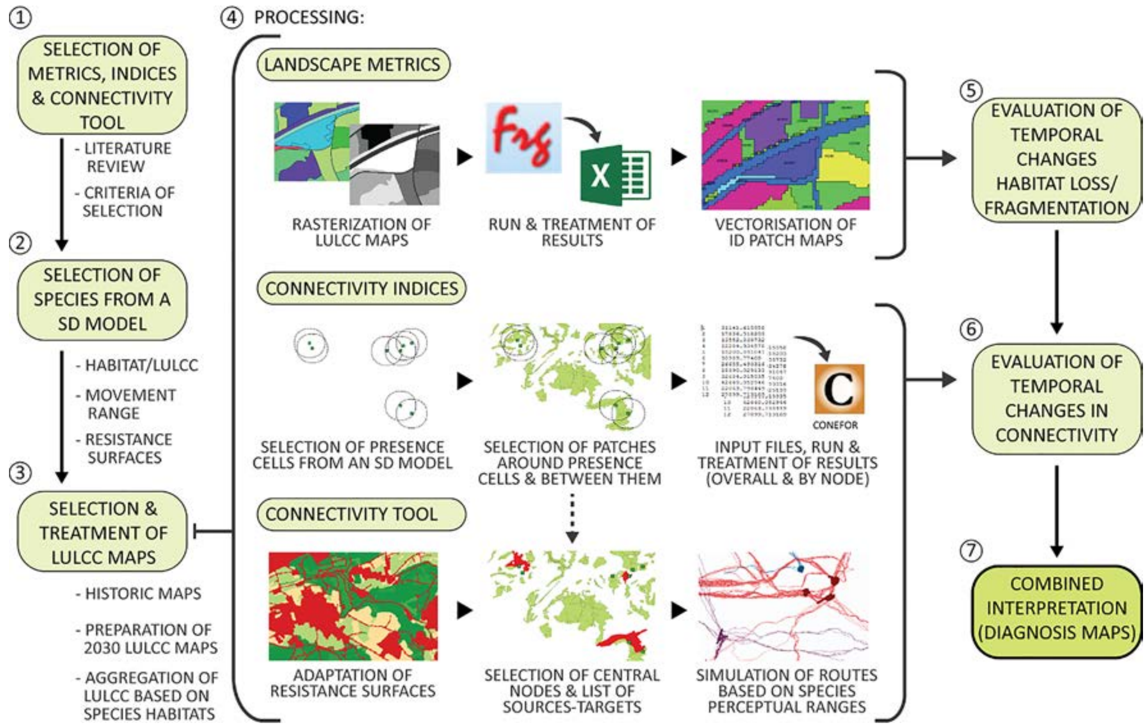

Fig. 1. Flowchart of the methodological steps; SD = Species Distribution; LULCC: land use/cover classes.

absence of species (see Section 2.5 for further details). Hence, four potential tools/software were preselected (i.e. Circuitscape, Condatis, Graphab, and LSCorridors) and the differences in the rationales and underlying assumptions of their modelling methods were further described in Table 2. Circuitscape (McRae, Shah, & Mohapatra, 2013) and Condatis (Hodgson, Thomas, Dytham, Travis, & Cornell, 2012) both apply circuit theory, while Graphab is based on graph theory, allowing calculations to be made based on Euclidean distance or cost distances (Foltête, Clauzel, & Vuidel, 2012). Conefor also allows the calculation of connectivity indices based on Euclidean and cost distance. Instead, LSCorridors uses the least-cost path analyses (Ribeiro et al., 2017).

Out of these four tools, LSCorridors was selected as the application for Luxembourg. The model mitigates a few of the common limitations of least-cost path and circuit theory models (i.e. assumption of omniscience and no influence of surrounding patches (Coulon et al., 2015; Delattre, Baudry, & Burel, 2018; Palmer, Coulon, & Travis, 2011)) by including stochastic variation, species perception, and landscape influence. Furthermore, LSCorridors permits the assessment of connectivity using a modelling approach different to graph theory only (i.e. least-cost path), which is already considered via the connectivity indices. Like other least-cost path models, LSCorridors requires the definition of a resistance surface with the cost of movement for each patch (cell) of the study area. The environmental stochasticity, as defined by Fujiwara and Takada (2017), is integrated through how the cost per cell is considered by using four different route simulation methods: measures by pixel (MP), measures by landscape-minimum, average, and maximum (MLmin, MLavg, and MLmax). The first method (MP) adds a random variability in the resistance surface, while the ML methods also integrate the landscape influence by considering how the value of the cells inside a moving window (equivalent to the species perception) influence the value of the central cell (Ribeiro et al., 2017). In other words, in MLmin, MLavg, and MLmax, the value of each resistance surface cell is substituted by the minimum, average or maximum value of the surrounding pixels inside the moving window (Ribeiro et al., 2017). It is suggested using MP, MLmin, and MLavg to model the movement of generalist species, while MLmax is recommended for specialist species because it generates more restrictive corridor routes (Ribeiro et al., 2017). Since we have selected species with different degrees of specialism (see Section 2.3), all four-simulation methods were used in our case study

2.2. Study area

Luxembourg is situated in Western Europe sharing borders with Belgium to the west, France to the south, and Germany to the east. The land cover in the northern part of Luxembourg (Oesling, a hilly area of 828 km^2) is mainly characterised by forests of spruce (*Picea abies, Pseudotsuga menziesii)* and oak (*Quercus robur*) in the hills with meadows, pastures, and arable land in the valleys and plateaus. The Gutland region (1758 km^2), which is less hilly and located in the southern part of Luxembourg, has a land cover mainly composed of arable land, meadows, pastures and extended deciduous forests *(Fagus sylvatica*, *Quercus robur*, *Carpinus betulus*). Currently, around 50% of the country's land is used for agriculture, with most of it in the southern part of Luxembourg, and of which, half is made up of pasture and meadows (Dietz & Pir, 2009; Schley, Dufrêne, Krier, & Frantz, 2008).

2.3. Selection of species

The animal species were selected from an existing dataset that included the potential distribution of species (i.e. presence/absence matrix) calculated using the species distribution model of Titeux et al. (2013). The following non-excluding criteria were used for the selection of species (Table 3):

i) Conservation status according to the European Habitats Directive. Priority was given to species with a bad or inadequate conservation status, but those with a favourable status were included if relevant for the other criteria. The use of the European Habitats Directive conservation status list was preferred to others because EU spatial planners are obliged to take this into account, since non-favourable conservation status and the priority species and habitats indicated in the Directive's Annexes are a means of establishing priority settings.

Table 1
Type and description of the selected landscape metrics and connectivity indices (see McGarigal et al., 2012; Saura & Torné, 2012 for detailed information about metrics and indices).

Type	Metrics/Indices	Name	Level	Units	Range	Function and rationale
Landscape Metric (Area)	PLAND	Percent land area	C	% of total land	0–100	Explains the amount of habitat (using land use/cover class as proxy) over time to understand habitat loss; 0 = all patches of habitat disappeared; 100 = One habitat occupies all the landscape.
	AREA (AW, CV)	Area	P/C	Ha	0-total class area	Information about the average-weighted (AW) amount of patch area in each land use/cover class and its coefficient of variation (CV) describes the viable area for habitat specialist species. A reduction in AREA at class level usually indicates increasing fragmentation of a land use/cover class. The AREA at patch level provides the dimension of each patch making use of the same raster used for class level analysis, which could be used in combination with class level results to ascertain which patches are below AW AREA.
	CORE (AW*, CV)	Core area	C	Ha	0-total class area	Average-weighted (AW) amount of inner patch area in each land use/cover class and its coefficient of variation (CV) of the patch areas; describe the suitable area for habitat specialist species taking into account the outer areas of the patch that they will not use. Reduction in CORE_AREA indicates fragmentation and loss of suitable habitats and shows whether the patches are below a minimum threshold for specific species.
	LPI	Largest patch index	C	% of total land	0–100	Percentage of total land occupied by the largest patch in a specific land use/cover class. Reductions in LPI indicate fragmentation of an LCC (class level) or increased patchiness (landscape level).
	ED	Edge density	C	Edge Metres/Ha	0-Limitless	Increase usually indicates fragmentation of patches. If (CORE) AREA increases and ED decreases, growth occurred as an expansion of existing patches. Together with AREA and LPI, ED reduction shows increased patchiness of each land use/cover class.
Landscape Metric (Shape)	SHAPE (AW*, CV)	Shape	P/C	None	1-Limitless	Average-weighted (AW) shape of patches of each land use/cover class and its coefficient of variation (CV) explain the naturalness of the patches. Values close to one indicate that patches are quite regular (man-made). When a value increases beyond one, patches are irregular in form and more naturalised. However, for urban land use/cover class, irregular patches usually indicate increased sprawl.
	PD	Patch density	C	No./100 Ha	0-Limitless	Amount of fragmentation (increase of PD) or aggregation (decrease of PD) of patches of a land use/cover class or all the land cover patches in the study area.
Landscape Metric (Aggregation)	NLSI	Normalised landscape shape index	C	None	0–1	Values close to one mean that patches are isolated or uniformly distributed, whilst values close to zero indicate increased clumpiness**.
	MESH	Effective mesh size	C	Ha	Ratio of cell size to Total landscape area	Probability that two random patches of a land cover class (or different land cover classes at the landscape level) are connected in the study area. A decrease indicates higher fragmentation, indicating loss of structural connectivity.
	ENN (AW*, CV)*	Euclidean nearest-neighbour distance	C	Metres	0-Limitless	Metric that informs about distance to the nearest patch of the same land use/cover class. It measures loss of structural connectivity without considering the characteristics of the other land use/cover class or the presence of barriers and how these increase or decrease the cost of movement for different species.
	CONTAG	Contagion index	L	None	0–100	Overall clumpiness of all the land use/cover class in the landscape; but also the interspersion of patches of different land covers in the study area. Values close to zero indicate patches maximally disaggregated or equally interspersed; a value approaching 100 shows that all the LCC are maximally aggregated.
Landscape Metric (Diversity)	SHDI	Shannon's diversity index	L	None	0-Limitless	Evaluate the increase in the diversity and heterogeneity of land covers in the landscape. For the same area of study, a decrease in values indicates increased homogenisation of the land use/cover class, which can be interpreted as loss of habitats.
Connectivity Indices***	BC, BC(IIC), BC(PC)	Betweenness centrality	N	None		These correspond to the degree to which the movement (Euclidean distance or cost-distance***) between other nodes (patches) passes through a particular patch. *BC* only considers the number of movements between patches that go through a particular patch. *BC(IIC)* and *BC(PC)*, however, take into account an additional attribute (in this paper, the attribute is area) of the patches that are being connected through a particular node from a binary approach (IIC) and a probabilistic one (PC).
	IIC (dIntra, dFlux, dConnect)	Integral index of connectivity	O/N	None	0–1	A binary index (graphs with unweighted links) that measures whether a patch (node) is connected (value 1) or not (value 0), taking into account a maximum distance of dispersal. The value increases with increased connectivity. For an overall connectivity assessment ("class level"), a value of one indicates that the entire area of study is occupied by the habitat studied. Their components provide the following information at the patch (node)-

(*continued on next page*)

Table 1 (*continued*)

Type	Metrics/Indices	Name	Level	Units	Range	Function and rationale
						level: internal connectivity in each patch (dIntra); importance of the patch for the current dispersal of individuals (dFlux); and loss of connectivity in the network if a specific patch is lost (dConnect).
	PC (PCintra, PCflux, PCconnect)	Probability of connectivity	O/N	None	0–1	A probabilistic index (graphs with weighted links) that indicates the probability that two animals randomly located in the study area are in habitats connected to each other, instead of binary values such as IIC. Similar to an IIC increase from 0 to 1, PC can be run to obtain an overall value or value by patch accounting for the same components.
	EC, (EC(IIC), EC(PC))	Equivalent connected area	O	Area (m^2, ha, km^2,…)	0-Total Landscape Area	EC is defined as the area of a single habitat patch that would provide the same connectivity as the existing habitat patterns of the area of study. EC(IIC) corresponds to the area equivalent to the connectivity value of IIC and EC(PC) to the area equivalent to the connectivity value of PC. This index can be run only for overall connectivity assessments.

* AW offers a landscape-centric perspective that considers the abundance of patches, giving more weight to bigger patches showing the average patch area/core area/shape/distance to other patches that an individual from a species in a random point of the study area may encounter.

** Clumpiness refers to the level of aggregation of each of the different land use/cover class patches, indicating whether or not they are distributed as clumps or as close adjacent groups in the landscape.

*** If the connectivity indices are calculated based on Euclidean distances, the analysis is structural. However, with modifications, these can be calculated based on cost distances by using resistance surfaces, which makes them adequate for functional connectivity analysis. **P** = patch, **C** = class, **L** = landscape; **O** = Overall connectivity analysis (equivalent to class level); **N** = node level analysis (equivalent to patch level).

ii) Balance distribution of taxonomic classes and types of consumers. At least one species, if possible two, per taxonomic class were selected to ensure the presence of different taxonomic classes. In the case of mammals, differentiation between primary consumers (e.g. rodents) and secondary to quaternary consumers (e.g. foxes, wildcats) was also taken into account. Birds were preselected (*Accipiter gentilis, Anthus pratensis,* and *Terastres bonasia*), but due to the lack of data, they were eventually excluded. Fish were not included in the study, since they would require a very specific habitat fragmentation and connectivity analysis that cannot be developed by making use of national land use/cover class maps.

iii) The use of representative or surrogate species. Surrogate species are those that can provide a good representation of a larger group of species and types of habitats they are associated with, such as keystone, umbrella and flagship species among others (Caro & O'Doherty, 1999; Favreau et al., 2006). We prioritise species that were recognised as habitat specialists, instead of generalists, as well as those already recognised in the literature as adequate surrogates for other species in forest, grassland and wetland habitats. In connectivity analysis, surrogate species can be also used (e.g. Mortelliti, Santulli Sanzo, & Boitani, 2009) to represent species with a different capacity of movement. As a result, we ensured some variety in the mobility range of the selected species.

The use of the criteria stated above prevented skewing the analysis towards a specific taxonomic group and specific habitat specialist. This ensures that locally vulnerable species were considered, whilst reducing the economic burden of addressing individual species' requirements. This methodological choice was chosen to simulate a scenario similar to the ones environmental planners might face in practice during the definition of urban development strategies or ecological corridors.

2.4. Selection and treatment of land use/cover class maps

The landscape metrics and connectivity indices were calculated for 1999, 2007 and 2030 by using the Luxembourgish land use/cover class maps of 1999 and 2007 (scale 1:20.000, a minimum mapping width measured by the authors of 4 m), the Urban Atlas of 2012 (minimum mapping unit of 0.25 Ha and minimum mapping width of 10 m), and a set of potential urban and infrastructure developments for 2030, which were taken from the Luxembourgish online geographic portal (geoportail.lu). The land cover maps of 1999 and 2007 are the only existing Luxembourgish national land cover maps. The development plans found on the geographic portal came from the Luxembourgish sectoral plans (*Plans sectoriels*, *Administration du Cadastre et de la Topographie*) and were digitalised by the authors. In order to create a land use/cover class map for 2030, the urban areas of the Urban Atlas of 2012 (European Union, 2018) were extracted and overlapped on the land use/cover class map of 2007, substituting non-urban land covers with new urban ones. Next, the digitalised 2030 future urban and infrastructure developments taken from the geographic portal were overlapped. This was used as a plausible scenario of urban growth for 2030, assuming that the changes in the land use/cover class will mainly be attributed to urban development. It was not possible to see changes between non-urban land use/cover class (e.g. grasslands converting to croplands or vice versa). The aggregation of land use/cover class for the raster (Table 4) was applied taking into account the habitat preferences of the species studied (Table 3).

2.5. Landscape metrics, connectivity indices and models

For the calculation of landscape metrics, all land use/cover class maps were rasterised at a resolution of 10 m (maximum resolution possible due to the minimum mapping width of the Urban Atlas 2012). The use of a high resolution minimises the loss of accuracy when transforming land cover maps into raster, especially for transport

Table 2
Connectivity modelling approaches selected (rationale and assumptions). The organisation follows the classification of modelling approaches of Kool et al. (2013).

Modelling approaches	Rationale	Assumptions
Circuit theory	A mathematical approach to calculate the path of least resistance through which an electrical current can travel in a circuit of multiple parallel paths (Svoboda & Dorf, 2003). Its application to ecological connectivity is more flexible resulting in a more complex and unpredictable set of possible pathways (Mcrae, Dickson, Keitt, & Shah, 2008).	Models usually assume patch homogeneity, usually employing land use/ cover class as the main attribute and do not consider the direction of movement through a cell or the characteristic of surrounding patches. It assumes the individual has perfect knowledge of their surroundings (omniscience).
Graph theory	This explains the landscape as a set of nodes and edges (paths connecting nodes). Movement (called a "walk") can occur between nodes (usually geometrically represented as the centroid of patches) only if an edge connection exists between those nodes (Bunn, Urban, & Keitt, 2000; Kent, 2009).	Distance between unconnected nodes (nodes that are not connected by a walk of edges) is infinite. Least-cost path and circuit theory can be integrated with graph theory by adjusting the Euclidian length of edges according to their weighted length (cost-weighted or resistance weighted, respectively) (Bunn et al., 2000; Mcrae et al., 2008).
Least-cost path	This assumes a cost per type of patch (or raster cell) based on their attributes. Euclidian distances are weighted by their costs and the minimum sum of cost-weighted distances is the least-cost path (Bunn et al., 2000; Zetterberg, Mörtberg, & Balfors, 2010)	As circuit theory, these models usually assume patch homogeneity, do not consider direction of movement, characteristics of surrounding patches, and assume omniscience.

infrastructure land use/cover class, and therefore minimising the impacts on metrics results calculated in Fragstats v4.4. Also, none of the selected species required an edge depth below 10 m since their adequate minimum habitat was higher (Olsson, 1997; Edgar & Bird, 2006; Pereboom et al., 2008; Dietz & Pir, 2009; Lozano, 2010; Bosch, Beebee, Schmidt, Tejedo, Martinez Solano, Salvador, García París, Recuero Gil, Arntzen, Díaz-Paniagua, & Marquez, 2016; Bani et al., 2017). In the maps, to ensure the continuity of the roads and rail infrastructure in rural areas and their disappearance in favour of urban LULLCs inside settlements, urban land use/cover classes and later transport infrastructure were prioritised in the rasterisation. Otherwise, the fragmentation effect created by these barriers (i.e. transport infrastructure and urban settlements) is underestimated. The results obtained in Fragstats v4.4 provided the increase/reduction of metric values between 1999 and 2007 and 2007 and 2030. The patch maps were vectorised in QGIS v2.14, and the patch level metric values were joined to their attribute tables. This permits the spatial association of patch level values to specific patches, which is necessary for comparisons between class level and patch level values. Since the rasterisation slightly affects values of area and shape, this step was necessary to ensure coherence between class level and patch level values.

For the calculation of connectivity indices, the species distribution model from Titeux et al. (2013) was used to narrow down the nodes analysed to patches that show presence. This step was necessary since the use of all possible patches in Luxembourg at 10x10m resolution required an excessive computational demand. This step reduced the computational power demand and made the analysis feasible in terms of time-consumption, keeping in mind constraints also relevant in real planning processes. Only preferred land use/cover class patches for each species in a 1 km buffer around the presence cells and those preferred land use/cover class patches in between buffers were selected as nodes for the calculation of connectivity indices. Overall, structural connectivity analysis was run for all species. Node-level connectivity analysis (i.e taking in consideration individual patches) was only done for the four non-mammalian species (*Maculinea arion, Triturus cristatus, Alytes obstetricans, Lacerta agilis*) since the computational power demand required was still excessive to model connectivity at node level for mammals. Once obtained, the differences in all connectivity indices between periods were calculated. At the node-level, the results of Betweeness Centrality (BC, BC(IIC) and BC(PC) variants), inter-patch components of Integral Index of Connectivity, and Probability of Connectivity (dConnector and dFlux (IIC and PC)) were associated with their specific patches to identify highly valuable patches (i.e. ones above the 95th percentile value for all the indices) for each year analysed (1999, 2007, 2030).

Preferred routes of movement were calculated with LSCorridors only for the four species for which node-level analysis was done to avoid excessive computational power demand. These will be the only species for which node-level (structural connectivity) and functional connectivity results were combined. The resistance surfaces of these species were obtained from studies in similar European contexts that developed them based on empirical studies for the same or similar species. For example, in the case of *Maculinea arion*, a grassland butterfly, only the resistance values of land covers existing in our study area were kept. The values of the resistance surfaces were harmonised for all species to a shared value range from 1 to 1000 (Table 4). The presence cells per species obtained from the species distribution models of Titeux et al. (2013) were used to select the pairs of sources (starting patches) and targets (end patches) for the routes that were calculated, as this was the most up-to-date species distribution data available for Luxembourg. For all species, 100 m was assumed as the perceptual range, since a low perceptual range was indicated in the literature for all of these species or similar ones.

3. Results

3.1. Landscape metrics

A first diagnosis of the landscape metrics shows that there are no dramatic changes over time (between 1999 and 2030) for all the metrics. Additionally, the values of Shape Average-weighted (SHAPE_AW), Largest Patch Index (LPI), and Normalised Landscape Shape Index (NLSI) are almost constant, which makes these metrics not sensitive enough for interpretation of changes in Luxembourg. Also, the changes in Core Area Average-weighted (CORE_AW) are equivalent to Area Average-weighted (AREA_AW). Because of this, AREA_AW, simpler than CORE_AW, seems to be sufficient for the interpretation of changes in Luxembourg (see further details in Table S5, Supplementary Material). An initial diagnosis as this one can inform spatial planners, in this case Luxembourgish, about metrics from the initial set selected that might not be sensitive enough or worth to be retained for the assessment of alternative planning options.

At the landscape level, the Shannon diversity index (SHDI) shows a slight increase in the diversity of land use/cover class (from 1.90 to 1.95), which could be result of the increase in urban land covers. Contagion (CONTAG) slightly decreases (from 53.09 to 49.37), which might indicate an initial tendency towards an increased uniformity in the spatial distribution of land use/cover classes. This kind of analysis can provide spatial planners with relevant information on changes in the relation among land cover/use classes, and therefore on the general landscape character.

At the class level, cropland, mixed woodland, coniferous woodland, deciduous woodland, and pasture are the types of non-urban land use/cover classes that occupy most of the landscape, and they are the most

Table 3
Description of the conservation status, land cover preferences, range of movement and representativeness as surrogate species of the species selected for the case study.

Species	Taxonomic group	Conservation status*	Land Cover preferences**	Range of movement***	Representativeness
Maculinea arion (Large blue)[a]	Butterfly	Bad	Grassland and Pasture (Spitzer, Benes, Dandova, Jaskova, & Konvicka, 2009)	390 m as the lowest mean distance to suitable patches (Schneider and Fry, 2001). 500 m assumed as maximum distance	A surrogate for the conservation of grassland invertebrates including other butterflies (Sielezniew, Włostowski, & Dziekańska, 2010; Spitzer et al., 2009)
Triturus cristatus (Great crested newt)[a]	Amphibian	Inadequate	Woodlands and scrubland surrounding ponds(Edgar & Bird, 2006; Vuorio, Reunanen, & Tikkanen, 2016)	Dispersal up to 860 (Edgar & Bird, 2006). 1 km assumed as maximum distance	A surrogate for wetland conservation (Denoël, Perez, Cornet, & Ficetola, 2013; Unglaub, Steinfartz, Drechsler, & Schmidt, 2015)
Alytes obstetricans (Common midwife toad)[a]	Amphibian	Inadequate	Woodlands, scrublands and scarce vegetated areas surrounding ponds (Bosch et al. 2016)	1 km assumed as maximum distance	Extensively studied, but it is not a surrogate. Included to ensure at least a second amphibian with similar land cover preferences
Lacerta agilis (Sand Lizard)[a]	Reptile	Bad	Grassland, pasture and rocky areas (Ceirans, 2007; Russell, 2012)	Evidence of short dispersal less than 150 m (Olsson 1997). 500 m assumed as maximum distance	A surrogate used in connectivity analysis since changes in structural connectivity of their habitats strongly match changes in functional connectivity (Rödder, Nekum, Cord, & Engler, 2016)
Myotis bechsteinii (Bechstein's bat)	Mammal	Inadequate	Deciduous woodlands (M. Dietz & Pir, 2009; Watts et al., 2010)	Less than 1 km to long distance foraging sites Dietz & Pir, 2009); 1 km assumed as maximum distance	Suggested as target species whose habitat protection could benefit other forest dwelling bat species in Luxembourg (M. Dietz & Pir, 2009)
Felis silvestris silvestris (European wildcat)	Mammal	Inadequate	Woodlands and scrublands (Klar et al., 2008, 2012; Lozano, 2010)	2 km assumed as maximum distance	The species is usually selected in connectivity studies as a surrogate of woodland medium size carnivores (e.g. Gurrutxaga, Lozano, & del Gabriel, 2010; Lozano, 2010)
Martes martes (Pine marten)	Mammal	Inadequate	Woodlands (Pereboom et al., 2008; Ruiz-González et al., 2014)	Recorded daily distance is 2.1 km, even if maximum linear distance 860 m (Pereboom et al., 2008). 2 km assumed as maximum distance.	The species is usually selected in connectivity studies as a surrogate of woodland medium size carnivores (Gurrutxaga et al., 2010; Pereboom et al., 2008)
Muscardinus avellanarius (Hazel dormouse)	Mammal	Favourable	Deciduous Woodlands (Bani et al., 2017)	Short dispersal of 500 m in forests and 300 m in open land (Bani et al., 2017). 500 m assumed as maximum distance	A surrogate used in connectivity models (Markus Dietz, Büchner, Hillen, & Schulz, 2018) representative of of red squirrels (Mortelliti et al., 2009), an endangered species

* Extracted from the Habitat Directive Report of 2007–2012 of Luxembourg (Titeux et al., 2013).
** Habitat preferences simplified based on land cover preferences without consideration of other features or microhabitat preferences.
*** Maximum distance used by the authors for LSCorridor and Conefor supported on data from literature review. The range of movement for *Alytes obstetricans*, and *Felis silvestris silvestris* was assumed similar to *Triturus cristatus* and *Martes martes*, respectively, due to lack of data.
[a] Species for which connectivity indices were also studied at patch (node) level and preferred routes of movement were calculated with LScorridors.

Table 4
Aggregation of land use/cover classes of Luxembourg maps and resistance values.*

Aggregated land use/cover class**	Maculinea arion	Triturus cristatus	Alytes obstetricans	Lacerta agilis
High-medium density urban areas	1000	1000	1000	1000
Low-density urban areas	1000	1000	1000	1000
Roads and railways	750	1000	1000	1000
Cropland	500	750	750	975
Pasture	100	250	250	1
Grasslands	100	500	500	1
Scrubland	1000	500	500	800
Deciduous woodland	1000	500	500	975
Coniferous woodland	1000	500	500	800
Mixed woodland	1000	500	500	900
Water	1000	1	1	1000
Wetlands	1000	250	250	1000
Rockland	100	500	500	1000

* The resistance surfaces were obtained from the following references: *Maculinea arion* (Schneider & Fry, 2005); *Triturus cristatus* & *Alytes obstetricans* (Arntzen, Abrahams, Meilink, Iosif, & Zuiderwijk, 2017); *Lacerta agilis* (Russell, 2012). Later, their range of values was harmonised to share the same scale.
** Land use/cover classes corresponding to the ATT Codes can be found in the SI (Table S4).

affected by changes from 1999 to 2007 and the expected changes from 2007 to 2030 (see Fig. 2). Cropland and mixed woodland in particular show a net increase of their area (increasing related habitats) during the whole period, while other land covers decreased. These land use/cover classes are the most relevant in terms of area and changes along time and are also the preferred land use/cover classes of our selected species. Therefore, the analysis of the remaining metrics (Table 5) only focuses on these thematic classes, since these would be the most informative for future land use planning in Luxembourg. Possible applications of the same approach to other contexts should be done according to a similar type of exercise. This means focusing the landscape metric interpretation on the most representative land covers (in area, changes along time, and relevance to surrogate species selected) to ensure time-effectiveness and relevance of the assessment to develop spatial planning recommendations.

In the case of cropland and mixed woodland, the increase in AREA_AW and effective mesh (MESH) from 1999 to 2007 indicate a reduction of the fragmentation and net gain of the two land use/cover classes. The increase in patch density (PD) also shows that new cropland and mixed woodland patches are generated. Additionally, the decrease of Euclidean neighbour (ENN) shows an increase of structural connectivity between cropland patches. From 2007 to 2030, for both cropland and woodland, the slight increase in ENN and the reduction of edge density (ED) and PD identifies a minor loss of entire existing patches.

For pasture and coniferous woodland, the decrease in AREA_AW and MESH explains the reduction in the size of patches. The decrease in ED and PD shows that this decrease was more related to the loss of entire patches than to their fragmentation. The overall increase in ENN, except for pasture, shows reduction of structural connectivity. A slight decrease of ENN in pasture from 2007 to 2030 seems to be the result of losing some of the most isolated patches. However, for deciduous woodland an increase in ED and PD and a decrease in AREA_AW and MESH up to 2007 shows the loss of area due to fragmentation. Instead,

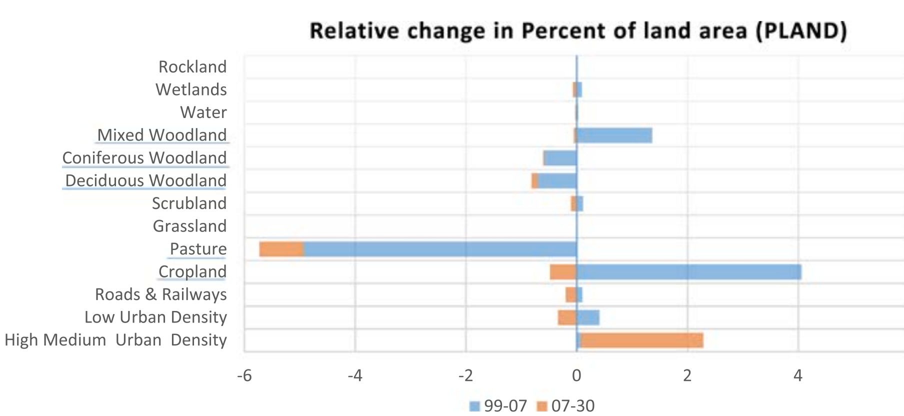

Fig. 2. Relative change in Percent of Land Area (PLAND) of each land use/cover class since 1999. The blue bars show the changes from 1999 to 2007, and the orange bars show the changes from 2007 to 2030. Pasture, cropland, and woodland land use/cover classes are underlined, since these are the classes discussed in depth. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 5
Relative change in percentage of class level metric values from 1999 (99) to 2007(07) and 2007(07) to 2030 (30).

Land Cover Classes and timeframes	Edge Density (ED)		Patch Density (PD)		Average-weighted area (AREA_AW)		Average Euclidean Nearest Neighbour Distance (ENN_AW)		Effective mesh size (MESH)	
	99-07	07-30	99-07	07-30	99-07	07-30	99-07	07-30	99-07	07-30
Cropland	12.65	−2.62	4.29	−2.16	22.33	−0.2	−12.55	0.47	47.7	6.52
Pasture	−12.22	−3.05	−2.44	−4.2	−10.58	−0.66	10.48	0.85	−25.33	−5.24
Deciduous Woodland	0.14	−0.9	0.9	−2.01	−6.77	−0.02	1.18	−0.22	−10	−3.92
Coniferous Woodland	−6.02	−0.5	−5.26	−1.01	−6.23	0.16	5.76	−0.09	−14.06	−2.72
Mixed Woodland	27.99	−2.02	23.92	−2.56	19.67	0.28	−17.99	0.37	58.38	2.64

in 2030 the reduction of ED and PD identifies the loss of entire patches. ENN shows changes equivalent to those of coniferous woodland for the isolation of patches.

Following landscape and class level analysis, a visualisation of AREA at the patch level shows that for pasture, cropland, and coniferous woodland, the larger patches (i.e. those above AREA_AW at class level) were mainly lost and gained from 1999 to 2007 (Fig. 3). However, for deciduous and mixed woodland, the changes in larger patches are more homogeneously distributed. The latter is also the case for the changes in all land use/cover classes from 2007 to 2030. The visualisation of landscape metric results at the patch level, supported on class level thresholds, can inform spatial planners, in this case Luxembourgish, about zones were the loss and fragmentation of habitats are more intense and for which mitigation measures might be more urgent. This information is useful when considering future land use/cover changes in specific areas, but also when developing landscape management interventions for them.

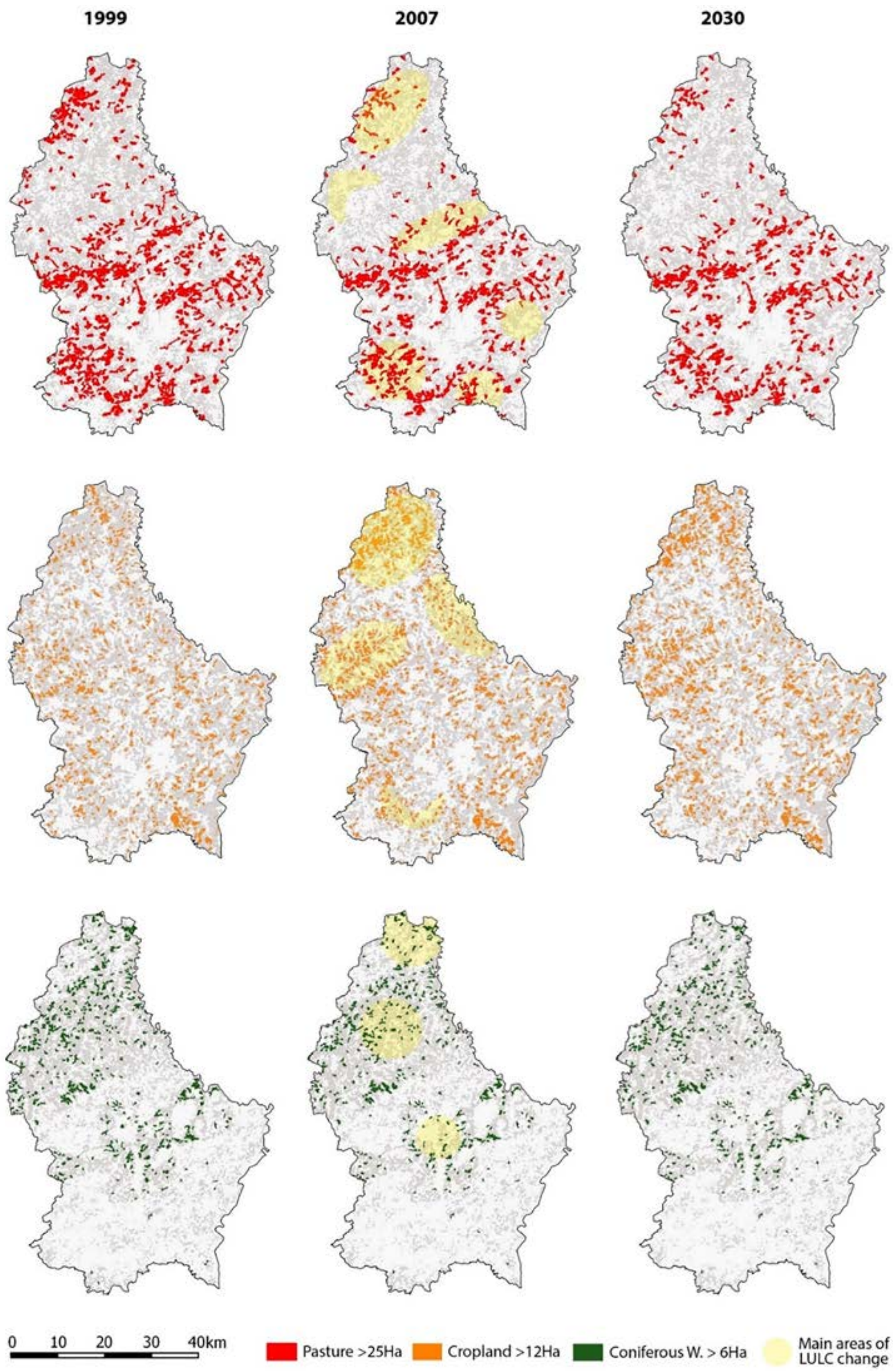

Fig. 3. Distribution of large patches (i.e. those above AREA_AW) in pasture, cropland and coniferous woodland in 1999, 2007 and 2030 (years organised by columns). The areas highlighted in yellow indicate zones where intense loss of large patches occurred for pasture and coniferous woodland. In the case of croplands, this indicates zones where intense increases of large patches occurred. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 6
Relative change (%) of the overall values of the connectivity indices since 1999.

Species	Timeframes	IIC	EC(IIC)	PC	EC(PC)
Maculinea arion	99-07	3.37	1.67	-9.59	-4.91
	07-30	-35.64	-19.37	-39.81	-23.95
Triturus cristatus	99-07	-12.87	-6.66	-17.23	-9.02
	07-30	-9.88	-5.45	-4.72	-2.63
Alytes obstetricans	99-07	5.54	2.73	-21.58	-11.45
	07-30	-8.14	-4.04	-11.98	-7.04
Lacerta agilis	99-07	-26.69	-14.38	-30.46	-16.61
	07-30	-8.72	-5.25	-7.83	-4.83
Myotis bechsteinii	99-07	-23.91	-12.77	-32.41	-17.79
	07-30	-0.81	-0.46	-0.54	-0.32
Muscardinus avellanarius	99-07	-17.81	-9.34	-26.46	-14.25
	07-30	4.62	2.51	-0.31	-0.18
Martes martes	99-07	0.46	0.23	-2.22	-1.12
	07-30	-1.16	-0.58	-2.1	-1.07
Felis silvestris	99-07	-34.24	-18.91	-55.27	-33.12
	07-30	-1.01	-0.63	-2.674	-2.03

3.2. Connectivity indices

An analysis of the results of connectivity indices showed changes in structural connectivity in Luxembourg using a graph-theory method as well as the observation of the performance of binary and probabilistic indices. The main results are described below, for the rest of the connectivity results please refer to Table S6–S10 in the Supplementary Material.

The relative change in the overall value for IIC and PC highlights a reduction of the ecological connectivity for all the selected species from 1999 to 2030 (Table 6). EC makes the implication of this loss clearer, by translating it into an equivalent area of habitat lost if all the connected patches were one single patch. This is quite relevant for species such as *Maculinea arion* or *Felis silvestris,* which lost an equivalent of almost 25% and 33% of habitat, respectively (Fig. 6). For *Maculinea arion, Alytes obstetricans, Martes martes,* and *Muscardinus avellanarius*, the values of IIC and EC (IIC) in one of the periods are contradictory with the values of PC and EC (PC), showing an enhancement of ecological connectivity. This is a consequence of the limitations of binary indices compared to probabilistic ones, which should be considered by spatial planners when using binary indices to analyse planning alternatives, since they consider if patches are connected or not in a more simple form (see Section 4.2 for further explanation).

In the case of *Maculinea arion*, the major decrease in structural connectivity will occur from 2007 to 2030 due to the urban development anticipated in one of the locations where this species is present. In addition, due to the reduced amount of patches for this species, any habitat loss will have a relevant effect on the decrease of ecological connectivity and therefore this sensitivity needs to be considered when making further changes to land use/land covers. For the rest of the species, the major decrease in connectivity occurred from 1999 to 2007. In other geographical contexts, similar exercises might be useful to inform spatial planners about relevant impacts for some species (especially those with a reduced local habitat distribution like *Maculinea arion* in Luxembourg), which could be overlooked if only landscape metrics analysis are performed.

The analysis of the connectivity indices by node for *Maculinea arion, Triturus cristatus, Alytes obstetricans,* and *Lacerta agilis* indicates that there is a low centrality in all patches (i.e. low values for BC, Tables S7–S10, Supplementary Material), and therefore, there are no key patches influencing the dispersal of individuals. However, if centrality is weighted by area (i.e. BC(IIC), BC(PC)), a few of the key patches for dispersal can be identified. This can be observed, for example, in the individual BC(IIC) results mapped in Fig. 4a. The combined analysis of dflux (IIC, PC), dConnector (IIC, PC), and BC(IIC) and BC(PC) identifies “key patches” that are simultaneously relevant as dispersal sources and sinks to maintain the connectivity between other patches and as current stepping stones from a probabilistic and a binary perspective (Fig. 4b). In the case of *Maculinea arion*, part of the “key patches” identified for 1999 and 2007 could be lost due to the urban development predicted for 2030. This result is useful to brief modifications on the Sectorial Plan of Luxembourg to avoid decline of this species (see Fig. 6 in Section 4). In other countries, similar applications might be useful to identify minor specific patch changes affecting species which show loss of overall connectivity along time (like *Maculinea arion* in Luxembourg). This can help spatial planners to draft local urban plans or to make more specific mandatory mitigation actions associated with these plans.

3.3. Functional connectivity tool (LSCorridors)

The functional connectivity analysis based on the least-cost path approach helped us to identify preferred routes of movement for the selected species in the expected land use/cover class mosaic of 2030. In some cases, preferred routes traverse urban areas, which could be explained by the adjacency of most of the sources and targets to urban areas (Fig. 5e). This is also explained by the much longer distances (and higher cost per route) that would be required to avoid them and by the introduction of stochastic variation in original resistance surfaces by LSCorridors. In Luxembourg, this situation is more common in the southern areas due to the increased urbanisation, highly limiting the options of movement of different species. The results also show that there are few overlaps between the routes of the different species (Fig. 5). This evidence a common spatial planning problematic, the difficulty of prioritising ecological corridors when preferences and distributions of several groups of species do not match and need to be taken into account.

Some of the routes for some species (e.g. *Lacerta agilis*) also show a good match with Natura 2000 areas (Fig. 5e). Overlaps like this one could be used by spatial planners to reinforce the relevance of protected

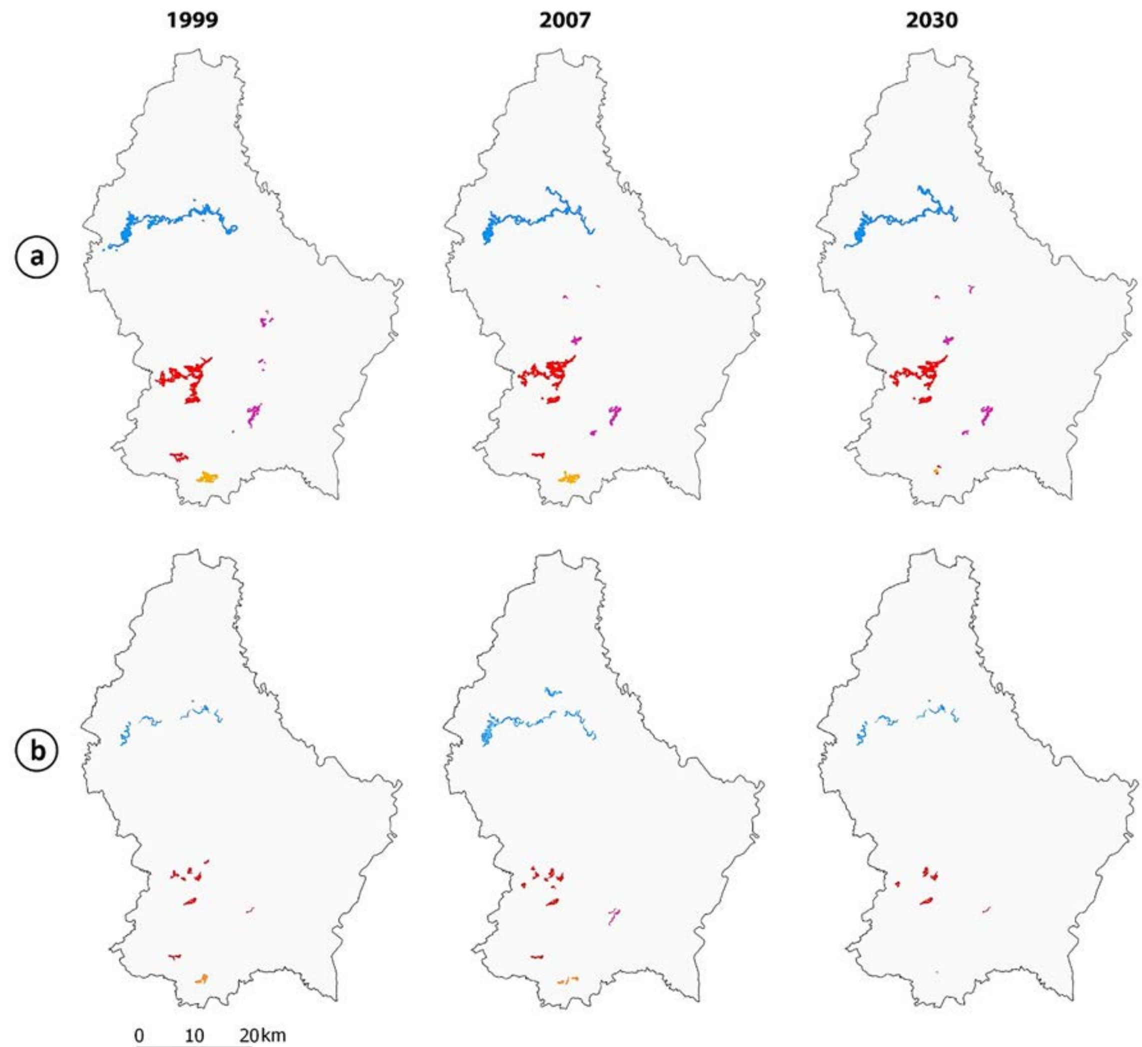

Fig. 4. a) Patches with values above the 95th percentile for BC(PC); b) Patches with values above the 95th percentile for dflux (IIC, PC), dConnector (IIC, PC), BC(IIC), and BC(PC). See reduction in key patches when the 95th percentile values for several indices need to be fulfilled. *Maculinea arion* (orange), *Lacerta agilis* (red), *Alytes obstetricans* (blue), and *Triturus cristatus* (purple) from 1999 to 2030. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

areas for potential animal movement at a national level, and not only for the conservation of the fauna and flora within these areas. In other cases, such as for *Alytes obstetricans*, there are certain areas, such as in the north of Luxembourg (Fig. 5e), where movement between sources does not match Natura 2000 since sources and targets are not yet associated with them. Spatial planners could use this kind of result when discussing new conservation that should be included in an existing network as well as to establish landscape management plans around protected areas that could also influence future local urban plans. Both outputs show an example of how spatial planners, in this case Luxembourgish, could use functional connectivity results together with existing protected areas, such as Nature2000, to prioritise conservation patches along preferred routes of movement to build ecological corridors.

Additionally, the results of the preferred routes of movement complement the connectivity analysis made by the indices, as these can help to identify whether the key connectivity patches identified in Fig. 4 in 2007 are still maintained in 2030. These results also identify whether the preferred routes of movement overlap with those patches. In terms of spatial planning, in this case for Luxembourg, the latter reinforces the value of protecting specific patches of habitats, since structural and functional analysis highlight their relevance, and act as another example of how to prioritise new protected areas for ecological corridors. Further explanations about the limitations and the relevance of the combination of outputs for spatial planning are discussed in Section 4.3.

4. Discussion

4.1. Habitat loss, fragmentation, and ecological connectivity in Luxembourg

The analysis of landscape metrics and connectivity indices shows that a reduction of structural connectivity for all selected species is associated with the loss and fragmentation of pastures, deciduous and coniferous woodlands, grasslands, and rocky areas. It should be noted that a decrease occurs in low density urban areas and transport infrastructure in PLAND (as shown in Fig. 2), which is due to an unavoidable aggregation in the base maps used as inputs. However, from the results, it is clear that the overarching trend is represented by an increase in total urban land area by 2030, consequently reducing non-urban land covers and related habitats.

The period from 1999 to 2007 has not only the greatest observed habitat loss, but also the highest reduction in ecological connectivity for all species, except *Maculinea arion*. However, a reduction in habitat loss

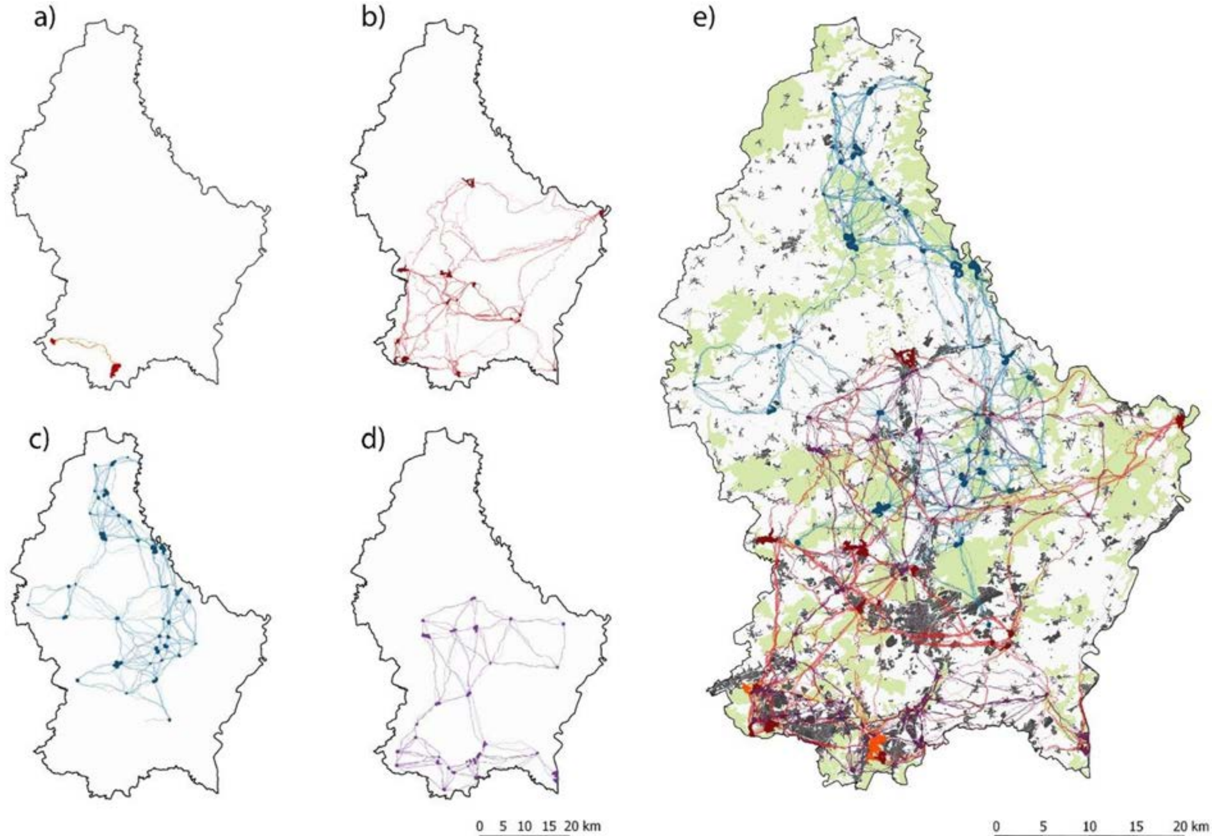

Fig. 5. Preferred routes of movement modelled in LSCorridors for 2030. a) *Maculinea arion*; b) *Lacerta agilis*; c) *Alytes obstetricans*; d) *Triturus cristatus*; e) Overlapping of the preferred routes of movements for the different species over urban areas (grey) and Natura 2000 sites (green). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

from 2007 to 2030, albeit smaller than the previous period, is not followed by a similar decrease in connectivity in all cases, as shown by connectivity indices. For some cases (e.g. *Martes martes, Alytes obstetricans*), the decrease in connectivity is equally as relevant as in the period from 1999 to 2007. This might be related to the fact that the analysis by connectivity indices only considered part of the preferred land use/cover class patches of each species (i.e. patches showing species presence and those in between them in the species distribution model of Titeux et al. (2013)). It is worth remarking, however, that the reduction in ecological connectivity is not always linearly related to habitat loss and fragmentation (Edelsparre et al., 2018; Thompson, Rayfield, & Gonzalez, 2017; Zeigler & Fagan, 2014), something which could further explain this result. For example, in the case of *Martes martes*, almost all the woodland patches in Luxembourg were taken into account in the analysis of connectivity indices due to the well-spread distribution of this species (presence cells) in the landscape. Despite a smaller reduction of preferred land use/cover classes in 2007, the loss of structural connectivity, as shown by connectivity indices, in 2007 and 2030 is almost the same. Moreover, the overall abrupt loss of connectivity for *Maculinea arion* in 2030, supported by the identification of highly valuable patches when applying connectivity metrics, may be caused by the potential loss of key patches in 2030, a result of the new developments proposed in the sectoral plans of Luxembourg (see Fig. 6, in Section 4.3); these impacts cannot be ascertained only from applying landscape metrics.

Regarding the spatial configuration of land use/cover classes, a potential loss of the most isolated patches of pastures and coniferous and deciduous woodland for 2030, shown by a decrease in ENN, might imply a reduction in the spatial distribution of species such as *Muscardinus avellanarius* or *Maculinea arion*, which are specifically dependent on those land use/cover classes. Concurrently, the mapping of patches above the AREA_AM (Fig. 3) identifies a concentrated loss of pastures and coniferous woodland from 1999 to 2007 in zones where preferred movement routes for *Lacerta agilis* and *Triturus obstetricans* exist. As a consequence, a loss of redundancy in potential habitats might be occurring in Luxembourg for several species, which could affect the connectivity of their habitats by jeopardising the movement of individuals between local populations or their future migration to alternative habitats if changes in the local conditions occur.

The results are coherent with a few previous studies in Luxembourg or surrounding areas. Regarding landscape fragmentation, studies from the European Environmental Agency (2011, 2017), using MESH as landscape metric, show that Luxembourg and its surrounding territories are highly fragmented, being one of the most fragmented in Europe. Regarding connectivity, a study by Filz, Engler, Stoffels, Weitzel, and Schmitt (2013) shows low butterfly connectivity for calcareous grasslands in an area of south-western Germany very close to Luxembourg, being similar to our results. No other research for Luxembourg or adjacent territories looking at temporal changes in habitat fragmentation and ecological connectivity were found that could inform or be compared against these results.

4.2. Limitations of metrics, indices and the connectivity model

The application of different landscape assessment techniques in this paper points toward a number of potential limitations that need to be further discussed to support the interpretation of the results obtained, such as:

i) the sensitivity of landscape metrics to spatial and thematic resolution and the difficulty of their interpretation when subtle changes occur. It is well known that the values of landscape metrics strongly

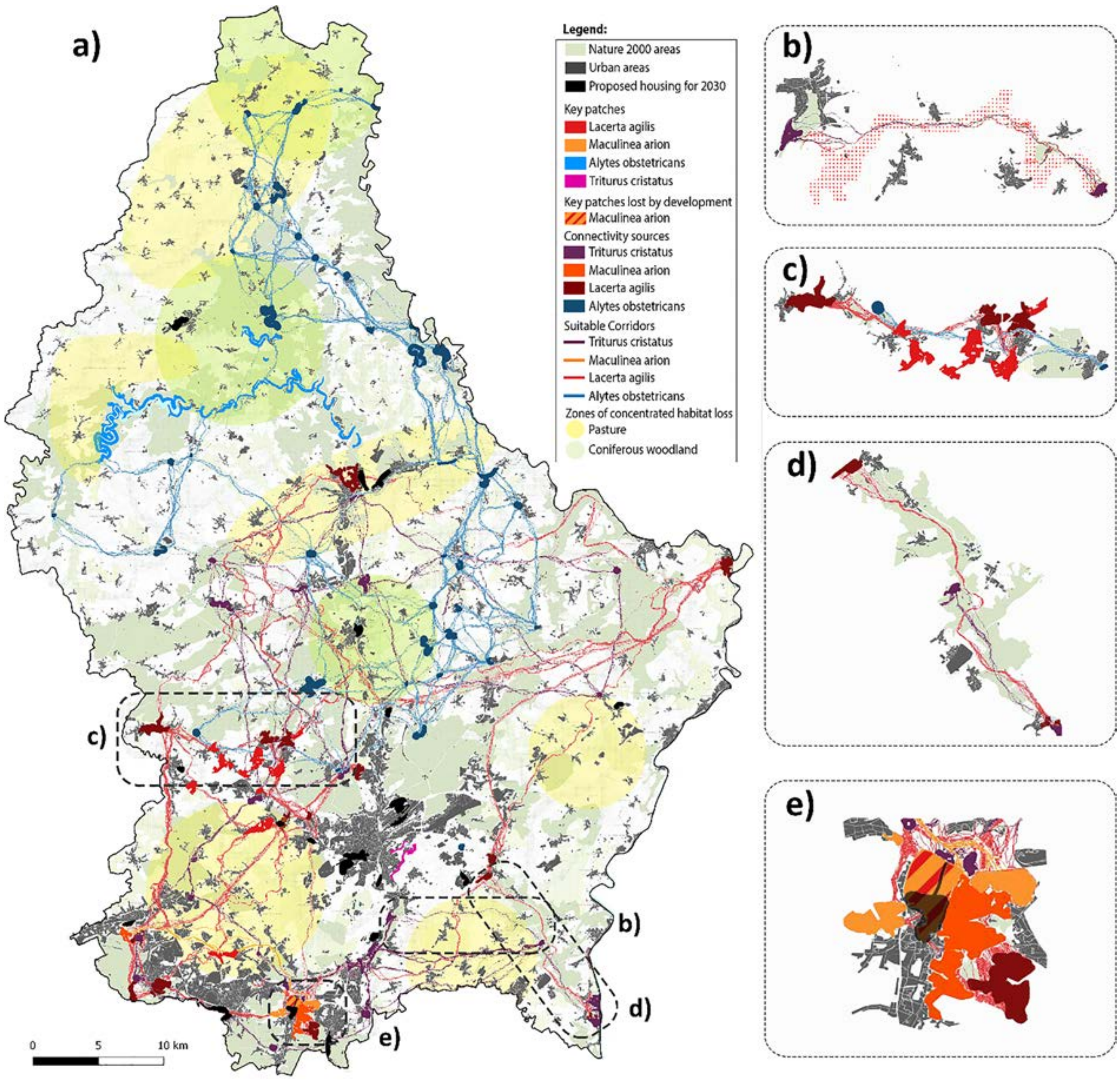

Fig. 6. a) Illustrative diagnosis based on the combination of outputs overlapped onto the "réseaux écologiques" map extracted from the Plan Sectoriel du Paysage (2014) and the current and future development areas (the new housing proposed by the Plan Sectoriel du Logement (2014) is included in black); b) Zoom of proposed ecological corridor (highlighted in red) matching the simulated route of movement for *Triturus cristatus*; c) Zoom to a simulated route matching key patches; d) Zoom to simulated routes for *Lacerta agilis* and *Triturus cristatus* matching Natura 2000 areas; e) Zoom to a settlement in the south of Luxembourg, overlappingg the specific housing development (semi-opaque polygon in black) proposed in the Plan Sectoriel du Logement that contributes to the loss of a key patch for *Maculinea arion*. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

depend on the resolution of the rasterisation process and also are affected by the aggregation of land use/cover class used (Buyantuyev, Wu, & Gries, 2010; Huang, Geiger, & Kupfer, 2006). For example, in the case study proposed here, a resolution of 15 m was also tested (Table S10, Supplementary Material) for which the PLAND value of roads and railways was more overestimated due to rasterisation than at 10 m (since keeping transport infrastructure land covers was prioritised in the rasterisation), further impacting other metrics. The problem of maintaining adequate proportions of transport infrastructure classes during rasterisations has already been shown in previous studies (e.g. Wickham & Riitters, 1995). Additionally, in cases such as that of Luxembourg (i.e. no dramatic changes in the land use/cover class), the values of some metrics might not help to explain fragmentation trends (e.g. LPI, LSI). For other metrics, transformation might be required to facilitate their interpretation and explanation to non-experts (e.g. showing their value changes relatively), which could in some cases misinterpret the meaning.

ii) the potential contradictions between binary and probabilistic connectivity indices. The connectivity indices we have considered are either binary or probabilistic. Binary indices are deterministic and only tell us that the patches are connected or not connected. On the other hand, probabilistic indices incorporate randomness based on probability distributions. The probability distributions work as weighting values for the likelihood of a given decision. A probabilistic model provides sets of connectivity indices according to their probability (Saura & Pascual-Hortal, 2007). For example, agent-based models depend on probabilistic indices for the likelihood of the agent's choices of movement from one patch to another. Sometimes we found that these two types of indices gave different results. For example, IIC connector (binary) gives a higher value to short and intermediate distance patches than PC connector (probabilistic), which affects the overall connectivity value (Bodin & Saura, 2010). In this sense, if land use/cover class conversion generates an increase in adjacent patches of the preferred land use/cover class, and only a few patches are lost, the overall IIC value could increase. This seems to be the reason for results with a positive relative change in overall IIC values when PC values were negative (see Table 5). Hence, as recommended by Saura and Pascual-Hortal (2007), when data is available, spatial planers should prioritise PC above IIC analysis, since it seems to be more adequate and will avoid oversimplification of patch connections.

iii) an under-estimation of urban land use/cover classes resistance by the modelled preferred routes and connectivity indices. Regarding the ecological connectivity model, in some cases, the preferred routes of species cross urban areas, even if this is not very likely to occur since the selected species would tend to avoid them. However, the extensive presence of settlements (i.e. southwestern Luxembourg, Luxembourg City area) in between source and target patches limits the creation of alternative paths, since the accumulated cost due to an increasing length would be much higher than for paths crossing cells classified as urban. Also, the MP, MLmin, and MLavg paths (most of those crossing urban settlements) created with LSCorridors add stochastic variation to the resistance values. This affects the cost of movement, and makes the paths less restrictive than in the case of MLmax. In order to better adapt the resistance surfaces to Luxembourg, and to adjust the stochastic variation applied in LScorridors, their refinement based on empirical animal movement studies applied to Luxembourg would be relevant. This refinement is a common step in the creation of resistance values, but something that has not yet been done in Luxembourg. With respect to the identification of key patches based on connectivity indices, these are not sensitive to the presence of settlements as the case of Triturus cristatus demonstrates (Fig. 6), where key patches are identified in zones surrounded by urban areas, and these are challenging for animals to traverse. This is a limitation of a simple application of connectivity indices based on a structural connectivity perspective, which uses Euclidean distance instead of a functional perspective that makes use of the least-cost path analysis (Saura & Pascual-Hortal, 2007). But also, it is affected by the fact that many patches with the presence of the study species were adjacent to existing settlements.
To cover the limitations of least-cost path (LSCorridors) and the simple application of graph-theory indices (Conefor), models using more advanced heuristic mathematical algorithms could be applied to reproduce ecological corridors. For example, particle swarm (e.g. Liu, Lao, Li, Liu, & Chen, 2012) and ant colony optimisation (e.g. (Yang, Zheng, & Lv, 2012) are two special variants of genetic algorithms based on the movement of animals (bees and ants, respectively) which make use of machine learning. They incorporate a random mutation of weighting values with a clustering algorithm to generate the most probable paths of movement (Dorigo, Birattari, & Stutzle, 2006). However, these methods could be too complex to be technically accessible to planning professionals and no application of them was found during our initial literature review.

iv) *the high computational capacity required to run the models*. The analysis of different species at a national level required the authors to reduce the number of patches to be considered for Conefor 2.6 and LSCorridor due to the excessive computational power demand (for three computers between 2.4 and 2.7 Ghz processors and 8 Gb of RAM). However, for the mammalian species (*Muscardinus avellanarius, Martes martes, Myotis bechsteinii,* and *Felis silvestris*), this was still too heavy to process with the available equipment, and it was not possible to run the analysis at node level (Conefor 2.6). In many cases, running the tools required more than 24 h of processing per studied year and species (e.g. input files for Conefor 2.6, and node level analysis). Moreover, for LSCorridors, although the number of simulations was limited to 40 per pair of patches, the outputs for some species occupied more than 20 Gb. The computational power demand may make the use of these tools difficult for extensive areas by spatial planning practitioners who may not have access to advanced IT infrastructure. Therefore, spatial planners in Luxembourg as well as from other contexts should consider computational power demand from the very beginning before applying this methodological approach to new assessments.

4.3. Implications and opportunities for spatial planning

Despite the abovementioned limitations, outputs likes the ones obtained from using the selected techniques may be useful for spatial planners during the assessment or the drafting of strategies and plans. Furthermore, the specific combination of techniques linking structural (landscape metrics and connectivity indices) and functional analysis (LSCorridors) might be useful to advance the practical utility of landscape ecology techniques for spatial planning and similar purposes. By modelling the preferred routes of movement, the value of some key patches identified by connectivity indices were reinforced, and others were marked as less relevant as a result of the lack of consideration of barriers (i.e. urban areas) by connectivity indices.

As part of spatial planning processes, the combined outputs could be used to improve the diagnosis of current (or potential) habitat status by linking connectivity loss to habitat loss and fragmentation and showing relevant routes of movement and areas to protect in comprehensive maps. In this sense, exercises like this one could be useful for spatial planners in the development (or modification) of strategies and plans. The most relevant routes of movement could be selected by manually removing paths crossing urban areas and giving priority to routes where more simulated paths are adjacent or overlap. These routes could be combined with the key connectivity patches, and the visualisation of patch level results. Then, these outputs can be overlapped onto key features of existing plans (e.g. ecological corridors, protected areas, new areas for housing allocation), and used to support future planning decisions (e.g. selection among alternative spatial development strategies).

To illustrate the above suggestions, Fig. 6a shows the results of our case study overlapped onto the current Landscape Plan (*Plan Sectoriel du Paysage*) and the Housing Plan (*Plan Sectoriel du Logement*). Map windows (boxes b-e) present examples of the potential use of the results to inform planning. Fig. 6b, which shows a match between a preferred route of movement and a specific ecological corridor, can be used to confirm the relevance of the latter, and to identify which specific group or surrogate species (in this case *Alytes obstetricans*) moves through this corridor (see other illustrative examples in Pereira et al., 2017; Pereira, 2018). As another example, as indicated in section 3.3, an overlap of key patches from the connectivity indices and preferred routes of movement could reinforce the conservation value of specific patches. If these overlaps are adjacent to existing protected areas (as shown in Fig. 6c for *Lacerta agilis*), the outputs could support the designation of new protected areas, the extension of existing ones or could inform specific landscape management interventions to enhance routes of movement. Similarly, adjacency of preferred routes of movement of different surrogate species, could serve to prioritise new ecological corridors or strengthen the importance of areas already protected. An example is shown in Fig. 6d where the routes of *Lacerta agilis* and *Triturus cristatus* are adjacent and greatly overlap with a Nature2000 area. Moreover, the outputs could be used to identify areas not to be urbanised. This is illustrated in Fig. 6e, which shows a new housing area proposed in the Housing Plan that will cause the loss of the key connectivity patch of *Maculinea arion*, already described in Section 3.2.

Regarding the innovation of this combination of techniques for spatial planning, very few studies were found that simultaneously used landscape metrics, connectivity indices and models based on circuit theory, least-cost path, or techniques such as agent-based modelling (Chen et al., 2017; Loro et al., 2015; Simpkins, Dennis, Etherington, &

Perry, 2018). In the literature review, there were studies combining landscape metrics and connectivity indices (e.g. Elliot, Cushman, Macdonald, & Loveridge, 2014; Zemanova et al., 2017) or connectivity indices with least-cost path or circuit theory (e.g. Lechner et al., 2015; Poodat, Arrowsmith, Fraser, & Gordon, 2015). However, these studies did not go from landscape metrics to least-cost path or circuit theory. To the authors' best knowledge, a combination of the three types of tools has never been applied to study an entire country before. This is most likely due to the difficulty of assessing habitat loss, fragmentation, and connectivity at a high resolution for vast areas. Additionally, the use of surrogate species is considered useful when optimising the conservation of a small set of species with similar ecological requirements and for limited environmental gradients (Mortelliti et al., 2009). The case of Luxembourg is a suitable exception to facilitate and demonstrate such a methodological approach.

In the case of Luxembourg, its small size combined with its intense population growth requires that planners balance smartly the growth and associated urban development with the protection of habitats. Due to this urgent need and its relatively small size, Luxembourg offers an ideal context to advance the combination of structural and functional landscape ecology analysis for the optimisation of national spatial plans. The coincidence of governmental and study area boundaries could foster the integration of these types of analysis into broader socio-ecological evaluations of national policies and strategies, such as urban development evaluations. Moreover, the scope of the present work offers an appropriated context for socio-ecological transboundary spatial planning studies by making use of the Greater Region (a transnational cooperation structure between the territories of Luxembourg, Belgium, France, and Germany) or Benelux (Belgium, the Netherlands, and Luxembourg) as case study areas. Such studies might foster international collaboration around Luxembourg for the protection of species, particularly those that share political borders. As urban plans are developed in Luxembourg, and the Greater Region, we advise detailed, up-to-date studies such as this one before the urban plan is put into place. In such instances, the future urban development is an added factor in how species will distribute themselves, becoming a main part of the future of urban planning.

Finally, replication of studies like the present one can add strength to existing international conservation networks, such as Natura 2000 (overlapping with Nature 2000 illustrated for Luxembourg in Figs. 5 and 6), to ensure that the most valuable areas are protected (e.g. Pereira et al., 2017; Santiago Saura & Pascual-Hortal, 2007) and to support spatial planning processes.

5. Conclusion

The combined analysis of metrics and connectivity indices shows an increased fragmentation and loss of habitats as well as a reduction of ecological connectivity in Luxembourg from 1999 to 2007 with regard to selected species (*Maculinea arion, Lacerta agilis, Triturus cristatus, Alytes obstetricans, Martes martes, Felis silvestris silvestris, Muscardinus avellanarius*). Our analysis of the proposed urban development up to 2030 shows that this trend will continue, potentially causing a decline in the species populations. The selected species are representative of different groups (mammals, reptiles, amphibians, butterflies), habitat specialists (e.g. grasslands, woodlands), and ranges of animal movements. Hence, the conversion of land use/cover classes from non-urban to urban up to 2030 might also affect other species with similar characteristics.

This combined use of landscape metrics and connectivity indices selected can be easily replicated by spatial planners, providing a better understanding as to how land use/cover class conversion or changes in the landscape structure affect ecological connectivity. This combination aids to notice significant impacts of proposed land use/cover changes that when using one of the techniques could be missed due to the potential lack of a linear relationship between habitat fragmentation/loss and changes in ecological connectivity. Additionally, as we did in our case study the relevance of key patches identified by connectivity indices can be supported by outputs of LSCorridors when preferred routes of movements overlap with those patches. Therefore, as shown in our exercise, the combined use of different tools proved to be effective in providing useful spatial information for planning processes.

In future studies, analyses of landscape metrics applied on a regular grid or at the municipal or canton level could improve the comparison of the different levels of fragmentation and habitat loss among zones in a region, in our case Luxembourg. Also, when running connectivity indices, the quality of habitats should be incorporated as an attribute, not only relying on area size to prioritise patches for conservation (i.e. assuming similar properties for all land use/cover class, bigger patches are more relevant than smaller ones). When applying functional connectivity models, such as LS Corridor, the use of national empirical studies monitoring animal movement, if available, could allow better adaptation of resistance surfaces improving the quality of the simulated routes. Finally, functional connectivity outputs may be compared against results of other connectivity models/software (e.g. Circuitscape, Condatis, Graphab) or advanced models such as particle swarm (Liu et al., 2012), which are based upon other methods (i.e. circuit theory, graph theory, genetic algorithms) to support testing and validation (from different angles) of the robustness of simulated routes.

When measuring habitat loss and fragmentation, coupling landscape metrics, connectivity indices and least-cost path models for the concurrent analysis of several surrogate species reduces the limitation of applying individual techniques focused on single species. Hence, in spatial planning exercises similar uses of a multitude of techniques at different levels of detail should be encouraged to support nature conservation policies, strategies or plans to better anticipate the negative ecological effects of future land use change, and their impact on biodiversity conservation.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.landurbplan.2019.05.004.

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