Combining spatial modeling tools and biological data for improved multispecies assessment in restoration areas

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Title page

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Highlights

- Habitat restoration or creation is one of the actions to reduce fragmentation
- Our goal was to improve multiscale and multispecies functional connectivity.
- We modeled habitat suitability and ecological network for eight pond-dwelling species.
- Forest edges appeared strategic for improving multispecific connectivity.
- The results provide insights into central issues of biodiversity offset and habitat restoration.

Abstract

Habitat restoration is one of the actions to reduce landscape fragmentation by promoting connectivity and thus biodiversity. But knowing where to implement these habitats is a major issue and planners lack guidance for answering this question, in particular when it involves multiple species and over a large area. We proposed to combine biological data, habitat suitability models and spatial graphs to improve multiscale and multispecies connectivity in Ile-de-France, a highly artificialized region of 12,000 km². The framework consisted of i) modeling habitat suitability for eight pond-dwelling species (*Alytes obstetricans, Bufo bufo, Epidalea calamita, Hyla arborea, Rana temporaria, Salamandra salamandra*, *Triturus cristatus, and Natrix natrix*), ii) modeling the ecological network for each species, iii) prioritizing each sampling point depending on the gain in connectivity if a new pond was created there and iv) combining single-species results to identify the areas that could improve multispecies connectivity. The multivariate statistical analysis revealed that transitional forest environments appeared to be the most strategic areas for improving multispecific connectivity (at least for 5 species). Targeted addition of habitat within an ecological network can increase habitat density in deficient areas and reconnect network sub-parts. This approach is therefore promising to guide conservation actions and "no net loss" biodiversity measures, especially the final stage of offset in the mitigation hierarchy.

Keywords: multispecies approach, amphibian, habitat suitability models, landscape graph, functional connectivity, biodiversity offset

1. Introduction

Urbanization and agricultural intensification lead to a reduction and a fragmentation of natural and semi-natural habitats. Wetlands and ponds have particularly been affected, experiencing a global 70% decrease since the beginning of the 20th century (Davidson, 2014). This reduction has direct consequences on the viability of animal populations. Among the current mass extinction of biodiversity, amphibian and reptile species are recognized as the most threatened vertebrate group. According to the International Union for Conservation of Nature (IUCN), more than half (59%) of amphibians and 42% of reptiles are declining worldwide. These trends are probably underestimated because a large proportion of species (23%) are "data

deficient" and are not integrated into population trend analyses (Howard and Bickford, 2014). The drivers of this decline are mostly related to human activities, habitat loss and landscape fragmentation, as well as environmental pollutants, infectious diseases and global climate change (Hayes et al., 2010). Their vulnerability is notably due to their biphasic life cycle, which induces many movements between aquatic and terrestrial habitats.

Many studies have documented this extinction crisis and proposed conservation actions mostly related to protected area design, sustainable conservation measures, species translocation or habitat restoration/creation (Godet and Devictor, 2018). Since many amphibians can live in artificial wetlands and ponds, habitat restoration and even the creation of new ponds could be an effective solution to reduce landscape fragmentation. But Grant et al. (2019) noted that species conservation, especially amphibian conservation, had failed. They advocate an improved complementarity between research and management to increase the effectiveness of conservation actions. For example, in the case of amphibian populations living in fragmented habitats and highly dependent on fluxes between patches (Hanski and Ovaskainen, 2000), aquatic habitat restoration should integrate both local-scale factors such as microtopography, water quality or nearby terrestrial habitat and broad-scale factors such as connectivity between habitats (Hodgson et al., 2011) to maintain regional connections and, consequently, the viability of populations (Briers, 2002; Moilanen et al., 2005). If expert opinions and field data could provide information about local-scale factors, then their large-scale generalization would be complex due to the large amount of data required. In addition, landscape managers lack information on where to restore future habitats, how many and how to arrange them, e.g., many habitats close together or habitats scattered to cover a large area (Schmidt et al., 2019). Recently, several studies have attempted to answer these questions by performing dynamic models (Scroggie et al., 2019) or connectivity models (Clauzel et al., 2015; Jeliazkov et al., 2019; Matos et al., 2019). Despite promising results for conservation actions, these studies focused on a single species. Designing a method to target restoration areas depending on regional connectivity for multiple species is still challenging.

We hypothesized that bringing together field expertise (expert opinion and biological data) and spatial modeling tools (prediction and simulation) could fill this gap. Several studies have been published on multispecies assessment of connectivity to prioritize core habitats and corridors (Khosravi et al., 2018; Lechner et al., 2017; Meurant et al., 2018), to reduce road fragmentation (Mimet et al., 2016; Santini et al., 2016) and to quantify the impacts of land cover changes (Sahraoui et al., 2017). But to our knowledge, no studies have implemented it on the assessment of habitat restoration, which is a major challenge for biodiversity conservation. We proposed to combine habitat suitability models and landscape graphs to take advantage of their respective strengths and partially overcome their limitations. Graph-based modeling is a widely used method for analyzing connectivity in habitat networks (Dale and Fortin, 2010; Foltête, 2019; Galpern et al., 2011; Minor and Urban, 2008; Urban et al., 2009). Landscape graphs are considered spatially explicit models of ecological networks designed from both environmental and biological data. Similar to any spatial graph (Fall et al., 2007), landscape graphs constitute a mathematical object on which connectivity metrics can be calculated at different levels (Rayfield et al., 2011). These metrics provide indicators for prioritizing habitats to preserve, assessing the potential impact of land-use changes and identifying the best locations to restore habitats or corridors (Foltête, 2019). However, like any modeling method, landscape graphs also have limitations, especially regarding the reliance of the representation of the actual habitat network (Moilanen, 2011). One solution to improve this limitation is to incorporate biological data in graph modeling through habitat suitability models (HSMs). Based on the concept of ecological niche, a HSM predicts species potential distribution by analyzing and extrapolating the statistical relation between species presence and environmental variables (Guisan and Zimmermann, 2000). The resulting HSM maps allow the identification of the most suitable areas for habitat patches. However, they cannot provide information about the connections between these suitable areas, for which a connectivity analysis is required. Combining HSM and landscape graphs has already been performed using various alternative techniques and input data for a single species (Almpanidou et al., 2014; Clauzel et al., 2013; Decout et al., 2012; Duflot et al., 2018; Schank et al., 2020; Ziólkowska et al., 2012). In most cases, HSM

has been used to define both habitat patches and least-cost paths, thus mixing two different ecological processes, habitat selection and movement, which may be a questionable practice. Radio-telemetry data (Ziólkowska et al., 2012) or individual-based simulations (Coulon et al., 2015) appear relatively more relevant but require complex data that are difficult to collect for several species and over a wide area. Furthermore, GPS data provide information on actual movements but not on alternative routes that could be used in case of disturbance. To overcome these difficulties, we used HSM to delineate optimal habitat patches as well as previous field experimentations combined with expert opinions to calibrate least-cost paths from a resistance landscape map.

We applied this protocol to the simultaneous conservation of eight species to search for the best locations for pond creation, i.e., optimizing connectivity for as many species as possible. The analysis was applied in the Ile-de-France region (France), a highly disturbed region, which is poorly represented in dispersal studies that tend to occur in less disturbed semi-natural habitats (Bailey and Muths, 2019).

2. Materials & Methods

2.1. Study area and studied species

The study area (12,000 km²) is the administrative region of Ile-de-France surrounding the city of Paris (France) (48.6°N; 3.2°E). The landscape is dominated by intensive agriculture (50%), urbanized areas (24.5%) and forests (24%). Water bodies and rivers occupy only 1.5% of the area (IAU, 2019). The Ile-de-France region is home to 12 reptile species and 17 amphibian species (Zucca et al., 2019). The species under study were selected according to several criteria: ponds as one of the habitats, sufficient occurrence data, various optimal habitat types and various dispersal abilities between species. Species occurrence data were extracted from the naturalist database CETTIA, which has included both protocoled and opportunistic data at the regional level since 2012. Eight species with distinct ecological preferences were retained: 7 amphibians (*Alytes obstetricans, Bufo bufo, Epidalea calamita, Hyla arborea, Rana temporaria, Triturus cristatus,* and *Salamandra salamandra*) and 1 reptile (*Natrix natrix*). Literature including naturalist guides (Bensettiti and Gaudillat, 2004 ; Grand et al., 2014 ; Lescure and Massary, 2012), regional studies (Sordello et al., 2011) and scientific studies (Sahraoui et al., 2017) helped us to identify the ecological characteristics of the species in terms of aquatic and terrestrial habitats, environments favorable or unfavorable to movement and daily and annual movement capacity. Some species are specialized more than others with a preference for either forest ponds or open-area ponds. Some tolerate artificial environments such as quarries or sandpits, while others avoid them (Table 1). Their dispersal abilities vary from 100 m for *S. salamandra* to 9,000 m for *R. temporaria.*

Table1 – General species' ecology, freshwater habitat types, number of occurrence data in CETTIA database, daily and dispersal distances for each of the eight species under study, based on information from the literature.

General species' ecology	**Preferred freshwater habitat type**	**Species**	**Number of observations in CETTIA database**	**Maximum dispersal distance**	**Daily movement**
Can use different kind of ponds, including large bodies of water	Ponds and all water surfaces	*Bufo bufo*	9,608	2,500 m	200 m
Dependent on a network of varied types of ponds	Ponds	*Hyla arborea*	372	4,000 m	500 m
Dependent on low-density forest, shrublands, and grasslands	Ponds in or near the forest	*Natrix natrix*	750	3,000 m	200 m
		Rana temporaria	1,038	9,000 m	200 m

Dependent of forest	Ponds in or near the forest	*Salamandra salamandra*	130	100 m	50 m
Dependent on open environments and temporary ponds. Tolerant of artificial environments (quarry and sandpit)	All ponds, except those in forest cores	*Epidalea calamita*	322	2,500 m	200 m
Dependent on open environments. Urban areas tolerant		*Alytes obstetricans*	413	150 m	100 m
Dependent of open and shrubby environments and on a dense network of ponds		*Triturus cristatus*	485	1,000 m	100 m

2.2. Habitat suitability modeling

For each species, habitat suitability was modeled by linking occurrence records, which varied from 130 points for *S. salamandra* and 9,608 for *B. bufo,* and a set of environmental variables. These predictive variables were chosen according to their potential ecological relevance for pond-dwelling species (Wilson et al., 2013). Thirteen variables corresponding to four different data categories were selected (Table 2). Two topographic variables (slope and roughness) were obtained from the digital elevation model of the Ile-de-France provided by IGN. Temperatures were extracted from BIOCLIM data derived from MODIS LST reconstructed at a resolution of 250 m pixels (Metz et al., 2014) and precipitations from CHELSEA (climatologies at high resolution for the earth's land surface areas) data (Karger et al., 2017). The NDVI (normalized difference vegetation index) was obtained from Landsat 8 satellite images. Landscape and proximity variables described the habitat quality of the pixel neighborhood (availability of daily resources or local disturbances). As the extent of this neighborhood could be different depending on the ecology of the species, three radius buffers were selected to calculate the percentage area of the land cover categories. Landscape and proximity variables were calculated from a landscape map built from the combination of three databases: i) the Ile-de-France's land use produced by the L'Institut Paris Region, ii) the BD TOPO® IGN for linear landscape elements such as roads and rivers and iii) the pond database of the National Society for the Protection of Nature. The resulting landscape map had 17 categories (Appendix A) and was rasterized at a 10 m resolution.

Table 2. Description and sources of the 13 environmental variables used for modeling habitat suitability of each species

Category	Variable	Resolution	Data source
Bioclimatic	NDVI	30 m	Landsat 8 (layers band 5 et band 4) NDVI = (NIR – R)/(NIR+R) August 2019
	Temperatures	250 m	BIOCLIM data derived from MODIS LST
	Precipitations	1 km	Chelsea (Climatologies at high resolution for the earth's land surface areas)
Topographic	Slope	25 m	MNT
	Roughness	25 m	MNT
Landscape composition with a buffer size of 50 m; 200 m; 500 m	Forest	10 m	Landscape map
	Grassland	10 m	Landscape map
	Quarry	10 m	Landscape map
	Water	10 m	Landscape map
	Artificial areas	10 m	Landscape map
Proximity	Distance to the nearest road	10 m	Landscape map
	Distance to the nearest river	10 m	Landscape map
	Distance to the nearest pond	10 m	Landscape map

Habitat suitability modeling was performed with MaxEnt (Phillips et al., 2017), an open-source software based on the maximum-entropy approach for modeling species niches and distributions. To avoid potential bias (Fourcade et al., 2014; Kramer-Schadt et al., 2013), we analyzed the data set before modeling to check for inconsistencies or outliers. We then removed duplicates in each 10mx10m resolution cell so that there were no overestimates in some places. We maintained the default settings that are recognized to perform as well as the adjusted settings (Phillips and Dudík, 2008). Models were replicated ten times, and the average probabilities of predicted presence were retained for further analysis. The robustness of the models was examined using a *k*-fold cross-validation procedure, wherein species presence points are randomly split into *k* equal-sized subsets to successively serve as test data, while the remaining *k*-1 folds are used as training data (Guisan and Zimmermann, 2000). Prediction performance is related to the error rate (misclassification) of the test data, which is measured by the extrinsic omission rate and the area under the curve (AUC) (Guisan and Zimmermann, 2000). AUC is a threshold-independent standard measure of model accuracy that ranges from 0 to 1. It can be interpreted as the probability that a randomly chosen species presence point will be correctly classified by the model (Phillips et al., 2006). Maxent indicates which variables most contribute to the presence of each species and what the shape the relationship is. As a result, the habitat suitability maps were created by applying each species distribution model to all cells in the study area using a logistic function to obtain a habitat suitability index (HSI) ranging from 0 to 1 (Phillips and Dudík, 2008).

2.3. Landscape graph construction

From each habitat suitability map, corresponding to the presence probability of each species, a landscape graph, composed of a set of habitat patches (nodes) potentially connected by links, was built at the dispersal scale. Habitat patches were defined as the highest values of habitat suitability (Duflot et al., 2018). The threshold value used corresponded to the maximum sum of sensitivity and specificity (Max SSS) (Liu et al., 2013) and could be different according to the species. Habitat patches were associated with an attribute representing their potential quality for pond-dwelling species. As the habitat patches derived from the HSI map could include both aquatic and terrestrial environments, the quality was determined by multiplying the area of the patch by its average HSI value.

The links of the graph were defined in a complete topology, i.e., all the links between patches were potentially taken into account. Their impedance was calculated in cost distances based on a resistance map. From a previously constructed landscape map, each category was classified according to its resistance to species movement, using the ecological literature and local experts' opinions (see Appendix A for all the resistance values for each species). Habitat patches, i.e., the highest habitat suitability values, were assigned a resistance of 1. The favorable landscape elements were assigned a low value (10), neutral elements a value of 100, unfavorable elements a value of 1,000, and barrier elements the highest value (10,000). This logarithmic scale was chosen based on several studies (Clauzel et al., 2013; Verbeylen et al., 2003) that have shown the importance of contrasting resistance values between favorable and unfavorable elements to explain the presence of species. These resistance values were then submitted to several experts in herpetology, who allowed the values to be refined according to the local characteristics of the landscape and/or the species. Only the links with distances shorter than the dispersal capacity of the species were retained. Each resulting graph thus represented the potential ecological network of a species, taking into account the environmental variables that best explain its presence in the Ile-de-France region.

2.4. Patch addition process

The graphs constructed in the previous step were used to identify the best locations for pond creation. We applied the method developed by Clauzel et al. (2015) and Mimet et al. (2016). The method consists of (1) calculating a global metric quantifying the initial connectivity of the network, (2) applying a sampling grid of a given resolution to the study area and then (3) evaluating the potential contribution of each centroid of cells by quantifying the increase in the connectivity index provided by the addition of a new node and of

new potential links from this node to other existing nodes (Fig. 1). After testing all the cells, the algorithm validated the one for which patch addition produced the largest increase in the metric value.

The global connectivity metric to be maximized was the Equivalent Connectivity (EC) index, defined as the "amount of reachable habitat" for a species at the landscape scale (Saura et al., 2011):

$$EC = \sqrt{\sum_{i=1}^{n}\sum_{j=1}^{n} a_i a_j P_{ij}^*}$$

where n is the number of nodes, a_i is the attribute of node i, a_j is the attribute of node j and P_{ij}^* is the maximum probability of all potential paths between nodes i and j. P_{ij} is determined by an exponential function such that:

$$P_{ij} = e^{-\propto d_{ij}}$$

where d_{ij} is the least-cost distance between these nodes and α is a constant expressing the intensity of the decrease in the probability of movement (p) with distance (d). As d corresponded to the dispersal distance, the setting of the metric was specific to each species.

Running these calculations (graph construction and patch addition process) over the whole region was very time consuming and not necessarily ecologically relevant. We therefore choose to limit the connectivity analysis to a 150 km² subpart for the demonstration. The patch addition process was applied on a sampling grid of 15,093 points evenly spaced 100 m apart.

The landscape graph construction and the patch addition method were performed using Graphab 2.4 software (Foltête et al. 2012; see http://thema.univ-fcomte.en/productions/graphab/).

2.5. From single-species to multispecies connectivity improvement

The protocol described above was used to calculate the connectivity gain G_{ki} from each location tested k and for each species i. A multivariate analysis was then performed to identify the best locations for creating a new pond with a multispecies approach, i.e., optimizing connectivity for as many species as possible. The values of G_{ki} were grouped in a table and processed in a principal component analysis (PCA). To obtain a sufficiently satisfactory approximation, we used eigenvalues to determine the number of principal components to be retained (Kaiser, 1961) and the graph of eigenvalues (scree plot). The number of axes was determined by the point beyond which the remaining eigenvalues were all relatively small and of comparable size (Jollife, 2002; Peres-Neto et al., 2005).

We also performed cluster analysis on the observations, i.e., for each of the 15,093 cells of the grid to group together points that had similar values of G_{ki} using the *k-means* classification algorithm. From an ecological point of view, this allows to identify which species could benefit at the same time from the creation of a same pond. The appropriate number of clusters was determined by the elbow method. It consisted of plotting the explained variance as a function of the number of clusters and picking the elbow of the curve as the number of clusters to use. A Kruskal-Wallis test was then used to study the variations in the species abundance between the different clusters. Subsequent post hoc pairwise Wilcoxon rank sum test was carried out to reveal the differences between each pair of clusters regarding the values of G_{ki} of each species.

3. Results

3.1. Habitat suitability models (HSM) and significant environmental variables

For each species, the variables were selected from a collinearity study (<70%) and the contribution of the variables in an HSM for each species, including all environmental variables. A 10-fold cross-validation procedure indicated good models for our studied eight species (see Appendix B, AUC > 0.7). In most cases, "distance to the nearest ponds" and "water surface area" were logically the environmental variables that contributed most to the best predictive model (Appendix C). Distance to the nearest pond was negatively correlated with the presence of *T. cristatus* (an average contribution of 69.5%), *H. arborea* (44.6%), *A. obstetricans* and *R. temporaria* (34.4 and 33%, respectively), *E. calamita* (22%), *N. natrix* and *B. bufo* (15% and 12%). Proportion of the water surface was positively correlated with the presence of *B. bufo* (51%), *N. natrix* (36.5%), *R. temporaria* (31%), *S. salamandra* (24%), *H. arborea* (21%), *A. obstetricans* (16%), and *T. cristatus* (13%). Some variables were significant only for a few species depending on their ecological preferences, such as the proportion of forests (*S. salamandra* 30.5%, *R. temporaria* 27.7%, *B. bufo* 18.6%, and *N. natrix* 16.9%) or the proportion of artificial environments (*A. obstetricians* 24.2% and *E. calamita* 14.8%). The first variable was positively correlated with species presence (the greater the proportion of forest, the higher the probability was), while the response of the second variable had a Gaussian form; i.e., only the moderate values were positive (see Appendix C). For all the landscape composition variables, the most significant buffer radius was 500 m for the species except for *A. obstetricans* and *T. cristatus* (200 m). Temperatures were significant only for *E. calamita* (32.1%), for which the probability of presence was a maximum temperature between 12°C and 13.6°C. High annual amounts of precipitation (< 700 mm) were correlated with the presence of *S. salamandra* (17.4%).

Given the different responses of the variables between species, the maps of the probability of presence were very different (Appendix D). The proportion of the Ile-de-France region occupied by habitat patches varied according to the species, between 0.55% for *S. salamandra* and 15.30% for *R. temporaria*. The combination of the eight habitat binary maps (Fig. 1) highlighted that 68% of the region had no potential habitat (mainly urban areas and intensive agricultural land), and 14% was habitat for only one species. In addition, 13% of the region (1617 km²) was habitat for 2 to 4 species and 7% (846 km²) for more than 4 species. Only 0.002% (0.24 km²) was habitat for all eight species. These areas had a high density of water bodies (ponds, rivers, and wetlands), located either in a few forest massifs (Fig. 1a) or along river valleys such as the southeastern Seine valley (Fig. 1b).

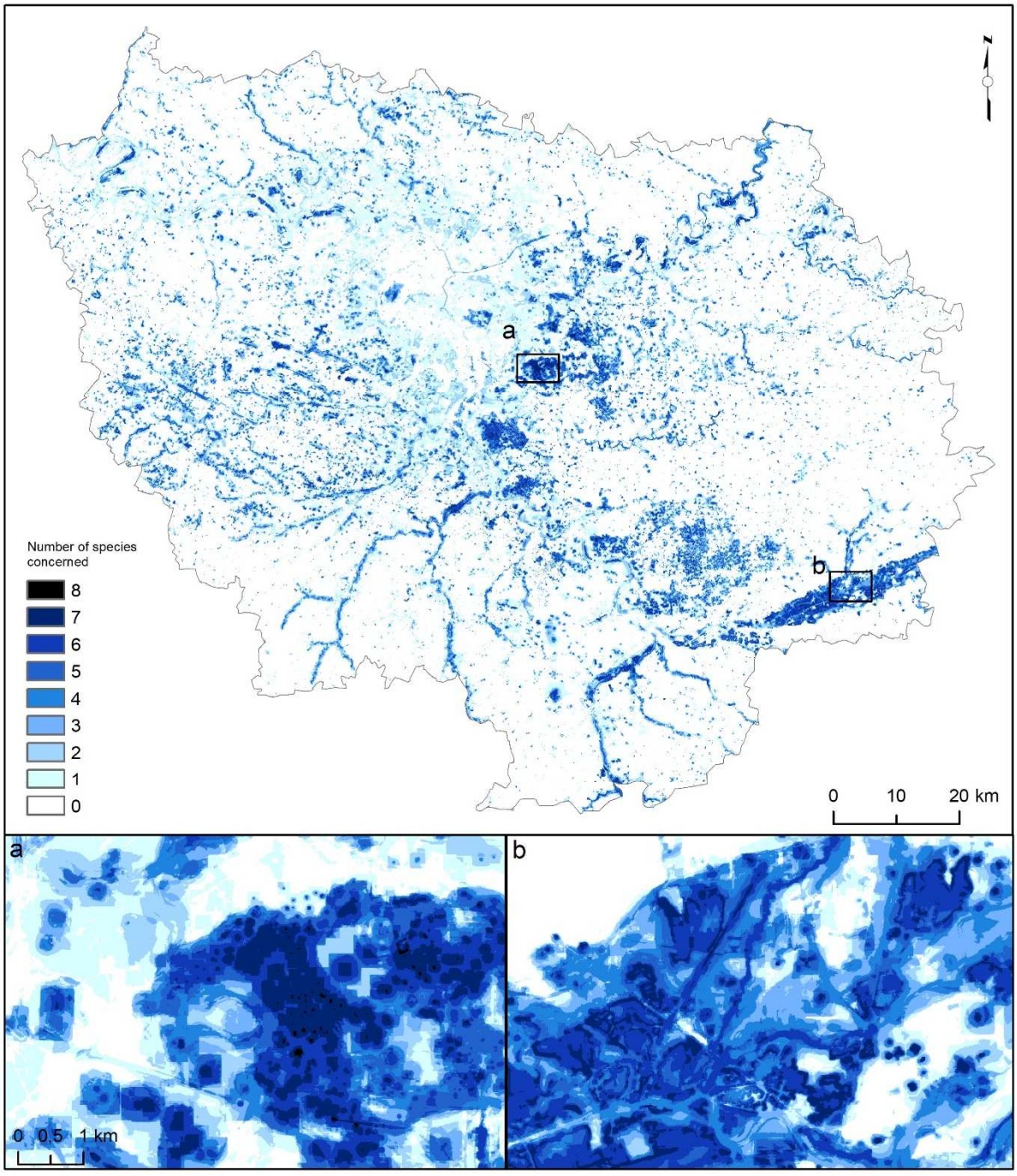


Fig. 1: Combination of the eight habitat binary maps extracted from the habitat suitability models. The colors indicate the number of concerned species by habitat patches.

3.2. Ecological network modeling

From these HSM maps, we selected a subpart of the region based on two criteria: i) the area must contain optimal habitat for the eight species, ii) habitat must be fragmented so that the creation of a new habitat is of ecological interest. A complete-topology graph was built for each species by keeping only those links whose distance was less than the dispersal distance. Connectivity evaluated by the Equivalent Connectivity metric varied greatly between species (Table 3 and Appendix E). The ecological networks of *B. bufo*, *R. temporaria* and to a lesser extent *N. natrix* had the highest connectivity due to the large area of potential habitat. The ecological networks of *T. cristatus, H. arborea*, *E. calamita* and *A. obstetricans* had seven

times less connectivity than those of the other species. Their ecological networks contained fewer habitat patches and were more fragmented, including that of *A. obstetricans. S. salamandra* was the only species that had extremely low connectivity, as the 16 potential habitat patches were almost all disconnected.

3.3. Improving single-species connectivity

The patch addition process was applied on a sampling grid of 15,093 points evenly spaced 100 m apart to cover the entire 150 km² regional subpart. The connectivity gain provided by the best locations for the creation of a new pond was very low overall (< 2%), except for *T. cristatus,* for which the gain reached 38.4% and to a lesser extent for *S. salamandra* (8.6%).

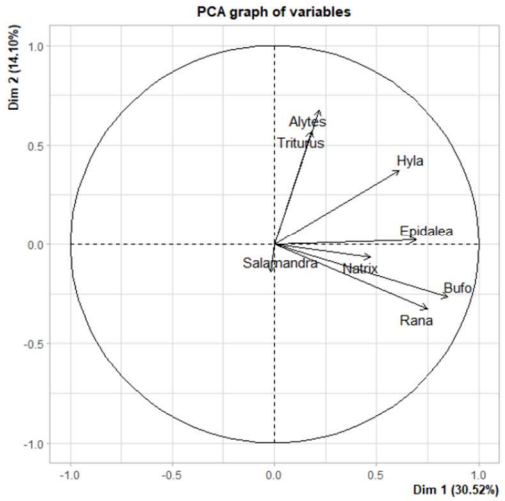
Table 3- Initial Equivalent Connectivity (EC) metric (expressed in m²) and the minimum, average and maximum values of the rate of change (%) in the EC provided by the addition of a new pond in the network of each species.

		Rate of change (%)		
Species	**Initial EC (m²)**	**Minimum**	**Mean**	**Maximum**
Alytes obstetricans	2,328,493	0.00108	0.0148	2.0039
Bufo bufo	17,066,498	0.00054	0.2238	0.3408
Epidalea calamita	1,847,265	0.00042	0.1335	1.5207
Hyla arborea	2,562,923	0.00043	0.0629	1.7516
Natrix natrix	13,797,042	0.00095	0.0731	0.3616
Rana temporaria	16,125,400	0.00029	0.2062	0.2450
Salamandra salamandra	17,265	0.55110	0.5614	8.6042
Triturus cristatus	3,267,325	0.00168	0.1357	38.3911

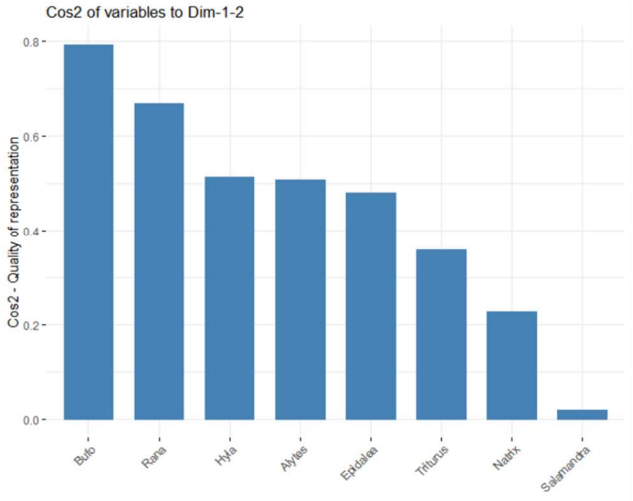
3.4. Improving multispecies connectivity

From the PCA analysis, the first two components explained 45% of the total variance (Table 4). The species that were best represented by these components were *B. bufo* (80%), *R. temporaria* (65%), *H. arborea, A. obstetricans* and *E. calamita* (50%). Only *S. salamandra* was not well represented by the first two components (Fig. 2b). The first component hierarchized the new pond locations for five species *(R. temporaria, B. bufo, N. natrix, E. calamita,* and *H. arborea*) and the second axis for two species (*A. obstetricans and T. cristatus*). The nearly orthogonal arrangement of several species in the PCA (Fig. 2a) indicated that there was no spatial correspondence in the best locations, and no compromise could be found to account for the eight species.

A)



B)



297

298 Fig 2. – A) The eight species projected onto the planes formed by the first two components of the PCA; B)
299 histogram of the contribution of each species to the first two components.

300 Table 4. Eigenvalue and amount of variance accounted for by each component of the PCA.

Component	Eigenvalue	% of variance	Cumulative %
1	2.4412414	30.515517	30.51552
2	1.1277741	14.097176	44.61269
3	1.0391739	12.989674	57.60237
4	0.9782465	12.228082	69.83045
5	0.9220738	11.525923	81.35637
6	0.7297676	9.122094	90.47847
7	0.4675788	5.844735	96.32320
8	0.2941439	3.676799	100.00000

301

302 We classified the 15,093 locations for the new ponds into 4 groups using the *k-means* classification
303 algorithm (Fig. 3) and spatially projected these clusters on the study area (Fig. 4). The connectivity gain
304 varied significantly between the clusters for each species (Appendix F). The percentage increase in the EC
305 was the highest in cluster 2 for most species, except for *B. bufo* and *R. temporaria*, which had their highest
306 EC value in cluster 3. The landscape of cluster 2 was dominated by forests (43%) but also contained urban
307 green spaces, artificial areas and cultures (approximately 15% each). The landscape of cluster 3 was
308 dominated by agriculture (49%), followed by forests (28%) and artificial areas (12%). Cluster 1,
309 characterized by a strong dominance (89%) of artificial surfaces and urban green spaces (9%), seemed to
310 have the lowest EC increase values for all species, whereas cluster 4 (containing both artificial areas at 39%
311 and forests at 34%) had average values for *B. bufo*, *R. temporaria*, *N. natrix* and *E. calamita*.

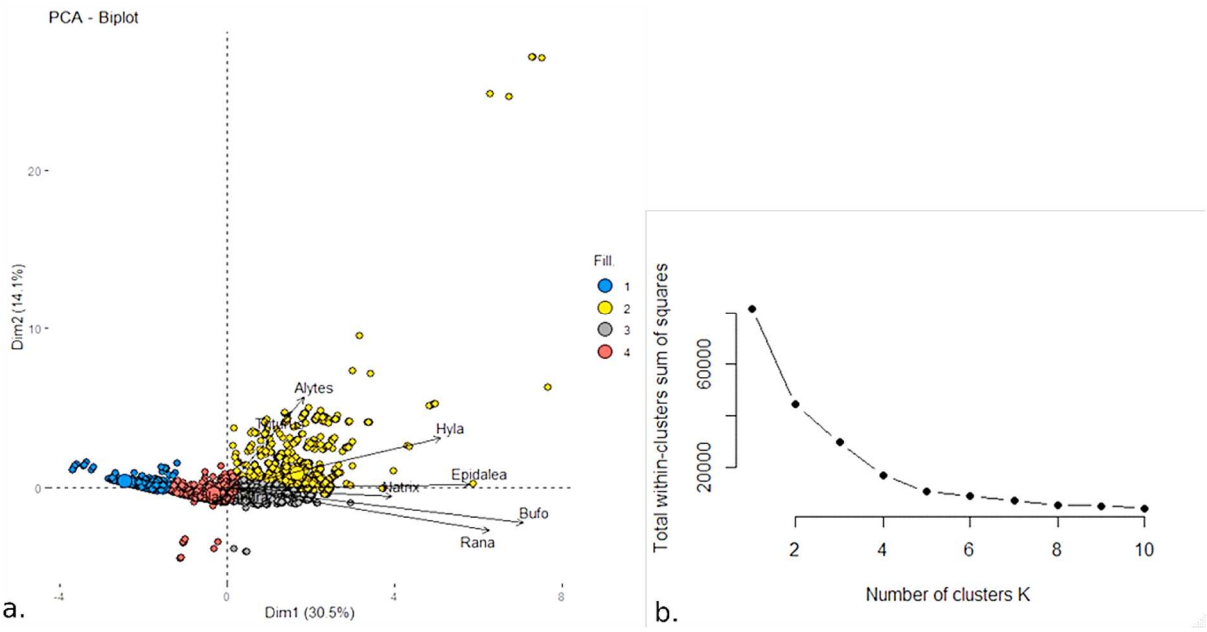


Fig. 3. The locations for new ponds were projected in the factorial planes formed by the first two components of the PCA (a). The colors of the points were related to the four different clusters attributed by the *k-means* method (b): cluster 1 (artificial areas) ; cluster 2 (forest edges) ; cluster 3 (mainly agriculture) ; cluster 4 (artificial areas and forest cores).

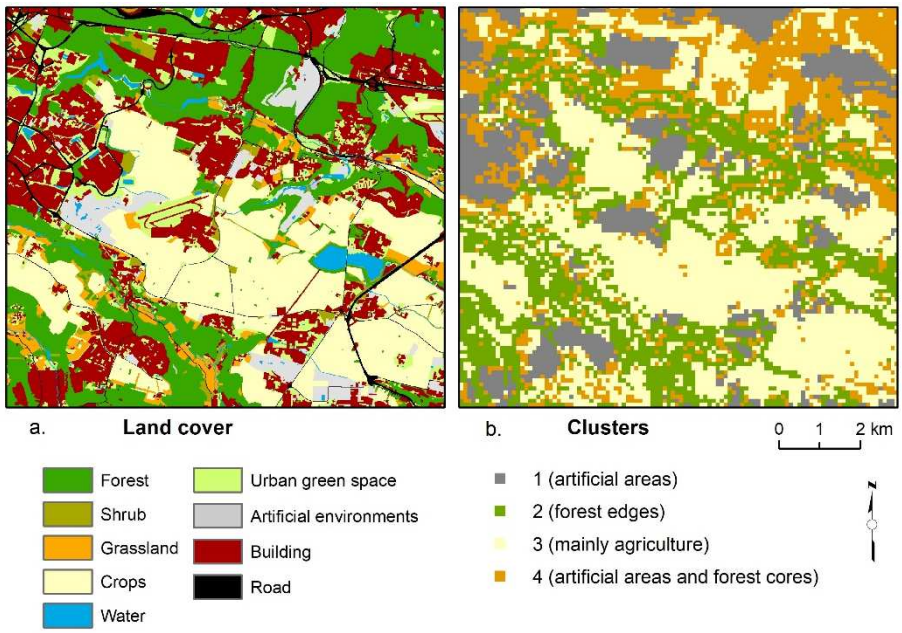


Fig. 4 – Land cover map of the patch addition area (a) and spatial projection of the four clusters grouping the 15,093 points according to the connectivity gain for the eight species (b).

4. Discussion

Our approach for restoring habitats prioritized areas based on their contribution to multispecies regional connectivity. Targeted addition of habitat within an ecological network can increase habitat density in deficient areas and reconnect network sub-parts. This approach is therefore promising to guide

conservation actions and "no net loss" biodiversity measures, especially the final stage of "offset" in the mitigation hierarchy (Ermgassen et al., 2019). Indeed, depending on the structure of the network, it may sometimes be more ecologically relevant to create habitat at a strategic location in the network, rather than necessarily near the habitat destroyed by the project (Bergès et al., 2020). However, managers currently lack information on the contribution of biodiversity offset areas to regional connectivity (Moilanen and Kotiaho, 2018). This involved taking into account the spatio-temporal nesting of ecological processes to propose effective and relevant conservation actions. Among the many studies on amphibian movement that have been published (Pittman et al., 2014; Smith and Green, 2005), most are focused on a single scale and life stage (habitat use, migration or dispersal), and very few have tried to integrate multiple spatial scales (Bailey and Muths, 2019). The modeling of ecological networks based on graph theory included both daily movements, through the definition of the patch quality, and dispersal events in maximizing the connectivity metric. Furthermore, the same protocol can be applied to other scales depending on the ecological process (e.g., seasonal migrations, range shifts related to climate change) we want to support through habitat restoration. Here, we focused on connectivity at the dispersal scale, using the global metric EC, which integrates both the amount of habitat and the degree of connections between habitat patches. Selecting this metric to optimize allowed us to take into account both the gain in local connectivity through additional habitat area and in regional connectivity through connections at the dispersal scale. Habitat restoration in areas with high connectivity gains could therefore enhance existing local populations and promote colonization of new habitats (Bailey and Muths, 2019). However, connectivity values should be analyzed in relation to the network configuration to recommend the most appropriate measures for the conservation of the species under study. Indeed, low gains in connectivity may correspond to radically different connectivity situations. The first situation related to very well-connected ecological networks with a high density of habitat patches and connections, such as that for *B. bufo*, *R.temporaria* or *E. calamita.* In this case, adding a new pond would only marginally improve an already high level of regional connectivity. In contrast, another connectivity situation may also correspond to a highly fragmented ecological network, either due to a low density of habitat (e.g., *S. salamandra*) or due to an unfavorable landscape matrix separating main habitat areas (e.g., the central part of the networks of *H. arborea* and *N. natrix*). In these two situations, adding a unique pond is not enough to significantly improve regional connectivity. Nevertheless, in the latter case, adding several ponds cumulatively, as in Clauzel et al. (2015), could reconnect the two main subparts of the network and thus greatly improve connectivity. The proposed protocol can therefore not only provide indications on where to restore a habitat but also on how many habitats in order to significantly improve connectivity, or to restore the original state of connectivity destroyed by a development project.

A major challenge for modeling is to build models that are realistic and robust enough to propose relevant conservation actions. This point is crucial and involves the integration of species observation data (presence, abundance, genetic diversity, etc.) into modeling. However, a recent review (Foltête et al., 2020) showed that among the large number of graph-based connectivity studies, very few articles used biological data in combination with landscape graphs. This scenario is probably related to the difficulty in obtaining relevant data, especially when studies involve multiple species and a large area. For example, in Clauzel et al. (2015), the ecological network of *H. arborea* was modeled from occurrence data to retain only occupied ponds as the graph nodes and not all potential habitats, as it is often the case in graph-based connectivity studies. However, this study was applied to a region of 4,000 km² and focused on a single species. Recently, Jeliazkov et al. (2019) integrated occurrence data for three amphibian species for an area of 430 km^2 and a set of environmental variables to provide information about structural and functional connectivity on several scales but without providing management recommendations. In our framework, occurrence data of each species was confronted with environmental variables to predict habitat suitability and to delineate optimal habitat patches. This part of the results is interesting in itself for biodiversity conservation because it allows managers to detect – and preserve – shared habitats or conversely species-specific habitats. The large differences in the potential distribution between species could be explained by the degree of habitat specialization. *R. temporaria*, which is a ubiquitous species, had the widest predicted

distribution, with 15.30% of the region classified as potential habitat. Conversely, *S. Salamandra,* a more specialized species with low movement abilities, had the lowest predicted distribution (0.55%), but the small number of observations could have limited the relevance of the model.

Finally, the major contribution of our paper is the multispecies assessment of restoration areas. In multispecies connectivity studies, the aggregation of the results between species is still challenging (Meurant et al., 2018). Most of them analyzed the results on a species-by-species basis and eventually combined them by simple spatial overlay. The sum or average of the connectivity values obtained per species provides an overall diagnosis on high connectivity areas but with a risk of giving more weight to species that already have a well-connected network. By normalizing the values beforehand, more weight is given to species with rare habitats, which may be consistent with biodiversity conservation objectives (Sahraoui et al., 2017). However, in any case, knowing precisely which species is more concerned is made impossible by these combinations. Here, we combined the results with a multivariate statistical analysis to potentially identify different clusters, i.e., sets of points where connectivity gains are close for some species. This method allowed to identify more robustly the restoration areas that were simultaneously strategic for species that do not have the same ecological network or movement capabilities. If our results revealed that no area seemed to benefit all species, the landscapes dominated by forests and located near agricultural land (cluster 2) were the most strategic area for improving multispecific connectivity (at least for 5 species). Secondly, areas dominated by agriculture appeared to be more suitable for habitat restoration for *B. bufo* and *R. temporaria* (cluster 3).

5. Conclusions

By coupling biological data, habitat suitability models and spatial graphs, the described method in this paper appears to be useful for targeting habitat restoration areas that would simultaneously benefit several species. Integrating functional connectivity into this research increases the probability of colonization of the new habitat as well as potentially reconnecting isolated habitats and thereby improving the robustness and the resilience of the ecological network. The value of this method goes beyond the creation of ponds and can be applied to any type of habitat that can be the subject of restoration measures or a complete creation. The results provide insights into central issues of biodiversity offset and habitat restoration (Moilanen and Kotiaho, 2018): where and how many new habitats should be created to optimize connectivity for multiple species with various movement abilities and within different habitats.

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Appendices

Appendix A: Resistance values assigned to each category of the landscape map for each species, based on information from the literature.

Species	Forest edges	Forests	Open shrubby environments	Grasslands	Crops	Quarries	Urban green environments	Artificial environments	Major roads	Minor roads	Buildings	Small rivers	Surface waters	Large rivers	Ponds
Alytes obstetricans	10	100	10	10	100	10	10	100	10000	1000	10000	10	10	100	1
Bufo bufo	10	10	10	100	100	1000	100	100	10000	1000	10000	100	1	1000	1
Epidalea calamita	100	1000	10	10	100	10	100	100	10000	1000	10000	10	10	100	1
Hyla arborea	10	100	10	10	1000	1000	100	1000	10000	1000	10000	10	10	100	1
Natrix natrix	10	100	10	10	1000	100	1000	1000	10000	1000	10000	10	1	100	1
Rana temporaria	10	10	10	10	100	100	100	10	10000	100	10000	10	1	1000	1
Salamandra salamandra	10	10	100	100	1000	1000	100	1000	10000	1000	10000	10	10	100	1
Triturus cristatus	10	10	10	10	1000	100	100	100	10000	1000	10000	10	10	1000	1

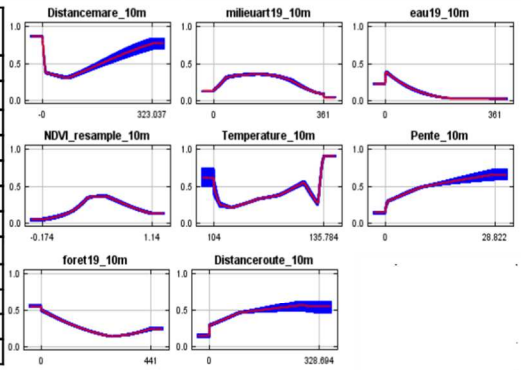
Appendix B: Results of the average accuracy of the predictive models for the 8 species using Maxent. AUC = area under the curves of relative operational characteristics. The results of the threshold "maximum test sensitivity plus specificity" = max SSS and the extrinsic omission rate (proportion of test localities not included in the prediction) are given for each of the 10 random data partitions. For all 8 species, the binomial test was highly significant for all partitions ($p < 0.001$, one-sided).

	AUC	Max SSS	Percentage of habitat area
Alytes obstetricans	0.902 +/- 0.012	0.24	11.62%
Bufo bufo	0.843+/-0.008	0.33	11.03%
Epidalea calamita	0.955 +/-0.013	0.16	4.55%
Hyla arborea	0.940 +/- 0.016	0.18	8.31%
Natrix natrix	0.900 +/- 0.015	0.24	15.13%
Rana temporaria	0.839 +/- 0.009	0.32	15.30%
Triturus cristatus	0.951 +/- 0.006	0.13	8.48%
Salamandra salamandra	0.976+/- 0.025	0.25	0.55%

Appendix C: List of the contributive variables and Maxent response curves for the variables that contributed the most (> 2%) for each of the eight pond-dwelling species.

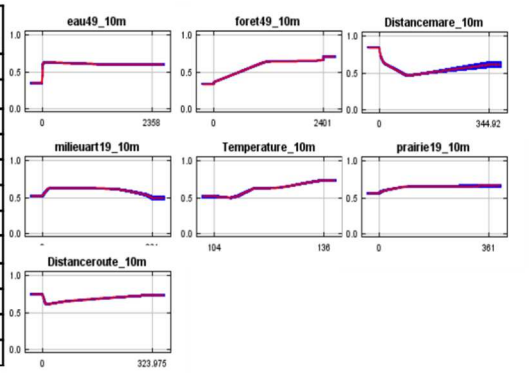
Alytes obstetricans

Variable	Percent contribution
Distancemare	34.4
milieuart19	24.2
eau19	15.7
NDVI	6.4
Temperature	5.6
Pente	3.5
foret19	2.4
Distanceroute	2.1
Distanceeau	1.8
prairie19	1.6
Precipitations	1.6
carriere5	0.7



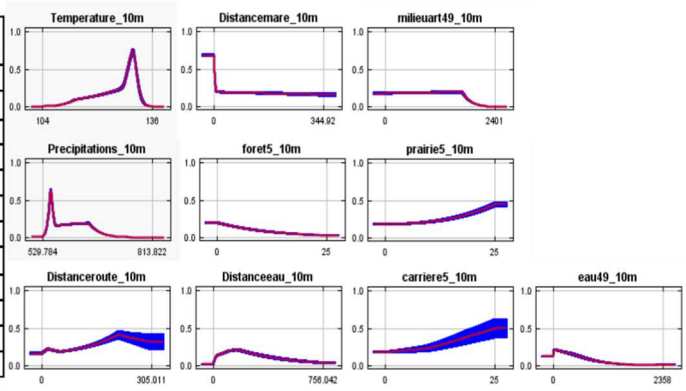
Bufo bufo

Variable	Percent contribution
eau49	51
foret49	18.6
Distancemare	12.7
milieuart19	6.7
Temperature	3
prairie19	2.7
Distanceroute	2
Distanceeau	1.2
eau5	0.9
Precipitations	0.7
NDVI	0.2
Pente	0.2



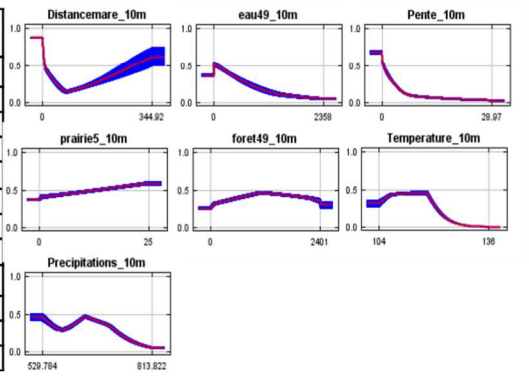
Epidalea calamita

Variable	Percent contribution
Temperature	32.1
Distancemare	22
milieuart49	14.8
Precipitations	8.6
foret5	5.4
prairie5	5
Distanceroute	3.4
Distanceeau	2.9
carriere5	2.5
eau49	2.1
NDVI	0.9
Pente	0.3



Hyla arborea

Variable	Percent contribution
Distancemare	44.6
eau49	20.9
Pente	8.4
prairie5	7.8
foret49	5.8
Temperature	3.7
Precipitations	2.3
milieuart49	1.9
NDVI	1.9
Distanceroute	1.7
Distanceeau	0.6
carriere49	0.4



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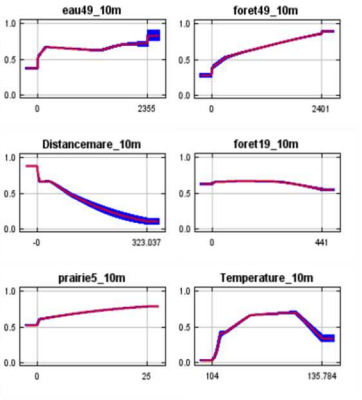
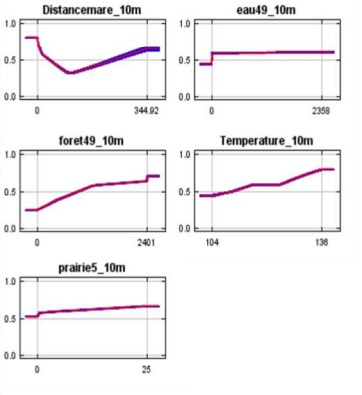
Natrix natrix

Variable	Percent contribution
eau49	36.5
foret49	16.9
Distancemare	15
foret19	9.4
prairie5	7.9
Temperature	6.5
Distanceeau	1.7
NDVI	1.6
milieuart49	1.5
Precipitations	1.4
Distanceroute	1.1
Pente	0.4



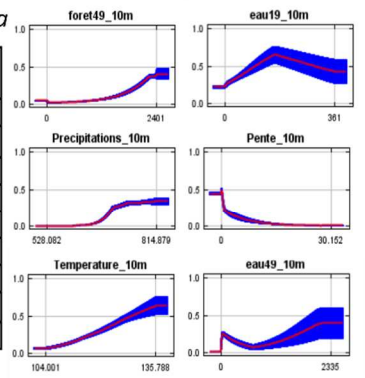
Rana temporaria

Variable	Percent contribution
Distancemare	33
eau49	30.8
foret49	27.7
Temperature	2.9
prairie5	2
Precipitations	1.3
milieuart5	0.8
Distanceroute	0.4
Pente	0.4
Distanceeau	0.3
NDVI	0.3
carriere19	0.1



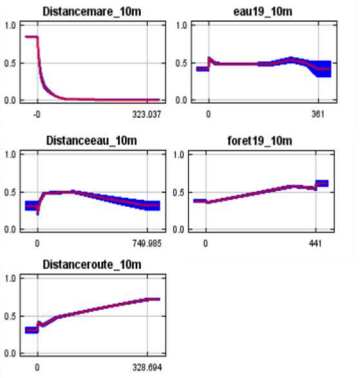
Salamandra salamandra

Variable	Percent contribution
foret49	30.5
eau49	23.9
Precipitations	17.4
Pente	13.1
Temperature	6
eau19	5.3
prairie49	1.8
NDVI	1.5
Distanceeau	0.5



Triturus cristatus

Variable	Percent contribution
Distancemare	69.5
eau19	13
Distanceeau	4.3
foret19	3
Distanceroute	2.1
milieuart49	1.8
prairie5	1.7
Temperature	1.6
Precipitations	1.2
Pente	1.2
NDVI	0.6



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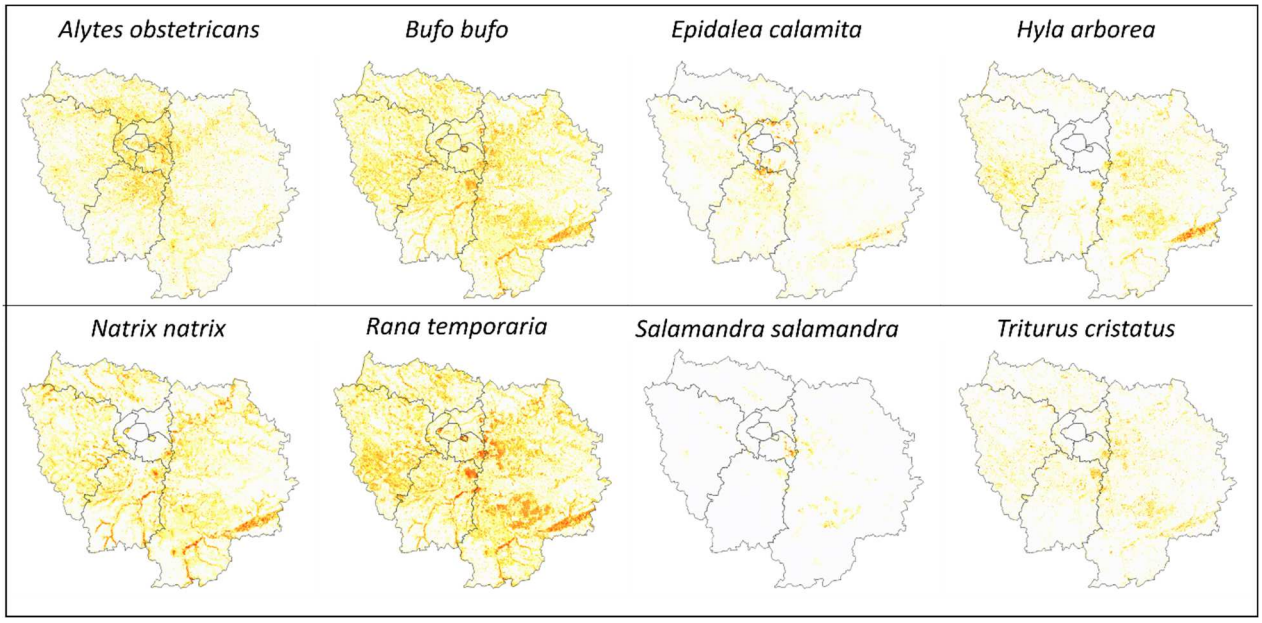
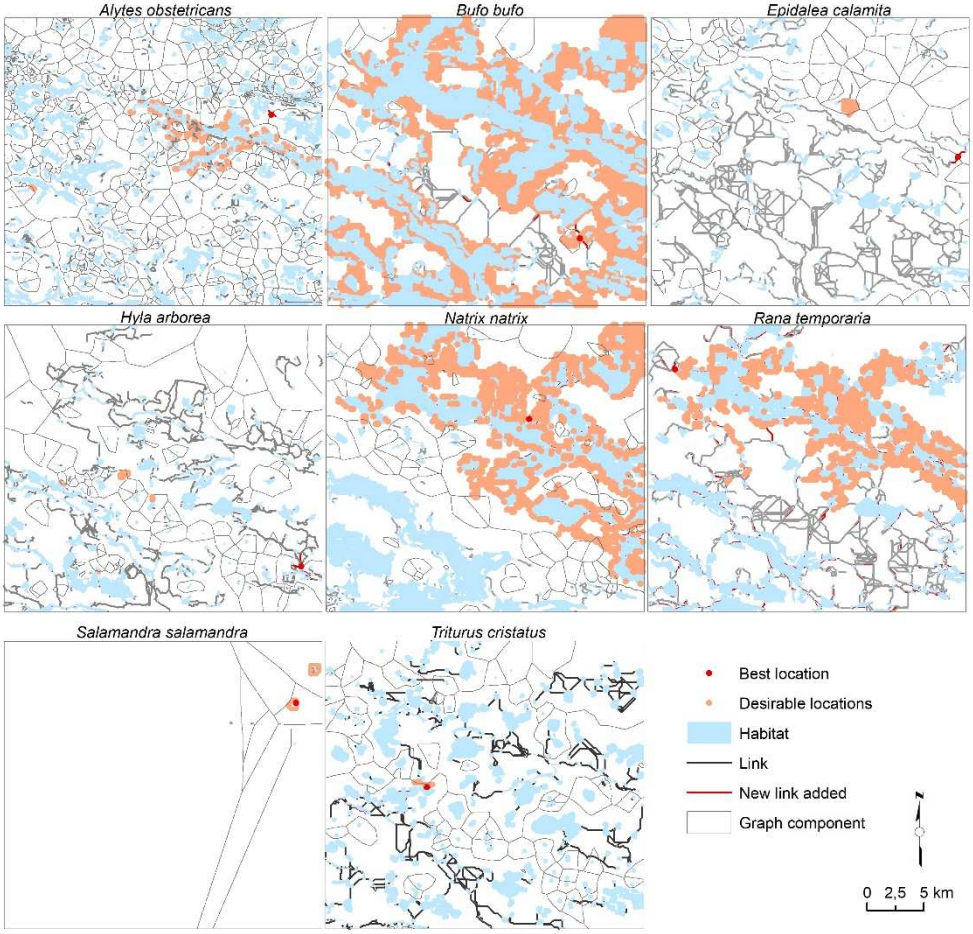
Appendix D: Habitat suitability models (HSM) corresponding to each species (red = highest probability of presence; white: zero probability of presence)



Appendix E: Landscape graphs representing the ecological network of each species and the best locations for adding a new pond according to the gain in connectivity. The desirable locations corresponded to the class with the highest increase in the Equivalent Connectivity (EC) metric. Their number varied according to species. The best location was the one that provided the highest increase.



Appendix F: Boxplots of the values of the percentage increase in the EC metric for each species. The outliers are in red. Following the Wilcoxon post hoc tests, the letters (a, b, c, and d) corresponded to the representation of significance. If two clusters have the same letter, then they are not significantly different and vice-versa.