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COUPLING LANDSCAPE GRAPH MODELING AND BIOLOGICAL DATA: A REVIEW

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Abstract

Context

Landscape graphs are widely used to model networks of habitat patches. As they require little input data, they are particularly suitable for supporting conservation decisions (and decisions about other issues as e.g. disease spread) taken by land planners. However, it may be problematic to use these methods in operational contexts without validating them with empirical data on species or communities.

Objectives

Since little is known about methodological alternatives for coupling landscape graphs with biological data, we have made an exhaustive review of these methods to analyze links between the main purposes of the studies, the way landscape graphs are constructed and used, the type of field data, and the way these data are integrated into the analysis.

Methods

We systematically describe a corpus of 71 scientific papers dealing with terrestrial species, with particular emphasis on methodological choices and contexts of the studies.

Results

Despite a great variability of types of biological data and coupling strategies, our analyses reveal a dichotomy according to the objective of the studies, between (i) approaches aimed at improving ecological knowledge, mainly based on land-cover maps and using biological data to test the influence of landscape connectivity on biological responses, and (ii) approaches with an operational aim, in which biological data are directly integrated into the graph construction and assuming a positive effect of connectivity.

Conclusions

Beyond these main contrasts, the review shows that landscape graphs can benefit from field data of different types at varying scales. The great variability of approaches adopted reveals the flexible nature of these tools.

1. Introduction

Landscape connectivity modeling is a powerful tool for analyzing the movements of species living in fragmented habitats (Correa Ayram et al. 2016; Zeller et al. 2018). Connectivity models integrate information about species behavior and landscape structures (Cushman et al. 2013). However, designing realistic models of the ecological processes involved while providing tools likely to be used by landscape managers remains a major issue (Beier et al. 2008). Even if data acquisition is difficult and local records of species are scarce (Pressey 2004; Pe'er et al. 2005), it is essential to integrate field data in landscape connectivity modeling (Crooks and Sanjayan 2006; Kadoya 2008).

Graph-theoretic approaches are considered both promising (Calabrese and Fagan 2004; Minor and Urban 2008; Kadoya 2008; Urban et al. 2009) and of uncertain ecological relevance (Moilanen 2011) in landscape connectivity modeling. Among the spatial graphs used in ecology and conservation (Dale and Fortin 2010; Fall et al. 2007), landscape graphs (also named habitat networks) have emerged in the last 15 years, following the seminal paper of Urban and Keitt (2001). They are mainly used to model networks of discrete habitat patches in many geographical contexts and for numerous species. In these graphs, nodes usually represent habitat patches of the species under study while links represent potential movements (Urban et al. 2009; Galpern et al. 2011). As initially designed, landscape graphs are constructed from a landscape map defined in accordance with species' habitat requirements and movement abilities. They are an interesting compromise among other modeling approaches given the little input data needed and their capacity to represent ecological fluxes (Calabrese and Fagan 2004). This makes them particularly suitable for supporting conservation decisions taken by land planners (Foltête et al. 2014; Zetterberg et al. 2010). However, it has been recognized that combining them with empirical data about species would improve their current

implementation (Kadoya 2008). Indeed, when landscape graphs are constructed from land cover maps without field data on species, their ability to represent ecological networks relies entirely on the assumption that the land-cover types identified as potential habitats or corridors are actually suitable for a species to settle in or disperse through. Since this assumption is not always confirmed (Clevenger et al. 2002; Shirk et al. 2010; Wasserman et al. 2010), it may be problematic to use these methods to support decisions in operational contexts without considering empirical data on species (Cushman et al. 2013; Beier et al. 2008). This issue is even more acute when the outcomes of connectivity modeling lead to significant funds being committed to concrete operations of conservation, compensation, or restoration.

While many studies using landscape graphs are based on land-cover maps alone (e.g. Avon and Bergès 2016; Dondina et al. 2018; Martensen et al. 2017; Poor et al. 2019; Tannier et al. 2016), others include field data on species. These data may be of various types (presence records, genetic data, movement monitoring, etc.), they may characterize several biological levels (populations, species, communities) and may be integrated at different stages of modeling (Correa-Ayram et al. 2016). For example, Estrada-Peña (2005) constructed a graph in which the nodes were defined from a species distribution model (SDM), directly using the presence records to calibrate the connectivity model. This approach, followed by other researchers since then, was recently summarized by Duflot et al. (2018). Another way of including field data has been experimented by O'Brien et al. (2006) who made use of telemetry data to calibrate the cost values assigned to the inter-patch links. In a quite different approach, other researchers have correlated local connectivity metrics and presence or abundance data, to investigate species' responses to habitat accessibility (Clauzel et al. 2013; Foltête et al. 2012a; Ribeiro et al. 2011). While the number of studies based on landscape graphs has increased in ecology and conservation (Correa-Ayram et al. 2016; Fletcher et al. 2016), favored by the diffusion of open access specialized software applications (Csardi and Nepusz 2006; Foltête et al. 2012b; Saura and Torné 2009), it is becoming difficult to have a clear view of the methodological options improving the ecological relevance of landscape graphs. Some reviews have already been published about graph construction methods (Galpern et al. 2011), connectivity metrics (Rayfield et al. 2011), and types of operational applications (Bergsten and Zetterberg 2013; Foltête et al. 2014; Zetterberg et al. 2010), but little is known about the combination of these spatial graphs with empirical data on species. Therefore, practitioners involved in landscape management as well as researchers working in ecology and conservation would benefit greatly from a comprehensive state-of-the-art review of the current implementation of such combinations.

In this paper, we propose a systematic review of the coupling of landscape graphs with field data on species (limited to terrestrial species). As connectivity analyses can be conducted in studies aimed at (i) improving our theoretical knowledge in ecology or alternatively at (ii) implementing operational approaches in landscape planning and management, we question the link between the main objective of the studies, the way landscape graphs are built and used, the type of field data and the way these data are integrated into the analysis. From a corpus of scientific papers, our aim is to take stock of the methods of coupling in relation to characteristics of the context of the studies. As we suspect these characteristics to be interrelated, we seek to identify the main rationales behind the use of field data, to finally define profiles of landscape graph applications. Our main hypothesis is that the purpose of

the studies determines the way biological data are considered, thereby making a contrast between operational applications where landscape graphs are constructed in a simple, time-saving and cost-efficient way (i.e. nodes and links directly delineated from a land-cover map), and scientific applications where researchers integrate field data in complex ways to maximize the fit between model and reality.

2. Data and methods

2.1. The corpus of landscape graph applications

We used the online database Scopus to gather the scientific literature dealing with landscape graphs combined with field data on species. We restricted our search to scientific publications in English. As the terminology of landscape connectivity may vary among authors (Moilanen 2011; Gippolitti and Battisti 2017), we defined a final request after several tests, by evaluating the efficiency of each request by the percentage of inclusion of a checklist of 33 papers meeting our specifications. Four sets of criteria were defined and combined into a single request (see appendix 1):

- The first criterion required the presence of "ecological networks" or equivalent terms in the title, the abstract, or the key-words: (landscape OR habitat OR ecological OR patch) AND (graph OR network).
- The second set of criteria was related to the use of field data on species. It was mainly represented by words expressing types of data or techniques of data acquisition in the title, the abstract, or the key-words: ("field data" OR population OR demographic OR occurrence OR abundance OR presence OR richness OR suitability OR "radio-tracking" OR telemetry OR GPS OR CMR OR genetic OR roadkill).
- The third set of criteria required the papers to focus on terrestrial biodiversity and to remove the papers on hydrographic networks that are too specific to be mixed with non-aquatic networks. Papers whose title, abstract, or key-words include (maritime OR marine OR dendritic OR riverscape OR "river network" OR stream) were excluded.
- The fourth criterion was the presence of at least one key paper on landscape graphs in the references. Based on the number of citations given by Scopus, we listed six key papers cited more than 300 times: Urban and Keitt (2001), Saura and Pascual-Hortal (2007), Urban et al. (2009), Bunn et al. (2000), Minor and Urban (2008), and Pascual-Hortal and Saura (2006).

2.2. Systematic description of the papers

Each article was summarized using a systematic grid including first the type of biological data, corresponding to the following non-exclusive items: presence, abundance, species diversity, telemetry, genetic diversity, other.

Five topics were also described: (1) geographical and biological framework, (2) purpose of the study, (3) involvement of stakeholders, (4) graph construction, (5) connectivity analysis.

(1) The geographical framework was documented by the country and the region of the study. The biological characteristics were the species under consideration, its habitat, and the type of movement represented in the graph (daily movement, dispersal). To perform the statistical analyses, the geographical locations were clustered by continent, and the species were grouped into the following taxa: mammals, birds, amphibians, insects (or arachnids), chiropterans, plants and "other taxa" in other specific cases.

(2) From reading the title, the abstract, and the introduction, the purpose of the study was categorized into one or more of the following items:

- Understanding: the aim is to understand the link between a biological feature of the population, the species, or the community, and the functional connectivity modeled by the landscape graph.
- Prioritization: the aim is to identify key elements of the network likely to be protected or monitored.
- Impact evaluation: the aim is to assess the impact of a potential or actual landscape change on the network functionality.
- Network design: the aim is to define new components of the ecological network to improve its global connectivity.
- Method design: the aim is to improve methods of ecological network modeling.

The purpose of each article was also described by the global design of the analysis, concerning temporality and a posteriori analysis. Temporality (i.e. the way the temporal dimension was managed) included static, retrospective, and prospective approaches. Analyses linked biological data and connectivity metrics to each other as follows:

- No link between biological data and metrics in analyses.
- Biological data correlated with metrics, i.e. in a descriptive approach based on a visual or statistical investigation.
- Biological data modeled with metrics, i.e. used as the target variable in a statistical model in which metrics are considered as explanatory variables of the biological response.

(3) The level of involvement of stakeholders (e.g., land-planning practitioners) was documented by three non-exclusive possibilities corresponding to a growing order of involvement:

- Acknowledgment of stakeholders: the acknowledgments at the end of the paper mention a land-planning practitioner or a non-academic organization.
- Data from stakeholders: in the method section, the authors explicitly mention a non-academic organization (and non-national, i.e. not a national topographic service) as a data source.
- Stakeholders as co-authors: some of the authors of the papers come from a non-academic area.

(4) Items related to the graph construction itself concerned mainly the patch and link definitions. By investigating the method section of the articles, we listed three approaches concerning patches:

- Land-cover-based patch: the patches are designed from land-cover classes only.
- Suitability-based patch: they are defined from a suitability map or another SDM output.
- Protected areas: patches are a set of protected areas or zones designed by field experts.

In landscape graphs, each patch may have its own weight in the connectivity analysis. This weight is usually considered as a proxy of its demographic or carrying capacity (Urban and Keitt 2001). We observed three possibilities:

- Uniform weight patch: all patches have the same weight.
- Area-based weighting: each patch is weighted by its area, which is a priori the most common option. In some specific cases, the patch is weighted by the area of a nearby resource patch (e.g. Tournant et al. 2013).
- Suitability-based weighting: the patches are weighted by a statistical indicator (specifically sum or average) computed from the pixel values of a suitability map.

The links are also characterized by a weight which is most of the time the edge-to-edge distance separating the patches connected by these links. Focusing on the data used to compute these distances rather than on the computation details, we found three types of distance weighting:

- Euclidean link.
- Land-cover based link, resulting from least-cost distances (or resistance distances derived from circuit theory) where a cost value is assigned to each land-cover class.
- Suitability-based link, i.e. least-cost distances where the costs are derived from a suitability map, for instance the inverse of the presence probability.

(5) The connectivity analysis was first described by the level of analysis among the following non-exclusive possibilities:

- Network-level: the analysis deals with the entire graph's connectivity.
- Component-level: the analysis deals with the comparison of connectivity between components (i.e. sub-graphs resulting from link pruning) or between clusters, i.e. compartments resulting from a clustering method.
- Patch-level: the analysis is focused on the local connectivity computed for each patch.
- Link-level: the analysis is focused on the links' attributes (e.g. potential fluxes).

The graph analysis was then characterized by the type of connectivity metric computed from the graph. We listed eight metrics among the most used ones, plus a class "other" corresponding to more specific measures, and a class "no metric" when no measure was computed. The eight metrics are:

- Probability of Connectivity (PC), a global metric integrating both patch and link weights in a measure of spatial interaction (Saura and Pascual-Hortal 2007).
- Integral Index of Connectivity (IIC), a global metric of spatial interaction integrating patch weight and a topological distance between patches (Pascual-Hortal and Saura 2006).

- Delta Probability of Connectivity (dPC), a local metric used to identify the key patches, computed from the iterative removal of each patch with PC as the global reference (Saura and Pascual-Hortal 2007). We also included in this item the decomposition of this metric into three fractions (Saura and Rubio 2010).
- Delta Integration Index of Connectivity (dIIC), a local metric similar to dPC but using IIC as a global reference (Pascual-Hortal and Saura 2006). As previously, the decomposition of dIIC into three fractions was included in this item.
- Betweenness Centrality Index (BC), applied with (Foltête et al. 2012b) or without (Zetterberg et al. 2010) weighting of the graph elements. It represents the theoretical level of local transit.
- Flux (F), also named Area Weighted Flux (Foltête et al. 2012b), a local metric expressing the potential of dispersal from a given patch.
- Degree (Dg), a topological measure derived from the global framework of graph theory and equivalent to the number of links connected to a given patch.
- Expected Cluster Size (ECS), a landscape level metric corresponding to the area-weighted mean cluster size (O'Brien et al. 2006).

2.3. Statistical analysis of the corpus

After the review stage, the topics of the previous grid were analyzed statistically by combining the related variables and the types of biological data. Because of the qualitative nature of all the variables, we performed multiple correspondence analyses (MCA). The principle of a MCA is to define orthogonal factors synthesizing the variance of a qualitative dataset (Tenenhaus and Young 1985). All categories and all individuals (here the articles) are given coordinates in this multidimensional space. We considered only the first two factors. When strong relationships were found between biological data and the variables of a given topic, we expected biological data categories to be widely distributed across the factorial space. Otherwise, this would mean no significant link existed between biological data and the topic.

The link between biological data and the first topic (geographical and biological framework) was analyzed separately using a first MCA. The topics 2 (purpose of the study), 3 (involvement of stakeholders), and 4 (graph construction) were grouped because they form a consistent set to be compared with biological data. As this part of the analysis includes numerous variables, the second MCA was followed by Hierarchical Clustering (HC) applied using the Ward criterion to summarize information and identify the main types of articles. The resulting typology was mapped to investigate the possible geographical effect in the use of landscape graphs. Finally, the last topic (connectivity analysis) was investigated separately by means of a third MCA.

3. Results

The request implemented on 12 December 2018 returned 338 articles. As several methods of landscape connectivity modeling rely on a partially similar vocabulary (e.g. approaches focused on spatial genetics), many of the 338 articles were outside the scope of our investigation. After a

systematic reading to finalize the selection, our corpus included 71 articles (see list in Appendix 2). The articles were published from 2005 to 2018, although a large majority (82%) was published after 2012 (Fig. 1).

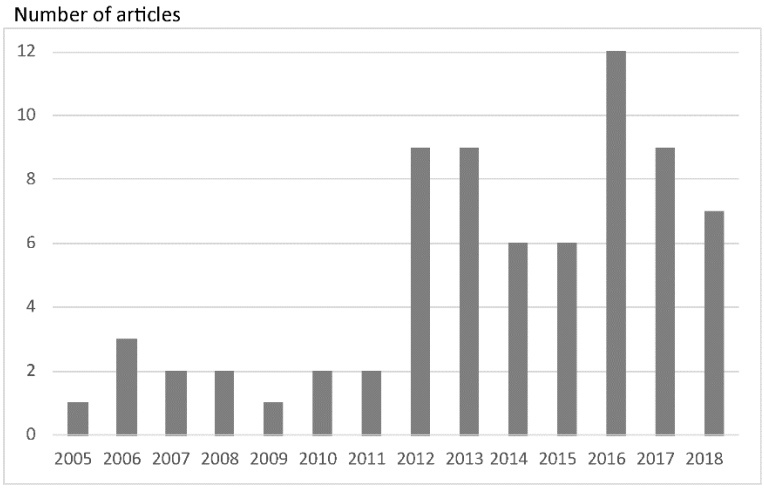


Figure 1. Number of articles combining landscape graphs and biological data published every year from 2005 to 2018

Among the five types of data, presence data are used in 61% of the articles, followed by abundance data (18%), genetic diversity and GPS-track data (11% for each type), and species diversity data (8%). Other data amount to 7% and include for example evidence of breeding, density, or roadkill data.

3.1. Are biological data specific to the geographical and biological framework?

Studies are unequally distributed over the five continents, with 52.1% of them in Europe, 23.9% in North America, 12.7% in South America, 11.3% in Asia, and only 1.4% in Africa. The two dominant taxa are mammals (35.2%) and birds (23.9%), the other main taxa being plants (16.9%), insects (11.3%), and amphibians (8.5%). The studied habitats are mainly forests (57.7%), followed by grasslands and agricultural habitats (14.4%), and wetlands and aquatic habitats (11.3%). A large proportion of the articles (26.8%) dealt with more complex habitats such as hedgerows or urban areas (hereafter "other habitats"). The type of movement analyzed is mainly dispersal (87.3%) and secondarily daily movements (12.7%).

The MCA combining biological data and geographical and biological characteristics primarily highlights studies concerning wetlands and amphibians, without evidencing any connection with a particular type of biological data (Fig. 2). The location of the items "plants", "insects", and "grasslands" close to "species diversity", "genetic diversity", and "abundance" also suggests a link between them, in studies more frequently conducted in Europe. However, the investigation of cross frequencies (Appendix 3) shows that these associations are only partial. For example, genetic data never come from grasslands in these studies but concern plants and insects in 37.5% and 12.5% of the cases. Over half of the abundance estimations concern insect populations. Almost all the species diversity measures concern plants (five out of six studies), a third of them in grasslands. The location of the

other items in the factorial space suggests that studies using presence or telemetry data frequently concern forest species of mammals and birds. Among these former studies some deal with daily movements on other continents than Europe.

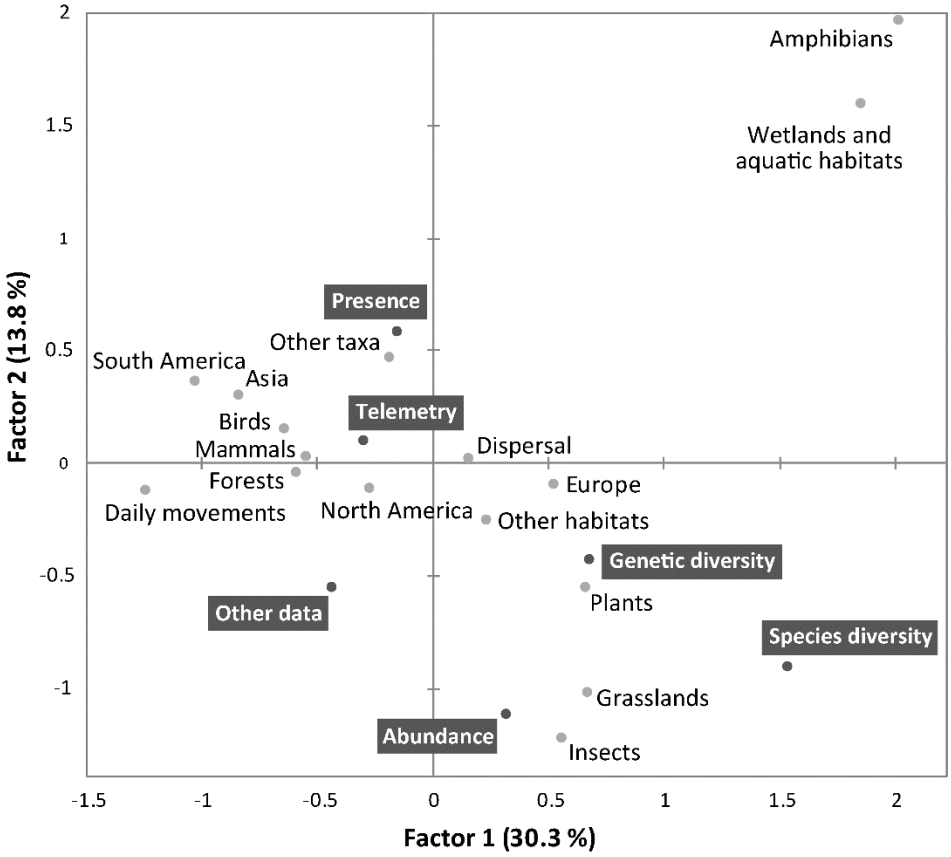


Figure 2. Factorial space of the variables describing the geographical and biological framework of the articles. The terms in the grey rectangles represent the types of biological data. Note that the single study applied to Africa was removed to avoid

3.2. Does the use of biological data depend on the objective of the graph analysis?

The studies aimed at understanding the relationships between landscape connectivity and populations, species, or communities amount to not quite half of the corpus (46.5%). The prioritization of elements or components of the ecological networks is present in 25.3% of the articles. Then comes the impact evaluation (16.9%) followed by the network design (12.7%) and the methodological approaches (9.9%). Most of the studies rely on a static approach (80.3%) as only 12.7% and 7.0% of them are based on prospective and retrospective approaches respectively. Among the 71 articles, 57.7% integrate stakeholders through acknowledgements and/or by the use of their data. Stakeholders are among the authors in only 16.9% of the articles.

Globally, biological data are included in graph construction (i.e. before the connectivity analysis) in 45 articles (63.4%). This integration more frequently concerns the definition of patches, delineated (36.6%) and/or weighted (21.1%) by using a suitability map or another SDM output. Biological data can

also be used to define and weight the links (23.9%), either by converting presence probabilities into a set of cost values (15.5%) or less frequently following other approaches from telemetry data or genetic differentiation measures (8.4%). Conversely, biological data are used after the graph analysis in 42.2% of the articles, correlated with connectivity metrics (14.1%) and more frequently used as target variables in explanatory models (28.2%).

The MCA applied to all these criteria results in a marked decrease in inertia from the first factor containing 46.9% of variance (Fig. 3). Given the position of categories along the x-axis, the first factor contrasts (1) studies where biological data are integrated in graph construction, and (2) studies where biological data are a posteriori correlated or modeled with connectivity metrics. In the first case (left side of Fig. 3), more related to presence and other data, patches and links are preferably defined and weighted from suitability maps or other outcomes of SDM. This approach is often adopted when pursuing operational objectives such as prioritization and network design. In the second case (right side of Fig. 3) where species diversity and abundance data are preferably used, graph elements are more frequently defined from land-cover maps only. This approach tends to be implemented when the main purpose is to understand the relationships between the species' ecological response and the connectivity levels inferred from metrics. Beyond this main contrast, the second factorial axis provides complementary information by emphasizing a gradient of stakeholder involvements, that is more prominent in approaches of method design and using telemetry data and secondarily genetic data (high side of Fig. 3), but is less frequent in studies dealing with impact evaluation either retrospectively or prospectively (low side of Fig. 3).

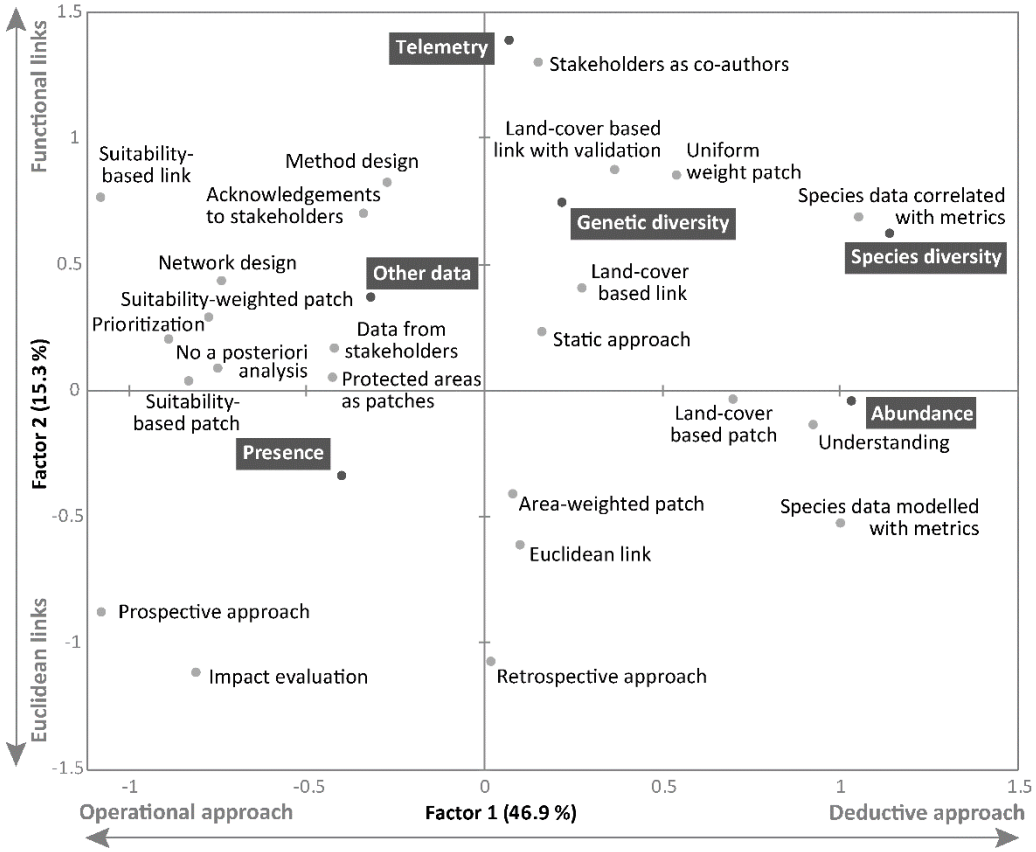


Figure 3. Factorial space of the variables describing the aim of the articles, the graph applications, and the involvement of the stakeholders. The terms in the grey rectangles represent the types of biological data.

The application of the HC to the factorial axes provided the dendrogram we cut to define four classes (Fig. 4). These classes have relatively homogeneous frequencies and can be nested into a higher-level where classes 1 and 2 contrast with classes 3 and 4. According to their position in the factorial space and to the frequencies of each category (see Appendix 3), these classes can be summarized as follows:

- Class 1 “deductive approach, Euclidean links”: studies aimed at understanding the relationships between populations, species, or communities and habitat connectivity, by correlating biological data with metrics after the graph analysis. The data used are mainly presence (55%), abundance (40%), and/or species diversity (15%). In these studies, patches are mainly defined from land-cover maps (90%) whereas links are most often Euclidean (80%). They rarely mention non-academic stakeholders.

- Class 2 “deductive approach, functional links”: studies directed at similar objectives as those from class 1 but using a larger panel of data types. Patches (85%) as well as links (77%) are mainly defined from land-cover maps. A strong link with stakeholders is mentioned in the papers (role in data acquisition and/or presence as co-author).

- Class 3 “operational approach, impact evaluation”: studies aimed at evaluating the impact of a past or future landscape change. Presence data are used to define the patches from an SDM (62%) whereas links are mainly Euclidean (76%). Few links with stakeholders are mentioned.

- Class 4 “operational approach, network design”: studies with an operational aim in which presence data are integrated in graph construction via an SDM to define patches (65%) and to weight links (47%). The connectivity analysis does not lead to a statistical investigation with biological data. An explicit link with stakeholders is frequent.

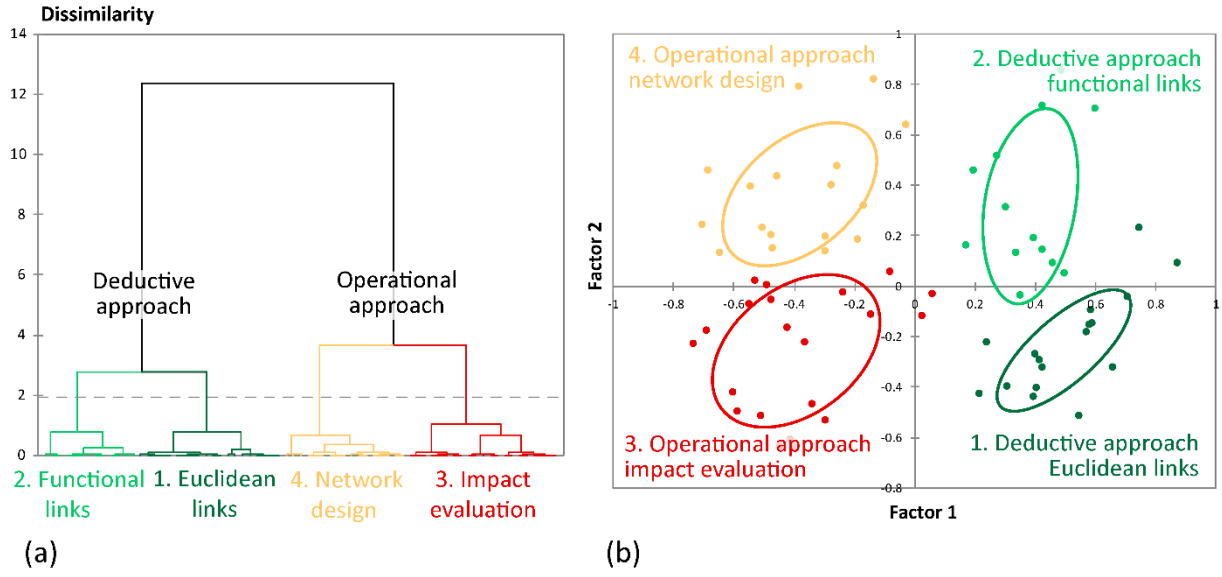


Figure 4. Hierarchical Ascendant Classification applied to the first two factors of MCA. (a) The dotted line represents the cutoff defining four classes. (b) These classes are represented by individual positions and 50% ellipses in the factorial space.

The map of field locations shows that the four classes are distributed worldwide (Fig. 5). But, deductive approaches tend to be more commonly adopted in Europe (specifically in Spain and France) than in North America.

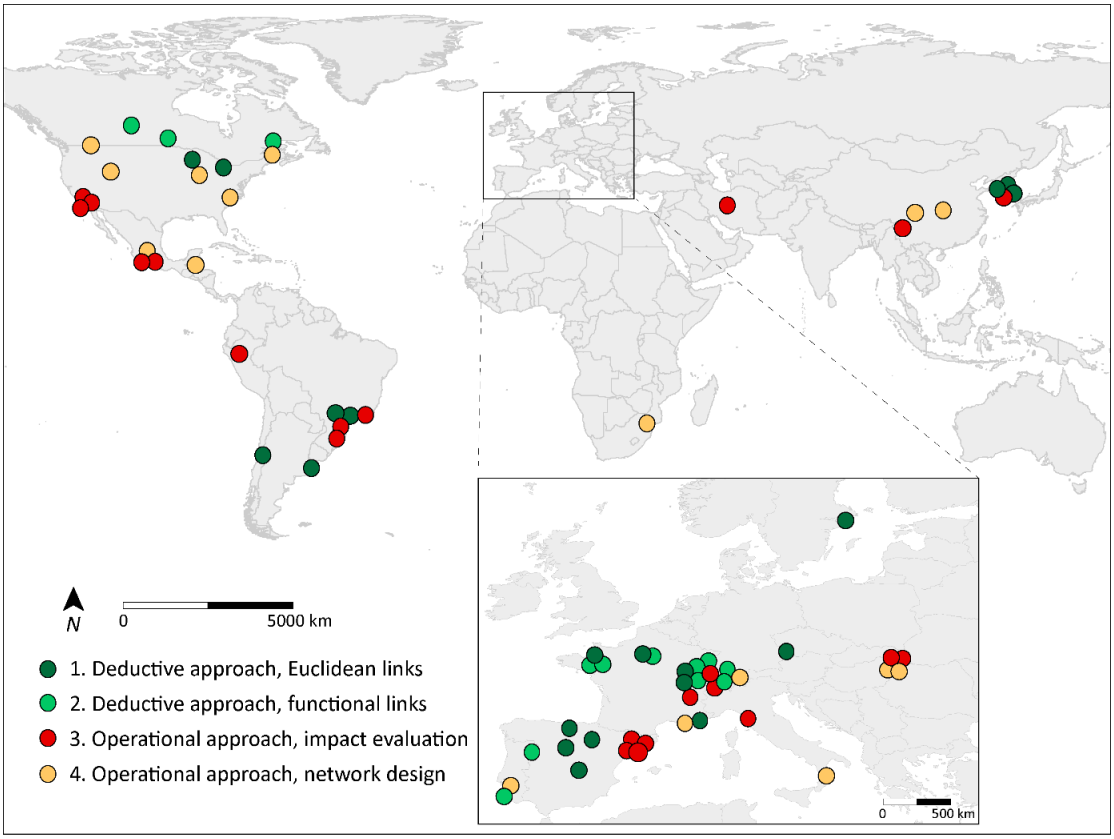


Figure 5. Map of the typology of use of biological data in landscape graphs.

3.4. The connectivity analyses

The connectivity analyses sometimes rely on a visual interpretation of maps without computation of connectivity metrics (eight articles). Overall, patch-level analyses are the most common (71.8%), being much more frequent than global-level (25.4%), component-level (15.5%), and link-level analyses (11.3%). The dominance of patch-level analyses is supported by the frequent occurrence of the metrics dPC (26.8%), F (16.9%), dIIC (15.5%), BC (15.5%), and Dg (9.9%). Global-level metrics such as PC and IIC are used only eight (11.3%) and seven (9.9%) times respectively. The most frequent component-level metric is the ECS (5.6%). It should be noted that a total of 20 other metrics (28.2%) are used in only one or two articles.

An analysis combining the biological data and the graph analysis outcomes is carried out in 42.2% of cases. Among the articles in which these data are analyzed jointly, we can distinguish (i) explanatory approaches based on statistical modeling (e.g. regression) where connectivity metrics are used as explanatory variables of biological responses measured by biological data (28.1%), and (ii) descriptive approaches in which biological data and graph analysis are simply correlated, statistically or visually (14.1%).

In the factorial space combining connectivity analyses and the types of biological data, genetic data prove to be specific to particular approaches (right side of Fig. 6). These data, sometimes used in patch-level analyses, are more frequently associated either with link-level analyses conducted without

metric computation, as for example in Galpern et al. (2012) and Keller et al. (2013), or with analyses performed at the component-level as in Moran-Lopez et al. (2016). These specific approaches contrast with common patch-level analyses linked to presence data and based on a series of local metrics such as delta PC, delta IIC, BC index, or Degree (left side of Fig. 6). The categories positioned at both extremities of axis 2 represent two specific cases encountered in the articles: (1) the studies in which a global-level analysis is conducted, frequently based on PC or IIC metrics, but without any particular link with a type of biological data, (2) the studies dealing with species diversity and abundance data, more often based on the metric flux.

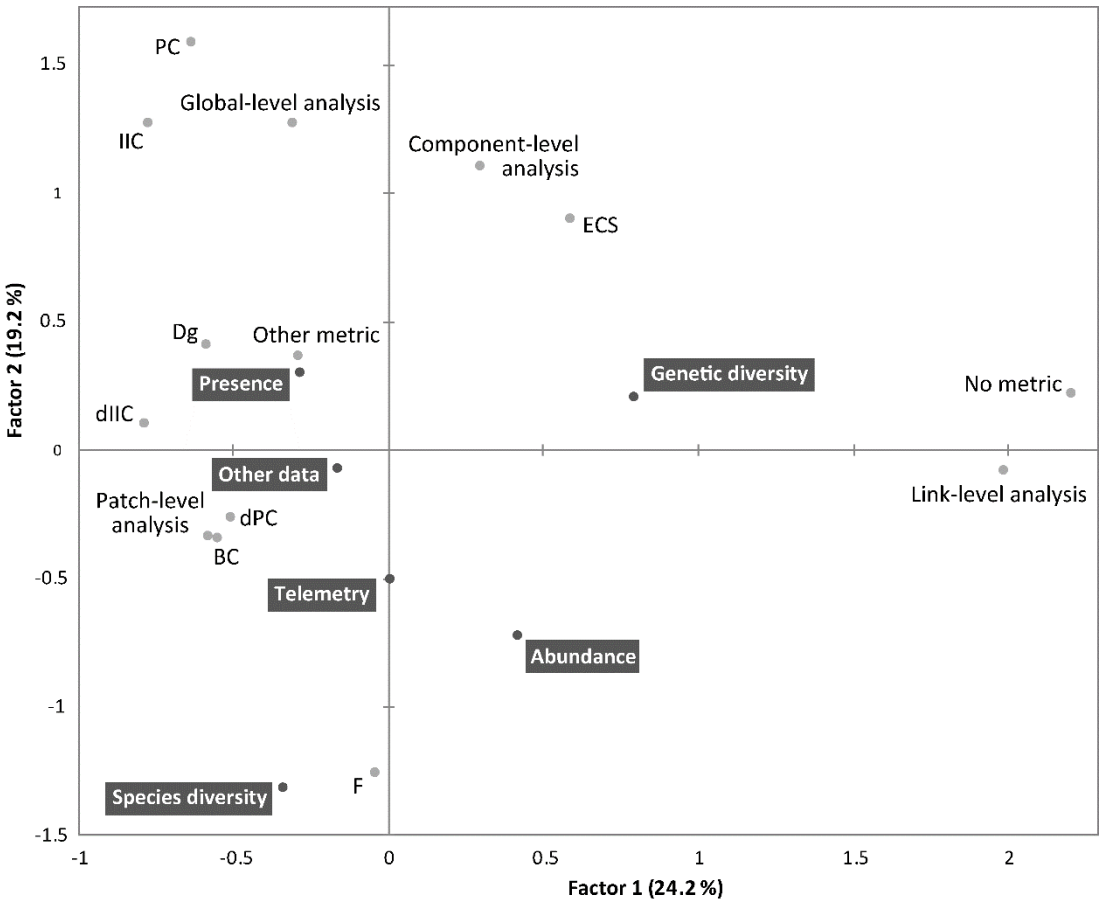


Figure 6. Factorial space of the variables describing the connectivity analyses. The terms in the dark grey rectangles represent the types of biological data.

4. Discussion

The number of studies of landscape connectivity has been rising at a sustained pace since 2005 (Correa-Ayram et al. 2016; Fletcher et al. 2016). Among these studies, approaches based on landscape graphs have been employed frequently, especially since 2012. The success of these approaches may be explained by the publication of reviews about graph construction (Galpern et al. 2011) and graph-theoretic metrics (Rayfield et al. 2011), by empirical research into connectivity metrics (e.g. Saura and Rubio 2010), by the availability of software to perform graph-based analyses (Foltête et al. 2012b; Saura and Torné 2009), and by the rising interest of stakeholders and policy-makers in connectivity

conservation (Correa-Ayram et al. 2016). Despite growing interest in connectivity modeling, and considering the large number of references reviewed in the syntheses by Fletcher et al. (2016) and Correa Ayram et al. (2016) about landscape connectivity (370 and 162 respectively), we found relatively few articles (i.e. 71) using biological data in combination with landscape graphs. This is all the more unfortunate because many studies assume (1) that connectivity has a positive influence on biodiversity or (2) that the connectivity model is a reliable representation of the actual habitat network, but without validating these assumptions from field data. Although the small number of articles using biological data was quite limiting for carrying out statistical analyses, our review clearly highlighted a preponderance of articles dealing with mammals and birds in forests of Europe and North America. This result recalls that obtained from a larger pool of articles in the review by Correa-Ayram et al. (2016), and this should encourage a greater diversity in the studied topics as connectivity conservation is a pervasive issue across taxa and regions.

A main contrast in the use of biological data: Prior coupling vs a posteriori analysis

Our review shows that biological data are integrated into the analysis at different stages depending on the objective, and that this integration is performed in many different ways. Specifically, the second MCA encompassing variables describing the purpose and application of landscape graphs and the involvement of the stakeholders revealed a main contrast between two objectives (Fig. 3). First, articles from classes 1 and 2 (Fig. 4) aim at providing knowledge about relationships between biological responses and landscape connectivity. In these articles, graph nodes are identified from relatively simple data, e.g. a land-cover map, without integrating biological data in the initial graph's construction stage. Once the connectivity metrics have been computed, biological data are considered as target variables in a statistical analysis in which connectivity metrics are used as explanatory variables. Examples of such a hypothetico-deductive approach can be seen in Martín-Queller and Saura (2013) or Mony et al. (2018). Separating the connectivity modeling step and the use of biological data amounts to considering connectivity, measured by metrics, as a potential driver of the biological response. This deductive reasoning aims at (i) providing new knowledge about the influence of landscape connectivity on species, (ii) evaluating the strength of this relationship, and (iii) identifying the spatial scale at which it occurs. It is worth noting that such an approach requires land-cover data that are suitable for mapping the habitat of the focal species and its dispersal paths. It also assumes that graph-based modeling captures connectivity patterns well so that connectivity metrics actually account for the influence of landscape connectivity on biological responses.

We return to the initial data by focusing on classes 1 and 2 to specify how these deductive approaches were conducted. The most frequent design is to analyze a given species at patch-level. This consists in explaining species presence (e.g. Anderson and Bodin 2009; Awade et al. 2012; Foltête et al. 2012a; Melles et al. 2012; Song and Kim 2016) or abundance (e.g. Estrada-Peña 2005; Betbeder et al. 2017) in habitat patches by including connectivity metrics in a regression model. In some cases concerning birds or plants, regression or correlation analyses performed at the community level attest to the effect of connectivity either on patch richness (Mony et al. 2018) or on an inter-patch dissimilarity measure (Muratet et al. 2013). Of the papers referring to the deductive approach, only a smallish proportion (27%) includes a sensitivity analysis to evaluate how statistical dependence is influenced by cost values (Foltête and Giraudoux 2012), minimum patch size (Anderson and Bodin

2009), the distance of graph pruning (Koh et al. 2013; Muratet et al. 2013) or the setting of the dispersal kernel in the metric calculation (Martín-Queller et al. 2017; Gil-Tena et al. 2014). Finally, several other papers report more specific protocols adapted to particular contexts.

Conversely, the opposite objective (represented by classes 3 and 4, Fig. 4) aims at prioritizing key habitat patches or supporting ecological network design. In this case, biological data, most of the time presence data, are directly embedded in the definition of patches from an SDM or another output of suitability modeling, following procedures synthesized in Duflot et al. (2018). In these approaches, a first step of modeling precedes the connectivity analysis, leading to map presence probabilities. These probabilities are thresholded to define the habitat patches, and sometimes used to set the cost values defining the links. The status given to the quantification of connectivity makes a big difference with the previous approach. Here, the connectivity computations derived from the landscape graph are not used to test a specific assumption about the landscape's influence. In contrast, they serve as a decision support tool in a rationale of action. This means that the positive influence of connectivity on species is not questioned but it is rather considered as an initial postulate.

Although percentages of articles corresponding to these contrasted objectives (66.2% including biological data in the graph construction compared with 42.2% analyzing biological data a posteriori) show that these rationales are in most cases exclusive, we found 12 articles (8.4%) in which both approaches are present. They correspond to various specific cases integrating different biological data. For example, Ribeiro et al. (2011) conducted a field campaign to select the patches with actual presence of amphibians. They then assessed the correlation between connectivity metrics and species richness in a second step. Other researchers have included field data in the definition of links, as in O'Brien et al. (2006) and Galpern et al. (2012) who brought into play telemetry data for defining the cost values used to compute the links. Galpern et al. (2012) finally compared genetic data with the outcomes of connectivity analyses, whereas O'Brien et al. (2006) used independent telemetry data to validate the cost values definition. In the same vein, Bergerot et al. (2013) carried out an individual release procedure to set up an inter-patch movement model. It was used to construct the landscape graph before comparing the graph's components with the results of a mass release-recapture operation.

The relationship between the purpose of the study and the region where it was carried out was not straightforward, but we observed a trend whereby studies with operational objectives were often performed in North America (Fig. 5). The involvement of public agencies in the research on connectivity such as the USDA, the US Fish and Wildlife service, or Parks Canada, already noticed by Correa-Ayram et al. (2016) and apparent in some of the articles we reviewed, may be a reason for such a result.

A secondary contrast related to functional connectivity

Apart from this dichotomy between operational and academic objectives, we observed in the same analysis (factor 2 in Fig. 3) a gradient in the way graph links are defined. This gradient contrasts Euclidean links (i.e. uniform matrix) on the one hand and, on the other hand, suitability-based links and land-cover based links (i.e. weighted by least-cost distances) that are validated or not by biological data. This gradient additionally suggests that studies aiming at modeling functional connectivity rather than structural connectivity make wider use of telemetry data. Indeed, eight articles from classes 2 and 4 are based upon this kind of data whereas no articles from classes 1 and 3 use them. Including

telemetry data in the definition of links is associated here with the greater involvement of stakeholders. Such a result may not be universal but more probably stems from the frequent use of telemetry in studies carried out in North America, where investment in the acquisition of data reflecting functional connectivity may be higher.

Focusing on the studies in which the functional aspect of connectivity is better considered (positive coordinates on factor 2 in Fig. 3), classes 2 and 4 differ both in their aims (providing knowledge vs supporting action, respectively) and the main types of data they include (54% using genetic or telemetry data vs 71% using presence data, respectively). Presence data can be easily and affordably obtained compared with genetic or telemetry data. The latter are technically more sophisticated and demand a more intensive collection effort in the field and/or in the lab. This probably explains the dominance of presence data (61%) in the literature we reviewed. This difference may also explain why studies with operational purposes are mainly based on presence data, because the time available for decision-making is often much more constrained than the time available for pure research. However, a direct link between the type of data and ecological processes underlying connectivity is critical to the graph's relevance whatever its purpose. In this context, several papers highlight that habitat suitability is often a poor predictor of dispersal or gene flow for numerous reasons, and that data directly related to movement or gene flow should be considered instead (e.g. Spear et al. 2010; Peterman et al. 2014; Khimoun et al. 2017). It does not mean that SDMs are pointless in graph construction, as they could be particularly relevant for delineating patches. But their utility for calibrating the cost values used in the least-cost paths raises questions. In addition, designing movement corridors or reserves for conservation aims not only at satisfying biological needs in different places for a species of concern over its life-cycle, but it should also maintain some genetic exchanges between populations to warrant their long-term viability and adaptive potential (Lindenmayer and Fisher 2006; Allendorf et al. 2012). While movements and gene flow are both important and complementary for conservation purposes, connectivity modeling should integrate different ecological data depending on the precise biological response that is considered.

Two key-levels of integration for biological data

Although a large range of biological data were used in the studies we reviewed, different types of biological data were rarely used in the same study. Due to the influence of landscape structure on both extinction/colonization and migration/drift equilibria driving species and genetic diversities, respectively (Vellend and Geber 2005), diversity data have considerable potential for improving landscape graph-based approaches. It is noteworthy that these data were used in very different ways in papers coupling them with landscape graphs. Genetic data were mainly used at link level to analyze genetic differentiation between locations (seven out of eight articles, versus two articles only using within-location genetic diversity), whereas species diversity data were almost exclusively used at patch level to derive species diversity values within locations (i.e. alpha diversity; five out of six articles, versus one article only using between-locations diversity, i.e. beta diversity; see Figure 5). In addition, species alpha diversity was always used as a biological response to be explained statistically from some connectivity measures obtained from the landscape graph, whereas genetic data were used either as an input to help graph construction or as a biological response that was correlated with some connectivity metrics (six and four articles, respectively). This difference in treatment between species

diversity and genetic diversity has a long history despite their theoretical connections as responses to similar processes (Vellend and Geber 2005, but see Taberlet et al. 2012). Indeed, populations occurring in small and isolated habitat patches are exposed to a higher genetic drift and a lower gene flow than large and continuous populations, and both processes are expected to lead simultaneously to lower within-population genetic diversity and greater genetic divergence between populations (Keyghobadi 2007). In the same way, communities occurring in small and isolated habitat patches are expected to harbor a lower species richness and to differ more widely from each other, because of a higher extinction rate and a reduced colonization rate (MacArthur and Wilson 1967). Thus, whether diversity is measured within or between entities (patches, populations, communities, etc.), and whether it is assessed at the genetic or species level, the value obtained always results from (at least) two processes operating within and between the entities considered. In this framework, graph theory offers a flexible and valuable landscape modeling approach, as metrics can be extracted from graphs to reflect processes operating at the patch level only, at the link level only, or to integrate both kinds of processes in the same connectivity measure (Saura and Pascual-Hortal 2007; Pascual-Hortal and Saura 2006). However, this opportunity is still under-used because even in articles coupling species or genetic diversity with a landscape graph, we found only two articles (Schoville et al. 2018; Ribeiro et al. 2011) and a single article (Neel 2008) trying to explain levels of species diversity and genetic diversity, respectively, by connectivity metrics integrating both patch and link properties.

Which strategy should we adopt in applying landscape graphs?

In light of the findings of our review, one may ask which is the more relevant approach to landscape graph modeling. This mainly relates to the opposition discussed above between prior coupling and a posteriori analysis. Should we directly incorporate biological data in graph construction, or use it once the graph has been constructed, to validate it or to verify the influence of connectivity?

As researchers involved in scientific approaches, our initial reflex would be to advocate the second proposition, where the role of habitat connectivity and the reliability of the model have to be questioned before being applied in an operational rationale. Theoretically, if the connectivity metric assumed to represent the process under consideration proves to be significantly linked to biological data, the graph could be used as a decision support tool, but otherwise not. A positive statistical test provides reassurance about the approach, but such validation should not be overestimated, especially when biological data are limited to presence data. A significant relationship between a graph metric and biological data only provides a global validation of the entire modeling approach; it does not inform us about the details of the relationship and the strengths and weaknesses of the model. Indeed, uncertainty may remain with respect to (1) the definition of patches, (2) the definition of links, (3) the choice and the setting of a metric for quantifying connectivity, and finally (4) the role of connectivity. Only a sensitivity analysis applied to the first three parameters could help to clarify their area of validity. Thus, the deductive approach seems to be preferable because it enhances the model's overall legitimacy, but any application should be subject to a sensitivity analysis to justify and specify the modeling choices.

Let us turn now to the direct incorporation of biological data in graph construction. Our review shows that the more frequent approach is to delineate habitat patches from outputs of a species distribution model. Since such models are usually the output of statistical approaches including a

validation step, it can be taken that the patches are validated by empirical data. The interest of this approach is to provide more realistic habitat patches, consistent with the concept of ecological niches, and not based on a land-cover map alone. However, the absence of a posteriori validation concerns the subsequent graph construction choices as to the definition and weighting of the links and the parameterization of the other criteria mentioned above. Consequently, to be reliable, this approach should preferably be supplemented by a validation process focused on the links and the connectivity metrics. In this perspective, the "gold standard" approach should ideally include additional data to calibrate or validate the links. Zeller et al. (2018) show that the type of biological data best reflecting movement patterns are genetic and telemetry data. Because genetic structure mainly results from multi-generational dispersal movements (Keyghobadi et al. 2007), genetic data are therefore a reliable proxy for the dispersal movements which matter most for species conservation (Zeller et al. 2012). However, genetic data provide limited information about current habitat connectivity in cases where recent changes have not yet affected genetic structure due to time lags (Landguth et al. 2010). In such cases, telemetry data are probably more helpful. In sum, we think that genetic and telemetry data should be used to validate landscape graph models, especially when they rely only upon land use and presence data.

Conclusion

This review has shown a major contrast in studies coupling landscape graphs and biological data depending on their main objective. In approaches aimed at providing knowledge, patches are defined from land-cover maps and biological data are correlated a posteriori with connectivity metrics. Conversely, in operational approaches, patches are more frequently derived from SDMs while directly including biological data in graph construction. The second contrast concerns the more or less functional nature of links and highlights the role of telemetry and genetic data in validating them.

Beyond these main contrasts, the review shows that landscape graphs can benefit from field data of different types at varying scales. The great variability of approaches adopted in the articles we have reviewed reveals the flexible nature of these tools. Since field data allow us to understand empirically ecological processes such as dispersal and its dependence on landscape connectivity, we encourage others to multiply studies coupling landscape graphs and field data. While biological data may reflect a functional biological response to landscape connectivity, they are usually gathered from a limited set of locations. Therefore, their complementarity with landscape graphs, which represent the exhaustive set of potential habitat patches, is an additional reason for encouraging this coupling. This may theoretically improve the reliability of connectivity analyses and the way they are carried out. Nevertheless, we do not discard the results from all studies performed without field data as they indirectly benefit from methodological improvements and ecological knowledge acquired in studies based on field data. For example, Clevenger et al. (2002) showed that connectivity models based on information derived from the literature were a better proxy of empirical models than those designed exclusively from expert opinion. Finally, whether ecological data are used as input in the graph construction process or as a biological response that has to be explained statistically by certain landscape properties, it is crucial to choose both the appropriate data and graph metrics in accordance with the biological process under consideration.

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