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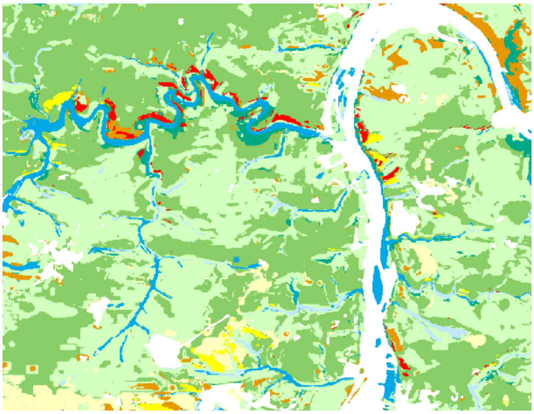

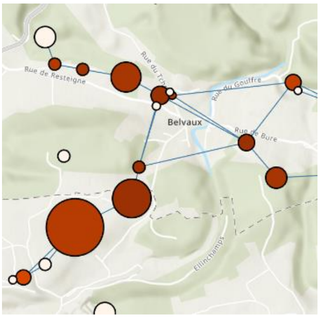

Prioritizing biodiversity conservation in degraded environments: mapping landscape connectivity challenges using biological data and local ecological knowledge

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PRIORITIZING BIODIVERSITY CONSERVATION IN DEGRADED ENVIRONMENTS: MAPPING LANDSCAPE CONNECTIVITY CHALLENGES USING BIOLOGICAL DATA AND LOCAL ECOLOGICAL KNOWLEDGE

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Abstract

This thesis aimed to develop methodologies for identifying biodiversity conservation priorities in fragmented landscapes while considering meta-population dynamics and species' habitat connectivity. The research encompassed several key aspects of biodiversity conservation in degraded landscape as mapping biotope and species corridors connecting them.

To begin, the study focused on delineating landscape elements using the concept of ecotopes, which are the smallest homogeneous units within a cartographic system. A novel approach utilizing spectral information and topography enhanced the ecological homogeneity of ecotope delineation. These ecotopes proved suitable for modeling biotope distribution, which is crucial for understanding landscape conservation priorities and guiding field inventories.

Subsequently, a biotope modeling framework was developed to accurately predict the presence of multiple biotopes within a region by incorporating vegetation dynamics. The concept of Potential Natural Vegetation (PNV) was utilized, assigning biotopes to PNV categories. This approach resulted in a robust presence/absence dataset for calibration and exhibited significant improvements in model sensitivity compared to traditional methods. The importance of PNV modeling in capturing the historical ecological envelope of biotopes was underscored.

Moving forward, the research explored the mapping of species corridors, using the case of the wildcat as an example. Various approaches were compared, including expert knowledge and modeling methods based on species observations. A data-driven approach utilizing presence-only data outperformed others in terms of efficiency, while all approaches identified the same critical corridors, emphasizing the importance of maintaining connectivity. Graph analysis revealed different central patches crucial for landscape connectivity, suggesting the data-driven approach when accurate data are available and the knowledge-driven approach when understanding of species habitat is well established.

The study then extended to modeling multiple species habitat networks to ensure landscape connectivity for species with different connectivity needs. A knowledge-driven approach was employed by considering fragmentation-sensitive focal species and their associated life history traits. Cluster analysis grouped species based on sensitivity to fragmentation, facilitating species choice to perform graph-based analyses for prioritizing connectivity stakes.

In conclusion, this thesis developed methodologies for identifying biodiversity conservation priorities in fragmented landscapes. The findings contribute to understanding and promoting landscape connectivity and emphasize the importance of incorporating such ecological considerations in landscape planning and management.

Résumé

Cette thèse a pour objectif de développer des méthodologies pour identifier les priorités de conservation de la biodiversité dans des paysages fragmentés en tenant compte de la dynamique des méta-populations et de la connectivité des habitats des espèces. La recherche a englobé plusieurs aspects clés de la conservation de la biodiversité dans les paysages dégradés, tels que la cartographie des biotopes et des corridors d'espèces les reliant.

Pour commencer, l'étude s'est concentrée sur la délimitation des éléments du paysage en utilisant le concept d'écotopes, qui sont les plus petites unités homogènes d’un système cartographique. Une nouvelle approche utilisant des données spectrales et la topographie a amélioré l'homogénéité écologique de la délimitation des écotopes. Ces écotopes se sont révélés adaptés pour modéliser la distribution des biotopes, ce qui est crucial pour comprendre les priorités de conservation du paysage et guider les inventaires sur le terrain.

Ensuite, une approche de modélisation des biotopes a été développé pour prédire avec précision la présence de plusieurs biotopes dans une région en intégrant l’aspect dynamique des communautés végétales. Le concept de Végétation Naturelle Potentielle (VNP) a été utilisé pour regrouper les biotopes par contexte écologique. Cette approche a permis d'obtenir un ensemble de données de présence/absence robustes pour la calibration des modèles et a présenté des améliorations significatives de la sensibilité du modèle par rapport aux méthodes traditionnelles. L'importance de la modélisation des VNP pour saisir l’enveloppe écologique historique des biotopes a été soulignée.

Par la suite, nous avons exploré la cartographie des corridors d'espèces, en utilisant l'exemple du chat sauvage. Différentes approches ont été comparées, notamment les connaissances d'experts et les méthodes de modélisation basées sur les observations d'espèces. Une approche basée sur les données de présence seule s'est avérée plus performante en termes d'efficacité, tandis que toutes les approches ont identifié les mêmes corridors critiques pour maintenir la connectivité du réseau. L'analyse des graphes a révélé différents points centraux cruciaux pour la connectivité du paysage, suggérant l'approche basée sur les données lorsque des données précises sont disponibles et l'approche basée sur les connaissances lorsque la compréhension de l'habitat des espèces est bien établie.

La recherche s'est ensuite étendue à la modélisation de réseaux d'habitats de plusieurs espèces afin de garantir la connectivité du paysage pour des espèces ayant des besoins de connectivité différents. Une approche basée sur les connaissances a été utilisée en tenant compte des espèces focales sensibles à la fragmentation et de leurs traits de vie associés. L'analyse statistique par cluster a regroupé les espèces en fonction de leur sensibilité à la fragmentation, facilitant le choix des espèces pour effectuer des analyses basées sur les graphes afin de prioriser les enjeux de connectivité.

En conclusion, cette thèse a développé des méthodologies permettant d'identifier les priorités de conservation de la biodiversité dans les paysages fragmentés. Les résultats contribuent à la compréhension et à la promotion de la connectivité des paysages et soulignent l'importance de prendre en compte ces considérations écologiques dans la planification et la gestion des paysages.

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AF: Acidophilous *Fagus* forests
AQC: Acidophilous *Quercus* and *Carpinus* forests on wet soils
AS: *Alnus* Swamp woods
AUC: Area Under the ROC Curve
CFQ : Calcareous *Fagus* and *Quercus* forests
CICES : Common International Classifications of Ecosystem Services
CS: Citizen Science
DEMNA : Département de l'Étude du Milieu Naturel et Agricole
DHM : Digital Height Model
DSM : Digital Surface Model
EEA : European Environment Agency
EN : Ecological Network
ES : Ecosystem Services
ESS : Ecosystem Services supply
EUNIS : European Nature Information System
FQC: Fammenian *Quercus* and *Carpinus* forests
GEOBIA: Geographic Object-Based Image Analysis
GI: Green Infrastructure
GIS: Geographic Information System
HIHF: Human Induced Habitat Fragmentation
HIHFS: Human Induced Habitat Fragmentation Sensitive species
IGN : Institut de Géographie National
IPBES : Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services
IUCN : International Union for Conservation of Nature
LCP : Least Cost Path
LIDAR : Light Detection And Ranging
MNS : Modèle Numérique de Surface
MSS : Maximizing Sensitivity and Specificity
NF: Neutrophile *Fagus* forests
NQF: Neutrophile *Quercus* and *Fraxinus* forests on wet soils
PA : Producer Accuracy
PAM : Partition Around Medoids
PCA : Principal Component Analysis
PNV : Potential Natural Vegetation
QBM: *Quercus* and *Betula* forests with *Molinia*
RF: Random Forest
RG: Riparian and Gallery woodland
ROC: Receiver Operating Curve
SB: *Sphagnum Betula* woods
SDM: Species Distribution Model

SLOSS: Single Large Over Several Small
SMOTE: Synthetic Minority Oversampling Technique
STD: Standard Deviation
TAQ: Thermophile acidophilous *Quercus* forests
TPI: Topographic Position Index
TPR: True Positive Rate
UA: User Accuracy
VSURF: Variable Selection Using Random Forest
WSR: Wet and Shady Ravine forests
XFQC: Xerophile Fammenian *Quercus* and *Carpinus* forests

Chapter 1

Introduction

1. Of landscapes and men

1.1. *Biodiversity loss: impacts and causes*

The current biodiversity loss we are facing represents an important threat as much important as climate change in spite of the low current media coverage (Cardinale et al., 2012). It negatively impacts the way ecosystems produce biomass, recycle nutrients and decompose. In other words, poorly diversified ecosystems perform less. Diverse ecosystems are more stable, insure their well-functioning through time and are more productive (Cardinale et al., 2012). As we depend on ecosystem products such as food, wood or medicines, we also depend on diversified ecosystems. This urgent topic caused the emergence of ecosystem services concept which encompass all goods and services provided by ecosystems to humans. Pollination, food production, hedges protection from floods and landslides and many more services important for human well-being (MILLENNIUM ECOSYSTEM ASSESSMENT (PROGRAM), 2005). More recently, teams of researchers are studying the link between biodiversity loss and pandemic emergence. The increasing frequency of infectious disease outbreaks such as wildlife disease and zoonose can be attributed to climate change, biodiversity loss, habitat degradation and increasing rate of wildlife-human contact (Schmeller et al., 2020). Given the profound implications of biodiversity loss for humanity, it has become imperative to promptly tackle this imminent peril.

Main drivers of biodiversity loss were identified by researchers and there are five of them (IPBES, 2019), ordered by decreasing impacts:

- change in land and sea use,
- direct exploitation of organisms,
- climate change,
- pollution,
- invasive alien species.

Change in land and sea use is considered as the most important driver of biodiversity loss worldwide and the expansion of agriculture is one of the main reasons in terrestrial ecosystems. One third of them are now dedicated to crop or livestock production. Along with the expansion of urban areas, all these land-use changes are made to the detriment of natural ecosystems such as natural forests, grasslands and wetlands (IPBES, 2019). These changes in land use leads to a phenomenon that we all witness. Every day, we walk along roads or railroads to go to work, to do our shopping and to eat in the evening. On the ground, it is difficult to realize the impact these movements have on the landscape. However, a very small country has managed to make this phenomenon visible from space: Belgium. With a dense network of highways that are lit up all night long, Belgium has quickly become a landmark for astronauts living on the ISS. By crossing the territory from one side to the other with its luminous features, the Belgian highways cut the territory and the terrestrial ecosystems. The large forests are thus cut into parts that will be very quickly nibbled by the expansion of intensive agriculture until only small natural areas remain, isolated from each other. This phenomenon which takes place throughout the world is called: landscape fragmentation. This alteration of landscapes due to human activities exerts a significant influence on species populations and the fundamental functioning of ecosystems, thereby threatening biodiversity.

1.2. Definitions and components of landscapes

Many disciplines study landscapes and there are as many different definitions. If we focus on common features, landscapes are characterized by the arrangement of different elements - called “patches” - and the variety of those elements creates heterogeneity in a defined area (Wiens, 2002). In a conservation perspective, landscape is for instance composed of vegetation community and/or different land-cover. Those different patches, their spatial arrangement and their relations can be analysed to characterize the landscape (Wiens, 2002). Here is everything that is commonly used to define the landscape. In ecology, the concept of landscape is commonly interpreted as a scale. A landscape is therefore composed of different ecosystems and multiple landscapes could be encompassed in a biome (Forman, R.T.T. & Godron, M., 1986; Noss, 1991). This use of the landscape term as a scale portrays how humans love to order everything hierarchically. This view is clear when focusing on the different sub-topic in ecology. Community ecology focuses on the interaction between multiple species that can be studied separately in population ecology while the individual can be studied in autecology. The term landscape can also be used to refer to a holistic approach of ecology to find solutions to better manage natural resources (Soulé et al., 1991; Wiens, 1997). Finally, the last use of the landscape term in ecology of conservation is to emphasize on the effect of spatial patterns on ecological processes (Wiens, 1995; Wiens et al., 1993). This independently of the size of the studied area but more about the characteristics of the studied organism (Haila, 1999; Mac Nally, 1999). This can concern a region of thousands of kilometres square for large mammals but also a dozen ponds for amphibians. The concern of this approach is about how landscape structure can affect mechanisms influencing elements of conservation value such as populations or biodiversity. This is the approach we will follow to understand how landscape fragmentation affects landscape patterns and therefore species populations and biodiversity.

But “spatial patterns” and “heterogeneity” may remain nebulous concept if we do not go further in understanding the features characterizing landscapes that are needed to understand what fragmentation is and how to measure it. Three features are generally used to characterize landscape. First, we have the composition designating the nature of the elements composing landscapes. Then, the structure of the landscape is how those elements are arranged in space. Finally, the processes refer to the flows of organisms, material or disturbance within the landscape mosaic (Wiens, 2002). Landscape processes are more complicated to depict and measure as it relies on multiple and complex relationships. On the contrary, multiple features and measure can be easily extracted from maps or image of landscapes to describe its composition and structure (Wiens, 2002). We have measures that focuses on patches characteristics such as size, shape, perimeter or contrast. And others focusing on the mosaic such as the number of patches, patches diversity, patch size frequency distribution, edge density and many more. All these measures with the use of spatially referred biological data are the core of understanding and assess how landscape affects ecological processes. However, this implies that we characterize landscapes with elements that have defined border. Yet, those borders such as vegetation classifications are born from scientist’s mind after long debates (Bailey, 1996; Monmonier, 1996). But these do not exist in nature where environmental variation occurs along a gradient. It is therefore important to keep in mind that maps and other representations are a simplification of the reality based on available data and knowledge and that results, and conclusion should be presented in consideration of this bias (Monmonier, 1996).

1.3. Landscape changes

1.3.1. Classification of landscape changes

Some natural events have always altered the landscape to a greater or lesser extent, such as volcano eruptions, fires or long-term climate change (Bradstock et al., 2002; Croizat, 1960; Franklin, 1985; Thomas et al., 2004). However, only human activities have had such an impact on the landscape that causes enough habitat loss and landscape fragmentation to lead to a significant loss of biodiversity (Kerr and Deguise, 2004; Saunders, 1987). Significant landscape changes can take different forms because their reasons are also very different. However, landscape change has followed similar patterns around the world and can therefore be classified. The first classification of landscape modification was established by Forman (1995) who identifies 5 main categories of changes that affect the landscape in its spatial configuration: perforation, dissection, shrinkage, fragmentation and attrition (reducing the absolute number of patches) (Figure 1.1). The impact of these different modifications has been experimentally studied on insects and it has been shown that their populations react significantly differently depending on the type of spatial patterns they face (Collinge and Forman, 1998). Insect species richness falls significantly in a landscape affected by the reduction while it increases in a fragmented landscape. This can be explained by a refuge effect of species located in the area impacted by the changes. Individuals moving toward less impacted areas increase species richness in remnant patches. Other authors have also worked to describe changes in the landscape. They have developed a classification of these changes by adding a temporal component influenced by an ever-increasing impact of human modifications over time (McIntyre and Hobbs, 1999). The landscape can thus be intact, then variegated, then fragmented and finally relictual (Figure 1.2). In this model, the authors suggest that the greater the human modifications, the less intact habitat remains. They also add that landscape elements obtain sharper boundaries as a result of human modification. These two models used to describe landscape changes can be seen in complementary ways. Indeed, both identify that landscape changes tend to create discontinuities in the remaining habitats and result in a decrease in the amount of vegetation. Vegetation patches are therefore increasingly distant from each other, connectivity between patches is decreasing and the edge surrounding the patches tends to increase.

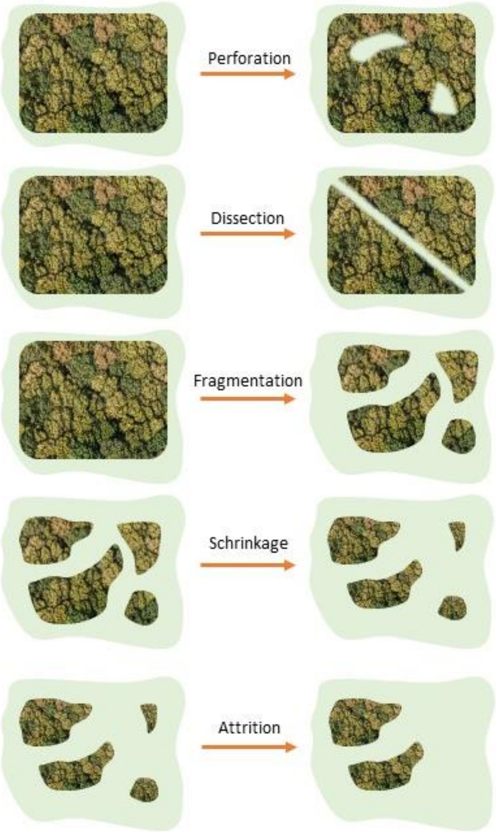

Figure 1.1: Visual examples of the 5 main type of landscape changes: Perforation (1), dissection (2), shrinkage (3), fragmentation (4) and attrition (5). Inspired from Forman (1995).

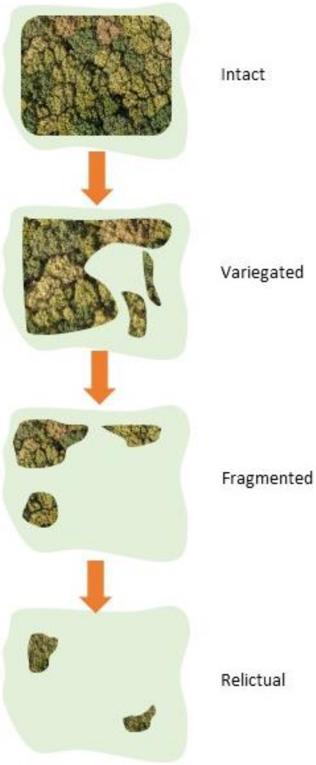

Figure 1.2: The evolution of human impacts on landscapes through time: Intact (1), variegated (2), fragmented (3) and relictual (4). Figure inspired from S. McIntyre & Hobbs (1999)

1.3.2. Distribution and dynamic of landscape changes

A particularity of landscape modifications that strongly impact the observed patterns comes from the fact that these modifications are not random. Man will tend to implement production activities in the most productive areas (Landsberg, J., 1999). The remaining habitat patches will therefore tend to be limited to less productive areas such as steep slopes, poor soils, those where the rock is outcropping or too wet areas (Hall, 1988). This non-random trend of landscape change will then have different impacts on biodiversity. Firstly, species growing on productive soils will be more likely to become scarcer as a result of habitat loss since they cannot survive in more extreme conditions (Braithwaite, 2004; D. B. Lindenmayer et al., 1991). It also implies that species abundance records in current landscapes are potentially far from what existed before human activities (Seabloom et al., 2002). This is the case for some previously abundant plant species that will only be found in low numbers in hedgerows in agricultural landscapes where they persist (Godwin

H., 1975). This implies that it is important to keep representative elements of the ancestral landscape in productive areas (Lindenmayer and Burgman, 2005). Even if these elements may seem strongly degraded or having too small surfaces. Finally, it is important to take into account this non-random character of landscape changes when studying their effect on species populations (Fischer and Lindenmayer, 2007; Hobbs and Yates, 2003). Indeed, factors other than landscape fragmentation or patch size may impact species distribution. Some species may be absent from some relictual patches because they simply do not persist under these conditions. It is therefore important to understand the needs of species in depth before studying the impact of landscape changes on their populations.

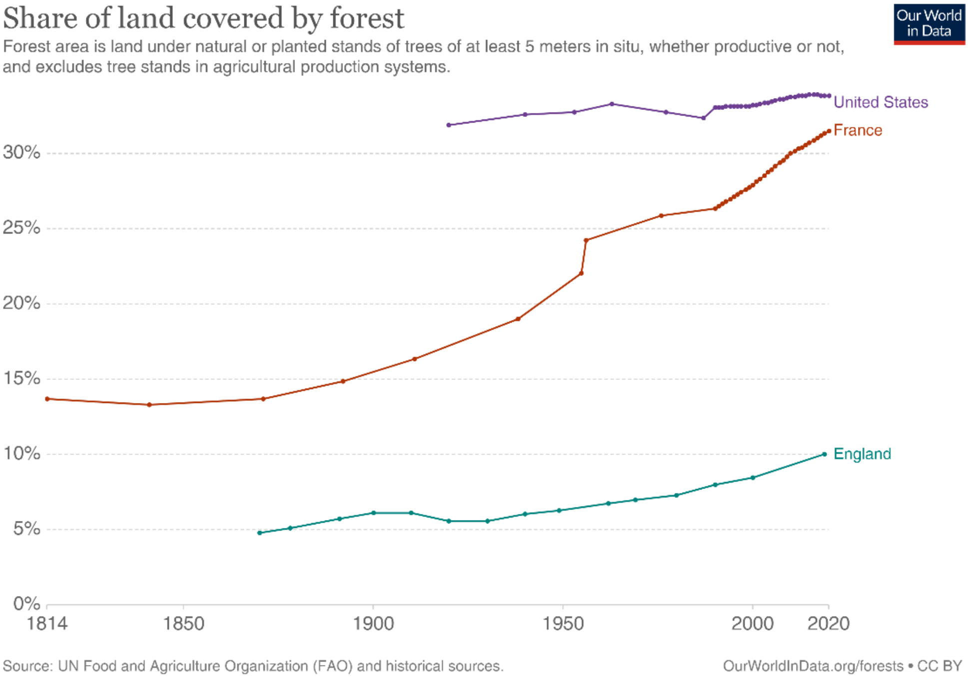

Figure 1.3: Evolution of forested area in France, England and the USA from the 1814 to 2020.

Another important aspect to consider when studying landscape change is the dynamics of these changes and the dynamics of ecosystems. The first example that comes to mind when we talk about landscape change is the degradation of large forest areas that are fragmented and reduced to small patches. However, this is not the evolution encountered everywhere on earth. In many parts of the world such as in the USA or in Europe, forest areas have increased for over a century (Figure 1.3). But these new forest areas, however, do not host as much biodiversity as natural old-growth forests and it will take a long time before they reach similar levels (Hall et al., 2002). The potential of these forests to support biodiversity will be further reduced if they are given over to silvicultural plantations. European landscapes have been managed by humans for a long time, which led to the concept of socio-ecosystems. Human activities have maintained ecosystems that fostered unique biodiversity, which now require protection from intensified agricultural and forestry practices. Therefore, it is important to consider the distinctiveness of these ecosystems and the species' needs when managing the landscape. (Aanderaa et al., 1996; Ratcliffe and Peterken, 1995). Ecosystems managed by humans can also be of paramount importance for critically endangered species such as the open cork oak plantation for the nearly extinct Lynx pardinus (Ferreras, 2001).

Drivers of landscape changes in Europe

As previously presented, the situation of the European landscape is complex. This is mainly due to an important cultural heritage of ancient agricultural practices that have shaped the landscape into a mosaic hosting an important biodiversity. The main source of landscape change in Europe is therefore its homogenization. Two main causes can be identified (Fry and Gustavsson, 1996). Firstly, the old agricultural and forestry practices have been pushed aside to the point of becoming marginal and have given way to an extreme intensification of raw material and food production. This phenomenon then leads to a second one. Agricultural and forestry areas with low productivity and high biodiversity occupied large areas. As they became more productive, they therefore tended to decrease in size, to specialize to the extreme, to become more intensive and therefore hosting less biodiversity. As a result of this homogenization, the landscape has lost its multi-functionality. There is therefore limited flexibility and few opportunities for recreational tourism and nature conservation due to the lack of available space.

This land management has had a significant impact on European landscapes. In the Netherlands, the forests located in alluvial plains lost 90% of their surface area between 1900 and 1980. Over the same period, the country lost 80% of its hedgerows (Jongman & Leemans, 1982). In Provence (France), the abandonment of silvo-pastoral practices have led to a simplification of the landscape structure which is nevertheless very important for many species such as chiropterans (Hubert, 1991). Add to this the disappearance of agricultural areas in the urban fringe that has given way to other urban functions such as business park (Lucas and van Oort, 1993). This urban expansion has led to the creation of impermeable soils, barriers, and roads. The same holds true outside urban areas. The development of transportation infrastructure has also increased barriers for species in the landscape. This reduction of species' habitats, favoring intensive agriculture and forestry, along with the presence of impermeable barriers, is known as landscape fragmentation, as described by Forman. (1995).

1.4. Effect of landscape changes on species populations dynamics

1.4.1. First theories and concepts

To fully understand how landscape fragmentation affects species populations, we need to develop some conceptual frameworks used in ecology. The first concept is known as the habitat patch size – species richness relation. It has been repeatedly observed by naturalists in islands or patch of habitat that more the area sampled increases, more species are found in it (Gotelli, 1995; Rosenzweig, 1995; Wilcox, 1980). The best-known example is the one of West Indies Island where multiple ecologists have studied this relation for numerous taxa (Wilcox, 1980). In all cases, they described a positive relationship between island area and species richness. To explain this observation, three important theories have been expressed. The first explanation to this phenomenon called passive sampling hypothesis says that if you increase the sampled area, you are more likely to observed individuals (Arrhenius, 1921; Connor & McCoy, 1979; Williamson, M., 1981). If you increase your chances to see individuals, you therefore increase your chances to see new species. The habitat heterogeneity hypothesis suggests that bigger areas are more likely to contain a wider range of habitat types (Boecklen, 1986; MacArthur and Wilson, 2001; Rosenzweig, 1995; Williamson, M., 1981). Thus, more habitat type will host more species and increase species richness.

The theory of island biogeography completes previous concept an states that species richness increases on larger islands due to a balance between the colonization and extinction rates of the island's populations. (MacArthur and Wilson, 2001). This hypothesis originated from studies of ant and bird populations on tropical islands, where an increase in species richness corresponded to larger island sizes. Ecologists explain this phenomenon by proposing a balance between the rates of extinction and colonization experienced by species on the island. The colonization rate is primarily influenced by the distance of the island from the mainland, as species tend to disperse more easily to nearby islands. On the other hand, the extinction rate is influenced by the island's size, with smaller islands having a lower capacity to support large populations and thus being more vulnerable to extinction events. The equilibrium population size on each island is reached when the extinction rate intersects with the colonization rate (Figure 1.4). Based on this theory, larger islands close to the mainland are more likely to have higher species richness, while smaller remote islands are more likely to have lower species richness. Although initially observed on oceanic islands, this theory has been applied to fragmented terrestrial ecosystems with some modifications.

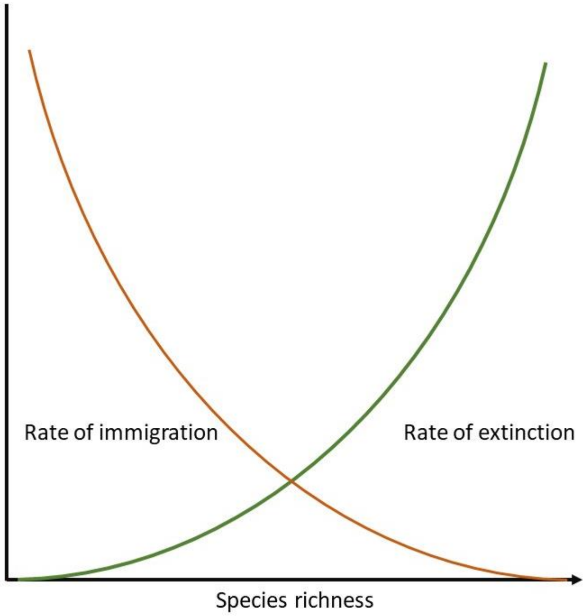

Figure 1.4: Persistence of specie populations depending on extinction rates and colonization rates. Figure inspired from Collinge (2009).

The first modification comes from the rescue effect theory (Brown and Kodric-Brown, 1977). The classical theory of island biogeography explains that the rate of colonization within islands is only influenced by the distance between the islands and the mainland. Although, these islands may be particularly close to the mainland as it is often the case with terrestrial ecosystems between large patches of habitat that function as springs and smaller patches undergoing immigration. In this case, the migration flow is so great that it may be greater than the extinction rate. This high rate of colonization therefore makes it possible to come to the rescue of remote populations before they reach a critical threshold of extinction. In this particular case, the extinction rate is no longer influenced only by the size of the islands but also by the distance between the islands, also affecting the species richness pattern. The appropriation of these theories on terrestrial ecosystems quickly led to the emergence of the concept of corridors (Diamond, 1975). These linear zones of vegetation/habitat connecting habitat patches to each other would reduce the distance between patches and improve the rates of immigration leading to a rescue effect to counterbalance extinction rates and thus increase species richness within fragmented landscapes. Small remote populations connected to bigger population would therefore be less vulnerable to extinction. This solution was therefore very quickly proposed for conservation purposes (A. F. Bennett, 1990; Saunders & Hobbs, 1991; Simberloff & Cox, 1987). However, when applied to terrestrial habitats surrounded by a landscape of the same nature, it is interesting to also take into account the effect that the landscape matrix can have on species populations. In this case, species richness within habitat patches is no longer explained solely by colonization and extinction dynamics but also by other components of the landscape (R. T. Forman, 1995; J. A. Hilty et al., 2006; Murphy & Lovett-Doust, 2004; Wiens, 1996). Certain landscape features can indeed have a positive effect on species richness such as landscape heterogeneity, habitat diversity and the size of patch core areas (R. T. Forman, 1995).

1.4.2. Metapopulation theory

The island biogeography theory and its modification made prediction of how isolation and patch size affects species richness of the local population. However, landscape level usually hosts multiple populations of the same species in interaction to each other. Levins (1969) conceive the metapopulation theory that explains how local population can undergo local extinction and colonization while the metapopulation persists if rates of extinction are balanced by colonization. The way the different populations are structured within the fragmented landscape will have an impact on the observed meta-population dynamics. For the same landscape composed of the same isolated habitat patches, it is possible that populations differ functionally. Different types of metapopulation have been studied in theory and practice (Figure 1.5). The classical representation of the metapopulation theory defines that even if patches can differ in size, quality and isolation they still have the same probability of extinction and colonization. Furthermore, each of these patches undergo fully independent dynamics. A possible variation of this theory is to state that the probability of extinction is not the same within patches. Patches with larger populations are less susceptible to extinction, while patches with smaller populations may experience local extinctions, but still persisting indefinitely. These mainland-island metapopulations (Harrison et al., 1988) echo the concept from biogeographic island theory, except that the designation as mainland or island depends on habitat quality and not necessarily on patch size. Another possible configuration of metapopulations is the patchy population, which is not a metapopulation per se but rather a single, very large population that occupies different patch habitats. This is the case for populations of species that must distribute themselves in different patches to meet their food needs. Finally, a fourth variation of the metapopulation theory is that of the "non-equilibrium" metapopulation. It appears when the habitat patches are so isolated from each other that colonization phenomena are non-existent. The small populations that die out are never replaced. Finally, it is important to note that different configurations can exist in the same landscape (Harrison, 1991; Harrison and Taylor, 1997). Conservation biologists must clearly identify the different variations of metapopulation theory because the solutions needed depend on the specific configuration being dealt with. A mainland-island configuration requires a high degree of protection on the patch hosting the mainland population. But the protection effort must be distributed in a balanced way in the case of a classical configuration where all the patches are equally important to maintain the metapopulation. This metapopulation theory has long been applied by the scientific community to study population dynamics in fragmented landscapes. Researchers have identified that failed colonization leading to local extinctions were due to patches of habitats isolated from each other. It became clear that creating corridors, stepping stones or managing the landscape matrix to make it more permeable to movement could reduce the impacts of human-induced fragmentation (Fahrig and Merriam, 1985; Hansson, 1991; Harrison, 1991).

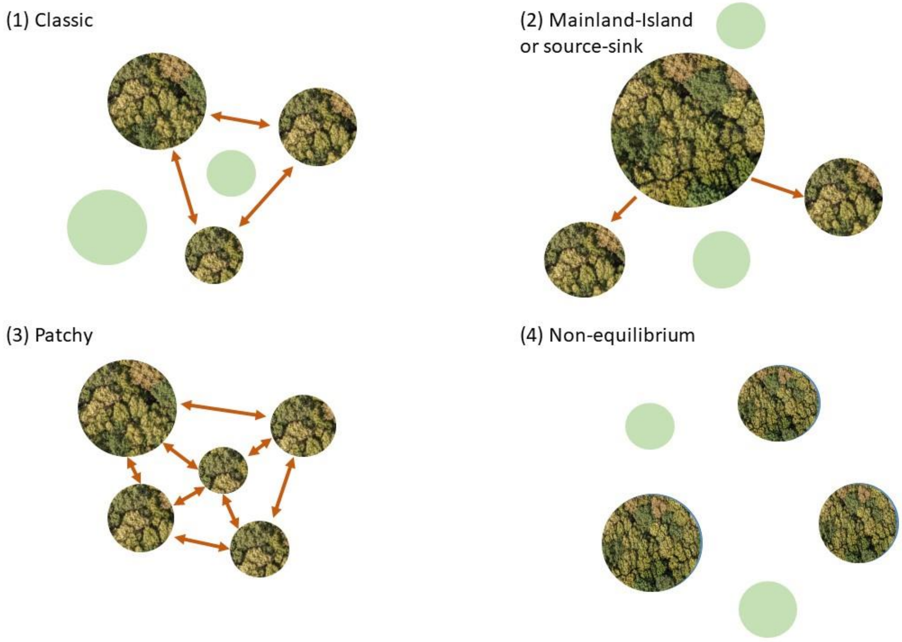

Figure 1.5: Different possible states of metapopulation according to landscape situations. A classical situation (1). Mainland-island metapopulation (2). Patchy population (3). Non-equilibrium metapopulation (4).

1.5. Effects of fragmentation on habitat patches

1.5.1. Habitat loss and degradation

The different theories presented above emphasize the importance of immigration and extinction processes on population dynamics. Obviously both processes are affected by habitat loss and fragmentation. Habitat destruction and degradation is indeed a major element impacting the survival of local populations. The need for habitat is vital for species that require an environment that meets their needs for food and reproduction (Fahrig, L., 1999; C. D. Thomas et al., 2004). It is therefore logical that the very first impact of landscape changes on species is obviously the disappearance of this vital habitat (Fahrig, 2003). However, it is important to specify that each species has specific habitat needs (Morrison et al., 2012). The habitat of one species is not necessarily a favorable habitat for another. The loss of vegetation is therefore not a universal criterion for measuring the loss of species habitat (Armesto et al., 1998; Braithwaite et al., 1993). Indeed, some species need forest environments, others live in open environments while others live at the edge of two contrasting environments (L. Brooker, 2002; M. Brooker & Brooker, 2001). This is why the notion of favorable habitat is essential in conservation biology to correctly identify the habitat areas of each species. However, the destruction of a habitat patch does not necessarily mean the death of the population. It is also necessary to consider the spatio-temporal processes that these habitats undergo. The presence of a part of these habitats can only exist by the destruction of another such as the forest fires maintaining in the past certain open environments like the savanna today (Agee, 1996; Bradstock et al., 2002). Ecosystems are in constant evolution, and a return to first successions of vegetation community is sometimes essential for certain species. At the extreme of the temporal scale, some species are sometimes totally dependent on temporary habitats that remain only part of the year. This is the case for example for the Natterjack Toad which needs temporary ponds in which predators are absent in order to complete their short reproduction cycle. Its historical habitat was once the river flood plains, which after flooding left a network of small temporary ponds that dried up over time (B. Banks & Beebee, 1988; Denton & Beebee, 1994). Today, the rivers being mostly canalized, the species which is now protected has found refuge in the quarries in activity where the extraction activity creates temporary ponds (Sanuy et al., 2000; Schlüpmann, 1995).

In contrast to habitat loss, habitat degradation is also a major factor in the decline of species populations, but is much less visible at first glance. In addition, habitat degradation is more likely to occur when human activities are carried out, resulting in a long decline in habitat quality that will lead to its disappearance (Ambuel & Temple, 1983; New, 2000; Saunders et al., 2003). Habitat degradation is therefore a slower and more pernicious phenomenon that can have devastating long-term effects if not identified early enough. Habitat degradation has been widely studied around the world, and two main factors have been identified to maintain an animal population within its habitat. These two factors are food and shelter and both can be degraded by human activity (Elton, 2001; Morrison et al., 2012). Modern forestry tends to cut down old trees which unfortunately have cavities that are a refuge and nesting place for many species that reduces presences of proper shelters (Saunders et al., 2003; Saunders and Ingram, 1987). Intensive agricultural practices using pesticides kill prey and therefore the food source of many insectivores. Finally, the main problem with habitat degradation is that it is not easily detectable. The habitat has not been totally lost, so the species remains present. But for how long? It is therefore possible that an anthropogenic factor is slowly driving a species to extinction and that it is detected once the dynamics cannot be reversed (D. B. Lindenmayer & Fischer, 2013). This is the case for species with very slow reproductive cycles on which the effects of degradation are not easily measurable and where it is already too late to do anything (Forshaw, 2002). This time lag between habitat degradation and its effect on the species population is what is more commonly called the extinction debt (McCarthy et al., 1997; Tilman et al., 1994).

1.5.2. Characteristics of habitat fragments

Habitat size

As noted above, much of the early work on habitat size (island and terrestrial) and fragmentation focused primarily on the relationship between habitat fragments size and species richness. Research has shown that the probability of extinction increases with decreasing fragments size in multiple species taxa (Blake and Karr, 1987; Cane et al., 2006; Crooks et al., 2001; Cutler, 1991; Lindenmayer et al., 2000) and herbaceous plants (Guirado et al., 2006). This widely demonstrated positive correlation between habitat size, and species richness has long served as a basis for guiding nature conservation initiatives. To understand the parameters explaining the species-area pattern, many authors have studied the response of individuals to the decrease in fragments size.

It turns out that some species are more tolerant of reduced habitat size. This could be explained by particular life history traits (Deng and Zheng, 2004; Ewers and Didham, 2006). Indeed, the ability to disperse is an important trait. Some species with a low dispersal ability will be more sensitive to habitat reduction because they will not be able to move enough to find a more favorable habitat (Hokit et al., 1999). This sensitivity to habitat loss could also be explained by landscape characteristics. A large meta-analysis was conducted on 25 studies involving 134 bird, mammal and insect species (Fahrig, 1998). This study demonstrated the link between habitat loss on species populations, landscape factors and life history attributes such as species preferred habitats, migratory or sedentary nature, taxonomic group, trophic level, geographic position, and percentage of suitable habitat remaining in the landscape.

For example, edge species are positively impacted by the reduction in patch size, while core species suffer from it. On the contrary, when the size of the patch increases, the relationships are reversed for these species. The more generalist a species is, the less sensitive it seems to be to the reduction of habitat fragments. Resident species are more sensitive than migrant species. Finally, species from Europe and Africa show a weaker response than those from North and South America. This last point may seem surprising but would be explained by a longer presence of man and his activity in Europe and Africa (Bender et al., 1998). All these factors influence the survival of species populations because they directly influence the basic processes of population maintenance which are births, deaths, immigration and emigration. It has indeed been shown that some species see their birth rate decrease when their habitat is reduced (Porneluzi et al., 1993). In the same way, mortality rates may also increase in small habitats where resources are scarce (Villafuerte et al., 1997).

Isolation

Although the relationship between habitat size and species richness now seems obvious from the studies presented above, the effect of patch isolation on species populations is less clear and not always consistent. Some studies have found that patch isolation had less effect on population densities or species richness than patch size or even no effect at all (Bruun, 2000; Fernández-Juricic, 2004; Krauss et al., 2004). Other studies have shown an equal or greater impact of isolation than patch size (Deng and Zheng, 2004; Francesco Ficetola and De Bernardi, 2004; Parris, 2006; Piessens et al., 2004). These conflicting results are principally due to the difficulty of measuring patch isolation as opposed to patch size.

Correctly measuring the isolation of fragments therefore allows us to identify important relationships between this isolation and species richness in the landscape. Piessens et al. (2004) has made the experience by studying plant populations in a network of residual heathland fragments in Belgium. It turned out that species richness was strongly influenced by patch size but even more so by different measures of patch isolation. These results also clearly showed a spatial and temporal rescue effect. Species that dispersed relatively easily were able to maintain viable populations within nearby habitat patches through emigration and immigration, thus preventing population extinction. In addition, species with low life expectancy seeds were more sensitive to isolation than species producing a high life expectancy seed bank. This last point underlines the existence of a temporal rescue effect. In general, it appears that the species most sensitive to isolation are the most sedentary species (such as vascular plants) and those that require different habitats to complete their life cycle (such as amphibians).

Edge effect

Changes in the landscape due to human activity also have an effect on the shape of habitat fragments in the landscape (Sharpe et al., 1981). More complex shapes generally have a larger perimeter to area ratio (Figure 1.6). This greatly increases the area of the interface between the fragment and the landscape matrix. These fragments are therefore more prone to edge effects (Laurance, 2000; Siitonen et al., 2005). Edges between natural ecosystems often host significant and sometimes unique biodiversity (Whitham et al., 1991). However, an abrupt edge between a landscape fragment and an area dedicated to intensive human activity tends to increase negative edge effect (R. T. Forman, 1995; Sargent et al., 1998). This edge effect can be defined in two categories (Harper et al., 2005). The abiotic effects are mainly related to the microclimatic modifications that will be measured within the edge and in the patch. Biotic effects refer to changes in ecological processes, community modifications and species interactions.

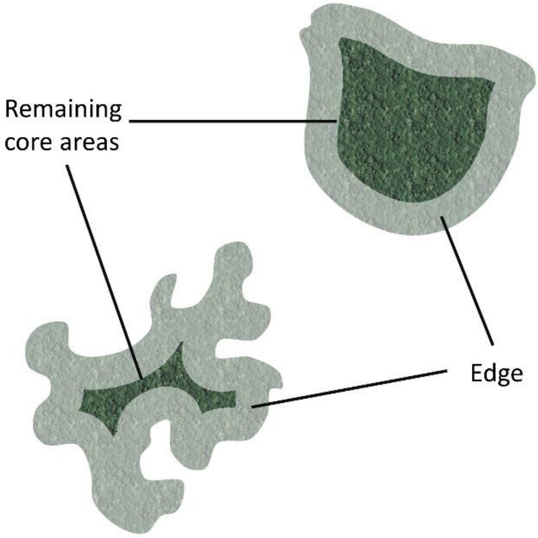

Figure 1.6: Visual representation of the effect of fragment shape on the edge area. For a same edge of 20m inside fragments of the same area, the more complex the fragment shape is the more the edge is important.

In general, the more disturbed the matrix is, the more negative the edge effect will be on the communities within the fragments(Chen et al., 1992). For instance, clearcutting at the edge of the forest will enhance reproduction and growth of mature forest trees along the edge (Chen, 1991). However, these steep edges will see their microclimatic conditions change to the benefit of invasive grasses or exotic invasive species disrupting the plant communities (Honnay et al., 2002; Yates et al., 2004).

Microclimatic conditions also strongly influence animal populations to such a point that some species are considered as "heart of the forest" species (Margules et al., 1994; Marini et al., 1995). This is the case for many birds that do not find a sufficient amount of food in the edges (Huhta et al., 1999; Zanette and Jenkins, 2000). In addition to access to food, many species also avoid edges due to the presence of predators which will then negatively influence their reproduction rate (Chalfoun et al., 2002; Marini et al., 1995). Different predators have been studied in the context of edges. These include corvids, small mammals and mustelids as well as foxes and badgers (Andrén and Angelstam, 1988; Huhta et al., 2004; Small and Hunter, 1988; Tellería and Santos, 1992). The edge is therefore a habitat suitable to biodiversity if it is natural and soft and if it fits properly in the landscape. However, its management must be correctly applied to favor the development of rare species living there while keeping the balance of communities living in the heart of the fragments, in the edge and in the matrix (Baur and Jaggi, 1999; Peterken and Francis, 1999).

1.6. Observed effect of fragmentation on individuals

1.6.1. Change in biology, behavior and species interactions

Changes in the landscape can have significant effects on the behaviour and biology of species. For example, breeding patterns are impacted by habitat size. Studies have shown that bird populations in smaller habitat patches have shorter breeding seasons, produce lighter eggs, and have smaller and fewer broods compared to populations in larger habitat patches (Hinsley et al., 1999; Zanette et al., 2000). These populations also produce offspring with lower growth rates and reduced survival chances (Saunders, 1980). Similar observations have been made for other species groups (Peacock and Smith, 1997).

Changes in species behaviour due to landscape changes also affect species interactions. Reducing habitat patch size can potentially intensify competition between species, although this relationship remains theoretical and understudied (Matthysen et al., 1995). Some studies show no change in feeding behaviour or niche overlap with patch size, while others demonstrate increased aggression and competition. Predation and parasitism are also exacerbated in altered landscapes, with certain predator species thriving in human-altered environments (May and Norton, 1996; Robinson et al., 1995). Positive interactions are endangered due to increased human activity. Many plants are losing their pollinators and many scientists tend to say that many ecosystems are facing a pollinator crisis that may lead to their decline (Kearns et al., 1998). Another relatively well-known mutualistic relationship between plants and animals is seed dispersal. Many plants are zoochorous, meaning that they depend on animals for dispersal. However, it has been found that these dispersal phenomena tend to decrease in fragmented environments where the remaining fragments are small while the rate of dispersal is higher in large patches (Galetti et al., 2006).

Dispersal of individuals plays a crucial role in species distribution and abundance (Chepko-Sade and Halpin, 1987). Landscape fragmentation greatly affects dispersal processes, limiting the number and distance of dispersal events. This has consequences for the emigration, colonization, and metapopulation dynamics, leading to increased species extinction rates (Banks et al., 2005; Hanski, 1994; Matthysen et al., 1995; Stow and Sunnucks, 2004). Fragmentation also hampers reproductive success by reducing the chances of individuals meeting and forming mating pairs, resulting in inbreeding within small patches and decreasing the survival of subsequent generations (Banks et al., 2005; Madsen et al., 1999).

Landscape fragmentation can even lead to changes in the biological traits of species. For instance, some arthropods have increased in size to cope with more severe drought events in small habitat patches where the edge occupies a significant portion of the patch, affecting microclimate conditions (Weishampel, 1997).

1.6.2. Parasite, Pathogen and Disease Emergence

The increase in disease outbreaks has been attributed to various factors such as climate change, invasive species, and water pollution (Anderson et al., 2004; Derraik and Slaney, 2007; Hrudey and Hrudey, 2007). However, there is growing evidence that changes in the landscape configuration also contribute to the emergence of parasites and pathogens (Ostfeld et al., 2005). The complex relationships between hosts, vectors, and pathogens play a crucial role in disease emergence. Landscape changes, including human activity and habitat loss, make the landscape more complex, impacting the abundance and diversity of hosts and vectors. Decreased spatial connectivity affects the dispersal and transmission rates of hosts, vectors, pathogens, and diseases. Habitat loss and degradation can weaken populations, making them more susceptible to pathogens due to stress and reduced immune response (Ostfeld et al., 2005).

While diseases and pathogens are not the main threats to biodiversity, there have been cases of species extinction caused by pathogen outbreaks. The modification and degradation of landscapes reduce species abundance and richness, leading to an increase in hosts and pathogens. Habitat modification tends to homogenize species communities, resulting in higher pathogen prevalence (Ostfeld and Keesing, 2011). Species-rich communities have a lower risk of pathogen contamination due to a dilution effect, reducing encounters and transmission between hosts, limiting host abundance, and improving recovery through mutualistic relationships (Keesing et al., 2006).

The spatial configuration of the landscape can isolate certain populations, potentially protecting them from specific pathogens. However, poor management decisions, such as protected areas surrounded by human settlements, can lead to contamination of isolated populations. Domestic animals can act as incubators for pathogens that are dangerous for wildlife and humans, highlighting the need for proper management (Vial et al., 2006; Woodroffe and Frank, 2005).

Intensive human activities and habitat degradation directly contribute to the development of certain diseases. For example, fertilization of sugarcane in Belize has been linked to increased risk of exposure to malaria due to eutrophication and favorable habitat for mosquito vectors (Rejmánková et al., 2006, 1998, 1996). Eutrophication of water bodies from intensive livestock activities has also been associated with severe amphibian limb malformations (Johnson et al., 2002).

Models using epidemiological data have helped understand the spatio-temporal patterns of epidemics. They have shown that less frequent movements like dispersal and migration have little impact on disease transmission compared to frequent movements within a species' home range. Overall, the positive impact of corridors on species populations outweighs the losses due to disease and pathogen dispersal (Hess, 1996).

2. Landscape Connectivity

2.1. Definitions

The concept of connectivity is universally recognized as a critical aspect in the study of landscape changes (Taylor et al., 1993). While there are multiple approaches to characterizing connectivity, it is important to differentiate between its functional and structural components. Functional connectivity refers to the movement of genes, gametes, propagules, or individuals across the landscape (Rudnick et al., 2012; Weeks, 2017). It therefore refers to realized connectivity. On the other hand, structural connectivity assesses landscape permeability based on the arrangement of vegetation features and patches, which can potentially influence species movement (Hilty et al., 2019). Until know, by referring to landscape component and characteristics, we focused on structural connectivity which depict a potential.

However, the term "connectivity" and its association with other terms encompass various themes that entail distinct implications (Bunnell, 1999). First, we have habitat connectivity, which is defined as the connectivity between different patches of favourable habitat for a species. It is therefore the opposite of habitat isolation. Second, we have landscape connectivity, which is an entirely anthropocentric view and concerns the connectivity of different vegetation or land-cover types across the landscape. Finally, we have ecological connectivity, which concerns the connectivity of ecological processes across different scales of study. These different types of connectivity are related to each other. Reducing habitat connectivity for a species that performs a primary ecological function such as seed dispersal will also reduce ecological connectivity (Galindo-González et al., 2000). This reduction in connectivity will have serious implications for a range of plant species that depend on animals for dispersal (Cascante et al., 2002). However, it is important to note that not all these terms are synonymous and opposite effects can occur. One can improve landscape connectivity and improve habitat connectivity for some species but not for others. In other words, landscape connectivity can be improved from a human perspective, but this does not correspond to an increase in habitat connectivity for certain species (Lindenmayer and Fischer, 2013).

2.2. Negative impacts on landscape connectivity

Landscape connectivity is one of the main elements for studying vegetation patterns in the landscape along with other attributes such as composition and configuration. Like these two other attributes, landscape connectivity can be assessed using many indices (Gustafson, 1998; Moilanen and Nieminen, 2002). Most of these indices are based on the same principles of distances between patches, the number of physical connections between them and sometimes the size and/or shape of patches (Schtickzelle and Baguette, 2003).

It can therefore be assumed that landscapes that still have connections between isolated patches have better landscape connectivity and are therefore more likely to maintain viable populations of various species (Brown and Kodric-Brown, 1977; Haddad and Baum, 1999). In contrast, a decrease in landscape connectivity will have a multitude of negative effects on these populations. This has been illustrated for many taxa. This is particularly true for forest birds that are unable to cross open areas (Bierregaard et al., 1992; van Dorp and Opdam, 1987). Similarly, species located in patches surrounded by an unfavorable matrix are more likely to suffer extinction than populations located in a matrix with better landscape connectivity (Laurance, 1991; Viveiros de Castro and Fernandez, 2004). A particularly well-known case of decreased landscape connectivity is the presence of roads intersecting habitat patches. These dissections in the landscape have the effect of profoundly altering the landscape patterns and thus greatly reduce habitat connectivity for many species (Spellerberg, 1998). The impact of roads on habitat connectivity has been demonstrated for many different taxa such as invertebrates (Haskell, 2000), small and large mammals (Burnett, 1992; Epps et al., 2005; Forman and Deblinger, 2000). Even small roads can have a significant impact on some species (Bright, 1998). In addition, beyond the impact on connectivity, roads are sources of long-term mortality due to vehicle collisions (Bennett, 1991; Trombulak and Frissell, 2000). This is particularly important for roads that cut across important migration routes, such as the seasonal migration of amphibians during the mating season, which may have to cross roads to reach their breeding grounds (Hels and Buchwald, 2001).

The decrease in landscape connectivity is not necessarily the result of a change in land-cover. The different uses that humans assign to certain areas can have a direct effect on landscape connectivity. For example, intensive agricultural plains can alter the sedimentation processes of amphibian habitats, thus decreasing landscape connectivity (Gray et al., 2004). A significant decrease in landscape connectivity can also have a strong cascading effect on ecological connectivity. Food webs (Holyoak, 2000), organic matter decomposition processes (Klein 1989), seed dispersal (Cordeiro and Howe, 2003), and pollination (Paton, 2000) can all be severely altered.

2.3. Fostering landscape connectivity

On the other hand, some landscape features are favorable to landscape connectivity. These are corridors, stepping stones and a "soft" matrix (Figure 1.7). Corridors are physical links between patches of native vegetation (Bennett, 1998). These corridors can improve landscape connectivity for some species but not all (Beier and Noss, 1998; Hewittson, 1997; Thomas, 1990). Numerous studies have been conducted to understand the effect of corridors on species populations and it has been found that population density of some species are significantly higher in patches connected by corridors than in others (Haddad and Baum, 1999). In general, many benefits are attributed to corridors. They facilitate the movement of species by providing suboptimal habitat between suitable habitat patches (Palomares et al., 2000). They can also serve as habitat and host populations within them (Bennett, 1998; Mönkkönen and Mutanen, 2003). They improve dispersal success (Kirchner et al., 2003; MacMahon and Holl, 2001) and can also decrease mortality during dispersal (Beier, 1993). They can limit local extinctions by promoting recolonization (Burbrink et al., 1998; Fahrig and Merriam, 1985). They facilitate gene flows between populations (Aars and Ims, 1999) and thus reduce the risks of genetic drift and inbreeding (Newman and Tallmon, 2001). Finally, they contribute to increasing species richness within patches and on a landscape scale (Gilbert et al., 1998; Harris and Scheck, 1991).

In general, corridors are most useful for species that cannot use the landscape matrix for movement and for species that can only move within their optimal habitat (Berggren et al., 2002; Martin and Karr, 1986). The corridor can also act as a directional barrier by intercepting the movement of species and redirecting them away from the matrix (Levey et al., 2005). This is a phenomenon that can be used, for example, to prevent species from crossing a road and to guide them toward a wildlife crossing. Stepping stones represent a network of small patches of native vegetation scattered across the landscape that provides improved habitat connectivity for a number of species (Dramstad et al., 1996; R. T. Forman, 1995). Finally, the "soft" matrix is a matrix whose vegetation cover and structure resembles that of the patches. This improves habitat connectivity for species for which vegetation cover is essential to their movement (Lindenmayer and Franklin, 2002; Metzger, 2001; Rosenberg et al., 1997).

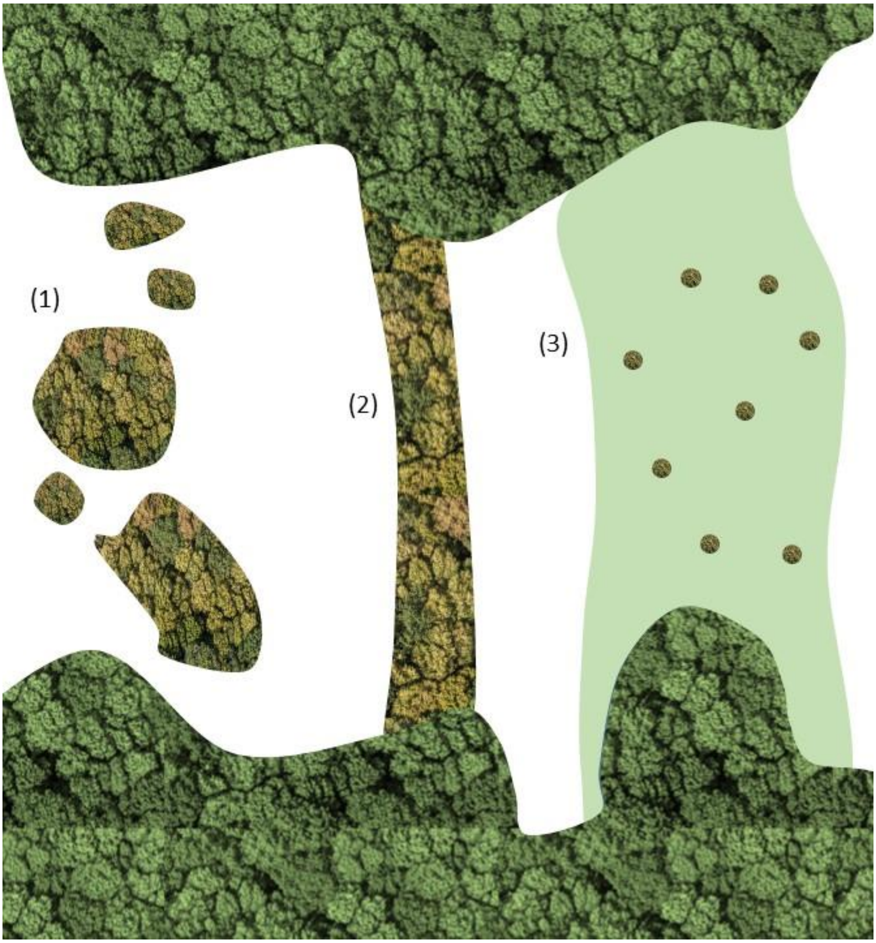

Figure 1.7: The three main types of landscape feature improving landscape connectivity: corridor (1), stepping stones (2), soft matrix (3).

3. Managing Landscape to Mitigate Landscapes Changes and Fragmentation

3.1. Protect and restore habitat patches

As discussed above, habitat patch size is one of the primary factors influencing population density and species richness within the landscape. Large patch sizes and a variety of habitat types are therefore important in reducing the negative effects of landscape change on species and communities (Lindenmayer and Fischer, 2013; MacArthur, 1964; Preston, 1962). The priority for terrestrial ecosystem conservation is to protect as much of the existing habitat as possible (Margules and Pressey, 2000a). This helps to maintain native vegetation, which limits the possible loss of populations of species that depend on them (Fahrig, 2003). This allows to keep a variety of habitat useful for generalist species while keeping habitats of specialist species. Finally, protecting a maximum of surface area will make it possible to maintain large population sizes that will be less sensitive to negative external disturbances (Lindenmayer and Franklin, 2002; Noss and Cooperrider, 1994). It is also important to protect the existing vegetation cover because some vegetation community require sophisticated restoration programs with high economic costs (Margules and Pressey, 2000b). Numerous studies have also shown the importance of maintaining a network of nature reserves at the landscape scale in order to provide sufficient habitat for species (Noss and Harris, 1986; Soulé and Terborgh, 1999).

In addition to protection, some of the more heavily modified landscapes require restoration efforts so that the patches can regain their former structural, ecological and functional characteristics (Franklin et al., 1981). Two aspects of restoration should be considered: the improvement of conditions within an existing patch or the creation of a new patch with native vegetation. In many cases, changing the management of the ecosystem will allow a natural return to a structural complexity that approximates the original habitats (Lindenmayer et al., 2003). For example, in grazed grassland ecosystems, a decrease in livestock density allows for the redevelopment of vegetation dynamics that approximates the original ecosystems present before intensive human activities (Jansen and Robertson, 2001; Spooner et al., 2002). In other cases, active restoration is necessary because natural regeneration has not occurred or because of the absence of a viable seed bank in the soil, or because species important to the maintenance of ecological processes have disappeared (Covington, 2003; Linder and Östlund, 1998). Restoration of important structural elements for biodiversity should also be a priority to rapidly improve the biological value of a habitat patch (Tews et al., 2004). Examples of such structures are temporary water bodies or standing dead trees with cavities. In addition to the improvement of existing patches through ecological restoration, it is also worthwhile to prioritize the enlargement of existing natural areas in order to increase their surface and their potential to host biodiversity (McCarthy and Lindenmayer, 1999). At the extreme, a complete restoration of the vegetation cover resulting in the creation of a new habitat patch is necessary following a destructive human activity such as mining or major land clearing (Martin et al., 2004). This type of restoration is much more complex as it depends on many factors such as soil conditions, target species and communities, and potential competition with invasive plants (Bennett et al., 2000).

3.2. Managing matrix

As explained above, the matrix plays an important role in patch-corridor-matrix systems because it represents the major part of the landscape and has a strong influence on ecological processes (R. T. Forman, 1995). In general, a "soft matrix" is characterized by a vegetation structure similar to that of patches which will produce more benefits for native species (Lindenmayer and Fischer, 2013). These include increased habitat availability, improved landscape connectivity and reduced edge effects. Studies have shown that a landscape matrix with a similar vegetation structure to that of native patches supports a greater number of native species in both agricultural and forested landscapes (Dunn, 2004; Thompson et al., 2003). Vertical structure has an enormous influence on landscape connectivity and management measures to maintain these vertical structures can facilitate the dispersal of animals and plants (Hokit et al., 1999; Wiens, 1997). Examples of this include retaining trees during forest harvesting or when the vegetation cover around patches of native vegetation is altered (Forest Ecosystem Management Assessment Team, 1993). Finally, as demonstrated above, the negative impact of edge effects is greater when the transition between the patch and the matrix is abrupt. Maintaining a patch-like vegetation structure around the patches therefore reduces the importance of the edge effect (Rodríguez et al., 2001; Tubelis et al., 2004). Management measures for the spatial arrangement of matrix elements can also be considered to minimize the effects of the matrix on species habitats. For example, in managed forests, the spatial arrangement of clearcuts can be optimized to reduce the negative impact of clearcuts through matrix arrangement. Indeed, grouping clearcuts in large blocks rather than scattering them across the landscape can limit the magnitude and extent of negative edge effects (Yates et al., 2004).

A complementary strategy to reduce negative edge effect is to maintain or restore buffer zones around ecologically sensitive areas. Typically, buffers are intended to limit the negative impacts of disturbance regimes on an ecosystem or to maximize species richness in a protected area (Baker, 1992; Spackman and Hughes, 1995). However, it should be noted that each buffer can be different depending on the disturbance regime it is trying to counter. To limit the effects of the wind, the buffer must be several hundred wide (Harris, 2013; Saunders et al., 1991). The width of the buffer can also change significantly depending on the species being targeted (Darveau et al., 1995; Kilgo et al., 1998).

3.3. Protect and restore ecological corridors

In addition to properly managing the landscape matrix, providing corridors or stepping stones that link habitat patches together are effective ways to improve landscape connectivity. However, corridors for some species can also have negative impacts on other species. Managing wildlife corridors is therefore complex and requires asking the right questions. For example, it is important to identify which species move without the need of corridors and which do (Berggren et al., 2002; Mabry and Barrett, 2002). Does the corridor serve only as a travel area or will it serve as a habitat area? What types of movement are targeted by the corridors (commuting, dispersal or migration)? How might the corridor be influenced by surrounding human activities (Rosenberg et al., 1997)? Several studies have shown, for example, that specialist species, those living in habitat that are highly sensitive to edge effects, or taxa that disperse poorly, may not be able to use all types of corridors. In contrast, generalist species that disperse very easily and are not very sensitive to edge effects do not need corridors to survive (Lindenmayer D. B. et al., 1993). Similarly, it is likely that if the alteration of the landscape is too great, a corridor within that landscape will lose its functionality (Tilman, 1987). In much the same way that corridors are managed as habitat patches, it is always best to first conserve existing landscape connectivity before thinking about restoring it to a greater or lesser extent. Stepping stones can act as a complement to wildlife corridors for more mobile taxa (such as bats and butterflies) that can disperse more easily across the matrix but are not able to move long distances to isolated patches (Bennett, 1998; Law et al., 1999; Lumsden et al., 1994). Corridors and stepping stones can also help provide additional habitat for species that are not sensitive to patch size. Even small areas of native vegetation are therefore useful. In areas of intensive human activity, small patches of habitat are all that are left. They require special protection and management because of their relictual nature (Saunders, 1987; Schwartz and van Mantgem, 1997).

3.4. Improve landscape heterogeneity

Finally, heterogeneous landscapes due to human activity tend to support more native species than homogeneous landscapes of human origin. Ecosystems are indeed naturally heterogeneous (Whelan et al., 2002). Natural disturbance regimes produce a mosaic of landscape elements corresponding to different stages of vegetation succession depending on the time of the disturbance. Species generally live and complete their life cycles under different environmental conditions. Providing a heterogeneous landscape that is close to a mixture of different natural environmental conditions is therefore beneficial to the native species assemblage associated with the landscape. To be more effective, landscape heterogeneity must be applied across different gradients of environmental conditions present within the landscape while providing natural disturbances of varying types and intensity

(Fischer et al., 2005). This landscape heterogeneity is, for example, essential in European agricultural landscapes to maintain the few species that have survived in these intensive landscapes (Benton et al., 2003; Tscharntke et al., 2005).

3.5. Conclusion

To summarize, concepts and theory in landscape ecology identify five major principles that should be incorporated into nature conservation to reduce the decline of species sensitive to landscape fragmentation. These are:

- maintain or increase the size of hosting biodiversity patches to increase species richness and reduce the risk of extinction in the long term,
- adjust the structural characteristics of the matrix and its composition to reduce its negative impact on patches and landscape connectivity,
- reduce the negative effect of edges using buffers,
- improve landscape connectivity using linking elements such as wildlife corridors or stepping stones,
- and finally maintain or improve landscape heterogeneity.

The way nature conservation integrates those principles are presented in the next section.

3.6. Conservation controversies

3.6.1. SLOSS

It has been shown that as the size of a patch increases, so does its species richness. It is therefore natural to assume that a large reserve will support more species than a set of small reserves whose surface area is the same as the large one. However, this assumption may only be true for homogeneous patches with the same type of vegetation cover (Quinn and Harrison, 1988; Wilson and Willis, 1975). Indeed, we know that if the set of small patches presents the heterogeneity of vegetation type and thus different species compositions, the cumulative species richness will be higher than a single large homogeneous patch (Diamond, 1975). Indeed, heterogeneity plays an important role on species richness patterns as it has been demonstrated for different ecosystems such as grasslands and forests (Simberloff and Gotelli, 1984). In both cases, it has been shown that for equal areas, clusters of small reserves hosted more species than in the large reserve. This has been demonstrated several times with different taxa such as vascular plants (Virolainen et al., 1998), grassland butterflies (Tscharntke et al., 2002), day-active butterflies and grasshoppers (Peintinger et al., 2003) and pond-dwelling animals (Oertli et al., 2002). However, the basis for assessing whether a large patch is preferable to a set of small patches depends strongly on what is being measured to make the comparison. Some species populations are unable to persist in patches that are too small because of their size, home range demand, or dispersal patterns. A set of small reserves can indeed host a greater species richness but a large patch would reduce the probability of extinction of a population, especially for mammals (McCarthy and Lindenmayer, 1999; Newmark, 1986; Picton, 1979). A study on American national parks has indeed shown that the largest parks have maintained a greater number of species over time than have smaller parks (Newmark, 1987). In conclusion, it can be said that the option chosen in the SLOSS (Single Large Or Several Small) debate will depend primarily on conservation objectives. Whether to maximize species richness or to reduce the risk of extinction will differ. In the best case scenario, a mix of large and small reserves is the best solution (Wiersma and Urban, 2005). However, it is rare to be able to build a management strategy from scratch, and it is therefore relevant to assess which strategy to choose depending on the conservation issues we face.

3.6.2. Land-sharing or lands-sparing?

Another up-to-date debate in land-management for nature conservation concerns the land-sharing versus land-sparing strategies. Well debated among ecologists, this theory is based on the actual land scarcity and proposes two land management options to protect and increase biodiversity while still keeping sufficient productive areas (Fischer et al., 2014). The land-sharing option offers a generalized wildlife-friendly human activity where production lands and natural areas are overlaying while land-sparing split strictly those two allowing a high-yield nature-proof agriculture while biodiversity is restrained in protected areas (Green et al., 2005).

In the past, lots of scientists used a trade-off analysis to find the balance between farming and conservation. The most used framework is the one proposed by Green et al. (2005) and is globally based on the production goals of the country and the analysis of the relation between the species sensitivity to a gradient of agricultural yields. For instance, a growing number of studies are indicating that a significant number of species are even absent from low-intensity farmland supposing that the best strategy is the land-sparing. This, especially in developing countries where a lot of species fleeing agricultural areas are still present and that increasing yields could protect remaining intact habitat. In the case of countries with long histories in agriculture, it’s not so simple and the land-sparing strategy relies on the possibility to increase the yield in suitable area and restore less productive agricultural lands into natural areas (Green et al., 2005; Jones-Walters, 2007). If we focus on plant diversity, the choice is more shared and it seems that land-sparing could be the best strategy in crop-dominated landscape and that land-sharing is the best choice when the landscape becomes more complex (Egan and Mortensen, 2012).

But this framework isn’t perfect despite its strength, indeed it is strongly focused on food production and some scholar would welcome some improvement to it. Also the framework doesn’t take into account any socio-cultural aspect (Fischer et al., 2014). Many scientists argue that a big threat for biodiversity is the loss of connection between people and nature leading to a preference for the land-sharing option (Folke et al., 2011; Miller, 2005).

Recently, Kremen (2015) suggest that the debate of choosing between those two management strategies will lead only to undesirable options for nature conservation. She proposes that a "both-and" strategy where natural area patches (land-sparing) are only useful if they are linked together by a wild-friendly matrix (land-sharing). Thus, the real question must not be anymore: "Which strategy is the best in that case?" But rather: "What kind of agricultural practice can promote both biodiversity and yields?"(Kremen, 2015). If we focus on the case of El Salvador, a country with a lot of pressure on nature and almost no forest left, it seems that the only efficient choice is to apply a "both-and" strategy because the only solution to maintain biodiversity is to reconnect the landscape with a wildlife-friendly matrix and protect all of its remaining natural patches (Crespin and García-Villalta, 2014).

3.6.3. Conclusion

The conclusion of those two debates is that no choice must be made and that a mixture of land-sharing, land-sparing, small and large nature reserves can coexist. We must strictly protect existing areas of biodiversity interest through land-sparing either they are small or large and go toward a land-sharing strategy in intensive landscape were reducing landscape fragmentation is needed to reconnect fragmented populations. To implement this statement in landscape management, we must follow a framework proposing a gradient of nature protection degree including progressively sustainable primary production in less sensitive areas.

4. Toward Ecological Networks

4.1. History of ecological network

Historically, the establishment of protected areas was the primary focus for in situ conservation to counter the decline of species populations and natural ecosystems. In response, the area under protection status was increasing steadily worldwide (Figure 1.8). In addition, protected areas are now supported by the increasing designation of OECMs (Other Effective Area-Based Conservation Measure). These other areas dedicated to nature conservation offer long-term sustainable management methods that have a favorable impact on biodiversity without necessarily being subject to a strict protection status (Hilty et al., 2020). Nevertheless, biodiversity decline continues to accelerate at a global scale. Protected areas are not always effective in conserving biodiversity, either because they are poorly located or because of inadequate management (Jones et al., 2018; Venter et al., 2018). Indeed, many protected areas are isolated from each other (Wittemyer et al., 2008). Various advances and theories in landscape ecology have demonstrated the high risk of extinction in isolated ecosystems. Researchers have shown that the protection of species, populations and ecosystems can only be achieved if protected areas are functionally connected (Resasco, 2019; Trombulak and Baldwin, 2010). It is therefore widely accepted that protected areas approach alone cannot address the decline in biodiversity (Hilty et al., 2019) further burying a pure land-sparing strategy.

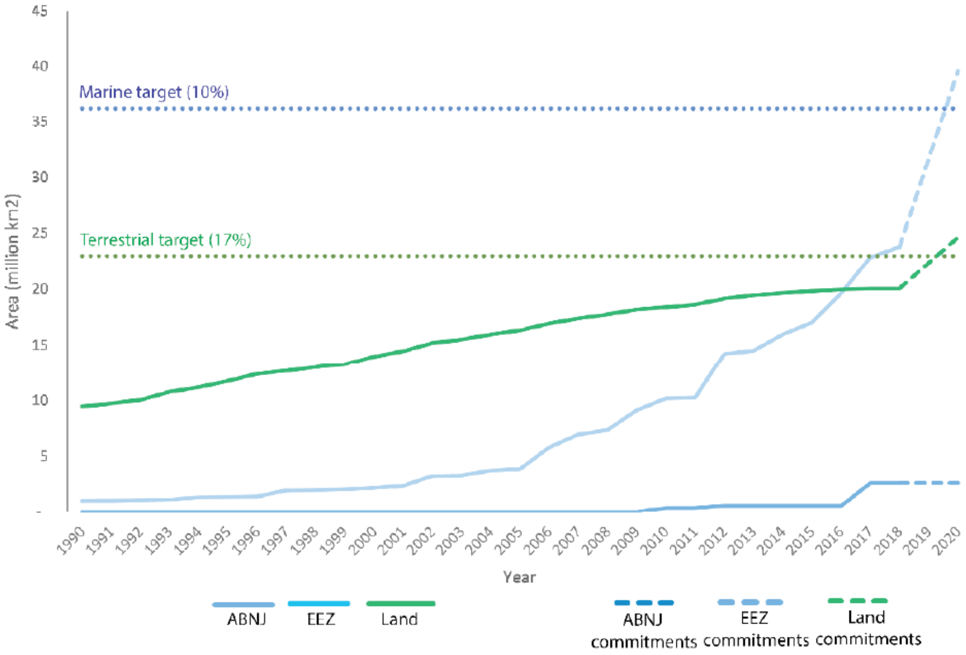

Figure 1.8: Global trends in protected areas coverage on land and in the ocean in the world from 1990 to 2018 extracted from Hilty et al. (2020). Projected growth from 2018 to 2020, according to commitments from countries and territories. ABNJs: Areas Beyond National Jurisdiction (i.e. those more than 200 nautical miles from the coast); EEZs: Exclusive Economic Zones (i.e. marine areas under national jurisdiction that are less than 200 nautical miles from the coast).

The integration of landscape ecology theory into nature conservation and land-use planning has led to the development of the concept of ecological networks. This concept has many definitions but could be defined as a set of homogenous ecosystems linked together through flows of organisms into a spatially coherent way and interacting with the surrounding landscape matrix (Opdam et al., 2006). The IUCN has a more operational definition stating: “A system of core habitats (protected areas, OECMs and other intact natural areas), connected by ecological corridors, which is established, restored as needed and maintained to conserve biological diversity in systems that have been fragmented”(Hilty et al., 2020). The main strategy behind ecological networks is to conserve and re-establish natural corridors to facilitate the spatial conductance of the landscape and the linkage between core areas sheltering species populations. These corridors can take various forms such as linear elements of the landscape or in a more halted way like stepping stones (Jongman et al., 2004). The goal is no longer only to maintain high patrimonial population but focus on a regional level to ensure the future of populations, interesting sites and ecosystems dynamics (Dufrêne, 2005; Melin, 1997).

The potential negative impacts of this kind of strategy were heatedly debated among ecologists and conservationists (Anderson and Jenkins, 2006; Hilty et al., 2019). Negative effects noted included increased predation, invasive species and disease dispersal (Weldon, 2006). However, it turns out that the benefits are far greater than the negative effects identified (Hilty et al., 2019). Ecological networks then became the dominant operational strategy to face biodiversity loss (Jongman et al., 2004).

The last decades of the 20th century saw a strong development of ecological networks in nature conservation with many examples developed by public authorities and institutions in Europe, America and Australia (Bennett and Mulongoy, 2006). In Europe a quasi-global approach has emerged in reaction to the recent development of the Convention on Biological Diversity. This policy was carried out with the help of the creation of different European directives and allowed the development of the NATURA 2000 network and the Pan-European Biological and Landscape Diversity Strategy (Jones-Walters, 2007; Jongman et al., 2011). Numerous scientific studies and national initiatives ranging from the adaptation of their conservation policies to the creation of ecological networks. Today, many ecological networks are the basis of regional and national policies of European countries (Amsallem et al., 2010a; Sordello, 2018; Sordello et al., 2013a).

4.2. Zonation of Networks

The way to conceptualize this strategy can widely differ from a region to another depending of the ecological but also political context (Jongman et al., 2004). The ecological network framework is usually based on a zonation corresponding to different purposes of the landscape units and it appears that the different components of the networks widely differ depending the author (Bennett and Mulongoy, 2006; Bernier and Théau, 2013; Melin, 1997). But a common basis can be highlighted resulting to three main components (Figure 1.9):

- Core areas, devoted to nature conservation and the protection of biodiversity. They allow to protect a target species or an ecosystem of interest. They act in the network as sources of species and as shelters.
- Corridors, serving to enhance the connectivity of the landscape to ensure the population dynamics and good-functioning of the ecosystem by maintaining tangible linkage between core areas. They are not necessarily linear and can take various forms such as stepping stone (relay patches).
- Buffer zones, surrounding the network, they are destined to protect it by mitigating negative externalities like pollution (pesticides, eutrophication).

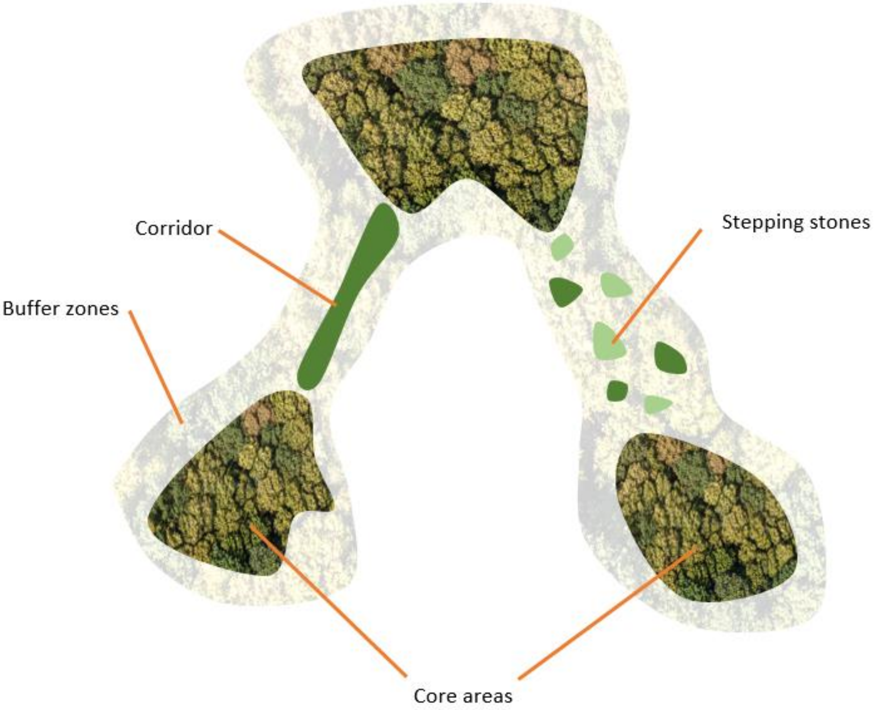

Figure 1.9: The common ecological network scheme

To this framework, some authors add more components like development/sustainable-use areas where intensive management is discarded in favor of sustainable management. These areas could play both the role of buffer zones or corridors (Bennett and Mulongoy, 2006; Melin, 1997). Some of them distinguish fine-scale ecological elements like hedges and isolated trees in meadows from the corridors and consider it as a particular area called " ecological gridding "(Melin, 1997). These solutions aim to soften the matrix and make it more permeable to species movements.

These different elements of ecological networks echo the principles to be integrated in nature conservation to address landscape fragmentation. With its core areas hosting biodiversity, its linkage areas identifying corridors, soft matrix areas and stepping stones in the landscape, its buffer areas or development areas that try to make the matrix more permeable to species movements and reduce negative edge effect. This framework integrates components that could easily allow implementation of both land-sharing and land-sparing strategy through a gradient of protection degree with core areas with maximal protection degree and development areas including sustainable production activities.

5. Developing Tools to Guide Ecological Network Mapping Initiatives

As previously discussed, an effective ecological network is composed of two main elements: core areas that protect biodiversity and ecological corridors that provide connectivity within the study landscape. Conservation objectives for ecological networks can target different issues such as focal species, key biodiversity areas, populations or habitat areas. The configuration of the final ecological network is intended to optimize the different conservation objectives that have been established (Hilty et al., 2020).

Different approaches exist to cover multiple conservation issues in complex landscapes. First of all single species can be studied based on their conservation value, the interest of its habitat or its capacity to reflects connectivity needs of multiple species such as focal species (Brennan et al., 2020; Brodie et al., 2015; Epps et al., 2005). Indeed, focal species are species that have connectivity needs similar to a group of species, so creating an ecological network that meets their needs will also meet the connectivity needs of many other species(Brennan et al., 2020; Pliscoff et al., 2020). The use of focal species is therefore a widely used network mapping strategy since decades and has been successful. In parallel, key biodiversity issues are very often linked to particular ecological conditions supporting habitats that host important biodiversity dependent on them (Jongman et al., 2011; Laita et al., 2010). Thus, many ecological network mapping initiatives are organized around different networks targeting conservation issues dependent on particular ecosystems and the species living there (Jongman et al., 2011). These different thematic networks can target connectivity issues in forests (Laita et al., 2010), peatlands (Grzybowski and Glińska-Lewczuk, 2020) or wetlands (McIntyre et al., 2014). The mapping of ecological networks components is therefore highly dependent on targeted objectives and on the selected approach. A variety of approach could be followed to map (multi-) species habitat, ecosystems and corridors supporting a single species or aggregating connectivity need of multiple species.

5.1. Mapping core areas

Different approaches exist to identify core areas of ecological significance that must be connected by ecological corridors. The areas identified first are generally those that have already been assessed and granted protection status. In addition to areas with protection status, other areas of biodiversity interest may have already been identified in maps and can also be used. Secondly, various mapping analyses cross-referencing different criteria established by expert assessments can be used to identify areas of major interest that have not yet been identified (Hoctor et al., 2000). These analyses can be supported by different data such as land use maps, aerial photos or cadastral maps (An et al., 2020; Hoctor et al., 2000).

Other authors will identify the habitat areas of the species using species occurrence data. Long considered as of paramount importance, species occurrence data have always been used to map biodiversity issues and guide conservation actions accordingly (De Ornellas et al., 2011). However, systematic sampling requires qualified agents, is particularly time consuming and therefore need important funding. Therefore, such sampling focuses on some areas and take time to be updated (Grantham et al., 2009). As a result, current biodiversity related studies are increasingly relying on citizen science and naturalist observation platforms (Petersen et al., 2021). Those datasets are continuously updated, observations can be validated by experts and highly precise observations are becoming more current thanks to easily accessible geolocation using smartphones. Although those data are complementary to systematic sampling because they can cover wider areas and are better updated, there are not exempt of biases(Kadmon et al., 2004; Tye et al., 2017). For instance, naturalists often visit area of high biodiversity concerns neglecting others and the absence of systematic sampling does not allow to identify true absences (Botts et al., 2011; Tulloch et al., 2013). Species occurrence data are also sensitive to location errors as people often encode the occurrence where they are and not necessarily where the species was. Moreover, animal species have a specific problem as they are moving species. Their presence is therefore not necessarily related to the presence of their habitat. Fortunately, other information’s and approaches can be used to put these data to good use.

Land-cover and land use data are important to map and infer biodiversity pattern or processes (Falcucci et al., 2007). Those data are largely used to study species distributions and helped to understand how land use changes negatively affects species populations (Sahraoui et al., 2017). Associated with abiotic data such as topography and climate, land-cover data and species occurrence can be used to calibrate species distribution models (SDMs) (Wilson et al., 2013). With some good practices and specific algorithm, modelling approaches can be adapted to available data and their biases. Those good practices refer to the preferred use of validated data and those with an accuracy concordant to study aims. The choice of predictors is also important as variable distribution and autocorrelation impact model quality (Guisan et al., 2017). Moreover, the selection of a set of uncorrelated variables with little redundancy is an important step of data processing before modeling (Guisan et al., 2017). Due to the increasing availability of opportunistic naturalist observation data characterized with no true absence, presence-only algorithms have been developed such as Maxent (for maximum entropy) (Phillips et al., 2006). This model creates in the study area a random set of pseudo-absence that are compared to presence to identify potential presence following the principle of entropy. Although that the algorithm is quite complex, results are often convincing and is therefore largely used by the biodiversity conservation related scientific community (Kramer-Schadt et al., 2013). However, when true absences are available, presence/absence model are still more recommended (Guisan et al., 2017).

But models remain models and do not depict reality. How model's results are used is of paramount importance and their limits must be clearly understood before guiding conservation practices. SDMs can be used to compensate for sampling issues by identifying potential presence of species in less sampled areas that can be confirmed with localized systematic sampling (Peterman et al., 2013).

Species distribution models can be used as it is when the primary purpose of the network is to connect habitat patches of the species in question (Duflot et al., 2018a). However, as previously mentioned, the conservation objectives of ecological networks sometimes go beyond the species alone and also include the whole ecosystem type. Ecosystem types are often simplistically derived from land use maps, which are generally limited to units differentiating only open and forest land-cover or the coniferous or deciduous character of a forest (Hoctor et al., 2000). In order to match as closely as possible ecological conditions on which certain species depend, it is necessary to move towards biotope mapping. Along species occurrence data, community level data also exists. Indeed, vegetation community are used for a long time to define biotopes that compose species habitats (Delescaille et al., 2021; Löfvenhaft et al., 2002). Many countries perform biotope surveys and therefore dispose of map allowing their monitoring (Sukopp and Weiler, 1988; Vihervaara et al., 2012). These biotope maps can be seen as a refined and species related land-cover classification. Those data are therefore powerful to identify high biological stakes areas.

Biotope mapping and their protection is at the heart of European nature conservation policies such as Habitat Directive (Weber and Christophersen, 2002). For that reason, biotopes mapping is performed by qualified team to be the most accurate possible allowing to differentiate all biotopes. But they unfortunately cannot cover an entire country as they are time consuming surveys. Therefore, most biotope maps have the same biases that species occurrence data due to unbalanced sampling effort. To fill unmapped areas, scientists have turned to SDM approaches that can also help to identify stakes of species dependent of specific biotopes (Álvarez-Martínez et al., 2018; Horvath et al., 2019). Indeed, many example of calcareous grasslands and peatland modelling to identify new areas hosting a specific biodiversity exist (Burnside et al., 2002; Horvath et al., 2019). The use of presence-only and presence/absence datasets for modelling is also a redundant question in biotope modeling. Some authors prefer using the Maxent algorithm with presence-only data while other consider the presence of other biotopes as absence of the targeted one (Álvarez-Martínez et al., 2018). But many question can be raised as ecological conditions suitable for biotopes can be present in considered absence even by using other biotope presences as absences.

Indeed, vegetation communities are dynamic through time. Pioneer communities give way to different stages of succession until they reach a stage of pseudo-equilibrium named "climax" (Niering, 1987) (Figure 1.10). Various successional patterns can occur due to natural or artificial disturbances, such as processes that restart the succession, regressive dynamics, or locking into specific stages (Blasi et al., 2004; Rees et al., 2001; Woodward, 2009). Humans actively maintain various stages within vegetation successions, which results in a complex coexistence of biotopes at different developmental stages, all sharing similar ecological conditions. Consequently, accurate modeling of biotope distribution becomes intricate, as building presence/absence calibration datasets gain in complexity.

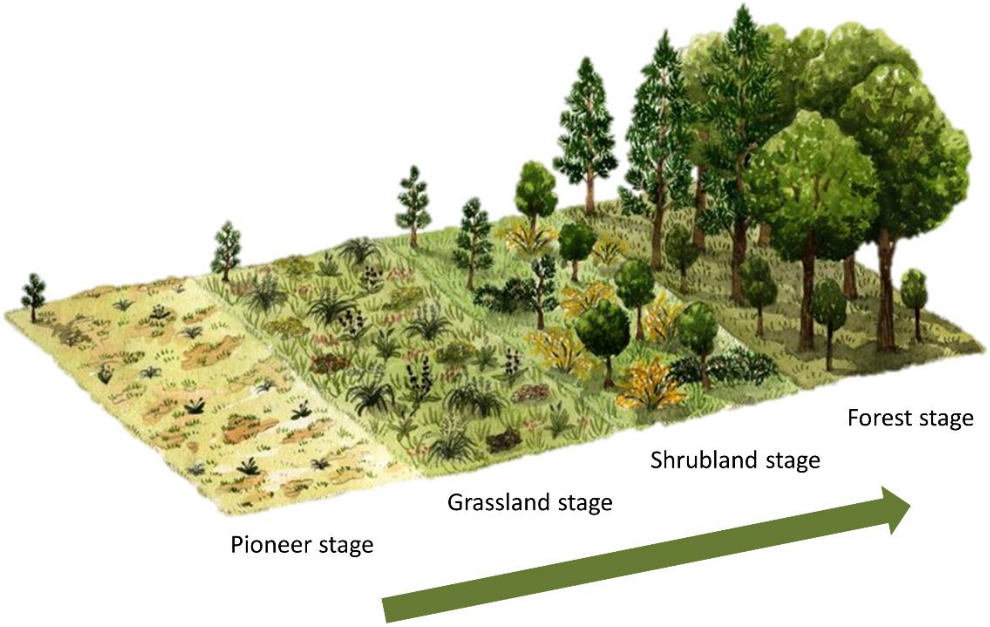

Figure 1.10: Example of vegetation succession dynamic (© Illustration : Florence Dellerie).

A practical solution involves the concept of Potential Natural Vegetation (PNV). PNV refers to the vegetation that would develop in a specific ecological zone if human intervention ceased, assuming stable climatic conditions (Gallizia Vuerich et al., 2001; Tuxen, 1956). It defines ecological conditions necessary for associated succession stages, regardless of the natural vegetation stage (Loidi and Fernández-González, 2012; Prach et al., 2016). PNV allows the definition of landscape units with similar ecological contexts that were initially used to guide sylviculture, conservation, and landscape planning (De Keersmaeker et al., 2013). Mapping PNV may also play a vital role in designing ecological networks by delineating the maximum potential distribution of vegetation succession. These maps can serve as the foundation for ecosystem-oriented ecological networks, providing essential backbones for their establishment. Furthermore, these maps offer valuable guidance for conservation and restoration efforts, ensuring both network coherence and ecological integrity. Consequently, integrating the PNV concept into biotope distribution models holds significant promise. This integration can enhance the consistency of presence/absence calibration datasets and significantly improve model accuracy.

However, PNV mapping primarily focuses on differentiating ecological contexts such as abiotic factors, favoring the presence of biotopes belonging to the same vegetation succession. This approach alone does not suffice to identify the specific stage of vegetation succession that characterize biotopes. Accurate identification of these stages is crucial for mapping biotopes outside surveyed regions. To bridge this gap, a meticulous analysis of vegetation physiognomy is imperative to distinguish various stages of vegetation succession. Additionally, considering the dynamic nature of vegetation cover, it is essential that any mapping technique adopted is easily updatable. Fortunately, advancements in Geographic Object-Based Image Analysis (GEOBIA) and automated segmentation algorithms have paved the way for the creation of easily updatable vectorized land-cover maps. Current methodologies commonly employ the concept of ecotopes, defined as the smallest homogeneous landscape unit within a cartographic system (Radoux et al., 2019). Ecotopes are currently delineated using different remotely sensed data. For instance, digital height models are used to distinguish open areas from forests. Moreover, incorporating environmental predictors in the segmentation process could help ecotopes approximate biotope limits and therefore differentiate them within predicted PNV. Consequently, combining ecotopes with PNV modeling offer a viable solution for approximating biotopes distribution beyond surveyed areas.

To prevent confusion regarding the various mapping units used in this thesis, the following definitions are employed :

- Biotope: An environmental area, such as a forest or wetland, characterized by specific environmental conditions and a distinct species community (Löfvenhaft et al., 2002).
- Habitat: The area where species or a population can survive and reproduce, often comprising a mosaic of biotopes necessary for the species' life cycle (Löfvenhaft et al., 2002).
- Ecotopes: The smallest ecologically distinct landscape features within a landscape mapping and classification system (Radoux et al., 2019).

A biotope signifies a specific landscape element defined by precise ecological conditions. In contrast, an ecotope, while not reflecting ecological reality, aids in identifying distinct landscape elements based on segmentation predictors. Information derived from PNV modeling allows for the prediction of species community presence. By combining ecotope delineation and PNV predictions, a more accurate approximation of biotopes can be achieved. These biotopes serve as fundamental components for constructing species habitats or identify cohesive ecosystems, enabling the identification of core areas critical for conservation efforts (Figure 1.11).

Finally, it is crucial to exercise caution in the usage of terms such as habitat and biotope, especially in light of the European Habitat Directive, which lacks a clear distinction between these terms (Loidi, 1999). The directive provides a list of habitats of interest corresponding to specific plant communities, aligning with our definition of biotopes. Therefore, it is essential to specify that the habitats mentioned in the directive are to be understood as biotopes, ensuring consistent interpretation throughout this thesis.

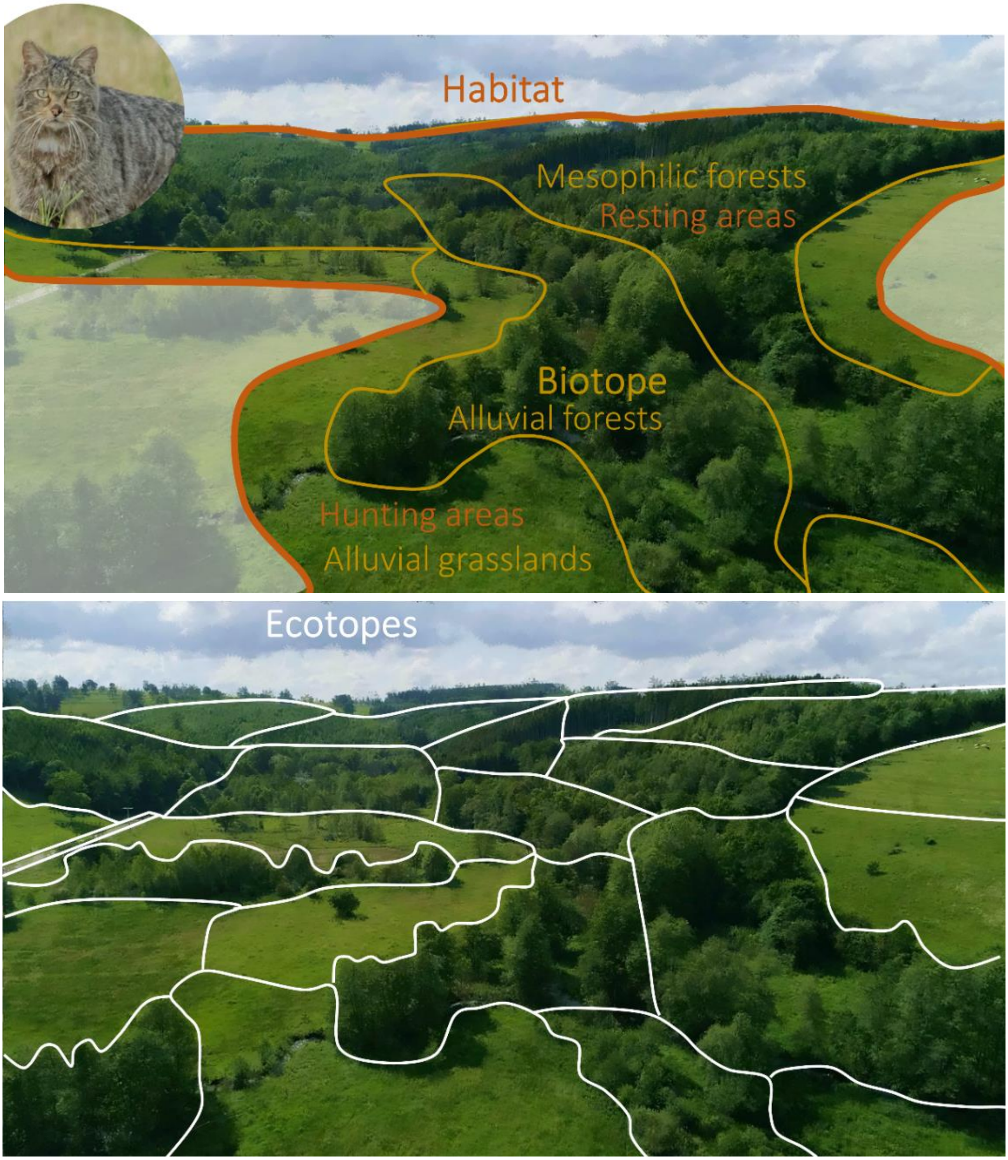

Figure 1.11: Distinction between concepts of habitat, biotope and ecotope. An illustrative example using the case of the wildcat, a forest species hunting in open areas bordering forests. Ecotope do not necessarily matches with biotope and habitat limits as its segmentation depends on predictors used.

5.2. Identifying ecological corridors

Reconnecting protected areas and other areas of conservation interest has become a priority for biodiversity conservation. To this end, many researchers have studied how to measure, model and map connectivity over the last twenty years. A wide variety of approach have been developed to consider functional and structural connectivity. Identifying elements that support population connectivity by directly measuring the movement of individuals across the landscape is an effective method for identifying functional corridors (Hilty et al., 2019; Sawyer et al., 2009; Seidler et al., 2015). However, this can be very time consuming to track sufficient numbers of individuals over the long term, so other approaches have been developed (Rudnick et al., 2012). Some study focal species to identify areas of connectivity for a represented species group (Weeks, 2017). Genetic approaches can also be used but are generally limited to preliminary steps to identify the status of a population and whether it is fragmented or not (Proctor et al., 2012).

Concerning structural connectivity, multiple approaches have emerged to identify areas of the landscape through which species can move. Some trivial approaches rely on the expert opinion on the species studied to draw corridors using landscape information such as land-cover or land use. Others apply GIS processing to identify areas hosting species that are sufficiently close to each other using buffers corresponding to the dispersal capacity of the studied species (Amsallem et al., 2011). Beside these simple but often used approaches in applications of the ecological network concept, other approaches based on modeling are particularly studied by the scientific community but are far more complex. (Hilty et al., 2020).

Beside the important use of species or biotope models to map biodiversity conservation stakes, modeling landscape connectivity require to implement complex concept to identify ecological corridors. Many approaches have been developed such as least cost paths, circuit theory, graph theory, Resistant Kernel, Reserve design and individual-based-modeling (McRae et al., 2008; Rudnick et al., 2012; Theobald, 2006; Urban and Keitt, 2001). Least cost path (LCP) is the most widespread and can be performed using both expert knowledge and data at different proportion. To model corridors, this approach needs the location of habitat patches that must be connected and a matrix representing the landscape in term of cost for movement for the considered species. Then the LCP between two patches is identified by the path with the least cumulated cost (Figure 1.12). Some authors use only expert knowledge to identify patches that must be connected and assign a cost for movements to each class of a land-cover map (Stevenson-Holt et al., 2014). At the opposite, we find authors modelling species suitable habitat to identify patches and use this model to infer the cost matrix by identifying less suitable areas as the costliest (Duflot et al., 2018a). Each of these approaches has its pros and cons and no consensus has been found while those approaches are still being compared.

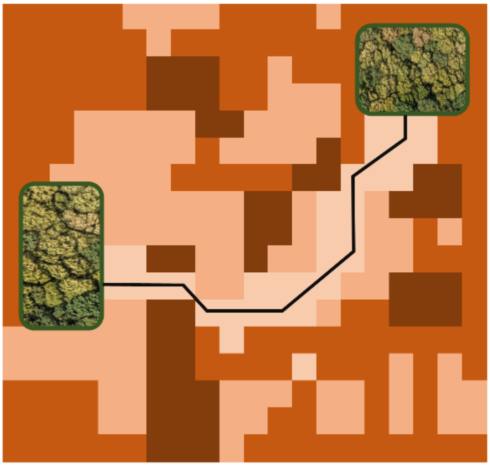

Figure 1.12: Schematization of LCP modeling between two vegetation patches: the matrix is represented with cells depicting the most costly land-cover in darker orange and the less costly ones in lighter orange. The LCP, shown as a black line, represents the path connecting the two vegetation patches with the least accumulated cost.

Amidst the myriad techniques employed in biodiversity conservation and landscape connectivity modeling, an essential aspect pertains to the definition of corridor and its distinction from a least cost path. Various definitions of corridors have evolved over time. In the early stages of landscape connectivity conceptualization, corridors were perceived as tangible landscape features, serving as physical links between patches of native vegetation (Bennett, 1998). This definition gained significance in operational planning, where demarcating zones and ecological network features was essential. For instance, the European Environment Agency defines ecological corridors as "thin strips of vegetation used by wildlife, potentially enabling the movement of biotic factors between two areas" (“EEA Glossary — European Environment Agency,” n.d.). However, from a species-centric perspective, corridors are not confined to specific vegetation features in the landscape. Species movements are intricate processes shaped by both abiotic factors (such as topography) and biotic interactions (including predation and competition) (Costa-Pereira et al., 2022). Therefore, our definition of corridors should be widened to areas where potential individual movements may occur (Foltête et al., 2021). Fortunately, these considerations are now being integrated into corridor definitions for landscape planning guidance. For example, Hilty et al. (2020) define ecological corridors as "clearly defined geographical spaces governed and managed over the long term to maintain or restore effective ecological connectivity." This definition offers the advantage of considering a broad area conducive to supporting species movements without restricting it to specific landscape features.

In contrast to corridors, LCP is always represented as a line traversing the least resistant matrix category between two habitat patches. LCP modeling stands as one of the most widespread and useful tools in habitat network mapping. However, its sole representation does not accurately capture the realistic and unique movements of species. Therefore, careful attention should be given to its representation before categorizing it as an ecological corridor.

6. Research questions and structure of the thesis

6.1. Objectives and research questions

Various studies have shown the importance of preserving and enhancing landscape connectivity to counteract the negative effects of landscape fragmentation. This notion has become of paramount importance in nature conservation and is increasingly integrated into landscape management through various biodiversity conservation strategies. This has given rise to the concept of ecological networks, which is rapidly becoming a key approach to conserving landscape connectivity.

Many researchers aim to better map habitat network and understand dynamics of species population in fragmented landscapes. But few studies seek to understand the potential effect on results of multiples choices made at different step of habitat network analysis from the identification of habitat patches to real-case conservation actions. The present work focuses on three factors greatly influencing habitat network analysis that correspond to the three main research question of this work:

<u>RQ1:</u> How do we represent ecological network elements?

This research question dwell on the representation of smallest landscape units that can be used to represent elements of ecological networks : biotopes. Indeed, species habitat are defined as the set of biotopes the species need to complete its life cycle. Therefore, biotopes are the brick used to construct the landscape as it is perceived by the species. **RQ1** is addressed in **Chapter 2** and **3**. In those two chapters, we focused on two aspect of biotopes mapping: a) representing their limits b) and their distribution.

<u>RQ2:</u> How to best evaluate landscape resistance to species movements?

This research question aims at investigating the different possibilities to translate the landscape as a resistance map to model species paths. The question is about the use of knowledge versus data to identify habitat but also to translate a land-cover map to a resistance to species movement matrix. Few studies have compared these two approaches (Stevenson-Holt et al., 2014) and none compared them based on connectivity analysis aiming to identify connectivity issues. This question is addressed in **Chapter 4**.

<u>RQ3:</u> How can be applied habitat network mapping to complex landscape reality having multiple ecosystem and species stakes?

This question concerns the application of habitat network mapping considering multiple stakes that are present in complex landscapes. This question is addressed in **Chapter 5** where we tested the concept of focal species to take account of multiple species with similar connectivity needs. We also modeled multiple focal species to get a range of connectivity needs to evaluate the fragmentation of an entire ecosystem and propose conservation actions. Two different ecosystems were also considered to evaluate potential overlap in connectivity issues and arising management measures. With this study, our purpose is to present a reproductible method to tackle connectivity issues at regional scale taking into account landscape complexity.

6.2. Structure of the Thesis

After presenting landscape connectivity stakes (Chapter 1), the present study is split in five parts (Figure 1.13):

Chapter 2. Representing landscape components

This chapter investigate the concept of ecotope which is considered as the smallest homogenous unit of the landscape and how it can summarize ecological feature at landscape level and help to delimit biotopes (Article 1 – Published) (**RQ1a**).

Chapter 3. Identify high biological value areas through vegetation dynamic series concept.

This chapter will address the modeling of potential biotope distribution to complete actual biotopes mapping suffering of sampling biases (**RQ1b**). These models also allow to identify landscape areas where habitat patches can be restored. We present a methodological approach including the PNV concept in biotopes modeling approaches (Article 2 – Published).

Chapter 4. Modeling and analyze species habitat network. Comparing approaches.

This chapter dwell on the comparison of two different approaches used to create the species movement resistance matrix (**RQ2**): the use of expert opinion and the use of species occurrence datasets. We compare the divergence in the different results for the wildcat. Different analysis to identify LCP, their respective importance for the connectivity of the network and their obstacle were performed (Article 3 – Published).

Chapter 5. Modeling habitat networks for multiple species using fragmentation-sensitive focal species

The aim of this chapter is to analyze the application of the focal species concept to map networks of species habitats that meet the connectivity needs of multiple species. In addition, we are interested in mapping networks of multiple focal species dependent on two major ecosystems with opposing connectivity stakes. We aimed to identify if the concept of focal species is efficient when applied to a larger scale and to more specific applications (**RQ3**). In a second step, it is also to see if the connectivity issues of two opposite ecosystems overlap or not.

Chapter 6. Discussion, Perspective and Conclusion

This chapter takes up the various research questions of the thesis and discusses how they were answered. This is followed by a general discussion of various aspects common to the different chapters and about the application of thesis results. A perspective section proposes to re-contextualize the concept of ecological networks in the face of new initiatives applying related concepts such as green infrastructure. Based on a review of scientific literature, we analyzed the inclusion of the concept of ecosystem services in the mapping of habitat and biotope networks for the purpose of building green infrastructure to see if the concept of ecological network can be used for green infrastructure mapping or if it has become obsolete. Then a general conclusion of the thesis completes this manuscript.

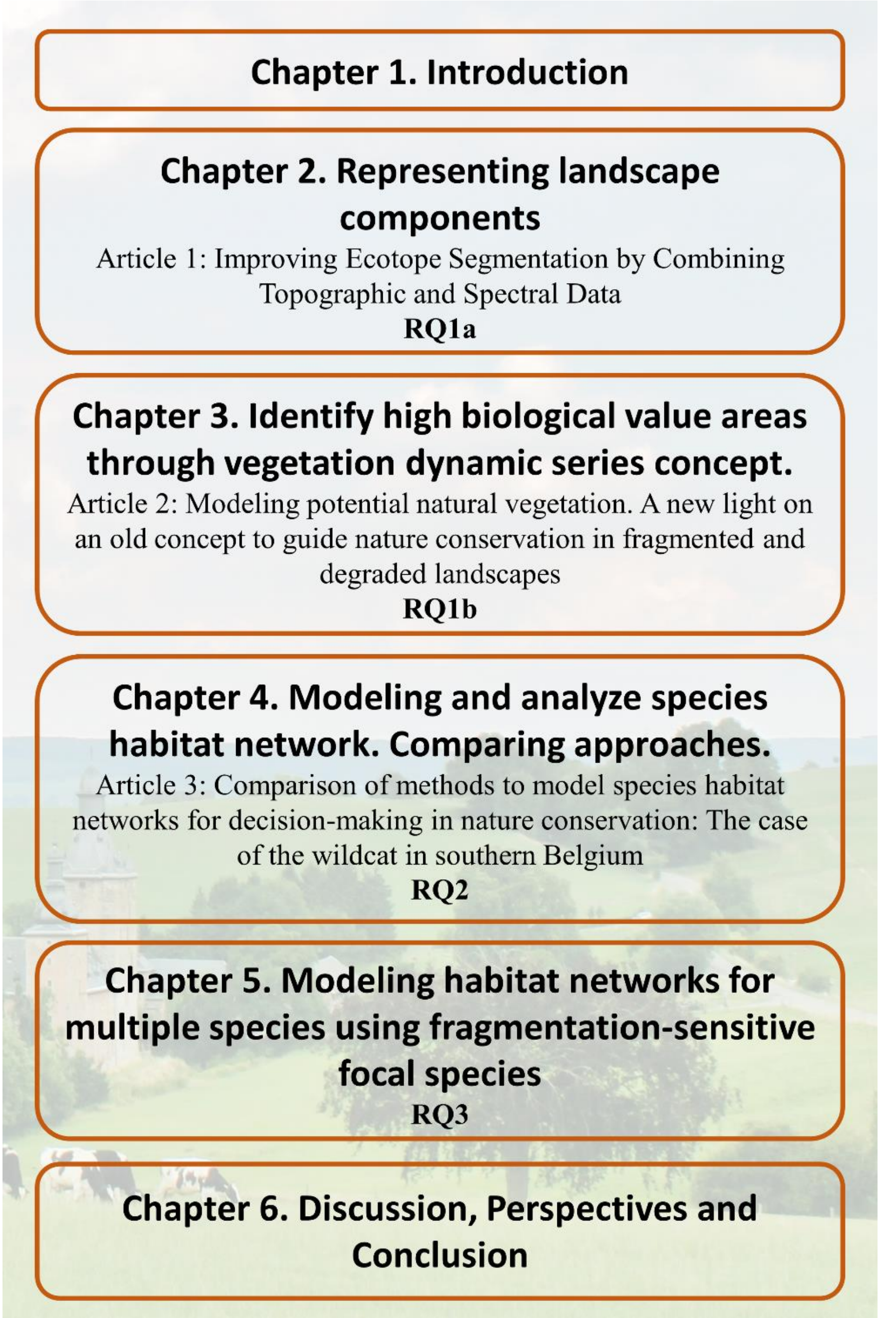

Figure 1.13: Conceptual framework of the thesis with links between chapters

Chapter 2

Representing Landscape Components

1. Preamble

In this chapter, we conducted an evaluation of the concept of ecotopes as a means to map ecologically distinct units of the landscape. Our focus initially lay on the segmentation process of ecotopes, utilizing topographic data to enhance the delineation of vegetation cover and environmental characteristics, such as soil attributes. To assess segmentation performance, we analyzed the homogeneity of soil characteristics, such as drainage, or land-cover classes, within ecotopes. Additionally, we investigated the influence of topographic variables in segmentation, taking into consideration the results of biotope distribution models using ecotopes as the modeling unit.

Subsequently, we proceeded to compare ecotopes with other landscape representations to perform ecological analyses for landscape conservation. We compared raster grids with ecotopes for biotope distribution modeling, and hexagonal grids with ecotopes for habitat network modeling. During this comparison, we evaluated biotope modeling performances and structural differences in habitat networks.

The first section of this chapter is adapted from : Radoux, J., Bourdouxhe, A., Coos, W., Dufrêne, M., Defourny, P., 2019. Improving Ecotope Segmentation by Combining Topographic and Spectral Data. Remote Sensing 11, 354.

2. Improving Ecotope Segmentation by Combining Topographic and Spectral Data

2.1. Introduction

2.1.1. Context

In order to mitigate biodiversity loss and destruction of ecosystems with heritage value around the world, we have to know where biodiversity hotspots and threatened areas are located. Facing the actual threats and due to a big extinction rate, the urgency leads to a race to become aware and map theses area before they don’t exist anymore. This logic was followed at many scales. Worldwide, biodiversity hotspots were identified and outlined in order to prioritize conservation actions (Mittermeier et al., 2011; Myers et al., 2000).

At the European scale, two directives have defined the need for the conservation of habitats and species with the adoption of appropriate measures. They allow to give a protection status for species and biotopes of interest, but also defining protected areas corresponding to species habitats or group of biotopes. Within this Pan-European ecological network known as “Natura 2000 network” of special areas of conservation, natural habitats will be monitored to ensure the maintenance or restoration of their composition, structure and extent (Ostermann, 1998).

Monitoring the evolution of the territory (land-cover, habitats of species, biotopes, . . .) is an essential activity to identify major changes, economic, social and environmental issues but also to assess the impact of public policies and private initiatives. This monitoring is held by each country and requires a large amount of data, mainly obtained through field surveys having a high financial and time cost. These mapping results are used to mitigate problems such as conservation measures of the kind at national and local level(Loidi, 1999), planning and development of green infrastructure (Wells et al., 2011), agro-environmental assessments (Donald and Evans, 2006), landscape changes monitoring (Bryn, 2008; Bunce et al., 2008), ecological forest management (Pokharel and Dech, 2011) or identification of ecosystem services (Egoh et al., 2012; Maes et al., 2012). However, existing maps are often limited to categorical land-cover characterization which does not provide a precise legend for habitat and biotope types and are hardly interoperable. Innovative remote sensing products could, however, facilitate the status monitoring and the detailed characterization of large areas, even sometimes for fine scale quality indicators (Spanhove et al., 2012). While it does not replace field data collection, remote sensing integration could thus be a first step towards a more cost effective monitoring of natural habitats (Vanden Borre et al., 2011).

Because of the limitations of remote sensing, habitat suitability mapping and biotope prediction models are necessary to fill the gaps of field observation for biodiversity monitoring. Nevertheless, remotely sensed data are of paramount importance in providing some spatially comprehensive information that is necessary to the prediction over large regions (Guisan and Zimmermann, 2000; Osborne et al., 2001). In this context, models are often based on regular grids linked with permanent structured inventories. However, with the democratization of geopositioning devices and the rise of citizen science, the precision of the observation has tremendously increased. An alternative approach to grid based habitat and biotope prediction could therefore emerge with a landscape partitioning into ecologically meaningful irregular polygons.

2.1.2. Remote Sensing for Ecotope Mapping

Previous studies showed that irregular polygons were supportive of habitats model that outperformed the standard grid-based approach with more than half of the investigated species (Delangre et al., 2017). This partition of the landscape into spatially consistent regions can be related to the concepts of ecotopes (Ellis et al., 2006) or of land use management units (Gerçek, 2017). Ecotopes are the smallest ecologically distinct landscape features in a landscape mapping and classification system. Mapping ecotopes therefore enables the measurement of ecological patterns, process and change (Chan and Paelinckx, 2008) with much more details than categorical land-cover classes or continuous field of a single class land-cover feature.

Ecotope maps are often created by overlaying a large number of components, such as physiotope (topographic and soil features) and biotope (vegetation) layers (Haber, 1990; Haber et al., 1990). As a result, ecotope maps are classified into hundreds of types and dozens of groups by combining biological and geophysical variables (HONG et al., 2004). Furthermore, the different scales and precision of the boundaries of the overlaid thematic layers may create many artifacts which need to be handled with advanced conflation rules.

Alternatively, Geographic Object-Based Image Analysis can be used to delineate spatial regions by grouping adjacent pixels into homogeneous areas according to the objectives of the study (Nemmaoui et al., 2018; Shen et al., 2017). For biodiversity research, image segmentation has been used to automatically derive homogeneous vegetation units based on spectral (Ruan and Ren, 2007) or a combination of spectral and structural (height) information(Delangre et al., 2017; Geerling et al., 2009). These approaches helped to reduce the number of polygons and improved the matching of those polygons with entities derived from the field.

On the other hand, GEOBIA was also used to delineate physiotopes, which can then be overlaid with land-cover polygons to derive meaningful spatial regions (Gerçek, 2017) or directly used to map aquatic habitats (Janowski et al., 2018). The delineation of physiotopes is a difficult task to assess because their definition depends on the purpose of the study (Guilbert and Moulin, 2017). Different GEOBIA methods have therefore been developed, based on curvature indices (Gerçek, 2017; Gerçek et al., 2011), decision rules using elevation and slope (Drăguţ and Eisank, 2012), network properties (Guilbert and Moulin, 2017) or a large set (70) of indices including slope, aspect and various texture indices (Janowski et al., 2018). However, the methods designed for terrestrial landscapes focused on global to regional scales, where the relative position (ridge, side or valley) plays a major role for the classification and do not directly take the orientation of the slope into account.

Our study aims at improving the large scale delineation of ecotopes applied on ecological modeling in Delangre et al. (Delangre et al., 2017). Our hypothesis is that this improvement can be achieved by simultaneously processing the topographic information from a LIDAR DEM and the vegetation structure information from optical image and LIDAR DHM. Topography is indeed a major driver of other abiotic components such as soil properties (which is more difficult to obtain at high precision) (Gessler et al., 2000; Kravchenko and Bullock, 2000)or insulation (depending on the orientation of the slope) (Sternberg and Shoshany, 2001).

2.2. *Data and Study Area*

The study area is located in the Walloon region (Southern part of Belgium). This is a very fragmented landscape including coniferous forests (mainly spruce and other sempervirent species), deciduous broadleaved forests (mainly oaks and beeches), crop fields, natural and managed grasslands, peatlands, small water bodies, extraction areas as well as dense and sparse urban fabrics.

There are no mountainous terrains in Belgium, but a topography that is mainly driven by a dense hydrological network. In order to test our hypothesis, the experimental study focuses on the ravine maple stands, which grow on relatively steep slope and rocky soil. This biotope is particularly sparse, but at least present in five of the biogeographical regions of Wallonia. A rectangular study area (Figure 2.1) was delineated to include the majority of these biotopes present in Belgium. This region is relatively flat (slopes smaller than 7 percents) except in the valleys.

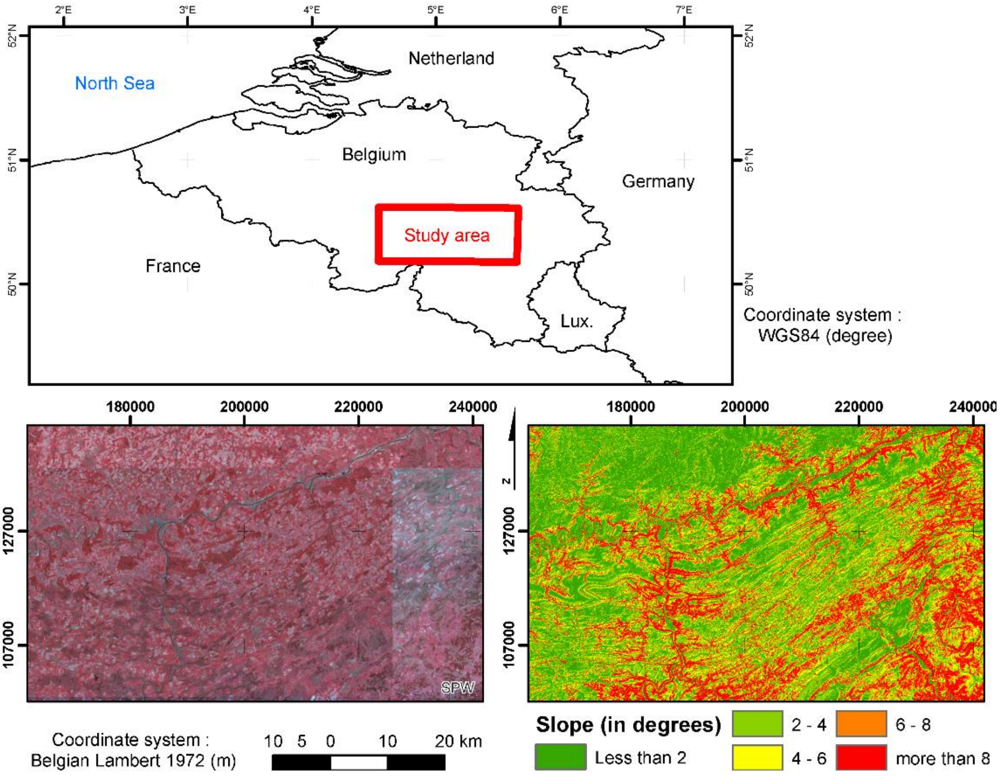

Figure 2.1: Aerial orthophoto (left) and slope derived from the LIDAR images (right) on the study area.

Two types of input data were available in the study area. First, a mosaic of ortho-rectified aerial photographs upscaled to 2 m resolution and including four spectral bands; Second, a LIDAR point cloud dataset rasterized at 2 m resolution.

The aerial photographs cover the entire study area. This coverage was done with several flights between March and April 2015. Image acquisition included four spectral bands (blue, green, red and near-infrared) at a spatial resolution of 0.25 m.

The images available for the analysis were already ortho-rectified, mosaicked and rescaled in bytes. In order to avoid too much local heterogeneity, which would affect classification process, the original images were resampled at 2 m resolution using the mean values of all contributing pixels.

The LIDAR dataset was acquired in spring 2013 and 2014. The minimum sampling density is of 0.8 points per square meter. First and last returns were used to extract the ground elevation and the vegetation canopy height. In addition, this dataset required specific mathematical morphology analysis in order to remove some artifacts: a gray scale opening was applied in order to remove power lines. A digital elevation model (DEM) and a Digital Surface Model (DSM) of the vegetation were derived from the last and first returns, respectively. A Digital Height Model (DHM) was then obtained by subtracting the DEM from the DSM.

In addition to the remote sensing data, a vector database describing the biotopes inside Belgian protected areas from the European network of natural sites (NATURA2000) was available. This database was produced by the Walloon administration for Nature and Forest based on expert knowledge and exhaustive field inventories (all polygons). It is considered as the best available information about ravine forests in Wallonia and was therefore used as a reference. In order to ensure and improve the reliability of this map, polygons with visible clear cuts on the 2015 othophotos were manually removed from this reference.

2.3. Method

The core of the proposed process is the simultaneous segmentation of the topographic, spectral and height information. The resulting image segments are then enriched by computing a set of attributes based on remote sensing and ancillary data. The potential of the proposed method to automatically delineate meaningful spatial regions is assessed based on two expected properties of the ecotopes: a large homogeneity and the ability to build high performance ecological models. These steps are summarized on Figure 2.2.

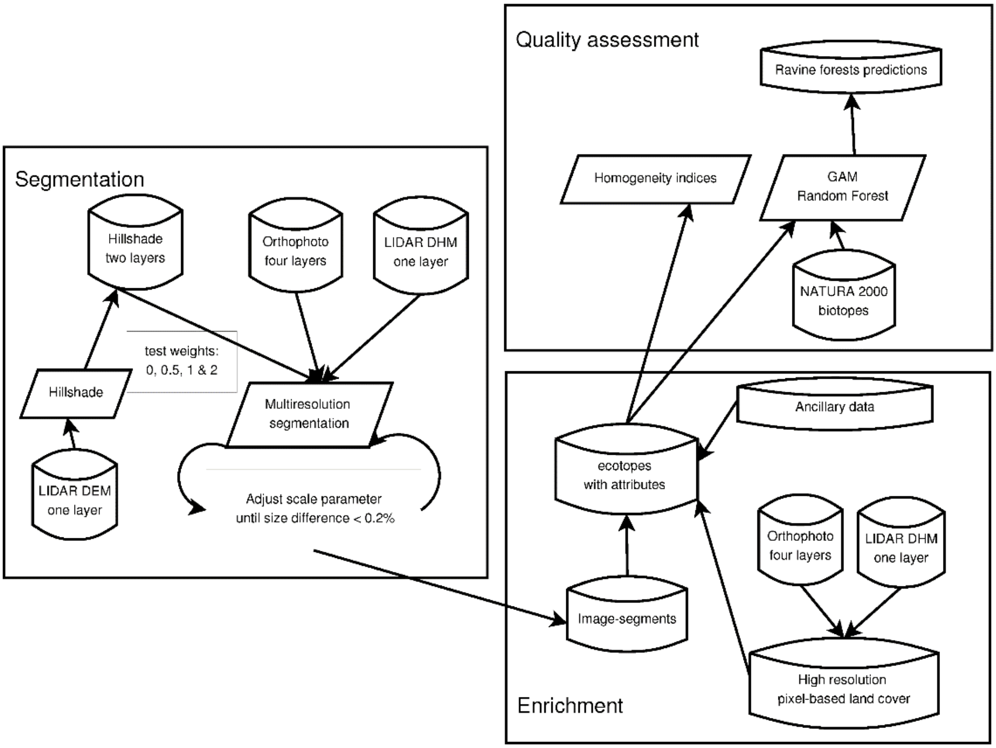

Figure 2.2: Overall flowchart of the proposed method.

2.3.1. Automated Ecotope Delineation

The three variables of interest to discriminate ecological function at the scale of the analysis are the land-cover, the topography and the soil type. However, the available soil type information was not precise enough and could be partly inferred by the topography. We therefore focused on variables that could be directly inferred by remote sensing: topography and land-cover.

The multiresolution segmentation algorithm (Baatz and Schape, 2000) was used to automatically delineate ecotopes. This algorithm can be tuned by a set of four parameters: the scale, the weight of the raster layer, the shape and the compactness. The scale parameter defines the maximum acceptable value of the change of heterogeneity when merging two neighboring image-segments. Increasing the scale parameter therefore increases the size of the image-segments. The weight of the layers defines how much each raster layer will contribute to the heterogeneity difference of the merged image-segments as shown in Equation 1:

Equation 1.

$$h_{diff} = \sum_{L} w_L \left(n_1\left(h_{mergedL} - h_{1L}\right) + n_2\left(h_{mergedL} - h_{2L}\right)\right/ \sum_{L} w_L$$

where h_{diff} is the total heterogeneity difference after merging based on the raster layers, w_L is the weight of each raster layer, $h_{mergedL}$ is the heterogeneity of image-segments 1 and 2 for layer L; n_1 and n_2 are the number of pixels in image-segments 1 and 2; h_{2L} and h_{2L} are the heterogeneity indices of image-segments 1 and 2. Then, the shape parameter defines the proportion of the heterogeneity index that is based on the shape of the image-segment. Increasing the shape parameter therefore reduces the contribution of a large heterogeneity difference after merging the image-segment. The compactness parameter determines if this shape index should favor compact image-segments (similar to a disk) or smooth image-segments (similar to a rectangle).

The efficiency of a segmentation combining LIDAR height and multispectral image had already been proven (Geerling et al., 2009). Our working hypothesis is that simultaneously combining the topographic information with the spectral values of the orthophotos and the DHM derived from the LIDAR would improve the delineation of the ecotopes. The segmentation results are therefore compared with different weights to the topographic information with respect to the other layers. For the sake of a fair comparison, the average size of the image-segments is fixed to approximately 2 ha (Two hectare on average corresponds to smallest ecological management units according to a group of users including biodiversity researchers and managers.) To do so, the composite image was first segmented with a scale parameter of 50, a shape parameter of 20% and a compactness of 100%. The shape parameter was then reduced to 10% and a larger scale parameter was obtained using binary search algorithm with a tolerance of 0.2% on the total number of polygons obtained on the reference image segmentation (that is 318,380). Apart from the size that was fixed after the first segmentation, no other optimization of the segmentation was performed. The only difference between the segmentation is therefore the weight of the topographic component that is being tested with values of zero (only spectral and structural information), 0.5, 1 and 2 (increasing the influence of topographic information).

Including topography in segmentation required a transformation of the DEM data to highlight the different slope types and identify breaks. Because the segmentation algorithm is based on the minimization of the variance inside each image-segment, using DEM values would indeed tend to create many linear spatial regions along contour lines in areas of steep slopes, even if the slope is constant. Previous studies used the slope together with some curvature indices (Gerçek, 2017). This is interesting for pedomorphic mapping, but (i) it then relies on arbitrary window size to compute minimum and maximum curvature and (ii) both sides of ridge and valley lines are in the same segment despites different sun illumination. In the case of ecotopes, the slope and the aspect of the slope are therefore more closely related to the functionnal homogeneity However, slope aspect could not be used by the segmentation algorithm because (i) it is undefined when the slope is null and (ii) it is a circular metric that jumps from 360 degrees to 0 degree for the same azimuthal direction. For those reasons, Janowski et al. (Janowski et al., 2018) used easting and northing instead of azimuth. For the ecotopes, two synthetic hillshade maps were derived along the North-South and the East-West transects using Equation 2, because this is the variable that is the most directly linked with the potential solar energy.

Equation 2.

$$hillshade = 255 \times ((\cos(SZA) \times \cos(Slope)) + (\sin(SZA) \times \sin(Slope) \times \cos(SAA - Aspect)))$$

where SZA and SAA are the hypothetical sun zenithal and azimuthal angles, respectively, and $Slope$ and $Aspect$ are derived from the DEM using a 3-by-3 moving window. The use of 3-by-3 windows corresponds to local hillshade at a high spatial resolution (2 m), so that only pixels with similar hillshade values are likely grouped together by the segmentation algorithm. The shape parameter of 20% that is used in the segmentation process aims at preserving the compacity of the image segment when isolated pixels have a markedly different orientations than their surroundings, but image-segments are expected not to merge when there is a change of slope.

In practice, synthetic hillshade maps were created by setting a large sun zenith angle (75°) for four sun azimuth angles (0°, 90°, 180°, 270°). The difference between the results of both pairs of opposite theoretical sun azimuth angles were then computed. Cast shadows were ignored in this process because the aim of the hillshade is only to provide a continuous topographic characterization. As can be seen on Figure 2.3, the values of the hillshade are equal on flat surfaces and on slopes oriented with 45° or 135° azimuths. In the case of flat areas, the value in two opposite directions is indeed equal, so that their difference is zero for all azimuths. In the other case, the values are either positive or negative and they are equal for the orthogonal direction because 45° is the bisector of those azimuthal angles.

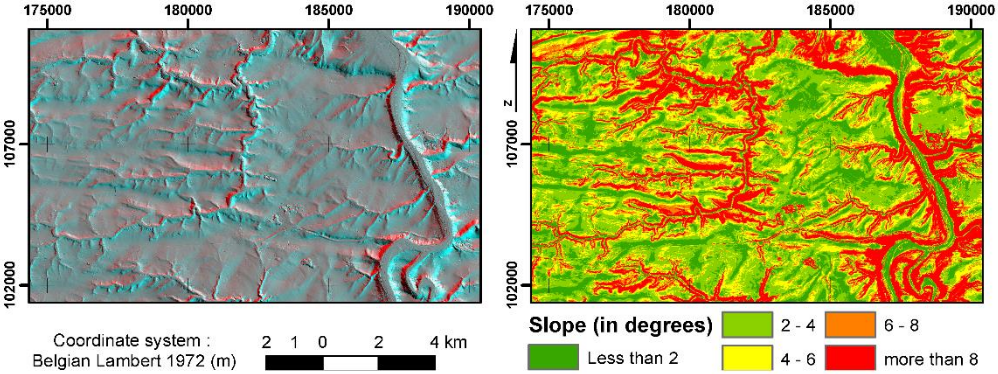

Figure 2.3: False color composite of the hillshades along the North-South and East-West directions (left) and slope derived from the LIDAR images (right) on a subset of the study area. Shades of grey indicate that the hillshade values in the two orthogonal directions are equal while colored areas highlight the differences between the two directions.

2.3.2. Quality Assessment

For the sake of ecological models, image-segments are enriched based on the proportion of land-cover features that they contain as well as various soil and contextual attributes (Delangre et al., 2017). With all attributes being derived from external databases, the quality assessment focuses on the homogeneity of the image-segments (which is a key feature for ecotopes) (Section 3.2.2) and the ability to run performant ecological models (Section 3.2.3).

Due to the lack of other up-to-date high resolution land-cover map of the Walloon region at the time of the study, a high resolution pixel-based land-cover map was produced in order to characterize the ecotopes and build some of their homogeneity indices. While the production of this high resolution land-cover database is out of the scope of this paper, it is briefly described in Section 3.2.1.

2.3.3. High Resolution Pixel-Based Land-cover

A Bayesian classifier with automated training sample extraction method (J. Radoux and Bogaert, 2014) was used to classify 8 land-cover types: bare soil, artificial, grassland, crops, coniferous, broadleaved, water and shrubs. The input image was based on the same datasets as the segmentation: the 4 spectral bands of the aerial photograph and the height information extracted from LIDAR. The a priori probability was computed based on the frequency of each land-cover type within two height classes (below and above 50 cm). Because of the high reliability of the LIDAR DHM, this step was particularly useful to discriminate forests, shrubs and buildings from the other land-covers. The training dataset was compiled based on existing datasets covering the study area, including a 2007 land-cover map from the Walloon Region, Open Street Map data (OpenStreetMap contributors, 2017) and forest inventory data from the Nature and Forest Department. The results were then consolidated with a crop mask in order to discriminate grassland and cropland. Furthermore, the classification of forest types was consolidated in the homogeneous region thanks to a classification of Sentinel-2 cloud-free images of early spring and mid summer 2016 (assuming that the forest type does not change from year to year and excluding clear cuts from the analysis).

For the validation, a simple random sample of 700 points was photointerpreted on the orthophoto with a geolocation tolerance of 5 m and ambiguous points were verified on the ground. The estimated overall accuracy of the consolidated product (93% with a 95% confidence) was above the other products, therefore it was considered as our best reference in the frame of this paper.

2.3.4. Homogeneity Measures

In order to test the hypothesis of this study, different homogeneity indices have been computed. Those indices look at the homogeneity from land-cover (based on the high resolution land-cover layer), from the topography and from the soil types. They are compared with an arbitrary regular grid with the same cell area than the average polygon size, which provides a reference considering the segmentation ratio. Because of the specific interest towards a biotope that is mainly present in areas of steep slopes, the homogeneity indices were not only computed for all the study area, but also for a subset composed of the polygons with an average slope above 10 degrees.

Giving more weight to the topographic bands could affect the homogeneity in terms of land-cover delineation. In order to control a potential loss of land-cover homogeneity, the average purity level was computed for each segmentation. The proportion of each land-cover class was computed inside each polygon based on the high-resolution pixel-based land-cover classification presented in Section 3.2.1. The purity index is then defined as the average of the maximum values of land-cover proportions of each image-segment.

From the topographic point of view, the primary variable of interest is the slope. The slope was measured on a smoothed version of the 2 m DEM in order to remove micro-topography effects and to remove artifacts due to the noise of the dataset. Because the slope is a quantitative variable, its heterogeneity was estimated using the standard deviation (STD) inside each polygon. For the aspect of the slope, standard deviation could not be used because of the break between 0 and 360°. The azimuth values were therefore converted into nine categories, including in eight directions (North, North-East, East, South-East, South, South-West, West and North-West) plus one class for the flat areas (where the aspect is undefined). The purity index of these nine categories is then computed like in the case of the land-cover.

Finally, an independent data source was also considered: the soil map. The purity index for soil drainage classes and soil depth classes was used as an additional indirect indicator of the polygon homogeneity. Those two soil classes were derived from the digital soil map of the Walloon region. The precision of this map corresponds to a scale of 1/25,000, which is coarser than the polygons delineation, but this uncertainty affects all polygon boundaries in a similar way.

2.3.5. Biotope Models

In addition to the homogeneity measures, a fitness to purpose analysis was implemented. The sensitivity of two state-of-the-art algorithms, namely Random Forest (RF) and Generalized Additive Model (GAM), has been tested for the detection of ravine maple forests. Each model was calibrated using the same workflow for each of the segmentation results.

First, a large set of attributes have been derived from existing database and GIS analysis. This set includes bioclimatic variables interpolated from Worldclim (Hijmans et al., 2005), soil variables, topographic variables and land-cover variables obtained by zonal statistics within each ecotope. Those variables have been selected based on expert knowledge and their contribution to habitat suitability models have been assessed in a previous study (Delangre et al., 2017). Calibration and validation polygons were then selected by crossing the ecotope database with the polygons of the NATURA 2000 database. An ecotope was labeled as a ravine maple forest biotope if more than half of its area was covered by its equivalent in the Natura 2000 cartography. To obtain a presence/absence dataset, ecotopes matching with ravine maple forests were considered as presence, while ecotopes matching with any other forest biotope were considered as an absence.

Different quality indices were used to validate the model, including the Overall Accuracy (OA) and the Area Under the Curve (AUC) of the model as well as producer and user accuracy (PA and UA) of the optimal binary classification between ravine forest and other forest biotope. In order to evaluate the accuracy of the model to detect ravine forests among all other biotopes, another overall accuracy was calculated taking into account all surfaces covered by Natura 2000 surveys (OA_Tot).Those indices were computed for the validation polygons which have been separated from the rest of the dataset before the calibration step. In order to provide an unbiased estimate of the correctly classified areas, the ecotope polygons were used as sampling units and their areas were taken into account (Radoux and Bogaert, 2017). The optimal binary classification was automatically determined based on the best compromise between sensitivity and specificity.

2.4. Results

By design, approximately 318400 image-segments were automatically created in the study area (with a range of 500 polygons, that is less than 0.2 percent). A visual check did not catch any macroscopic errors, but revealed most of the topographic features hidden by the vegetation on the aerial image. Figure 2.4 shows a subset of the segmentation result, highlighting the impact of the topography on the image-segments created inside patches of homogeneous land-cover. As expected, areas of homogeneous slope are well delineated in addition to the land-cover induced partitioning. Furthermore, the limits of the ecotopes are consistent with the pattern of slope curvature, which were not used for the segmentation.

Quantitative results related to the homogeneity of the image-segments are summarized in Tables 2.1 and 2.2. Overall, the advantage of automatically partitioned landscape against a regular grid of the same size is obvious. The results indeed show that the heterogeneity of the topographic attributes decreases and the separability of ecotopes increases when the partition of the landscape is determined by topography and land-cover. As shown in Figure 2.4, the results within the subset of polygons with a slope above 15 percent further highlight the differences where the terrain plays a bigger role in the definition of the polygons.

Table 2.1: Homogeneity of the image-segment as a function of the segmentation weights. The grid is composed of squares with the same area as the average of image-segments. Large purity values and low average variance of the slope indicate a good segmentation.

	0 (No Topographic Layers)	**0.5**	**1**	**2**	**Grid**
Slope variance	4.21	4.00	3.90	3.83	4.82
Aspect purity	94.4	94.4	94.5	94.5	94.3
Soil depth purity	82.8	82.8	84	83.1	79.9
Soil drainage purity	80.1	80.9	81.3	81.7	80.4
Land-cover purity	75.9	76.5	76.6	76.4	72.2

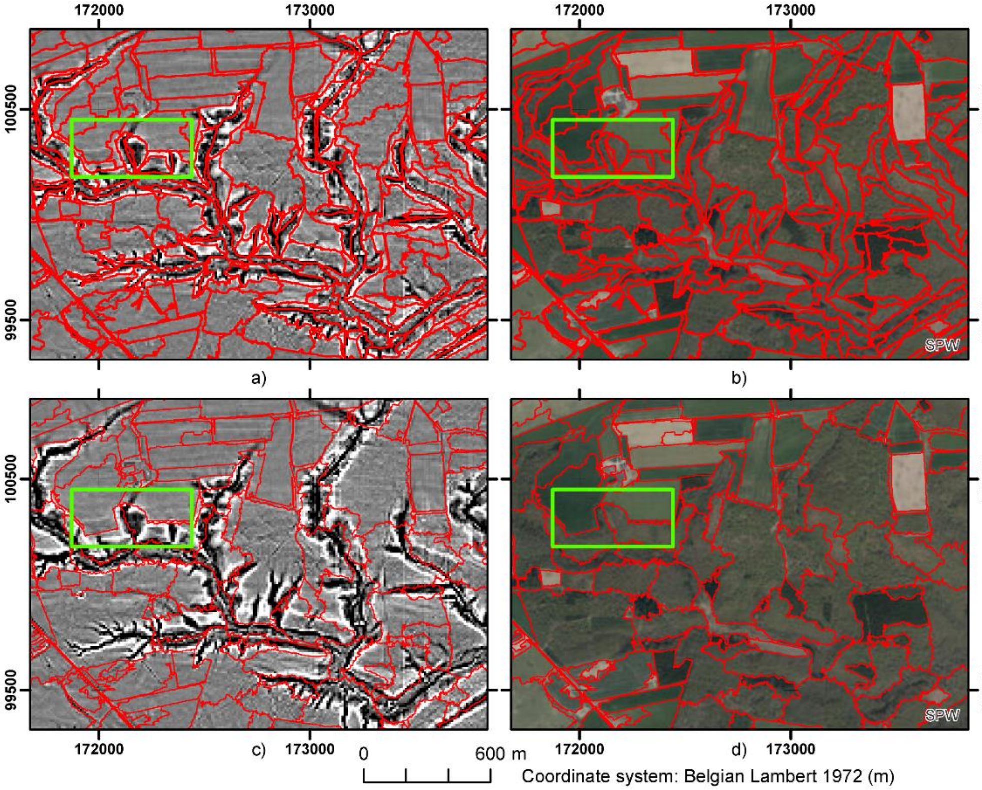

Figure 2.4: Image-segment boundaries (in red) overlaid on the curvature of the DEM at 10 m resolution (left) and the orthophoto from the Walloon Region (right, copyright SPW 2015). The images at the top (a,b) display the segmentation with the topographic bands (weight of 1); the images at the bottom (c,d) display the segmentation without the topographic bands. The green rectangle highlights an area where the land use boundaries follow the topography.

Table 2.2: Homogeneity of the subset of image-segments with a slope greater than 15 percent. The grid is composed of squares with the same area as the average of image-segments. Large purity values and low average of slope variance indicate a good segmentation.

	0 (No Topographic Layers)	**0.5**	**1**	**2**	**Grid**
Slope variance	10.6	8.1	7.1	6.2	11.6
Aspect purity	93.7	95.2	95.9	96.4	93.7
Soil depth purity	80.2	81.9	82.7	83.5	75.6
Soil drainage purity	79.7	81.8	82.4	82.5	78.3
Land-cover purity	69.4	75.0	75.4	76.4	64.8
Mean area (m^2)	20 466	17 379	16 432	15 577	19 016

The analysis of the predictive model indicate that the ecotopes are appropriate mapping units to map ravine forest in the study area. The overall accuracy of the best model is indeed 99.9% (Table 2.3). However, this value does not completely reflect the errors of the model because ravine forests are rare in the study area and specific to the polygons with a majority of broadleaved trees. Additional indices measured on a subset of the ecotopes with a majority of broadleaved trees are therefore more relevant to compare the different scenarios. On this subset, the use of topographic information to delineate polygons had a significantly positive impact on the results of the models. This confirms the results obtained by homogeneity measures (Tables 2.1 and 2.2). However, the best prediction is achieved for the GAM model when the weight of the topographic information is equal to the weight of the spectral information and the performances of the model decrease with the weight of 2.

Table 2.3: Results of the different models of ravine forest predictions with respect to the weight of topography in the segmentation. Matches correspond to the number of ecotopes matching at more than 50 percent with biotopes survey polygons. The next rows show the different quality indices including the overall accuracy of ravine forest mapping in the study area (OATot), the Overall Accuracy (OA), Area Under the Curve (AUC), Producer Accuracy (PA) and User Accuracy (UA) of the ravine forests for each model based on ecotopes covered by a majority of broadleaved trees.

	0	**0.5**	**1**	**2**
Matches	17	60	87	109
RF OA Tot	99.7	99.8	99.8	99.7
RF OA	93.2	94.7	95.5	92.7
RF AUC	79.6	97.1	96.8	94.3
RF PA	77.9	97.0	95.3	92.7
RF UA	8.90	18.9	25.3	16.1
GAM OA Tot	99.8	99.8	99.9	99.8
GAM OA	96.1	95.7	97.3	95.2
GAM AUC	81.4	95.6	97.6	95.2
GAM PA	77.2	93.1	97.0	92.7
GAM UA	15.0	21.9	37.2	22.5

The number of matching polygons increases when the segmentation uses more topographic components (Table 2.3). This is due to the fact that the polygon boundaries match the Natura 2000 boundaries closer than in the case without topographic contributions, but also because the polygons become on average smaller in rugged terrain when the topography is taken into account, as shown in Table 2.2.

2.5. Discussion

This study demonstrates that automated image segmentation simultaneously combining topographic information from LIDAR with the spectral information from optical sensors provides ecologically relevant polygons. Two facets of the results are discussed in this section: the technical quality of the results and the usefulness of the model for biodiversity studies.

2.5.1. Consistency of the Polygons

The objective of this paper was to build homogeneous polygons that would better match the concept of ecotopes than a delineation solely accounting for the land-cover. While it was foreseen that the addition of topographic information to the segmentation process would reduce the topographic heterogeneity, the increased land-cover homogeneity was surprising. This could be due to the long term land management practices that optimized land use based on the topography (for example, most crop fields are located on flat areas while steep slope are mainly covered by forests). Such patterns have been observed in the landscape, but the causality should be further investigated.

The results of the model shows that including topographic information improves the correspondence between ecotopes polygons and the field mapping of ravine forest biotope. The increased number of matches is partly due to the reduction of the average polygon size inside rugged terrain (about 25% for the weight of 2). The reduction of the size is however not sufficient to explain the large increase in the number of matches. This could be better explained by the fact that presence of biotope is highly dependent on the topographic situation. Indeed, contrasted situations such as south or north hillside leads to very different abiotic features. Furthermore, even a small difference of slope leads to different water intakes leading also to different vegetation communities.

Even if the model weren’t created in the best conditions due to the scarcity of the biotope, we can stress that we see a large leap in the AUC of the models (more than 16% for both RF and GAM) by adding topographic data in the segmentation process. Concerning the model accuracy, the big increase observed by adding topographic data is consistent with the improvement observed by the heterogeneity indices. However, we can see that the indices of the models don’t follow the same trend than the heterogeneity indices and are less correlated with the level of contribution of topographic data. This is probably due to the fact that we model a rare biotope with scarce presence data. Thus, the overall quality of the models is sensitive to the polygons selected in the calibration/validation process.

In this study, the average size was selected according to user requirements and fixed in order to fairly compare the contributions of the models. However, the size could also be optimized based on data driven features (Drăguţ et al., 2010; Radoux and Defourny, 2008) In this case, the weight of the topography, the vegetation height and the spectral values of the images should be considered to determine an optimal size. However, the observed difference between the trend in terms of ecotope purity and the trend of the fitness-to-purpose analysis should be further investigated as a potential issue to the use of a single optimization criteria.

On the other hand, landscape and landform analysis very much depends on the scale of the process being addressed and a hierarchical approach could help to extract additional characteristics from the landscape. For instance, elevation and curvature are important features at coarser scale to identify ridges or valleys. However, ridges and valley landforms include two sides facing opposite directions, which is not homogeneous in terms of insulation. The use of hillshade at local scale obviously placed the emphasis on potential insulation, but it also split image-segments in places of strong positive or negative curvature, which contributed to the improvement of characteristic soil properties. Identifying pattern from another scales could however be necessary to cover the processes that occur in more mountainous areas.

2.5.2. Usefulness of Biotope Models

The high (above 95% for both GAM and RF) AUC of the best models shows that models based on ecotope polygons are very consistent. However, despite the high specificity and sensitivity of the models, the user accuracy of the ravine forest class is very low. This low user accuracy can be explained by three different factors.

First, the ravine forests are rare in the study area. As a result, even a very small proportion of false positive had a strong impact on the user accuracy. Nevertheless, the absolute number of forest remains small, so that the models could help field prospecting by narrowing the search area to fewer than five percents of the total surface of forests.

Second, the models were used to test a concept and compare different segmentation strategies, but they could be tuned for other specific purposes. The selected optimization criteria, based on the sensitivity and the specificity, favored a solution that maximized the sensitivity because the specificity computed on a large proportion of absences was rapidly very high (above 97%), then slowly increased. This type of optimization is particularly useful for restraining the surveyed area in order to exhaustively map a specific biotope. Another threshold for binary classification could seek an optimum between producer’s and user’s accuracy based on the F-Score. With this alternative, the UA would be 0.63 and the PA would be 0.65, which is a good compromise for a generic result but less interesting for the identification of unknown biotopes of high biological interest.

Third, the model is limited by the available data, which does not replace field based observations. For instance, typical ferns in the understory are not visible by remote sensing. On the other hand, the ecotope might include all conditions for the development of maple ravine forests, but a different type of forest could have developed because of historical land management of the ecotope. From this point of view, a substantial proportion of the false positives could be considered priority zones for biotope restoration.

Nevertheless, values of user accuracy that we are discussing about are dependent of the correctly classified ravine forest among other broadleaved forests. If we take a look at total overall accuracy values, they show an excellent prediction of ravine forest in our study area therefore moderating the poor user accuracy previously discussed.

Referring to the field data, forest communities don’t follow a logic of tangible frontier, but they look like a gradient of vegetation communities mixing with another one. Limits are vague, but the conceptual model of the geographic database uses crisp boundaries to represent those transition areas. This conceptual mapping model into the so-called spatial regions is not specific to the GEOBIA, but it is also performed on the field when a boundary has to be drawn. While about half of the boundaries are matching the boundaries of the reference polygons with precision close to 10 m, diverging delineation occurs on the other half of the boundaries (Example on Figure 2.5). An independent field campaign was unable to undoubtedly and consistently arbitrate between the two datasets. Despite its limitations, the repeatability of the automated image segmentation makes it very useful in prospective studies or to guide interpretation on the field. However, the use of sharp boundaries could be an issue to represent gradients of vegetation or to be associated with punctual observations. It is therefore of paramount importance to remember that the proposed mapping strategy is a model used to represent the landscape in a way that closely matches the definition of biotopes from the field, but that there is no universal representation of nature.

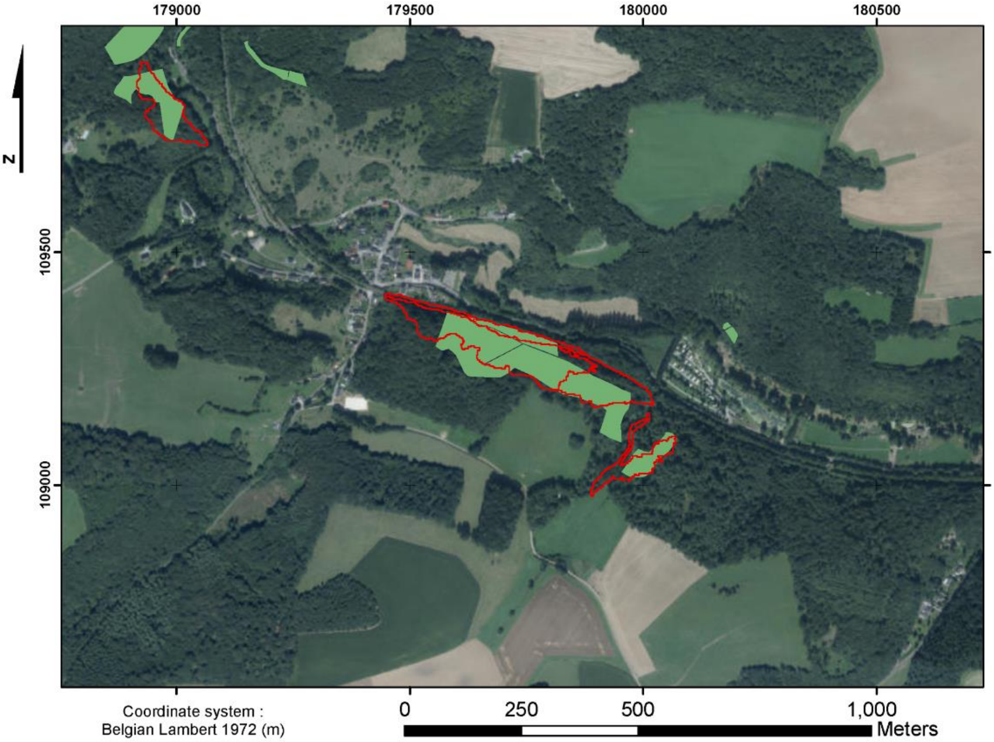

Figure 2.5: Divergences of delineation of ravine forest in the Natura 2000 database (green polygons) and the automated segmentation (red outlines).

2.6. Conclusions

This study demonstrates that hillshade layers can be used simultaneously with spectral information to improve the automated delineation of ecotopes in a GEOBIA framework. The AUC of predictive ecological models was improved by 15% when the ecotopes were delineatd using these topographic layers. Furthermore, the inclusion of topographic features in the segmentation process also improved the purity in terms of land-cover, probably due to the indirect impact of the topography on the land use in the study area.

The good results at small scale factor suggests that the proposed GEOBIA workflow could be tested at larger scale factor in combination with curvature indices in order to generate homogeneous landforms with minimal arbitrary decisions.

Chapter 3

Identify High Biological Value Areas Through Vegetation Dynamic Series Concept

1. Preamble

After evaluating the performance of delineating ecotopes with incorporating topographic data to obtain homogenous and ecologically distinct landscape units, we focused on mapping biotope potential distribution to serve as the most precise unit or mapping habitat patches to connect in a fragmented landscape. In this chapter, our primary objective was to propose an efficient approach for biotope distribution modeling that encompasses multiple biotopes across the entire territory while considering the temporal dynamics of vegetation in human-dominated landscapes. To accomplish this, we focused on the concept of potential natural vegetation (PNV), which considers vegetation communities belonging to the same vegetation succession and sharing ecological contexts as a unique mapping unit.

We evaluated this approach by analyzing its modeling performance, comparing our results to distribution models that focus on individual biotopes separately, and utilizing floristic observation data for independent quality assessment.

This chapter is composed of a preliminary analysis evaluating the use of ecotope as biotope modeling unit. The next section is a study about implementing PNV concept in biotope modeling approaches and is adapted from : Bourdouxhe, A., Wibail, L., Claessens, H., Dufrêne, M., 2023. Modeling potential natural vegetation: A new light on an old concept to guide nature conservation in fragmented and degraded landscapes. Ecological Modelling 481, 110382.

2. Preliminary analysis

2.1. Introduction

Segmenting ecotopes offers a promising method for defining coherent landscape features and effectively synthesizing ecological information, as highlighted in previous study (Radoux et al., 2019). These ecotopes could serve as fundamental units for conducting ecological analyses like Species Distribution Models (SDMs). Available ecotope databases precisely delineate landscape feature (at a 2m scale), in contrast to their larger 2ha average size. This approach not only reduces the number of computing units but also has the potential to improve the predictive power of ecological models by optimizing computational efficiency and enhancing environmental homogeneity. While raster datasets are commonly employed in such analyses, they are often arbitrarily defined and lack ecological significance. Consequently, it is natural to question the efficacy of both approaches. A comparative evaluation of segmented ecotope datasets and traditional raster datasets is vital for determining their respective performance and reliability in ecological analyses, such as SDMs. A sensitivity analysis was previously conducted to compare the performance of raster and ecotope representations for SDMs. Various sizes were used to be compared as grain size affect model predictive power (Gottschalk et al., 2011; Guisan et al., 2007). The results revealed that, for the majority of the species species, ecotopes measuring 2 hectares on average outperformed raster representations of comparable size (Delangre et al., 2017). However, it is worth noting that the observed differences were not consistent across both representations.

Given that biotope distribution models primarily rely on SDM approaches, it is imperative to conduct a comprehensive analysis comparing ecotope and raster data, especially in the context of biotopes characterized by specific species communities. The following analysis seeks to provide valuable insights into the most effective modeling approach in accurately predicting biotope distribution patterns before applying it more generally.

2.2. Method

2.2.1. Ecotope database

The ecotope database used in this study is an environmental database composed of polygons representing ecotopes, the smallest homogeneous unit of the landscape. This database was produced in the framework of LifeWatch-WB project and covers whole Belgian territory (Radoux et al., 2019). The segmentation of ecotopes is performed by an algorithm using orthophotoplan, vegetation height and hillshade fixing a mean polygon size of 2 hectares. A multitude of environmental predictors are resumed at the ecotope scale such as land-cover, soils attributes, climatic conditions and many more.

2.2.2. Modeling biotope distribution

For biotope distribution modeling, we opted for a 10m resolution raster which has a finer grain size than ecotope to better catch environmental predictor variability and improve modeling performance. This raster size is far from ecotope delineation accuracy (2m) but is a compromise between sufficient delineation and keeping a dataset with a manageable size for modeling.

To test this approach, we focused on a 1558 km² area located at the south of the city of Liège in eastern Belgium where a wide diversity of biotopes is present.

Two different calibration datasets are then constructed using Natura 2000 map. This map is composed of polygons delimiting biotopes, i.e. an environmental area characterized by particular environmental conditions and a specific community of species (Löfvenhaft et al., 2002). But, as biotope rarely follow tangible limits and is more a gradient of changing vegetation communities, polygons often describe complex of biotopes. Each polygon is therefore linked to one or multiple biotopes that are identified by an unique EUNIS (European Nature Information System) code. To facilitate the integration of this dataset we used biotope proportion inside Natura 2000 polygons and the majority biotope was further considered.

For this study, we focused on four forest biotopes: Medio-European acidophilous *Fagus* forests (EUNIS: G1.61), Medio-European acidophilous non-thermophilic *Quercus* forests (EUNIS: G1.87a), *Acer* and *Tilia* forests with *Asplenium* *scolopendrium* (EUNIS: G1.A41a), and Sub-Atlantic calciphile *Quercus* - *Carpinus betulus* forests (EUNIS: G1.A17). To ensure the good differentiation between presence and absence of biotopes, only other natural biotopes of the same succession stage are considered as absence during modeling (i.e. natural forests biotopes).

The environmental dataset uses a 10m resolution raster environmental dataset. This dataset is composed of 8 predictors: annual mean temperature, standard deviation of temperature, solar radiation the first day of spring, soil depth categories, presence of marginal soils, soil drainage categories, topographic relative position (TPI, topographic position index calculated in a 200m radius), and slope percentage. For the raster approach, biotope reference dataset was then used to attribute biotope EUNIS code to each cell of our environmental dataset with their center covered by Natura 2000 biotope polygons.

The ecotope approach uses the same environmental dataset but summarized at the ecotope scale. Continuous predictors (annual mean temperature, standard deviation of temperature, solar radiation the first day of spring, normalized topographic relative position and slope percentage) are summarized based on mean value inside the ecotope. Categorical predictors (soil depth categories, presence of marginal soils and soil drainage categories) are splitted by each category and the proportion of each category inside the ecotope is measured. The EUNIS code from Natura 2000 biotope map is attributed to the ecotope if overlapping surface area between the two polygons concern at least 50% of the ecotope.

The modeling approach uses a Random Forest algorithm and by splitting randomly the same dataset to obtain a calibration and validation dataset. Prediction accuracies are evaluated using four accuracy metrics (AUC, Overall Accuracy, Producer Accuracy and User Accuracy). The overall accuracy (OA) measures the proportion of correctly classified pixels (both presence and absence) compared to the total number of pixels used for validation. The producer accuracy (PA) assesses the proportion of reference pixels that are correctly classified, as evaluated from the perspective of the cartographer examining the model's predictions. The user accuracy (UA) gauges the proportion of accurately classified presence pixels in relation to the total number of predicted presences. This metric evaluates the model's ability to predict the presence of a biotope from the perspective of the map user. For these metrics, which are dependent on threshold values, the threshold that maximizes the F-score was utilized to convert the model's probability estimates into presence or absence predictions. The F-score is calculated as the harmonic mean of precision and recall. To ensure an impartial estimation of accurately classified landscape unit, ecotope polygons were utilized as sampling units, and their respective areas were considered inaccuracy metric calculation.

2.3. Results

Results of biotope model prediction for both approaches are available in Table 3.1.

Table 3.1: Accuracy metrics resulting from modeling biotopes using ecotope segmentation or 10 meter resolution raster to summarize environmental data. AUC: Area Under the Curve, OA: Overall accuracy, PA: Producer accuracy, UA: User accuracy.

	AUC		**OA**		**PA**		**UA**	
Biotopes	Ecotope	Raster	Ecotope	Raster	Ecotope	Raster	Ecotope	Raster
G1.61	0.90	0.99	0.87	0.97	0.80	0.84	0.44	0.87
G1.87a	0.84	0.99	0.88	0.97	0.56	0.89	0.51	0.89
G1.A17	0.95	0.99	0.90	0.96	0.88	0.90	0.75	0.94
G1.A41a	0.90	0.97	0.94	0.98	0.66	0.67	0.34	0.66

We can observe that modeling directly using raster data perform largely better than summarizing information at the ecotope level. We see a mean increase of 33% for UA when using raster. This increase is far more important in UA than in other accuracy metrics.

2.4. Discussion

Our results of modeling biotope distributions showed improvements in accuracy metrics when using a raster approach. Improvement is more important in terms of UA which means that model predictions are more precise. Different factors may explain these differences.

First, using ecotope data to gather information from another vectorized datasets using overlap thresholds limits the quantity of calibration data. At the opposite using rasterized environmental predictor and attribute calibration data to each cell with their center inside vectorized objects allow to increase the quantity and variability of predictor values. Therefore, the ecological envelope of biotopes may be better evaluated using raster data. However, this variability in predictor values may also increase the negative impact of border effect and even more when considering operator effects during biotope mapping. Rare biotopes are often present in specific marginal ecological context dependent of oro-hydrographic context. Therefore, their shape is often linear which increase confusion with neighboring ecological context not representative of modeled biotope. However, such effect did not negatively impact accuracy metric results for raster approach.

The ecotope approach may encounter limitations due to the exclusion of certain ecological predictors during its automated segmentation process. Restricting the use of environmental predictors closely related to ecotopes could potentially narrow the disparity between the ecotope approach and other methodologies. However, this constraint may also curtail the model's predictive power by overlooking crucial predictors. Additionally, the threshold of 50% coincidence between ecotope delineation and biotope maps could impact model performance. This threshold aids in selecting biotope polygons that exhibit purity in terms of topography and land-cover, thus potentially enhancing model accuracy by limiting the use of polygons representing a complex mixture of different biotopes. However, this might lead to a reduction in the number of calibration data, consequently decreasing model sensitivity (Figure 3.1). Adjusting the minimal threshold value may further influence the calibration data size and, consequently, the model's sensitivity and precision. Raising the threshold can result in reduced calibration data and diminished model sensitivity, while lowering the threshold may introduce environmental data distant from the ecological context of the model biotope, leading to decreased model precision. In our study, we selected a 50% threshold to strike a balance between sensitivity and precision. It is essential to acknowledge these considerations while employing the ecotope approach for predictive modeling and to be mindful of the potential trade-offs between sensitivity, precision, and model accuracy.

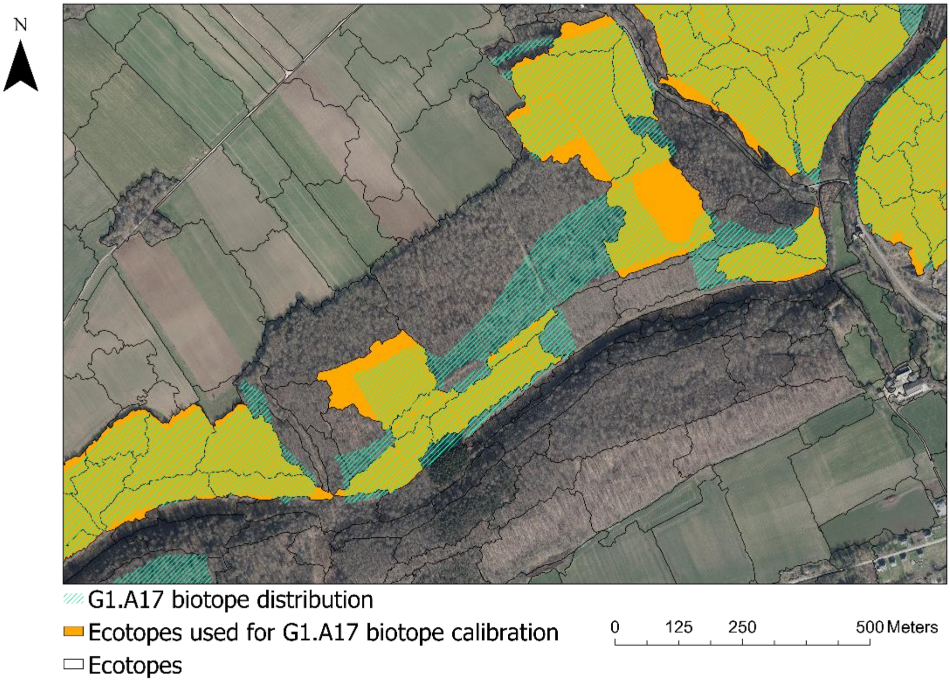

Figure 3.1: Ecotope polygon used to represent presence of Sub-Atlantic calciphile Quercus - Carpinus betulus forests (G1.A17) for calibrating distribution model (orange) compared to actual distribution of the same biotope in Natura 2000 biotope map (hatched green). Ecotope segmentation is represented by black line.

It is important to precise that categorical ordinal predictors must have been processed before their implementation in the ecotope database. Environmental predictors are therefore not identical between the two approaches. Moreover, grain size is not equivalent. Ecotopes have an average size of 2 hectares while 10m raster resolution have a 0.01ha size. Multiple authors have measured the importance of grain size on species distribution models with divergent results depending on the studied species (Graf et al., 2005; Li et al., 2006). Studies on the relationship between model accuracy and grain size have indicated minimal variations. However, a consistent pattern emerges, suggesting that reducing the grain size enhances the model's accuracy (Gottschalk et al., 2011; Guisan et al., 2007). This can be attributed to a more precise identification and differentiation of habitats, as well as the possibility to use more accurate observation data (Gottschalk et al., 2011). In our study, we opted for a raster resolution of 10 meters, striking a balance between improved delineation and manageable size. It is important to note that this resolution does not align with the accuracy of ecotope delineation, which stands at 2 meters. Consequently, we can argue that the utilization of a raster representation reduced the grain size without necessarily improving the distinction between landscape elements. Nonetheless, this approach ultimately led to improved predictive model accuracy.

Delangre et al. (2017) conducted a sensitivity analysis on the accuracy of SDMs for multiple species, considering various grain sizes of raster and ecotope representations. While there were small but statistically significant differences in accuracy metrics, no clear trends emerged to definitively recommend one representation type over the other. However, the study did confirm a general trend that finer grain sizes tend to yield better prediction results confirming the findings of previous studies (Guisan et al., 2007). It is worth noting that this study solely assessed model accuracy using the AUC metric, and other metrics could have been employed to further validate these trends. Metrics such as User Accuracy or Producer Accuracy have the potential to reveal differences in model accuracy that may not be evident when relying solely on AUC (Bourdouxhe et al., 2023). Moreover, confusion matrices offer a comprehensive solution by providing detailed insights into the distribution of errors. Derived from these matrices are numerous accuracy metrics, facilitating their interpretation based on the specific requirements of the study. Nonetheless, the utilization of confusion matrices is contingent upon two key factors: the ability to transform predicted values into discrete values and the presence of adequately balanced calibration data (Anderson et al., 2003; Peterson et al., 2008).

Regarding biotope distribution modeling, the 10-meter raster resolution demonstrates significant improvements compared to the utilization of ecotope segmentation with an average size of 2 hectares. The 10-meter raster resolution strikes a favorable balance between fine grain size, ecological context delineation, and manageable data size. Hence, when precise calibration of data is crucial for well-defined areas, we advocate employing raster datasets for predictive modeling. In such instances, local contexts may lose some ecological significance, but the advantage lies in the absence of disadvantages associated with fine grain representation. Conversely, when modeling species, an excessively fine grain could potentially lead to certain drawbacks. For instance, it might not effectively represent complex species habitats that comprise diverse vegetation structures, or it might be uninformative when delineating forest gaps with isolated trees. Furthermore, there is a potential for vectorized data, such as ecotopes, to assist in synthesizing point-based observations into ecologically distinct entities. This approach holds promise in providing a means to represent ecological contexts more comprehensively and distinctly. However, it should be acknowledged that further research is needed to explore and validate the efficacy of this method fully.

2.5. Conclusion

In conclusion, this study demonstrated that using a 10-meter raster resolution improves the accuracy of biotope distribution models compared to ecotope segmentation with an average size of 2 hectares. The raster approach provides a balance between delineation of ecological contexts while maintaining manageable data size. However, ecotope segmentation remains relevant in certain situations, when local context has an ecological significance that exceeds the importance of better delineating ecological contexts.

3. Modeling potential natural vegetation: A new light on an old concept to guide nature conservation in fragmented and degraded landscapes

3.1. Introduction

The restoration of functional species habitat networks became a priority to tackle landscape fragmentation, one of the key factor of biodiversity loss (Hilty et al., 2020a; IPBES, 2019; Resasco, 2019). This implies the use of multiple information sources involving the recording and mapping of species of interest, vegetation, ecological conditions, land use, pressures, management, dispersal barriers and many more. One key source of information is vegetation mapping using the biotope concept. A biotope is a landscape unit characterized by specific environmental conditions and supporting a characteristic community of species. A species habitat is considered as the set of biotopes it needs to complete its lifecycle (R. T. T. Forman, 1995; Löfvenhaft et al., 2002). Biotope level can therefore be considered as the finest unit of landscape management for conservation purpose. Biotopes are commonly described by the vegetation species assemblages depending on more or less precise ecological conditions (Davies et al., 2004). Generally, these ecological conditions are defined by topography, hydrography, climate, soil type and human management, justifying that biotope units are significant landscape features. However, as biotope surveys require skilled teams that sometimes have to cover large territories (Lillesand et al., 2008), biotope mapping is therefore limited by time-consuming surveys, which restricts their capacity to be up-to-date in a land-use change context. To circumvent these technical limitations, biotope modeling using available environmental predictors and remote-sensing data is increasingly being developed (Horvath et al., 2019; Maggini et al., 2006). This approach, derived from species distribution modeling (SDM), produces relatively accurate maps of the current or the potential distribution of biotopes when, taking into account land-cover or not (Álvarez-Martínez et al., 2018; Horvath et al., 2019). Current and potential biotope distributions are also strategic information to design ecological networks. Biotope restoration can then target areas to increase species habitat patches and limit fragmentation impacts to compensate habitat loss due to human activities (Jones et al., 2021).

The interest and quality of biotope distribution modeling (BDM) is however limited because several biotopes can occupy similar ecological conditions (soil, climate and topography) during the vegetation successions. Indeed, plant communities characterizing biotopes evolve naturally from pioneer open biotopes to mature forest biotopes reaching one or several stages of equilibrium called climax (Niering, 1987). Different types of successional patterns are possible with dynamics of natural or artificial disturbances that, for example, restart the process of succession, regressive dynamics, lock-in at certain stages, etc (Blasi et al., 2004;

Rees et al., 2001; Woodward, 2009). BDM accuracy is thus disturbed by the competition between different biotopes belonging to the same succession in similar ecological conditions and the difficulty of having descriptive variables to discriminate the different stages. Some authors consider this issue by focusing only on climax stage biotopes (Horvath et al., 2019; Maggini et al., 2006). The presence of some stages/biotopes of a vegetation succession is also impacted by human management that restricts them to less productive areas such as the steepest slopes or the most superficial soils (Hall, 1988). The observed relationship between some biotope distribution and environmental conditions, therefore, can only be one part of the potential biotope ecological envelope .

One pragmatic solution to consider temporal dynamics of ecosysems is to use the concept of “potential natural vegetation” (PNV). PNV concept was defined by Tuxen (1956) as ‘the vegetation that would develop in a particular ecological zone or environment, assuming the conditions of flora and fauna to be natural, if the action of man on the vegetation mantle stopped and in the absence of substantial alteration in present climatic conditions’ (Gallizia Vuerich et al., 2001). By convention, PNV therefore refer to climax vegetation but it designs the ecological conditions necessary for the development of the main stages of the associated succession (Loidi and Fernández-González, 2012; Prach et al., 2016). The concept of PNV makes it possible to define landscape units that share similar ecological contexts, regardless of the stage of natural vegetation succession (Leguédois et al., 2011; Stumpel and Kalkhoven, 1978). This concept was used in the past to classify the landscape to guide nature oriented sylviculture, conservation and landscape planning (De Keersmaeker et al., 2013). Such PNV maps can also be used as one of multiple approaches to determine the conservation status or naturalness of areas by measuring the difference between PNV and current land-cover (Hemsing and Bryn, 2012) or to identify gaps and completion of networks of protected areas such as Natura 2000 (Bohn and Gollub, 2006). PNV mapping can be seen as an integrative approach that better considers vegetation dynamics, which is important for the design and connectivity of ecological networks and their management. It has the advantage of better delineating the maximum potential distribution of biotopes depending on the ecological context and therefore ensures network coherence. It also helps to guide the management of conservation and restoration actions based on natural disturbance to create a more heterogeneous landscape.

However, the expected link between PNV typology and ecological conditions is well debated among experts (Chiarucci et al., 2010). Pioneer or intermediate biotopes are sometimes shared by different vegetation succession series. The dynamic drivers influencing a biotope to develop to a specific vegetation succession may be subtle variations in ecological factors and vegetation composition that are undetected in the field, the result of biological processes (competition and predation favoring certain species) or the impact of direct (management) or indirect (pollution, eutrophication, etc.) effects of present and past human activities. However, a lot of example of vegetation communities evolving to the expected climax exist thanks to a better understanding of these successions (Loidi and Fernández-González, 2012; Prach et al., 2016).

The most important prerequisites to map PNV are therefore (Loidi and Fernández-González, 2012):

1. a PNV typology that is sufficiently validated with quite exclusive biotopes belonging to each PNV,
2. a validated mapping of the different biotopes belonging to each PNV
3. a precise mapping of ecological factors which are supposed to play an essential and proximal role in biotope distribution.

PNV mapping also benefited from the development of distribution modeling approaches and multiple examples of PNV modeling exist (Reger et al., 2014; Somodi et al., 2017). Recent studies addressed different topics such as the best modeling approach (Hemsing and Bryn, 2012), the representation of multiple overlapping modeled PNV (Somodi et al., 2017), the definition of PNV (De Keersmaeker et al., 2013) or the modeling of numerous PNV at larger (Liu et al., 2009) and smaller scales (Longcore et al., 2018). When PNV and related vegetation communities are well identified, they are mainly based on national classification systems and models are calibrated on stable/climax forest or open areas stages reference data (Hemsing and Bryn, 2012). Building PNV based on species assemblage using floristic occurrence data is far more complex and raise many methodological questions (De Keersmaeker et al., 2013). The presence of characteristic species is highly dependent of natural sites condition and some PNV may not have any highly characteristic species (De Keersmaeker et al., 2013). The integration of multiple PNV predictions into a single map allows to better apprehend such useful results but current aggregation method are complex (Somodi et al., 2017).

In the other hand, single biotope modeling – i.e., peat bogs, calcareous grasslands, moors, etc. – is still being applied (Horvath et al., 2019). In the literature, PNV concept seems to be a closed study field as many biotopes modeling study cases do not even mention PNV concept (Álvarez-Martínez et al., 2018; Horvath et al., 2019).However and as mentioned earlier, modeling PNV present many advantages to produce accurate and useful prediction map of biotopes.

In this paper, we propose a methodological framework which aims to be as most replicable as possible using biotopes classification systems and mapping used in all European countries. In contrast to last PNV modeling applications using stable forest stages, we suggest modeling PNV using multiples biotopes from the same vegetation succession to better cover the ecological envelopes of PNV in disturbed landscapes. Our methodological framework also proposes a simpler aggregation technique to deliver a unique map of all PNV considering also potential overlaps. We will also compare PNV modeling approach to individual biotope modeling and assess performance of both approaches. Finally, we also suggest an independent qualitative assessment of modeled PNV distributions using floristic occurrence data.

3.2. Materials and methods

3.2.1. Study area

Wallonia is an administrative region covering southern Belgium (17 000 km2). It is characterized by a temperate climate with precipitation distributed throughout the year. However, the precipitation can double within the territory (from 800 to 1600 mm/year) and its rate increases with altitude. The summit of the region is a high peaty plateau that culminates at 694 m above sea level. The Walloon region can be split into six principal parallel biogeographic zones that are well defined by a large gradient from recent to oldest geological substrates going from NW to SE. This explains a wide diversity of very different ecological contexts, ranging from boreo-alpine peatlands to Mediterranean limestone lawns less than 30 km away (Dufrêne and Legendre, 1991).

3.2.2. Methodological framework

The proposed approach was carried out in four steps:

1. Biotopes developing in the same ecological context were identified and referred to one specific PNV by using historic and recent expert knowledge to maximize the difference between PNV ecological contexts.
2. PNV distributions were individually modeled using environmental predictors including topographic information, soil conditions and climatic parameters.
3. To obtain a unique typology for the territory, possible PNV prediction maps were used as predictors to produce a classification to test the potential presence of the different PNV.
4. Finally, overlaps between individually modeled PNV distributions were identified. These mixed PNV areas allowed us to identify where the proposed classification is more uncertain.

The general workflow of our method is summarized in Figure 3.2.

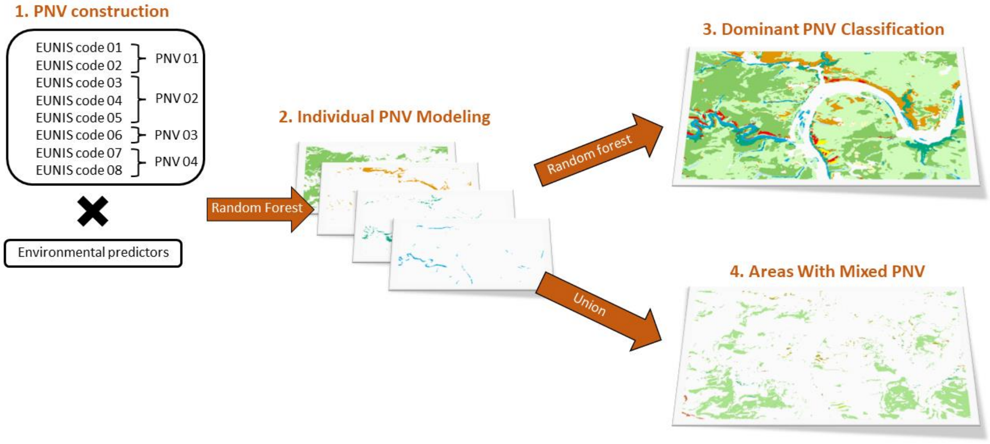

Figure 3.2: Schematization of the general workflow for the proposed approach with the different results. 1. Biotopes are attributed to defined PNV. 2. Individual PNV are modeled. 3.These individual predictions are used to produce a classification map. 4. Individual prediction maps are overlapped to identify potential areas with multiple PNV predicted.

3.2.3. PNV construction

The biotope classification and denominations used in this study are based on the EUNIS (European Nature Information System) classification for biotope types (Davies et al., 2004). EUNIS is a hierarchical classification describing every biotope and habitat present in Europe, from natural to artificial, and covering terrestrial, freshwater and marine ecosystems. The EUNIS classification was adapted to Wallonia by the public research agency in order to match regional variations (Dufrêne and Delescaille, 2005). Each biotope is characterized by a unique code.

The PNV modeled in this study were identified to cover almost all ecological contexts of the region using phytosociological literature (Delescaille et al., 2021) complemented by expert opinion. The region has historically hosted several famous authors working on phytosociology and vegetation successions, who precisely described the different vegetation stages, their dynamics and links with ecological contexts making expert opinion highly robust (Duvigneaud, 1949; Herbauts and Tanghe, 1987; Noirfalise, 1984; Venseveren, 1969). Common and scarce biotopes were selected if there was sufficient data to model them and if they belong to only one vegetation succession. Some open biotopes such as sub-montane *Vaccinium* and *Calluna* heaths can evolve toward two different climax stages (medio-European acidophilous *Fagus* forests and medio-European thermophile acidophilous *Quercus* forests) and were therefore discarded. Biotopes corresponding to intensive agricultural practices or exotic tree plantations were also eliminated as they are not linked to a particular ecological condition. All biotopes and PNV assignations are compiled in Table 3.2. For further details, Appendix 1 presents all biotopes belonging to a PNV even if they are present in multiple PNV.

Table 3.2: List of biotopes considered in this study and their related PNV. Biotopes are referred to by their EUNIS classification adapted to Wallonia and Habitats Directive classification (asterisks indicate habitat of priority European interest). PNV are sorted by a humidity gradient of their ecological context from marshy to xeric.

EUNIS Code	Habitats Directive code	Biotopes names	Potential Natural Vegetation	Code	Area mapped in reference dataset (ha)
D1.1	**7110***	Raised bogs	***Sphagnum Betula*** **woods**	**SB**	**485**
G1.51	**91D0***	*Sphagnum Betula* woods			
D5.21^e		Beds of large *Carex spp.*	***Alnus*** **swamp woods**	**AS**	**229**
G1.4		Broad-leaved swamp woodland not on acid peat			
F4.11b	**4010**	Wet heathland with *Vaccinium* and *Erica tetralix*	***Quercus*** **and** ***Betula*** **forests with** ***Molinia***	**QBM**	**1 510**
F4.13		*Molinia caerulea* wet heath			
G1.81	**9190***	Atlantic *Quercus robur – Betula* woods			
G1.911a	**9190***	*Betula* facies of *Quercus robur* forests			
F9.12	**91E0***	Lowland and collinear riverine *Salix* scrub	**Riparian and gallery woodland**	**RG**	**1 087**
G1.1	**91E0***	Riparian and gallery woodland, with dominant *Alnus, Betula, Populus* or *Salix*			
G1.2	**91E0*, 91F0**	Mixed riparian floodplain and gallery woodland			
G1.A15a	**9160**	Famennian *Quercus – Carpinus betulus* forests on schist	**Fammenian** ***Quercus*** **and** ***Carpinus*** **forests**	**FQC**	**9 482**
G1.A1ba		Atlantic neutrophile *Quercus* and *Fraxinus* forests on hydromorphic soils	**Neutrophile** ***Quercus*** **and** ***Fraxinus*** **forests on wet soils**	**NQF**	**3 231**
G1.A1da	**9160**	Sub-Atlantic neutrophile *Quercus* and *Fraxinus* forests on hydromorphic soils			
G1.A1aa		Atlantic acidocline *Quercus* and *Carpinus* forests on hydromorphic soils	**Acidophilous** ***Quercus*** **and** ***Carpinus*** **forests on wet soils**	***AQC***	**38**
G1.A1ca	**9160**	Sub-Atlantic acidocline *Quercus* and *Carpinus* forests on hydromorphic soils			

G1.63	**9130**	Medio-European neutrophile *Fagus* forests	**Neutrophile *Fagus* forests**	**NF**	**6 055**
G1.A1bb	**9130**	Atlantic neutrophile *Quercus* and *Fraxinus* forests substitute to *Fagus*			
G1.A1db	**9130**	Sub-Atlantic neutrophile *Quercus* and *Fraxinus* forests substitute to *Fagus*			
G1.A41b	**9180***	*Acer* and *Ulmus* Ardennes forests	**Wet and shady ravine forests**	**WSR**	**640**
G1.A41a	**9180***	*Acer* and *Tilia* forests with *Asplenium scolopendrium*			
G1.61	**9110**	Medio-European acidophilous *Fagus* forests	**Acidophilous *Fagus* forests**	**AF**	**42 199**
G1.62	**9120**	Atlantic acidophilous *Fagus* forests			
G1.82	**9120**	Atlantic acidophilous *Fagus* – *Quercus* forests			
G1.87a		Medio-European acidophilous non-thermophilic *Quercus* forests			
G1.A1ab	**9120**	Atlantic acidocline *Quercus* and *Fraxinus* forests substitute to *Fagus*			
G1.A1cb		Sub-Atlantic acidocline *Quercus* and *Fraxinus* forests substitute to *Betula*			
E1.26	**6210***	Sub-Atlantic semi-dry calcareous grassland	**Calcareous *Fagus* and *Quercus* forests**	**CFQ**	**2 443**
E1.27	**6210***	Sub-Atlantic very dry calcareous grassland			
G1.66	**9150**	Medio-European limestone *Fagus* forests			
G1.71		Western *Quercus pubescens* woods and related communities			
G1.A17	**9150**	Sub-Atlantic calciphile *Quercus* – *Carpinus betulus* forests			
G1.87b		Medio-European thermophile acidophilous *Quercus* forests	**Thermophile acidophilous *Quercus* forests**	**TAQ**	**67**
G1.A15b		Famennian xerophile *Quercus* – *Carpinus betulus* forests	**Xerophile Fammenian *Quercus* and *Carpinus* forests**	**XFQC**	**133**

3.2.4. Environmental dataset

Belgium has the particularity to be covered by a multitude of environmental datasets at high resolution. For instance, the country is covered by a soil dataset with detailed information on soil structure, composition and humidity at a precise scale (1/10 000) (Bah et al., 2007). More modern tools like digital elevation models based on LIDAR (light detection and ranging) are also available at high resolution (1m). These precise environmental informations make it possible to better capture the relationship between environmental predictor and vegetation assemblages than it could be with generic and larger scale dataset such as Soilgrids (Poggio et al., 2021).

The environmental variables used as predictors to model PNV distributions were split into three categories: climatic variables, soil dependent variables and topographic variables.

Bioclimatic variables were extracted from high-resolution (1 km²) climate data derived from the downscaling of EURO-CORDEX regional climate model (RCM) datasets representing the historical climate between 1971 and 2005 and covering all Europe (De Troch et al., 2020). EURO-CORDEX RCM is considered as more spatially coherent at fine-scale than widely used models such as Worldclim or Climate-EU (Chakraborty et al., 2021). This dataset proposes a subset of best climatic predictor for species distribution modeling and integrate original interesting climatic variable such as annual mean potential evapotranspiration. Soil related variables were principally extracted from the digital soil map of Wallonia (Bah et al., 2007; "Carte Numérique des Sols de Wallonie - Série," 2015). Different soil types (Calcareous, Podzol, Organic, Sandy, Alluvial and Source) were stored as binary variables. Natural soil drainage (Drainage), hydric level (Hydric_lvl) and trophic level (Trophic_lvl) were extracted as ordinal variables. Natural drainage was subdivided into 5 ordinal classes directly derived from the soil –ap (dry and very dry soils; moderately dry and wet soils; wet soils with temporary water table; very wet soils with temporary water table; very wet and peaty soils).

Two variables were derived from a dataset created to guide sylvicultural practices (Petit S. et al., 2017). Hydric level (Hydric_lvl) is a variable evaluating the humidity level of a soil based on the combination of natural drainage, soil texture and topographic position. Trophic level (Trophic_lvl) is also a variable quantifying the amount of nutrients available to the plants based on a dichotomous key using soil characteristics. These cartographic data are available online in open access ("Forestimator," 2021).

Soil texture (Sand and Silt) proportions present in the soil were not available on maps but from another data source by performing a convolution between texture information from the Walloon digital soil map and the kriging of more accurate and latest field observation points (D'Or Dimitri, 2021). These are continuous variables with the proportion of sand and silt measured at a 50 m resolution.

Finally, topographic continuous variables included elevation (Elevation), slope percentage (Slope_prc), topographic position index calculated in a 200 m radius normalized from 0 to 100 (TPI) and the potential incident light energy in W/m² for the first day of spring (SunSpring). These predictors are derived from 1m LIDAR acquisition resampled at 10m and produced for the study purpose (“Relief de la Wallonie - Modèle Numérique de Surface (MNS) 2013-2014 – Hillshade,” 2015). The radiative subsector (Radiative_SS) and the potential water intake (Water_int) are categorical variables constructed with dichotomous keys based on relative position, slope and exposure to guide sylvicultural practices (Petit S. et al., 2017). They are also available online in open access (“Forestimator,” 2021).

Predictors used in this study have different resolutions ranging from 1km for climate data to 10m for topographic ones. We chose to resample all predictors to 10m resolution to match the finest resolution which is also a compromised between computing time during modeling and precision at a regional scale (study area of 17 000 km^2). Different approaches exist to consider multiscale relations between predictors. Some authors perform a first model at larger scale then use the results as a predictor to perform a second model at finest scale with other predictors (Source). More than increase complexity of our approach, this kind of method does not improve significantly model results to be chosen (Source).All predictors were therefore resampled and assembled in a raster stack of 10 m resolution.

Autocorrelation was tested to conserve independent variables for modeling. Elevation and all climatic variables except the annual variation of precipitation (AnnualVariationPrecipitation) showed a Pearson correlation coefficient higher than 0.7 or lower than –0.7 and were considered to be strongly correlated (Ratner, 2009). But bioclimatic variables are considered of high biological significance influencing plant and species distribution (Bede-Fazekas and Somodi, 2020). They were summarized by using the two main principal component axes resulting from a principal component analysis (PCA) (Climatic_pca_1 and Climatic_pca_2) to limit correlation but keep the maximum amount of information (88% and 10% of explained variance). This use of multivariate analysis to create a composite predictor has already been used and give convincing results in species and ecosystem distribution modeling (Ejrnæs, 2000; Santos et al., 2020; Simensen et al., 2020).

Normality of each variable was tested and values were transformed if necessary. Slope percentage and annual variation of precipitation were transformed with a logarithmic function. In total, 19 environmental predictors were kept for modeling (Table 3.3).

Table 3.3: List of environmental predictors used in this study and their descriptions.

Predictor alias	Description	Unit	Range	Native Resolution	Transformation	Source
Climatic_pca_1	First principal component axis coordinate of climatic predictors and elevation	-	-500 – 709	1000 m (climatic) – 1 m (elevation)	-	(De troch et al., 2020)
Climatic_pca_2	Second principal component axis coordinate of climatic predictors and elevation	-	-358 – 336	1000 m – 1 m (elevation)	-	(De troch et al., 2020)
AnnualVariationPrecipitation	Mean annual variation of precipitation between 1971 and 2005	Millimeter	7-23	1000 m	Log(x+1)	(De troch et al., 2020)
Calcareous	The presence of calcareous soil	-	0-1	75 m	-	(Bah et al., 2007)
Podzol	The presence of podzolic soil	-	0-1	75 m	-	(Bah et al., 2007)
Organic	The presence of organic (peaty) soil	-	0-1	75 m	-	(Bah et al., 2007)
Sandy	The presence of sandy soil (very high proportion of sand)	-	0-1	75 m	-	(Bah et al., 2007)
Alluvial	The presence of alluvial soil	-	0-1	75 m	-	(Bah et al., 2007)
Source	The presence of source related soil	-	0-1	75 m	-	(Bah et al., 2007)
Drainage	Classes of natural soil drainage: Dry and very dry soils; Moderately dry and wet soils; Wet soils with temporary water table; Very wet soils with temporary water table; Very wet and peaty soils	-	1-5	75 m	-	(Bah et al., 2007)
Hydric_lvl	Includes 10 categories of soil humidity from xeric to marshy soils + 3 categories of alternative water regime (moving water table)	-	1-13	10 m	-	(Petit S. et al., 2017)
Trophic_lvl	Categories of trophic level from oligotrophic soils to carbonate soils	-	1-6	10 m	-	(Petit S. et al., 2017)

Sand	Proportion of the sandy texture found in soil sample extrapolated with kriging	-	0-0.88	50 m	-	(D’Or Dimitri, 2021)
Silt	Proportion of the silty texture found in soil sample extrapolated with kriging	-	0-0.82	50 m	-	(D’Or Dimitri, 2021)
Slope_prc	The slope percentage	-	0-50	10 m	Log(x+1)	Created for the study purpose based on LIDAR data
TPI	Topographic position index. The relative position in terms of elevation of the pixel compared to other pixels in a 200 m radius	-	0-100	10 m	-	Created for the study purpose based on LIDAR data
SunSpring	The potential incident light energy on the pixel for the first day of spring	W/m²	16-3434	10 m	-	Created for the study purpose based on LIDAR data
Radiative_SS	Categories of different radiative sub-sectors identified by slope and exposure: 1 = cold sub-sector (from 285° to 125° oriented slopes and valley bottom); 2 = neutral sub-sector (plains, plateaus and gentle slopes); 3 = hot sub-sector (from 125° to 285° oriented slopes)	-	1-3	10 m	-	(Petit S. et al., 2017)
Water_int	Categories of water intake: 1= areas without lateral water inflows (convex plateaus and slopes); 2 = areas with variable water inflows (bottom of slopes, flats, valleys and concave areas); 3 = areas with permanent water inflows (areas connected to the	-	1-3	10 m	-	(Petit S. et al., 2017)

Areas not described in soil maps, i.e., urban areas, watercourses and parts of military domains, were not considered in the model. They appear as ‘no data’ on maps presented in this paper.

3.2.5. Vegetation data

As part of the implementation of the European Union Council Directive 92/43/EEC on the conservation of natural habitats and of wild fauna and flora (Loidi, 1999), detailed mapping of biotopes has been carried out by the different member states. Field biotope inventories realized in the Walloon region between 2005-2020 as part of the implementation of this directive were used as a reference dataset for PNV. Biotope limits were identified as polygons mapped at 1:10.000 and each of them is characterized by a EUNIS code. This field mapping is perfomed using vegetation inventories to identify vegetation communities that are linked to the EUNIS classification. Limits are drawn using IGN to differentiate open areas from forest and digital soil maps are used to refine limits identified on the field. Precise biotope mapping is not published and was provided directly by the public service in charge (SPW/DGARNE/DEMNA). As natural vegetation rarely follows tangible limits, the change from one biotope to another is not always a sharp edge but rather a continuous local gradient (Kuchler, 1973). Transitions and mosaics between biotopes can also be complicated and difficult to map. Field survey agents address this problem by identifying and mapping complexes of several biotopes which are intertwined (Dufrêne and Delescaille, 2007; Hearn et al., 2011). Those complexes may negatively affect a model’s accuracy by decreasing strong differences between ecological conditions of biotopes, and were therefore discarded (Horvath et al., 2019). We therefore only selected polygons containing a unique EUNIS code that could be linked to a PNV (following Table 3.2), covering 65 599 ha.

To limit the imprecision of biotope and ecological variable mapping, we shrank biotope polygons greater than 1 ha and corresponding to more widespread PNV with a 20 m inner buffer. Fammenian *Quercus* and *Carpinus* forests, neutrophile *Fagus* forests, acidophilous *Fagus* forests and calcareous *Fagus* and *Quercus* forests are the most widespread biotopes in Wallonia (Delescaille et al., 2021). The area covered by theses PNV potentially affected by errors and polygon limit inaccuracies is not negligible compared to scarcer biotope areas which are more typical of extreme ecological conditions. The rarest biotopes have been subject to more precise mapping because nearly all are biotopes of community interest (*sensu* the European Habitat Directive defining aims of Natura 2000 network) (Loidi, 1999). They are also easily delineable on the ground. This step of shrinking the most widespread biotopes improved the quality of scarcer biotope models.

Modified biotope polygons were then used to link each PNV to every cell of the environmental predictor raster stack that falls into them. To reduce the spatial autocorrelation effect, we applied a random spatial sampling to select a maximum of 50 pixels per km² for each PNV. That reduced the dataset to approximately 200 000 rows (5% of the complete dataset). This sampling helped to initially balance the distribution of PNV occurrences by limiting those dominating the landscape. The evolution of PNV areas following the different sampling steps is available in Appendix 2.

3.2.6. Individual PNV modeling

A first modeling step was performed for each PNV with presence/absence data. The presence of a PNV was attributed to each pixel where an EUNIS habitat associated to the PNV have been mapped on the field. All other EUNIS habitat associated to other PNV were considered as absence (Horvath et al., 2019; Maggini et al., 2006). We could have used presence only models such as Maxent (Álvarez-Martínez et al., 2018) but the way PNV were defined with unambiguous biotopes related to specific ecological context made it possible to perform robust presence/absence models.

Models were calibrated through a Random Forest algorithm using the randomForest R package (Breiman, 2001). Random forest algorithm is recognized for its accuracy and its computational efficiency. It can easily handle small sample size and high dimension models which make it perfect to model scarce PNV (Biau and Scornet, 2016). Random forest is also known to be less sensitive to overfitting when calibrated with large sample size which is interesting in our case for common PNV (Belgiu and Drăguţ, 2016). Finally, Random forest performs for both regression and classification that make it versatile enough for our methodological framework achieving individual modeling and global classification without complexifying the method (Biau and Scornet, 2016).

The model was calibrated using 70% of the selected presence/absence dataset. On this calibration dataset, a SMOTE (synthetic minority oversampling technique) algorithm was applied to balance presence/absence frequency without losing too much information (Chawla et al., 2002). The SMOTE algorithm decreases dominant class (generally absences) and artificially increases the minority class (generally presences). Before modeling, a variable selection was performed on the calibration dataset using VSURF (Variable Selection Using Random Forest) (Genuer et al., 2015). All variables selected at the prediction step of the VSURF algorithm were kept for modeling. Random Forest model tuning focused on the mtry argument – i.e., the number of variables randomly sampled as candidates at each split – as it is considered to be the most influential parameter (Probst et al., 2019). Multiple tests were performed to choose the best mtry value giving low error and less computational time. These tests resulted in the use of the square root of the number of variables kept after selection, which corresponds to what is found in the literature (Probst et al., 2019).

Model results were first validated using the 30% remaining test set. The area under the curve (AUC) was used to evaluate model robustness using this test set. A second validation was performed on the 95% dataset discarded by spatial sampling to measure the accuracy of predictive maps. Different accuracy metrics were calculated in order to compare predictive maps and assess their adequacy: the overall accuracy

(OA), the producer accuracy (PA) and the user accuracy (UA). OA is the proportion of well-classified pixels (presence and absence) compared to the total number of pixels used for validation. PA is the proportion of correctly classified reference pixels compared to the total number of reference pixel that represent the point of view of the cartographer evaluating the model prediction. UA is the proportion of well-classified presence pixels compared to the total number of predicted presences. This evaluates the model performance to predict PNV presence from the point of view of the map user. For these threshold-dependent metrics (OA, PA and UA), the threshold maximizing the F-score was used to transform model probability to presence/absence. The F-score is the harmonic mean of the receiver operating characteristic (ROC) curve. The five most important environmental predictors for the Random Forest model and their importance for the model were also identified based on the Gini index (Aldrich, 2020).

3.2.7. Dominant PNV classification

A second modeling step was performed using results of each PNV prediction as an input for a new Random Forest classification to produce a unique classification map of PNV. Results of specific PNV probabilities cannot be compared to identify what the dominant PNV is for a pixel. Specific PNV probabilities are average results from multiple specific classification trees with specific distributions of values. However, they can be used as variables for a new classification that will identify the most likely PNV for each pixel based on PNV probabilities.

The SMOTE algorithm can only be performed on a two-class dataset. To balance the different PNV frequencies before modeling, we decided to weight PNV classes as this is the recommended approach to balance a dataset for Random Forest classification of more than two classes while keeping all the information (Chen and Breiman, 2004). We weighted PNV classes according to their prevalence by applying Equation 1 to each class:

Equation 1.

$$Weight = (1 - freq_{class})^2$$

Where freq_class is the proportion of the class – i.e., the PNV.

This helped to give more weight to less-represented PNV. For instance, the weight of the rare xerophile Fammenian *Quercus* and *Carpinus* forests is 0.99 while the weight of the common acidophilous *Fagus* forests is 0.53. The same OA, PA and UA metrics used for the specific PNV modeling were calculated. We also calculated the Cohen's kappa coefficient that measures the global accuracy of a classification comparing the proportion of well-classified pixels to the total number of pixels compared to a random classifier. To interpret Cohen's kappa coefficient results, we used the classification proposed by Landis and Koch (1977) that consider a kappa value below 0.2 as slight, between 0.21 and 0.40 as fair, between 0.41 and 0.60 as moderate, between 0.61 and 0.80 as substantially good and above 0.81 as an almost perfect classifier.

3.2.8. Identification of areas with mixed PNV

As previously explained, biotope distributions do not follow tangible and exclusive limits. In the field, gradients and complexes of multiple biotopes are common where biotope ecological envelope overlap. Dominant PNV classification attributes to each pixel the dominant PNV even in less ecologically specific areas where multiple PNV could overlap. In order to get closer to reality and identify less certain classified areas, we chose to identify areas where several PNV are in competition. To do so, predictive distributions of each individual PNV were transformed to binary presence/absence maps using the threshold maximizing F-score. These binary maps were therefore all added together and areas where the presence of multiple PNV overlapped were considered as mixed areas. The area of each type of PNV present in mixed areas has been measured and compared to the total area of the concerned PNV. If the mixed area represented more than 10% of the total surface of one PNV in question, it was kept; those below 10% were discarded. This allowed most PNV associated with important confusion after classification to be kept, discarding small and irrelevant confusion issues. All retained mixed areas were added to the PNV classification map as an overlay. Then we recalculated accuracy metrics for each PNV with validation data by considering the potential presence of the PNV in single and mixed areas. Mixed areas were therefore considered as a presence for the validation of each PNV concerned.

3.2.9. Complementary analysis

Individual biotope modeling vs. PNV

To identify gains or losses of using the PNV approach compared to individual biotope modeling that consider biotopes independent, we also performed modeling of biotopes composing the PNV for calcareous *Fagus* and *Quercus* forests. We chose this PNV as it includes several biotopes of different succession stages that are exclusive to the PNV. It is also the only one with sufficient data about open and semi-open biotopes to enable accurate and robust individual models.

Biotopes belonging to calcareous *Fagus* and *Quercus* forest succession were modeled considering the targeted biotope as presences and all other biotopes of the dataset – i.e., also other biotopes belonging to the same PNV – as absences, as is done in individual biotope modeling approaches (Horvath et al., 2019). All independent models were used to predict presence/absence maps using the threshold maximizing F-score. To make individual biotope models and the PNV model comparable, we added together all biotopes' predicted ranges, which was compared to the PNV predicted presence range. Producer accuracy was calculated for each individual biotope – i.e., the proportion of reference pixels related to each biotope belonging to the PNV or the cumulative biotope distributions. Furthermore, each total area of the PNV predicted presence and the cumulative individual biotope predicted presence were calculated to evaluate the specificity of the model. A presence prediction that is too large can increase producer accuracy, but the model specificity may be low.

Quality assessment with floristic data

Indicator plant species observations were also used to complete the quality assessment of PNV predictions. A validated plant dataset compiled for the Walloon Flora Atlas (Delescaille and Delaitte, 2011) was filtered to keep only observations of indigenous plants between 2000 and 2020 and location with precision below 100 m. PNV information was then assigned to each observation of a plant species. A Chi² test was performed to measure the dependence between the presence of a plant taxa and each specific PNV, discarding mixed PNV.

The dependence is based on residual Chi² (T) calculated with Equation 2:

Equation 2.

$$T = \sum_{ij} \frac{\left(O_{ij} - E_{ij}\right)^2}{E_{ij}}$$

where O_{ij} is the number of observations of a taxon i in a PNV j and E_{ij} is calculated based on Equation 3:

Equation 3.

$$E_{ij} = \frac{O_{i+} \times O_{+j}}{N}$$

where O_{i+} is the total number of observations for a taxon, O_{+j} is the total number of observations in a PNV and N is the total number of observations in all PNV.

Chi² test was preferred to similar metric such as Indval (Dufrêne and Legendre, 1997). Indeed, using Indval to compare species occurrence to PNV prediction should results to low values of indicative level as it depends on the proportion of species occurrence on PNV occurrences. PNV occurrences is far wider than as it is a potential prediction and could not be compared to species occurrence that are linked to actual distribution of biotopes.

3.3. Results

3.3.1. Dominant PNV classification

PNV were firstly modeled individually using the Random Forest algorithm. Complete results are available in Appendix 3. Random Forest prediction results were then used as independent predictors to perform a classification to identify the dominant PNV for each pixel. Results of accuracy metrics show that global accuracy metrics for the classification are almost perfect with 0.95 and 0.91 for OA and Cohen’s kappa coefficient, respectively.

If we go into further detail, we can see that the classification increases producer accuracy for almost all PNV (Table 3.4). The PA increase is particularly important for 5 PNV out of 13 with an increase higher than 10%. The results for UA are more heterogeneous with some PNV gaining in UA and others decreasing. Two PNV particularly lost accuracy according to UA: riparian and gallery woodland and *Alnus* swamp woods. To better understand these accuracy losses, we performed a confusion matrix that highlights an important confusion between the predicted value for some PNV and reference pixels of acidophilous *Fagus* forests (Table 3.5).

Table 3.4: Accuracy metric results of the classification map for each PNV. Producer (PA) and user accuracy (UA) above 0.8 (considered to be highly accurate for our objectives) are highlighted in bold text. To better view trends in accuracy metrics between individual PNV modeling and dominant classification, differences of PA and UA were added. Absolute differences higher than 0.1 are highlighted in bold font.

Potential Natural Vegetation	**Code**	**Area used for calibration (Ha)**	**PA**	**PA differences**	**UA**	**UA differences**
***Sphagnum Betula* woods**	**SB**	50.8	**0.898**	+0.075	**0.829**	+0.000
***Alnus* swamp woods**	**AS**	141.1	**0.936**	**+0.122**	0.678	**−0.148**
Quercus* and *Betula* forests with *Molinia	**QBM**	144.9	**0.912**	+0.096	**0.827**	−0.034
Riparian and gallery woodland	**RG**	337.8	**0.930**	**+0.114**	0.689	**-0.129**
Fammenian *Quercus* and *Carpinus* forests	**FQC**	64.8	**0.968**	+0.082	**0.932**	+0.023
Neutrophile *Quercus* and *Fraxinus* forests on wet soils	**NQF**	156.5	**0.936**	+0.059	**0.888**	−0.026
Acidophilous *Quercus* and *Carpinus* forests on wet soils	**AQC**	8.1	**0.868**	**+0.244**	0.731	+0.099
Neutrophile *Fagus* forests	**NF**	338.8	**0.921**	+0.046	**0.914**	−0.005
Wet and shady ravine forests	**WSR**	94.9	**0.820**	**+0.185**	0.688	+0.018
Acidophilous *Fagus* forests	**AF**	559.0	**0.959**	−0.010	**0.990**	+0.018
Calcareous *Fagus* and *Quercus* forests	**CFQ**	131.3	**0.918**	+0.066	**0.884**	+0.021
Thermophile acidophilous *Quercus* forests	**TAQ**	24.5	**0.836**	**+0.330**	0.580	**+0.137**
Xerophile Fammenian *Quercus* and *Carpinus* forests	**XFQC**	8.4	**0.856**	**+0.195**	**0.842**	+0.003

Table 3.5: Table resulting from classification of PNV. Columns concern predicted classes and rows refer to reference classes. Values in the matrix correspond to the number of pixels divided by the total number of pixels predicted in each PNV. The diagonal therefore corresponds to UA values. SB: *Sphagnum Betula* woods; AS: *Alnus* swamp woods; QBM: *Quercus* and *Betula* forests with *Molinia*; RG: riparian and gallery woodland; FQC: Fammenian *Quercus* and *Carpinus* forests; NQF: neutrophile *Quercus* and *Fraxinus* forests on wet soils; AQC: acidophilous *Quercus* and *Carpinus* forests on wet soils; NF: neutrophile *Fagus* forests; WSR: wet and shady ravine forests; AF: acidophilous *Fagus* forests; CFQ: calcareous *Fagus* and *Quercus* forests; TAQ: thermophile acidophilous *Quercus* forests; XFQC: xerophile Fammenian *Quercus* and *Carpinus* forests.

	Prediction												
Reference	**SB**	**AS**	**QBM**	**RG**	**FQC**	**NQF**	**AQC**	**NF**	**WSR**	**AF**	**CFQ**	**TAQ**	**XFQC**
SB	**0.83**	0.02	0.02	0	0	0	0	0	0	0	0	0	0
AS	0	**0.68**	0	0	0	0	0	0	0	0	0	0	0
QBM	**0.14**	0.02	**0.83**	0	0	0	0	0	0	0	0	0	0
RG	0	0.01	0	**0.69**	0	0	0	0	0.01	0	0	0	0
FQC	0	0.04	0	0.05	**0.93**	0.01	0	0.01	0	0	0.02	0.02	0.09
NQF	0	0.01	0	0.05	0	**0.89**	0.02	0	0	0	0.01	0	0
AQC	0	0	0	0	0	0	**0.73**	0	0	0	0	0	0
NF	0	0.02	0	0.04	0	0.02	0.01	**0.91**	0.08	0	0.05	0.03	0.01
WSR	0	0	0	0.01	0	0	0	0	**0.69**	0	0.02	0.02	0
AF	**0.03**	**0.21**	**0.15**	**0.15**	0.06	0.08	**0.24**	0.05	**0.11**	**0.99**	0.02	**0.33**	0.03
CFQ	0	0	0	0	0	0	0	0.01	**0.11**	0	**0.88**	0.02	0.02
TAQ	0	0	0	0	0	0	0	0	0	0	0	**0.58**	0
XFQC	0	0	0	0	0	0	0	0	0	0	0	0	**0.84**
Total	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**1**

This is particularly the case – in decreasing order of confusion importance – for thermophile acidophilous *Quercus* forests, acidophilous *Quercus* and *Carpinus* forests on wet soils, *Alnus* swamp woods, riparian and gallery woodland, *Quercus* and *Betula* forests with *Molinia* and wet and shady ravine forests. All these PNV are scarce except for *Quercus* and *Betula* forests with *Molinia* and riparian and gallery woodland. We can also see a notable confusion between wet and shady ravine forests and calcareous *Fagus* and *Quercus* forests. Figure 3.3 shows the results of classification as a unique map of PNV potential presence.

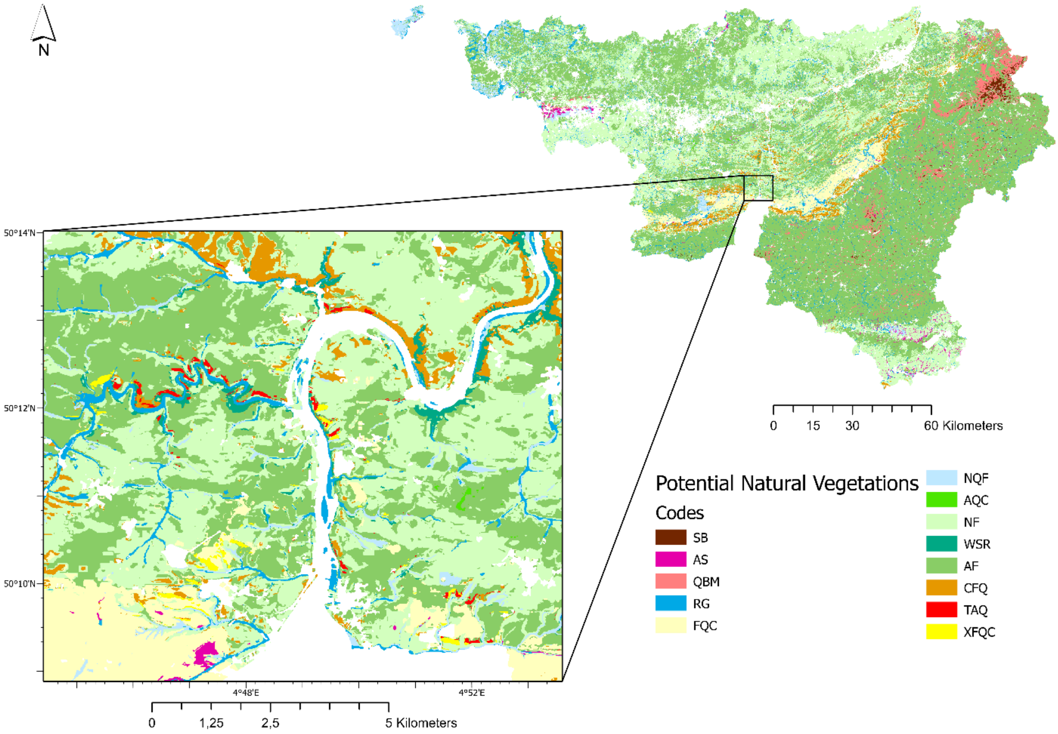

Figure 3.3: Result of classification map of PNV with a close-up of the Hermetton Valley region where important diversity of PNV can be seen. SB: *Sphagnum Betula* woods; AS: *Alnus* swamp woods; QBM: *Quercus* and *Betula* forests with *Molinia*; RG: riparian and gallery woodland; FQC: Fammenian *Quercus* and *Carpinus* forests; NQF: neutrophile *Quercus* and *Fraxinus* forests on wet soils; AQC: acidophilous *Quercus* and *Carpinus* forests on wet soils; NF: neutrophile *Fagus* forests; WSR: wet and shady ravine forests; AF: acidophilous *Fagus* forests; CFQ: calcareous *Fagus* and *Quercus* forests; TAQ: thermophile acidophilous *Quercus* forests; XFQC: xerophile Fammenian *Quercus* and *Carpinus* forests.

Results of PNV individual modeling and classification can be viewed online (“Lifewatch-FWB : UCL - Geomatics,” 2022).

3.3.2. Identification of areas with mixed potential natural vegetation

The identification of potential zones with competition between PNV resulted to ten mixed PNV complexes where the sum of PNV proportions is higher than 10% . These complexes are presented in Table 3.6. Here, the PNV concerned with mixed areas representing a large proportion of their presence range are generally those with a lot of confusion, as shown in the confusion matrix. This is particularly the case for scarcer PNV such as thermophile acidophilous *Quercus* forests, acidophilous *Quercus* and *Carpinus* forests on wet soils and xerophile Fammenian *Quercus* and *Carpinus* forests. There is an important overlap between neutrophile *Fagus* forests and acidophilous *Fagus* forests, involving 30% of neutrophile *Fagus* forests. This overlap is not present in the classification as there is not a notable confusion between the two PNV in the confusion matrix. An example of the resulting map of mixed areas overlaid with the classification is given in Figure 3.4. Accuracy metrics were recalculated considering the potential presence of PNV in mixed areas. Global results were logically better, with a slight decrease of PA in some cases and an appreciable increase of UA for almost all PNV. OA slightly increased by 0.004 while kappa increased by 0.019. Trends in accuracy metrics with and without mixed areas are available in Appendix 4.

Table 3.6: List of PNV mixed areas identified and mapped. The proportions of each PNV in the association compared to the total area of each PNV concerned are presented, beginning with the first PNV in the association. QBM: *Quercus* and *Betula* forests with *Molinia*; FQC: Fammenian *Quercus* and *Carpinus* forests; AQC: acidophilous *Quercus* and *Carpinus* forests on wet soils; NF: neutrophile *Fagus* forests; WSR: wet and shady ravine forests; AF: acidophilous *Fagus* forests; CFQ: calcareous *Fagus* and *Quercus* forests; TAQ: thermophile acidophilous *Quercus* forests; XFQC: xerophile Fammenian *Quercus* and *Carpinus* forests.

Mixed PNV	Proportion of PNV 1	Proportion of PNV 2
TAQ+AF	66.4%	0%
NF+ AF	29.5%	7.9%
AQC+AF	35.8%	0.0%
QBM+AF	18.7%	0.4%
XFQC+AF	17.8%	0.0%
XFQC+ FQC	16.9%	0.1%
WSR+AF	15.4%	0.0%
CFQ+NF	12.3%	1.6%

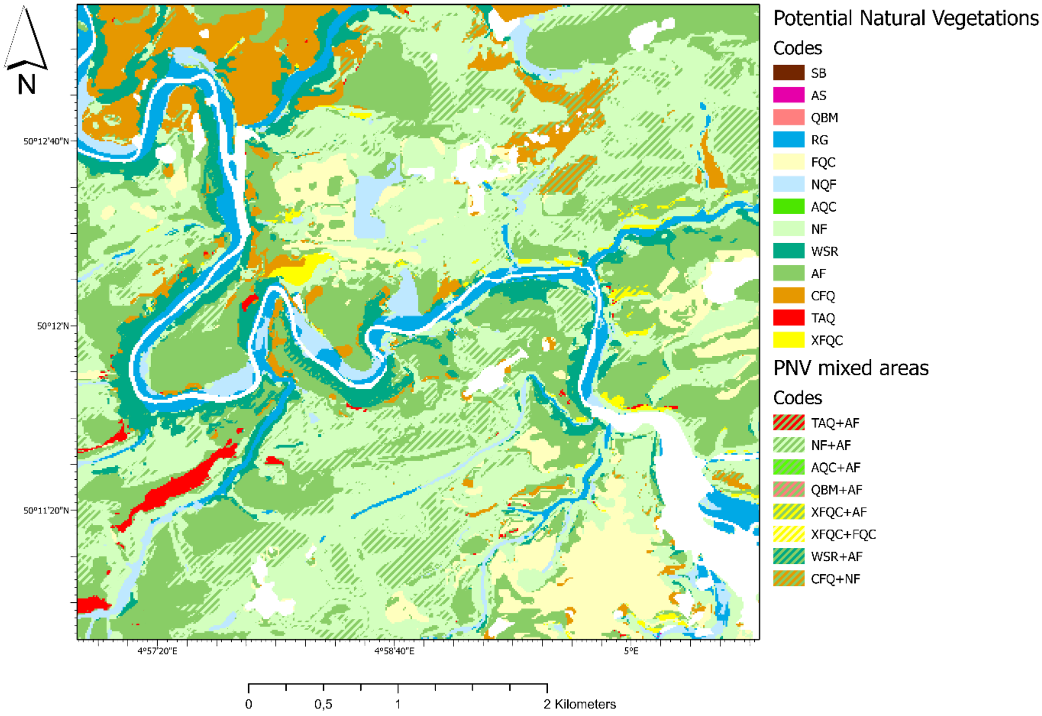

Figure 3.4: Presentation of the different complexes of multiple PNV identified with PNV classification on a fine scale. SB: *Sphagnum Betula* woods; AS: *Alnus* swamp woods; QBM: *Quercus* and *Betula* forests with *Molinia*; RG: riparian and gallery woodland; FQC: Fammenian *Quercus* and *Carpinus* forests; NQF: neutrophile *Quercus* and *Fraxinus* forests on wet soils ; AQC: acidophilous *Quercus* and *Carpinus* forests on wet soils; NF: neutrophile *Fagus* forests; WSR: wet and shady ravine forests; AF: acidophilous *Fagus* forests; CFQ: calcareous *Fagus* and *Quercus* forests; TAQ: thermophile acidophilous *Quercus* forests; XFQC: xerophile Fammenian *Quercus* and *Carpinus* forests.

3.3.3. Complementary analysis

Individual biotope modeling vs. PNV

Results of the modeling of the calcareous *Fagus* and *Quercus* forests PNV were compared to the remodeling of each of the biotopes that characterize the vegetation succession of this PNV. Results are presented in Table 3.7. We can see that PA values were low for individual biotope predictions, except for sub-Atlantic calciphile *Quercus* and *Carpinus betulus* forests. The PA values increased when biotope predictions were grouped, but the PNV approach performs better for all biotopes except for sub-Atlantic calciphile *Quercus* - *Carpinus betulus* forests where the difference is only 0.4%. In other words, more biotope reference pixels were encompassed in the PNV range than in the addition of individual biotope predicted presences. This represents a mean PA increase of 29% compared to individual biotope predictions and 8% compared to when they are grouped. In addition, areas of grouped biotope predictions and PNV are similar, with 30 250 ha for the PNV and 25 250 ha for the addition of individual biotopes model. The large PA for the PNV approach is therefore not due to an excessively large potential distribution.

Table 3.7: Producer accuracy (PA) of each biotope used to define calcareous *Fagus* and *Quercus* forests considering PNV range or addition of individual biotope models. Highest values of PA are represented in bold text.

Biotopes	**Biotopes (EUNIS code)**	**PA of individual biotope predictions**	**PA of individual biotope predictions inside grouped area**	**PA individual biotope predictions inside PNV**
Sub-Atlantic semi-dry calcareous grassland	**E1.26**	0.609	**0.843**	**0.905**
Calcareous thermophilic thickets and scrub	**F3.1b**	0.488	0.710	**0.861**
Medio-European limestone *Fagus* forests	**G1.66**	0.615	0.720	**0.817**
Western *Quercus pubescens* woods and related communities	**G1.71**	0.304	0.781	**0.871**
Sub-Atlantic calciphile *Quercus* and *Carpinus betulus* forests	**G1.A17**	**0.857**	**0.863**	**0.859**

Quality assessment with floristic data

An additional validation of the PNV models assessed to what extent most dependent species of each PNV based on Chi² are known to be indicators of the different related biotopes. Chi² analyses were performed on plant occurrence data using a PNV classification map to identify most dependent species without considering aquatic species and very rare species (Appendix 5 summarized in Table 3.8).

Table 3.8: This table presents the five species with the highest values resulting from the Chi² test for each PNV, excluding aquatic and too scarce species. Species names in bold with bigger font are those typical of the associated biotopes (but not necessarily exclusive). In bold but with smaller font: companion species of the associated biotopes. Small normal font is used for generalist species. Finally, underlined species names are those not corresponding to the biotope according to their ecological requirements or corresponding to ruderal species. Exponents above the names denote if species are typical of open environments (O), develop in open and forest environments (M) or strict forest species (F).

Potential Natural Vegetation	**Five most dependent species**
***Sphagnum Betula* woods**	***Vaccinium oxycoccos*^{M}, *Eriophorum vaginatum*^{M}, *Narthecium ossifragum*^{O}, *Eriophorum angustifolium*^{O}, *Drosera rotundifolia*^{O}**
***Alnus* swamp woods**	***Carex appropinquata*^{O}, *Filipendula ulmaria*^{M}, *Cirsium oleraceum*^{M}, *Caltha palustris*^{M}, *Triglochin palustris*^{O}**
Quercus* and *Betula* forests with *Molinia	***Erica tetralix*^{O}, *Molinia caerulea*^{M}, *Vaccinium uliginosum*^{M}, *Juncus squarrosus*^{O}, *Viola palustris*^{M}**
Riparian and gallery woodland	***Filipendula ulmaria*^{M}, *Phalaris arundinacea*^{M}, *Caltha palustris*^{M}, *Iris pseudacorus*^{M}, *Scirpus sylvaticus*^{M}**
Fammenian *Quercus* and *Carpinus* forests	***Orchis morio*^{O}, *Silaum silaus*^{O}**, *Dianthus armeria*^{O}, ***Colchicum autumnale*^{O}, *Selinum carvifolia*^{O}**
Neutrophile *Quercus* and *Fraxinus* forests on wet soils	*Lythrum salicaria*^{M}, ***Alnus glutinosa*^{M}**, ***Filipendula ulmaria***^{M}, ***Glechoma hederacea*^{M}**, *Phragmites australis*^{M}
Acidophilous *Quercus* and *Carpinus* forests on wet soils	*Dactylorhiza praetermissa subsp.praetermissa var.j,*^{O} *Oxybasis rubra*^{O}, ~~*Dipsacus pilosus*^{F}~~, *Lathyrus nissolia*^{O} *Senecio vulgaris*^{O}
Neutrophile *Fagus* forests	***Galium odoratum*^{F}**, ***Paris quadrifolia*^{F}**, *Saxifraga granulata*^{O}, *Viscum album*^{M}, *Equisetum arvense*^{O}
Wet and shady ravine forests	***Asplenium scolopendrium*^{F}, *Polystichum aculeatum*^{F}**, ***Asplenium trichomanes*^{M}**, ***Mercurialis perennis*^{F}**, *Biscutella laevigata*^{O}
Acidophilous *Fagus* forests	***Pteridium aquilinum*^{M}, *Teucrium scorodonia*^{F}, *Cytisus scoparius*^{O}, *Vaccinium myrtillus*^{M}, *Luzula luzuloides*^{F}**
Calcareous *Fagus* and *Quercus* forests	***Helianthemum nummularium*^{O}, *Vincetoxicum hirundinaria*^{M}, *Teucrium chamaedrys*^{O}, *Globularia bisnagarica*^{O}, *Gymnadenia conopsea*^{O}**

Thermophile acidophilous *Quercus* forests	***Asplenium septentrionale***^{O}, ***Asplenium adiantum-nigrum***^{M}, *Filago minima*^{O}, ***Silene nutans***^{M}, ***Galeopsis segetum***^{O}
Xerophile Fammenian *Quercus* and *Carpinus* forests	***Silene nutans***^{M}, ***Dianthus carthusianorum***^{O}, ***Asplenium adiantum-nigrum***^{M}, ***Potentilla argentea***^{O}, *Ulmus laevisF*

Most dependent species resulting from Chi² analyses are generally indicative or related to biotopes concerned by the modeled PNV. These results indicate that the predictive map of PNV concerns the corresponding environmental conditions and expected species communities. Species characteristic of both open and forest stages of the PNV are present in the five most dependent species. For open habitats species, this is true for *Helianthemum nummularium* that is indicative of open stages of calcareous *Fagus* and *Quercus* forests or *Erica tetralix*, typical of open stages of *Quercus* and *Betula* forests with *Molinia*; for forest species, *Asplenium scolopendrium* that is typical of forest stages of wet and shady ravine forests or *Luzula luzuloides* that is present in forest stages of acidophilous *Fagus* forests. Two PNV had poorer results: neutrophile *Quercus* and *Fraxinus* forests on wet soils and acidophilous *Quercus* and *Carpinus* forests on wet soils. Some species of these two PNV highlighted by the analysis are not related to the expected environmental conditions.

3.4. Discussion

3.4.1. Dominant PNV classification

Classification results to identify dominant PNV had an important global PA increase at the expense of UA, which shows that the modeled distribution of PNV had been widened after classification. This is especially the case for riparian and gallery woodlands and *Alnus* swamp woods. A detailed analysis of the confusion matrix performed on classification results revealed a significant confusion between acidophilous *Fagus* forests and scarcer PNV. Acidophilous *Fagus* forests is the largest of all PNV representing 64% of reference data and its high prevalence in the validation dataset could also explain why prediction errors are more widely detected in widespread biotopes. Even if areas of confusion between acidophilous *Fagus* forests and other PNV are small and rare compared to acidophilous *Fagus* forests' total area, the impact on accuracy metrics may still be significant for the rarest PNV for which less validation data is available. This confusion can be explained by different hypotheses.

Firstly, *Fagus* forests are the natural dominant vegetation on the Walloon territory and can sometimes extend in the smallest and 'linear' areas with ecological conditions at the border of their range, especially as *Fagus* sylvatica is a shady and highly competitive species that can counter the colonization of other woody species.

This effect is accentuated by conventional silvicultural management favoring the homogenization of stands, and by game pressure on less common tree species. Therefore, the presence of *Fagus* sylvatica in less ecologically suitable conditions can be explained by its competitiveness, stand management and high game pressure.

Secondly, biotopes present in scarce PNV are often represented as sliver polygons due to their specific ecological conditions defined by topography and hydrography. Therefore, the extraction of rasterized environmental predictors of 10 m wide may have created border effects where predictor values of specific ecological conditions may be attributed to the scarce PNV or to the surrounding common PNV. This issue has been considered and its impact limited by removing a 20 m inside buffer from common PNV polygons.

Thirdly, biotope maps are susceptible to biases. It is likely that the mapping of common biotopes may be coarser, including smaller areas with ecological conditions suitable to other PNV. A detailed analysis of the acidophilous *Fagus* forests reference data showed that a bigger proportion of riparian and gallery woodlands reference polygons are on wet alluvial soils (43%) than that of acidophilous *Fagus* forests (1%) but the latter has a greater absolute area of wet alluvial soil (83 398 ha) than riparian and gallery woodlands (47 972 ha). This issue was anticipated by balancing calibration datasets; firstly with spatial sampling and secondly by weighting PNV before classification. By giving more importance to scarce PNV we also gave more importance to biotope polygons for which we can have better confidence as more attention was given to them during their mapping. The operator effect is also potentially present in soil maps. The digital soil map of Wallonia is an interpolation of field surveys performed by different agents. For instance, soil texture value leaps with artificial limits are present in this map. Biases present in reference and environmental datasets can explain an overlap between ecological envelopes of different PNV and thus the confusion measured.

3.4.2. Complementary analysis

Individual biotope modeling vs. PNV

The analysis of the independent biotope models of calcareous *Fagus* and *Quercus* forests showed that our approach better covers the existing biotope distributions compared to single biotope modeling. Furthermore, PNV modeling using only climax stage vegetation as reference would have used Medio-European limestone *Fagus* forests (Delescaille et al., 2021). However, we can see that using this vegetation alone to model the PNV leads to missing 20% more cells of this biotope than our approach. For this example, using multiple stages biotopes to calibrate the PNV better encompass ecological envelope and leads to better predictive results.

The better results of our approach can be explained by the fact that open biotopes are maintained by human management. In our case, only a portion of them have resumed their succession and another part had their succession stopped by human activities, which mimics historical vegetation dynamics. Our hypothesis is that human activity restricts the distribution of open biotopes to local ecological contexts that could be only a limited part of the actual ecological envelope of the biotope. By modeling calcareous *Fagus* and *Quercus* forests we therefore better consider the ecological envelope of sub-Atlantic semi-dry calcareous grassland, as evidenced by our results.

Quality assessment with floristic data

Quality control of the potential distribution of PNV using floristic data demonstrates that the most dependent PNV species are those that are found in corresponding biotope floristic assemblages (Delescaille et al., 2021). Some of them are even considered as indicator species, such as *Asplenium scolopendrium*, which is indicative of ravine or slope forests. We can also mention *Paris quadrifolia* and *Galium odoratum* which are two indicative species of neutrophile *Fagus* forests. Species of open environments are also identified in addition to these different forest species indicative of climax vegetation, as for calcareous *Fagus* and *Quercus* forests. *Helianthemum nummularium*, *Globularia bisnagarica* and *Teucrium chamaedrys* are typical of calcareous grasslands that are the pioneer stage of the PNV, while *Vincetoxicum hirundinaria* is typical of forest edges and woody stages of the PNV.

Most important issues concern neutrophile *Quercus* and *Fraxinus* forests on wet soils and acidophilous *Quercus* and *Carpinus* forests on wet soils. This can be explained by too low accuracy of available observations, poorer sampling inside the biotopes concerned and inherent PNV scarcity – especially acidophilous *Quercus* and *Carpinus* forests on wet soils – that impact Chi² analysis.

3.4.3. Strength and limitations of the approach

Our approach helped to tackle different issues related to biotope mapping. In our case, biotopes that are part of other vegetation series were therefore considered as true absences which improved the model's capacity to distinguish them. The use of independent models for each PNV to produce a classification as well as the distinction of the mixed zones allowed potential PNV distributions to be refined. Important PA values for classification and the small change in UA showed that this model was very powerful, avoiding omitting the presence of different PNV while keeping a good detection of true presences. Other approaches have allowed a map to be built with the most dominant biotope from multiple predictions (Álvarez-Martínez et al., 2018), but the probabilities between two concurrent biotopes were compared and the dominant biotope was assigned to the pixel if the difference of probabilities was higher than a subjective threshold. In our approach, any subjectivity was avoided through the classification based on individual PNV predictions.

The identification of mixed areas revealed the difficult distinction and blurred delimitation between different PNV where ecological conditions are very close. These transitional areas between different biotopes reflect those typically encountered in the field. Other methods to tackle overlapping of multiple PNV predictions are complex and do not provide convenient maps but give a more complete information with different comparable probabilities for all overlapping PNV (Somodi et al., 2017) Our approach is simpler and we discard some complexes but all information is available in a single convenient map. Moreover, marginal complexes of PNV that were discarded are mainly unrealistic in term of ecological condition that should not overlap. The filter that was performed improve therefore consistency to the final map while proposing a clear visualization of results.

PNV modeling can identify possible important areas for restoration, which could target forests or open biotopes as well. The distinction between forest and open biotopes can then be identified using available land-cover data, which is becoming increasingly accurate and easily available through remote sensing approaches (Bourdouxhe et al., 2020; Radoux et al., 2019). Then, mixed areas where several PNV may be present could be discarded to greater specify the modeled distribution and gain in certainty. This more precise information about actual biotope distribution is of paramount importance for monitoring habitat distribution (Stevens et al., 2004). This refining of the resulting distributions of PNV to match different objectives of biotope maps is similar to recent initiatives in biotope modeling (Álvarez-Martínez et al., 2018). Actual distributions may also help to measure the frequency of appearance of the different biotopes belonging to a vegetation succession series. This could help to determine if the different stages of succession are well represented and to guide restoration actions to diversify the landscape.

To model PNV, we assumed a deterministic evolution of vegetation succession toward a climax stage, which is not agreed upon by all the scientific community (Chiarucci et al., 2010). We therefore paid attention to PNV definition and identifying biotopes belonging to each PNV. Our results showed a good distinction between the different PNV, which proves they were well defined and that our hypothesis about a deterministic evolution of vegetation succession covered by this study is true. Furthermore, these results underline the benefits and sturdiness of a prior definition of PNV compared to more complex methods where PNV are constructed based on vegetation occurrence datasets (De Keersmaeker et al., 2013). However, the existence of mixed areas shows some important overlaps between independent PNV predictions. These mixed areas are mainly distributed in more productive areas that are intensified and have fewer biotopes of reference for model calibration. Nevertheless, modeling PNV has many advantages presented in this paper that brings new light to this old concept.

3.5. Conclusion

This study helped to develop a modeling approach that presents new possibilities for biotope modeling on large scales and increased prediction accuracy. A range of different datasets and methods were used to evaluate our approach, which highlights its robustness. However, PNV modeling is not free from limitations; attention must be paid to PNV definitions and important phytosociological knowledge is recommended. As with many models, we must be careful in the selection of reference datasets and environmental predictors to better distinguish modeled ecological envelopes.

Chapter 4

Modeling and Analyze Species Habitat Network. Comparing Approaches

1. Preamble

For this chapter, we conducted a comparison of various habitat network modeling approaches found in the literature, aimed at connecting habitat patches and analyzing the resulting networks. Our focus was on the case of the wildcat in southern Belgium, and we examined three different approaches.

The first approach involved a data-driven method that utilized species observations and models to identify habitat patches and evaluate the landscape's resistance to movement. The second approach employed a knowledge-driven method to map habitat patches based on the species' preferred land-cover and identified land-cover resistance to movement using information from existing literature. The third approach combined elements of both data-driven and knowledge-driven approaches. It involved identifying habitat patches based on species distribution models and determining landscape resistance based on information obtained from the literature. To compare the different approaches, we examined their structural differences and assessed how they identified obstacles in the landscape.

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2. Preliminary analysis

Habitat network modeling is an important tool to restore and conserve degraded landscape (Hilty et al., 2020). Those analyses are of paramount importance to limit impacts of landscape fragmentation. Until now, ecotopes and raster were used as fundamental unit to perform ecological analysis and particularly biotope distribution models. Ecotopes has an interesting potential to precisely represent landscape features that favor species movements. For instance, hedgerows are known to favor movement in open areas of forest dependent species (Burel, 1996; Hinsley et al., 1999; Schlinkert et al., 2016). Bats are also known to precisely follow hedgerows in open areas when foraging and also to move from a habitat patches to another (Heim et al., 2016).

However, hexagonal grids are also used to map ecological processes and especially when it concerns fluxes such as individual movements in landscape connectivity analysis. Hexagonal grid provides a significant advantage for data visualization, as it enhances clarity in depicting the relationships between neighboring hexagons. This representation is therefore advised to improve performance of habitat connectivity analysis. This clearer representation also enables more effective presentation of connectivity analysis results, facilitating a better understanding of ecological connectivity patterns (Birch et al., 2007; Molné et al., 2023).

In this first analysis, we propose to test the use of ecotopes delineation for representing species habitat patches and corridors in habitat network modeling in comparison to a 1 ha hexagonal grid.

2.1. Method

2.1.1. Ecotope database

The ecotope database used in this study is an environmental database composed of polygons representing ecotopes, the smallest homogeneous unit of the landscape. This database was produced in the framework of LifeWatch-WB project and covers whole Belgian territory (Radoux et al., 2019). The segmentation of ecotopes is performed by an algorithm using orthophotoplan, vegetation height and hillshade fixing a mean polygon size of 2 hectares. A multitude of environmental predictors are resumed at the ecotope scale such as land-cover, soils attributes, climatic conditions and many more.

2.1.2. Habitat network modeling

To assess the representation of species' habitat patches and corridors, we employed two types of references: a ecotope segmentation (mean size of 2ha) and a 1ha hexagonal grid. We opted for a hexagonal grid instead of a raster (squared) grid to better depict results of connectivity analysis (Birch et al., 2007; Molné et al., 2023).

Our habitat network modeling focused on *Limenitis camilla*, a diurnal forest butterfly with an approximate dispersal distance of 1000m. For this purpose, we considered habitat patches as forest patches with a minimum size of 1ha. This size was chosen as a compromise between being sufficient for multiple butterfly species (Hill et al., 1996; Lewis et al., 1997; Mennechez et al., 2003) while not being too small to increase computational time. Habitat patches were identified as adjacent ecotope with forest land-cover, forest edges were then removed with an internal buffer of 50m. Subsequently, we overlapped habitat patches to a random hexagonal grid and hexagons were considered as habitat when the overlap concern at least 50% of the hexagon.

To assign costs to each land-cover class, we employed a logarithmic cost scale (Savary et al., 2021a). Land-cover information was extracted from the ecotope database and summarized at the ecotope level. Then ecotope were rasterized at a 10m resolution to be implemented in the Graphab software to test ecotope representation. The same rasterized land-cover dataset was used to attribute the majority land-cover to each hexagon. Then hexagons were rasterized at a 10m resolution and implemented in Graphab to test hexagon representation. Using Graphab software, we modeled least-cost paths (LCP) for each representation of landscape and habitat patches. For both approach LCP modeling was parametrized as follow. Patch connexity was set to an 8-connexity type to ensure to keep alluvial forest continuity. We chose for a planar topology to keep only LCP that connect neighboring patches which reduce number of LCP and computational time. Finally, LCP crossing patches were ignored.

Resulting LCP were then synthesized using ecotopes and hexagons by selecting polygons that were intersected by LCP. Consequently, we compared the number of habitat patches (groups of adjacent ecotopes or hexagons with habitat land-cover) and LCP generated for each representation.

2.2. Results

Table 4.1 shows the different results of comparing ecotope and hexagons representation to map habitat patches and LCP.

Table 4.1: Results of comparing ecotopes and hexagons to represent elements of habitat networks.

	Hexagon	**Ecotope**
Number of habitat patches	2595	1218
Habitat patches area (Ha)	68 539.68	68 124.88
Number of LCP	2702	1519
Connected areas by LCP	717	274

The most important difference resides in the different number of resulting patches. Ecotope representation regroup more adjacent forest ecotopes into single patch than hexagons leading to half as many habitat patches. However, surface areas are similar with a slightly bigger surface for hexagons. The number of LCP logically follow the number of patches. The number of connected areas decrease more for the ecotope representation.

Figures 4.1 display the outcomes of employing hexagons and ecotopes to represent habitat patches, as well as LCP results. This figure focuses on an area where significant variations in habitat patches and their effects on LCP modeling are evident.

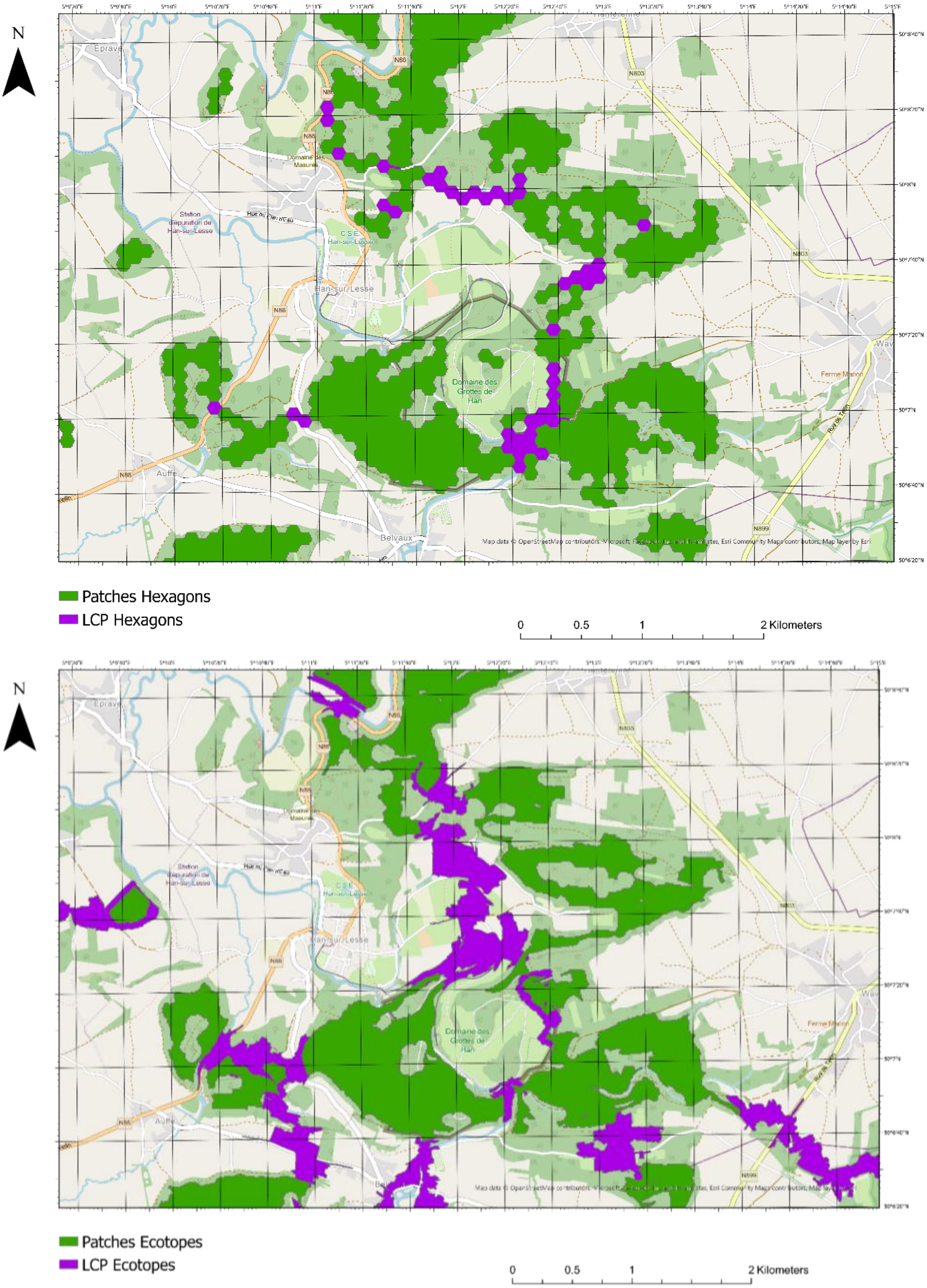

Figure 4.1: Results of habitat network modeling using hexagonal (above) and ecotope (below) representations to model habitat patches and LCP.

We can see that already connected patches thanks to adjacent forest ecotope radically changes habitat patches and LCP number and layout. New LCP also appear which can be explained by a more permeable matrix using ecotope approach. The hexagonal approach identifies LCP that avoid clearly some areas used in ecotope approach.

2.3. Discussion

The evaluation of representing habitat network components, such as habitat patches and LCP, using hexagons or ecotopes involved comparing multiple structural attributes of the networks. The primary distinction lies in the number of identified habitat patches, which significantly affects other measured attributes. Hexagonal representation identifies 2 times more habitat patches compared to ecotope representation, while the surface areas are similar. Consequently, the number of LCPs follows the increase in the number of habitat patches, as there are more patches to connect. This highlights that the hexagon representation identifies a more fragmented landscape. The reason behind this can be attributed to the fact that linear forest cover connected to habitat patches does not provide sufficient area to be summarized at the hexagon level. The inclusion of linear forest elements in the ecotope representation allows for the connection of forests, leading to the identification of larger and less fragmented forest patches (Figure 4.2 and Figure 4.1). In fact, the mean habitat patch size identified using ecotope representation is 56 hectares, while it is 26 hectares for hexagon representation.

Figure 4.2: Exemple of ecotope delineation of deciduous forest land-cover which allow to connect two forest patches using a small linear element.

We observed that the hexagon representation identify less connected patches which leads to an increase in number of distinct connected areas, while ecotope segmentation allows for the connection of more patches. This could be explained by the fact that ecotope segmentation may include linear elements, whether present or not, that facilitate species movement or act as barriers (Figure 4.2). In our case, such element favorized evaluated species movements.

It has been observed that hedgerows, whether connected or isolated, serve as shelter habitats or corridors for various species, including birds and specialized small mammals that inhabit forests mammals (Burel, 1996; Hinsley et al., 1999; Schlinkert et al., 2016). However, it is important to consider the influence of edge effects and small patch size as significant landscape characteristic that can have a negative impact on population survival and species richness within habitat patches (Chalfoun et al., 2002; Chen et al., 1992; Crooks et al., 2001; Lindenmayer et al., 2000). Consequently, it is incorrect to assume that habitat patches connected by such elements form a single, larger patch with high capacity. The use of such ecotope delineation can therefore underestimate the measurement of landscape fragmentation.

Studies have emphasized the effectiveness of hexagons in representing connectivity analysis results (Birch et al., 2007). It is crucial to recognize that LCP alone does not capture realistic species movement patterns. By representing LCP using ecotopes or hexagons, a more nuanced delineation of movement patterns can be considered. Ecotope representation offers the advantage of depicting ecologically distinct areas in the landscape and more precisely delimiting vegetation cover used for species movements. However, it is important to acknowledge that such precise delimitation may inadvertently create a false impression of precision, as automated ecotope segmentation is not immune to biases. Conversely, an abstract representation such as hexagons may better reflect the inherent imprecision and biases of ecological analyses. Further investigation is required to comprehensively evaluate the strengths and limitations of each representation method for accurate visualization of connectivity analysis results.

For this comparative analysis, we opted to directly convert land-cover data synthesized at the ecotope level into hexagons. This decision was made to enable a comparison between two representations that capture a similar local context. Alternatively, attributing local land-cover context using a moving window sampling approach with native 2-meter resolution land-cover data could be employed to provide land-cover information to the hexagons.

2.4. Conclusion

In conclusion, this study demonstrated that the choice of method to represent habitat network elements significantly impacts the assessment of landscape fragmentation. Ecotope segmentation results in fewer but larger connected habitat patches, whereas hexagon representation identifies a more fragmented landscape with a higher number of patches. The choice between these representations depends on the specific requirements of the studied species. It is important to consider potential segmentation artifacts when using precise representations, as inaccuracies in data calibration can lead to unrealistic boundaries and false impressions of accuracy. Automated segmentation methods are not immune to biases, and careful interpretation is necessary.

3. Comparison of methods to model species habitat networks for decision-making in nature conservation: The case of the wildcat in southern Belgium.

3.1. Introduction

Despite the establishment of protected areas, anthropogenic pressures on landscapes cause significant fragmentation of species habitats, increasing species extinction rates (Hanski, 2005; Stanners and Bourdeau, 1995). This is particularly the case in landscapes strongly shaped by human activities, such as Western Europe, where natural areas are reduced to small and isolated habitat remnants embedded in an anthropogenic matrix (Jongman et al., 2004; Luck , 2007). Significant fragmentation restricts population movements of species in the landscape, limiting metapopulation functioning (Hansson et al., 1992; Jongman et al., 2004). Populations can suffer genetic drifts, including inbreeding, further increasing their extinction risk (Hansson et al., 1992). In addition, lack of habitat connectivity prevents recolonization of potential habitats after local extinctions (Verboom et al., 1991).

The lack of connectivity could be efficiently addressed by implementing ecological networks, also known as habitat networks (Melin, 1997; Opdam et al., 2006), which are progressively integrated into conservation planning (Albert et al., 2016; Rayfield et al., 2016). The ambition of this conservation tool is to connect isolated populations of targeted species by linking their habitats in a coherent way and in interaction with the landscape matrix (Opdam et al., 2006). To implement ecological networks, habitat areas or biodiversity cores and the corridors connecting them must be identified (Bennett & Mulongoy, 2006; Bernier & Théau, 2013; Sordello et al., 2017). To identify them, many scientists use the concept of landscape connectivity, which can be defined as functional or structural. Functional connectivity identifies how well genes, gametes or individuals move through the landscape (Rudnick et al., 2012; Weeks, 2017). Structural connectivity measures habitat permeability to species movements based on the spatial arrangement of habitat patches, and the disturbances and other lands in the matrix (Hilty et al., 2019). This help to identify existent and potential landscapes features through which species may be able to move (Hilty et al., 2020). However, evaluation of connectivity requires spatial analyses of large and various sets of spatially explicit data that describe landscapes and the habitats corresponding to the natural life history traits of targeted species (Duflot et al., 2018a; Gurrutxaga et al., 2015; Sordello et al., 2017; Sordello, 2016).

An increasingly used method to model ecological networks and support decision making regarding their implementation is based on spatial graphs theory. Spatial graphs are a simplification of landscapes where habitat patches are considered as nodes and potential movements of species as links connecting pairs of nodes

(Galpern, Manseau, & Fall 2011; Urban & Keitt 2001; Urban, Minor, Treml, & Schick 2009). This method allows landscape elements (habitat patches and corridors) to be prioritized for their contribution to the overall connectivity of a habitat network (Avon and Bergès, 2016; Duflot et al., 2018a; Gurrutxaga et al., 2015; Saura and Rubio, 2010). A key step is to evaluate the potential connectivity between habitat patches, which is most commonly done in current scientific literature through use of least cost paths (LCP; Sawyer, Epps, & Brashares 2011). The landscape is interpreted as a resistance raster map representing the resistance to species movements, where each pixel has a travel cost specific to the targeted species, or group of species. Then, the path analysis identifies LCP connecting pairs of patches through the series of pixels with the lowest cumulative cost (Liu, Newell, White, & Bennett 2018). Hence, to model spatial graph and LCPs for maintaining ecological networks, two steps must be completed: (i) identify the habitat patches to be (re)connected, and (ii) create a resistance map to describe landscape permeability to species movements.

The habitat and resistance maps used for LCP and spatial graph modeling have been defined in different ways. Some studies have built maps on the basis of expertise, using land-cover maps: some land-cover categories are considered as habitat, while every other land-cover category is assigned a resistance value according to the ecology of the targeted species (Liu et al. 2018; Watts et al. 2010). However, this method has some limitations due to the potential subjectivity of experts in identifying habitat patches and assigning resistance values to the land-cover classes (Sawyer et al., 2011; Stevenson-Holt et al., 2014). In view of the increasing use of species habitat suitability models, other studies have defined habitat patches and calculated resistance maps by transforming the map of habitat suitability derived from species distribution models (Duflot et al., 2018a). Such data-driven approaches are expected to better reflect reality. However, this method assumes that factors influencing species movement behaviors are the same as those influencing the habitat suitability, which may not always be true (Zeller et al., 2018; Ziolkowska et al., 2012). Nevertheless, the use of a habitat suitability model is preferred when species observation data are available (Stevenson-Holt et al., 2014).

The emergency state of biodiversity loss pushes local stakeholders to value ecological networks as a leading strategy in nature conservation stakes (Amsallem et al., 2010; Sordello, 2016). However, the lack of suitable species data often forces local nature conservation practitioners to use expert knowledge to perform ecological analyses (Stevenson-Holt et al., 2014). In this context, we compared data-driven and knowledge-driven approaches to assess if expert-based ecological network modeling could be used as an alternative solution to approaches based on habitat suitability models, when data are missing. In this study, three approaches were compared: a “knowledge-driven method” based on expert opinion, a “data-driven method” based on a habitat suitability model, and a “mixed method” combining data and knowledge-driven methods to potentially compensate for their respective weaknesses. The rationale behind the mixed approach is that a habitat suitability model is more accurate in identifying the species habitat, but may be less relevant to inform about the species movement behavior. The resistance map was therefore created following expert opinion. To align our results to the needs of nature conservation practitioners, our aim was to identify the differences between habitat, resistance, and priority action maps obtained by the alternative methods. We therefore focused on easily reproducible workflows based on available datasets.

To carry out this comparison, we studied the potential corridors of the wildcat (Felis silvestris Schreber, 1777) in the Walloon region (southern Belgium). The Walloon forests are the core part of a large group of forests at European scale. They play an important role for the connectivity of the species at a supra-population scale with the Alsatian and Black Forest areas. However, Belgium has one of the most fragmented landscapes of Western Europe, reducing the connectivity of forest habitats (Jaeger et al., 2011). These issues have pushed local nature conservation stakeholders to view the wildcat and the connectivity of its habitat as a top priority. In this study, we address the following questions:

- What are the differences between the ecological network and priority action maps derived from knowledge-driven, data-driven and mixed approaches?
- Can expert knowledge lead to similar conclusions as approaches using species observation data?
- Which components generate the main differences between the different approaches tested?

3.2. Materials and Methods

3.2.1. Focal Species and Observation Data

Like other forest species, the wildcat is particularly vulnerable to historical and present fragmentation, mainly due to increased agricultural practices and the development of urbanized areas (Foley et al., 2005; Gibson et al., 2013). The species - once widespread in Europe - has suffered a significant decline over the past century, mainly due to the destruction of its habitat (Stahl et al., 1994; Sunquist, M., Sunquist, F., 2002), but also to hunting. Its registration as a protected species has enabled the gradual recovery of its populations, but it remains sensitive to habitat fragmentation caused by transport infrastructure, mainly roads (Hartmann et al., 2013; Klar et al., 2008). In addition, hybridization with domestic cats is a significant threat to the genetic integrity of the species (Hertwig et al., 2009; Hubbard et al., 1992; Lecis et al., 2006; Pierpaoli et al., 2003).

The wildcat is mainly a forest animal that prefers dense understory vegetation. It needs a spatial continuity of forest cover and therefore very rarely visits isolated groves (Libois 1991; Libois & Maréchal 1994; Klar et al. 2008). The wildcat is also looking for undisturbed areas that are rich in prey such as small mammals. At night, the cat leaves the forest to roam the open spaces to search for prey (Libois 1991;

Libois & Maréchal 1994; Klar et al. 2008). The wildcat also strongly avoids village areas and isolated houses (Klar et al. 2008; Libois & Maréchal 1994; Libois 1991).

For this study, we used wildcat observations (occurrence points) that combined two different databases: a field survey performed by public-service agents, and a public database built upon opportunistic observations made by naturalists (Source: Observations.be, Natagora, Natuurpunt et la Fondation "Observation International"). The former is more accurate, but the extent of the sampled area is smaller than the area covered by opportunistic records. The latter is less accurate regarding species identification and often also less precise in terms of geographic location. To limit bias due to this dataset, we excluded opportunistic observations not confirmed by experts: only observations i) flagged with a high degree of certainty and ii) validated by an expert were retained. Observation coordinates located in an artificialized area were also relocated to the nearest neighboring ecotope (see “Environmental Data Layers” section) which is not artificial. These observations usually result from an observer recording the observation from where he/she was and not where the animal was. While this dataset has some limitation, it is representative of the data usually available to nature conservation practitioners, which gives more pertinence to the results of this study.

3.2.2. Study Area

The study was located in the Walloon region (southern part of Belgium) and the studied area extent was defined based on the wildcat observation range in the region. This was done to ensure that the constructed models stay ecologically coherent, without taking into account the large diversity of ecological factors associated with different landscape entities present in the Walloon region. To do so, a convex hull polygon was created from wildcat observations and an additional 10 km buffer (average dispersal distance of the species) was applied (Figure 4.3). This buffer ensures that the wildcat habitat patches of interest are not considered in isolation from neighboring regions. This also ensures that it takes into account a recurring problem of graph analysis: the measured importance for connectivity of external habitat patches may be underestimated (Avon & Bergès 2016; Duflot et al. 2018a; Gil-Tena et al. 2014; Saura & Pascual-Hortal 2007). This buffer is only used to perform consistent spatial graph analyses. Therefore, comparisons between approaches and other analyses were only performed inside the convex hull polygon. Any further mention of the study area refers to the area of data availability without the buffer.

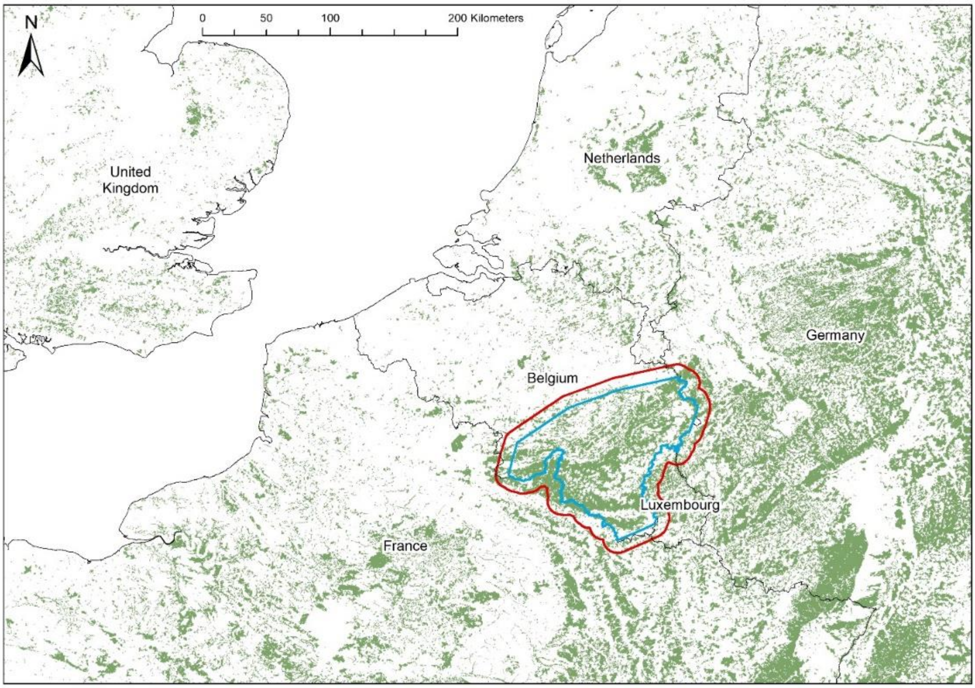

Figure 4.3: Location of the study area delimited by data availability (blue line) and the buffer of 10 km around it (red line) in the regional context of Belgium and its neighboring countries. It covers most of the Walloon region in southern Belgium. Forest areas are represented in dark green.

The study area corresponds to the Ardenne plateau, representing the highest region of the country (200 – 700 m) and dominated by forests. The center of the study area contains a slightly undulating plateau covered by coniferous forests, with deep valleys covered by deciduous forests on its edges (CPDT, 2014). The northern and outermost southern parts of the study area lean at the bottom of the Ardenne plateau and exhibit a mixed landscape where forests give way to croplands and grasslands. The whole study area is fragmented by villages, small cities, and a dense road network, including highways; although it is less fragmented than the rest of the country (CPDT, 2010; Quadu et al., 2014). The northern edge of the study area includes large town suburbs (namely Liège and Namur).

3.2.3. Environmental Data Layers

Land-cover and environmental maps were extracted from the ecotope database (Radoux et al., 2019). This database consists of a polygon map where each polygon represents an ecotope, which is considered to be the smallest ecologically distinct landscape feature (Bastian et al., 2002; Chan and Paelinckx, 2008). The ecotope map of Wallonia was obtained by segmentation and classification of a multispectral remote sensing imagery and elevation model derived from LIDAR (Julien Radoux and Bogaert, 2014). The ecotope map has 106 descriptors including land-cover variables, land-cover of the neighborhood (e.g. percentage of broad-leaved forest in a 250 m radius around the polygon and of each land-cover with 250 and 500 m radius), bioclimatic variables (e.g. rainfall of the wettest month, minimum temperature of the coldest month), soil variables (e.g. percentage of wet or alluvial soils), or topographic variables (e.g. mean slope of the ecotope, azimuthal exposure). This set of 106 variables resulted from an optimization for building ecological models performed in a previous study (Delangre et al., 2017). (For further information about the ecotope database, visit the website : http://maps.elie.ucl.ac.be/lifewatch/ecotopes.html)

For the study, the ecotope data layer was transformed into a raster of 20 m resolution. As highways and large roads are the major obstacles for mammals (Gurrutxaga et al. 2011), and to prevent them from becoming discontinuous during the conversion to raster, a 20-meter buffer was built around these structures and was then superimposed onto the resistance maps for all methods.

This complete and precise dataset was only available for the Walloon region at the time of the study. To consistently complete the environmental data set in neighboring regions, a new set of patches was created, which covers the Netherlands, Luxembourg, Belgium, and neighboring parts of France and Germany. Due to this much larger area and non-availability of accurate data in every overlapping country, this expanded dataset has a lower resolution and a less complete set of environmental data. It was based on a supervised classification of Sentinel-1 (C-Band Synthetic Aperture RADAR) and Sentinel-2 (13 bands visible and infra-red sensor) images, using the ecotopes as training data. The resulting classification was consolidated based on Open Street Map data (© OpenStreetMap contributors) and the Copernicus high resolution layers. The source of elevation data was the EU-DEM from the Copernicus land monitoring service. Only factors useful to model wildcat habitat suitability were included in this dataset (see “Results” section).

3.2.4. Knowledge-Driven Approach

Expert-based habitat and resistance maps were derived from the land-cover classes of the ecotope database. The following land-cover classes are related to the forest environment and were considered wildcat habitats: deciduous, coniferous, and mixed forests, as well as clear-cuts including regeneration growth. A cost of resistance to movements between 1 for the habitat and 1,000 for the most resistant land-cover was assigned based on scientific knowledge (Table 4.2). For other costs, we followed the order of magnitude of cost values used by Gurrutxaga et al. (2011) for studying habitat connectivity of mammals. A cost value of 5 was assigned to wildcat hunting territories which are open habitats with little disturbance, such as diversified grasslands and shrublands. Open habitats with disturbance such as crops were given a cost value of 60. Finally, the avoidance behavior of the wildcat towards built-up areas was taken into account by assigning the maximum cost value of 1,000 to artificialized areas. The other land-cover classes also received relevant cost values according to their similarity with previously mentioned ones (Table 4.2). In the case of the mixed approach, a resistance of 2 was assigned to land-covers corresponding to the knowledge-driven habitats that the data-driven model did not identify as optimal. Those land-covers are considered as sub-optimal habitat for the mixed approach.

Table 4.2: Summary table of land-cover classes in the ecotope database showing the travel costs assigned to each land-cover class to create the resistance map.

Land-cover class	Cost
Broad-leaved deciduous forest	1 (Habitat)/ 2 (suboptimal)
Needle-leaved sempervirens forest	1 (Habitat)/ 2 (suboptimal)
Needle-leaved deciduous forest	1 (Habitat)/ 2 (suboptimal)
Mixed forest	1 (Habitat)/ 2 (suboptimal)
Recently cleared areas with forest regrowth, also includes forest gaps and Christmas trees	1 (Habitat)/ 2 (suboptimal)
Mixed herbaceous and tree cover (with a majority of trees)	5
Diversified grassland and shrubland	5
Shrub and herbaceous flooded	5
Mixed herbaceous and tree cover (with a majority of herbaceous)	10
Mixed crop cover (with a minority of crops)	20
Permanent mono specific productive grassland	20
Mixed crop cover (with a majority of crops)	50
Periodically herbaceous	60
Mixture of vegetation and bare soil	60
Bare soil	500
Water	500
Densely artificialized (>50% artificial surface)	1000
Sparsely artificialized (>25% artificial surface)	1000

3.2.5. Data-Driven Approach

We followed an adapted version of the data-driven method described in Duflot et al. (2018a). MaxEnt package in R (Phillips et al., 2006) was used to model the habitat suitability for wildcats in the study area. Opportunistic observations may lead to some bias due to the lack of true-absence data. However, precautions have been taken to diminish this bias by using Maxent model which can handle pseudo-absence. The model was built using validated observations of the wildcat as presence points, while pseudo-absences were simulated by randomly projecting points onto the study area. To prevent pseudo-absence points from being projected into areas potentially covered by wildcats, buffers with a radius of 800 m were created around points of presence in order to be excluded from the area where the pseudo-absences were projected (Klar et al., 2008). This radius corresponds to that of a circle whose surface area is the average area of the wildcat's home range, which is 200 ha according to the literature (Libois 1991; Klar et al. 2008; Sordello 2012). The predictive variables used to train the model were extracted from the ecotope database. The set of 106 predictors was filtered to keep only variables relevant to wildcat ecology on the basis of the aforementioned literature. Then, the values of these variables were extracted for each of the presence and pseudo-absence points. Collinearity across environmental variables (or predictors) was tested (Spearman rho), and variables that were overly correlated (> 0.80) were removed to improve the quality of the model (Guisan et al., 2017). This was done manually (using "corrplot" package in R to visualize correlations) and iteratively to obtain the less correlated set of predictors. Then, the selected environmental variables were used to train the habitat suitability model, which was tested by cross-validation. The quality of the obtained model was assessed using the Area Under the Curve (AUC) and True Positive Rate (TPR), i.e., the percentage of correctly predicted presences compared to actual presence (also called sensitivity or recall). To calculate the latter, a presence/absence threshold was defined by maximizing the sensitivity and specificity (MSS) of the model as recommended in the literature (Liu, White, & Newell 2013). The obtained model was used to predict the habitat suitability over the entire studied area, using the environmental variable layer.

The habitat suitability index (HSI) map was used to determine the species habitat and define costs of movements for the non-habitat landscape matrix. The threshold selected for the calculation of TPR (MSS) was reused to determine which elements of the prediction map would be used as habitat patches for the species (Duflot et al., 2018a). Thus, all pixels whose prediction probability was greater than the identified habitat/matrix threshold were considered as habitat and all others were considered as the landscape matrix. The resistance map was computed by applying a negative exponential transformation function (Equation 1) to the HSI values of pixels not predicted as habitat (Keeley et al., 2016):

Equation 1.

$$resistance = e^{\frac{\ln(0.001)}{threshold} \times HSI} \times 10^3$$

where threshold is the habitat/matrix threshold and HSI is the value resulting from the habitat suitability model. The decay parameter of the negative exponential is set to provide resistance values ranging from 1 to 1,000.

3.2.6. Connectivity Analysis

The habitat and resistance maps obtained by each method were then used to perform a connectivity analysis using Graphab software (Foltête et al., 2012). Three spatial graphs were built based on (i) knowledge-driven habitat and resistance maps, (ii) data-driven habitat and resistance maps, and (iii) data-driven habitat maps and knowledge-driven resistance maps (the mixed approach). All following analyses were performed for all three approaches.

Habitat patches were further selected using a minimum surface area threshold that was set to 200 ha, which is commonly considered to be the home range area of wildcats (Libois 1991; Klar et al. 2008; Sordello 2012). Habitat area was used as the attribute for patches. With the use of the resistance maps, LCP analysis was performed to calculate the cost distance between neighboring patches (minimum planar graph).The cost distance was used as the attribute of links connecting pairs of habitat patches.

To build spatial graphs, we used the average dispersal distance of the wildcat, that is 10 km (Klar et al. 2008; Libois 1991; Sordello 2012). The dispersal distance must be multiplied by the median value of the resistance map. Thus, this distance is weighted within the reference frame used, i.e., the resistance map, and therefore is independent from the chosen scales of cost values (Avon and Bergès, 2016; Duflot et al., 2018a; Gil-Tena et al., 2014; Gurrutxaga et al., 2015). The obtained distance values, which are different in each approach because the resistance maps are different, were then used as a threshold to sort corridors that must be preserved or restored (i.e., those links with lower distance than the mean dispersal distance).

Then, the Probability of Connectivity index (PC, Equation 2) and its partitions were calculated to assess the importance of each habitat patch and the corridors that connect them for the overall connectivity (Saura & Pascual-Hortal 2007). For this analysis, all links were retained (i.e., no threshold was applied). The PC index evaluates the global connectivity of the ecological network:

Equation 2.

$$PC = \frac{\sum_{i=1}^{n} \sum_{j=1}^{n} a_i \, a_j \, p_{ij}^*}{A_L^2}$$

where n is the number of nodes (or habitat patches), a_i is the attribute characterizing node i (here patch size), a_j is the attribute of node j, A_L is the total area of the study area, and p_{ij}^* is the maximum probability product, i.e., the maximum value of the product of the attribute of the links for all possible paths, between patch i and j (Saura & Pascual-Hortal 2007).

Habitat patches and links were evaluated for their contribution to overall connectivity using the percentage change in PC (dPC_k) when removing the element k in question (Saura & Pascual-Hortal 2007).

Equation 3.

$$dPC_k = \frac{PC - PC_{remove}, k}{PC} \times 100$$

Finally, this dPC_k can be split down into three additive components:

Equation 4.

$$dPC_k = dPC_k intra + dPC_k flux + dPC_k connector$$

where $dPC_k intra$ is the contribution of the patch or link to habitat availability, $dPC_k flux$ is the dispersion flow in patch k from and to all other network patches, and $dPC_k connector$ is the contribution of the patch or link k to the connectivity of network elements based on their topological position. The higher the connector value, the more essential the element is to the network (Saura and Rubio, 2010). $dPC_k connector$ is recommended to measure the importance of patches and links for the overall connectivity of a habitat network, independently of patch size (Saura and Rubio, 2010). $dPC_k connector$ corresponds to a part of the sum of $a_i \times a_j \times p_{ij}^*$ (eq. 2) for each pair of patches i and j in which $i \neq k$, $j \neq k$ and k is part of the maximum probability path between them (p_{ij}^*) (Saura and Rubio, 2010).

The $dPC_k connector$ values allow the creation of priority action maps needed to maintain or increase the connectivity of the Walloon landscape for wildcat populations (Amsallem et al., 2010b; Duflot et al., 2018a). Because of the generalist behavior of the wildcat regarding habitat selection, we focused mainly on corridors, but $dPC_k connector$ was also calculated for habitat patches. For each method, corridors (LCPs) are sorted based on $dPC_k connector$ values to remove less important corridors for landscape connectivity and to prioritize the remaining ones. To do so, $dPC_k connector$ values were divided into four categories on the basis of Jenks natural breaks (that create groups maximizing differences between groups and minimizing variance within groups). A quantitative comparison between the three resulting habitat networks has been done regarding the priority class given by $dPC_k connector$ values to habitat patches and corridors. The category with lowest $dPC_k connector$ value was then put aside in order to keep only the most important corridors for landscape connectivity.

The remaining corridors have been categorized according to their state of conservation to differentiate corridors that must be conserved or restored. When the cumulated cost of a corridor was lower than the dispersal distance weighted to the median cost of resistance map, the corridor was considered as “conservation”, corridors were otherwise categorized as “restoration”.

Restoration actions can take several forms, such as forest patches or hedges and riparian forest restoration, to improve the landscape matrix for wildcat movements (Jerosch et al., 2018). However, when a corridor must cross a road, actions to facilitate the crossing are more specific. While road infrastructure without fences are not always blocking elements compared to those with fences, some enhancements could prevent and reduce mortality such as wildlife bridges (Hartmann et al., 2013; Klar et al., 2009). Potential locations for such specific actions were identified by intersecting corridors considered as important to maintain overall connectivity with the road network. Roads are still important obstacles even if the corridors crossing them are below the weighted dispersal distance threshold, therefore both "conservation" and "restoration" corridors were included. Restoration corridors that do not cross roads were put into a "non-suitable habitat" category if no obstacles could be identified.

In order to quantitatively measure if priority conflicts with roads were located at the same places, we used a Jaccard similarity index. To do so, a buffer of 5 km was calculated around intersections between priority corridors and roads. Then, the area of intersection between those buffers from the two compared approaches was calculated and divided by the total area of buffers of the two approaches. This was done between all three approaches. A higher value explains a higher similarity in terms of location between identified conflicts with roads. This value of 5 km was arbitrarily chosen as a compromise between study extent, the precision needed for corridor spatial location, and a sensitivity analysis performed to find the best value to highlight similarities and differences. The study extent plays a role in the potential convergences of buffers and the precision should not be too excessive because precise location of corridor restoration actions should also align with actual land-use planning opportunities.

A selection based on the different priority categories was made to study the variation in the Jaccard index while taking into account i) all conflict points, ii) conflict points of first and second priority, and iii) conflict points of first priority only.

3.3. Results

3.3.1. Wildcat Habitat Maps

After refining the wildcat observation data, there were 1319 presence points available, and as many pseudo-absences were generated to calibrate the MaxEnt model. Among presences, 40 points located in artificial areas were relocated to avoid any unintended effect on the model. The obtained model has satisfactory accuracy with an AUC of 0.79 and a TPR of 0.75. The presence/absence threshold that maximizes the sensitivity and specificity of the model is 0.56. Pixels with Habitat Suitability Index above this value were considered as potential habitats of the wild cat, representing 35.9% of the study area. As a comparison, the area considered as habitat in the knowledge driven approach represented 56.4% of the study area. However, the TPR calculated for this approach reaches 0.47 which is 0.28 lower than data-driven approach. Maps of the suitable habitat obtained by the two approaches can be found in Appendix 6. Concerning the data-driven approach, the main factors influencing habitat suitability for the wildcat were contextual variables. For instance, the most important factor was the presence of forests dominated by coniferous trees within a 250 m radius, which is positively correlated to the habitat suitability. The second most important factor was the presence of artificial light in the neighborhood, which is negatively correlated to the habitat suitability and positively correlated to the presence of artificial areas. The list of variables retained in the final model and their relative importance in predicting habitat suitability can be found in Appendix 7.

3.3.2. Resistance Maps

The two resistance maps created following data-driven and knowledge-driven approaches are available in Appendix 8. To help in comparing those results, we calculated the absolute difference of costs between the two approaches for each land-cover category (Figure 4.4). Land-cover were grouped in a broader category if they share similar costs for both approaches. Forest environment land-covers can be related to the habitat of the species and generally have a mean difference close to zero but a large variance. Land-covers related to artificialized areas also had a mean difference near zero and an even larger variance. Those land-covers are generally well identified as habitat or blocking elements but differences still exist, as shown by large variances. In contrast, important differences exist between the two resistance maps for other land-covers, particularly water bodies and bare soils with a mean difference higher than 100, while crop and productive pastures showed differences near 100 in absolute difference of resistance values. Bare soils represent only 0.06% of the study area and were not taken into account in the model of the data-driven model which explain the important difference of cost. Yet, their sporadic location should diminish their impact on connectivity. In contrast, water bodies such as rivers are linear elements which have a potential role of blocking elements. Crop and pastures occupy larger areas. Therefore, differences of cost for these two land-cover should have a strong influence on the connectivity results. Differences measured can be explained by their location near forests or cities and the use of contextual variables in the data-driven approach. A high cost is given in the surrounding areas of cities, villages, and roads, whereas the opposite applies to water bodies, crops, and pastures near forests, i.e., a lower resistance due to proximity to forest. This proximity effect was not considered in the knowledge-driven approach. As a consequence, rivers are less well identified as blocking elements in the data-driven approach, particularly in forest environments. However, crop and pastures near forests can contribute to corridors and can be identified as more favourable element for species movement with this approach. Proximity variables also affected land-cover related to forest environments (when forest was part of the landscape matrix) explaining some of the differences. In the data-driven resistance map, forests located in artificial landscapes are less favorable for wildcat connectivity. This influence of local context does not emerge from the knowledge-driven method because ecotope polygons are considered independently from each other. For instance, the mean percentage of presence of artificialized areas in a 500 m radius around each ecotope identified as habitat of the species has been calculated. This mean percentage is 0.9% for the knowledge-driven approach and 0.4% for the data-driven one. This result indicates that more knowledge-driven habitat patches are surrounded by artificialized areas than data-driven ones. This converges with our hypothesis that proximity to artificialized areas impacts forest habitat suitability in the data-driven approach and not in the knowledge-driven one.

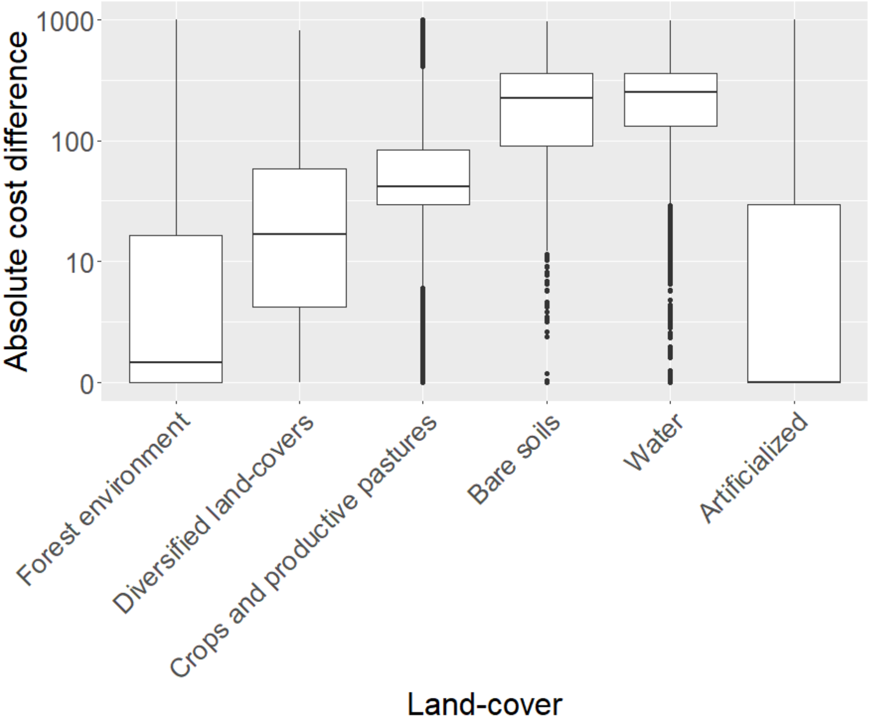

Figure 4.4: Boxplots of absolute costs differences between resistance maps from knowledge and data-driven approaches, for each land-cover class. A log 10 transformation has been applied to the y axis while land-cover categories are arranged from least to highest resistance (left to right).

The median values of resistance per meter traveled for the expert-based, data-based, and mixed methods are 40, 5, and 2 (cost/meter) respectively. The resulting weighted dispersal distances for each method are 20,000, 2,500, and 1,000 (in cost units).

3.3.3. Connectivity Analysis

To visualize priority corridors, a schematization of habitat patches and corridors was performed, using the graph representation, i.e., nodes and links (Figure 4.5). Gaps between forest patches would not be visible on a land-cover map at the regional scale. Because Figure 4.5 stays complex despite the schematization, it was not possible to highlight the cumulated cost of each corridor. This useful information, that makes it possible to quickly visualize actual connectivity between patches, is available in Appendix 9. We compared the three resulting habitat network regarding the priority class given by $dPC_k connector$ values to habitat patches and corridors (Table 4.3). As a reminder, the lowest priority class entities (priority 4) are not considered important for connectivity in further analysis. For each approach and each priority class, habitat area in hectares and number of corridors were calculated. We can see that for all three approaches tested, $dPC_k connector$ identified a few main patches and corridors needed to maintain connectivity in the network. The data-driven is the approach that identified the most first priority corridors (3). Besides, big habitat patches are often considered as important for the connectivity which increase habitat area of importance except for the mixed approach. The knowledge-driven and the data-driven approaches both identified large and central patches along the Ardennes as the most important patches for connectivity. The mixed approach showed a different result with large external patches marked as important. It is crucial to note that all approaches also identified small patches as important for connectivity, particularly the data-driven and the mixed approaches. For the mixed approach, three patches in the southern part of study area were classified in the top two categories of priority. All three methods identified several important corridors following the Ardenne high plateau summits. Those central corridors were also generally those with the highest cumulated cost for all methods (Appendix 9). The knowledge-driven approach identifies about twice as many corridors (248) than the other methods (Table 12). This approach highlighted an important path in southern Ardennes (southwest of the study area), which was not shown by other approaches. It also identified corridors connecting central patches with southernmost ones and also with south-eastern patches. In general, the knowledge-driven approach identified a much more connected landscape.

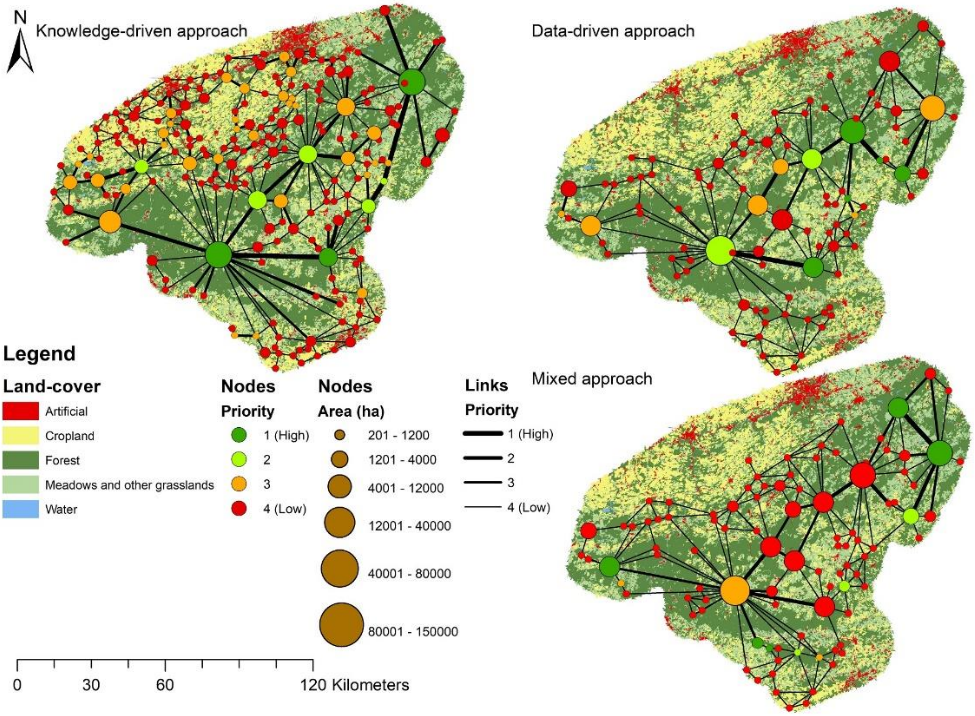

Figure 4.5: Schematic representation of the connectivity of habitat patches for each approach, overlaid on land-cover map. Habitat patches are represented by nodes whose size is proportional to their area, the different colors represent the respective importance of each patch for the connectivity based on the dPC Connector calculation. Corridors are represented by links, the thicker they are the more important they are to support global connectivity.

Table 4.3. Habitat area and number of corridors are compared across the three approaches tested according to their importance to maintain connectivity. Priority classes were created using Jenks natural breaks on $dPC_k connector$ values ranking them from lowest (Priority 4) to highest priority (Priority 1).

Habitat area (km²)	**Priority 4**	**Priority 3**	**Priority 2**	**Priority 1**	**Sum**
Knowledge-driven	864	1357	668	2567	5456
Data-driven	801	885	1081	703	3470
Mixed	1647	813	138	872	3470
Number of corridors					
Knowledge-driven	199	44	4	1	248
Data-driven	115	6	1	3	125
Mixed	113	7	3	1	124

For the knowledge-driven approach, 49 out of 248 corridors were considered as important for connectivity based on their $dPC_k connector$. Those 49 corridors were all considered for conservation objectives as their cost did not exceed the weighted dispersal distance. Concerning conflict with obstacles, 19 were related to roads. The others were not related to a lack of suitable habitat because their cost did not exceed the weighted dispersal distance.

Concerning the data-driven approach, 10 out of 125 corridors were considered important for connectivity and all of them had conservation goals. 6 of them were related to road conflict.

In the case of the mixed approach, 11 out of 124 corridors were important for connectivity. 4 of them had conservation goals, while 6 had restoration and 7 had road conflict.

This sorting helped to build priority action maps that show, for each method, habitat patches, corridors that must be preserved (important conservation corridors), and road conflicts (intersection between important corridors of conservation or restoration and major road networks). Due to high values of weighted dispersal distance, no corridors with a lack of suitable habitat were identified (restoration corridors not crossed by a road).

The different priority action maps showed that the corridors needing restoration to improve overall connectivity are small corridors crossing important road infrastructure such highways or 2×2 lane national roads (Figure 4.6). These roads split important forest areas from north to south. Knowledge-based priority action maps identified more obstacles in accordance with the higher number of corridors in that map.

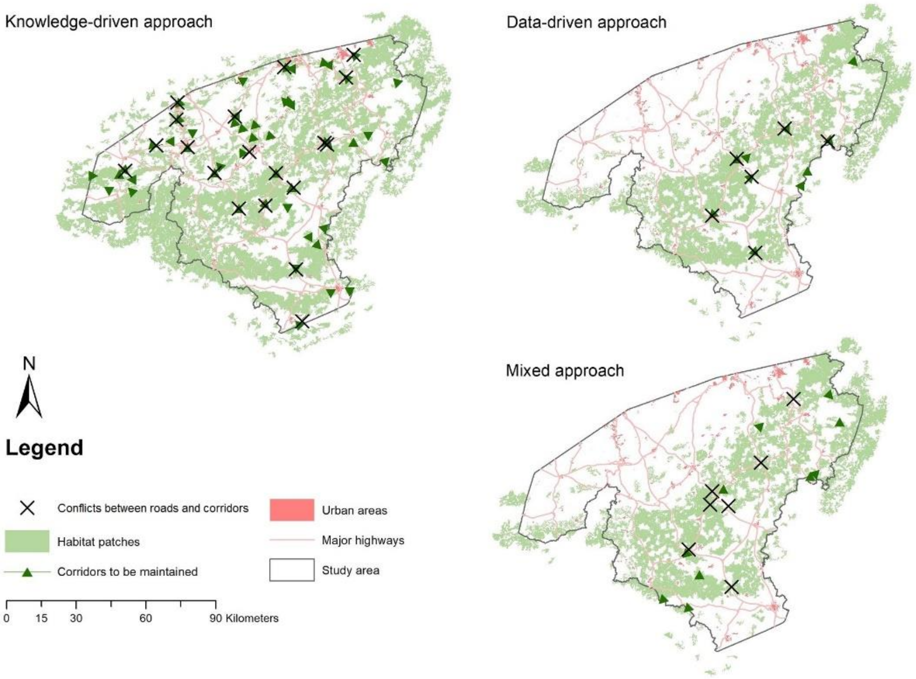

Figure 4.6: Action maps identifying obstacles and important corridors that need to be taken into account to improve general connectivity of the Walloon landscape. Priority obstacles include conflicts with conservation and restoration corridors crossing a road (represented by black crosses). "Corridors to be maintained" corresponds to all important corridors for connectivity with conservation goals, they are represented by green triangles.

Table 4.4 shows the different values of the Jaccard index measuring location proximity of corridors in conflict with roads between the three approaches. We can see that the mixed and data-driven approaches share the most similarities but few are shared with the knowledge-driven approach. However, the similarity between the knowledge-driven approach and the two others doubles when we focus on high priority conflicts. With first priority conflicts, this similarity approaches 50%.

Table 4.4: Results of Jaccard index analysis performed on priority conflict between corridors and roads based on priority action maps. Values range from 0 to 1, higher values indicate that conflict points are closely located to each other.

Comparing all priority conflicts (1,2 and 3)			
	Knowledge-driven	**Data-driven**	**Mixed**
Knowledge-driven	1	0.18	0.15
Data-driven		1	0.49
Mixed			1
Comparing conflicts with priority 1 and 2			
	Knowledge-driven	**Data-driven**	**Mixed**
Knowledge-driven	1	0.37	0.31
Data-driven		1	0.44
Mixed			1
Comparing conflicts of maximum priority (1)			
	Knowledge-driven	**Data-driven**	**Mixed**
Knowledge-driven	1	0.57	0.48
Data-driven		1	0.69
Mixed			1

3.4. Discussion

3.4.1. Modeling Habitat and Resistance Maps

The different methods used to model the habitat network of the wildcat led to different results. First, there were important differences in identification of suitable habitat patches. Despite a much larger area was predicted as habitat in the knowledge driven approach (1.5 times larger), the habitats mapped by the data-driven approach included 28% more of total observations, suggesting a better identification of habitat suitability. The knowledge-driven map shows its limitations by only considering the local land-cover. In contrast, the data-driven approach accounted for local characteristic and surrounding context, which is closer to wildcat ecology. It does not come close to villages and human-related land-cover types and prefers proximity with forests, particularly the ecotone between forests and open natural areas to hunt (Klar et al., 2008). Accordingly, the final habitat suitability model included contextual variables such as presence of needle-leaved forest in a 250 m radius and artificial light. The knowledge-driven approach did not use contextual variables, so the quality of the identified habitat patches can be questioned as there are more of them in densely populated areas than in the data-driven approach. Contextual variables such as proximity to built-up areas or forests could also be considered in the knowledge-driven approach, but would be much more difficult to parameterize (i.e., define proximity distance) and would require additional time-consuming GIS (Geographic Information System) data manipulations. The resulting networks are therefore very different. The habitat map resulting from the data-driven approach may be considered conservative and focused on higher quality patches. However, the generalist behavior of the wildcat makes it difficult to map its suitable habitat, hence the intermediate predictive accuracy of the habitat suitability model (AUC = 0.79). It is known that wide-ranging species produce models with a lower accuracy than habitat-specific ones (Segurado and Araújo, 2004). However, modeling the habitat suitability of the wildcat is also sensitive to calibration data. The observation data used here is not optimal and may represent biased reality, and contains less information than presence-absence data. Radio-tracked data could be used as relevant data to create very performant resistance maps, with more realistic information related to movements, but there is a recognized shortage of such data (Eycott et al., 2012). Approaches based on expert opinion and opportunistic observation data are therefore most often used (Stevenson-Holt et al., 2014). It remains important to stress that the effectiveness of either method compared in this study may depend on the data available, the species considered, and on the landscape in which the study is carried out (McClure et al. 2016). In our case, the obtained model represents the probability of seeing the wildcat rather than identifying its current habitat. It is thus important to take those limitations into consideration when designing a conservation action plan from such a method.

Second, the resistance maps obtained from the two approaches were partially divergent. However, forest and densely populated areas were still distinctly identified in both maps (Appendix 8). The main differences were due to smoother transitions between habitat and matrix in the data-driven approach, as a result of contextual variables, and leading to huge differences in costs for areas near forests and artificial areas (Figure 4.4). The huge variance within land-covers corresponding to blocking elements suggests that the data-driven approach did not correctly identify obstacles as such. This could be explained by a high proportion of forest land-cover decreasing the cost value of surrounding obstacles such as rivers or roads crossing forests. It is therefore sometimes difficult to handle the effect of contextual variables because it does not always give the results sought. This problem may be avoided in the mixed method by using the knowledge-driven resistance map. However, in that approach, assigning cost values to land-covers other than obvious obstacles remains subjective, or even speculative. Also, in this approach, the use of local context variables, although possible, remains even more questionable. As a compromise, the data-driven method could be combined with manually defined costs for certain obstacle elements, herein roads (Stevenson-Holt et al. 2014). However, this would require case-specific adaptations, which may be too time consuming to be performed on a regular basis.

3.4.2. Connectivity Analysis

Connectivity analysis through use of $dPC_k connector$ allowed prioritization of elements that are important to maintain overall connectivity. All approaches located these elements between the large forest patches along the Ardennes plateau (Figure 4.5). Additional smaller habitat patches and connections located in the southern part were also identified as important. The data-driven approach prioritized a lower area of habitat patches and fewer corridors, which can help to reduce the number of priority actions when resources available for conservation are limited.

In general, the $dPC_k connector$ values for patches and corridors were low, showing a relative weak effect of fragmentation in the study region. Nevertheless, road infrastructures still have a negative impact on the wildcat population (Hartmann et al., 2013; Klar et al., 2008), and their effect on connectivity may have been compensated here by the high dispersal capacity of the wildcat, its generalist behavior, and relatively high habitat availability. Furthermore, the study area is one of the less fragmented regions of Belgium (Quadu et al., 2014). The use of $dPC_k connector$ values is therefore best suited for relative comparisons between elements of the network.

The differences in the $dPC_k connector$ range of values across approaches resulted from the use of different habitat and resistance maps. $dPC_k connector$ calculations were also based on the dispersion distance derived from the dispersal capacity of the wildcat adjusted by the median cost value of resistance maps. These median cost values were different across the three approaches. The lowest median travel cost value was in the mixed approach (2/meter), indicating a more permeable matrix. This was probably due to suboptimal habitats, which were excluded from favorable habitat patches in the data-driven habitat map, but considered permeable (low costs) in the knowledge-driven resistance map. In addition, habitat patches from the data-driven approach overlap areas considered as less favorable in the knowledge-driven one (reducing areas with higher costs in the mixed approach).

Calculating the weighted dispersal distance using the median cost value allows comparisons to be made between the cumulated cost of LCP and the dispersal distance of the focal species, independently from the scale of cost allocated to the landscape (Avon and Bergès, 2016; Duflot et al., 2018a; Gil-Tena et al., 2014; Gurrutxaga et al., 2015). However, comparing different approaches highlights, again, the fact that weighted dispersal distances and related $dPC_k connector$ values are useful for relative comparisons (e.g. ranking/prioritization) within one particular map/approach, but may have limited relevance out of their context. Therefore, we advise to limit the use of $dPC_k connector$ values to the comparison of element importance within the same approach and not between different methods. Instead, priority ranks should be used for comparison.

3.4.3. From Connectivity Analysis to Conservation Actions

Despite large differences, the most important conflict points between high priority corridors and roads were similarly identified across the different approaches (Figure

4.7). These high priority conflicts can be considered with certainty as priority areas for conservation and used to guide nature conservation practitioners in their efforts to restore landscape connectivity. Therefore, the knowledge-driven approach still identified similar high priority conflicts and this approach should not be totally excluded when qualitative datasets are missing. However, many important corridors that must be preserved differ significantly between approaches. The data-driven and mixed approach share the most similarities with regard to the locations of the conflict points compared with knowledge-driven one. This is probably because data-driven and mixed approaches share the same habitat patches while knowledge-driven identified habitat patches in other areas. Corridors have therefore more chance to be in similar places. But difference still exists between data-driven and mixed approach due to the use of different resistance map. Differences in location of priority action between approaches can be, at least in part, explained by the dispersal distance weighted by the median cost value of the resistance map. Those weighted dispersal distances influenced the categorization of corridors as "conservation" or "restoration" sites and the way obstacles were identified as blocking elements or not. Therefore, those categories may be seen as indications for practitioners, but do not directly infer the probability of movement through them.

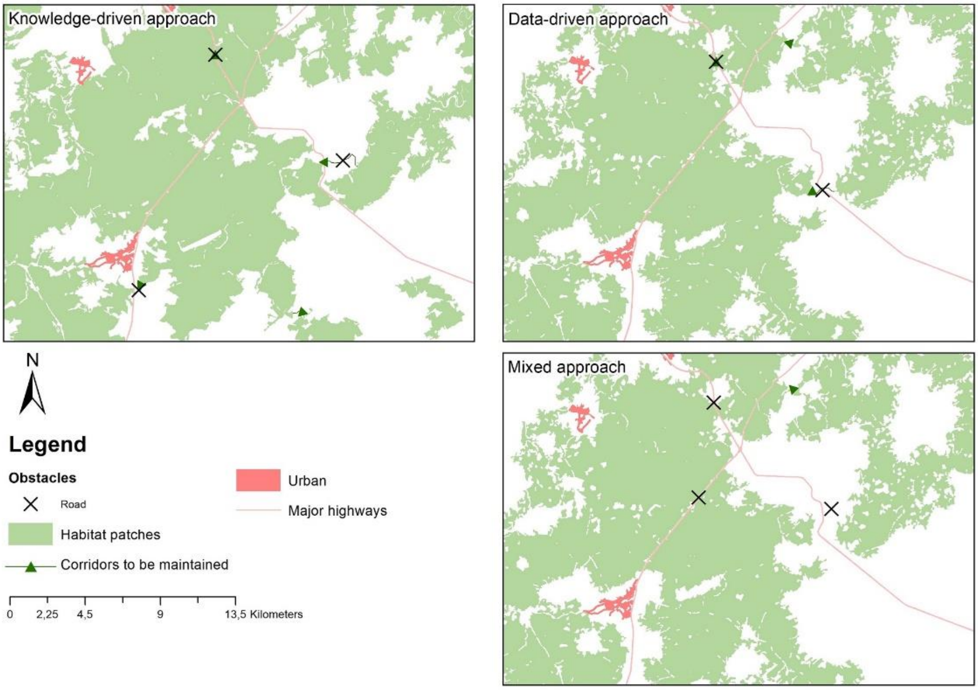

Figure 4.7: Zoom on similar conflicts with roads identified on the different action maps.

Nature conservation practitioners should bear in mind that quantitative comparison of priority action maps remains difficult because of the spatial aspect. We propose in this study the use of a Jaccard similarity index. Although the method has its own limitations due to arbitrary choices made, the results were useful and relevant. We therefore advise the use of such a quantitative comparison method. Also, some arbitrary choices have been made following the up to date knowledge (e.g. dispersal distance, resistance scales, connectivity metrics), with potential consequences on the results.

3.5. Conclusion

Our study tested different approaches to habitat network modeling from habitat and resistance maps to the creation of priority action maps. It comes out that core habitats and corridors are confirmed, but that only the data-driven method could take advantage of the multiple impacts of contextual information on the final results. Although we do not have access to the true use of space by the wildcat, the comparison of the results therefore seems to indicate the data-driven approach correspond best to the known ecology of the species. Moreover this approach can be improved by systematically identifying obstacles based on expert opinion. The knowledge-based method could be more competitive with additionnal parameters in case of absence of observation, but a robust and systematic method to gather expert opinion is needed as well as in-depth sensitivity analysis. In the end, the data-driven approach with presence-only data was more efficient in this study. However, all approaches identified the same important corridors, showing the importance of maintaining the continuity of the Ardennes plateau. The graph analysis of the mixed approach did not highlight central patches important for landscape connectivity. Also, this method requires more inputs (gathering expert opinion and performing habitat suitability models) for less accurate results. The study shows some limitations as arbitrary choices were made throughout, but precautions were taken and discussed. We highlight that one important parameter is the weighted dispersal distance. We suggest therefore that the graph-based metrics should be used for prioritizing connectivity of landscape elements, rather than the direct use of LCP values. We also encourage using sensitivity analysis of dispersal distance to detect uncertainty associated with this parameter. In the end, the different priority action maps, albeit different, identified similar conflict points between important corridors and roads. Those conflict points could guide nature conservation practitioners in their efforts to improve landscape connectivity.

Chapter 5

Modeling Habitat Networks for Multiple Species Using Fragmentation-Sensitive Focal Species

1. Preamble

In this chapter, we present an innovative approach that utilizes the concept of fragmentation-sensitive focal species to conduct habitat network modeling, which takes into account the connectivity needs of multiple species. Our primary aim was to model habitat networks that support the movements of a diverse array of species with varying connectivity requirements. To achieve this, we identified multiple focal species that represent different connectivity needs, all dependent on the same type of ecosystem.

We applied this approach to two types of ecosystems: deciduous forests and dry grasslands. By doing so, we compared the resulting network structures to evaluate various aspects of this approach. These included assessing how well the focal species represented the broader array of species, exploring the benefits of using multiple focal species to map habitat networks within an ecosystem, and examining the contrasting results obtained when mapping networks for different ecosystems with divergent conservation objectives (e.g., forest versus open ecosystems).

Throughout this chapter, we utilized hexagonal grids to conduct and illustrate the outcomes of our knowledge-driven habitat network modeling approach.

2. Introduction

In landscapes where human activities have altered the matrix to include developed and degraded land, the movement of animals across these mixed-use areas can be disrupted, limited, or completely impeded (Harris et al., 2009). Consequently, conservation strategies implemented in such landscapes must prioritize connectivity to facilitate animal movement and safeguard biodiversity (Baldwin et al., 2018; Dinerstein et al., 2019; Heller and Zavaleta, 2009). These strategies aim to protect biodiversity by preserving essential ecological patterns and processes that sustain ecosystem functioning and enhance climate resilience, including habitat and species distributions, migration patterns, and gene flow (Baldwin et al., 2018). As landscapes become fragmented, conservationists aim to maintain or create linkages between habitat patches through corridors. Habitat corridors can also help species track their fundamental ecological envelope in response to climate change (Heller and Zavaleta, 2009).

Traditionally, corridor planning initiatives have predominantly focused on a single species (Brennan et al., 2020), overlooking the connectivity needs of other species due to disparities in resource requirements, movement strategies, and susceptibility to human influences (Brodie et al., 2015; Epps et al., 2011; Taylor et al., 1993). Large-bodied, wide-ranging mammals have often been selected as the primary research focal point for connectivity studies due to their conservation status, ecological significance, and sensitivity to human disturbance (Beier et al., 2008; Epps et al., 2011). Moreover, these species possess charismatic qualities and can potentially function as umbrella species, offering connectivity corridors that benefit other species (Beier et al., 2008; Epps et al., 2011). However, the efficacy of using umbrella species for connectivity purposes can vary depending on the species involved, their body size, and life-history traits (Beier et al., 2008; Breckheimer et al., 2014; Brodie et al., 2015; Wang et al., 2018). For instance, the promotion of connectivity among wide-ranging species may not extend beyond those belonging to the same trophic guild (Brodie et al., 2015; Epps et al., 2011). Additionally, habitat generalists may not serve as effective umbrella species for habitat specialists, and larger-bodied animals may not always be the optimal candidates for promoting connectivity (Beier et al., 2008; Cushman and Landguth, 2012).

To address these discrepancies and assess connectivity across multiple species, researchers have proposed separate modeling of connectivity for individual species, followed by integration of the results to identify areas where movement pathways coincide (Brodie et al., 2015; Epps et al., 2011; Wang et al., 2018). However, multispecies connectivity models should not solely rely on species with the same life-history traits or vulnerability to landscape fragmentation (Brennan et al., 2020; Pliscoff et al., 2020).

In parallel, Amici and Battisti (2009) developed an approach for selecting fragmentation-sensitive focal species based on their sensitivity to land use change processes and human-induced habitat fragmentation. This method enhances the coherence of the focal species approach and holds potential for selecting species with varying degrees of sensitivity to fragmentation. Consequently, it enables the modeling of connectivity for multiple species with distinct and unique requirements in fragmented landscapes, as currently emphasized in the research field (Brennan et al., 2020; Pliscoff et al., 2020). Despite this potential, the construction of habitat networks based on such focal species and their quantitative evaluation has not yet been undertaken.

In this study, we propose a methodological approach to model a habitat network that aims to preserve connectivity for multiple species dependent on the same ecosystem, utilizing the concept of fragmentation-sensitive focal species. Our methodology involves the identification of multiple focal species, representing groups of species with similar life-history traits, through the application of multivariate analysis. Subsequently, the habitat network for each focal species is modeled, and these networks are then overlaid to map the ecosystem network.

To evaluate our approach, we compare the resulting least cost paths (LCP) to answer the following questions:

- Do fragmentations-sensitive focal species networks encompass the connectivity needs of species with similar life-history traits?
- Does modeling multiple focal species with different life-history traits help identify new and unique connectivity priorities?
- How can we account for different connectivity needs that compete for the same areas when considering different ecosystem networks?

3. Method

3.1. Study area

To evaluate the effectiveness of our ecological network mapping approach, we selected the Fagne-Famenne-Calestienne bioregion in southern Belgium as our study area (Figure 5.1). This bioregion is characterized by a diverse landscape, consisting of a depression with fluctuating water tables and waterlogged soils in winter, surrounded by hilly terrain with calcareous formations and resurgences. The hills are covered by extensive forests and pastures, while the valleys have thicker silt deposits suitable for intensive agriculture. The region supports a variety of conservation targets, including European priority habitats such as calcareous grasslands and slope and ravine forests. The landscape structure reflects the typical rural Western European pattern, with (semi-)natural habitats occupying marginal areas such as hills or wetlands, while intensive agriculture or forestry dominates the more mesophilic conditions. The competition for limited marginal areas results in a diversity of habitat conservation priorities.

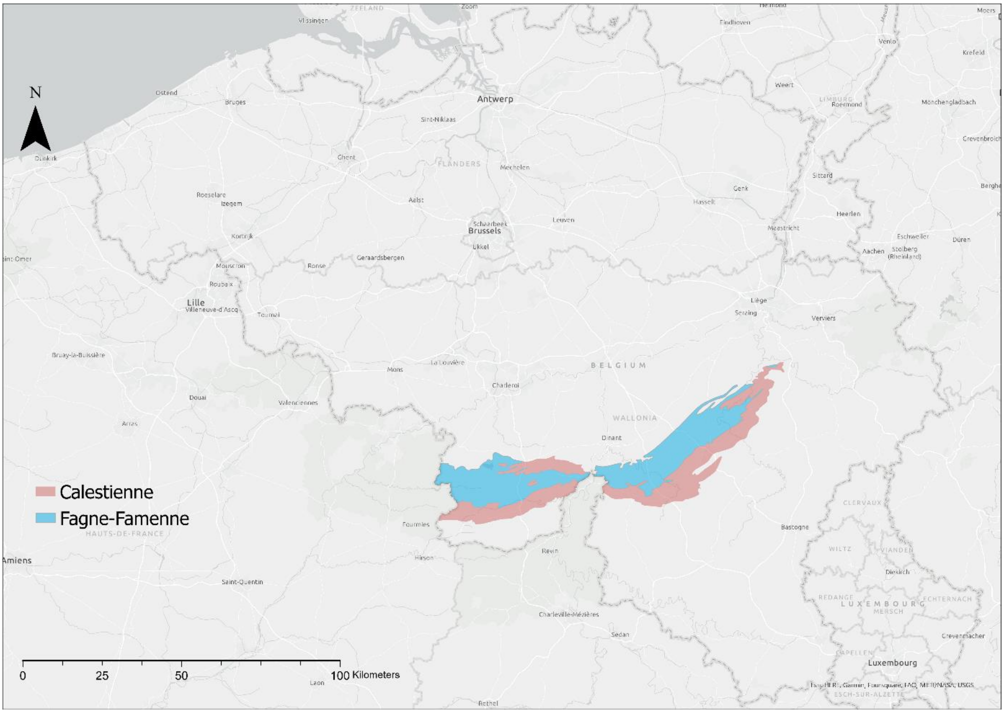

Figure 5.1: Location of the study area in southern Belgium. Calestienne bioregion in red and Fagne-Famenne in blue.

We focused on two ecosystems, dry grasslands, and deciduous forests, which compete for the same areas. Our goal was to assess potential overlapping connectivity priorities that may arise when applying our approach at such spatial scale.

3.2. Methodological framework

To map the thematic networks using the fragmentation-sensitive focal species concept, we followed a four-step process:

1. We compiled a database of species traits related to fragmentation sensitivity, using occurrence data and scientific literature.
2. These traits were then used in a multivariate analysis for each ecosystem type to group species with similar connectivity needs. This analysis helped us select three focal species representing each group.
3. Connectivity analyses were performed for each focal species to model the least-cost path (LCP) and evaluate the importance of patches and LCPs in maintaining ecosystem connectivity.
4. Thematic networks were constructed by adding the focal species networks together. We compared these networks by analyzing the overlap between the most important LCPs.

Additionally, we chose two other species belonging to the same groups as the previously selected focal species and mapped their habitat networks. We then compared their habitat networks with the related focal species networks to evaluate the application of this concept. We also compared their common network with the corresponding thematic network to determine if non-focal species' connectivity priorities are also considered in the thematic network.

Finally, we analyzed the overlap of the most important connectivity priorities between the dry grassland and deciduous forest networks. This analysis aimed to answer whether generalized approaches to habitat networks create highly competitive areas for connectivity priorities.

The overall methodological framework is presented in Figure 5.2.

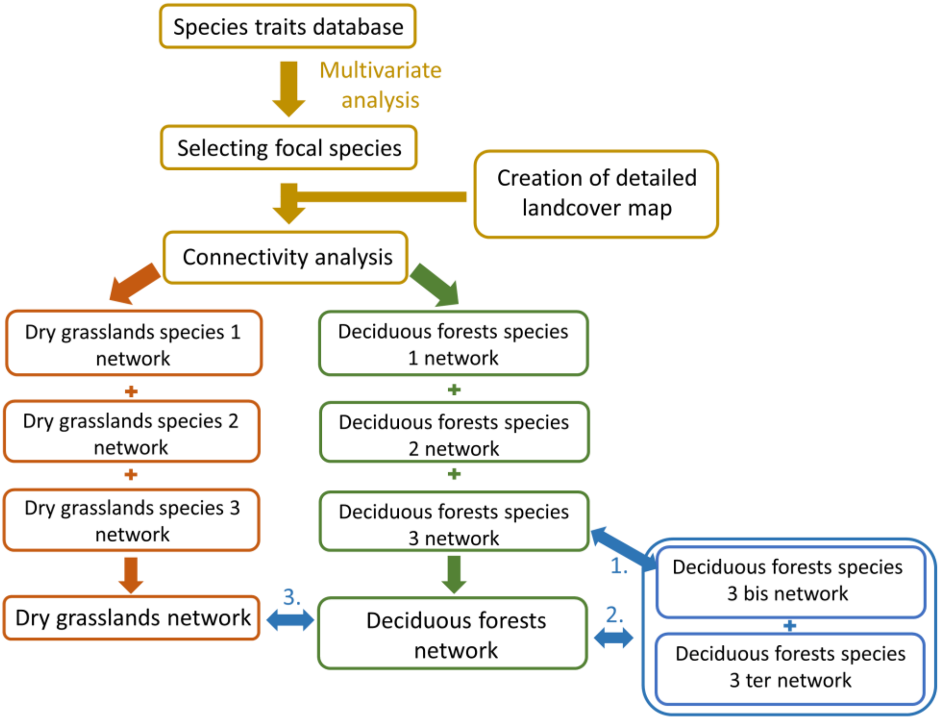

Figure 5.2: Global methodological framework used for the study. 1. Overlap comparison between networks of two non-focal species and the focal species network representing them. 2. Overlap comparison between the merged network of two non-focal species and their thematic network. 3. Connectivity stakes overlap between the two studied thematic networks.

3.3. Datasets

3.3.1. Species occurrences

We extracted species occurrence data from online platforms for opportunistic observations (source: Observations.be, Natagora, Natuurpunt, "Observation International” Fundation and SPW/DGARNE/DEMNA). To ensure up-to-date and qualitative data, we filtered the dataset by keeping only validated data and recent observations (after December 31, 1999) with a location precision finer than 100 meters.

3.3.2. Habitat mapping

Our method aims to map the ecological network of ecosystems based on different focal species to account for multiple connectivity needs. For this purpose, we identified habitats to connect the different biotopes within each studied ecosystem. We used biotope field inventories conducted in the Walloon region between 2005 and 2020 as part of the implementation of the European Union Council Directive

92/43/EEC on the conservation of natural habitats and wild fauna and flora (Loidi, 1999). These inventories resulted in a biotope map composed of polygons at a 1:10,000 scale. The precise biotope mapping, not yet published, was provided directly by the public service responsible (SPW/DGARNE/DEMNA).

Each polygon in the biotope map is characterized by an EUNIS code (European Nature Information System) used for classifying biotope types. (Davies et al., 2004). The EUNIS classification describes biotopes and habitats present in Europe, including terrestrial, freshwater, and marine ecosystems. The EUNIS classification was adapted to Wallonia by the public research agency to match regional variations (Dufrêne and Delescaille, 2005). Each biotope is characterized by a unique code. However, in the field, complexes of multiple biotopes may exist as natural ecosystems do not follow tangible limits. Therefore, numerous polygons are described by a complex of multiple EUNIS codes. To avoid omitting this significant part of the dataset, biotope complexes were kept if one biotope code belonging to a studied ecosystem is present.

However, such biotope map is not exempt of sampling biases as the whole region is not yet covered by field inventories. To complete this dataset, we used recently developed potential natural vegetation (PNV) predictions that correspond to ecological context that favor the development of specific vegetation successions (Bourdouxhe et al., 2023). We combined calcareous *Fagus* and *Quercus* forests PNV with grasslands with extensive practices land-cover to identify calcareous grasslands outside existing biotope maps.

3.3.3. Land-cover information

The first data source is the ecotope land-cover map (Radoux et al., 2019). This vector map delimits the landscape into ecotopes, considered as the smallest homogeneous landscape units. Each ecotope polygon has an attributed majority land-cover type based on a 2m resolution land-cover raster (Radoux et al., 2023). The advantage of the ecotope database compared to other land-cover datasets such as Corine is the use of small polygons (average size of 1.4 ha), which ensures the integrity of landscape elements, important for connectivity analysis and particularly for identifying obstacles. However, the ecotope land-cover classification does not distinguish dry, mesophilic, and wet ecological contexts for forests and open natural areas, which may be useful for our analysis.

To address this, we used a PNV to distinct various ecological contexts from wet to xeric, with further distinction between oligotrophic and eutrophic contexts. PNVs were used to improve the ecotope land-cover map by adding a distinction between dry, mesophilic, and wet natural habitats.

We also enhanced the ecotope land-cover classification by overlaying the linear road network using Open Street Map data, distinguishing highways, primary, and secondary road networks. Additionally, we created a map identifying high densities of forest edges, tree lines, and orchards to further refine the land-cover map for connectivity analysis. This land-cover information may help identify landscape connectivity paths for species that disperse better or find sub-optimal habitat in open areas with such structures than in other open areas (Duflot et al., 2018b; Fischer et al., 2013; Schlinkert et al., 2016).

Finally, we utilized a European-scale land-cover dataset to integrate our study area into the neighboring landscape, improving the coherence of connectivity analysis (Bourdouxhe et al., 2020). The ecopatches dataset is an implementation of the ecotope database method at a lower resolution on a European scale, within the framework of the LifeWatch project (“Lifewatch-FWB : UCL - Geomatics,” 2022). Ecopatches are polygons with a majority land-cover class and an average size of 10 ha. The use of this dataset helped complete the land-cover map in a 20 km buffer outside the Walloon region, where ecotope database and PNV models are not available. The precision level of land-cover is therefore different outside the Walloon region limits.

Utilizing land-cover information from outside the study region enables us to consider neighboring habitat patches and accurately calculate the importance of patches and landscape connectivity within the study area. By neglecting this approach, network elements at the borders would be limited to the external boundaries of the network, resulting in a lower importance for landscape connectivity due to underestimated species potential fluxes compared to the actual scenario (Bourdouxhe et al., 2020).

3.4. Building species traits database

We constructed a comprehensive database to compile all the necessary information for identifying species sensitive to habitat fragmentation, following the approach of Amici and Battisti (2009). We focused on species listed in the regional red list belonging to two taxonomic groups: mammals and lepidoptera. These groups provided the most complete and readily available information on dispersal ability. The database consists of the following descriptors: species name, relevant thematic networks, trophic level, dispersal ability, body size, niche breadth, and rarity. All traits were populated by combining expert opinions and information from the literature, except for rarity.

Rarity was determined by using validated species occurrences from the regional naturalist encoding platform. We calculated the proportion of 1-km squares where a species was observed, relative to the total number of 1-km squares where species from the same taxonomic group were observed in the study area. This approach helped account for variations in sampling effort across taxonomic groups. The proportion values were then grouped into three classes (R = rare, QR = quite rare, C = common) using a PAM (partitioning around medoids) clustering. This analysis was performed independently for each species group.

The remaining traits were assigned three different ordinal qualitative values representing low, intermediate, or high levels for each trait. For example, species niche breadth was characterized as "specialist," "intermediate," or "generalist."

These values were determined based on the range observed within the respective group. For instance, a large butterfly would have a high value for body size.

The list of species and their corresponding traits is provided in Appendix 10.

3.5. Identifying focal species

The identification of focal species was carried out in two steps.

First, we applied the method proposed by Amici and Battisti (2009) to identify human-induced habitat fragmentation-sensitive (HIHFS) species. This method is based on a meta-analysis by Ewers & Didham (2006), which examines species responses to fragmentation based on their traits. We considered three components of human-induced habitat fragmentation (HIHF): habitat patch area, isolation, and edge effect. Species populations respond differently to these components based on their traits. A score ranging from 1 to 3 was assigned to each species trait value, with higher scores indicating higher sensitivity to fragmentation. These scores were then summed to obtain a global fragmentation sensitivity score. Instead of using a subjective threshold to identify HIHFS species, we applied a PAM clustering based on the global score, resulting in the creation of two groups: sensitive and non-sensitive species.

Secondly, we performed a multivariate analysis (PCA) on the HIHFS species related to each thematic network. This analysis utilized the trait scores related to fragmentation sensitivity calculated earlier. Subsequently, a PAM clustering was applied to identify three groups of species based on their trait characteristics. We chose three groups as a reasonable compromise to capture different connectivity requirements without excessively increasing the number of analyses. This multivariate analysis served as a tool to assist in selecting focal species that were closest to the center of each group.

Finally, information regarding dispersal distance and minimum patch area necessary for modeling the habitat network was gathered for each focal species. This information was obtained from studies that provided precise results on species dispersal, and approximations based on scientific literature were used for species lacking accurate evaluations of dispersal distance.

3.6. Habitat networks analysis

3.6.1. Habitat patches

The native ecotope land-cover classification already differentiates deciduous broadleaved forests and needle-leaved forests effectively. Therefore, we selected deciduous broadleaved forests and applied a negative 50m buffer to exclude forest edges, focusing only on distinct forest patches connected by tree rows to account for edge effects. To identify dry grassland areas, we initially used current biotope mapping, using EUNIS codes corresponding to dry grasslands. To supplement this dataset and address biases resulting from heterogeneous sampling efforts in biotope mapping surveys, we incorporated the ecotope database augmented with PNV information, as it does not provide this distinction for open natural areas. To align with the existing distribution of biotopes, we combined PNV distributions of dry biotopes such as Calcareous Fagus and Quercus forests, Thermophile acidophilous Quercus forests, and Xerophile Fammenian Quercus and Carpinus forests, intersecting them with the current land-cover of natural open areas to identify potential dry grasslands.

To enhance reliability, we utilized validated botanic and faunistic occurrence datasets to identify verified biotopes where indicative species (highly specialized species) are observed in potential dry grasslands. We also expanded the selection of habitats to be connected by incorporating potential distribution models of specialized butterflies in dry grasslands. Potential dry grassland areas not covered by indicative species occurrences or potential distribution models of specialized butterflies were excluded from the habitat patches.

3.6.2. Cost Matrix

The landscape map used in the analysis is a land-cover map that assigns travel costs to each land-cover type based on species capacity. To create a detailed land-cover map suitable for connectivity analysis, we refined the ecotope database with PNV models, road networks, and interface environments (bocage and forest edges). For each thematic network, a landscape map was generated by integrating the identification of habitat patches.

For each species, travel costs were assigned to each land-cover type in the landscape map based on expert opinions and literature. Four different travel cost values were used: [1, 10, 100, 1000]. This exponential scale was recommended by Savary et al. (2021) to maximize landscape heterogeneity during sensitivity analysis. The landscape map was then transformed into a resistance map, expressing the assigned cost values.

3.6.3. Hexagonal representation

Land-cover maps, PNV models, and current biotope mapping have inherent limitations in precision due to biases associated with their nature (e.g., operator effects, calibration data accuracy, environmental predictors). The cumulative effect of these biases, coupled with the high resolution of analysis (10m), may result in erroneous LCP modeling, creating links that may not be feasible. Furthermore, species affinity with the environment is also influenced by local land-cover context (Klar et al., 2008), which cannot be adequately captured using 10m resolution data.

To overcome these limitations, we decided to aggregate the land-cover and habitat patch information into 1 ha hexagons. The information regarding land-cover or biotopes was integrated into the hexagons by calculating the intersection proportion between different sources of information. Different rules were applied depending on the information to be summarized. For summarizing land-cover information, we rasterized the aforementioned land-cover data at a 10m resolution. The majority land-cover type within each hexagon was assigned. For habitat patches, the proportion of habitat coverage within each hexagon was calculated. A 50% threshold was applied to consider a hexagon as a deciduous forest habitat, while a lower threshold of 30% was used for dry grasslands due to their scarcity and typically smaller patch sizes.

3.6.4. Corridor modeling and connectivity metrics

The habitat network modeling for each focal species followed the same approach in Graphab© software. The software utilizes raster data to perform connectivity analysis. The different landscape maps represented as hexagons were rasterized at a 10m resolution. In this example, we considered the road network as a significant obstacle to species dispersal. Hence, we overlaid the road network rasterized at a 10m resolution. To preserve the integrity of the road network during rasterization, a 10m buffer was applied.

The first step involved translating the dispersal distance into a cost relative to the landscape typically traversed by the species. To accomplish this, an initial least-cost path (LCP) was modeled using a cost of 1,000,000 to connect all patches within the study region. Then, we utilized a built-in option in Graphab that performs a regression with cost values and metric distances of the previously modeled LCPs. This allowed us to establish a linear relationship between metric distance and cost, enabling the translation of dispersal distance into a maximum cost. The software also provides options to perform the regression on a subset of LCPs that do not cross land-cover types with high resistance to movement. This ensures that only LCPs that species would plausibly follow are considered, providing a better estimate of species' dispersion capacity in the studied landscape. The calculated cost values were then used to model the final LCP network.

Finally, a graph analysis was conducted to assess landscape connectivity by calculating the Betweenness Centrality (BC) index. BC evaluates the importance of each habitat patch and link in the network by measuring the extent to which a patch or least-cost path (LCP) holds a central position. It is computed as the sum of the shortest paths passing through a focal patch or LCP, with each path weighted by the product of the connected patches' capacities and their interaction probability (Saura and Pascual-Hortal, 2007):

Equation 1.

$$BC_i = \sum_j a_j^\beta a_k^\beta \, e^{-\alpha d_{jk}}$$

$$j, k \in \{1..n\}, k < j, i \in P_{jk}$$

where n is the number of habitat patches, a_j is the attribute characterizing patch j (here patch size), a_k is the attribute of patch k, P_{jk}represents all the patches crossed by the shortest path between the patches j and k and $e^{-\alpha d_{jk}}$ is the probability of movement between the patches j and k (Saura and Pascual-Hortal, 2007).

The BC calculation can be configured with two parameters: α and β. α correspond to $\frac{-\log(p)}{d}$,where *p* is the probability of movement and *d* the distance. This can help to modulate dispersal movement found in the literature if this movement is a maximum observed (p=0.05), a mean (p=0.5) or a minimum (p=0.95). β is used to weight more or less capacity of patches. The default value of 1 was used in this study.

The BC metric was selected for its ease of interpretation, its ability to evaluate the importance of network elements for connectivity, and its applicability to both patches and links.

3.7. Comparing networks

Networks were compared by processing the modeled LCPs and analyzing their overlapping stakes. Different buffers were applied based on species' dispersal distances. A 250m buffer was used for dispersal distances exceeding 5000m, a 100m buffer for distances between 1000m and 5000m, and a 50m buffer for distances below 1000m. The processed LCPs were then reintegrated into the hexagon representation, considering a 33% overlap proportion.

Regarding connectivity metrics, BC values of patches and LCPs were categorized into four priority classes using the Jenks Natural Break method, which minimizes variance within groups. This classification was performed for each species to enable standardized comparison of patches and corridors.

The first comparison involved evaluating whether the focal species networks correctly encompassed important connectivity areas for similar species (Species_3_1 and Species_3_2). The proportion of LCP areas overlapped by Species_3 LCPs was calculated, considering different priority class combinations (third, second, and first classes; first and second classes only; and first-class only).

Next, the focal species networks of the same thematic networks were merged using GIS software. Patches and LCPs were merged, and the highest priority for connectivity was assigned to each merged element. This merging process was also applied to the two other species (Species_3_1 and Species_3_2) belonging to the same group as the evaluated focal species (Species_3).

The second comparison aimed to assess if the deciduous forest networks identified important connectivity areas for similar species not used in building the network (Species_3_1 and Species_3_2). The proportion of LCP areas of Species_3_1 merged with Species_3_2 overlapped by the deciduous forest networks' LCPs was calculated.

The third comparison analyzed the added value of multiple focal species with different dispersal distances. Overlaps of different LCP categories between focal species within the deciduous forest network were compared. The focus was primarily on LCPs of species with lower dispersal distances compared to LCPs of species with the highest dispersal distance, as the latter covers a wider surface area. The plus-value represented the surface area of priority class LCPs not covered by LCPs of the same or higher priority class of the compared species.

The final comparison involved the dry grassland and deciduous forest networks to identify potential connectivity overlaps between the two networks with different habitat structures. The same method was applied, calculating proportions of LCP overlaps between dry grasslands and deciduous forests based on the total area of LCPs for each habitat type.

3.8. Quality assessment of thematic network mapping

To validate the LCP mapping, occurrence data of dry grassland focal species were used to assess their spatial distribution within the study area. Frequencies inside and outside the modeled LCPs were compared. This analysis was specifically performed for the dry grassland network due to its specificity and limited coverage, while the larger coverage of deciduous forest LCPs could include species observations that might affect the analysis's relevance. To exclude the fact that most species are observed in specific LCP priority category because this category is more prevalent in the landscape, we calculated the difference of frequency between observations and LCP surface areas in each priority category.

4. Results

4.1. Identifying focal species

Species were grouped in 3 cluster following a PAM algorithm for each ecosystem type. Species of dry grasslands are well differentiated with 3 groups. One group concerns rare species with larger ecological envelope with *Spialia sertorius* chosen as focal species. The second group is made of high disperser with larger ecological envelope. The chosen focal species is *Melitea cinxia* due to its higher dispersal distance than any other species that must be considered for connectivity analysis. Finally, the third group is composed of rare species with specific ecological envelope. The focal species of this group is *Erebia aethiops.*

Concerning deciduous forests species, two groups are overlapping. Species with low dispersal distance are hardly separated by rarity and body size while species with high dispersal distance are not separated by those two criterions (Figure 5.3). Species inside groups are more fragmented for deciduous forests. We therefore chose species at the center of group as focal species of deciduous forests: *Myotis nattereri* for species with high dispersal ability, *Limenitis Camilla* for common species with low dispersal ability and *Neozephyrus quercus* for rare species with low dispersal ability. To test our hypothesis of using multivariate analysis on traits linked to sensitivity to fragmentation to select focal species, we selected two species belonging to *Limenitis camilla* group : *Lucanus cervus* which is also overlapped by the third group ellipse (*Neozephyrus quercus*) and *Meles meles* located at the extremity of its group.

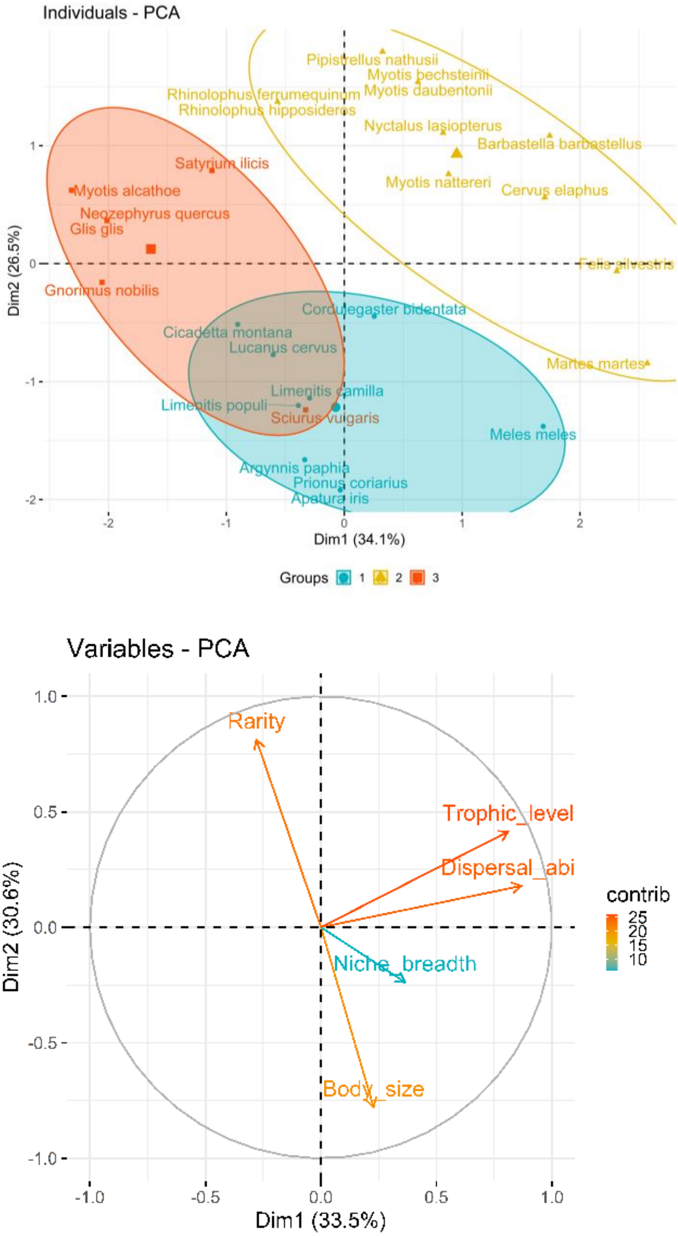

Figure 5.3. Results of PCA analysis and PAM clustering on species related to deciduous forests. Species distributed depending on the first two principal component axis and their cluster (top) and variable contribution projected on the first two principal component axis (below).

4.2. Modeling thematic networks

A review of the literature has been made for the selected focal species to gather information on measured dispersal distance and size of habitat patches to perform connectivity analysis.

In total, 21 land-cover categories were compiled. Costs of dispersion were assigned to each land-cover for each species based on literature and expertise. The different cost of dispersion for each species are available in Appendix 11. All resulting categories of land-cover with an example of cost for *Limenitis camilla* are presented in Table 5.1.

Table 5.1: Cost attribution to land-cover for Limenitis Camilla.

Code	**Land-cover**	**Costs**
10	Water	100
21	Open natural wetlands	10
22	Dry natural open areas	100
23	Mesophilic natural open areas	10
31	Crops	1000
32	Permanent intensive pasture	1000
33	Other agricultural areas	1000
40	Forest edge and orchads	1
51	Alluvial or wet deciduous forests	1
52	Mesophilic deciduous forests	1
53	Dry deciduous forests	1
61	Needleleaved sempervirens forest	1000
62	Young forests and Christmas trees	100
71	Artificialized areas	1000
72	Other artificialized areas	1000
73	Urban forests	100
74	Urban grasslands	100
80	Bare soils	1000
91	Highways	1000
92	Primary road network	100
93	Secondary road network	10

Habitat network of each focal species have been modeled such as habitat network of *Lucanus cervus* and Meles meles who belong to the focal species Limenitis camilla group. Habitat network of each focal species were merged to create thematic networks of deciduous forests and dry grasslands. A graph analysis was performed for each network to evaluate importance for connectivity of each patches and LCP using BC metric. The Figure 5.4 shows an example of visualization of patches ad LCP importance for network connectivity.

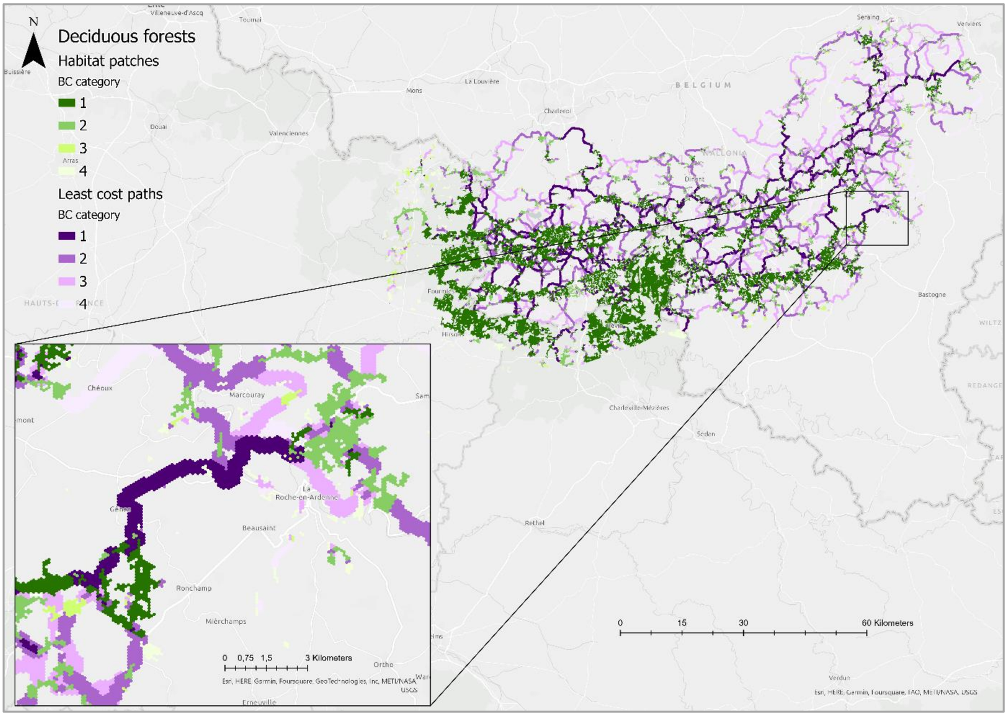

Figure 5.4: Result of network modeling for deciduous forests species. Here, a visualization of importance for connectivity of each element of the network using BC metrics reclassified into four categories (1 = highest importance, 4= lowest importance).

4.3. Comparing networks

To evaluate the use of focal species to ensure needs for connectivity of multiple species, we quantified overlaps between the focal species *Limenitis camilla* LCP and LCP of *Meles meles* and *Lucanus cervus* (Table 5.2). As *Meles meles* has a dispersal distance of 8300m which imply a larger buffer around LCP, the same buffer as *Lucanus cervus* and *Limenitis camilla* is performed (100m) before the transposition to hexagonal representation for this comparison.

Table 5.2: Proportion of surface area of *Lucanus cervus* and Meles meles LCP included by Limenitis camilla LCP for each catego importance for connectivity based on BC metric.

	Limenitis camilla									
	1		**2**		**3**		**4**		**Outside**	
Priority	*Lucanus cervus*	*Meles meles*	*Lucanus cervus*	*Meles meles*	*Lucanus cervus*	*Meles meles*	*Lucanus cervus*	*Meles meles*	*Lucanus cervus*	*Meles meles*
1	0.76	0.11	0.01	0.12	0.01	0.06	0.00	0.02	0.22	0.70
2	0.85	0.04	0.04	0.09	0.02	0.09	0.00	0.06	0.08	0.71
3	0.09	0.02	0.65	0.08	0.03	0.10	0.01	0.05	0.21	0.76
4	0.02	0.00	0.38	0.07	0.34	0.09	0.06	0.01	0.21	0.82
Outside	0.05	0.10	0.22	0.22	0.39	0.32	0.34	0.35		

We can see that *Lucanus cervus* LCP are better included by *Limenitis Camilla* LCP with only 22% of most important LCP for connectivity surface areas outside *Limenitis camilla* LCP. At the opposite, only 30% of *Meles meles* LCP surface areas are comprised.

Then *Lucanus cervus* and *Meles meles* LCP were merged to be compared with deciduous forests LCP (Table 5.3).

Table 5.3: Proportion of surface area of merged *Lucanus cervus* and Meles meles LCP included by deciduous forests species LCP for each category of importance for connectivity based on BC metric.

		Deciduous forests LCP				
	Priority	**1**	**2**	**3**	**4**	**Outside**
Lucanus cervus and Meles meles LCP	*1*	0.43	0.28	0.13	0.05	0.11
	2	0.25	0.25	0.27	0.07	0.15
	3	0.19	0.28	0.29	0.09	0.15
	4	0.13	0.24	0.28	0.13	0.22
	Outside	0.19	0.27	0.37	0.16	

Here, most important LCP in the first BC class are better comprised with only 11% of surface areas outside deciduous forest LCP. For other BC class, at least 78% of surface areas a comprised in the thematic network.

To evaluate the plus-value of modeling networks of species with low and medium dispersal distance in addition to high dispersal species, the different priority LCP surface areas of *Limenitis camilla* and *Neozephyrus quercus* were compared to *Myotis nattereri* LCP (Table 5.4).

Table 5.4: Surface area of *Limenitis Camilla* and *Neozephyrus quercus* LCP not overlapped by *Myotis nattereri* LCP. Sufaces area are also compared to total surface areas of concerned species LCP.

	Limenitis camilla		***Neozephyrus quercus***	
Priority	**Ha**	**Prop**	**Ha**	**Prop**
1	304	0.13	100	0.17
1-2	1289	0.19	575	0.28
1-3	2758	0.23	1130	0.32
1-4	4349	0.27	1327	0.32

We can see that, for both species, 27 to 32% of LCP are not comprised in *Myotis nattereri* network. However, for first-priority LCP, the proportion of surface area not intersected by *Myotis nattereri* network decrease to 13 and 17%.

Finally, dry grasslands and deciduous forest LCP were overlapped to evaluate how much open and forest ecosystems connectivity stakes may compete for the same areas (Table 5.5).

Table 5.5: Proportion of surface area of deciduous forest species LCP intersected by dry grassland species LCP for each category of importance for connectivity based on BC metric.

		Deciduous forests LCP				
	Priority	**1**	**2**	**3**	**4**	**Outside**
Dry grasslands LCP	***1***	0.08	0.19	0.24	0.07	0.43
	2	0.10	0.19	0.25	0.04	0.42
	3	0.06	0.14	0.19	0.06	0.55
	4	0.16	0.16	0.08	0.02	0.59
	Outside	0.25	0.29	0.33	0.13	

We can see that an overlap exists, but it concerns less important LCP based on BC metric. High priority LCP do not concern same areas except for 8% of them.

3.3.4. Quality assessment

We analyzed dry grassland focal species distribution inside study area to evaluate the quality of LCP modelling. 84% of species observations are located inside the network and in a 100m buffer (corresponding to data precision). The distribution of species occurrence inside LCP along the different priority categories is available in Table 5.6. We also compared this distribution to the distribution of LCP surface areas between priority categories to evaluate if species are more often observed inside most important LCP for connectivity. This analysis identified that 83% of species observation inside LCP are distributed around the most important priority category. We also highlighted that species distribution inside LCP priority categories is not only due to the distribution of LCP surface areas between priority categories. Species are therefore comparatively more located in most important LCP for connectivity.

Table 5.6: Distribution of dry grassland focal species inside LCP priority categories. The frequency is compared to the distribution of LCP surface areas between priority categories.

LCP Priority	*Occurrence*	*Frequency*	*Compared frequency*
1	1309	83%	+50%
2	208	13%	-31%
3	58	4%	-18%
4		0%	-1%
Total	1574		

5. Discussion and Conclusion

5.1. Multivariate analysis to identify focal species

In this study, multivariate analyses were conducted to identify focal species that could be used to model habitat networks. Candidate species were compared based on traits related to their sensitivity to HIHF. This analysis was useful for visualizing species characteristics and how they can be grouped. It revealed that certain species have extreme trait values compared to others in their group. For example, *Meles meles* is located far to the right of its group. The variable contribution projected in the first two dimensions of the PCA indicated that this remoteness could be explained by trophic level and dispersal ability. *Meles meles* is omnivorous and can disperse up to 3500 m, while *Limenitis camilla* (located at the center of the same group and selected as a focal species) has a lower trophic level and disperses up to 1000m. This difference is reflected in the overlap analysis, which shows that 79% of *Meles meles* LCP are overlapped by its focal species LCP. On the other hand, *Lucanus cervus* is closer to *Limenitis camilla* with the same dispersal distance (1000m), and 95% of its LCP are considered in the *Limenitis camilla* network.

This important difference of dispersal distance for species in the same group may raise questions on the automated choice of most centered species in the group as focal species. Indeed, PCA analysis must be considered as a tool to help choosing focal species. In our case, a fourth focal species as *Felis sylvestris*, *Martes martes* or *Meles meles* should have been chosen to ensure connectivity needs for more common species with high dispersal ability and high trophic level. But this analysis is easily done thank to the PCA who allows to summarize connectivity needs of species.

However, species traits used in PCA are not the only factor influencing results of graph analysis. Dispersal distance and patch size are two important parameters used to model habitat network. As we have seen, *Meles meles* has a dispersal distance higher than *Limenitis Camilla* but also different minimal patch size has been used with 1ha for *Limenitis camilla* and 100 ha for *Meles meles*. The minimal patch size affects the number of potential connections as a lower minimal patch size increase number of patches to connect. Therefore, number of LCP for each species are also different with 1441 LCP for *Limenitis camilla* and 339 LCP for *Meles meles*. Differences in dispersal distance and minimal patch size increases differences in networks. The choice of focal species must be done with care, also considering these two parameters.

Moreover, PCA analysis is based on traits summarized by ordinal values. A slight change may significantly affect how species are grouped. A limited number of possible values may increase the effect of value change on PCA results but also increase stability of value attribution as difference between values are more important. The choice of focal species is also dependent on dispersal data and available literature rather than choosing only central species. This strengthens the use of PCA analysis as a choice guiding tool more than an automated method.

Furthermore, some species traits were built based on occurrence data such as rarity. This should be made with care as species have different sampling rate according to the interest we have in them. For instance, game species such a *Sus scrofa* or *Cervus elaphus* are underestimated in opportunistic observation database. This has led us to consider *Cervus elaphus* rarer than *Felis sylvestris*, which is not the case.

5.2. Using multiple focal species to identify different connectivity stakes

Overlap analysis between focal species of deciduous forests allowed to highlight the plus-value of modeling multiple networks of focal species with different connectivity needs to identify new connectivity stakes. For both species with lower dispersal distance, around 30% of LCP surface area are not considered by long disperser species. Furthermore, around 15% of first-class priority LCP are not considered to such priority by the long disperser species. This emphasizes the use of species with lower dispersal distance even for regional scale studies. This also underline that dispersal distance is not the only factor influencing species habitat network modeling and that it cannot be used alone to select focal species.

5.3. Overlapping of opposed objectives for landscape connectivity

Results of overlap analysis between LCP of deciduous forest network and dry grassland network have shown small overlaps between LCP of first-class priority. LCP prioritization based on BC metric may be useful to guide conservation actions for the ecosystem for which connectivity stakes are the most important. However, areas with an overlap of LCP of the same priority, even if they are rare, should benefit actions to improve landscape heterogeneity which favor biodiversity and species population maintenance (Ke et al., 2018; Malanson and Cramer, 1999). Moreover, it is important to consider local land-use plans or socio-economic context that may swing the choice to improve a particular ecosystem.

5.4. Quality assessment

Analysis of dry grassland focal species observations made interesting insights on LCP potential use. A large majority of individuals are observed in the network and are more often observed in first-class priority LCP. This may lead to believe that LCP are correctly modeled, and that priority classification made on BC metric well identified most important areas for species movements. However, these results should be confirmed by specific studies to correctly measure functional connectivity and the real use of LCP.

5.5. Limitations and perspectives

This study principally focuses on exploratory analysis made directly on resulting network or using already available data. This was sufficient to highlight the interest of using multiple fragmentation-sensitive focal species to model thematic networks. However, further studies could be performed to control and strengthen results made.

Empirical evaluation on LCP use are important to validate such approach (Brennan et al., 2020). This could be done using tracking device (Driezen et al., 2007) or following specific monitoring protocol (Powney et al., 2012). Using genetic analysis is also increasingly used to measure functional connectivity and give convincing results to measure realized movement leading to reproduction (Balkenhol et al., 2019; Dyer, 2015; Savary et al., 2021b). Such analysis could also be made in relation to results of graph analysis such as BC metric and the realized use of important LCP for species movements. Other connectivity metric could have been used such as dPC decomposed and sensitivity analysis could be performed on multiple metrics (Savary et al., 2021a). This could also be done to evaluate if connectivity stakes of different thematic network are really overlapping or not.

6. Conclusion

The method proposed in this study helped to identify focal species for modeling habitat networks based on multivariate analysis. The results showed that using only the most centered species in a group as focal species may not always ensure connectivity needs of all species. Additionally, dispersal distance and patch size are important parameters that must be considered in choosing focal species. PCA analysis proved to be a useful tool in summarizing connectivity needs of species, but it should be used as a choice-guiding tool rather than an automated method. Multiple focal species modeling was found to be effective in identifying new connectivity stakes. The study also highlights the importance of graph analysis and the use of connectivity metrics to prioritize network elements and identify which connectivity stakes are the most important. Especially when connectivity stakes correspond to opposed objective. A first quality assessment using species observation datasets highlighted the good modelling of LCP and stressed out that species are more present in most important LCP. Finally, it was suggested that future studies should confirm the functional connectivity and the real use of LCP using tracking devices or genetic analysis.

Chapter 6

Discussion, Perspectives and Conclusion

1. Major findings

The objective of this thesis was to examine and develop methodologies for identifying biodiversity conservation priorities in a fragmented landscape while considering meta-population dynamics. Our approaches focused on assessing species' habitat availability and potential, including their connectivity.

Initially, we concentrated on the representation of landscape elements, particularly on the delineation process (**RQ1a**). **Chapter 2** centered on the concept of ecotopes, which are considered as the smallest homogeneous units within a cartographic system. To capture the ecological conditions shaped by topography, we incorporated topographic data in the ecotope segmentation process. Topography plays a significant role in influencing water intake, insolation, and soil depth, which are important predictors of biotopes and species habitats (Pradervand et al., 2014). **Chapter 2** demonstrated that topography also has a substantial impact on the spatial distribution of land-cover. Human activities tend to favor intensive agricultural and sylvicultural production in flat and deep soil areas, while restricting (semi-)natural vegetation to slopes, superficial soils, and wetlands (Hall, 1988).

In **Chapter 3**, we developed a biotope modeling framework that incorporated vegetation dynamics to accurately predict the presence of multiple biotopes within a region (**RQ1b**). This modeling framework was calibrated on raster environmental datasets. A preliminary analysis showed that employing raster data with a finer grain than ecotope data (10m resolution) strikes a balance between achieving a more precise delineation of biotope ecological envelopes and maintaining a manageable data size. Consequently, the use of raster data significantly enhances the accuracy of biotope modeling.

The concept of potential natural vegetation (PNV) was used to assign multiple biotopes sharing the same ecological envelope to a PNV category. This enabled the creation of a robust presence/absence dataset, which was used to calibrate classification models. Overall, the prediction results were highly satisfactory, with some exceptions for the rarest PNV categories. Independent quality assessments using floristic observation data validated these positive outcomes. We also compared our approach with a conventional biotope modeling method that models biotopes separately. Our approach exhibited significant improvements in model sensitivity compared to the traditional approach. Furthermore, it underscored the significance of PNV modeling in fragmented and degraded landscapes to get closer to the historical ecological context of biotopes. Human activities have favored certain biotopes, especially in marginal areas, thereby constraining their ecological context.

Having addressed biotope distribution and representation as a foundation for identifying species habitat patches, our research subsequently focused on connecting these habitat patches to facilitate meta-population dynamics. In **Chapter 4**, we explored the use of expert knowledge and modeling approaches to map species corridors, using the case of the wildcat (*Felis sylvestris*) as an example (**RQ2**). First of all, a initial assessment was conducted to evaluate the use of ecotope delineation in habitat network analysis compared to another type of representation used that are hexagonal grids. We noticed significant disparities between using ecotope and 1ha hexagonal grids. The utilization of ecotope representation indicated a less fragmented landscape compared to the results obtained using hexagonal grids. This difference can be attributed to the presence of linear elements in ecotope delineation, which tends to facilitate patches connection and species movements, whereas hexagonal grids primarily reflect the local land-cover context. However, it's essential to consider that ecotope delineation may introduce biases that create artificial linear elements lacking ecological reality. Therefore, these considerations must be carefully evaluated when selecting the appropriate representation type based on the requirements of the studied species.

In our study case on the wildcat, we employed LCP modeling approach in combination with spatial graph analysis to map species corridors and evaluate their significance for habitat network connectivity. We compared the use of expert knowledge in assessing landscape resistance to movement and identifying habitat patches with modeling methods based on species observations. Additionally, we proposed a third approach that combined data-driven identification of species habitats with expert knowledge-based evaluation of landscape resistance. The data-driven approach, utilizing presence-only data, outperformed the other methods in terms of efficiency. However, all approaches identified the same critical corridors, highlighting the importance of maintaining connectivity in the Ardennes plateau. The graph analysis in the mixed approach revealed different central patches crucial for landscape connectivity compared to the other approaches. Hence, we recommend employing the data-driven approach when accurate and easily accessible data are available, while the knowledge-driven approach may be preferable when a better understanding of species habitat is established beforehand.

In **Chapter 5**, we delved into modeling multiple species habitat networks to ensure landscape connectivity for a diverse array of species (**RQ3**). This study built upon the results of previous investigations. We demonstrated that it was possible to model multiple species habitat networks even with limited and unvalidated data, thanks to a robust knowledge-driven approach. Precise habitat identification was facilitated by the utilization of PNV, which enables a more nuanced consideration of land-cover types within their ecological context (e.g., wetlands or dry grasslands). We developed a methodology based on the concept of fragmentation-sensitive focal species, initially proposed by Amici and Battisti (2009). Our approach involved identifying species sensitive to fragmentation and subjecting them to a multivariate analysis using life history traits associated with their sensitivity. Subsequently, the species were grouped using cluster analysis. This allowed for a visual representation of different species types and guided the selection of focal species for graph-based analyses. We compared the modeled LCPs and highlighted the importance of incorporating species with varying dispersal distances. Furthermore, we demonstrated that multivariate analyses based on life history traits related to fragmentation sensitivity served as a reliable proxy for assessing the divergence within resulting networks. Lastly, we underscored the capability of graph-based analyses to prioritize connectivity priorities, even in contrasting ecosystems such as grasslands and deciduous forests.

2. Discussion

2.1. Representing landscape elements and ecological data

Throughout this thesis, various types of landscape element representations have been utilized. Throughout this thesis, we extensively covered the ecotope delineation and its application in landscape ecology analyses. This representation was employed for tasks such as mapping potential biotope distributions and species habitat networks. Ecotopes provide a valuable approach for fine-scale landscape delineation and managing the complex distinction of vegetation cover and different land-use in complex human dominated landscapes (Ellis et al., 2006). Our research has demonstrated that ecotopes exhibit high purity in terms of land-cover, soil predictors such as drainage and depth. Ecotope grain size was fixed to 2 hectare considered as the smallest ecological unit of management for biodiversity conservation purpose (Radoux et al., 2019). For its consistent delimitation of ecological distinct element such as land-cover and vegetations in human dominated landscape, ecotope representation was used to represent land-cover for connectivity analysis in **Chapter 4**. Furthermore, as SDM approach were used in this chapter, the existence of previous studies highlighting SDM accuracy improvement using ecotope have set the choice for this representation (Delangre et al., 2017). Furthermore, ecotope database produced in the framework of LifeWatch ERIC dispose of interesting contextual land-cover information known to be good predictors of wildcat habitat suitability (Klar et al., 2008). However, using ecotope with such fine-scale delimitation makes this type of representation sensitive to errors present in raster layers used for segmentation. Even small errors can have larger-scale repercussions, and especially in connectivity analysis where the presence of linear elements can help connect habitat patches as demonstrated in **Chapter 4**.

Yet, it should be noted that ecotope segmentation can be adjusted to improve the delineation of environmental data or address specific issues. As discussed in **Chapter 3**, ecotopes demonstrated less favorable outcomes in modeling biotope distribution compared to using a finer raster grid (10m). The utilization of a finer raster grid allowed for better differentiation of the ecological variables utilized in the model, including soil variables. Consequently, these pedological data could be employed to enhance the ecotope segmentation process. Nevertheless, integrating continuous ecological data covering an entire territory, such as the Walloon soil data (map derived from kriging based on 75m resolution point-specific dataset), with the fine-grained ecotope segmentation (2m resolution) poses challenges and question about using such precise delimitation to represent limits of coarser ecological conditions.

In **Chapter 3**, fine-grain raster data were employed to model PNV. A raster grid with a 10-meter resolution was selected to represent environmental predictors. This choice aimed to capture the ecological context's variability within reference biotopes while using only biotope map delimitations and retaining a maximum of reference data. The ecotope approach, on the other hand, necessitates the use of an overlap threshold to assign a biotope to the ecotope. This threshold introduces a dilemma, where one must decide between underestimating the ecological envelope of the biotope, overestimating it, or finding a balance between the two.

Alternative approaches to represent landscape elements have also been investigated. Hexagonal grids are known for their potential advantages in the analyses conducted and in the spatial representation of complex ecological processes, such as the movement of individuals in a fragmented landscape (Birch et al., 2007; Molné et al., 2023). In **Chapter 5**, we employed 1-hectare hexagons to perform habitat network modeling and represent resulting habitat patches and corridors. Hexagons were also utilized to address inaccuracies in ecotope delineation and to better incorporate the influence of the global environment. Certain species disperse along narrow structures like tree rows or hedges (Davies and Pullin, 2007; Forman and Baudry, 1984), which can't be properly represented by regional-scale hexagons. To address this, we introduced a land-cover class for areas with high hedge and forest edge density. Additionally, for species hindered by hedges in their dispersal (Klaus et al., 2015), these structures can be included in connectivity analysis, akin to roads in **Chapter 5**. However, the choice of hexagon size was subjective and based on a compromise between the scale of the study and the size of species habitat patches. Sensitivity analysis should be further performed to deeply evaluate the potential effect of hexagon size on connectivity analysis results.

Incorporating landscape connectivity considerations into landscape planning practices is of utmost importance, highlighting the significance of properly representing biological stakes. Utilizing precise representations, such as ecotopes offers a more intuitive understanding for policy makers who often rely on vectorized formats like cadastral maps and development plans for landscape planning purposes. However, using fine scale delimitation may induce a false impression of precision given numerous biases of biological data. By employing abstract representations, decision-makers can better comprehend the complexities of the landscape and make informed choices that promote effective nature conservation strategies for the future. To address this issue, there is a need for research on landscape representation and how stakeholders in the field of nature conservation perceive it, as the current scientific literature lacks comprehensive studies in this area.

In conclusion, throughout this thesis, multiple landscape representations were utilized, each having its advantages and drawbacks depending on the ecological analysis's objectives and the specific focus of the study (such as particular species or biotopes). In our research, ecotope delimitation was primarily employed when punctual observation data were available for SDM and when habitat network analyses were derived from this modeling approach. On the other hand, raster grids were chosen for biotope modeling, especially when reference data were mapped as polygons. Finally, hexagonal grids were utilized for knowledge-driven habitat network analysis, which heavily relies on land-cover information (see Figure 6.1).

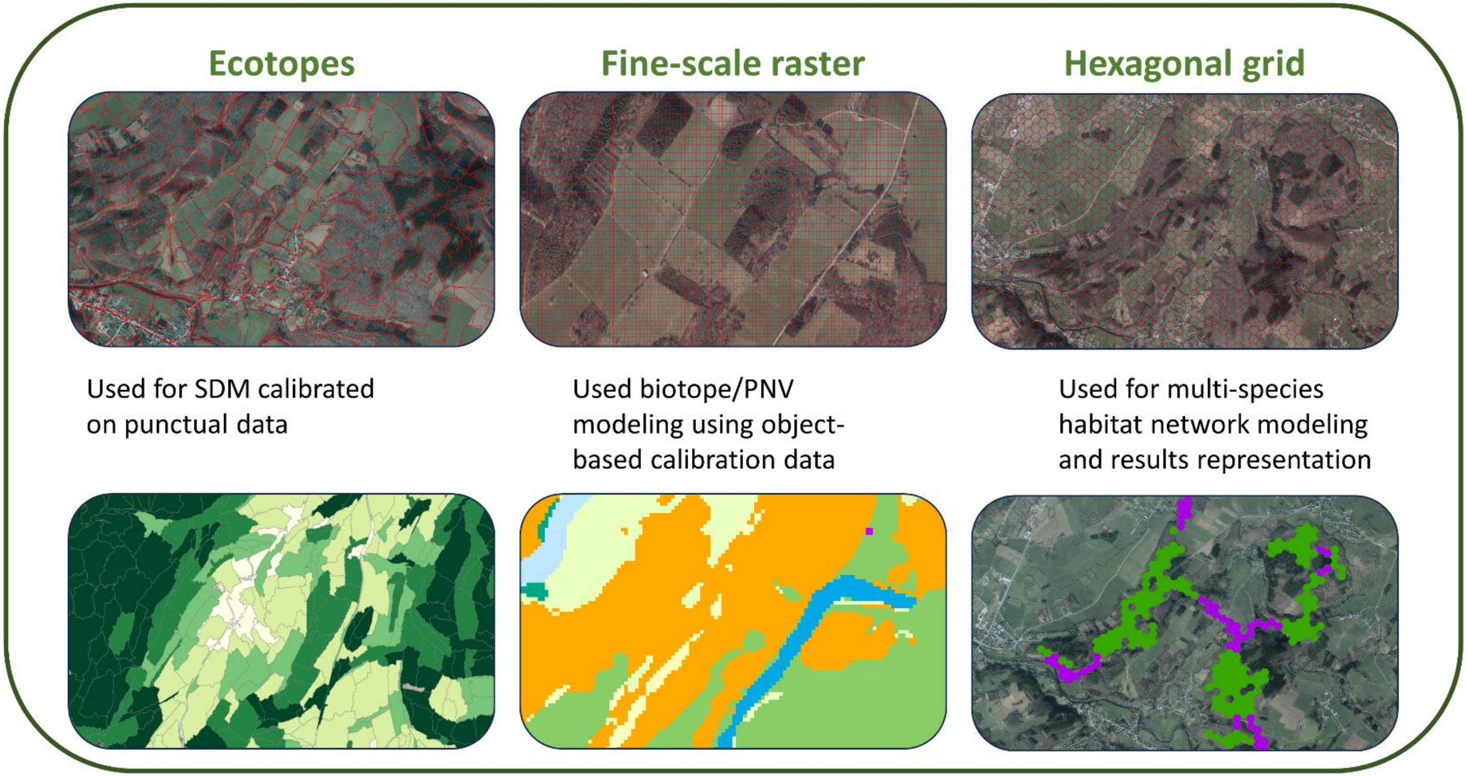

Figure 6.1: Summary of different landscape unit representation types used throughout this thesis.

2.2. Multiple uses and limits of potential natural vegetation concept

2.2.1. A dynamic management as a response to habitat fragmentation

The utilization of PNV as an approach for biotope prediction in habitat survey and monitoring was extensively explored in **Chapter 3**. However, PNV also holds potential for various applications relevant to ecological network objectives.

Given that PNV considers vegetation dynamics, mapping its distribution across an entire territory provides an opportunity to utilize natural or human-induced ecosystem perturbations for the natural restoration of biotopes. This approach can facilitate spontaneous colonization and the achievement of required biotope conditions through appropriate management practices. By modeling the potential distribution of the primary ecological contexts that cover the region, restoration and conservation efforts can enhance their coherence by identifying areas where restoration activities can defragment patches and consequently increase patch areas. This, in turn, reduces the extinction rate of populations.

Furthermore, presenting such predictions across the entire territory enables the identification of the maximum distribution of biotopes, serving as a backbone for ecological networks. Such maps can serve as initial decision-making tools before undertaking numerous and time-consuming habitat network analyses. Biotopes belonging to the same ecological context can be protected or restored to promote the continuity previously identified, enhancing the overall coherence of landscape management in fragmented settings.

In **Chapter 5**, PNV was employed to generate a refined land-cover map that accurately reflects specific species habitats, such as dry grasslands or peatlands. This detailed mapping of species habitats plays a crucial role in conducting precise connectivity analyses, relying solely on expert knowledge, as demonstrated in **Chapter 4**. Additionally, this approach enables the assignment of movement costs to precise land-cover classes, enhancing the accuracy of such analyses.

2.2.2. Vegetation dynamics in human dominated landscape

One major finding from the application of the PNV approach in biotope distribution modeling is its ability to better identify the historical ecological envelope of biotopes. This highlights the value of incorporating this concept into biotope distribution modeling. This phenomenon can be attributed to the impact of human activities, which may have favored specific vegetation communities in localized areas that do not fully represent the entire ecological envelope but rather a limited and potentially extreme portion of it. However, further investigation is required to verify this assumption through specific studies that correlate vegetation community surveys with environmental predictors to depict the ecological envelope of biotopes belonging to the same PNV. This could partly be done with our results by analyzing potential distribution overlaps as it is already made in the literature (Stigall, 2012).

2.3. Scope and Scale Considerations in the Study Area

In **Chapter 3**, we emphasized the utility of the PNV modeling approach, which enabled the collection of more calibration data for modeling PNV than for rare open biotopes. This expanded dataset significantly enhanced prediction accuracy, although certain PNV categories remained scarce, resulting in less precise predictions. It's crucial to note that this scarcity was specific to the study area's scale. For instance, calcareous grasslands and peatlands, although scarce in the study area, have more important surfaces in neighboring regions. To enhance the calibration datasets, the study area could have been expanded to a biogeographical region and include ecological contexts similar to those found in the Walloon region. However, replicating our PNV modeling approach in a transborder study area poses challenges.

Firstly, our study employed a 10m resolution grid. Our analysis demonstrated a notable improvement in prediction accuracy compared to coarser resolutions, primarily due to the availability of environmental datasets containing fine-scale information, such as soil predictors, which significantly influenced our models. However, precise environmental datasets, especially regarding soil characteristics, are not universally available across different countries or regions. This lack of consistency in data accuracy and grain size among various administrations responsible for environmental inquiries complicates the homogenization of datasets for modeling in international study areas. Additionally, enlarging the study area while maintaining high resolution could increase computational demands, necessitating advanced expertise in managing substantial datasets. This computational complexity might hinder large-scale modeling of biotope distribution.

Nevertheless, potential solutions exist to extrapolate the application of PNV modeling to a global scale, primarily through the utilization of remotely sensed data. Ecosystem functioning attributes measured via remote sensing have gained popularity in ecological niche modeling (Regos et al., 2022). This approach offers the advantage of incorporating ecosystem dynamics in modeling approaches by utilizing time series of spectral vegetation indices (Mayor et al., 2017; Thorup et al., 2017). Available predictors include soil moisture, land surface temperature, primary productivity, among others. It also facilitates access to vast amounts of open-access data with substantial spatial continuity, mitigating the aforementioned limitations (Alcaraz-Segura et al., 2017; Arenas-Castro et al., 2019). While this approach has shown improvements in ecological niche models and significant correlations between ecosystem function attributes and species richness (Radeloff et al., 2019; Toszogyova and Storch, 2019), its application has primarily been at the species level. No known examples exist of its application at the community level, necessitating further research to evaluate the potential in utilizing ecosystem functioning attributes derived from remote sensing for biotope modeling.

Additionally, considering neighboring regions is crucial when mapping connectivity stakes, as metapopulational dynamics do not adhere to national borders. As discussed in **Chapter 4**, considering the landscape of neighboring areas is essential for unbiased habitat connectivity analysis and to avoid treating the studied landscape as an isolated region. In our study, we accounted for this by implementing a 10km buffer around the study area. However, this buffer extended into other administrative regions, where equivalent precise datasets were unavailable. Instead, a less detailed land-cover dataset was utilized. Although adequate for identifying deciduous forest patches around the study area, this issue persists in a transborder study necessitating a precise land-cover dataset. While not insurmountable, extensive preliminary work is required to standardize the data used in such cases.

2.4. Knowledge-driven and data-driven approaches

2.4.1. Knowledge-driven

Throughout this thesis, we employed and compared both data-driven and knowledge-driven approaches. Expert knowledge, like any other source of information, carries uncertainties (O’Hagan et al., 2006), but it remains widely utilized in landscape management decision-making (Kangas and Kangas, 2004). The presence of uncertainties, without a clear understanding of their extent, can be particularly detrimental. Therefore, it is highly recommended to evaluate the uncertainty associated with expert knowledge before applying it, to ensure its appropriate utilization (Davis and Ruddle, 2010; Mackinson, 2001).

Expert knowledge played a crucial role in defining the modeled PNV by categorizing biotopes based on their ecological requirements (**Chapter 3**). The evaluation of uncertainties related to expert knowledge in forest succession has been the focus of a previous study (Drescher and Perera, 2012), which identified certain limitations, including lower accuracy in common forest succession scenarios compared to better understanding of forest succession in marginal environmental conditions. However, alternative data-driven approaches exist. Analytical techniques such as PCA or hierarchical clustering could have been employed to establish links between biotopes and ecological predictors. However, conducting such an analysis would rely on biotope survey data that may be subject to biases. As discussed in **Chapter 3**, the delimitation of common PNV biotopes could be challenging in the field, given that multiple rare PNVs with extreme ecological conditions were predicted within the common PNV reference data. Moreover, we observed that the most frequently occurring PNV reference data (Acidophilous Fagus forests) contains more surface areas of alluvial soils compared to riparian and gallery woodland PNVs. This further highlights the less well-defined nature of common PNVs.

Interestingly, the results of modeling PNVs built with expert knowledge demonstrated accurate predictions and better overall accuracy than modeling individual biotopes separately. Indeed, when modeling distinct biotopes belonging to the same PNV and combining their resulting predictions, lower accuracy was achieved compared to the PNV approach. This further emphasizes that, in our case, expert knowledge based on a century of studying vegetation communities and dynamics provides a robust foundation for PNV modeling (Duvigneaud, 1949; Noirfalise, 1984).

Considering habitat network analysis, it is common to utilize expert knowledge in constructing the resistance matrix (Liu et al., 2018; Watts et al., 2010). In **Chapter 4**, we compared this expert-knowledge approach with a data-driven approach using observation data to conduct habitat suitability models. The results revealed few differences, except for better habitat patch identification when employing modeling approaches and improved identification of less permeable land-cover using expertise. These findings align with previously identified limitations (Stevenson-Holt et al., 2014; Zeller et al., 2018). Nevertheless, we emphasized that the knowledge-driven approach could serve as a strong foundation for habitat network modeling if habitat patch identification is meticulously executed. Therefore, knowledge-driven approach can act as a strong basis for habitat network modeling of species with few observation data or unstructured survey.

Leveraging the advancements made in this thesis concerning biotope modeling and its delimitation, we were able to enhance habitat patch identification and create a precise resistance matrix based on a finer land-cover classification. As a result, the knowledge-driven approach was deemed sufficiently robust and was selected for habitat network modeling in **Chapter 5**. Furthermore, the knowledge-driven approach is not reliant on the quality of observation data, which allowed us to incorporate multiple focal species regardless of the available data.

2.4.2. Data-driven

Data-driven approach was principally followed to model potential distribution of species and biotope. Such models are of paramount importance to apply robust conservation management decision taking into account future climate, potential invasion or lack of biological data (Guisan et al., 2013). However, such modeling approach are sensitive to sample size and biases in the distribution of data (Araújo and Guisan, 2006). But, correctly structured surveys are rare even from official source such as museum or other collection (Stockman et al., 2006). Recently, scientists modeling species distribution are more and more looking toward opportunistic observation gathered in open access collection known as “Citizen Science data”. "Citizen Science" - increasingly referred to as "Community Science"- defined as the "active engagement of the general public in scientific research tasks" (Vohland et al., 2021). It involves non-professional individuals voluntarily contributing to data collection for scientific research. In the field of ecology, Citizen Science (CS) data comprises a diverse range of observation types. However, we focus on a narrower scope of CS data: direct species observations obtained through unstructured and semi-structured protocols, where observers independently decide where, when, how, and whether to record different species.

Such data source is attractive as this makes possible to cover wider areas and temporal windows to complete existing collection or encode observation in area with no formal data collection (SoIB, 2020). However, the growth of such database recently observed goes together with less structured and formal monitoring (Pocock et al., 2017). It is therefore important to correctly understand the multiples biases related to the use of CS data (Johnston et al., 2023).

First, CS data can be influenced by observer choices, leading to spatial bias. Observers may select locations based on accessibility such near their home or close to roads (Mair and Ruete, 2016; Tiago et al., 2017), or for ecological reasons by focus on protected area or those known for their high biodiversity (Botts et al., 2011; Tulloch et al., 2013). This bias results in non-representative samples of the target population which can affect ecological inferences, especially when the drivers of observer site selection align with the ecological process of interest (Chakraborty et al., 2021). Observers in CS projects vary in their skills, experience, behavior, and equipment, which can lead to differences in their ability to detect and identify species (Sunde and Jessen, 2013). As CS projects expand, older participants learns to identify new species (Sharma et al., 2019). In addition, new participants with less experience may join, which contribute to a variability of observer's skills for detection over time(Sunde and Jessen, 2013). Observers may also preferentially report certain species due to personal interest, species rarity, or detectability leading to reporting preferences (Johnston et al., 2023). This preference can introduce bias when comparing different species and can be particularly problematic when species preferences vary spatially and temporally (Schuetz and Johnston, 2021; Steger et al., 2017). Finally, false positive errors occur when a species is reported as present when it is not. While false negative errors are routinely accounted for in ecological analyses (Royle and Nichols, 2003), false positive errors due to a lack of skill from beginner observers in CS data present an additional challenge. They can lead to biased estimates of species occupancy rates and distributions (Cruickshank et al., 2019).

The biases mentioned earlier are not exclusive to CS data but can also occur in more traditional data collection methods. To address and mitigate multiple biases in observation data used, we incorporated various strategies throughout this thesis.

In **Chapter 3**, we specifically examined the potential spatial biases in the Natura 2000 biotope survey maps. To minimize the impact of poorly delimited common PNV and their overrepresentation in the dataset, we implemented a spatial subsampling approach. This involved selecting a maximum of 50 occurrences of a PNV within a 1km² cell. Similar spatial filtering approaches have been recommended for handling species data with strong spatial biases (Kramer-Schadt et al., 2013).

Addressing observer preference bias, we accounted for it in **Chapter 5** while calculating the rarity of species to identify HIHFS species. As different taxonomic groups may have varying levels of interest among CS observers (Johnston et al., 2023), we conducted rarity calculations considering the sampling of each taxonomic group separately for each bioregion as abundance of protected area vary among them. By adopting these methods, we aimed to minimize the impact of biases and ensure the robustness of our analyses.

2.4.3. Conclusion

Upon reflection, it is evident that neither approach inherently surpasses the other. Instead of competing, these concepts should be viewed as complementary, and it is crucial to fully comprehend the inputs used in the analyses and recognize their limitations. Striking a balance between leveraging expert knowledge and utilizing data while considering their specific biases should be a conscientious consideration throughout all research process.

2.5. Guiding biodiversity conservation actions

Conservation of landscape connectivity is universally acknowledged as crucial for maintaining healthy ecosystems, biodiversity, and adapting to climate changes (Hilty et al., 2020). Throughout this thesis, our primary focus has been on developing and evaluating precise methods to map the components of connected landscapes, including habitat patches and the corridors linking them. These components are designed to be integrated into a cohesive landscape zonation known as ecological networks (ENs). This integration, in turn, facilitates the incorporation of connectivity concerns into landscape planning and conservation decision-making (Amsallem et al., 2010a; Sordello, 2018; Sordello et al., 2013).

As demonstrated in this thesis, the Walloon region, situated in the heart of Western Europe, possesses a highly fragmented landscape, making it an ideal testing ground for innovative approaches to mapping ecological network elements. Despite the growing importance of addressing nature conservation issues related to landscape connectivity, Wallonia lacks a comprehensive ecological network map. Such a map is essential for organizing land use planning while preserving landscape connectivity. Nevertheless, Wallonia is not devoid of nature conservation efforts.

Wallonia's conservation law of 1973, updated in 2001, defines site protection statuses, supplemented by government decrees on wetlands and underground caves. While 240 Natura 2000 sites covering 220,000 hectares were designated in Wallonia, a 2017 EU report highlighted Belgium's lag in implementation, especially regarding conservation objectives and ecosystem services mapping, compared to Flanders, a leader in ES evaluation initiative.

Several biological inventory initiatives have occurred in Wallonia, starting with Jean Massart's 1912 inventory. In the 1980s, projects mapped natural habitats, and the concept of Sites of High Biological Interest (SGIB) was introduced, leading to a database of over 2,500 sites (Dufrêne, 2000)

+. However, these inventories failed to establish a comprehensive protection strategy, update the SGIB database, or modify sector plans. The ecological network, developed by the “Cercle des Naturalistes de Belgique” in 1992, classified habitats into central, development, and connecting zones, covering 25% of Wallonia. The approach extended to Communal Plans for Nature Development (PCDN), where 7% of the territory was identified as central and 20% as development zones. Natura 2000, designated in 2002, covers sites based on the Birds and Habitats Directives. Although 60% of SGIB areas fall under Natura 2000, detailed mapping and SGIB boundary restructuring lag. Recently, Wallonia, along with the environmental governing bodies, has endorsed the implementation of a novel biodiversity strategy. This strategy aligns with the objectives and pledges outlined in the "Kunming-Montreal Global Biodiversity Framework" and the "European Biodiversity Strategy 2030". The primary goals of this strategy encompass completing the regional network of strictly protected areas to encompass 5% of the territory by 2030 and enhancing the conservation status of a minimum of 30% of endangered biotopes and species. The future demands detailed, functional ecological networks that consider local biodiversity, akin to France's approach, necessitating coordination among various stakeholders and administrations to create a coherent, effective ecological framework.

Thanks to a new political determination to establish a functional ecological network in Wallonia, mapping this network has once again become a top priority since 2018. Based on an assessment that analyzed existing initiatives and identified bottlenecks, a comprehensive methodology for mapping a functional ecological network was developed and is currently being implemented (Boeraeve et al., 2020a; Harchies et al., 2018). In the following section, we will outline how the results obtained in this thesis could provide valuable guidance for mapping an ecological network within the specific context of Wallonia.

2.5.1. Mapping and restoring core areas

As previously mentioned, biotopes are fundamental units for mapping core areas within ecological networks, particularly when considering an ecological network approach based on ecosystem types. The PNV modeling approach has been recognized as a valuable tool for guiding future inventories, aiding in the completion of existing biotope maps, or generating potential maps across a given territory. Using models also offers the advantage of comprehensive coverage compared to surveys, which are typically limited to public areas due to restrictions in accessing private forests or parcels based on owner agreements. However, PNV predicts the ecological conditions necessary for the development of vegetation successions without specifying the stage of succession. Therefore, ancillary data are necessary to refine the specific stage being sought. This can be achieved with increasing accuracy using the latest land-cover data obtained through remote sensing. Land-cover data can serve as a basis for distinguishing open areas from forested biotopes and approximating biotopes from PNV predictions. Moreover, this approach's advantage lies in the automation of producing land-cover data, enabling the integration of land-cover change dynamics and facilitating continuous updates of biotope maps to assess their conservation status.

However, distinguishing biotopes from PNV based solely on current land-cover data may have limitations. This is particularly evident in open areas where available land-cover data derived from remote sensing does not differentiate between permanent intensive grasslands and more extensive management practices leading to biotopes significant for biodiversity. Recent studies showed promising results in using remote sensing to detect mowing intensity, aiding in the identification of extensive practices in open biotopes (De Vroey et al., 2022). These results could be utilized as-is or integrated into models along with other vegetation-related indices obtained through remote sensing to enhance performance in detecting extensive grasslands.

When assessing connectivity stakes in degraded landscapes and identifying potential core areas for ecological networks, the primary objective is to pinpoint regions with significant constraints on socio-economic development. However, it's crucial to acknowledge the inherent limitations of models. Field inventories remain essential to confirm the presence of ecological interest. Despite the necessity for additional surveys, these endeavors often cover vast areas, prompting the need to refine predicted biotopes to more specific regions. Our methodological approach to PNV modeling preemptively acknowledged potential model imprecision. To address this, we proposed mapping potential PNV overlaps. This approach helps in avoiding areas with significant overlap of PNV if a specific biotope is sought. However, it's important to note that overlaps of scarce and endangered biotopes should not be avoided deliberately. Accuracy metrics, such as User Accuracy, can further aid in identifying areas with the highest model accuracy. Additionally, complementary data sources can be utilized alongside the biotope model to further narrow down the areas requiring field validation. Observations of indicator species, which are species closely associated with the biotope and not/less with another, can be valuable. Although observational data are not free from bias, the presence of species typical of a biotope in a predicted area of said biotope is not negligible. Hence, it gains relevance when integrated with modeling approaches. Alternatively, habitat suitability models for these species could be employed if sufficient and high-quality observation data are available. However, it's worth mentioning that this latter option may have a comparatively lesser impact than the use of direct observation.

Conservation efforts in degraded landscapes should primarily focus on preserving existing biotopes to safeguard the remaining natural areas. However, in such landscapes, biotopes in good condition are scarce. In Wallonia, for instance, 95 to 96% of biotope types are in an unfavorable conservation status (SPW - DGO3 - DEMNA - DEE, 2017). Therefore, it is crucial to restore these habitats. Restoration initiatives must be enhanced to align with regional biodiversity strategies aiming to improve the conservation status of 30% of biotopes and endangered species.

To achieve this objective, it is imperative to employ tools such as PNV modeling. As mentioned earlier, the PNV modeling results obtained in this thesis enable the identification of the most accurate predictions. These predictions can serve as a guide for restoration efforts in areas with more typical ecological conditions suitable for the target biotope. PNV prediction maps also help identify the maximum potential range of biotopes, aiding in directing restoration efforts to more relevant areas, such as those isolated ecologically or situated within potential connectivity pathways. These decisions can be further informed by landscape connectivity evaluations, as presented in other sections of this thesis.

2.5.2. Mapping ecological corridors

Incorporating scientific diagnostics into operational planning requires sufficient informative data to perform tradeoff analyses between socio-economic and connectivity conservation aspects (Foltête et al., 2014). To achieve this, prioritizing network components based on their importance for connectivity analysis is made possible through spatial graph analysis (Clauzel et al., 2015; Foltête et al., 2014). Spatial graphs have been increasingly employed in habitat network studies (Clauzel et al., 2018; Foltête, 2019; Pereira, 2018). In this thesis, LCP were used to evaluate landscape connectivity, and serve as a basis to map ecological corridors. Combined with graph theory, they helped to identify most important areas of the network for connectivity. In **Chapter 5**, spatial graph analysis results were instrumental in prioritizing ecosystems when their related network overlaps with the potential to guide conservation or restoration decisions in favor of the most priority ecosystem. Similarly, in **Chapter 4**, identifying obstacles in the landscape connectivity pathways (LCPs) based on their importance for connectivity provided valuable information for selecting specific obstacles before implementing potentially costly conservation actions (Ascensão et al., 2019). These findings could be subsequently validated through independent surveys or data sources, such as radio tracking or road collision records. For instance, road collision data were utilized in Wallonia to pinpoint conflict zones within the road network (Dubois and Renglet, 2020). Their results affirmed the selection of the wildcat as a focal species, as many forest mammals also faced road collisions in the same regions. They identified collision hotspots where our study recognized one of the most significant obstacles for the wildcat habitat network (Bourdouxhe et al., 2020). Additionally, this hotspot already has a wildlife crossing in place, underscoring the importance of evaluating the functionality of wildlife crossings in Wallonia, especially in critical conflict zones identified in **Chapter 4**.

PNV modeling results were utilized to enhance land-cover distinctions, creating a more precise identification of areas conducive to species movement, as elaborated in **Chapter 5**. Moreover, PNV prediction maps can play a pivotal role in restoration initiatives. They enable the identification of potential restored habitat patches, facilitate the assessment of their significance within the network, and pinpoint the most crucial areas for restoration efforts. Another set of analyses could be undertaken to evaluate the region's entire restoration potential. This involves modifying land-cover classes associated with intensive agricultural and silvicultural practices to align with the targeted biotope, guided by PNV modeling. To refine this analysis, socio-economic factors could be integrated, limiting restorable areas to those with the most marginal ecological conditions. These conditions typically entail below-average productivity yields and the presence of biotopes of interest. It is worth noting that this approach closely aligns with a "land-sparing" strategy, which could serve as a compelling argument in regional planning. By favoring the biodiversity-friendly land-sparing approach, these insights could significantly influence land-use decisions, promoting biodiversity while accommodating developmental needs.

However, the wide variety of connectivity metrics may make their use sensitive to the specific aims being sought. Some may misuse the abundance of metrics to distort the results of connectivity analyses, particularly in cases where people seek to exclude areas from landscape connectivity conservation plans (Kindlmann and Burel, 2008; Walker et al., 2009). For instance, good connectivity of certain areas might be used to argue for a development project in an economically valuable area, even though it would result in habitat loss detrimental to species in that region (Falcy and Estades, 2007). It is essential to remember that areas should be conserved for reasons beyond just the connectivity of a species or a group of species, but rather for their intrinsic conservation value for species population (Fahrig, L., 1999; C. D. Thomas et al., 2004).

Providing straightforward information such as metric distance and cumulative cost, the results obtained from LCP modeling are already highly valuable without delving into complex metrics derived from spatial graph analysis. Through this approach, we can readily discern connected patches by filtering LCPs based on their cumulative cost and the dispersal capacity of the studied species. Furthermore, by selecting those LCPs with a cumulative cost higher than the species' dispersal capacity and a metric distance smaller than the dispersal distance, we can identify LCPs that potentially connect patches. This can be achieved without introducing new habitat patches, which could be both costly and intricate. Instead, the focus is on reducing matrix resistance to movement by incorporating smaller features, such as hedgerows. Hedgerows are well-known for enhancing connectivity for forest-related species in more open areas. Regional initiatives for hedgerow plantations could thus greatly benefit from such analyses, guiding the strategic planting of hedgerows in areas where connectivity improvements are essential.

The hexagonal representation of LCPs combined with buffer as proposed in **Chapter 5** also aids in depicting areas where conserving and restoring landscape connectivity is crucial. Due to the uncertainty in complex ecological processes, such as species movements (Hodgson et al., 2009), identifying larger areas for conservation actions instead of fine-scale operational landscape units appears to be a more truthful approach. These larger areas better depict the definition of ecological corridors proposed by Hilty et al. (2020). Such areas could encompass the protection of vegetation structures or more artificial features such as stone walls and vegetalized roadsides that favorize species movement. But this could also concern more punctual element such as isolated tree and old orchards or the maintenance of extensive agricultural practices. All these elements may concern fluctuating surfaces and an abstract representation such as hexagon may better reflect this uncertainty. Such corridors important for landscape connectivity could therefore be used to identify areas with a big potential to implement AECMs (Agri-Environment-climate Measures) supported by the European CAP (Common Agricultural Policy) that leads to landscape features that could helped to limit the resistance of the landscape matrix (Pe’er et al., 2019). AECMs could move from agricultural parcels to other inside such ecological corridors while still enhancing landscape connectivity.

3. Perspectives

The analyses conducted throughout this thesis, centered on the concept of ecological networks, can potentially be translated into tangible conservation actions, and serve as a guiding framework for making informed political decisions.

However, it is worth noting that other similar concepts to ecological networks (EN), particularly those focusing on incorporating the production of ecosystem services (ES), have emerged to inform green space network planning (MA, 2003). Numerous initiatives integrated this concept into a new landscape planning management, notably due to the European Green Infrastructure strategy (European Commission, 2013; Liquete et al., 2015). Green Infrastructures (GI) are defined as a network of natural or semi-natural ecosystems providing ES (European Commission, 2013). This definition is close to EN except it integrates the function of providing ES. However, EN are not completely implemented in all European countries and regions and initiatives are still in course. Due to the development of new strategies such as GI, it is important for practitioners to know if their efforts to implement EN will not be quickly outdated. Connected ecosystem through EN initiatives could also be used as a basis to GI planning which could avoid mapping another network. The question of compatibility between EN and GI framework is therefore a major issue.

The following discussion results from a literature review carried in 2020 about the inclusion of ES concept in studies aiming to map networks facilitating species movements in fragmented landscapes. The original review with details about methods and results is available in Appendix 12.

3.1. Evolution of inclusion of ecosystem services concept in ecological network planning

The way ES are integrated in EN research globally increased over time. First studies mentioning ESs cites them in their discussion as an added value delivered to give weight to some less natural part of ENs or to show a relative importance of ENs for policies (Leibenath, 2011; Zmelik et al., 2011). But it can be seen that even if the mention of ES has increased, few papers consider them as sufficiently important to be cited in their abstract (e.g. Mander et al. 2018; Hatziiordanou et al. 2019). The latest articles generally place the challenges of delivering ESs at the same level as those of conserving biodiversity in the core of their study but those studies are really scarces (Cunha and Magalhães, 2019; Ersoy et al., 2018; Marini et al., 2019). Some even consider ENs as multi-functional GI even speaking of socio-ecological networks/systems (Arnaiz-Schmitz et al., 2018; Capotorti et al., 2019a; Cunha and Magalhães, 2019).

Beyond scientific initiatives, national and regional initiatives of EN planning led by nature practitioners are also including ES concept in their planning (Sordello et al., 2013). But ES supply is only cited as an indirect product of EN restoration to give weight to EN in land-use planning thanks to the benefits provided by ecosystems and their economic value. Moreover, stakeholders are probably encouraged to cite ES because of the GI strategy developed by the European Commission. However, we are far from a complete integration such as the development of socio-EN as defined by some authors (Arnaiz-Schmitz et al., 2018; Capotorti et al., 2019a; Cunha and Magalhães, 2019). This is probably due to a lack of reproducible methods or a lack of expertise in an emerging research field.

It is interesting to highlight that the majority of papers evaluating ES supply use the term of GI as a concept integrating both EN and ES concepts (Cannas et al., 2018; Capotorti et al., 2019a; Liquete et al., 2015). Some GI papers are even not citing EN as such but still integrate species habitat networks issues (Rodríguez-Espinosa et al., 2019; Snäll et al., 2016). We can see that EN and GI are not complementary terms but GI has supplanted EN over time to englobe a concept including a multifunctional network strategy. Even if GI concept rely on a framework connecting natural and semi-natural elements such as EN. But this statement is only true for papers addressing EN issues, the use of GI concept with no link to EN concept and focusing only on ES supply is still in use (Badenhausser et al., 2020; Mullins et al., 2020).

3.2. Toward multifunctional ecological network planning

The integration of EN and ES concepts into one multifunctional framework was analyzed for papers including ES supply evaluation in EN planning. The resulting networks are now called “multifunctional network” to differentiate them from classic EN planning and from GI initiatives that do not consider EN issues.

Concerning the context within analyses are performed, the planning of multifunctional networks implies a demand for ES supply analysis +explaining why half the studies analysed are carried out in urban contexts (Capotorti et al., 2019b, 2019a; Rodríguez-Espinosa et al., 2019). By contrast, Liquete et al. (2015) include rural environments into GI, due to the scale of their study (EU) implying a high proportion of rural environment. Those different contexts also create different levels of complexity to choose between production and biodiversity conservation priority land-use (Lanzas et al., 2019; Liquete et al., 2015; Newton et al., 2012; Rodríguez-Espinosa et al., 2019; Snäll et al., 2016). This led to inherent trade-offs analysis affecting an important component of multifunctional network planning: the zonation of the network.

Preserving ES supply and biodiversity is difficult as it does not always lead to preserving the same areas (Venter et al., 2009). Thus, authors suggest a systematic planning approach based on prioritization of zones to help address conflicting issues (Lanzas et al., 2019). The multifunctional framework used through the papers scrutinized could be split into two types of zones: core areas and mixed zones. Cores areas are the most common zone represented in most of studies analyzed here (Cannas et al., 2018; Capotorti et al., 2019b, 2019a; Lanzas et al., 2019; Liquete et al., 2015; Niemelä et al., 2010; Rodríguez-Espinosa et al., 2019). They are principally devoted to biodiversity conservation or they also include ES supply that are compatible with biodiversity conservation (Lanzas et al., 2019). Cores areas of a multifunctional network represent also areas were biodiversity conservation and ES supply are both maximized (Liquete et al., 2015). The other kind of zones ("mixed zones") represents a gradient were we can find areas with ES supply but where biodiversity conservation has lower priority due to its conservation status or preservation state (Lanzas et al., 2019). Finally, we can find zones that are considered opposed to conservation goals and that only focus on ES supply (Lanzas et al., 2019). Those areas are often excluded from the multifunctional network and thus not considered (Lanzas et al., 2019; Liquete et al., 2015).

The question of connectivity between core areas is not put aside. Some authors use species corridors models as important structuring input for the multifunctional network planning (Cannas et al., 2018; Liquete et al., 2015; Snäll et al., 2016). However, methods to do it are not as complex and complete as dedicated studies (Gurrutxaga and Saura, 2014; Pereira, 2018). Others suppose that some components of their network could play a role of corridors to reconnect core areas (Capotorti et al., 2019b, 2019a; Lanzas et al., 2019). Indeed mixed zones with ES supply and lower biodiversity conservation goals can play an important role of connecting but also playing a role of buffers to protect conservation areas from pollution and other impact of intensive human activities (Mubareka et al., 2013).

This kind of land zoning is really similar to de different zonation known in EN planning with core areas, corridors and optional buffer zones (Bennett and Mulongoy, 2006; Bernier and Théau, 2013; Melin, 1997). Indeed, buffer zones may include areas under sustainable management taking into account portions of landscape devoted to production (Bennett and Mulongoy, 2006; Melin, 1997). Thus, this idea of landscape partitioning including socio-economic issues (hence ES) in EN planning is not recent. Indeed, dealing with trade-offs between nature conservation and food production was already brought forward by EN planners (Bennett and Mulongoy, 2006; Melin, 1997) . Yet, EN framework could gain importance in land management thanks to the ES concept. Biodiversity conservation priority networks could benefit from ES supply evaluations by enhancing the role of conservation areas but also those with lower conservation value but still important for the network as buffer or corridors (Lanzas et al., 2019). However, it can be seen that some approaches to map multifunctional networks do not evaluate ES supply consistently by taking only into account ES not endangering nature conservation actions and putting aside others such as food production (Capotorti et al., 2019b; Lanzas et al., 2019; Liquete et al., 2015). This can be explained by the chosen approach or aims of the study. For instance, focusing on regulating and maintenance to identify network elements with conservation purposes (Liquete et al., 2015). Areas with opposed objectives to nature conservation should be mapped and considered for any multifunctional network planning. This issue could be tackled by moving forward to a more flexible definition of zones in EN planning and developing a real gradient of conservation vs. exploitation (Lanzas et al., 2019). This may move EN concept toward multifunctional EN framework.

We saw that multifunctional networks planning are mainly performed in urban context (Capotorti et al., 2019b; Rodríguez-Espinosa et al., 2019),while EN concerns principally rural and natural areas (Bernier and Théau, 2013). But integration of EN planning in urban and peri-urban areas of paramount importance as most cities have nature conservation stakes in their close environment (Beckline and Yujun, 2014; Borgström et al., 2012). Due to the benefit of integrating nature and biodiversity in cities supplying an important amount of ES (Hamel et al., 2021; Hobbie and Grimm, 2020), multifunctional ENs could be easily implemented to reconnect urban and peri-urban populations to rural and natural ones. This may help to conserve urban and peri-urban biodiversity while reducing the permeability to nature of cities. This is also the case for intensive agricultural and forestry areas where improving ES supply could be an argument to improve connectivity within those areas by defining zones sharing conservation and exploitation stakes.

3.3. Conclusion

Although GI framework is newer, old EN concepts such as buffer zones are still relevant and proposed as important component within multifunctional network planning (Lanzas et al., 2019). Moreover, dealing with trade-offs between nature conservation and production has already been tackled by both EN and GI planners. It can be said that EN planning, and GI strategy are largely compatible. GI can be considered as multifunctional networks connecting the different conservation areas and not independent GI only aiming for ES supply (Rodríguez-Espinosa et al., 2019). EN are networks planned principally focusing on biodiversity conservation and an important part of recent studies focus on developing methods to map the most accurate corridors (Duflot et al., 2018a; Ersoy et al., 2018). In parallel, methodological research on ES evaluation is still in course (Boeraeve et al., 2020b; Maebe et al., 2019). However, a certain amount of papers build multifunctional network while putting biodiversity conservation as a top priority assuming that a well-functioning network of ecosystems supply better quality ES (Cannas et al., 2018; Liquete et al., 2015; Niemelä et al., 2010). This allows understanding that EN concept has not been superseded at all but has just evolved regarding consideration of ES. By including ES into EN planning, connectivity and nature conservation issues have now a chance to be put in the center of society’s interest.

Multifunctional networks are maybe oversimplifying connectivity issues or ES supply evaluation, but they offer promising avenues for EN research by mixing both conservation issues and human needs thanks to trade-off analysis (Newton et al., 2012). In the future, it could be interesting to see multifunctional network planning based on trade-offs analyses performed on results from more complete corridors mapping or ES supply evaluation.

4. Conclusion

In conclusion, this thesis represents a significant advancement in the field of biodiversity conservation in fragmented landscapes. The methodologies developed and applied throughout this research offer valuable insights into the identification of conservation priorities for various species in complex environments. Through a meticulous analysis of landscape elements, including the use of ecotopes and precise biotope modeling, this thesis provided a framework for accurate prediction and representation of multiple biotopes within a region. The incorporation of PNV in the modeling process further strengthened the good identification of ecological context.

The research also delved into the critical aspect of habitat connectivity, especially focusing on mapping habitat networks facilitating species movement. By comparing expert knowledge-based approaches, data-driven methods, and hybrid strategies, this study provided insights in landscape connectivity assessment. The findings emphasized the interest of using knowledge-driven approach while ensuring the effectiveness of habitat networks.

Furthermore, this thesis explored the modeling of multiple species habitat networks, demonstrating the feasibility of the approach even with limited data. The utilization of fragmentation-sensitive focal species chosen based on life history traits provided a comprehensive perspective, enabling the identification of key species and prioritization of connectivity efforts. The integration of multivariate analyses and graph-based techniques proved instrumental in assessing network divergence and establishing connectivity priorities across diverse ecosystems.

In summary, the outcomes of this thesis not only contribute significantly to the theoretical understanding of biodiversity conservation in fragmented landscapes but also offer practical methodologies for conservation practitioners and policymakers. By identifying critical habitat patches, mapping corridors, and prioritizing connectivity efforts, this research provides a roadmap for future conservation initiatives. These findings, rooted in a deep understanding of ecological complexities, will undoubtedly inform decision-making processes and guide the development of conservation strategies, ultimately fostering the preservation of biodiversity in fragmented landscapes.

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Appendices

Appendix 1: List of biotopes considered in this study and their related PNV. Biotopes are referred to by their EUNIS classification adapted to Wallonia and Habitats Directive classification (asterisks indicate habitat of priority European interest). Greyish biotopes are those shared by multiple PNV and are not considered in model calibration and validation. PNV are sorted by a humidity gradient of their ecological context from marshy to xeric.

EUNIS Code	Habitats Directive code	Biotope names	Potential Natural Vegetation	Code
D1.1	**7110***	Raised bogs	***Sphagnum Betula* woods**	**SB**
D2.2		Poor fens and soft-water spring mires		
D2.3		Transition mires and quaking bogs		
F9.2	**7140**	*Salix* carr and fen scrubs		
G1.51	**91D0***	*Sphagnum Betula* woods		
D5.21e		Beds of large *Carex spp.*	***Alnus* swamp woods**	**AS**
D4.1	**7230**	Alkaline fens		
E5.4		Moist or wet tall-herb and fern fringes and meadows		
F9.2		*Salix* carr and fen scrub		
G1.4		Broadleaved swamp woodland not on acid peat		
E2.11ba		Permanent grazed meadows with little or no fertilization (*Junco-Cynosuretum*)	***Quercus* and *Betula* forests with *Molinia***	**QBM**
E3.42		*Juncus acutiflorus* meadows		
E3.51	**6410**	*Molinia caerulea* meadows		
E3.52	**4010**	Humid *Nardus stricta* swards		
F4.11	**4010**	Northern wet heaths		
F4.11b	**4010**	Heathlands with *Vaccinium* and *Erica tetralix*		
F4.13		*Molinia caerulea* degraded wet heath		
G1.81	**9190**	*Quercus -Betula* woods with *Molinia*		
G1.911a	**9190**	*Betula* facies of *Quercus-Betula woods* with *Molinia*		
E2.11ba		Permanent grazed meadows with little or no fertilization (*Junco-Cynosuretum*)	**Riparian and gallery woodland**	**RG**
E2.2	**6510**	Low and medium altitude hay meadows		
E5.4	**6430**	Moist or wet tall-herb and fern fringes and meadows		
F9.12	**91E0***	Lowland and collinar riverine *Salix* scrub		
G1.1	**91E0***	Riparian and gallery woodland, with dominant *Alnus, Betula, Populus* or *Salix*		
G1.2	**91E0*, 91F0**	Mixed riparian floodplain and gallery woodland		
E2.11ba		Permanent grazed meadows with little or no fertilization (*Junco-Cynosuretum*)	**Fammenian *Quercus* and *Carpinus* forests**	**FQC**
E2.2	**6510**	Low and medium altitude hay meadows		
E3.51	**6410**	*Molinia caerulea* meadows		

E5.4		Moist or wet tall-herb and fern fringes and meadows		
G1.A15a	**9160**	Famennian *Quercus* - *Carpinus betulus* forests on schist		
E2.11ba		Permanent grazed meadows with little or no fertilization (*Junco-Cynosuretum*)	**Neutrophile *Quercus* and *Fraxinus* forests on wet soils**	**NQF**
E2.2	**6510**	Low and medium altitude hay meadows		
E5.4		Moist or wet tall-herb and fern fringes and meadows		
G1.A1ba		Atlantic neutrophile *Quercus* and *Fraxinus* forests on hydromorphic soils		
G1.A1da	**9160**	Sub-Atlantic neutrophile *Quercus* and *Fraxinus* forests on hydromorphic soils		
E2.11ba		Permanent grazed meadows with little or no fertilization (*Junco-Cynosuretum*)	**Acidophilous *Quercus* and *Carpinus* forests on wet soils**	**AQC**
E2.2	**6510**	Low and medium altitude hay meadows		
E2.3	**6520**	Mountain hay meadows		
E3.51	**6410**	*Molinia caerulea* meadows		
G1.A1aa		Atlantic acidoclinic *Quercus* and *Carpius* forests on hydromorphic soils		
G1.A1ca	**9160**	Sub-Atlantic acidoclinic *Quercus* and *Carpinus* forests on hydromorphic soils		
E2.11bb		Permanent grazed meadows with little or no fertilization (*Galio-Trifolietum*)	**Neutrophile *Fagus* forests**	**NF**
E2.2	**6510**	Low and medium altitude hay meadows		
G1.63	**9130**	Medio-European neutrophile *Fagus* forests		
G1.A1bb		Atlantic neutrophile *Quercus* and *Fraxinus* forests substitute to *Fagus*		
G1.A1db	**9130**	Sub-Atlantic neutrophile *Quercus* and *Fraxinus* forests substitute to *Fagus*		
H2.3	**8150**	Medio-European upland siliceous screes	**Wet and Shady Ravine forests**	**WSR**
H2.6	**8160***	Medio-European calcareous scree of hill and montane levels		
G1.A41a	**9180***	*Acer* and *Tilia* forests with *Asplenium scolopendrium*		
G1.A41b	**9180***	*Acer* and *Ulmus* Ardennes forests		
E1.71	**6230***	*Nardus strica* swards	**Acidophilous *Fagus* forests**	**AF**
E2.11bc		Permanent grazed meadows with little or no fertilization (*Festuco-Cynosuretum*)		
E2.2	**6510**	Low and medium altitude hay meadows		
E2.3	**6520**	Mountain hay meadows		
F4.2	**4030**	Dry heaths		
G1.61	**9110**	Medio-European acidophilous *Fagus* forests		
G1.62	**9120**	Atlantic acidophilous *Fagus* forests		
G1.82	**9120**	Atlantic acidophilous *Fagus* - *Quercus* forests		
G1.87a		Medio-European acidophilous non-thermophilic *Quercus* forests		
G1.A1ab	**9120**	Atlantic acidoclinic *Quercus* and *Fraxinus* forests substitute to *Fagus*		

G1.A1cb		Sub-Atlantic acidoclinic *Quercus* and *Fraxinus* forests substitute to *Betula*		
E1.26	**6210***	Sub-Atlantic semi-dry calcareous grassland	**Calcareous *Fagus* and *Quercus* forests**	**CFQ**
E1.27	**6210***	Sub-Atlantic very dry calcareous grassland		
E2.2	**6510**	Low and medium altitude hay meadows		
F3.1b		Calcareous thermophile thickets		
G1.66	**9150**	Medio-European limestone *Fagus* forests		
G1.71		Western *Quercus pubescens* woods and related communities		
G1.A17	**9150**	Sub-Atlantic calciphile *Quercus* - *Carpinus betulus* forests		
F4.2	**4030**	Dry heaths	**Thermophile Acidophilous *Quercus* forests**	**TAQ**
H2.3	**8150**	Medio-European siliceous scree		
G1.87b		Medio-European thermophile acidophilous *Quercus* forests		
E1.28	**6210***	Xerophilous grasslands on calcareous-siliceous rocks	**Xerophile Fammenian *Quercus* and *Carpinus* forests**	**XFQC**
F4.2	**4030**	Dry heaths		
H2.3	**8150**	Medio-European siliceous scree		
H2.6	**8160***	Medio-European calcareous scree of hill and montane levels		
G1.A15b		Famennian xerophile *Quercus* - *Carpinus betulus* forests		

Appendix 2: Evolution of PNV reference data areas through spatial sampling and calibration filtering.

PNV	Area before main polygon biotopes shrinking (ha)	Area before spatial sampling (ha)	Area after spatial sampling (ha)	Area used for calibration (ha)	Area used for validation (ha)
SB	485.3	485.3	72.5	50.8	412.8
AS	229.2	229.2	201.5	141.1	27.7
QBM	1509.9	1509.9	207.0	144.9	1302.9
RG	1086.9	1086.9	482.5	337.8	604.4
FQC	15367.7	9481.6	92.5	64.8	9389.1
NQF	3231.0	3231.0	223.5	156.5	3007.5
AQC	38.5	38.5	11.5	8.1	27.0
NF	12031.9	6055.4	484.0	338.8	5571.4
WSR	639.7	639.7	135.5	94.9	504.2
AF	75022.3	42199.3	798.5	559.0	41400.8
CFQ	5375.7	2442.6	187.5	131.3	2255.1
TAQ	67.2	67.2	35.0	24.5	32.2
XFQC	133.4	133.4	12.0	8.4	121.4
Total	115218.7	67600.0	2943.5	2060.5	64656.5

Appendix 3: Results of individual PNV modeling

Table 1: Accuracy metric results of predictive maps for each PNV. The total area of reference biotopes used to model each PNV is presented in hectares (ha). Area under the curve and overall accuracy are respectively referred as AUC and OA. Producer (PA) and user accuracy (UA) above 0.8 (considered to be highly accurate for our objectives) are highlighted in bold text. The five most important predictors based on the Gini index are also presented.

Potential Natural Vegetation	**Code**	**Area used for calibration (ha)**	**AUC**	**OA**	**PA**	**UA**	**5 most important variables (based on Gini Index)**
***Sphagnum Betula* woods**	**SB**	50.8	**0.997**	**0.998**	**0.824**	**0.829**	Organic; Drainage; Climatic_pca_1; Sand; Silt
***Alnus* swamp woods**	**AS**	141.1	**0.997**	**0.999**	**0.814**	**0.826**	TPI; Climatic_pca_1; Hydric_lvl; AnnualVariation Precipitation; Climatic_pca_2
Quercus* and *Betula* forests with *Molinia	**QBM**	144.9	**0.995**	**0.993**	**0.816**	**0.861**	Climatic_pca_1; Drainage; Slope_prc; AnnualVariation Precipitation; Sand
Riparian and gallery woodland	**RG**	337.8	**0.995**	**0.995**	**0.816**	**0.818**	Water_int; TPI; Hydric_lvl; Climatic_pca_1; AnnualVariation Precipitation
Fammenian *Quercus* and *Carpinus* forests	**FQC**	64.8	**0.996**	**0.971**	**0.886**	**0.909**	Climatic_pca_1; TPI; Trophic_lvl; Hydric_lvl; Silt
Neutrophile *Quercus* and *Fraxinus* forests on wet soils	**NQF**	156.5	**0.995**	**0.990**	**0.877**	**0.915**	Climatic_pca_1; AnnualVariation Precipitation; TPI; Climatic_pca_2; Silt
Acidophilous *Quercus* and *Carpinus* forests on wet soils	**AQC**	8.1	**0.998**	**1.000**	0.624	0.632	Climatic_pca_1; Climatic_pca_2; AnnualVariation

							Precipitation; Sand; SunSpring
Neutrophile *Fagus* forests	**NF**	338.8	**0.990**	**0.982**	**0.875**	**0.919**	Climatic_pca_1; AnnualVariation Precipitation; Climatic_pca_2; Silt; Sand
Wet and shady ravine forests	**WSR**	94.9	**0.989**	**0.994**	0.635	0.670	Slope_prc; SunSpring; Radiative_SS; Sand; Climatic_pca_1
Acidophilous *Fagus* forests	**AF**	559.0	**0.992**	**0.962**	**0.969**	**0.971**	Sand; Climatic_pca_1; Hydric_lvl; AnnualVariation Precipitation; Climatic_pca_2
Calcareous *Fagus* and *Quercus* forests	**CFQ**	131.3	**0.993**	**0.990**	**0.852**	**0.862**	Calcareous; TPI; Climatic_pca_1; Trophic_lvl; Sand
Thermophile acidophilous *Quercus* forests	**TAQ**	24.5	**0.994**	**0.999**	0.506	0.442	Slope_prc; TPI; Radiative_SS; Hydric_lvl; Climatic_pca_1
Xerophile Fammenian *Quercus* and *Carpinus* forests	**XFQC**	8.4	**0.997**	**0.999**	0.661	**0.839**	Radiative_SS; Climatic_pca_1; SunSpring; Trophic_lvl; AnnualVariation Precipitation

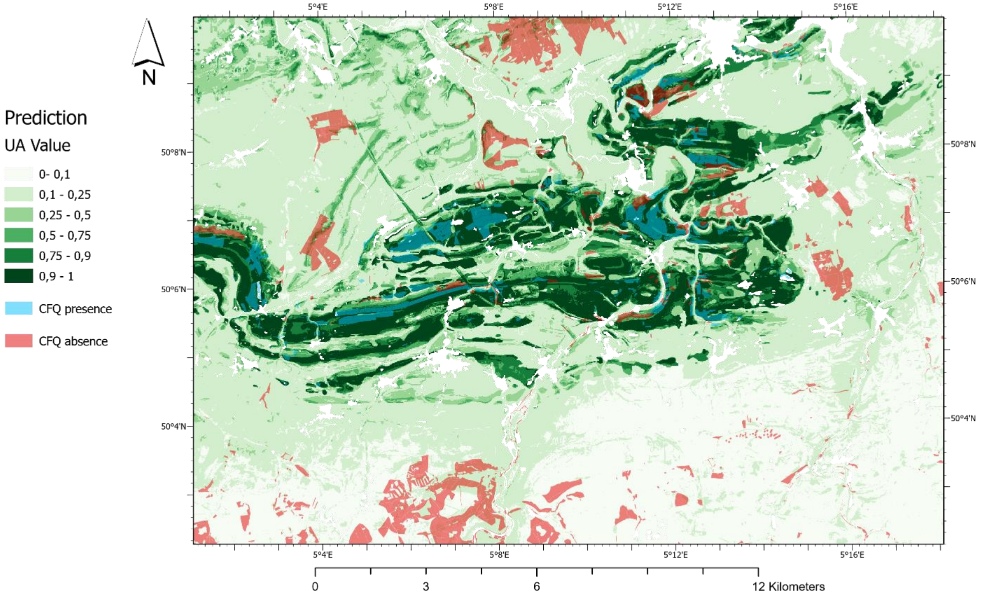


Figure 1: An example of individual PNV models with prediction of the presence of calcareous Fagus and Quercus forests succession. Transparent blue polygons represent the presence of biotopes used to model this PNV. Transparent red polygons refer to other biotopes surveyed. This predictive map was created using different thresholds of user accuracy. For instance, dark green represents areas where there is 90 to 100% chance of finding ecological contexts for the development of the calcareous Fagus and Quercus forests PNV according to the individual model. White areas are no data.

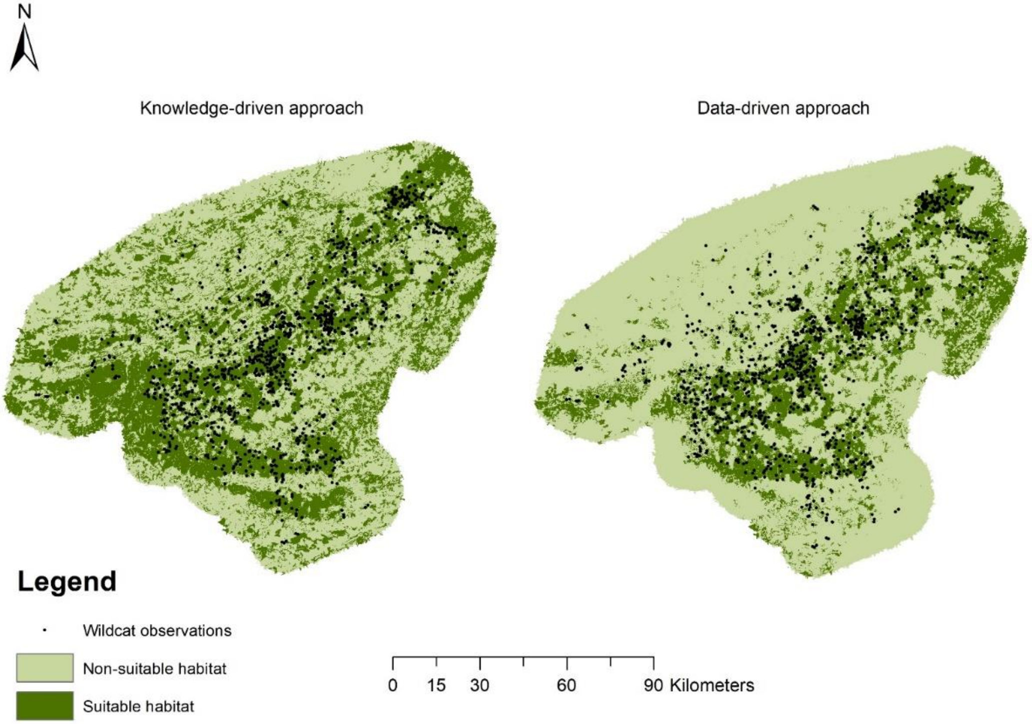
Appendix 4. Differences of accuracy metric results of the classification map for each PNV discarding mixed areas compared to previous classification. Producer (PA) and user accuracy (UA) above 0.8 (considered as highly accurate for our objectives) are highlighted with bold text. Values between 0.5 and 0.8 are in normal text (considered as sufficiently accurate for our objectives).

Potential Natural Vegetation	Code	Biotopes of reference extent (Ha)	PA trends	UA trends
***Sphagnum Betula* woods**	**SB**	214	+0.020	+0.041
***Alnus* swamp woods**	**AS**	220	+0.002	+0.058
Quercus* and *Betula* forests with *Molinia	**QBM**	1522	+0.016	+0.082
Riparian and gallery woodland	**RG**	1056	+0.005	+0.076
Fammenian *Quercus* and *Carpinus* forests	**FQC**	3222	+0.001	+0.051
Neutrophile *Quercus* and *Fraxinus* forests on wet soils	**NQF**	3222	+0.006	+0.013
Acidophilous *Quercus* and *Carpinus* forests on wet soils	**AQC**	35	+0.001	+0.066
Neutrophile *Fagus* forests	**NF**	11902	+0.001	+0.027
Wet and shady ravine forests	**WSR**	622	+0.007	+0.043
Acidophilous *Fagus* forests	**AF**	75059	+0.013	-0.006
calcareous *Fagus* and *Quercus* forests	**CFQ**	5285	+0.001	+0.022
Thermophile acidophilous *Quercus* forests	**TAQ**	66	+0.005	**+0.156**
Xerophile Fammenian *Quercus* and *Carpinus* forests	**XFQC**	133	+0.016	+0.058

Appendix 5. Extraction from complete Chi^2 analysis result

taxprio	freq_sp	AS	SB	TAQ
Carex appropinquata	116	1888.45172	-2.534498	-0.1913985
Filipendula ulmaria	5904	1211.43384	8.44347008	-9.7415255
Cirsium oleraceum	1388	1177.01879	-9.8992493	-2.2901825
Caltha palustris	3553	1155.8387	215.594892	-5.8624051
Triglochin palustris	101	1059.28885	-2.2067612	-0.1666487
Equisetum palustre	997	955.877643	3.89938375	-1.6450374
Oenanthe peucedanifolia	82	863.300563	-1.7916279	-0.135299
Carex limosa	54	793.307815	-0.0274161	-0.0890993
Comarum palustre	1855	783.61341	3117.65268	-3.0607266
Crepis paludosa	655	780.285694	70.1676642	-1.0807417
Juncus acutiflorus	2084	777.21961	1228.02529	-3.4385737
Lychnis flos-cuculi	3133	766.255859	55.3369513	-1.9431931
Cirsium palustre	4954	740.981261	253.843848	-8.1740375
Menyanthes trifoliata	1200	739.273929	3473.51138	-1.9799849
Persicaria bistorta	4058	723.343817	712.466265	-6.6956488
Carex disticha	710	714.766164	-1.3128481	-1.171491
Angelica sylvestris	4467	689.945784	153.501542	-7.3704936
Lotus pedunculatus	3133	685.692079	144.763609	-3.3628561
Phalaris arundinacea	2501	684.691742	17.9918405	-4.1266184
Galium palustre	2026	679.757877	173.883866	-3.3428744
Pedicularis palustris	111	675.283921	-2.4252524	-0.1831486
Ranunculus lingua	91	662.455552	-1.98827	-0.1501489

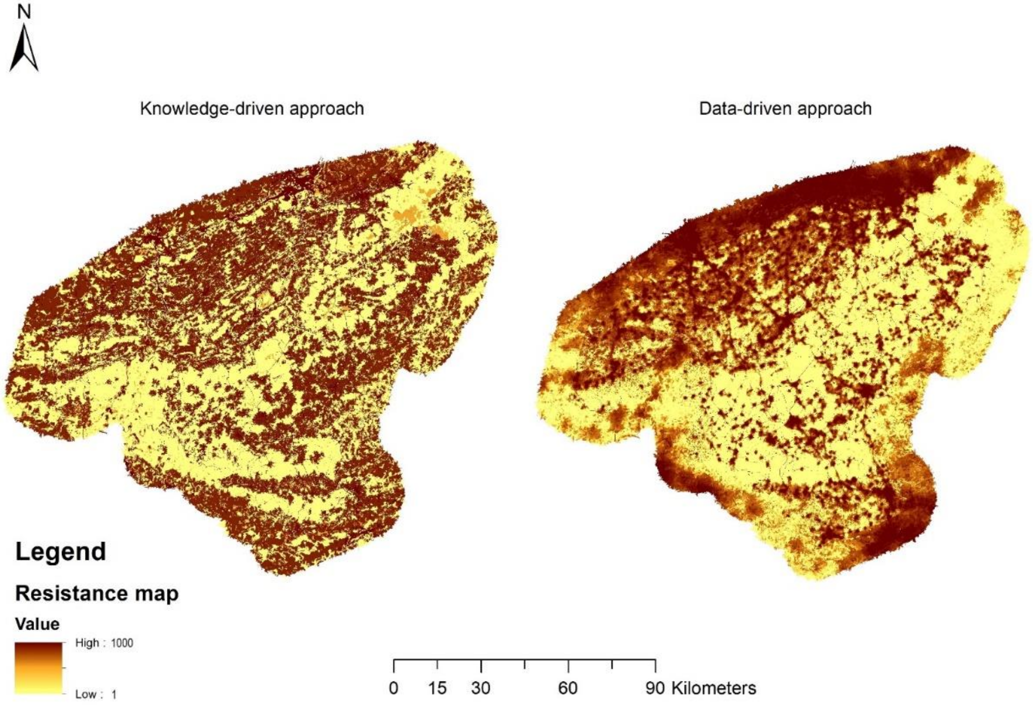
Appendix 6: Habitat suitability map of the wildcat in study area with wildcat observations used to build the model with the data-driven approach.



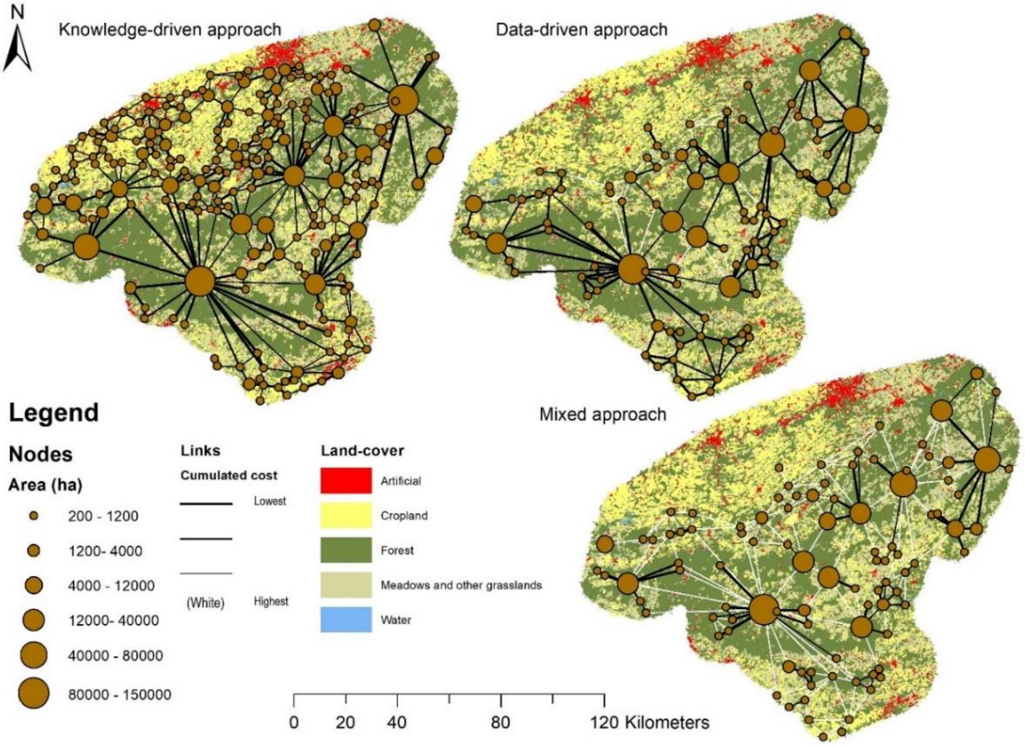
Appendix 7: Percent contribution of each variable used to build the MaxEnt model. Only variables with a contribution > 1% were retained to construct this table.

Variable code	Variable	Percent contribution
NeedLV250	Proportion of needle leaved forests in a 250m radius	36.5
Light	Artificial Light	21.1
Artif250	Proportion of artificialized elements in a 250m radius	8.5
Bare250	Proportion of bare soils in a 250m radius	7.4
NOpen	Proportion of natural open areas inside ecotope	2.8
BroadLV	Proportion of broad-leaved forest inside ecotope	2.8
Artif	Proportion of artificialized elements inside ecotope	2.6
COpen250	Proportion of forest gap or clear cut in a 250m radius	2.3
SunSpring	Incident sun light in spring	2.2
BroadLV	Proportion of needle-leaved forest inside ecotope	1.8
NOpen250	Proportion of natural open areas in a 250m radius	1.7
BroadLV250	Proportion of broad-leaved forest in a 250m radius	1.6

Appendix 8: Resistance maps used to perform connectivity analysis.



Appendix 9: Schematic representation of the connectivity of habitat patches for each approach.



Appendix 10: Data table gathering species traits information and ecosystem network affiliation.

Taxa	**Group**	**Network**	**Specialization**	**Size**	**Dispersal ability**	**Trophic level**
Apatura iris	Lepidoptera	Deciduous forests	Specialist	Tall	Medium	Low
Apodemus flavicollis	Mammals	Deciduous forests	Medium	Small	Low	Low
Arethusana arethusa	Lepidoptera	Dry grasslands	Specialist	Medium	High	Low
Argynnis adippe	Lepidoptera	Deciduous forests	Medium	Medium	Medium	Low
Argynnis paphia	Lepidoptera	Deciduous forests	Medium	Tall	Medium	Low
Barbastella barbastellus	Mammals	Deciduous forests	Specialist	Medium	High	High
Boloria dia	Lepidoptera	Dry grasslands	Medium	Small	Medium	Low
Boloria euphrosyne	Lepidoptera	Deciduous forests	Medium	Medium	Medium	Low
Calosoma inquisitor	Coléoptère	Deciduous forests	Specialist	Medium	Low	Medium
Cerambyx cerdo	Coléoptère	Deciduous forests	Medium	Tall	High	Low
Cervus elaphus	Mammals	Deciduous forests	Medium	Tall	High	High
Cicadetta montana	Homoptères	Deciduous forests	Medium	Tall	Medium	Low
Colias alfacariensis	Lepidoptera	Dry grasslands	Medium	Medium	Medium	Low
Cordulegaster bidentata	Odonates	Deciduous forests	Specialist	Tall	Medium	Medium
Cupido minimus	Lepidoptera	Dry grasslands	Specialist	Small	Low	Low
Erebia aethiops	Lepidoptera	Dry grasslands	Medium	Medium	Low	Low
Erynnis tages	Lepidoptera	Dry grasslands	Medium	Small	Low	Low
Felis silvestris	Mammals	Deciduous forests	Specialist	Medium	High	High
Glaucopsyche arion	Lepidoptera	Dry grasslands	Specialist	Small	Low	Low
Glis glis	Mammals	Deciduous forests	Specialist	Small	Low	Low
Gnorimus nobilis	Coléoptère	Deciduous forests	Medium	Medium	Low	Low
Hipparchia semele	Lepidoptera	Dry grasslands	Specialist	Tall	Medium	Low

Iphiclides podalirius	Lepidoptera	Dry grasslands	Specialist	Tall	Medium	Low
Lasiommata maera	Lepidoptera	Dry grasslands	Specialist	Medium	Medium	Low
Limenitis camilla	Lepidoptera	Deciduous forests	Specialist	Medium	Medium	Low
Limenitis populi	Lepidoptera	Deciduous forests	Specialist	Tall	Medium	Low
Lucanus cervus	Coléoptère	Deciduous forests	Specialist	Tall	Medium	Low
Meles meles	Mammals	Deciduous forests	Medium	Medium	Medium	High
Melitaea aurelia	Lepidoptera	Dry grasslands	Specialist	Medium	Low	Low
Melitaea cinxia	Lepidoptera	Dry grasslands	Specialist	Medium	Medium	Low
Melitaea didyma	Lepidoptera	Dry grasslands	Specialist	Medium	High	Low
Myotis alcathoe	Mammals	Deciduous forests	Medium	Small	Medium	High
Myotis bechsteinii	Mammals	Deciduous forests	Specialist	Small	High	Medium
Neozephyrus quercus	Lepidoptera	Deciduous forests	Specialist	Small	Low	Low
Nymphalis polychloros	Lepidoptera	Deciduous forests	Medium	Tall	High	Low
Polyommatus bellargus	Lepidoptera	Dry grasslands	Specialist	Small	Medium	Low
Polyommatus coridon	Lepidoptera	Dry grasslands	Specialist	Small	High	Low
Prionus coriarius	Coléoptère	Deciduous forests	Specialist	Tall	Medium	Low
Pyrgus armoricanus	Lepidoptera	Dry grasslands	Specialist	Small	Low	Low
Pyrgus serratulae	Lepidoptera	Dry grasslands	Specialist	Small	Low	Low
Rhinolophus ferrumequinum	Mammals	Deciduous forests	Medium	Small	Medium	Medium
Rhinolophus hipposideros	Mammals	Deciduous forests	Medium	Small	Medium	Medium
Satyrium ilicis	Lepidoptera	Deciduous forests	Specialist	Small	Medium	Low
Spialia sertorius	Lepidoptera	Dry grasslands	Specialist	Small	Low	Low
Thymelicus acteon	Lepidoptera	Dry grasslands	Specialist	Small	Low	Low

Appendix 11: The different cost of dispersion for each species

Land-cover	Erebia aethops	Spialia sertorius	Melitea cinxia	Neozeph-yrus quercus	Limenitis camilla	Myotis nattereri	Lucanus cervus	Meles meles
Water	1000	1000	1000	1000	100	100	1000	1000
Wet and alluvial grasslands	10	10	100	100	10	10	100	10
Dry grasslands	1	1	1	100	100	10	100	10
Mesophilic grasslands	10	1	10	100	10	10	100	10
Crops	100	100	100	1000	1000	100	1000	100
Intensive grasslands	100	100	100	1000	1000	100	1000	10
Mixed agricultural lands	100	100	100	1000	1000	100	1000	100
Groves and edges	10	10	10	1	1	1	1	10
Wet and alluvial deciduous forests	100	100	100	1	1	1	1	1
Mesophilic deciduous forests	100	100	100	1	1	1	1	1
Dry deciduous forests	100	10	100	1	1	1	1	1
Coniferous forests	1000	1000	1000	100	1000	100	100	100
Clearcuts and regenerations	10	10	10	10	100	10	10	10
Artificialized	1000	1000	1000	1000	1000	1000	1000	1000
Mixed arificialized	1000	1000	1000	1000	1000	1000	100	1000
Parks	100	100	100	10	100	100	1	1000
Gardens	100	100	100	10	100	1000	10	1000
Bare soil	100	10	1000	1000	1000	1000	1000	1000
Highways	1000	1000	1000	1000	1000	1000	1000	1000
Major roads	100	100	100	100	100	10	100	100
Minor roads	10	10	10	10	10	10	10	10

Appendix 12: Complete review on evaluation of ES supply in EN framework

1. Introduction

Despite considerable efforts made since the last century within the field of nature conservation, continuous anthropogenic changes have caused a wide fragmentation of the natural landscape. This fragmentation causes loss of natural habitats and their isolation in the landscape (Hanski, 2005; Stanners and Bourdeau, 1995). This is especially the case in areas with highly concentrated human populations, such as in Western Europe (Hansson et al., 1992; Jongman et al., 2004; Luck, 2007) where natural areas are becoming remnants in an anthropogenic matrix. With this high rate of fragmentation, flows of species populations through the landscapes are limited (Hansson et al., 1992; Jongman et al., 2004). Therefore, meta-population processes struggle which increases their extinction rates (Hansson et al., 1992).

To address the lack of connectivity into landscape planning, the concept of ecological network (EN) has been developed and seems to act as the main dynamic and pragmatic strategy to face biodiversity loss (Melin, 1997; Opdam et al., 2006). This concept could be defined as a set of homogenous ecosystems linked together through flows of organisms in a spatially coherent way and interacting with the surrounding landscape matrix (Opdam et al., 2006). Other authors see in EN a way to summarize a biological landscape and its different flows of organisms into an operational map useful for land-use management (Melin, 1997; Mougenot and Melin, 2000). Moreover, various definitions of the EN concept illustrate how malleable the concept is (Bennett and Mulongoy, 2006; Bernier and Théau, 2013; Melin, 1997).

More recently, the concept of ecosystem services has been developed, defined as the benefits provided by ecosystems to human populations (MA, 2003). Numerous initiatives integrated this concept into a new landscape planning management, notably due to the European Green Infrastructure strategy (European Commission, 2013; Liquete et al., 2015). Green Infrastructures are defined as a network of natural or semi-natural ecosystems providing ES (European Commission, 2013). This definition is close to EN except it integrates the function of providing ES. However, EN are not completely implemented in all European countries and regions and initiatives are still in course. Due to the development of new strategies such as GI, it is important for practitioners to know if their efforts to implement EN will not be quickly outdated. Connected ecosystem through EN initiatives could also be used as a basis to GI planning which could avoid mapping another network. The question of compatibility between EN and GI framework is therefore a major issue.

Last literature reviews on ENs and their application date back from more than fifteen years ago (Bennett and Wit, 2001; Jongman et al., 2004). The present paper will address this gap of knowledge by carrying a literature review on recent publications and applications of the EN concept and by analyzing how well the ES concept is integrated. Since the EN concept has already been debated and presented in those previous reviews, our objective focuses on clarifying the appropriation level of the EN concept and of its multifunctional ambition and its adequacy with GI strategy. To do so, the present study reviews peer-reviewed literature addressing EN and GI concepts. More precisely, the paper addresses the following aims:

- To present a review of the latest research based on the concepts of both EN and GI in Europe in order to identify trends in the inclusion of ES concepts.
- To assess to which point the scientific community integrates the ES concept into the creation and mapping of EN.
- Have ENs become obsolete since the arrival of GIs or are the two concepts compatible?

3.1. Method

A systematic review of the peer-reviewed scientific literature has been conducted using the Scopus database by searching the following terms: ("Ecological network" OR "Green infrastructure") in the title, keywords, or abstract AND (((species W/15 connectivity) OR (habitat W/15 connectivity) OR (landscape W/15 fragmentation) OR (habitat W/15 fragmentation) OR (species W/15 corridors) OR (landscape W/15 connectivity))) in all document. The W/15 operator allows to search two terms that can be separated by maximum 15 words. This allows getting a less strict research with resulting document that can cite, for instance, “connectivity of species” instead of “species connectivity”. This results to 511 papers (100%). All papers that are not in the scope of this review were discarded. To do so, all abstracts were screened and papers that did not address the subject of a network of natural or semi-natural habitats were eliminated. Thus, papers discussing only the evaluation of ES and not the connectivity of GI were also discarded as this review focus on the concept of EN. Also, book chapters, documents in other languages than English and case of studies out of Europe were eliminated. This led to 197 documents (38%). These papers were sorted in 4 categories using a dichotomous key (Figure 1). (1) Documents that did not mention ES were identified. The terms “ecosystem service” were searched through the entire document for all 197 papers. This represented 134 papers (26%). (2) 38 papers (7%) mentioned ecosystem services only in the body of the paper, and not in the abstract. Papers mentioning ecosystem services in their abstract were then entirely read. (3) Papers not evaluating them (14 papers, 3%) were split from (4) papers evaluating ES (9 papers, 2%). Evaluations of the regulating ES “Maintaining habitat of species” were not taken in account and reallocated in the previous category. This ES is too close to nature conservation objectives that are encompassed in classic EN planning. Indeed, the goal of this step is to identify elements bringing EN to a multifunctional purpose by ensuring ES delivery simultaneously to conserving biodiversity.

Papers evaluating ES were carefully examined and the following pieces of information were integrated in a table: the name of evaluated ESs, the sources or tools that helped the evaluation, the geographical extent of this evaluation and authors and year of publication. The different ES evaluated were also classified using the latest CICES classification (Haines-Young and Potschin-Young, 2018) to allow comparison across case studies. ES supply evaluation derived from existing map dataset are commonly used and the extent of the original data was indicated. To differentiate the use of pre-existing dataset of ES evaluation, "study area" was noted in the extent column if an evaluation was done for the purpose of the study.

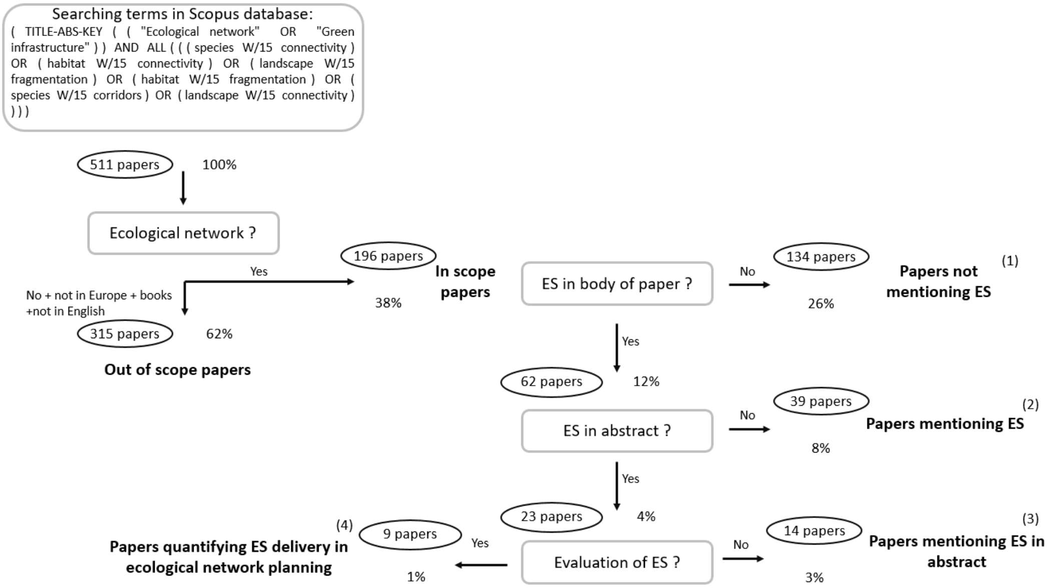


Figure 1: Dichotomy key used to sort the different papers of this review.

4.3. Results and Discussion

4.3.1. Evolution of inclusion of ecosystem services concept through time

Results from paper sorting were summarized with two temporal plots (Figure 29). First, a comparative plot with cumulative number of publications with and without ecosystem services mentioned (based on the second sorting) was realized to compare the evolution of the number of studies mentioning ES and those who does not. Then a second plot distinguish the different inclusion of ES concept in EN by addressing the number of publications only mentioning ES, those mentioning ES in their abstract too and those going further by dealing with ES supply evaluation.

While papers concerning ENs are published consistently, the mention about ES really starts after 2010 (even if the first mention was in 2004). This year corresponds to the development of the GI strategy by EU. Thereafter, an increase of publications mentioning ESs in ENs can be seen. The research about ENs is principally dedicated to methodological developments (Bruinderink et al., 2003; Meier et al., 2005; Villemey et al., 2018). On this topic, an important quantity of papers is studying the use of spatial graph theory in the identification of species habitat networks (Clauzel et al., 2018; Foltête, 2019; Pereira, 2018). Indeed, identifying species corridors connecting landscape patches is complex and different approaches exist with their respective pros and cons (Gurrutxaga and Saura, 2014; Stevenson-Holt et al., 2014). The other fields of research are more concerned by theoretical discussions about the integration of EN in policies (Andrian, 2015; Beunen and Hagens, 2009; Romano and Zullo, 2015) or by the ways to make ENs more reliable and coherent (Baguette et al., 2013; Battisti, 2013, 2003).

The way ES are integrated in EN research has changed over time (Figure 2). First paper mentioning ESs cites them in their discussion as an added value delivered to give weight to some less natural part of ENs or to show a relative importance of ENs for policies (Leibenath, 2011; Zmelik et al., 2011). But it can be seen that even if the mention of ES has increased, few papers (24) consider them as sufficiently important to be cited in their abstract (e.g. Mander et al. 2018; Hatziiordanou et al. 2019). The latest articles generally place the challenges of delivering ESs at the same level as those of conserving biodiversity in the core of their study (Cunha and Magalhães, 2019; Ersoy et al., 2018; Marini et al., 2019). Some even consider ENs as multi-functional GI even speaking of socio-ecological networks/systems (Arnaiz-Schmitz et al., 2018; Capotorti et al., 2019a; Cunha and Magalhães, 2019). Among these 9 papers, two are reviews speaking about the evaluation of ES supply and 7 are really applying a method of EN planning with ES's evaluation. This represents only 4% of the papers treating about EN planning and most of them were published in the last 2 years.

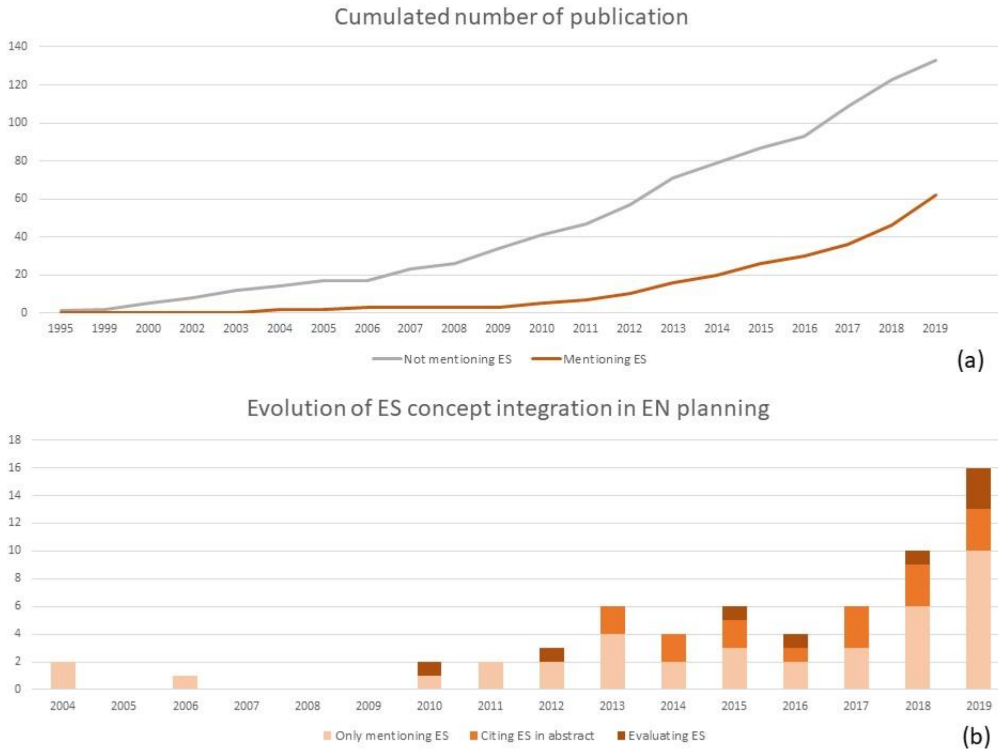


Figure 2: Cumulative line plot of number of publication by year for two categories of paper: those mentioning ES and those who do not. Papers published in 2020 were discarded for the plot construction because the year is not yet over.

Beyond scientific initiatives, national and regional initiatives of EN planning led by nature practitioners are also including ES concept in their planning (Sordello et al., 2013b). But ES supply is only cited as an indirect product of EN restoration to give weight to EN in land-use planning thanks to the benefits provided by ecosystems and their economic value. Moreover, stakeholders are probably encouraged to cite ES because of the GI strategy developed by the European Commission. However, we are far from a complete integration such as the development of socio-EN as defined by some authors (Arnaiz-Schmitz et al., 2018; Capotorti et al., 2019a; Cunha and Magalhães, 2019). This is probably due to a lack of reproducible methods or a lack of expertise in an emerging research field.

It is interesting to highlight that the majority of papers evaluating ES supply use the term of GI as a concept integrating both EN and ES concepts (Cannas et al., 2018; Capotorti et al., 2019a; Liquete et al., 2015). Some GI papers are even not citing EN as such but still integrate ecological corridors issues (Rodríguez-Espinosa et al., 2019; Snäll et al., 2016). Only one still considers that EN concept is sufficient to take into account ES supply issues and does not use the term of GI (Newton et al., 2012) but GI concept was not well spread at this time. We can see that EN and GI are not complementary terms but GI has supplanted ES over time to englobe a concept including a multifunctional network strategy. Even if GI concept rely on a framework connecting natural and semi-natural elements such as EN. But this statement is only true for papers addressing EN issues, the use of GI concept with no link to EN concept and focusing only on ES supply is still in use (Badenhausser et al., 2020; Mullins et al., 2020).

4.3.2. Toward multifunctional ecological network planning

The integration of EN and ES concepts into one multifunctional framework was analyzed for the nine papers including ES supply evaluation in EN planning. The resulting networks are now called "multifunctional network" to differentiate them from classic EN planning and from GI initiative that do not consider EN issues.

The first parameter is the ES typology relied on. Some authors use international nomenclatures, such as CICES (Common International Classifications of Ecosystem Services) or EEA's (European Environment Agency) classification (Lanzas et al., 2019; Liquete et al., 2015; Rodríguez-Espinosa et al., 2019). Others refer to ESs with a coarser definition due to the peculiarities of the method or software used (Arcidiacono et al., 2016; Cannas et al., 2018; Capotorti et al., 2019a, 2019b).

By analyzing the table summarizing the different ES evaluated, we can identify some patterns (Figure 3). Regulation and maintenance services are the most evaluated ones, in most cases. They regroup ES dealing mostly with "atmospheric composition", "mediation of wastes or toxic substances of anthropogenic origin by living processes" or "regulation of baseline and extreme events". The latter is also the most represented group of ES evaluated in the different studies. Provisioning evaluated ES are principally represented by "Cultivated terrestrial plants for nutrition, materials and energy" group. Cultural services are mainly represented by "Physical and experimental interactions with natural environment" and "Intellectual and representative interactions with natural environment". In half of the cases, ES supply are evaluated through a proxy calculation and is mostly used for "Regulation and maintenance" ES (68% of cases) while panel evaluation (interviews or expert panels) methods apply mainly for cultural ES (50% of cases), which are qualitative assessments. They are also sometimes evaluated through quantitative assessments by estimating ,for instance, touristic attractiveness using location data of social media Flicker (Cannas et al., 2018) or using monetary evaluation (Cannas et al., 2018; Newton et al., 2012). In general, ES are selected based on the availability of the different data or on regional specificities such as traditional mushroom picking by instance (Lanzas et al., 2019).

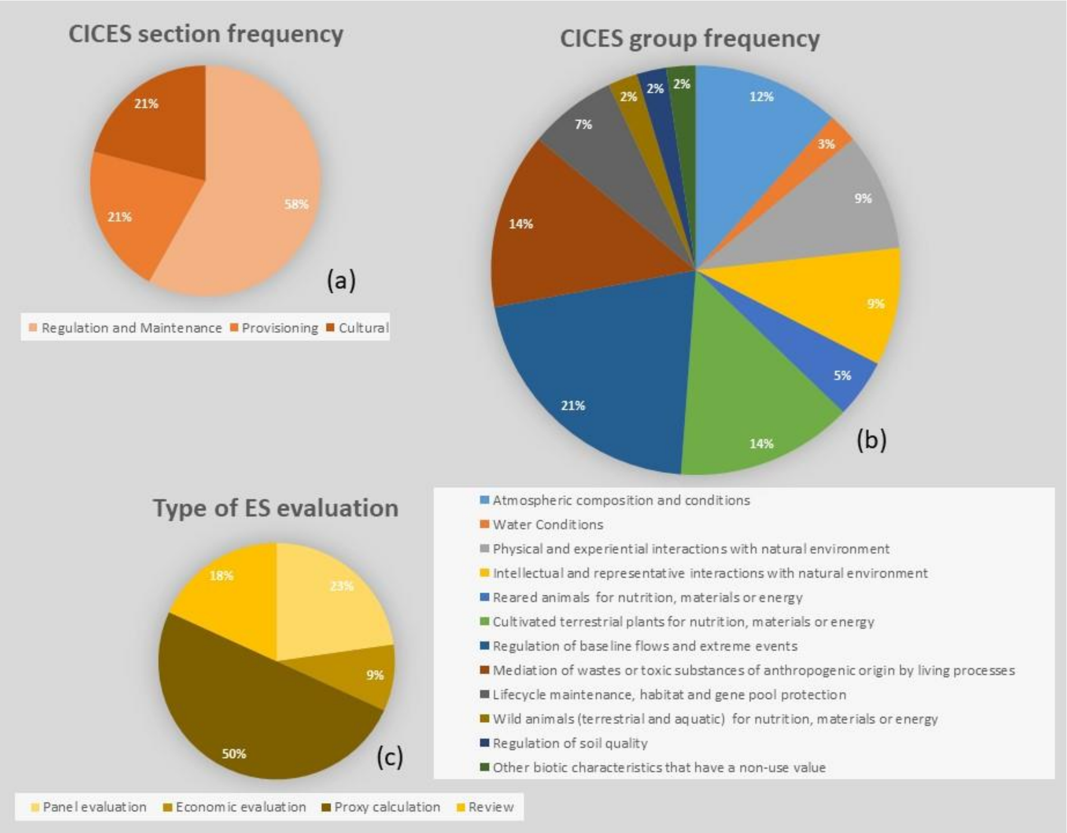


Figure 3: Pie charts resuming the different classification made to identify patterns in ES supply evaluation in EN context. We have, the proportion of CICES section to identify the main section of ES evaluated (a), a more precise identification based on the CICES group (b) and finally the different type of evaluation performed (c).

Concerning the context within analyses are performed, the planning of multifunctional networks implies a demand for ES supply explaining why a lot of studies (3 out of 7) are carried out in urban contexts (Capotorti et al., 2019b, 2019a; Rodríguez-Espinosa et al., 2019). By contrast, Liquete et al. (2015) include rural environments into GI, due to the scale of their study (EU) implying a high proportion of rural environment. Those different contexts also create different levels of complexity to choose between production and biodiversity conservation priority land-use (Lanzas et al., 2019; Liquete et al., 2015; Newton et al., 2012; Rodríguez-Espinosa et al., 2019; Snäll et al., 2016). This led to inherent trade-offs analysis affecting an important component of multifunctional network planning: the zonation of the network.

Preserving ES supply and biodiversity is difficult as it does not always lead to preserving the same areas (Venter et al., 2009). Thus, authors suggest a systematic planning approach based on prioritization of zones to help address conflicting issues (Lanzas et al., 2019). The multifunctional framework used through the papers scrutinized could be split into two types of zones: core areas and mixed zones. Cores areas are the most common zone represented in most of studies analyzed here (Cannas et al., 2018; Capotorti et al., 2019b, 2019a; Lanzas et al., 2019; Liquete et al., 2015; Niemelä et al., 2010; Rodríguez-Espinosa et al., 2019). They are principally devoted to biodiversity conservation or they also include ES supply that are compatible with biodiversity conservation (Lanzas et al., 2019). Cores areas of a multifunctional network represent also areas were biodiversity conservation and ES supply are both maximized (Liquete et al., 2015). The other kind of zones ("mixed zones") represents a gradient were we can find areas with ES supply but where biodiversity conservation has lower priority due to its conservation status or preservation state (Lanzas et al., 2019). Finally, we can find zones that are considered opposed to conservation goals and that only focus on ES supply (Lanzas et al., 2019). Those areas are often excluded from the multifunctional network and thus not considered (Lanzas et al., 2019; Liquete et al., 2015).

The question of connectivity between core areas is not put aside. Some authors use species corridors models as important structuring input for the multifunctional network planning (Cannas et al., 2018; Liquete et al., 2015; Snäll et al., 2016).However, methods to do it are not as complex and complete as dedicated studies (Gurrutxaga and Saura, 2014; Pereira, 2018). Others suppose that some components of their network could play a role of corridors to reconnect core areas (Capotorti et al., 2019b, 2019a; Lanzas et al., 2019). Indeed mixed zones with ES supply and lower biodiversity conservation goals can play an important role of connecting but also playing a role of buffers to protect conservation areas from pollution and other impact of intensive human activities (Mubareka et al., 2013).

This kind of land zoning is really similar to de different zonation known in EN planning with core areas, corridors and optional buffer zones(Bennett and Mulongoy, 2006; Bernier and Théau, 2013; Melin, 1997). Indeed, buffer zones may include areas under sustainable management taking into account portions of landscape devoted to production (Bennett and Mulongoy, 2006; Melin, 1997). Thus, this idea of landscape partitioning including socio-economic issues (hence ES) in EN planning is not recent. Indeed, dealing with trade-offs between nature conservation and food production was already brought forward by EN planners (Bennett and Mulongoy, 2006; Melin, 1997) . Yet, EN framework could gain importance in land management thanks to the ES concept. Biodiversity conservation priority networks could benefit from ES supply evaluations by enhancing the role of conservation areas but also those with lower conservation value but still important for the network as buffer or corridors (Lanzas et al., 2019). However, it can be seen that some approaches to map multifunctional networks do not evaluate ES supply consistently by taking only into account ES not endangering nature conservation actions and putting aside others such as food production (Capotorti et al., 2019b; Lanzas et al., 2019; Liquete et al., 2015). This can be explained by the chosen approach or aims of the study. For instance, focusing on regulating and maintenance to identify network elements with conservation purposes (Liquete et al., 2015). Areas with opposed objectives to nature conservation should be mapped and considered for any multifunctional network planning. This issue could be tackled by moving forward to a more flexible definition of zones in EN planning and developing a real gradient of conservation vs. exploitation (Lanzas et al., 2019). This may move EN concept toward multifunctional EN framework.

We saw that multifunctional networks planning are mainly performed in urban context (Capotorti et al., 2019b; Rodríguez-Espinosa et al., 2019),while EN concerns principally rural and natural areas (Bernier and Théau, 2013). But integration of EN planning in urban and peri-urban areas of paramount importance as most cities have nature conservation stakes in their close environment (Beckline and Yujun, 2014; Borgström et al., 2012). Due to the benefit of integrating nature and biodiversity in cities supplying an important amount of ES (Hamel et al., 2021; Hobbie and Grimm, 2020), multifunctional ENs could be easily implemented to reconnect urban and peri-urban populations to rural and natural ones. This may help to conserve urban and peri-urban biodiversity while reducing the permeability to nature of cities. This is also the case for intensive agricultural and forestry areas where improving ES supply could be an argument to improve connectivity within those areas by defining zones sharing conservation and exploitation stakes.

4.4. Conclusion

What emerges from this literature review is that EN et GI concepts share a lot of features. Although GI framework is newer, old EN concepts such as buffer zones are still relevant and proposed as important component within multifunctional network planning (Lanzas et al., 2019). Moreover, dealing with trade-offs between nature conservation and production has already been tackled by both EN and GI planners. It can be said that EN planning, and GI strategy are largely compatible. GI can be considered as multifunctional networks connecting the different conservation areas and not independent GI only aiming for ES supply (Rodríguez-Espinosa et al., 2019). EN are networks planned principally focusing on biodiversity conservation and we have seen that an important part of recent studies focus on developing methods to map the most accurate corridors (Duflot et al., 2018a; Ersoy et al., 2018). In parallel, methodological research on ES evaluation is still in course (Boeraeve et al., 2020b; Maebe et al., 2019). However, a certain amount of papers build multifunctional network while putting biodiversity conservation as a top priority assuming that a well-functioning network of ecosystems supply better quality ES (Cannas et al., 2018; Liquete et al., 2015; Niemelä et al., 2010). This allows understanding that EN concept has not been superseded at all but has just evolved regarding consideration of ES. By including ES into EN planning, connectivity and nature conservation issues have now a chance to be put in the center of society's interest.

Multifunctional networks are maybe oversimplifying connectivity issues or ES supply evaluation, but they offer promising avenues for EN research by mixing both conservation issues and human needs thanks to trade-off analysis (Newton et al., 2012). In the future, it could be interesting to see multifunctional network planning based on trade-offs analyses performed on results from more complete corridors mapping or ES supply evaluation.