Multiple habitat graphs: how connectivity brings forth landscape ecological processes

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Abstract: Habitat connectivity is integral to current biodiversity science and conservation strategies. Originally, the connectivity concept stressed the role of individual movements for landscape-scale processes. Connectivity determines whether populations can survive in sub-optimal patches (i.e., source-sink effects), complete life cycles relying on different habitat types (i.e., landscape complementation), and benefit from supplementary resources distributed over the landscape (i.e., landscape supplementation). Although the past decades have witnessed major improvements in habitat connectivity modeling, most approaches have yet to consider the multiplicity of habitat types that a species can benefit from. Without doing so, connectivity analyses potentially fail to meet one of their fundamental purposes: revealing how complex individual movements lead to landscape-scale ecological processes. To bridge this conceptual and methodological gap, we propose to include multiple habitat types in spatial graph models of habitat connectivity, where nodes traditionally represent a single habitat type. Multiple habitat graphs will improve how we model connectivity and related landscape ecological processes, and how they are impacted by land cover changes. In three case studies, we use these graphs to model (i) source-sink effects, (ii) landscape supplementation, and (iii) complementation processes, in urban ecosystems, agricultural landscapes, and amphibian habitat networks, respectively. We show that multiple habitat graphs help addressing crucial conservation challenges (e.g., urban sprawl, biological control, climate change) by representing more accurately the dynamics of populations, communities, and their interactions. A new version of the Graphab open-source software implements the proposed approach, thereby extending the ecologist's toolbox and fostering the alignment between landscape ecology theory and practice.

Keywords: habitat connectivity, spatial ecology, landscape ecology, urban planning, conservation biology, graph theory, ecological modeling

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1 Introduction

Landscape ecology has been key for unraveling the influence of landscape structure on ecological processes and resulting biodiversity patterns (Turner, 1989). It revealed how the heterogeneity of land cover and habitat types provides species with a variety of resources, and even allows them to colonize and survive in sub-optimal patches located nearby source patches. After Dunning et al. (1992) stressed the roles of landscape complementation, landscape supplementation, and source-sink effects, Taylor et al. (1993) relevantly pointed out that these processes tightly depend on species ability to move across the landscape, thereby giving birth to the landscape connectivity concept. This concept has first been widely acknowledged by ecologists as an overall landscape property (Forman, 1995), although it probably downplayed its relevance. It was then recognized that it should rather be associated with a given habitat type and/or a given species or taxon, and analyzed accordingly (Taylor et al., 2006). Habitat connectivity analyses are nowadays integrated into most conservation strategies (Crooks and Sanjayan, 2006), and prove helpful for understanding the influence of landscape and habitat structures on species responses (Baguette et al. (2013); Gonzalez et al. (2017); Resasco (2019); among others).

In the meanwhile, however, the processes stressed by Dunning et al. (1992), brought forth by connectivity, have often been overlooked in connectivity analyses. Indeed, most modeling approaches do not account for the fact that some species rely on different habitat types to complete their life-cycle, moving between them according to seasonal, transient, or permanent habitat changes, or over multi-generational time scales. For example, dispersal movements between several types of habitat can make it possible for some species to persist in apparently suboptimal habitats, such as urban or other human-made habitats (Snep et al., 2006). Besides, while many natural enemies feed on pest species that seasonally peak in crops, they reproduce and overwinter in semi-natural habitats (Gurr et al., 2017; Schellhorn et al., 2014). Similarly, many amphibian species reproduce in wet areas while overwintering in forest areas (Cayuela et al., 2020a). Consequently, failing to account for the heterogeneity of habitats and related connectivity patterns could limit our ability to properly understand biodiversity dynamics and design adequate conservation strategies.

The lack of consideration of such heterogeneity is partly explained by methodological shortcomings. Commonly used approaches for modeling habitat connectivity include pixel-based methods computing least cost paths or resistance distances to locate potential movement areas (McRae, 2006). Modelers often combine the identification of movement paths with the delineations of discrete habitat patches, and eventually represent habitat patch networks as landscape graphs (Galpern et al., 2011). For the latter approach, some authors have developed methods to analyze connectivity while considering land cover changes between several time periods (Martensen et al., 2017; Uroy et al., 2021). Yet, connectivity modeling tools available for these temporal analyses do not make it possible to distinguish several habitat types and the variation of movement types and timing between each of them. A modeling tool tailored to fit these cases will allow modelers to represent more realistically the processes at play. This could additionally reveal the importance of a given type of habitat patch for species' life stages occurring in other types of habitat patches. Finally, this will help designing conservation measures that increase the amount and reachability of one type of habitat while indirectly benefiting biodiversity in another type of habitat. Such an approach thus appears timely needed from both theoretical and applied perspectives.

To bridge these gaps, we propose an extension of the landscape graph modeling approach introduced by Urban and Keitt (2001), that aims to represent the connectivity of habitat networks made of different types of habitats. In an effort to foster the use of this approach, we released a new version of Graphab, an open-source software program (Foltête et al., 2012, 2021). Graphab 3.0 will allow ecologists to use multiple habitat graphs for analyzing connectivity and revealing the landscape-scale processes driving their biological responses of interest. In the following sections, we first present the theoretical underpinnings of this modeling approach. Next, we present how we adapted commonly used graph-based connectivity analyses and metrics (Rayfield et al., 2011) to multiple habitat graphs.

We then illustrate the interest of multiple habitat graphs through three case studies associated with an increasing diversity of modeled habitats and movement types. These examples showcase how to (i) consider potential source-sink dynamics for managing urban biodiversity, (ii) improve semi-natural area management as part of biological control strategies, and (iii) consider seasonal migrations for conserving composite habitat networks. We finally pinpoint future promising applications and developments of this new approach.

2 Background

Species need to move to accomplish different stages of their life cycles (e.g., foraging, breeding, overwintering), colonize new sites, extend their ranges or disperse between different populations (Schlägel et al., 2020). Some species occupy discrete habitat patches across the landscape, often after these habitats have been reduced and subdivided by human activities. The dynamics of these discrete populations and their dependence on species movements have been better understood following pioneering works on island biogeography theory (MacArthur and Wilson, 1967), spreading of risk (Den Boer, 1968), and metapopulation theory (Levins, 1969, 1970; Hanski, 1989). This body of research served as a basis for the connectivity concept, coined by Taylor et al. (1993). By allowing individuals to move across the landscape, habitat connectivity brings forth landscape-scale ecological processes, and is responsible for the fact that, in the words of Dunning et al. (1992), "*the sum of the parts of a landscape will likely not add up to the observed whole*". Indeed, individuals' movements give rise to the emergence of several types of spatial dynamics, depending on the types of habitat, resources and movements involved (Figure 1). Furthermore, because the quality and spatial distribution of habitats and resources change through time, these processes also possess their own temporal dynamics, largely driven by human activities and their consequences (e.g., land cover and climate changes). These spatial and temporal dynamics emerge from the structure of spatial networks made of habitat patches connected to different degrees depending on landscape composition and configuration (Nicoletti et al., 2023; Savary et al., 2024).

Connectivity modeling aims to map potential movements between habitat patches accurately, either for providing patch-scale or landscape-scale predictors of biological responses or for the design of spatially-explicit conservation strategies. Over the past decades, graph theory has been particularly helpful to study habitat patch networks at multiple scales and understand their ecological consequences (Borthagaray et al., 2014; Keitt et al., 1997). Landscape graph modeling has been the cornerstone of these graph-based frameworks, which represents habitat networks as sets of nodes featuring habitat patches connected by links supposed to match potential movement paths (Galpern et al., 2011; Keitt et al., 1997; Urban and Keitt, 2001).

We propose to further extend landscape graph modeling by accounting for different types of nodes and links corresponding to different types of habitats/resources and movement paths, respectively (Figure 1). Including an additional level of spatiotemporal heterogeneity in the modeling will represent more realistically the dynamics of the following landscape-scale ecological processes: (i) source-sink effects, (ii) landscape supplementation, and (iii) landscape complementation. On the one hand, when modeling habitat patch networks as multiple habitat graphs, we assume that the spatial dynamics of the latter processes takes place ON the multiple habitat graph (Fortin et al., 2021). On the other hand, their temporal dynamics is modeled by seasonal or permanent modifications of the graph components, which reflect the dynamics OF the graph.

Source-sink effects

Source-sink effects allow populations to survive in sub-optimal patches, where they cannot sustain long term growth rates, by benefiting from migrant inflow originating from optimal source patches

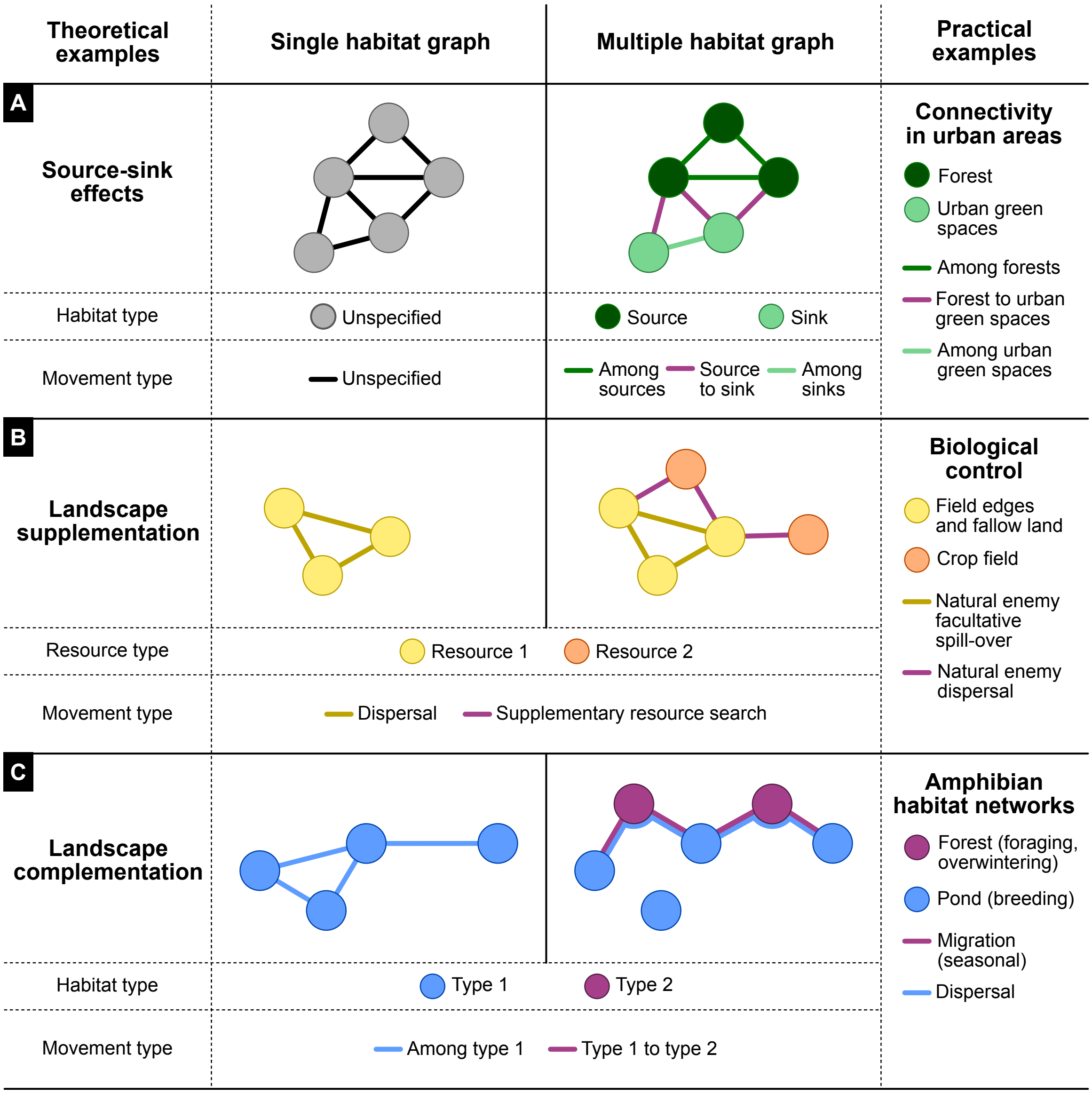

Figure 1: Multiple habitat graphs (center-right column) provide an advantage over single habitat graphs (center-left column) to model how the connectivity between different types of habitats and different movement paths brings forth the following landscape-scale ecological processes: (A) source-sink effects, (B) landscape supplementation, and (C) landscape complementation (vertically separated frames). Habitat patches (nodes) and movement paths (links) are represented by plain circles or thick lines, respectively; with colors specifying the habitat/resource types and movement types they correspond to, for multiple habitat graphs (single colored otherwise). The right-most column provides application examples (cf. Case studies section) where the multiple habitat graph approach will prove helpful.

(Pulliam, 1988). Beyond its dependency on patch quality, this landscape-scale process depends on the spatial configuration of source and sink patches as well as on the permeability of the matrix. We can expect this process to affect population demographics and community diversity in a wide range of contexts where patches of habitats of the same nature exhibit highly heterogeneous qualities (Mouquet and Loreau, 2003). For instance, in agricultural landscapes, permanent grasslands can be source patches, whereas regularly ploughed and/or fertilized temporary grasslands can be sink patches for insect or plant species that do not survive these practices, but can recolonize grasslands afterwards.

To model how source-sink effects impact population dynamics, multiple habitat graphs make it possible to distinguish habitat patches of different quality, as well as different types of movement paths connecting them (i.e., source-source, sink-sink, and source-sink links; Figure 1A). They model the connectivity between source and sink patches in a more realistic way than considering that patches and movement paths are all equivalent. Besides, changes in land use or patch quality affect these processes to varying degrees depending on the type of patches and paths they modify. For instance, the destruction of either source patches or movement paths between source and sink patches could affect the demography of sink patches in a substantial way. On the contrary, one can expect the destruction of sink patches, or movement paths among sink patches, to affect the overall population demographics to a much lesser extent. Note that a binary, and rather arbitrary, classification of habitat patches into sources and sinks can be assumed in order to quantify the connectivity between habitat types that are either highly affected by human activities, or subject to more natural dynamics. For example, such a distinction could help deriving separate estimates for the connectivity (i) among habitat patches located within protected areas, (ii) among other structurally similar habitat patches, and (iii) stemming from their inter-connections. Our first subsequent case study showcases a similar application of this approach to the connectivity of urban wooded habitat patches and peri-urban forests (Figure 1A).

Landscape supplementation

Landscape supplementation processes take place when the population occupying a focal patch increases in response to the availability of additional, and often substitutable, resources in nearby patches (Dunning et al., 1992). The focal patch is often heterogeneous and provides all the resources needed for the species' life cycle. In contrast, additional nearby patches can include one or several similar or substitutable resources to supplement the focal patch resources. In some cases, these nearby patches might not be suitable by themselves and only be used during a short period (e.g., for foraging on highly seasonal and/or patchy resources). For instance, some bird species can form large populations in small woodlots because their individuals also forage in surrounding forests (Whitcomb et al., 1977). Similarly, some insect populations breed in field margins and maintain large populations by foraging in crops (Figure 1B, and second case study).

Multiple habitat graphs can differentiate patches sustaining populations in the long term from patches only providing supplementary resources. They also distinguish the movement paths between these two types of habitat patches and can account for differences in the movement behaviors adopted for foraging, breeding, or dispersing. Based on the above, this can improve our ability to explain population sizes or predict predation pressure in nearby patches. Additionally, one can build these graphs for several dates by updating resource distributions as a function of land use changes. This provides better insights into the temporal dynamics of populations in complex and evolving landscapes. Figure 1B and a subsequent case study illustrate the use of such an approach for modeling biocontrol in agricultural landscapes.

Landscape complementation

Some species need to move to different habitat types throughout their whole life cycle to forage, breed, or overwinter. Consequently, they only survive in landscapes that provide these different types of habitats and are permeable enough to the movements between them. This defines the landscape-scale ecological process called "landscape complementation" (Dunning et al., 1992). Most amphibians are highly dependent on such processes (Figure 1C, and third case study), alike many aquatic species that separate their breeding habitats from other habitats (e.g., fish species spawning in flooded grasslands). However, several exclusively terrestrial taxa can also exhibit such a movement pattern, making them dependent on the connectivity of complementary habitats. For example, the lesser horseshoe bat (*Rhinolophus hipposideros*) differentiates foraging, roosting, and swarming sites. Given the sensitivity of this species to habitat connectivity (Tournant et al., 2013), this can largely affect the demography of its populations.

Multiple habitat graphs can distinguish several types of totally different habitats and the movements that functionally connect them (i.e., associated with foraging, breeding, or dispersal). This more realistic modeling approach is key for revealing the connectivity patterns underpinning landscape complementation processes. This will help detecting how minor land use changes can spark detrimental consequences for the dynamics of subsets of populations, and even put their survival at risk. Note that if the sole path ensuring seasonal migration movements is no longer functional or if the only habitat patch sustaining breeding is destroyed, populations could face extinction on a large scale. The corollary of these intricate dynamics is that depicting them in a more realistic manner also provides insights into which type of habitat should be best restored and, importantly, where. We next present our new modeling approach and its outputs, and how it is seamlessly implemented in the new version of Graphab.

3 Methods

To construct multiple habitat graphs and benefit from their theoretical advantages described above, we have released a new version of Graphab. This open-source software program makes it possible to build and analyze landscape graphs in a wide range of environments, including a GUI, command-line facilities, a QGIS plugin, and an R package (Foltête et al., 2012, 2021; Savary et al., 2021). The new version, Graphab 3.0, extends previous modeling options to operationalize the multiple habitat graph approach. Creating a project is the starting point of each set of analyses in this software program. At this stage, users can now consider several types of habitats, either by specifying the habitat codes from a categorical raster map of land cover, or by providing a vector map of habitat patches. They can then create sets of least cost paths according to the cost values they provide to define the resistance surface. The novelty of the new release is that these links can either connect pairs of patches of each habitat type separately, of all habitat types together, or alternatively, can be restricted to cross-connections between habitat types. After specifying topological criteria matching species movement types, landscape graphs are created and can include or not the different types of links created before.

Landscape graphs are easy to visualize using cartographical representations, either directly in Graphab or by exporting outputs to open them in other GIS applications. These graphs are usually analyzed by computing metrics at the graph-level or patch-level. The relevance and potential redundancy of the wide range of existing metrics have been investigated. Most often, a reduced set of metrics representing the amount of reachable habitat at the patch scale (e.g., patch carrying capacity or area), and beyond the patch at a local scale (e.g., local flux metrics) or network scale (e.g., betweenness centrality metric) is sufficient to represent the habitat network properties (Rayfield et al., 2011) and explain their effects on biological responses (Daniel et al., 2023; Mony et al., 2018; Savary et al., 2022). We adapted these metrics to multiple habitat graphs. First, when links are weighted for computing metrics, a movement kernel is defined to convert every distance between two patches into a dispersal probability. This is done by using a negative exponential function, as is commonly done in the metapopulation literature (Hanski, 1989). Because the multiple habitat graph approach distinguishes several movement types according to the habitat type they connect, the dispersal kernel can vary according to the link types. Second, the connectivity measurement can focus on specific connections between different types of habitat. This amounts to subdivide the overall connectivity into several components. We illustrate this below with both a global metric (i.e., computed at the scale of the entire graph) and a local metric (i.e., computed at the patch scale):

- The Equivalent Connectivity (EC) metric assesses the amount of reachable habitat at the scale of the entire habitat network. It corresponds to the area of a single patch that will provide species with an equal amount of reachable habitat as the studied habitat patch network, given its number of patches and the resistance of the landscape matrix (Saura et al., 2011). The generic formula is as follows:

  $$EC = \sqrt{\sum_{i}^{n}\sum_{j}^{n} a_i a_j e^{-\alpha \times d_{ij}}} \tag{1}$$

  The particularity of this computation in multiple habitat graphs is that it can distinguish several components of the overall metric according to the type of patches i and j connected by a link ij. Given two habitat types a and b, we can estimate the contribution of the connections between patches of habitat a alone (EC_{aa}), of habitat b alone (EC_{bb}) and of the connections between patches of habitat a and b (EC_{ab}), such that:

  $$EC_{all} = \sqrt{EC_{aa}^2 + EC_{bb}^2 + EC_{ab}^2} \tag{2}$$

- The Flux metric estimates the amount of reachable habitat from any given habitat patch. For that purpose, it sums the capacity of other patches weighted by the dispersal probability to these patches, such that:

  $$F_i = \sum_{j}^{n} a_j e^{-\alpha \times d_{ij}} \tag{3}$$

  with i the index of the focal patch, j the index of the other connected patches among the n habitat patches, d_{ij} the cost-distance between patches i and j, and a_j the capacity of patch j. Note that the capacity is akin to the patch carrying capacity. Although per default capacities correspond to patch areas, users can specify a custom value which serves as a reliable proxy for the patch demographic potential.

  In multiple habitat graphs, for a focal patch of habitat type a, F can be computed by considering only the connections to other patches of habitat a (F_{aa}) or to patches of habitat b (F_{ab}), and similarly for patches of habitat b (F_{bb}, F_{ba}).

- The Betweenness Centrality metric assesses the contribution of a given habitat patch to the connectivity between other patches. It is equal to the number of times the focal patch is located on the least cost paths on the graph between two other patches, when considering all possible patch pairs and by weighting each pair by the product of their capacities and the dispersal probability between them, such that:

  $$\begin{aligned} &BC_i = \textstyle\sum_j \sum_k a_j a_k e^{-\alpha d_{jk}} \\ &j, k \in \{1, \ldots, n\}, k < j, i \in P_{jk} \end{aligned} \tag{4}$$

  with P_{jk} the set of patch pairs to consider, corresponding to all patch pairs jk ($i! = j, i! = k$) connected by a least-cost path passing through patch i.

In that case, the multiple habitat graph approach makes it possible to assess the contribution of a patch of habitat a to the connectivity between patches of type a only (BC^a_{aa}), b only (BC^a_{bb}) or between a and b (BC^a_{ab}), and similarly for patches of habitat b (BC^b_{aa}, BC^b_{bb}, BC^b_{ab}).

The subdivision of metric values into several components described above is also possible when more than two habitat types are distinguished, and for all the other connectivity metrics already included in Graphab. Although not exhaustively described here for the sake of brevity, Graphab 3.0 made most of landscape graph analysis functionalities compatible with the multiple habitat graph approach (e.g., patch addition prioritization, link-level metrics). Similarly, users can identify habitat modules by partitioning the graph or analyze different corridors according to the types of habitats they connect and the movement types they support.

Additionally, to investigate the relationship between landscape graphs and biological data (Foltête et al., 2020), users can include nodes corresponding to their sampling sites in order to compute landscape connectivity metrics at this level with more flexibility. Graphab 3.0 and its user manual for both the GUI and command-line facilities are available at: https://sourcesup.renater.fr/www/graphab/v3/.

4 Case studies

In the three following case studies, we illustrate how the multiple habitat graph approach contributes to a better understanding of landscape-scale ecological processes and to decision-making in landscape and urban planning. The objective of this section is not to provide a detailed explanation of the data and methods employed in each study case, but rather to provide didactic examples corresponding to potential ecological applications of our framework.

4.1 Considering potential source-sink dynamics in urban biodiversity management

The local biotic and abiotic conditions affecting population eco-evolutionary dynamics in urban habitats are highly influenced by management practices and surrounding urbanization (Des Roches et al., 2021). Despite strong filtering effects reducing taxonomic and functional diversity in cities (Piano et al., 2020), urban habitats can still host a significant part of regional species pools (Aronson et al., 2014). However, the permanence of diversity patterns in these habitats probably depends to a large degree on their connections to peri-urban habitats (Snep et al., 2006; Stillfried et al., 2017; Lepczyk et al., 2017; Wang et al., 2022). Accordingly, the role of habitat connectivity for maintaining biodiversity in cities has given rise to a large body of research (e.g., Balbi et al. (2018); Beninde et al. (2015); Khiali-Miab et al. (2022); LaPoint et al. (2015); Tannier et al. (2012, 2016)), and the development of green infrastructures increasing connectivity is a key objective in urban biodiversity conservation strategies.

Determining to which point the biodiversity of urban habitats depends on peri-urban habitats (or conversely) is important for several reasons. First, if population growth rates in urban habitats cannot sustain populations without immigration from peri-urban habitats, these habitats could be considered as sinks (Lepczyk et al., 2017; Pulliam, 1988; Stillfried et al., 2017), and increasing their local suitability should then be the priority objective. Second, if movements from peri-urban to urban habitats are more important than movements between urban habitats for population dynamics and diversity patterns, connectivity conservation measures should target this type of movements. Third, these potential source-sink effects could also affect the ability of populations to adapt to urban environments (Szulkin et al., 2020; Verrelli et al., 2022). Finally, in certain contexts, urban habitat patches have been shown to act as refuges for various species (Baldock et al., 2015; Ives et al., 2016). Such a phenomenon is

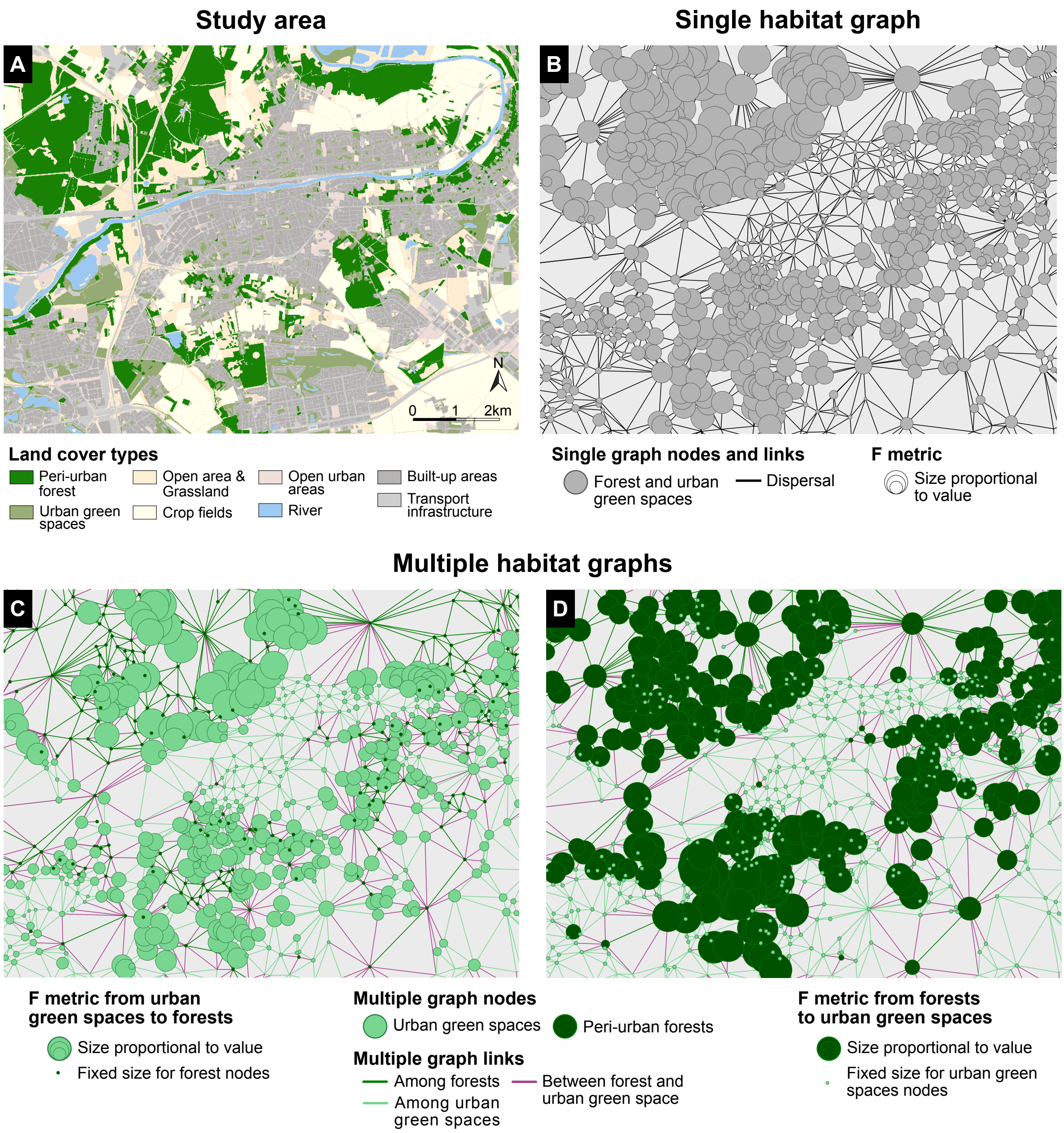

Figure 2: (A) Land cover of the study area, located in the Greater Paris, France (48°86'N, 2°72'E). Single habitat graph (B) and multiple habitat graph (C, D) representing the connectivity of a habitat patch network made of urban patches of wooded habitats (light green) and forests (dark green), both represented in grey in the case of the single habitat graph approach. The connectivity between each patch and the surrounding patches is assessed using the Flux metric (F). Values are displayed with circles at the patch (node) level, with sizes proportional to the metric values. In the single habitat graph (B), these circles are grey and the F metric assesses the amount of both forest and urban wooded habitat reachable from any type of patch. In contrast, in the multiple habitat graph approach, the circles are light green when the F metric assesses the amount of forest reachable from a urban habitat (C) and dark green when it assesses the amount of urban habitats reachable from a forest patch (D). Graph links are uniformly grey in the single habitat graph (B), whereas they take a dark green, light green, or purple color when they depict connections among forests, among urban green spaces, or between forest and urban green spaces, respectively, in multiple habitat graphs (C, D).

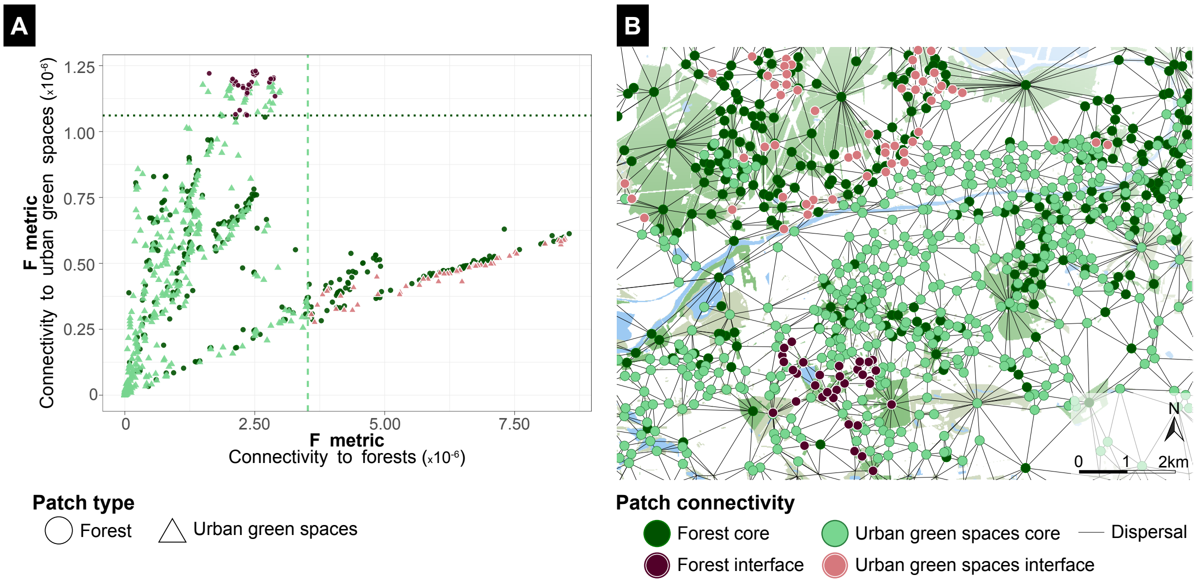

Figure 3: Connectivity contrasts revealed by multiple habitat graphs within each habitat type. (A) Relationship between the amount of forest reachable (x-axis) from forest patches (plain circles) or from urban green space patches (triangles), and the amount of urban green spaces (y-axis) reachable from forest or urban green spaces. The amount of reachable habitat is computed with the F metric (see details in main text). Every data point corresponds to a patch. Urban green space patches located on the right side of the vertical dashed line (pale orange) take values of the F metric measuring the connectivity to forest from the 9th decile of its distribution, and are therefore the most connected to forest patches. Similarly, forest patches located above the horizontal dashed line (purple) take values of the F metric measuring the connectivity to urban green spaces from the 9th decile of its distribution, and are therefore the most connected to urban green spaces. (B) Spatial location of the habitat patches according to the relationship between their connectivity to forest patches and urban green spaces. Forest patches above the horizontal dashed line on panel (A) and urban green space patches on the right of the vertical dashed line are represented in the same colors on panel (B).

expected when surrounding landscapes have been subject to substantial anthropogenic disturbances, and potentially turns urban populations into source populations for peri-urban populations.

To detect and map these dynamics towards guiding urban biodiversity conservation, it is therefore essential to consider the spatial heterogeneity of habitat types in cities and their surroundings. In that case, the heterogeneity does not reside on the fact that the species of interest use habitats that modelers commonly assign to different categories, or move between them at specific periods. Instead, the species of interest use structurally similar habitats (e.g., wooded urban parks and peri-urban forests, or private flowered lawns and grasslands) that are located in areas reshaped by humans to varying degrees, managed differently, and therefore varying in quality. Multiple habitat graphs can differentiate urban and peri-urban habitats, enabling modelers to assess the individual contribution of each habitat type to the overall habitat connectivity. It also allows for the identification of urban patches that contribute most to the connections with peri-urban habitats, and conversely, the peri-urban patches that facilitate movements to urban habitats.

We illustrate this approach by modeling the network of forest patches and urban green spaces in a highly urbanized area in the Greater Paris, France (48°86'N, 2°72'E; Figure 2; and see Appendix S1 for further modeling details). We used a 2017 land cover map provided by Institut Paris Région, simplified to include 9 different land cover types and rasterized at a resolution of 2 m. The least cost paths were computed between pairs of habitat patches, irrespective of their nature, following a minimum planar graph topology (see cost scenario in Appendix S1: Tables S1 and S2). On the obtained graph, all types of potential links were conserved such that two forest patches, two urban green spaces or one patch of each type could be connected. We then computed the Flux (F) metric at the patch level, and could thereby assess the connectivity of forest patches to urban green spaces or to other forest patches, and conversely. This analysis revealed the complementarity of forest and urban green space patches in this area for the movements and dynamics of forest species surviving urban conditions (Figure 2). Moreover, Figure 3 reveals the better resolution gained in the analysis by using multiple habitat graphs instead of single habitat graphs. Indeed, the new approach allows for patch prioritization at the habitat type level, while considering the connection among habitat types. This reveals both the forest patches most connected to urban green spaces and the urban green spaces that are the most connected to forest patches. Because these two sets of patches do not necessarily coincide in an urban context (Figure 3), these results could help managers identify the most important patches, both within and outside the urban fabric. These analyses could also provide relevant information for sampling populations when investigating urban adaptations and how gene flow moderates it.

4.2 Improving semi-natural area management as part of conservation biological control strategies

Our proposed model could also find applications when modeling ecological processes in agroecosystems. Indeed, disentangling trophic interactions and their consequences for population dynamics in agroecosystems is critical for ensuring sustainable crop production (Benton et al., 2003). Although pest populations have been increasingly regulated using pesticides in the past century, conservation biological control strategies can be implemented to prevent pest outbreaks (Tscharntke et al., 2007), either by managing their resources (e.g., with frequent crop rotations) or by favoring natural enemies (e.g., entomophagous arthropods; Gurr et al. (2017)). The success of the latter top-down strategy has been shown empirically (e.g., Aguilera et al. (2020); Woodcock et al. (2016)). It depends on landscape supplementation processes and is contingent upon natural enemy movements between semi-natural habitats and crop fields (Rand et al., 2006; Tscharntke et al., 2012). This stems from the fact that natural enemy species such as carabid species or other beetles often breed or overwinter in field margins or fallow land and then spill-over into arable crops to feed on pest species (Schellhorn et al., 2014). These processes have been studied for a long time (Rand et al., 2006; Tscharntke et al., 2005), and have justified subsidies for agri-environmental measures as part of the European Common Agricultural Policy (e.g., beetle banks, flower strips).

Notwithstanding their alleged advantages, some studies did not evidence the benefits of semi-natural areas for biocontrol (Duflot et al., 2015; Veres et al., 2013) and several explanations can be given. First, the legacy of intensive pesticide use or past extinctions of natural enemy species can explain why conserving semi-natural areas in the landscape falls short in favoring biocontrol. Apart from these mechanistic explanations, the way we account for landscape composition and configuration when testing for the influence of semi-natural habitats on biocontrol can also be brought into question (Martin et al., 2019; Veres et al., 2013). On the one hand, some types of semi-natural habitats can either favor or limit the presence of pest species, as for instance woody habitats (e.g., woodland and hedgerows) and open habitats (e.g., grassy strips or fallow land), respectively (Tougeron et al., 2022). On the other hand, landscape configuration may moderate the presence of natural enemies in crop fields (Perović et al., 2015), as the core of fields can be too far from semi-natural habitats to be reached or because some woody habitats are barriers for some flying arthropods.

In light of these aforementioned elements, we need to better account for the spatial heterogeneity and connectivity of habitats in agricultural landscapes if we are to shed light on biocontrol drivers, guide agricultural subsidy policies and farmer decision-making (Batáry et al., 2011; Veres et al., 2013). Multiple habitat graphs may prove helpful in that respect because they can model natural enemy movements between semi-natural habitats and crop fields in a spatially-explicit way. In that case, the habitat network would consist of distinct types of nodes, representing either crop fields or semi-natural open habitats. The set of links will only connect different types of nodes, in order to explicitly model landscape supplementation processes sustaining biocontrol while potentially accounting for variations in the matrix permeability to movements linked to its heterogeneity (e.g. hedgerows, thickets, roads). One can then assess the overall connectivity of the network at the landscape or farm level using global connectivity metrics. These metrics can be used to test the influence of semi-natural habitats on biocontrol when data on natural enemies, pest populations or crop damages are available at the

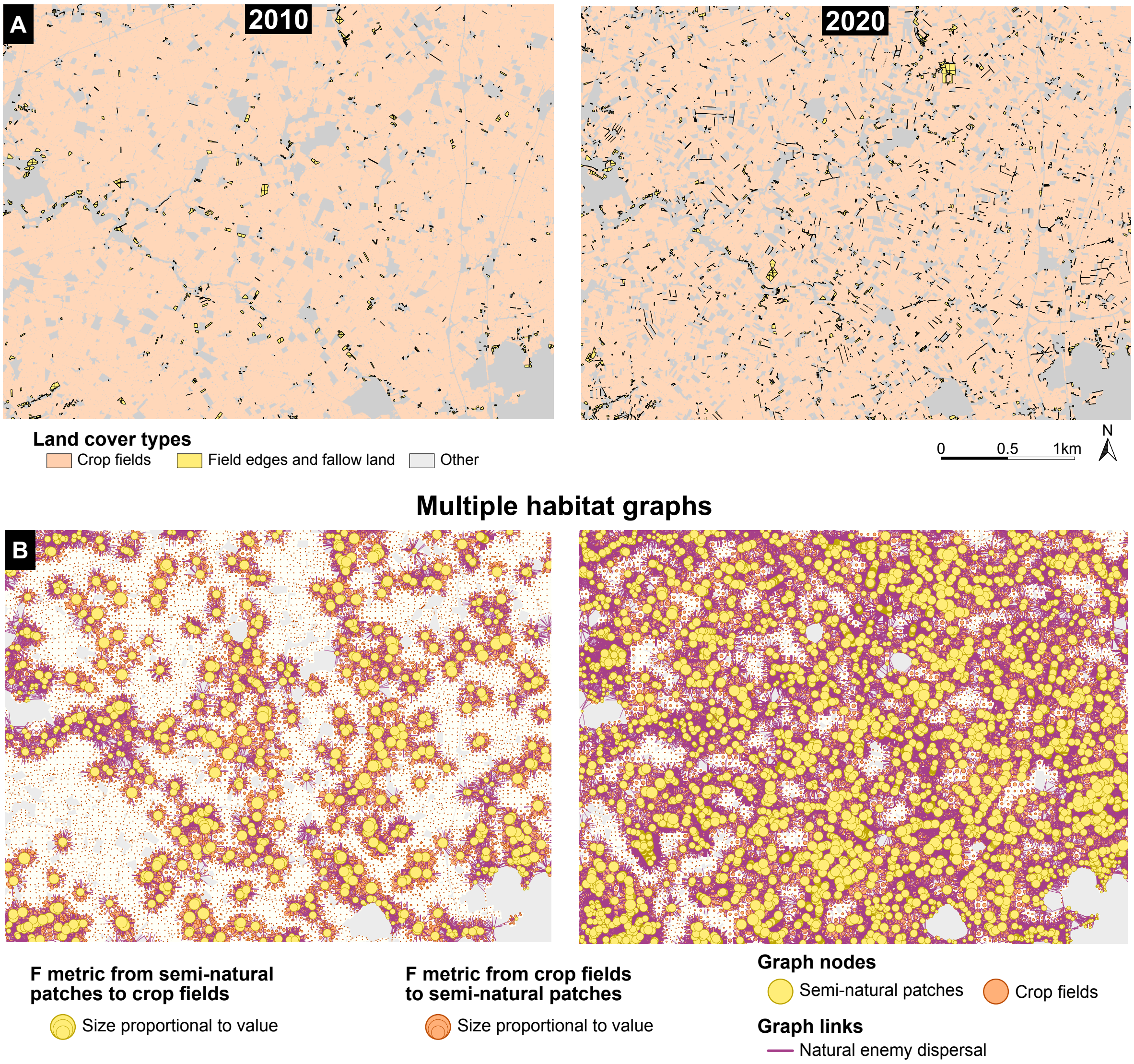

Figure 4: Connectivity of the network of annual crops and semi-natural habitats in a French agricultural landscape (48°08'N, 1°40'E), as modeled using the multiple habitat graph approach for the years 2010 and 2020. Annual crops (orange in A) include cereals, maize, beets, potatoes, oil-protein crops and other annual cash crops, and exclude grasslands, perennial fodder crops or plantations. Semi-natural patches (yellow in A) include field margins, fallow land, and grassy strips. The left column corresponds to the year 2010, and the right column to 2020. In the bottom panels representing multiple habitat graphs (B), the pruned links of the graph are represented in purple. The circles representing each node have a size proportional to the values of the F metric, assessing the amount of crop field habitat reachable from semi-natural patches (yellow), or of semi-natural habitat reachable from crop fields (orange).

landscape- or farm-level. Note that when data are available for several years, the influence of crop rotations on biocontrol and pest outbreak dynamics can also be assessed. Besides, metrics computed at the local-level, i.e., at the level of individual crop fields or semi-natural habitat patches, can reveal which fields are potentially more reachable by natural enemies, and which field margins, fallow land or grassy strips could favor most biocontrol. This information will give some leeway to improve parcel configurations towards maximizing local or farm-level biocontrol.

To provide an example of this modeling approach (Figure 4), we modeled the network of annual crops and semi-natural habitats in a French agricultural landscape (48°08'N, 1°40'E) for the years 2010 and 2020 (see Appendix S2 for further modeling details). We used the national agricultural parcel database (Registre Parcellaire Graphique, ASP) to identify two types of habitat patches: (i) annual crops, including cereals, maize, beets, potatoes, oil-protein crops and other annual cash crops, and excluding grasslands, perennial fodder crops or plantations, and (ii) field margins, fallow land, and grassy strips. We then computed the movement paths between crops and semi-natural habitats, excluding paths between habitats of the same type. We assumed that Euclidean distances reflected the cost of dispersal across mostly open areas of entomophagous arthropods regulating pest species such as aphids or butterflies. After building the two multi-habitat graphs (one for each year), we computed the Equivalent Connectivity (EC) metric at the graph level and the Flux metric (F) at the patch level for both years. This diachronic analysis revealed substantial changes from 2010 to 2020. First, the number of semi-natural habitat patches have increased nine-fold in 10 years, while their total area has increased by only 57 %. In contrast, the number of crop fields has increased by 26 % for an overall decrease in total area of 6 %. From 2010 to 2020, these contrasting changes jointly affecting the number, mean size, and total areas of crop fields and semi-natural patches translated into an increase by 28 % of the connectivity of the network they form. These changes in crop rotations and semi-natural area management are visible on the map, which sketches where local gains (or losses) of connectivity have occurred (Figure 4). Local metric values could be used to understand pest outbreaks, assess the performance of farming strategies, and help designing crop rotations maximizing the potential for biological control over time. They also reveal the consequences of agricultural policies implemented over the last decades in Europe, which have significantly increased the amount of semi-natural areas and modified crop planning in the study area.

4.3 Accounting for seasonal migrations for conserving amphibian composite habitat networks

Ecological processes and the movements they cause often go beyond the limits of a single habitat type. Some species use different types of habitats during their life cycle (e.g., amphibians, bats, fish) and are therefore particularly sensitive to the spatial arrangement of these different types of habitats and their connectivity. Amphibians are an example of biphasic species, breeding in aquatic areas (e.g., ponds), but spending the rest of their life-cycles in terrestrial habitats. This life history strategy leaves a typical imprint on their movement patterns, which deeply vary over spatial and temporal scales (Cayuela et al., 2020b). Individuals move between aquatic habitats and more or less distant terrestrial habitats during seasonal migrations, but also between two aquatic habitats via one or more intermediate terrestrial habitats during inter-annual dispersal.

Despite the peculiar pattern of these different types of movements, many amphibian conservation studies are focused on a single ecological process (mostly dispersal) and evaluate connectivity between breeding habitats (e.g., Clauzel et al. (2013)). However, focusing solely on one type of movement overlooks an integral aspect of their life cycle, namely seasonal migration, which plays a crucial role in maintaining the viability of amphibian populations (Bailey and Muths, 2019). Furthermore, assessing connectivity at the dispersal scale by focusing on direct connections between breeding habitats does not match the actual movement behavior of amphibians. The latter is best modeled by assuming that dispersal connections among breeding ponds involve an intermediate step through a terrestrial habitat used during and outside breeding periods.

In that context, multiple habitat graphs overcome the limitations of classical single habitat approaches. The graph created to illustrate the application of our approach to this biological model (Figure 5) includes two distinct habitat types (aquatic and terrestrial habitats) linked by a set of inter-habitat links. This model allows for quantitative and cartographic connectivity assessments that are specifically tailored to the ecological process of interest. Amphibian migration will be mostly affected by connectivity patterns driving fine-scale movements between aquatic and terrestrial habitats. In contrast, amphibian dispersal and gene flow will depend on larger-scale indirect movements between aquatic habitats stepping through terrestrial habitats. In that context, connectivity metrics computed assuming different connections and movement distances will be relevant predictors of different biological patterns. For instance, the Flux metric (F) parameterized for movement distances commonly covered during seasonal migrations assesses the amount of aquatic habitat reachable from a patch of terrestrial habitat, and vice versa. It therefore reflects the contribution of these habitat patches to annual population dynamics. In contrast, the same metric computed by assuming a movement kernel characterizing the behavior of dispersing individuals evaluates the potential gene flow between breeding habitats over multiple years. Note that in that case, the philopatry degree of breeders will determine the frequency and spatial distribution of gene flow events per breeding migration event (see Cayuela et al. (2020a), for an empirical evidence). Finally, the topology of inter-habitat links provides an advantage over single habitat graphs to realistically compute centrality metrics such as the Betweenness Centrality Index. This index can assess the contribution of each terrestrial habitat (or each link) to multi-generational dispersal movements among all breeding habitat pairs, thereby revealing the backbone of gene flow events. From a conservation point of view, mapping the most important migration paths can lead to targeted measures for reducing amphibians' road kills, while identifying gene flow patterns can help sustaining genetic diversity for long-term adaptation potential. Both endeavors are equally important for a taxon facing high extinction risks due to historical hydrologic management, climate change, and wildlife disease, among others (Díaz et al., 2019).

To provide an example, we modeled the network of amphibian species in a mainly agricultural area in the south of Paris (48°44'N, 2°17'E, Clauzel et al. (2024); see Appendix S3 for further modeling details). We built a land cover map for the year 2021 by combining land cover data from Institut Paris Région, the locations of the main linear transport infrastructures provided by the National Institute of Geographic and Forest Information (IGN), and a pond inventory from the SNPN naturalist association. The land cover map includes 21 different land cover types at a spatial resolution of 3 m. We compared the network structure and connectivity values (Flux metric) at the dispersal scale between a single habitat graph (Figure 5A) and a multiple habitat graph (Figure 5B).

This analysis revealed some differences in network structure. Some aquatic habitats (e.g., in the North) appeared to be rather isolated in the single habitat graph but were connected to other habitats via terrestrial habitats in the multiple habitat graph, although in a fragile way. The latter model thus highlighted the key role of terrestrial habitats for both migration and dispersal. When the local aquatic habitat connectivity was calculated at the dispersal scale, the Flux metric took similar values in both approaches. This suggests that the classical single habitat approach could be sufficient for an assessment of aquatic habitat connectivity. In contrast, the multiple habitat approach would be of greater interest for detailed and multi-scale connectivity analyses, making it possible to break down the modeling outputs reflecting either migration or dispersal processes. Accordingly, this approach can be particularly useful for habitat restoration. Clauzel et al. (2024) showed that improving connectivity sometimes requires the creation of a terrestrial habitat associated with an aquatic habitat. The efficiency of such a strategy is conditional upon a proper consideration of patch types and locations within ecological networks at the landscape scale. In that context, the approach we introduce will prove helpful for landscape managers to design conservation or restoration actions. Multiple habitat graphs can also be used to assess the effects of landscape transformations (e.g. conversion of grasslands to crops, urbanization, restoration of ponds, reforestation) affecting the different types of habitat used

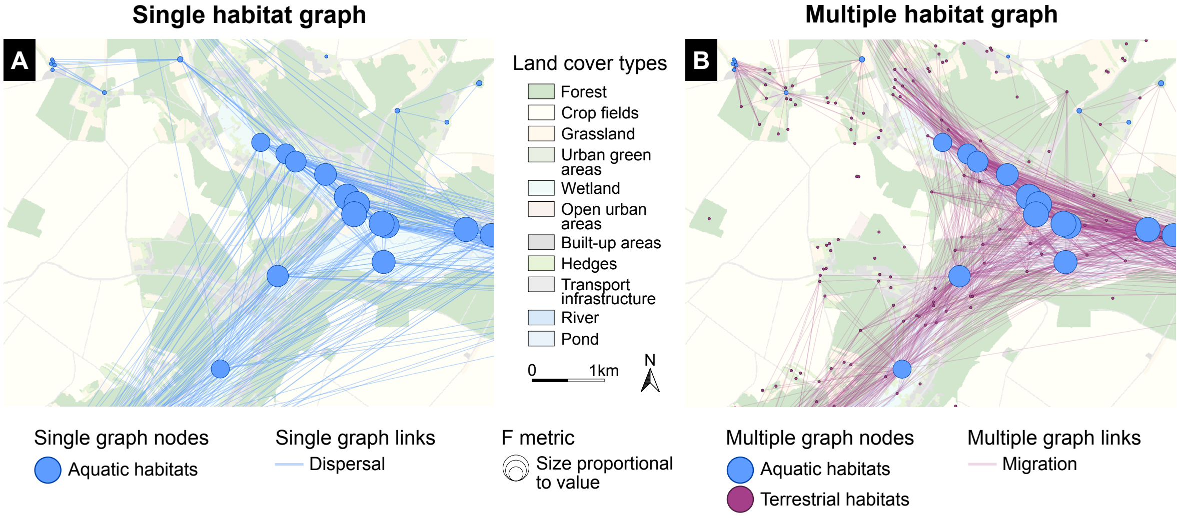

Figure 5: Connectivity of an amphibian ecological network in a French agricultural landscape (48°44'N, 2°17'E), modeled using a single habitat (A) and a multiple habitat graph approach (B). Whereas the single habitat graph contains only aquatic habitats, the multiple habitat graph contains aquatic habitats (blue) and terrestrial habitats (purple) connected by an inter-habitat link set. In both cases, the link topology is complete. The connectivity between each patch and its neighboring patches was assessed using the Flux metric (F). We assumed that the movement distances used for the computation match typical dispersal distances for aquatic habitats (A, B). Values are displayed with circles at the patch (node) level, with sizes proportional to the metric values. These circles are blue when the F metric assesses the amount of aquatic habitats reachable from another aquatic habitat patch by direct connections (A) or through indirect connections via an intermediate terrestrial habitat patch (B).

by amphibian species, thus revealing which ecological process would be most affected.

5 Perspectives for future applications and improvements

By focusing on a single type of habitat and movement, common connectivity models fall short in depicting how habitat connectivity gives rise to landscape-scale ecological processes driving population dynamics in significant ways. To bridge the gaps between landscape ecology theory and modeling approaches, and hopefully between models and reality, we propose a new version of the Graphab software program that operationalizes the concept of multiple habitat graphs. Although we described several examples in which these tools would be relevant for research and conservation applications in various landscape contexts, this new approach opens avenues for other applications and further extensions.

Landscape graph connectivity modeling is most relevant for a given species or a set of specialist species occupying the same type of discrete habitat patches (Galpern et al., 2011). However, by considering different types of habitats in the same model, our approach relaxes this constraint and offers the possibility to model simultaneously the connectivity for species having a wide range of ecological requirements, coexisting at landscape scales in partially overlapping habitats, and potentially sharing movement patterns. This could help explain how landscape structure drives the specialization degree of communities (Lami et al., 2021). Similarly, multiple habitat graphs can improve predictions in spatial epidemiology by modeling the interaction of species occupying the same type of habitat during their encounter period, but different habitat types most of the time (Gilbertson et al., 2023). For example, the spread of pathogens responsible for Lyme disease or echinococcosis depends on the movements of rodent and carnivorous mammal species potentially occupying different types of habitat (Giraudoux et al., 2003; Ostfeld et al., 2005; Raoul et al., 2015).

Besides, while connectivity conservation strategies often include several types of habitats (e.g., Mimet et al. (2013); Oehri et al. (2023)), the joint consideration of their connectivity is still lagging behind. Environmental management schemes based on ecological networks (e.g., green and blue infrastructures) tend to compartmentalize conservation issues by analyzing each habitat network independently. This partly stems from the current lack of methods and tools available to landscape managers for combining different networks and detecting areas with multiple-habitat connectivity issues (Savary et al., 2024). Multiple habitat graphs can also help analyze the respective contributions to connectivity of habitat types defined using administrative criteria, such as protected areas (Santini et al., 2016), private lands (Bargelt et al., 2020), or retention ponds (Clevenot et al., 2022).

While our approach allows for the consideration of multiple habitat types in connectivity models, it does not tackle the challenge of identifying these habitat types based on their ecological functions, such as being a source, sink, supplementing, or complementing habitat. If the main objective justifying connectivity analyses is to assess the respective contributions of areas that share comparable structural and environmental conditions but that differ in terms of management, conservation status, or ownership, the definition and delineation of habitat types can be arbitrary and based on these human-defined distinctions. Nevertheless, ecological differences among habitat types can be informed by expert knowledge, as for instance in our case studies. It is common practice when implementing the single habitat graph approach to select habitat patches from the output of species distribution models (Foltête et al., 2020). However, these models rarely consider the fact that species use different habitat and resource throughout the year. As a consequence, although this approach provided an empirically grounded solution to the identification of habitat patches for this approach, this workaround might not fit the multiple habitat graph approach as adequately. The usefulness of any ecological model highly depends on the relevance of its parameters to the pursued objectives. Because our modeling approach adds complexity to common modeling approaches, this novelty must go hand in hand with the use of advanced empirical methods and expert knowledge for defining multiple habitats in a realistic way. Resource Selection or Utilization Functions fitted from telemetry data at different life-cycle stages could, for instance, provide key insights into the seasonal use of habitats and resources by animals (e.g., Aiello et al. (2023); Boggie et al. (2017)).

Finally, in the new release of the Graphab software, we have adapted commonly used graph-based connectivity metrics to multiple habitat graphs. Nonetheless, new metrics directly inspired from this type of graph could further extend the toolbox of connectivity modeling. Besides, we did present the use of modularity analyses considering how subsets of habitat patches of different types can ensure the optimal accomplishment of the different stages in species life cycles. We believe these aspects represent promising research avenues for dedicated landscape ecologist and conservation specialists.

Authors' contributions

All authors contributed to the initial ideas of the project. GV developed the new version of the Graphab software program and updated users' manuals. PS and CC wrote the initial draft of the manuscript, which was significantly edited by all authors. GV, CC and PS carried out the case study analyses. XG made the figures.

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Conflict of interest statement

The authors declare no conflicts of interest.

Data availability statement

Data are available in Zenodo at https://doi.org/10.5281/zenodo.10576225.

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