Conservation networks do not match ecological requirements of amphibians

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Abstract

1. Amphibians are among the most threatened taxa as they are highly sensitive to habitat degradation and fragmentation. They are considered as model species to evaluate habitats quality in agricultural landscapes. In France, all amphibian species have a protected status requiring recovery plans for their conservation. Conservation networks combining protected areas and green infrastructure can help the maintenance of their habitats and while favouring their movement in fragmented landscape such as farmlands. Yet, assessing the effectiveness of conservation networks is challenging.
2. Here, we compared ecological requirements of amphibian species with existing conservation network coverage in a human-dominated region of western France. First, we mapped suitable habitat distributions for nine species of amphibian with varying ecological requirements and mobility. Second, we used stacking species distribution modelling (SSDM) to produce multi-species habitat suitability maps. Then, we defined species and multi-species core habitats and performed a connectivity analysis using Circuitscape theory to identify spatial continuity in suitable habitats at regional scale. Finally, we compared different suitability maps with existing conservation networks to assess conservation coverage and efficiency.
3. We highlighted a mismatch between the most suitable amphibian habitats at regional scale and the conservation network, both for common species and for species of high conservation concern. We also found two bottlenecks between areas of suitable habitat which might be crucial for population movements provoked by global change, especially for species associated with hedgerow mosaic landscapes. These bottlenecks were not covered by any form of protection and are located in an intensive farmland context.
4. *Synthesis and applications* - We advocate the need to better integrate agricultural landscape mosaics into protected areas as well as to protect the associated extensive agricultural practices suitable for biodiversity, including extensive livestock farming. We also emphasize the importance of interacting layers of green infrastructure for amphibian conservation and the need for it to be effectively considered in land-use planning policies. Further investigations are needed to strengthen and restore habitat continuities in area with regional bottlenecks marked by rare and degraded semi-natural elements.

Keywords

Green infrastructure, protected area, multi-habitat network, ecological network, stacked species distribution models, gap analysis, connectivity, citizen science data

1 Introduction

The biodiversity decline is still accelerating across the world affecting both scarce and common species (Dirzo et al., 2014; Gaston & Fuller, 2008) especially in agroecosystems (Kleijn et al., 2011; Seibold et al., 2019). To palliate this decline, the establishment of protected areas (PAs) is a relevant conservation tool in a human dominated world (Rodrigues & Cazalis, 2020). However, PAs alone are not sufficient to protect biodiversity and they should be part of an ensemble of management and planning strategies aiming to create functional conservation networks. Green infrastructure (GI) has been proposed as a way to address this issue (Chatzimentor et al., 2020; Salomaa et al., 2017). Such initiatives aim to maintain a coherent and functional network of suitable habitats and to improve biodiversity integration into land-use planning. GI design is based on the *ecological network* concept (Opdam et al., 2006) emphasizing complementarity of core habitat patches and ecological corridors at different spatial and temporal scales (Opdam et al., 2006; Salomaa et al., 2017).

Evaluating the efficiency of conservation networks (here PAs and GI) is a real challenge (e.g., Rodrigues & Cazalis, 2020). In France, GI has mostly been defined based on spatial analysis of land-cover data without considering species data. It is based on a simplistic classification of ecosystems reduced to broad categories of land cover data (i.e. different layers for forest or wetlands separately) with a poor consideration of habitat complementation. In contrast, PAs have usually been defined according to the needs of focal endangered species and/or habitats, often charismatic species such as birds and endangered plants, poorly representative of species-habitat relations (Rodrigues et al., 2004). Gap analysis and conservation prioritization are common approaches for a first-step assessment of the effectiveness of a conservation network and to inform decisions for conservation measures (Jennings 2000; Moilanen et al. 2005). To conduct a gap analysis, outputs of spatial modelling are particularly useful (Ahmadi et al., 2020). Species distribution models (SDMs) are commonly used to make spatially explicit predictions of the suitable environment of a given species from biological data (Guisan & Zimmermann, 2000) and multi-specific approaches have recently been developed (Scherrer et al., 2018; Thuiller et al., 2015). In addition, recent methods integrate both graph theory and SDMs for ecological network modelling (Duflot et al., 2018; Godet & Clauzel, 2020). These multi-species and integrative approaches could be relevant for gap analyses and spatial prioritization but remain underused (Foltête et al., 2020).

In western Europe, traditional hedgerow landscapes are of high conservation concern for numerous taxa such as plants, amphibians, birds, bats and arthropods (Baudry et al., 2000; Boissinot et al., 2019). These rural landscapes are associated with dense hedgerow networks interconnected with a mosaic of small interlocked patches of pastures, cultivated fields and bushes with high pond density (Burel & Baudry, 1995). They have been greatly impacted by agricultural intensification and have declined from 40 % to 80 % in Europe (Bazin & Schmutz, 1994). Amphibians are good candidates to assess the ecological quality of human-dominated landscape mosaics and to question the efficiency of existing conservation networks. Indeed, They are among the most threatened taxa with rapid and widespread population declines in both natural and modified habitats (Stuart et al., 2004). They have a bi-phasic life cycle with different ecological requirements inducing seasonal

migrations between habitat patches (Sinsch, 2014). Their poor mobility and their impermeable skin increases their sensitivity to anthropogenic disturbances, pollution and ecological fragmentation induced by urbanization and intensive agriculture (Cushman, 2006; Hamer & McDonnell, 2008; Stuart et al., 2004). Hence, some authors consider amphibians as good ecological indicators of general environmental health (Collins and Storfer 2003; Díaz-García et al. 2017 but see Sewell & Griffiths, 2009). In addition, amphibians have been the target of several citizen science programs in different countries around the world (De Solla et al., 2005; Petrovan & Schmidt, 2016) leading to a large amount of available data over wide areas which could be relevant for conservation tools assessment (Snäll et al., 2016).

In a human-dominated region of western France, we compared the predicted habitat requirements of amphibian species with existing conservation network coverage (of both protected areas and green infrastructure). Specifically, we: (1) produced single and multi-species habitat suitability maps for amphibians with differing ecological requirements and mobility (2) compared these habitat suitability maps with existing conservation networks (PAs and GI), and (3) identified gaps in conservation coverage which could be a priority for new potential conservation areas.

2 Material and Methods

2.1 Regional context and studied species

Ecological context

Our study was performed in a region of western France (Pays-de-la-Loire) covering 32,082 km². Intensification of agricultural practices have greatly transformed the landscape over the last century from a complex matrix of small fields, meadows and woody elements to more homogeneous landscapes with larger monocultural fields. With 21 species of amphibian (out of 43 species recorded at national scale), of which 12 are priority species for conservation, the region has considerable responsibility for the preservation of amphibian species and their habitats, including traditional hedgerow landscapes and wetlands.

Studied species

Nine amphibian species in the Pays-de-la-Loire region were studied (see Table 1 for species list). Three species have high conservation value (*Pelodytes punctatus*, *Triturus marmoratus* and *Rana temporaria* i.e., regional priority index > 1; Table 1). Three form a "FOR" group of forest species or species associated with dense hedgerow mosaic landscape (*T. marmoratus*, *R. temporaria* and *Salamandra salamandra*) and five form a "GEN" group of more generalist species (*Lissotriton helveticus*, *Bufo spinosus*, *Hyla arborea*, *Rana dalmatina* and *Triturus cristatus*). *P. punctatus* is a pioneer species mainly associated with disturbed open environments. Finally, the "ALL" group contained all nine studied species. Species were selected according to data availability and previous studies (Matutini, Baudry, Fortin, et al., 2021; Matutini, Baudry, Pain, et al., 2021).

Biodiversity conservation policies

In France, there are different conservation tools including protected areas, green infrastructures, and inventoried sites with recognised biodiversity value but that are not protected (Categories “PA”,”GI” and “INV” respectively in Table 2). We defined five groups of conservation tool based on IUCN categories and protection levels (Table 2 and Fig. 1). For two types of PAs (SCEN and ENS in PA-Group 2), site boundaries were not available. As a result, only a point location per site was considered in the analysis (see Appendix 2). If one conservation area was overlapped by another, we classed the area into the group with the strongest protection level and therefore all PAs were excluded from GI. French GI is divided into different land cover or landscape classes (Table 2). Each GI layer includes two types of elements: habitat nodes, considered as “biodiversity reservoirs”, and “corridors” ensuring potential continuity between nodes based on geographical criteria.

2.2 Single and multi-species habitat suitability maps

We used 100 m-resolution habitat suitability maps resulting from a previous study of the same nine species in Pays-de-la-Loire (Matutini, Baudry, Fortin, et al., 2021). This used heterogeneous data from citizen sciences completed by professional surveys to perform and evaluate (with independent dataset) presence-only habitat suitability modelling with functional friction-based and multi-scale predictors (see Matutini, Baudry, Fortin, et al., 2021 and Matutini, Baudry, Pain, et al., 2021 for full details and methods).

We produced multi-species suitability maps by compiling individual species maps (Stack-SDM, e.g. Ferrier & Guisan, 2006) using a simple probabilistic stacking method (pSSDM, see Zurell et al., 2019). We summed continuous individual maps without binary “presence-absence” conversion (Calabrese et al., 2014; Scherrer et al., 2020) for three focal species groups: (1) forest species (FOR), (2) generalist species (GEN), and (3) all species (ALL). According to the ecological context of our region for a best integration of mosaic effect for landscape evaluation, we summed species maps at 500 m-resolution after 100 m-pixels aggregation using maximum suitability values (see Appendix 1 for additional information and selection tests). Hence, we compiled single species standard deviation maps to obtain a general representation of levels of confidence in our mapped distributions. To assess the accuracy of the three pSSDMs, we compared multi-species suitability index (i.e., the sum of single species suitability values from 0 to 1) with species richness from independent pond monitoring (Matutini, Baudry, Pain, et al., 2021). We calculated a community-AUC (Scherrer et al., 2020) and R^2 value for each species group with 500 iterations.

2.3 Reclassification and core habitat node definition

For each species and stacked species group, we reclassified the final suitability map into five categories of potential habitat: not suitable (below the ten-percentile value P_{10th} method in Huang et al 2020), Less suitable (P_{10th}-55%), moderately suitable (55%-65%), suitable (65%-80%), and highly suitable (>80%).

2.4 Network patterns

To map potential connections between each highly suitable patch (i.e., patch with a suitability index up to 80%) at regional scale, we used circuit theory with Circuitscape

software (McRae et al., 2016). Circuit theory considered each cell as an electric node connected to neighbouring cells by resistors and defined by a landscape resistance (or conductance) value (McRae et al., 2008). We used highly suitable core habitats as source patches, and a friction map as a measure of conductance (i.e., conductance of each raster 100 m cell for movement). This method provides an exploration of potential links between nodes according to landscape permeability combining habitat suitability and connectivity modelling (Ahmadi et al., 2020; Koen et al., 2014).

Habitat suitability could however be a poor proxy of permeability as species may move in unsuitable habitats (Keeley et al., 2017). Hence, the friction map was computed using different friction cost values derived from the multi-species habitat map and landcover data (Keeley et al., 2016, 2017). Therefore, we considered moderately to highly suitable habitat classes (i.e., from 65% to 100%) as permeable features except for pixels crossed by a linear barrier. In less suitable habitats (i.e., under the 65% threshold), we calculated a friction cost based on a 100m-grid analysis performed over 10 m-resolution landscape layers followed by a classification procedure (see Appendix 3). 100m-resolution were selected to reduce computational power needed for Circuitscape analysis and to consider landscape complementation of fine-scale landscape elements (e.g., ditches, hedgerows and field margins, Pope et al., 2000; Mazerolle, 2005). The cost values of impermeable barriers (i.e., high-density urban area, highspeed train line, highway and dual carriageways) were considered as infinite. Permeable features facilitating movement across barriers (e.g., viaduct, wildlife pass and others, see Table 2) were digitized from aerial photographs. To reduce border effects, we allocated resistance values to a 5km-buffer around the studied region which were randomly selected if land-cover data were not available.

2.5 Gap analysis and prioritizing for conservation

We based the gap analysis framework on a method used by Ahmadi et al. (2020) that compared reclassified suitability maps with areas covered by PA or GI. We calculated "total conservation coverage" (i.e., the proportion of suitable habitat overlapping a conservation area), "conservation efficiency" (i.e., the proportion of conserved areas overlapping suitable habitats) and plotted histograms showing the total distribution of suitability values covered by different types of conservation area. To complete the analysis, we overlaid the existing conservation network with the final regional maps obtained using Circuitscape for each species group to discuss network configuration in relation to potential regional continuities. All spatial analysis were performed using R environment v. 3.5.3 (R Development Core Team, 2019).

3 Results

3.1 Multi-species maps and core habitat definition

For each group, the community-AUC varied from 0.76 (forest species) to 0.87 (generalist species) and R^2 from 0.23 (forest species) to 0.31 (nine studied species). The suitable maps are shown in Fig. 1 while associated confidence maps are available Appendix 4. For the nine studied species, highly suitable habitats covered 12% of the region and suitable habitats covered 49% of the region (Fig. 1). Highly suitable habitat for the forest species,

covered 11% and suitable habitat covered 17% of the region. Larger amounts of highly suitable and suitable habitats were available to generalist species, covering 33% and 40% of the region respectively.

3.2 **Protected areas (PAs)**

The distribution of protected areas along the habitat suitability gradients modelled for each species or species group (FOR, GEN, ALL) is shown Fig. 2.

Conservation coverage

PAs covered a relatively low proportion of highly suitable habitat: 15%, 19% and 8% for all species, forest species and generalist species respectively (Table 4). The most strictly protected areas protection (PA group 1) covered even lower proportions of suitable habitat: 1% of highly suitable habitat and 2% of suitable habitat for each species group. Similarly, for two of the three species of high conservation concern, PA covered only a relatively low 17% or 26% of highly suitable habitat, for *T. marmoratus* and *R. temporaria* respectively. Only for *P. punctatus* was conservation coverage high: 90% of highly suitable habitat was included in PA.

Conservation efficiency

Among PA-Group 1, no sites with the highest level of protection (names "RNN", see Table 2) contained highly suitable area for any species group or individual forest species except *P. punctatus* (12% of RNN areas contain high suitable habitat) (Table 4). Other PA-Group 1 protection levels were covered by 7 to 24% of multi-species core area and by 3 to 24% of species-specific highly suitable habitat, with a higher proportion for *P. punctatus*. Regional Park (PA-Group 2) and Natura 2000 network (PA-Group 3) included less than 16% multi-species core area and lower proportions for the two-forest species individually. For SCEN and ENS (in PA-Group 2) 26%, 12% and 8% of these sites were located in highly suitable habitats for generalists, forest species and all nine species respectively. Overall, PAs contain a higher proportion of highly suitable habitat for *P. punctatus* than for other species.

3.3 **Inventoried sites (INV)**

Inventoried sites with known ecological value but no legal protection (INV-Group 5) covered 13% of the region. 20% to 34% of their areas were covered by multi-species highly suitable habitat (24 to 57% for suitable area). 11%, 21% and 1% are covered by highly suitable habitat of *T. marmoratus*, *R. temporaria* and *P. Punctatus* respectively (Table 4). INV-Group 5 covered the most suitable and highly suitable habitat of all studied groups and species except for *P. punctatus* with a poor overlapping between this species issues and areas of INV-Group 5 (i.e., 2%).

3.4 **Green infrastructure (GI)**

GI included and covered a larger area of highly suitable and suitable habitat for amphibian species than PA particularly hedgerow networks BOCAGE followed by WOOD and WET (see Table 2). Globally, GI covered around 50% of potential habitat for amphibian species.

Among the five GI's classes (Table 4), GI relating to traditional hedgerow landscapes (BOCAGE) were the most widespread and covered from 16% to 33% of highly suitable habitat of species or species groups (especially *T. marmoratus* with 33% and excluding *P. punctatus* with only 2%). In addition, the GI BOCAGE contained 42% highly suitable habitat for generalist species and between 12-21% for other species except *P. punctatus*. GI relating to woodlands (WOOD) and wetlands (WET) covered more than 10% of highly suitable habitat except for *T. marmoratus* and *P. punctatus*. GI relating to coastland (COAST) and natural open grasslands (OPEN) covered small areas compared with other GI and also a low area of suitable habitat for studied species.

Potential multi-habitat continuities patterns

The distribution patterns associated with highly suitable and suitable habitats are shown Fig. 1 and supplemented in Fig. 3 by a more detailed analysis of the spatial organisation and potential links between habitat patches. The central and the southern parts of the region have a few patches of highly suitable habitat, especially for forest species. Generalist species have a more homogeneous distribution of suitable habitats spreads over the region. Suitable and highly suitable habitat distribution patterns associated with forest species are mostly common with other species, with the exception of large suitable forest patches especially at the north of the region. Indeed, 92% and 81% of highly and suitable habitat of FOR species (i.e., suitability index > 65%) are include in GEN and ALL species' high and suitable habitat respectively.

Regarding potential multi-specific regional continuities, two major sectors form "bottlenecks" to north-south (sector B, Fig. 3) or east-west continuity axis and potential movements (sector A, Fig. 3). This is particularly marked for forest species. These two sectors contain few protected areas and show a cover mismatch with GI (Fig. 3).

4 Discussion

We highlighted a mismatch between the most suitable amphibian habitats at regional scale and the existing conservation network, in particular protected areas (in coverage and efficiency). Indeed, habitat patches with a high suitability index associated with common or slightly rarer species were poorly covered by PA except for one species of high conservation concern: *P. punctatus*. Yet, most suitable areas were better covered by GI (especially GI layers associated with wood, hedgerow landscapes and wetlands) and by INV sites (inventoried sites with ecological value but no regulatory protection). Difference in coverage and efficiency obtain for PAs and INV highlight that some sites with amphibian conservation issues are known but not protected. In addition, we identified two narrow "bottlenecks" in suitable habitat continuities at regional scale which are only very sparsely covered by the conservation network (PAs and GI).

4.1 General limits and interpretation framework

In addition to the limits related to the presence-only SDM detailed in Matutini, Baudry, Fortin, et al. (2021) recently developed stacking-SDM methods require further development to improve their evaluation. SDM are useful tools to predict the distribution of habitat suitability but rarely predict the biology of populations (Lee Yaw et al., 2022).

The multi-species networks identified should be considered simply as maps of highly suitable habitat for biodiversity (habitat perspective) - measured with highly sensitive and biphasic amphibian species – rather than as a real multilayer network of amphibian communities (species perspective). In addition, resistance values based on literature and expert opinions or derived from SDM values are still debated (see Godet & Clauzel, 2020 for methods comparison and discussion) and information about species movement and dispersion processes are still very scarce in the literature (Pittman et al. 2014). A more rigorous approach would be to integrate independent genetic data to assess our final maps (in addition to the external presence-absence dataset use to evaluate our models), particularly in the two bottleneck sectors. However, these data were not available. This might be worthwhile pursuing for post-validation and further investigations.

Our results must also be interpreted keeping in mind the spatial and temporal scales involved. Amphibians have poor movement capacities, rarely exceeding a few kilometres during dispersal movements (Sinsch, 2014). In this work, continuities were identified from habitat distributions at regional scale and species level reflecting long-term ecological processes and population movements across decades. This study takes a first step towards assessing potential barriers to species distribution shifts in response to global change, but does not directly include landscape dynamics and climate change scenarios. Rather it provides elements at regional scale to guide regional policies and further studies to improve multi-scale integration and efficiency of measures for biodiversity conservation.

4.2 **A mismatch for the conservation of amphibians**

Two main reasons may explain the mismatch between location of PAs and amphibian habitat requirements. Firstly, PAs are generally defined according to the needs of rare and/or emblematic species or habitats). In the study region, most PA focus on birds or plants species, large open wetlands near the western coast or the Loire River valley but only a few target species of amphibian and these tend to be rare species (e.g., *Pelobates cultripes*, *Bombina variegata*). Most local, rare species of high conservation concern are pioneer species and/or associated with loose or sandy soils with poor vegetation that are found in particular on the coast, along the Loire River and in some quarries. Their ecology contrasts with the other studied species, except for *P. punctatus* which shares many of the same ecological requirements, explaining the better conservation coverage and efficiency of PA for this species.

Secondly, PA definition in the region presents a “location bias”. Indeed, PAs are defined primarily in areas of low economic interest, less used for human activities (Rodrigues et al., 2004). This bias is common worldwide and widely described in the literature (Ahmadi et al., 2020; Joppa & Pfaff, 2009). It can be especially problematic for species living in human-dominated landscapes, like most amphibian species. For example, Rodrigues et al. (2004) demonstrated that amphibians contain a large number of “gap species” worldwide, i.e., they are the biological group least covered by the global PA network. In addition, our results show a potential “network bias” similar to Ahmadi et al. (2020), i.e., the extension of PA is established without sufficiently considering their position within the network. Indeed, the current PA sites (and the sites intended for the

future extension of PAs – see Appendix 4) are not located in the two areas with highest potential defined by our primary analysis of the regional continuity of suitable habitats.

4.3 Green infrastructure (GI) as a complementary tool for biodiversity conservation

Our results show GI offers better coverage of highly suitable habitats than PAs for amphibian species groups, but this remains partial, in particular in the two identified "bottleneck" sectors. Indeed, agricultural areas are poorly covered by PAs, generally due to a conflict of economic interest (Rodrigues et al. 2004) while GI provides complementary coverage in areas dominated by human activities. Agricultural landscapes with high conservation value for biodiversity such as hedgerow mosaic landscapes depend on the maintenance of traditional farming practices that may even be inhibited by PAs conservation (Schmitz et al., 2017)

In addition, we underline the importance of GI layers associated with wetlands, woodlands and traditional hedgerow mosaic landscapes for amphibians. Consequently, our results highlight the importance of considering several GI layers with potential interactions. GI tends to compartmentalize conservation issues by splitting them into distinct layers of habitat types considered as independent "subnetworks", where the "habitat" concept is limited to landcover categories (see Pilosof et al., 2017 for general perspective on multi-layer nature of ecological networks). Species survival is however conditioned by different ecological processes which generally go beyond a single type of land cover class. Some bat species, for example, can roost in buildings or old trees in summer, caves in winter, forage in open areas and wetlands and use hedgerow networks to transit or migrate. Species other than amphibians may also have very contrasting requirements during their life cycle (e.g., many holometabolous insects and odonates) with, for example, distinct aquatic and terrestrial phases.

Lastly, we expected a higher overlap of the GI layer called Bocage (traditional hedgerow mosaics) based on knowledge of amphibian ecology (Boissinot et al., 2019). This GI layer was mapped using combined land use data (i.e., hedges, ponds and meadows only) at 1km-resolution with a poor consideration of the interactions between these elements (i.e., simple metrics as density or area related to hedges, ponds and meadows were combined independently). Of course, other elements of the landscape are important for amphibians, such as small streams and wooded patches, as well as more complex processes related to landscape complementation and structural heterogeneity (Boissinot et al., 2019). Amphibian habitat network studies mainly focus on pond networks but natural or semi-natural forest patches, especially mature forest (e.g. >70 years) and even small woodlots (Boissinot et al. 2015), are essential for amphibian population persistence, in particular in agricultural regions (Hartel et al., 2010; Collins & Fahrig 2017).

Therefore, current methods for defining green infrastructure, based on landcover data, should be complemented by integrating biological data. An integrative approach using habitat suitability mapping combined with connectivity modelling, using biological observations, seems relevant for integrating species-habitat relations into ecological network definition at different spatial scales (Clauzel & Godet 2020).

4.4 **Implications for conservation**

Protected areas seem insufficient and poorly suited to maintaining amphibians regionally. Green infrastructure (GI) has better efficiency and coverage but is not regulatory (unprotected) and covers only 16 to 33% of highly suitable habitat. An important weakness of GI is its exclusive reliance on land use data without including biological data and landscape complementation as well as the multi-layered nature of ecological networks. Ecological niche modelling tools such as SDM, coupled with ecological connectivity models, are of particular interest for improving the ecological realism of identified networks and supporting related decisions. To make this possible, strengthening the interactions between researchers and stakeholders is essential, especially because these modelling tools need to be used and interpreted with care.

The second major result concerns bottlenecks. We identified "bottleneck" sectors not covered by any conservation tools such as PA or GI despite high potential conservation value. These areas might be especially important for amphibian populations in a context of global change requiring distribution shifts to maintain suitable conditions for population viability. Indeed, according to Préau et al. (2019), important distribution shifts at regional scale are expected for certain amphibian species based on global change predictions. These two “bottlenecks” are located in a context of open fields and intensive farming which are considered by nature protection organisations to have limited potential for biodiversity. In these areas, some semi-natural elements such as small woods associated with wetlands may nonetheless play a key role in maintaining functionality and connectivity of the network at regional scale and should be strengthened. In these two areas, habitat continuities are maintained by riparian woods (sometime very thin and degraded) and associated river landscapes with a higher proportion of pastures and hedgerows, as well as small wood patches close to wetlands including ponds. As a result, these two areas need further investigation and could be targeted by conservation and restoration measures. These results also underline the importance of multi-scale and multi-level analysis for habitat and connectivity studies (e.g., McGarigal et al. 2016).

Finally, the different maps obtained from this study provide support for prioritizing certain regional policies with different objectives: (1) strengthening PA network and GI, in particular in the 2 bottleneck sectors. (Appendix 5 provides more specific information to prioritize new protected area from a regional preselected set of sites according to our results); (2) to identify potential conflict points with transport network (i.e., roads and railways); (3) spatially prioritize actions supporting agroecological transition, particularly in the two bottleneck areas considered as “degraded” for biodiversity. Conservation actions for amphibian conservation often focus on ponds and pond networks. The complementarity of ponds (or wetlands) and forest patches should be considered to define conservation actions (Cushman, 2006; Denoël & Lehmann, 2006; Pope et al., 2000) as well as certain associated traditional farming practices in western Europe (Boissinot et al., 2019; Hartel et al., 2010). In our region, amphibians have interactions with traditional agricultural practices and with related landscape dynamics. The success of conservation measures depends on our ability to integrate biodiversity issues into human-dominated agricultural landscapes shaped by farming practices.

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Authors' contributions

Florence Matutini: Conceptualization (Equal), Data curation (Lead), Formal analysis (Lead), Funding acquisition (Supporting), Methodology (Lead), Investigation (Lead), Visualization (Lead), Writing-original draft (Lead), Writing-review & editing (Lead); **Marie-Josée Fortin:** Conceptualization (Equal), Methodology (Supporting), Supervision (Supporting), Writing-original draft (Supporting), Writing-review & editing (Supporting); **Jacques Baudry, Guillaume Pain & Josephine Pithon:** Conceptualization (Equal), Methodology (Supporting), Supervision (Equal), Writing-original draft (Supporting), Writing-review & editing (Supporting)

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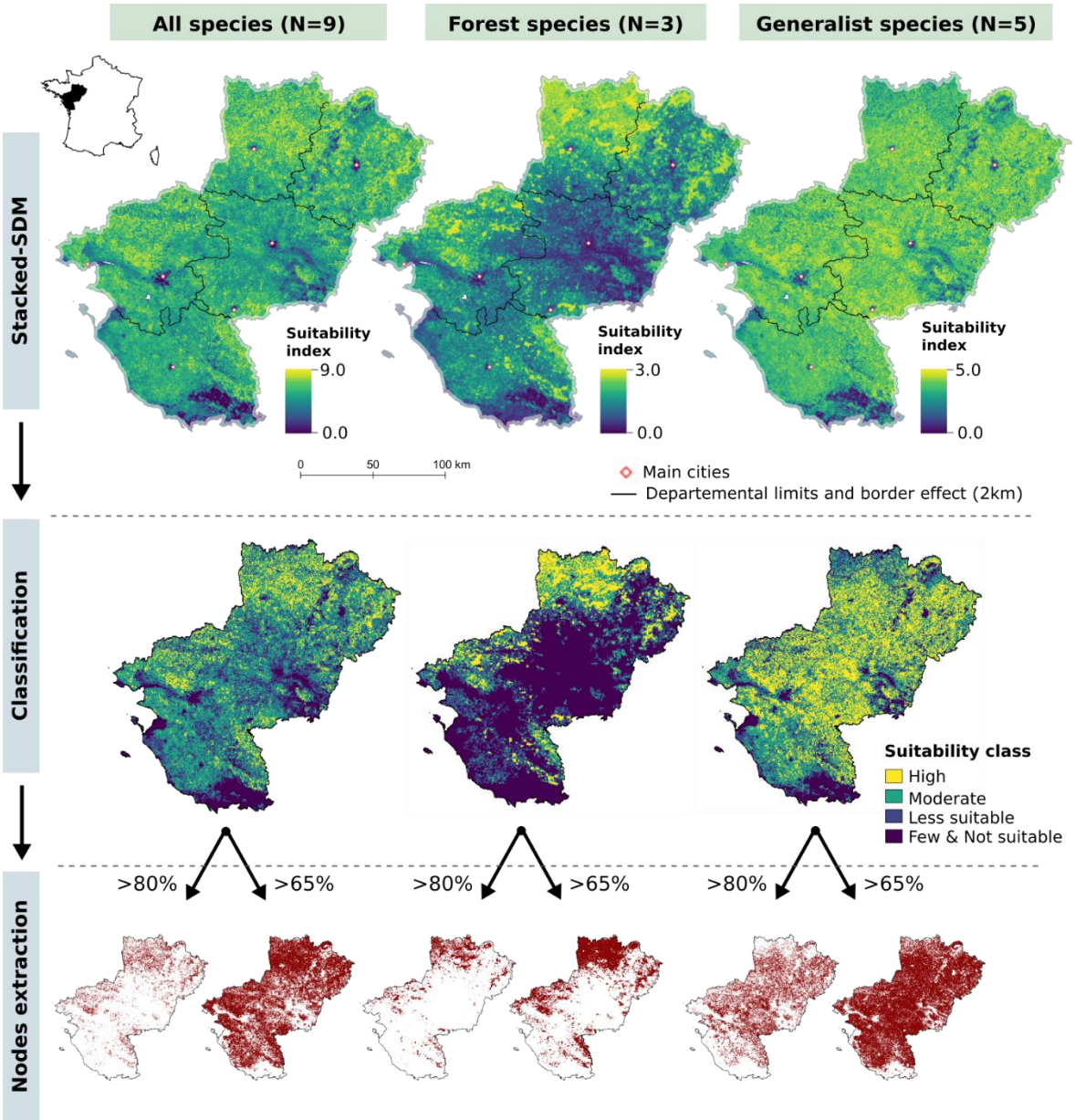


Fig. 1. Identification of highly suitable and suitable multi-specific patches of habitat using stacked habitat suitability map for three species groups.

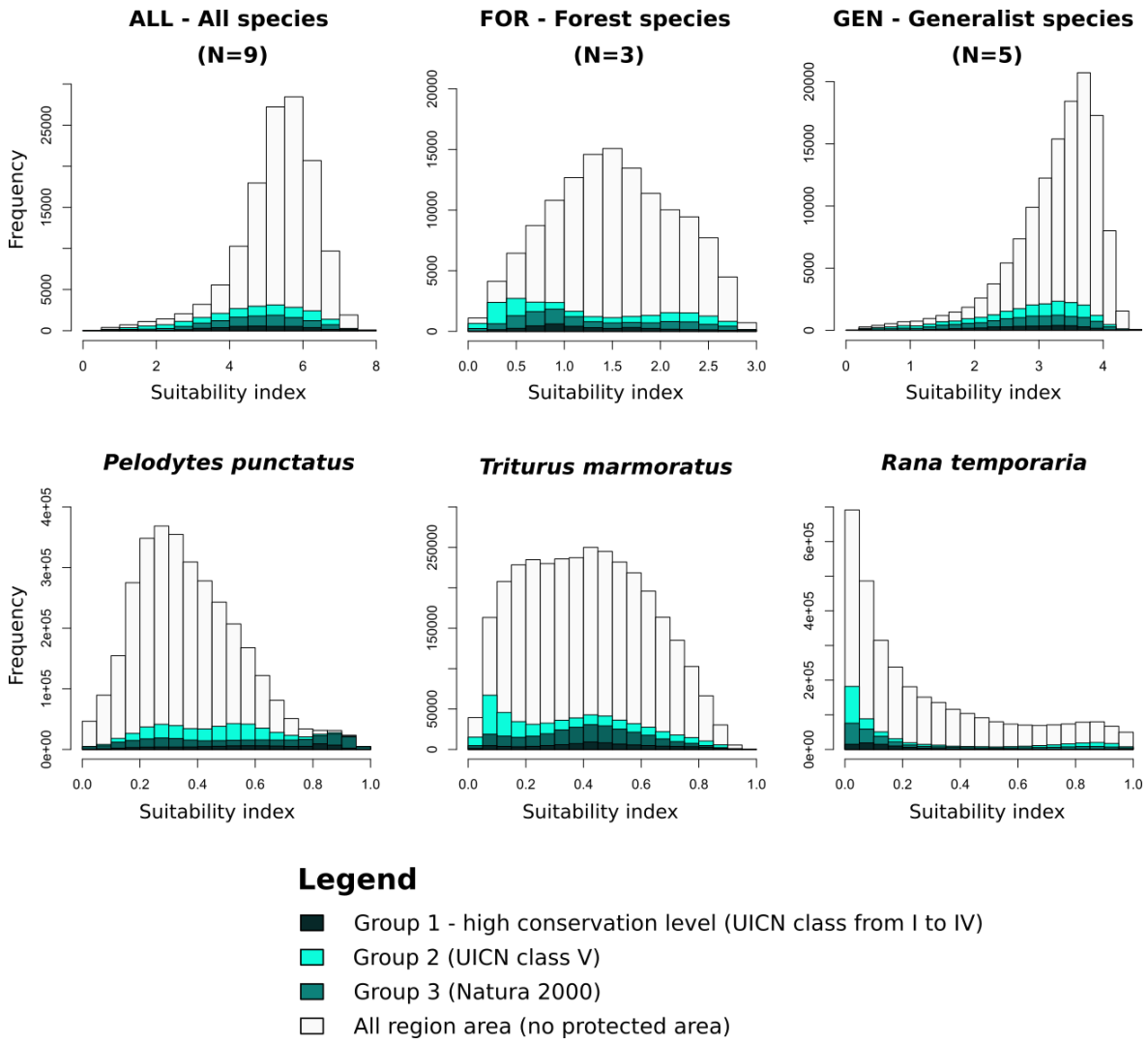


Fig. 2. Distribution of pixels along the regional habitat suitability gradient covered or not by protected area. Suitability index (from the habitat suitability map) is calculated for each species and varies from 0 to 1. Suitability index of the three groups (ALL, FOR and GEN) is the sum of the individual species index related to each group (pSSDM). The frequency corresponds to a number of pixels covered by protected areas from the Group 1, 2, 3 in relation to the whole region area.

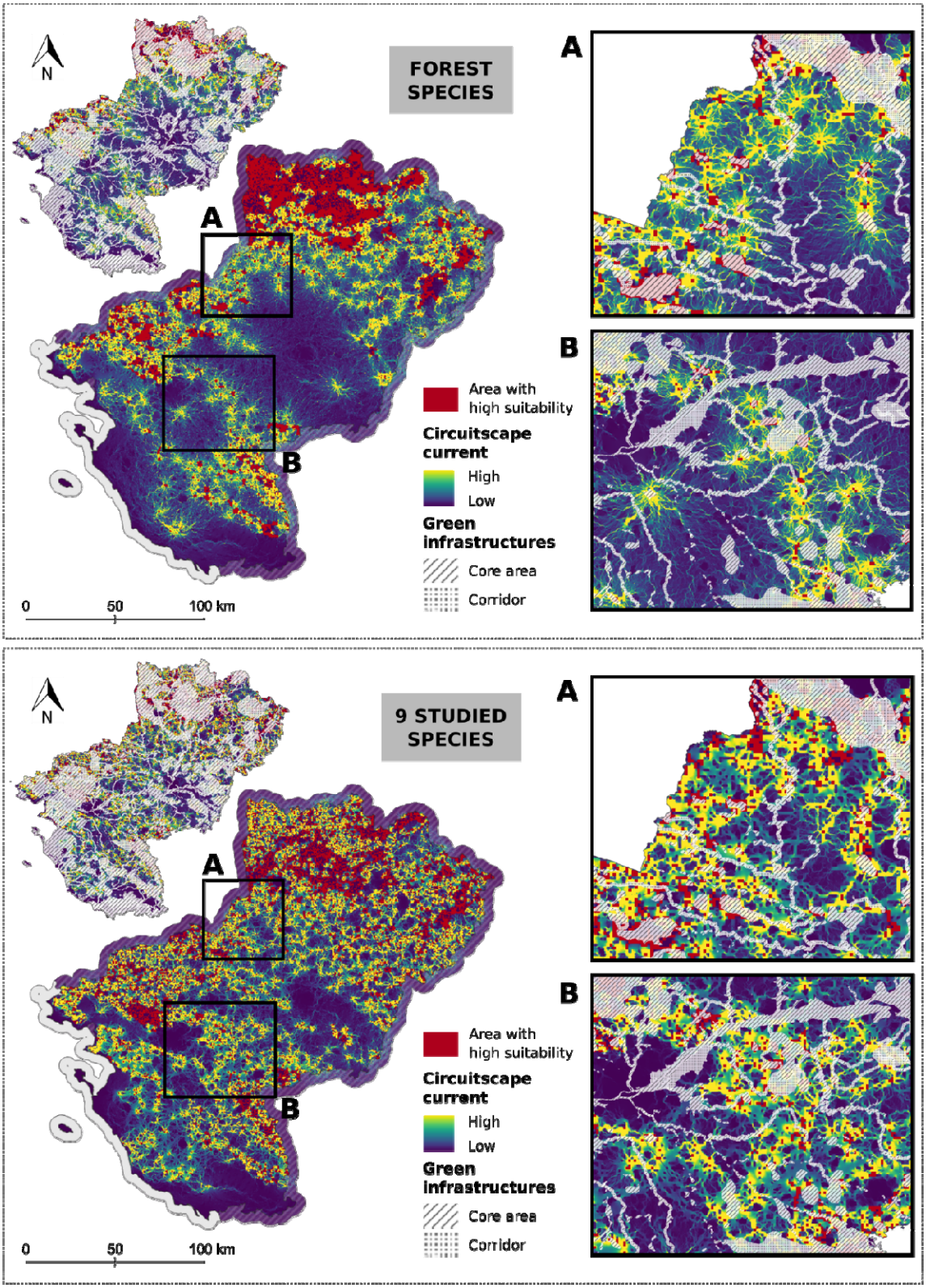


Fig. 3. Large scale permeability between high suitability areas and associated continuities patterns confronted with regional green infrastructure. A and B show potential conflict area and issues for continuity conservation at regional scale with a mismatch with the green infrastructure network.

Table 1. Description of the nine studied species: conservation status and number of presence-only data available for analysis. RL FR: France red list; RL Region: regional red list of Pays-de-la-Loire; Priority: regional priority level for species conservation from the regional red list defined by Marchadour et al. (2009); Hab. Dir. N2000: habitats directive classification (Natura 2000); Pop trends: regional population trends from Marchadour et al. (2009); Nb presence data: Number of presence-only data were calculated after a 100 m-resolution rasterization and correspond to the number of pixels with at least one observation of the species.

	Species	RL FR (2008)	RL Region (2009)	Priority (region)	Hab. Dir. N2000	Pop trends (1998-2008)	Nb presence data (Atlas)
Species used for SSDM	*Pelodytes punctatus*	LC	LC	2		↘	1714
	Triturus marmoratus	LC	LC	3	IV	↘	906
	Rana temporaria	LC	VU	2	V	↘	848
	Lissotriton helveticus	LC	LC	1		?	4580
	Bufo spinosus	LC	LC	0		?	6071
	Hyla arborea	LC	LC	0	IV	↘	4555
	Rana dalmatina	LC	LC	0	IV	?	6118
	Triturus cristatus	LC	LC	0	II & IV	↘	1040
	Salamandra salamandra	LC	LC	0		?	3514

Table 2. Classification of main conservation areas according to protection levels used in Pays-de-la-Loire (France). PA: protected area; GI: Green infrastructure; INV: area with an inventory of biodiversity and having a strong natural heritage interest but not protected by regulatory tools (ZNIEFF, type I and II).

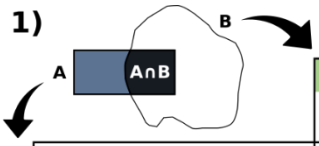
Cat.	Group	Protect. level	Code name	UICN class	Protection approaches	Level	French denomination
PA	1	+++	RNN	I-IV	Regulatory	National	National Nature Reserve
			SIN,SCL	III	Regulatory	National	Classified site and Registred site
			RNR,RB, SCL,APB	I-V	Regulatory essentially	National or Regional	Biological Reserve, Conservatoire du littoral Site, Regional Nature Reserve, Biotope Protection Order
	2		SCEN, ENS	I-VI	Regulatory, Contractual management or Land purchase and management	Regional	Area managed by Natural Area Conservation Societies (CENs)
			PNR	V	Contractual management	Regional	Regional Nature Park
	3	+	N2000	/	Contractual management	European	Natura 2000 sites (N2000)
GI	4	0	BOCAGE	/	Non-regulatory Advisory / informative	National to local	Traditional hedgerow mosaic landscapes Infrastructure
		0	WOOD	/			Woodlands infrastructure
		0	WET	/			Wetlands infrastructure
		0	COAST	/			Coastlands infrastructure
		0	OPEN	/			Natural open fields infrastructure
		0	Corridor	/			Ecological cooridors
INV	5	0	ZNIEFF	/	Biodiversity inventories only	National	Natural areas of special ecological, faunal and floral value

Table 3. Accuracy of stacked species distribution models for three species groups according to the nine studied amphibian species. Results obtained with external data with 100 permutations. Community AUC were obtained using species diversity results for each studied species group and for all species inventoried in the external dataset (*n*=17). Individual AUC and SEDI are from a previous study in Matutini, Baudry, Fortin, et al. (2021).

Species group	**R^2**	**cAUC**	**Min individual AUC / SEDI**	**Max individual AUC / SEDI**	**R^2 all**
All nine species	0.31	0.86	0.73 / 0.67	0.86 / 0.89	0.07
Forest species (*n*=3)	0.23	0.76	0.78 / 0.68	0.86 / 0.84	0.14
Generalist species (*n*=5)	0.30	0.87	0.73 / 0.67	0.81 / 0.89	0.02

Table 4. Proportion of the conservation area covered by different habitat suitability classes (1. conservation efficiency) and proportion of different habitat suitability classes covered by the conservation area (2. conservation coverage) for different species and species groups. Classes of conservation area: Protected (groups 1 to 3) – classes I to V derived from the UICN classification; EURO: European conservation network from Natura 2000; Non-protected: GI (Green infrastructure) and INV (inventoried sites define as "high naturalist interest"). Suitability class for each groups or species: "+++" = highly suitable (>0.80) ; "++" = suitable (>0.65) ; +/- = "moderately or not suitable" (<=0.55). See Table 2 for "code names" details. Names with * show sites with point data only (surface area is not available).

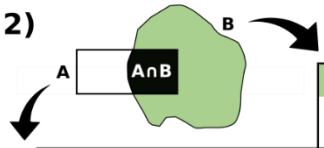
1)



AnB / A — CONSERVATION EFFICIENCY

					SSDM 500m resolution									SDM 100m resolution								
					All studied species (n=9)			Forest species (n=3)			Generalist species (n=5)			*Triturus marmoratus*			*Rana temporaria*			*Pelodytes punctatus*		
	Group	Name	Class	Area (ha)	+++	++	+/-	+++	++	+/-	+++	++	+/-	+++	++	+/-	+++	++	+/-	+++	++	+/-
Protected (PA)	1	RNN	I-IV	3183	0	23	26	0	19	26	0	21	24	0	3	21	0	4	12	12	1	4
		SIN,SCL	III	80912	7	33	36	7	11	18	12	35	29	8	13	19	4	2	3	24	18	20
		RNR,RB,SCL,APB	I-V	4902	17	30	28	20	12	8	24	32	28	3	12	17	22	4	2	14	11	15
	2	SCEN,ENS*	I-VI	/	12	50	26	12	24	23	26	44	19	8	21	20	6	7	7	6	10	15
		PNR	V	358668	11	28	27	15	15	10	13	32	24	5	10	13	15	8	4	10	12	24
	3	N2000	EURO	144070	10	33	36	10	16	12	19	34	26	2	10	23	10	8	6	24	14	13
Non protected (GI & INV)	4.1	BOCAGE	GI	424568	20	63	17	21	26	29	42	43	13	12	27	30	15	11	9	0	3	10
		WOOD	GI	176157	26	55	18	38	25	23	38	38	20	6	20	22	31	12	11	0	1	4
		WET	GI	270266	19	56	22	21	25	25	38	44	15	5	18	26	15	11	11	1	3	8
		COAST	GI	9376	2	51	35	0	12	30	4	59	26	12	34	25	0	0	0	13	20	26
		OPEN	GI	19445	15	53	28	11	22	20	42	41	13	1	5	11	13	11	12	1	5	17
	4.2	Total core hab.	GI	650572	20	60	19	24	25	27	40	43	15	9	24	26	18	10	9	0	3	9
		Corridor	GI	378391	17	52	25	13	21	26	39	41	16	5	14	20	9	8	9	0	4	14
	5	ZNIEFF	INV	279266	20	57	20	29	24	25	34	44	18	11	28	25	21	9	10	1	4	10
		REGION		**3236407**	**12**	**49**	**28**	**11**	**17**	**23**	**33**	**40**	**17**	**5**	**13**	**19**	**9**	**7**	**7**	**3**	**6**	**15**

2)



AnB / B — CONSERVATION COVERAGE

				SSDM 500m resolution									SDM 100m resolution								
				All studied species (n=9)			Forest species (n=3)			Generalist species (n=5)			*Triturus marmoratus*			*Rana temporaria*			*Pelodytes punctatus*		
	Group	Name	Class	+++	++	+/-	+++	++	+/-	+++	++	+/-	+++	++	+/-	+++	++	+/-	+++	++	+/-
Protected	1	RNN	I-IV	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
		SIN,SCL	III	1	2	3	1	2	2	1	2	4	4	2	2	1	1	1	19	8	3
		RNR,RB,SCL,APB	I-V	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
	2	SCEN,ENS*	I-VI	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/
		PNR	V	10	6	10	14	10	5	4	9	15	11	9	8	20	13	6	35	23	18
	3	N2000	EURO	4	3	6	4	4	2	3	4	7	2	3	5	5	5	4	35	11	4
Non protected	4.1	BOCAGE	GI	21	17	8	24	20	17	16	14	10	33	27	20	23	21	17	2	8	9
		WOOD	GI	11	6	3	18	8	5	6	5	6	7	8	6	20	9	9	1	1	2
		WET	GI	13	10	7	16	12	9	10	9	7	8	12	11	15	14	14	2	4	5
		COAST	GI	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	1	1	1
		OPEN	GI	1	1	1	1	1	1	1	1	0	0	0	0	1	1	1	0	0	1
	4.2	Total core hab.	GI	33	25	13	42	30	24	24	21	17	39	36	28	43	32	28	3	11	13
		Corridor	GI	16	13	10	14	15	13	14	12	10	12	12	12	12	15	16	2	9	11
	5	ZNIEFF	INV	14	10	6	22	12	10	9	9	9	21	18	11	21	12	12	2	6	6