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DEVELOPMENT OF AN INTEGRATED APPROACH FOR THE ANALYSIS AND OPTIMIZATION OF ECOLOGICAL NETWORKS IN AGRICULTURAL LANDSCAPES

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Abstract

In human-modified landscapes, biodiversity is often confined in remnants of natural habitats and there is an urgent need to take significant action to halt the loss of biodiversity, happening at a faster rate than ever, driven by many factors such as land use change, habitat fragmentation, pollution, natural resources exploitation, climate change, biological invasion, and many other. In this light, identifying actions that can be implemented to reduce the loss of biodiversity and simplification of landscapes has become a key topic in the field of landscape ecology and conservation biology. Management approaches to achieve protection and maintenance of natural ecosystems should consistently consider all landscape components so that they can be managed with the goal of maintaining or restoring pre-existing ecological functions. In fact, through the concepts of meta-population and ecological connectivity, as strategies to sustain biodiversity in fragmented landscapes by reconnecting natural habitat fragments in anthropogenic environments, Ecological Networks (EN) can be developed. Generally, territorial planning refers to models that allow for the reading of potential EN. However, their biodiversity content is often not verified, and/or they are never monitored over time once implemented.

The research activities described in this Thesis aimed to contribute filling the knowledge gaps with respect to biodiversity verification, EN structure and its monitoring, by identifying what elements drive the expression of biodiversity and the factors that influence its content. Specifically, starting from a EN model developed in north-eastern Italy, in the context of the landscape project of the region Friuli-Venezia Giulia, a vegetation sampling was planned to assess plant diversity contained within the nodes of the EN. Then, in the first part of the Thesis, I provided a method to determine the adequate number of replicates to effectively characterize biodiversity content of natural habitats within the nodes of the EN (Chapter 1). In fact, the field verification of the EN model represents the most expensive part both in terms of time and money. For this reason, it is often not carried out as well as the monitoring of the network over time. It is necessary, to identify the minimum number of

replicates to keep unchanged the characteristics of the observed communities thus reducing the sampling effort.

In the second part (Chapter 2), based on the vegetation sampled, I studied the relationships between α and β diversity pattern, landscape structure and connectivity in the nodes of the EN. I found that high node connectivity led to a higher species richness (α-diversity) but also increased plant communities' similarity (i.e., low β-diversity). The effect of landscape composition of semi-natural land covers (i.e., hedgerows, watercourses) showed a positive effect on species diversity as opposed to that of the configuration of anthropogenic elements. Finally, in the last part (Chapter 3), I investigated the potential of Spectral Variation Hypothesis (SVH) in linking field-collected and remotely sensed data in a complex landscape as the under study one. Specifically, I examined whether ecosystem heterogeneity was related to greater diversity and whether the estimated spectral diversity was consistent with the observed one. I found that spectral data can be used as a guidance to assess and/or monitor plant diversity conserved in the EN.

In conclusion, the three case studies contained in this Thesis, could provide novel insight in the planning and monitoring of ENs, through a multidisciplinary approach that considered different points of view with which to evaluate the effectiveness of plant diversity conservation within ENs.

Riassunto

Nei paesaggi modificati dall'uomo, la biodiversità è spesso confinata in frammenti di habitat residuali e c'è un urgente bisogno di intraprendere azioni significative per fermare la perdita di biodiversità, che avviene a un ritmo più veloce che mai, guidata da molti fattori come il cambiamento d'uso del suolo, la frammentazione degli habitat, l'inquinamento, lo sfruttamento delle risorse naturali, il cambiamento climatico, l'invasione biologica e molti altri. Sotto questa luce, identificare le azioni che possono essere attuate per ridurre la perdita di biodiversità e la semplificazione dei paesaggi è diventato un argomento chiave nel campo dell'ecologia del paesaggio e della biologia della conservazione. Gli approcci di gestione per raggiungere la protezione e il mantenimento degli ecosistemi naturali dovrebbero considerare coerentemente tutte le componenti del paesaggio, in modo che esse possano essere gestite con l'obiettivo di mantenere o ripristinare le funzioni ecologiche preesistenti. Infatti, attraverso i concetti di meta-popolazione e connettività ecologica, come strategie per sostenere la biodiversità in paesaggi frammentati attraverso la riconnessione dei frammenti di habitat naturale in ambienti antropogenici, è possibile sviluppare Reti Ecologiche (RE). Generalmente la pianificazione del territorio fa riferimento a modelli che consentono la lettura delle RE potenziali. Tuttavia, di esse spesso non viene verificato il contenuto di biodiversità, e/o non vengono mai monitorate nel tempo una volta implementate.

Le attività di ricerca descritte in questa Tesi vogliono dare un contributo per colmare le lacune di conoscenza rispetto alla verifica della biodiversità, alla struttura della RE e al suo monitoraggio, identificando quali siano gli elementi che guidano l’espressione della biodiversità e i fattori che ne influenzano il contenuto. Nello specifico, partendo da un modello di RE sviluppato nell'Italia nord-orientale, nell'ambito del piano paesaggistico della regione Friuli-Venezia Giulia, è stato pianificato un campionamento della vegetazione per valutare la diversità vegetale contenuta all'interno dei nodi della RE. Quindi, nella prima parte della Tesi, ho fornito un metodo per determinare il numero adeguato di repliche per caratterizzare efficacemente il contenuto di biodiversità degli habitat naturali all'interno dei nodi della RE (Capitolo 1). Infatti, la verifica sul campo del modello di RE rappresenta

la parte più costosa sia in termini di tempo che di denaro. Per questo motivo, spesso non viene effettuata così come il monitoraggio della rete nel tempo. È necessario individuare il numero minimo di repliche per mantenere inalterate le caratteristiche delle comunità osservate riducendo così lo sforzo di campionamento.

Nella seconda parte (Capitolo 2), sulla base della vegetazione campionata, ho studiato le relazioni tra i pattern di diversità α e β, la struttura del paesaggio e la connettività nei nodi della RE. Ho riscontrato che un'alta connettività dei nodi ha portato a una maggiore ricchezza di specie (α-diversità) ma anche a una maggiore somiglianza delle comunità vegetali (cioè, una bassa β-diversità). L'effetto della composizione paesaggistica delle coperture seminaturali (cioè, siepi, corsi d'acqua) ha mostrato un effetto positivo sulla diversità delle specie rispetto a quello della configurazione degli elementi antropici. Infine, nell'ultima parte (Capitolo 3), ho studiato il potenziale dell'ipotesi di variazione spettrale nel collegare i dati raccolti sul campo e quelli rilevati da remoto in un paesaggio complesso come quello oggetto di studio. In particolare, ho indagato se l'eterogeneità dell'ecosistema fosse legata a una maggiore diversità e se la diversità spettrale stimata fosse coerente con quella osservata. Ho scoperto che i dati spettrali possono essere utilizzati come guida per valutare e/o monitorare la diversità vegetale conservata nella RE.

In conclusione, i tre casi di studio contenuti in questa tesi, potrebbero fornire una nuova visione nella pianificazione e nel monitoraggio delle RE, attraverso un approccio multidisciplinare che considera diversi punti di vista con cui valutare l'efficacia della conservazione della diversità vegetale all'interno delle RE.

Preface

Due to rapid biodiversity loss worldwide, identifying actions that can be implemented to reduce the degradation and simplification of biodiversity and landscapes has become crucial and a key topic in the field of landscape ecology and conservation biology. Thus, the major aim of this Thesis is to provide an insight for testing and monitoring diversity and the factors that influence it in the habitats and nodes of an EN. Specifically, the Thesis explores the plant diversity content present in an EN, evaluating the possible effects of the surrounding landscape on the communities studied and possible methods for monitoring vegetation within habitats and nodes over time. The main objectives of this research were 1) to provide a methodological framework to support biodiversity data collection planning, to optimize the sampling effort and estimate the number of replicates sufficient to distinguish different habitats and gather data on species diversity within the EN. 2) to analyze plant diversity patterns within nodes of the EN investigating the effects of landscape structure and connectivity on plant communities. 3) to investigate the potential of remote sensing for quantitative analyzing the biodiversity content of the EN and the study area.

The Thesis is organized as follows: a general introduction, three chapters containing the articles that responded to the three research objectives, and overall conclusions.

Specifically, in the introduction I briefly presented some key concepts of landscape ecology, as landscape connectivity, and the concept of EN, as it is meant in this Thesis. In addition, I briefly mentioned some of the gaps existing in the field and described the EN under study, thus providing the necessary background for the reading and understanding of this research.

In the first Chapter, I provided a method to determine the adequate number of replicates to effectively characterize biodiversity content of natural habitats within the nodes of the EN, aiming at reducing the cost of future sampling and/or monitoring campaigns.

In the second Chapter, I focused on the relationships between α and β diversity pattern, landscape structure and connectivity in the nodes of the EN, aiming at identifying those factors that influence plant diversity within the EN and what suggestions can be applied for the management of the elements composing the EN.

Finally, in the last part I investigated the potential of remote sensing in linking field-collected and remotely sensed data in a heterogeneous landscape as the one containing the EN. Specifically, I examined the relationship between spectral diversity and heterogeneity and plant diversity, exploring the potential of remote sensing data as a guidance to assess and/or monitor biodiversity.

The conclusions section provides a general overview and synthesis on the key findings emerging from these three study cases presented in the Thesis, suggesting potential actions and directions for future research on the planning and managing of ENs.

General introduction

Landscape ecology

The term landscape ecology dates back nearly a century, developing in later years with theory and applications (Troll 1939, 1968; Schreiber 1990; Forman 1995). It encompasses several principles that unite ecology and landscape perspectives, focusing on spatial pattern and ecological process, biotic diversity, species flow, landscape structure and function, spatial and temporal scales, heterogeneity effect on fluxes and disturbance, changing patterns, and many others (Risser et al. 1984; Forman and Gordon 1986; Risser 1987; Forman 1995). The object of study of this subject is the landscape, defined as a mix of local ecosystem or land use types repeated over the land; it is a land mosaic, composed of spatial elements (patches, corridors or matrix, Urban et al. 1987; Forman and Gordon 1986; Forman 1995; see Table 1.1). Landscape ecology is largely founded on the notion that the patterning of landscape elements strongly influences ecological characteristics, including plant and animal populations.

From an ecological perspective, the patches represent relatively discrete areas of relatively homogeneous environmental conditions where the patch boundaries are distinguished by discontinuities in environmental character states from their surroundings of magnitudes that are perceived by or relevant to the organism or ecological phenomenon under consideration (Wiens 1976). What is outside the patches is called matrix and is the most extensive and connected element type, therefore plays the dominant role in the functioning of the landscape (Forman and Godron 1986). Finally, the elements that provide physical links between patches and facilitate the movement of an organism through the matrix are called corridors (Forman 1995; Bennet 1998). The types and distribution of the landscape elements determine the landscape structure, that is the spatial relationships among component parts, and can be divided in two further definitions: landscape composition and configuration (Turner 1989; Dunning et al. 1992). Landscape composition refers to features associated with the presence and amount of each patch type within the landscape, but without being spatially explicit while landscape configuration refers to the physical distribution or spatial character of patches within the landscape (McGarigal and Marks 1995).

Landscape connectivity

Landscape connectivity is the degree to which the landscape facilitates or impedes movement among resource patches (Taylor et al. 1993), or the functional relationship among habitat patches, owing to the spatial contagion of habitat and the movement responses of organisms to landscape structure (With et al. 1997). Connectivity is therefore a feature of a whole landscape, where the scale of interest is determined by the habitat use and movement scales of the organism in question (Goodwin and Fahrig 1998; Tischendorf and Fahrig 2000).

Table 1.1: Definition of key terms in landscape ecology used in the Thesis

Terms	Definitions	References
Corridors	Landscape elements that provide physical links between patches and facilitate the movement of an organism through the matrix.	Forman (1995); Bennet (1998)
Functional connectivity	Landscape features that facilitate or impede the movement of species between habitat patches.	Taylor et al. (1993, 2006)
Landscape	Mix of land use types repeated over the land.	Urban et al. (1987); Forman and Gordon (1986); Forman (1995)
Landscape composition	amount of each patch type within the landscape.	Turner 1989
Landscape configuration	physical distribution of patches within the landscape.	Turner 1989
Matrix	most extensive and connected element type in the landscape.	Forman and Gordon (1986)
Patches	Relatively homogeneous areas that differ from their surroundings.	Forman (1995)
Structural connectivity	Spatial relationships between the structural elements of the landscape.	Tischendorf and Fahrig (2000); Taylor et al. (2006)

The definition of landscape connectivity includes two fundamental concepts: structural connectivity, corresponding to spatial relationships (continuity and adjacency) between the structural elements of the landscape, which is independent on the ecological characteristics of the species (Tischendorf and Fahrig 2000; Taylor et al. 2006), and functional connectivity, which refers to landscape features that facilitate or impede the movement of species between habitat patches (Taylor et al. 1993; Taylor et al. 2006). Consequently, the ability of species to move or disperse through the landscape is driven also by structural features of the landscape (Adriaensen et al. 2003). When landscape connectivity is seen by a target organism, it is possible to introduce the term habitat connectivity, which refers to the degree of functional connectivity between patches of optimal habitat for that species (Lindenmayer and Fischer 2006; Taylor et al. 2006; Correa Ayram et al. 2016). In this way, landscape elements take on different levels of habitat suitability allowing to define areas of higher and lower suitability, on the base of both the ecological behavior of target species and of the matrix characteristics that facilitates or impedes species mobility, and which could be affected by human influence.

Conservation of biodiversity and Ecological Networks

Biodiversity loss is one of the main concerns in the Anthropocene, happening at a faster rate than ever, driven by many factors such as land use change, habitat fragmentation, pollution, natural resources exploitation, climate change, biological invasion, and many other (Landi et al. 2018; IPBES 2019; EEA 2020). As stated by the United Nations (2015a) there is a need to "take urgent and significant action to reduce the degradation of natural habitats, halt the loss of biodiversity and protect and prevent the extinction of threatened species". These actions could be achieved through a management approach that coherently consider all the landscape components.

In the beginning, protected areas (hereafter PAs) were designed to preserve endangered ecosystems, nowadays it is clear that biodiversity protection should rely on a smarter management of the anthropogenic surrounding landscapes and no longer be confined only to PAs (UN 2015a, 2015b; European Commission 2020). Thus, the concept of Ecological Network (hereafter EN) arose, defined as ''a coherent system of natural and/or semi-natural landscape elements that is configured and managed with the objective of maintaining or restoring ecological functions as a means to conserve biodiversity'' (Bennett 2004). The modeling of ENs, as useful tools to provide an integrated protection of biodiversity also considering biotic interactions among species in an ecosystem, was then introduced (Pascual and Dunne 2006). ENs are composed by habitat patches (or nodes of the EN graph) suitable for an organism and corridors (or links of the EN graph) that allow the movement of the species from a patch to another. However, EN are spatial patterns which are modeled by landscape ecologists to quantify connectivity using various methods such as individual-based movement models (Grimm and Railsback 2005), least-cost analysis (Adriaensen et al. 2003), circuit theory (McRae et al. 2008, 2012), centrality analyses (Rudnick et al. 2012) or landscape graphs (Urban and Keitt 2001). Other important methods to quantify connectivity are based on genetic data (e.g., Andreassen and Ims 2001) or on tracking animal movements over time (Turchin 1998; Gillis and Krebs 1999, 2000). These methods present limitations and they basically favored the spread of approaches based on habitat quality and analysis of the autoecology of animal species (Fichera et al. 2015; Gao et al. 2017; Cunha and Magalhães 2019).

All these techniques differ in their capacity to characterize the ecological processes and in the amount of input data required. Landscape graphs are an interesting compromise for both those criteria (Calabrese and Fagan 2004), making them useful tools, that mix methodological simplicity and ecological relevance, suitable for land planning (Urban et al. 2009; Foltete et al. 2014).

However, some studies have highlighted the exiting gaps among researchers and practitioners in the implementation of the ENs as tools to mitigate the effect of habitat fragmentation on biodiversity, such as the lack of monitoring to test their effectiveness and the evaluation of the network structure only from the structural perspective, ignoring the effective biodiversity hosted within the EN elements (Gippolitti and Battisti 2017; Luo et al. 2021). Moreover, many of the research analyzing the influence of landscape connectivity on biodiversity were studied for animal species, while the understanding of the role of EN connectivity on plants remains limited, especially at the community level (but see Uroy et al. 2019; McLeish et al. 2021).

These gaps will be thoroughly investigated in Chapter 1, by proposing an integrated method to determine the adequate sampling effort for the purpose of monitoring an EN, and in Chapter 2, by analyzing the effects of landscape structure and connectivity on plant communities with nodes in an EN.

Remote sensing

Remote sensing refers to gathering information about an object without coming into direct contact with it. In this Thesis, the concept of remote sensing is refired to the study of the Earth's surface characteristics from above. Remote sensing can be used to differentiate objects or materials based on their characteristic optical properties. These optical properties are characterized by its interaction with incoming electromagnetic radiation, that can be either absorption, reflectance, scattering or transmission (Jones and Vaughan 2010). Remote sensing instruments can be grouped into active and passive, but since only the passive one was used in the Thesis, only the latter will be described. Passive remote sensing instruments capture the reflectance of solar radiation. Most commonly, the output is an image consisting of layers that represent information from various parts of the electromagnetic spectrum. Such part of the spectrum is referred to as a spectral band, and can vary in band width, depending on the covered wavelength range. In addition to the spectral resolution, it is important to mention the spatial resolution (i.e., the physical size that represents a pixel) and temporal resolution (i.e., the revisiting time of the satellite on the same area) of the images (Woodcock and Strahler 1987). In the case of free access products, the images can have medium spatial resolution and high temporal resolution (e.g., Sentinel and Landsat) while the paid products can reach very high resolutions both spatially and temporally (e.g., WorldView and Pléiades neo).

Remote sensing of vegetation

Compared to non-living surfaces, remote sensing of vegetation is complicated by its high spatio-temporal variability. In general, the spectral reflectance of vegetation is characterized by strong absorbance in the visible wavelength region (VIS, 400-700 nm) and relatively high reflection in the near infrared (NIR, 700-1000 nm). In the transition zone from VIS to NIR, vegetation spectra are characterized by a strong increase of reflectance, which is referred to as red edge (690-790 nm).

Depending on the vegetation type, reflectance can differ considerably. Differences between vegetation types can be usually detected in the wavelength region ranging from 300 nm to 15 µm (Jones and Vaughan 2010). These differences are determined by the interactions of incoming radiation and components of the canopy. At the level of entire plants or plant communities, spectral reflectance is furthermore substantially influenced by the canopy structure (Asner 1998; Knyazikhin et al. 2013; Kattenborn et al. 2018). This includes canopy depth, density, and leaf arrangement (Ollinger 2011). Based on differences in spectral properties it is possible to differentiate single vegetation types (Ustin and Gamon, 2010), examples include discrete classifications of dominant vegetation types at the global scale (Bonan et al. 2002), to the delineation of single habitats at a local scale (Mack et al. 2016; Stenzel et al. 2017). Remote sensing can also be used to monitor biodiversity, specifically, the combination of remotely sensed and field data represents one of the most promising approaches to fill gaps in biodiversity monitoring (Vihervaara et al. 2017). Much research has considered the relationships between remotely sensed and field sampled data (e.g., Palmer et al. 2002; Rocchini et al. 2015; Lausch et al. 2020), based on the Spectral Variation Hypothesis (SVH), proposed for the first time by Palmer et al. (2002). This concept hypothesizes that the variability of the spectral response of a remotely sensed image could be used as a proxy to assess plant biodiversity. The ability of SVH to detect plant diversity was tested on several ecosystems covering large areas (e.g., Feret and Asner 2014; Heumann et al. 2015; Torresani et al. 2019) but few studies have investigated SVH application at a greater level of detail over small and complex areas. The potential of SVH in linking field-collected and remotely sensed data in a complex landscape will be investigated in Chapter 3. Furthermore, its suitability to assess and/or monitor plant diversity conserved in a EN or more generally in natural environments over time will also be explored.

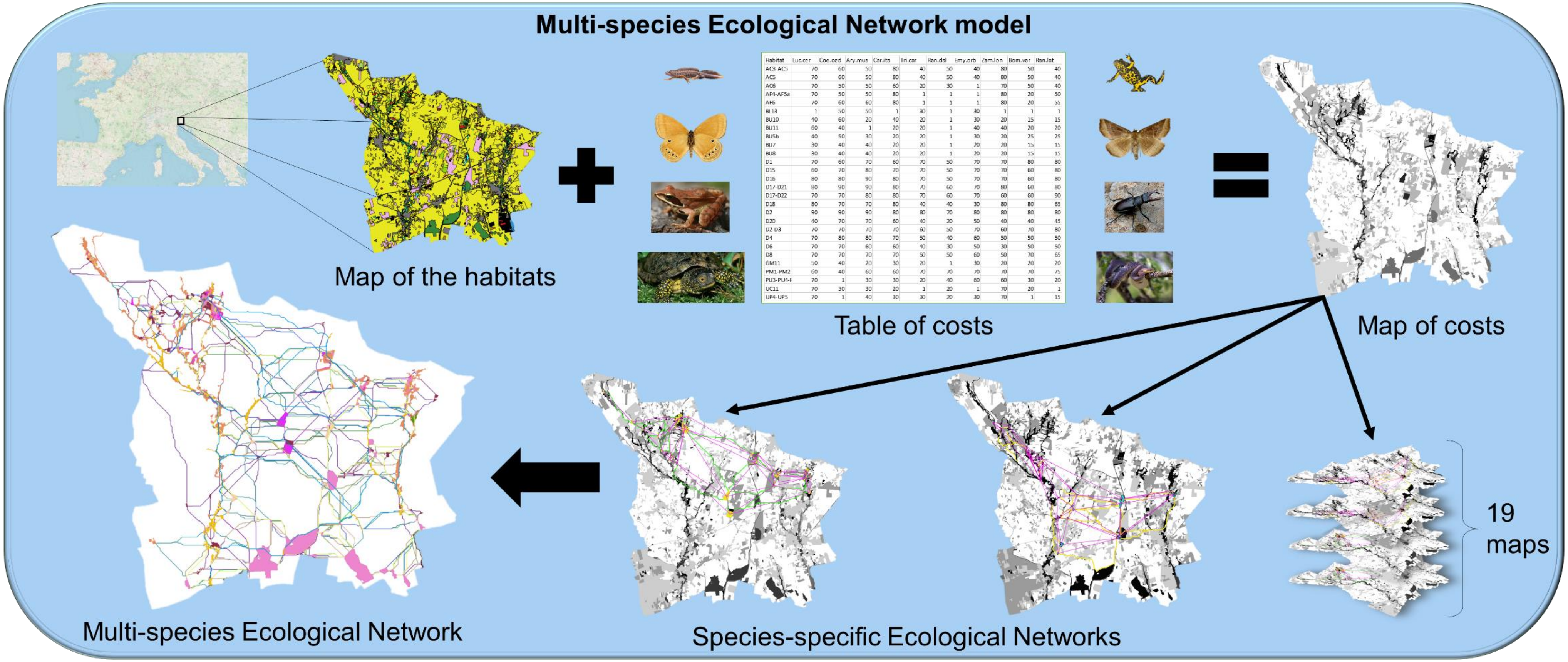
Ecological network model: the study case

The studied EN is located in the lowlands of the Friuli Venezia Giulia region (NE Italy; centroid coordinates: 45°48'13.4"N - 13°08'11.0"E), within an area that covers almost 300 km^2, including a large agricultural area embedded in two river systems (Stella and Corno, respectively). The landscape is characterized by a mixed mosaic of intensively and extensively cultivated areas, settlements, semi-natural (hedgerows and watercourses) and natural habitats (woodlands, shrubs, meadows and fens). The area includes eight Natura 2000 Special Area of Conservation (Habitats Directive 92/43/EEC) and nine regional protected sites (biotopes), mainly connecting remnants of wetland habitats and lowland forests.

The EN was designed using a habitat-species based model (considering flora and fauna, Figure 1.1) developed at the local scale in the context of the regional landscape planning project (Sigura et al. 2017). The model was based on least-cost path analysis and graph theory, which were used to obtain species-specific ENs that were later merged into the final composite multi-species network (Figure 1.1). The EN was originally modeled using the regional habitat map based on the habitat classification proposed by Poldini et al. (2006) and crossing costs for species were attributed by expert assessment and literature review data.

The nodes (target habitats), corridors and steppingstones (links between target habitats) were obtained for a set of 10 target animal species and 9 plant communities (assumed to be crucial for several plant species of conservation concern) to proxy favorable conditions for the overall network biodiversity. The animal species considered were: *Arytrura musculus*, *Bombina variegata*, *Carabus italicus*, *Coenonympha oedippus*, *Emys orbicularis*, *Lucanus cervus*, *Rana dalmatina*, *Rana latastei*, *Triturus carnifex*, and *Zamenis longissimus*. While the plant communities were: Alkaline fens dominated by *Schoenus nigricans* (*Caricion davallianae*), Alluvial forests with *Alnus glutinosa* and *Fraxinus excelsior* (*Alnion glutinosae*), Calcareous fens with *Cladium mariscus* (*Magnocaricion elatae*), Illyrian *Quercus-Carpinus betulus* forests (*Erythronio-Carpinion*), Low altitude mowing meadows (*Arrhenatherion elatioris*), *Molinia* meadows on calcareous, peaty or clayey-silt-laden soils (*Molinion caerulae*), Southeast European *Fraxinus-Quercus-Alnus* forests (*Alno-Quercion roboris*), Sub-Mediterranean arid meadows (*Scorzonerion villosae*), and Tunnel forests of *Salix alba* and *Populus albae* (*Salicion albae*).

The EN is composed of 108 nodes and 17 different habitats (14 terrestrial and 3 aquatic), corresponding to a total extent of 5900 ha, of which 1700 ha represent nodes and 4200 ha ecological corridors.



Habitat	Luc.cer	Coe.oed	Ary.mus	Car.ita	Tri.car	Ran.dal	Emy.orb	Zam.lon	Bom.var	Ran.lat
AC3-AC5	70	60	50	80	40	50	40	80	50	40
AC5	70	60	50	80	40	50	40	80	50	40
AC6	70	50	50	60	20	30	1	70	50	40
AF4-AF5a	70	50	50	80	1	1	1	80	20	50
AF6	70	60	60	80	1	1	1	80	20	55
BL13	1	50	50	1	30	1	30	1	1	1
BU10	40	60	20	40	20	1	30	20	15	15
BU11	60	40	1	20	20	1	40	40	20	20
BU5b	40	50	30	20	20	1	30	20	25	25
BU7	30	40	40	20	20	1	20	20	15	15
BU8	30	40	40	20	20	1	20	20	15	15
D1	70	60	70	60	70	50	70	70	80	80
D15	60	70	80	70	70	50	70	70	60	80
D16	80	80	90	80	70	50	70	70	60	80
D17-D21	80	90	90	80	70	60	70	80	60	80
D17-D22	70	70	80	80	70	60	70	60	60	90
D18	80	70	70	80	40	40	30	80	80	65
D2	90	90	90	80	80	70	80	80	80	80
D20	40	70	70	60	40	20	50	40	40	45
D2-D3	70	70	70	70	60	50	70	60	70	80
D4	70	80	80	70	50	40	60	50	50	50
D6	70	70	60	60	40	30	50	30	50	50
D8	70	70	70	70	50	50	60	50	70	65
GM11	50	40	20	30	20	1	30	20	20	20
PM1-PM2	60	40	60	60	70	70	70	70	70	75
PU3-PU4-	70	1	30	30	20	40	60	60	30	20
UC11	70	30	30	20	1	20	1	70	20	1
UP4-UP5	70	1	40	30	30	20	30	70	1	15

Figure 1.1: Flow chart of the main steps applied to model the multi-species Ecological Network: starting from a map of the habitats of the study area and combining it with a table of costs (time and effort to travel through an environment) it was obtained a map of costs for all 10 animal species and 9 plant communities (habitats) present in the landscape. From the overlay of all species-specific networks the multi-species ecological network was obtained as the sum of all identified elements.

Specific aims

The major aim of this Thesis is to provide an insight for testing and monitoring diversity and the factors that influence it in the habitats and nodes of an EN.

Specifically, in Chapter 1, I aimed at providing a methodological framework to support biodiversity data collection planning, estimating how many replicates are sufficient to represent plant diversity. Specifically, the addressed aims were:

a) to distinguish and maintain the typification among different habitats;
b) to gather data on species diversity and heterogeneity within the whole EN.

The second objective (Chapter 2) was to analyze plant diversity patterns within the EN investigating the effects of landscape structure and connectivity on plant communities at two scales. Specifically, the following specific aims were addressed:

a) investigate the effects of landscape structure and connectivity in different habitats on α diversity at the habitat scale;
b) examine the effects of landscape structure and connectivity in different habitats on β diversity at the habitat scale;
c) explore the effects of landscape structure and connectivity on α diversity at the node scale;
d) inspect the effects of landscape structure and connectivity on β diversity at the node scale.

The last goal (Chapter 3) was to investigate the potential of remote sensing for quantitative analyzing the biodiversity content of the EN and the study area. To do so, starting from the vegetation collected in the EN, two R packages were tested to analyze the relationships between spectral and observed (taxonomic) diversity. Specifically, I tested whether:

a) spectral diversity, considered as α and β diversity, can be compared with α and β taxonomic diversity and with what degree of relationship;

b) spectral heterogeneity (in pixel reflectance variation) is related to ecosystem, landscape heterogeneity and plant diversity in a complex landscape, where natural and anthropogenic elements interact;

c) spectral data can be used to assess and/or monitor plant diversity and its dynamics in an Ecological Network (EN) or more generally in natural environments over time.

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Chapter 1

Determining plant diversity within interconnected natural habitat remnants (ecological network) in an agricultural landscape: a matter of sampling design?

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ABSTRACT

In intensively used and human-modified landscapes, biodiversity is often confined to remnants of natural habitats. Thus, identifying ecological networks (ENs) necessary to connect these patches and maintain high levels of biodiversity, not only for conservation but also for the effective management of the landscape, is required. However, ENs are often defined without a clear a-priori evaluation of their biodiversity and are seldom even monitored after their establishment. The objective of this study was to determine the adequate number of replicates to effectively characterize biodiversity content of natural habitats within the nodes of an EN in north-eastern Italy, based on vascular plant diversity. Plant communities within habitats of the EN's nodes were sampled through a hierarchical sampling design, evaluating both species richness and compositional dissimilarity. We developed an integrated method, consisting of multivariate measures of precision (*MultSE*), rarefaction curves and diversity partitioning approaches, which was applied to estimate the minimum number of replicates needed to characterize plant communities within the EN, evaluating also how the proposed optimization in sampling size affected the estimations of the characteristics of habitats and nodes of the EN. We observed that reducing the total sampled replicates by 85.5% resulted to sufficiently characterize plant diversity of the whole EN, and by 72.5% to exhaustively distinguish plant communities among habitats. This integrated method helped to fill the gap regarding the data collection to monitor biodiversity content within existing ENs, considering temporal and economic resources. We therefore suggest the use of this quantitative approach, based on probabilistic sampling, to conduct pilot studies in the context of ENs design and monitoring, and in general for habitat monitoring.

Keywords: α diversity, β diversity, multivariate pseudo-standard error, plant biodiversity, protected areas, sampling optimization

Abbreviation: EN ecological network; ENRS ecological network resampled subset; HRS habitats resampled subset; PA protected area; RC rarefaction curve; SER spatial explicit rarefaction curve

INTRODUCTION

Biodiversity loss is one of the main concerns in the Anthropocene, happening at a faster rate than ever, driven by many factors such as land use change, habitat fragmentation, pollution, natural resources exploitation, climate change, biological invasion, and many other (Landi et al. 2018; IPBES 2019; EEA 2020). Although protected areas (hereafter PAs) were designed to face these problems through conservation actions focused on endangered target habitats and species, it is now clear that biodiversity protection should rely on a more efficient management of the anthropogenic surrounding landscapes and no longer be confined only to PAs (UN 2015a, 2015b; European Commission 2020). Urgent actions to mitigate habitat loss and fragmentation are needed. These actions must be achieved through a management approach that coherently consider all the landscape components, integrating also information about functional traits of species and landscape structures through connectivity models (Cushman et al. 2013). In this context, the Ecological Network (hereafter EN) was established as a useful tool to provide an integrated protection of biodiversity also considering biotic interactions among species in an ecosystem (Pascual and Dunne 2006). ENs were described and used as tools for conservation planning that rely on the concept of ecological connectivity between the more natural portions of a landscape (so called "nodes" of the EN), with the final aim to limit the effects of fragmentation of habitat patches (Fahrig 2003; Battisti 2004; Biondi and Nanni 2005; Rosati et al. 2010). ENs were thought as a patch matrix model (Forman 1995), a vision of landscape in which discrete homogeneous habitat patches, surrounded by a more or less inhospitable matrix, are connected in a network structure to support ecological connectivity at landscape scale (Foltete 2019). Research concerning ENs have developed different approaches directed to assess both the structural connectivity, that is a property of the landscape and concerns the spatial pattern of habitat patches and is independent on the ecological characteristics of the species (Tischendorf and Fahrig 2000; Taylor et al. 2006), and the functional connectivity, defined as the behavioral movement response of organisms towards habitat patches (Taylor et al. 1993; LaPoint et al. 2015). In this respect, many analytical tools were developed in recent decades such as least-cost modeling, circuit theory, graph-theoretic methods, aiming at design connectivity models (Foltete 2019).

The concept of EN is increasingly accepted as an operational tool for protecting biodiversity, improving ecological connectivity and sustainable development of landscapes (Damschen 2013; De montis et al. 2016; Keeley et al. 2018; Xu et al. 2019). Several studies have focused on the application of ENs, both from the theoretical and practical point of view, highlighting the complex interaction between structural and functional features of ENs, and the need for further research on the effects of their planning and implementation (Battisti 2013; Boitani et al. 2015; Gippolitti and Battisti 2017; Foltete 2019). In particular, the definition of the EN follows often an approach oriented only to the structure of the network, while there is a lack of standards in EN projects (e.g., no clear objectives, no monitoring activities) to make them a suitable tool for biodiversity conservation (Kareksela et al. 2013; Gippoliti and Battisti 2017; Jalkanen et al. 2020). Thus, it is essential to assess the spatial distribution of the habitats within the EN and to quantify their biodiversity content as they may be potentially altered due to anthropic activities of the surrounding matrix, or even by application of an improper management of the nodes (Brooks et al. 2002; Wiegand et al. 2005; Thiele et al. 2018). Moreover, the identification of the habitats suitable for a species should consider the plant communities that are fundamental to habitat definition adopted also in modern European habitat classifications (Devillers et al. 1991; Devillers and Devillers-Terschuren 1996; Davies et al. 2004; European Commission 2013). The term "habitat" has been used in various contexts with different meanings. In the context of EN, we refer to habitat as an assemblage of animals and plants, together with their abiotic environment, that contribute as patches of the network. Plant communities also have a key role in primary productivity, capturing that portion of solar energy that can support the life of all components of the biosphere, as well as in regulation of the nutrients' cycle and in soil protection (Lieth 1973) and stand for a large part of biodiversity of landscapes.

In this light, a robust and replicable method to detect the biological and structural characteristics of plant communities, within the ENs is needed. It should also aim at monitoring the distribution and biodiversity content of the habitats. A robust methodological approach which is based on probabilistic sampling of plant communities is fundamental to estimate how suitable a sample is for seizing the species diversity and relative abundance, avoiding bias (Cao et al. 2002). The adequacy of sampling methods able to reliably characterize ecological communities within a habitat have long been debated in literature (e.g., Yoccoz et al. 2001; Balmford et al. 2003; Del Vecchio et al. 2019, Maccherini et al. 2020). One recently introduced approach which proved to be useful consists of evaluating multivariate differences in the composition of plant communities (Anderson and Santana-Garcon 2015), using a measure of precision based on dissimilarity matrices called pseudo multivariate dissimilarity-based standard error (*MultSE*), which allows for determination of sample-size adequacy within communities. The *MultSE* is the multivariate analog of the standard error and measures the variability in the position of the centroid in the space of a chosen dissimilarity measure under repeated sampling for a given sample size (Anderson and Santana-Garcon 2015). This measure of multivariate precision was recently used in the context of European habitats monitoring for costal sand dunes by Maccherini et al. (2020), and it can represent a valid approach to estimating the optimal sample-size required to adequately characterize plant communities within habitats.

In this study, we provide an integrated method to determine the adequate number of replicates to effectively characterize biodiversity within habitats (considered as EUNIS habitat types; Davies et al. 2004) and nodes in an EN whose main novelty relies on the combination of i) *MultSE*, ii) rarefaction curves, and iii) diversity partitioning approaches. Our main contribution is to provide a methodological framework for practitioners to support biodiversity data collection planning, in the EN design process or in the monitoring of existing ENs and PAs, as requested by European Biodiversity Strategy for 2030 (European Commission 2020).

In an EN, modeled in the context of the regional landscape planning process at the regional level, we sampled 193 vegetation plots in 14 habitats contained within 74 nodes, aiming at estimating how many replicates are sufficient a) to distinguish and maintain the typification among different habitats and b) to gather data on species diversity and heterogeneity within the whole EN. We tested our framework on an EN in Friuli Venezia Giulia region (north-eastern Italy), which was developed in the context of the regional landscape planning project (Sigura et al. 2017). The sampled EN is composed of numerous PAs and biotopes, as well as several patches of semi-natural and natural habitats in an agricultural landscape matrix. These habitats, forming the nodes of the EN, consist mainly of wetlands, linked to the presence of rivers and fens, which are well-known for their ecological role and for the high levels of biodiversity (Liccari et al. 2020). These environments are usually underrepresented in EN studies and the few studies concerning wetlands tend to give more weight to animal diversity instead of plant diversity (Foltete et al. 2020).

METHODS

Study area and EN model

This study was carried out in a local EN in the Friulian lowland (Friuli Venezia Giulia region, NE Italy; centroid coordinates: 45°48’13.4” N – 13°08’11.0” E; Figure 2.1).

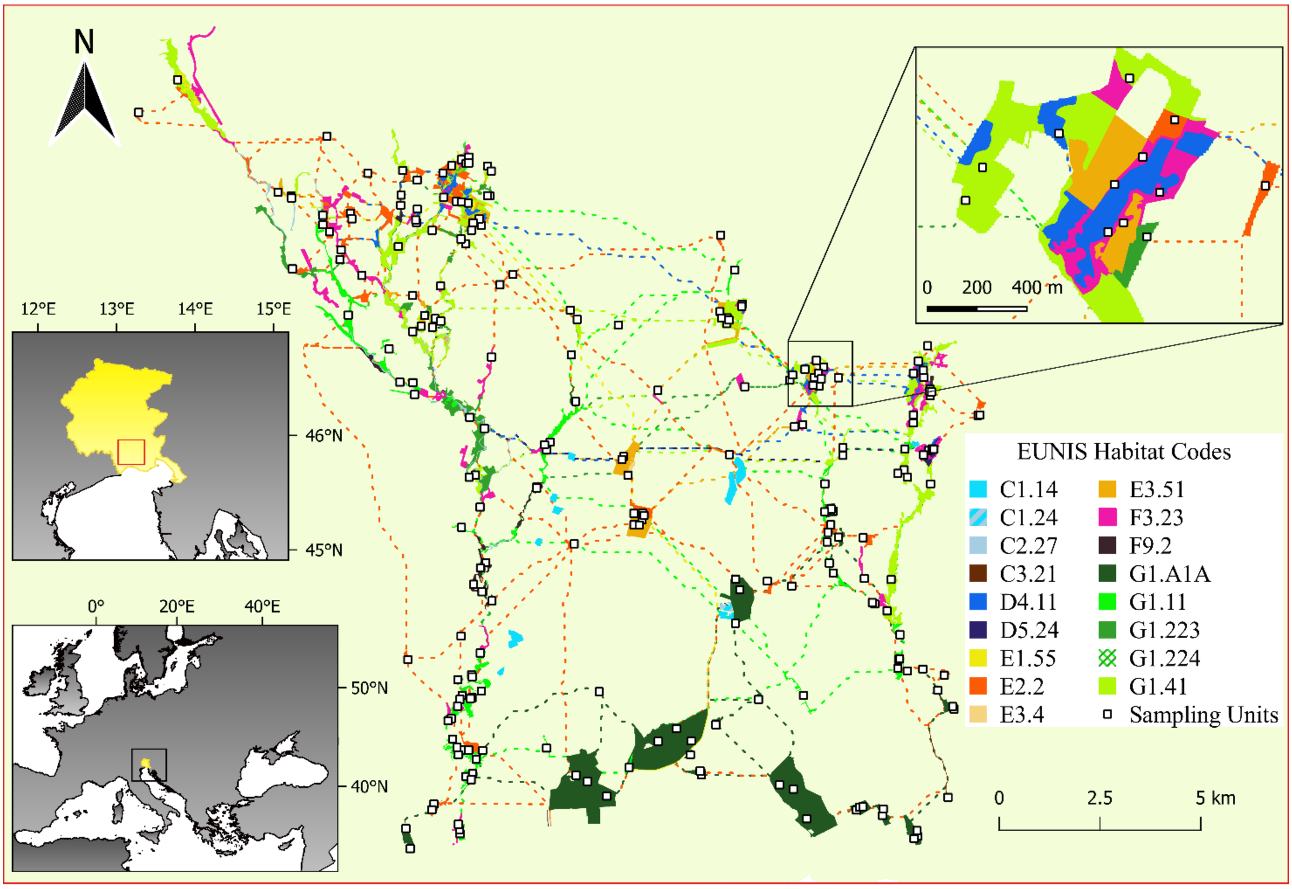

Figure 2.1: Study area location (Friuli Venezia Giulia region is represented in yellow) and ecological network representation (all the nodes of the EN are shown, including aquatic and smaller than 1 ha nodes). EUNIS Habitat Codes are as follows: C1.14 Charophyte submerged carpets in oligotrophic water bodies; C1.24 Rooted floating vegetation of mesotrophic water bodies; C2.27 Mesotrophic vegetation of fast flowing streams; C3.21 *Phragmites australis* beds; D4.11 *Schoenus nigricans* fens; D5.24 Fen *Cladium mariscus* beds; E1.55 Eastern sub-Mediterranean dry grassland; E2.2 Low and medium altitude hay meadows; E3.4 Moist or wet eutrophic and mesotrophic grassland; E3.51 *Molinia caerulea* meadows and related communities; F3.23 Tyrrhenian sub-Mediterranean deciduous thickets; F9.2 *Salix* carr and fen scrub; G1.A1A Illyrian *Quercus-Carpinus betulus* forests; G1.11 Riverine *Salix* woodland; G1.223 Southeast European *Fraxinus-Quercus-Alnus* forests; G1.224 Po *Quercus-Fraxinus-Alnus* forests; G1.41 *Alnus* swamp woods not on acid peat. Colored lines and patches are corridors and nodes of the network, representing different habitat types and species-specific networks. An example of the hierarchical sampling design in which each node was sampled stratified by habitat proportionally to habitat extent within the node is showed.

The study area has an extent of 298 km^2 and is included in an agricultural context bounded by two river systems (Stella and Corno rivers, respectively). The landscape is characterized by a mixed mosaic of intensively and extensively cultivated areas, settlements, semi-natural (hedgerows and watercourses) and natural habitats (woodlands, shrubs, meadows and fens), including eight Natura 2000 Special Area of Conservation (Habitats Directive 92/43/EEC) and nine regional protected sites (biotopes), connecting mainly wetland habitats.

The geology of the area is mainly composed of Quaternary sand sediments, silt sediments and silt-clay sediments generated by glacial fluvial transport during Pleistocene and by alluvial deposit during Holocene. The area is characterized by an average annual temperature of ca. 13°C and an average annual rainfall between 1100 and 1400 mm.

In this intensively cultivated landscape, connectivity was mapped on a habitat-species based model (flora and fauna), developed at the local scale in the context of the regional landscape planning process (Sigura et al. 2017). The model is based on least-cost path analysis and graph theory used to obtain species-specific ENs which were later merged into the final composite multi-species network, where the nodes (natural habitats), corridors and stepping stones (links between natural habitats) were obtained for a set of 19 target species (10 animal species and 9 plant communities, assumed to be crucial for several plant species of conservation concern) to capture favorable conditions for biodiversity. Specifically, the EN was originally modeled from the habitat map of the region (ISPRA 2017), using the habitat classification proposed by Poldini et al. (2006) (see Table 2.1), and crossing costs for species were attributed by expert assessment and literature review data. However, for a more comparable interpretation and replicability of this study, the adopted habitat classification was converted according to the European Nature Information System (EUNIS, Davies et al. 2004) classification which has a one-to-one correspondence with the previous classification (Table 2.1). The term habitat is here understood as an assemblage of plants together with their abiotic environment. The EN is composed of 108 nodes and 17 different habitats, for a total extent of 5900 ha of which 1700 ha represent nodes and 4200 ha ecological corridors.

Table 2.1: Habitat codes of the area according to Poldini et al. (2006) and correspondence with EU and EUNIS habitat classification along with descriptive statistics of the study area (i.e., area, number of patches, number of plots and average richness). Asterisk (*) in EU habitat codes denotes priority habitats according to Habitats Directive. Plus (+) before EUNIS habitat codes denotes habitats that were updated after the sampling (see main text).

Habitat FVG (Poldini et al. 2006)	**EU Habitat (Directive 92/43/EEC)**	**EUNIS Habitat**	**Area (ha)**	**N. Patches**	**N. Plots**	**Average richness (± SD)**
AC6	3260 - Water courses of plain to montane levels with the *Ranunculion fluitantis* and *Callitricho-Batrachion* vegetation	C2.27 - Mesotrophic vegetation of fast flowing streams	48.6	7	Not sampled	Not sampled
AF5	3140 - Hard oligo-mesotrophic waters with benthic vegetation of *Chara* spp.	C1.14 - Charophyte submerged carpets in oligotrophic water bodies	59.3	10	Not sampled	Not sampled
AF6	/	C1.24 - Rooted floating vegetation of mesotrophic water bodies	5.0	1	Not sampled	Not sampled
BL13	91L0 - Illyrian oak-hornbeam forests (*Erythronio-Carpinion*)	G1.A1A - Illyrian *Quercus* - *Carpinus betulus* forests	599.4	17	34	23.3 ± 5.7
BU10	91E0* - Alluvial forests with *Alnus glutinosa* and *Fraxinus excelsior* (*Alno-Padion*, *Alnion incanae*, *Salicion albae*)	G1.41 - *Alnus* swamp woods not on acid peat	410.5	43	28	23.3 ± 5.0
BU11	/	F9.2 - *Salix* carr and fen scrub	45.8	8	12	25.0 ± 5.2
BU5	92A0 - *Salix alba* and *Populus alba* galleries	G1.11 - Riverine *Salix* woodland	186.4	31	39	23.6 ± 6.9
BU7	91F0 - Riparian mixed forests of *Quercus robur*, *Ulmus laevis* and *Ulmus minor*, *Fraxinus excelsior* or *Fraxinus angustifolia*, along the great rivers (*Ulmenion minoris*)	G1.223 - Southeast European *Fraxinus* - *Quercus* - *Alnus* forests	112.4	20	8	25.9 ± 4.8
BU8	91F0 - Riparian mixed forests of *Quercus robur*, *Ulmus laevis* and	G1.224 - Po *Quercus* - *Fraxinus* - *Alnus* forests	1.9	1	1	18

	Ulmus minor, *Fraxinus excelsior* or *Fraxinus angustifolia*, along the great rivers (*Ulmenion minoris*)					
GM11	/	F3.23 - Tyrrhenian sub-Mediterranean deciduous thickets	153.1	41	27	22.5 ± 4.7
PC8	62A0 - Eastern sub-Mediterranean dry grasslands (*Scorzoneretalia villosae*)	+ E1.55 - Eastern sub-Mediterranean dry grassland	2.9	1	1	35
PM1PM2	6510 - Lowland hay meadows (*Alopecurus pratensis*, *Sanguisorba officinalis*)	E2.2 - Low and medium altitude hay meadows	127.2	37	19	29.7 ± 5.8
PU1	6430 - Hydrophilous tall herb fringe communities of plains and of the montane to alpine levels	+ E3.4 - Moist or wet eutrophic and mesotrophic grassland	4.1	1	2	12 ± 14.1
PU3	6410 - *Molinia* meadows on calcareous, peaty or clayey-siltladen soils (*Molinion caeruleae*)	E3.51 - *Molinia caerulea* meadows and related communities	71.7	20	7	33.9 ± 8.5
UC1	/	+ C3.21 - *Phragmites australis* beds	3.7	1	1	21
UC11	7210* - Calcareous fens with *Cladium mariscus* and species of the *Caricion davallianae*	D5.24 - Fen *Cladium mariscus* beds	9.9	2	3	14.3 ± 4.2
UP4UP5	7230 - Alkaline fens	D4.11 - *Schoenus nigricans* fens	75.5	28	10	14.9 ± 6.2

Sampling design and data collection within the EN

Among the nodes, we selected and sampled all the nodes larger than 1 ha. Purely aquatic habitats (i.e., C1.14, C1.24, C2.27, EUNIS codes; see Table 2.1) within the nodes were not sampled, since they require completely different assumptions for connectivity than terrestrial ones. Ecological corridors were not sampled. Thus, the final dataset relies on 74 nodes and 14 habitats. The adopted sampling design was hierarchical (Figure 2.1), where each habitat type was sampled within each node (that could contain more than one habitat), proportionally to habitat extent within the node. The sampling density with respect to the habitat extent was chosen as follows: a squared plot of 100 m^2 was randomly placed for a habitat area < 5 ha, 2 plots for an area ≥ 5 and ≤ 10 ha and, finally, 3 plots for an area > 10 ha. In total, 193 plots were randomly selected within the EN corresponding to an overall sampling density of 0.11 plot/ha. Occurrence and abundance (% visual cover estimation) of vascular plant species were recorded within each plot. Nomenclature and taxonomy of species followed Bartolucci et al. (2018) for native species and Galasso et al. (2018) for alien species. Data were collected during spring and summer 2019.

Data Analysis

Habitats and nodes within the EN were analyzed in terms of species richness (alpha diversity) and compositional dissimilarity as a measure of species complementarity among sampling units (*sensu* Whittaker 1972 defined as beta diversity). The latter was analyzed using the Bray–Curtis (BC) dissimilarity index (Bray and Curtis 1957). This index is defined as the sum over the whole species of the ratio between the difference of abundance values and the sum of abundance values for each species, and it represents the vegetation plots pairwise differences using quantitative species abundance data. The BC dissimilarity index ranges between 0, when two plots share the same elements, to 1, when the two sampling units are totally different. First, we performed a preliminary analysis to evaluate statistical differences in species richness among habitats and nodes using ANOVA test followed by Tukey post-hoc test (using the “`multcomp`” R package, Hothorn et al. 2008) when significant. These differences represented our baseline diversity values characterizing the EN in terms of biodiversity and its variability among habitats/nodes, given the maximum sampling effort available. Then, we characterized diversity patterns through sample-based rarefaction curves (RCs) using exact method and spatially explicit rarefaction curves (SERs, Chiarucci et al. 2009; Bacaro et al. 2012, 2016), using the function available in “`rarefy`” package (Thouverai et al. 2020) and in “`vegan`” R package (Oksanen et al. 2019). We compared first the habitat-based curve and node-based curve to the rarefaction curve for the whole dataset (both RC and SER) and then the curves for each habitat (RCs and SERs) to the whole dataset curve (both RC and SER). Finally, we compared RC for each node with respect to the whole dataset RC. The difference between RC and SER somehow expresses the amount of spatial autocorrelation among sampling units, based on the spatial structure of the collected data and already proved to be effective in different habitats (Bacaro et al. 2016; Tordoni et al. 2018).

Species richness patterns across different spatial scales (plot, habitat/node, whole EN) were also evaluated by means of additive partitioning techniques (Lande 1996; Crist et al. 2003) using the "adipart" function in the "`vegan`" R package (Oksanen at al. 2019) and their significance was tested using a null model that permutes the original data matrix 999 times to assess deviation from random expectations.

Pseudo multivariate dissimilarity-based standard error (*MultSE*) was computed following the method described by Anderson and Santana-Garcon (2015), and using the code and functions provided therein. *MultSE* (Equation 1 and 2) is based on the chosen dissimilarity measure, thus providing a powerful tool to examine the relative precision of a sampling procedure. It is calculated as follows:

$$MultSE = \sqrt{V/n} \tag{1}$$

where *V* is a multivariate measure of pseudo variance in the space of the chosen dissimilarity measure:

$$V = \frac{1}{(n-1)} \sum_{i=1}^{(n-1)} \sum_{j=(i+1)}^{n} \frac{d_{ij}^2}{n} \tag{2}$$

where *n* is the number of sampling units and *d* represents the squared distance between individual sampling points to their centroid, given a chosen dissimilarity measure.

To calculate *MultSE*, we first downweighted the abundance of the plant community matrix using a log (x + 1) transformation and then we computed the BC dissimilarity. This was computed both for habitats and habitats aggregated within nodes, and then for the whole dataset. A double resampling scheme was used to generate means for each sample size and 95% confidence intervals; in particular the first was obtained from 10,000 permutations and the latter from 10,000 bias-adjusted bootstrap resamples. When the profile of *MultSE* in relation to the increasing sampling size reaches an asymptote, we can consider that sample size as an adequate number of replicates beyond which only small fluctuations of sampling precision can be observed. The point where the slope of *MultSE* profile changes, was estimated using R package “`segmented`” (Muggeo 2003; Muggeo 2008). These were calculated only for the habitats and for the whole dataset. The number of plots for each node profile was often not large enough to estimate breaking points.

To verify if and how the proposed reduction in sampling size affects diversity, we reduced the whole dataset adopting resampling strategies as suggested by the results of *MultSE*. In particular, the complete dataset was resampled both randomly and stratified by habitats. The plots were resampled from the whole dataset, using the number of plots derived from *MultSE* estimation for the habitats (999 random resamples) and for the whole EN (999 random resamples). These subsets of plots were then tested to investigate if there were significant differences in species richness between habitats (only for habitats resampling). Species diversity patterns across different scales (plot/habitat/whole EN and plot/node/whole EN) were evaluated both for the habitats resampled subset (HRS) and for the whole EN resampled subset (ENRS). Finally, the resulting statistics were compared with those of the original dataset to determine the effect in sampling reduction in the ability to discriminate among habitats and EN nodes.

RESULTS

Overall, 74 nodes of the EN were sampled, of which 56 were formed by a singular habitat and 18 by multiple habitats. The most common habitats within the nodes were G1.11 Riverine *Salix* woodland (present within 26 nodes, see Table 2.1 for more details on habitats), F3.23 Tyrrhenian sub-Mediterranean deciduous thickets (19), G1.A1A Illyrian *Quercus*-*Carpinus betulus* forests (17), G1.41 *Alnus* swamp woods not on acid peat (14), E2.2 Low and medium altitude hay meadows (13), while the less common were F9.2 *Salix* carr and fen scrub (7), D4.11 *Schoenus nigricans* fens, E3.51 *Molinia caerulea* meadows and related communities, G1.223 Southeast European *Fraxinus-Quercus-Alnus* forests (5), D5.24 Fen *Cladium mariscus* beds (2), other habitats were present only within a singular node. Most of these habitats (11) were attributable to wetland habitats and were present in 78% of the nodes, occupying 84% of the total extent of the EN's nodes.

A total of 399 plant species were sampled in the EN, of which 42 were aliens and 20 were protected, rare or endemic species according to European, Italian, or Regional red lists. The most frequent native species were *Rubus caesius* (occurring in 126 plots), *Rubus ulmifolius* (118), *Quercus robur* (107), *Hedera helix* (106), *Cornus sanguinea* (104) and *Salix alba* (94). Concerning alien species, the most frequent were *Platanus hispanica* (61), *Robinia pseudoacacia* (33) and *Potentilla indica* (28). Finally, the most frequent protected species were *Ruscus aculeatus* (Habitat Directive 92/43/CEE Annex V, 18 occurrences) and *Neottia ovata* (CITES and (CE) N. 407/2009 Annex B, 8 occurrences).

The sampling activity, that aimed at verifying the biodiversity content of the EN, helped also to verify the correspondence between cartography and ground-data. Moreover, it permitted us to update the habitat attribution to a precise habitat type thanks to a greater level of detail and considering natural dynamism among plant communities (e.g., see Table 2.1 habitats distinguished by the symbol +).

Concerning species richness calculated at the habitat level (Figure 2.2), the higher values were in meadows (31.3 ± 8.8 species), the lowest ones in fens (14.9 ± 5.3 species), while intermediate values were observed in shrublands and forests (23.3 ± 5.8 species). Species richness was significantly different among these 3 groups, but not within the groups. Conversely, no significant differences emerged for species richness between EN nodes.

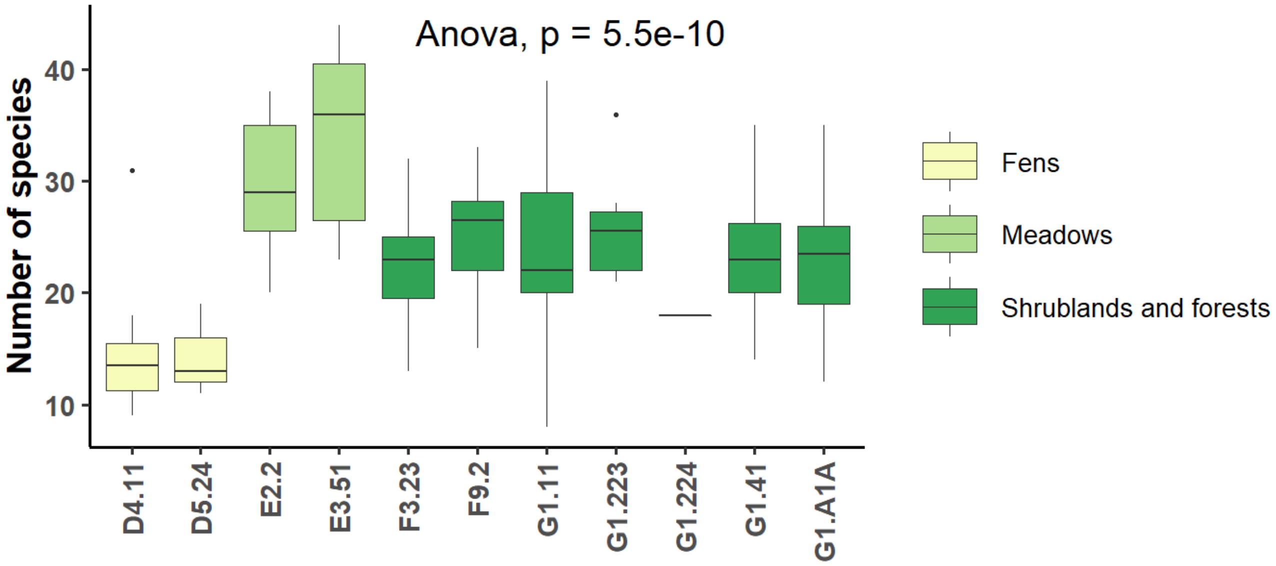

Figure 2.2: Species richness in habitats and ANOVA resulting p-value. The color scale identifies the 3 groups with significant differences resulting from ANOVA post-hoc analysis ($\alpha < 0.05$): fens (light yellow), meadows (light green) and shrublands and forests (green).

Rarefaction curves (RCs, Figure 2.3) calculated from the whole dataset confirmed that spatially explicit rarefaction curve (SER) accumulated a lower number of species than RC and revealed that the habitat-based RC accumulated species less rapidly than the node-based RC and SER. RCs for habitats (Figure S2.1) showed that none of the curves reached a plateau. A similar trend was observed also in the RCs for nodes (Figure S2.2).

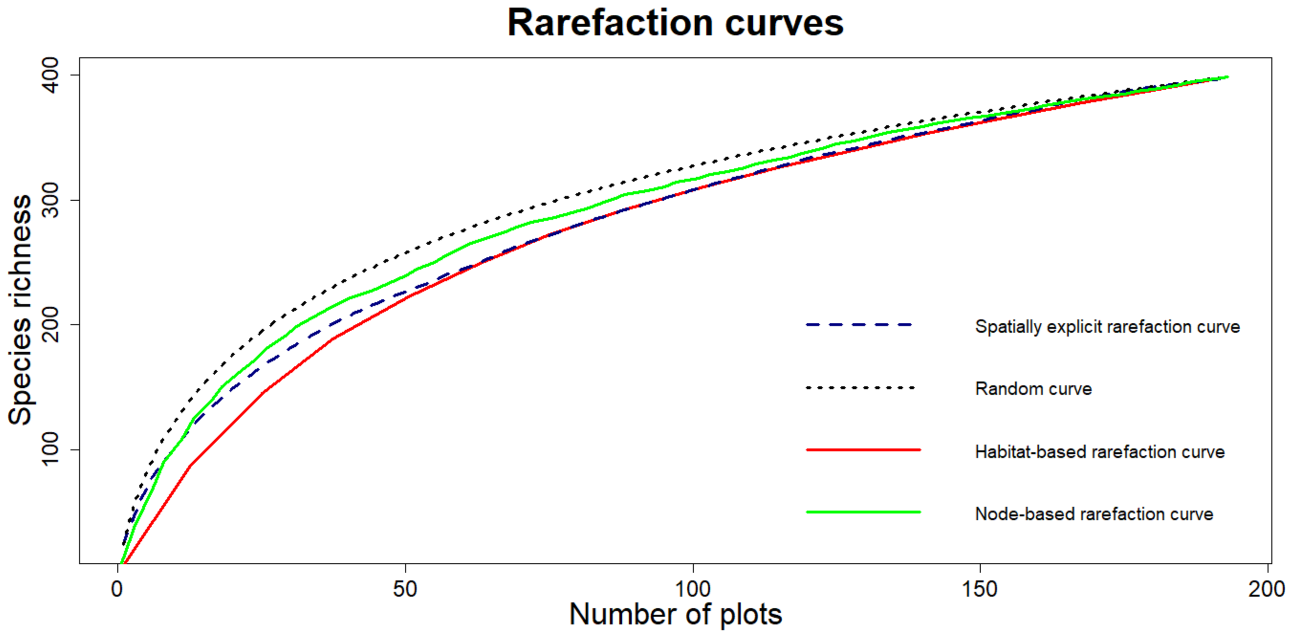

Figure 2.3: Spatially explicit rarefaction curve (SER, blue dashed line), traditional rarefaction curve (RC, black dotted line), habitat-based rarefaction curve (red solid line) and node-based rarefaction curve (green solid line) calculated from the whole dataset.

Additive partitioning (Figure 2.4) for habitats showed how within habitats diversity (i.e., the average inventory diversity) accounted for 15.61% of the total EN diversity and it was lower than between habitats diversity (78.43% of total diversity). For nodes, this pattern was even more evident, with a diversity within nodes (3.84% of total diversity) lower than between them (90.2% of total EN diversity).

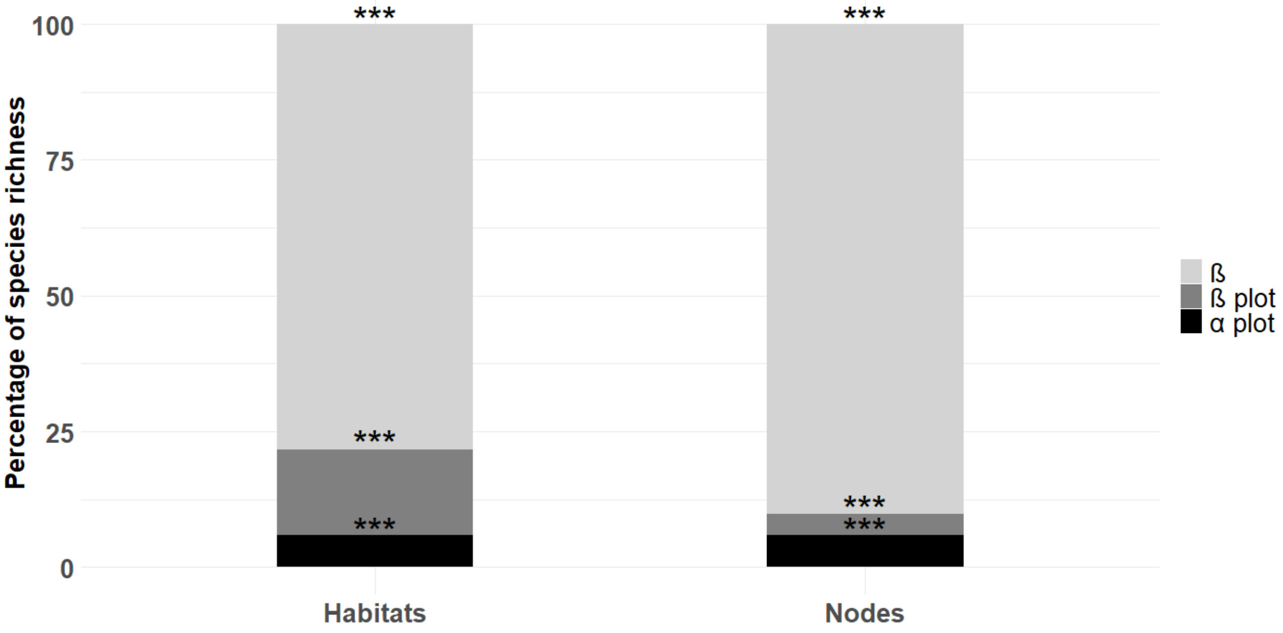

Figure 2.4: Additive partitioning of diversity across different scales: within each plot (α plot), within each habitat or node (β plot) and between habitats or nodes (β). Asterisks indicate a significant difference from random expectations resulting from a null model (*** p < 0.001).

MultSE profiles in relation to sample size for each habitat within the EN (Figure 2.5) flattened out between 7 and 10 plots depending on habitat type, a similar trend was observed also in the *MultSE* profiles of the nodes (Figure S2.3). The *MultSE* profile for the whole dataset (Figure S2.4) flattened out at around 25 plots.

Based on habitats' *MultSE* profiles, the minimum number of replicates needed to characterize the main features of each habitat was reported in Table S2.1, while the minimum number of replicates needed for the whole EN was 27.77 ± 1.77 (mean ± SD) according to the point where the slope of *MultSE* profile changed.

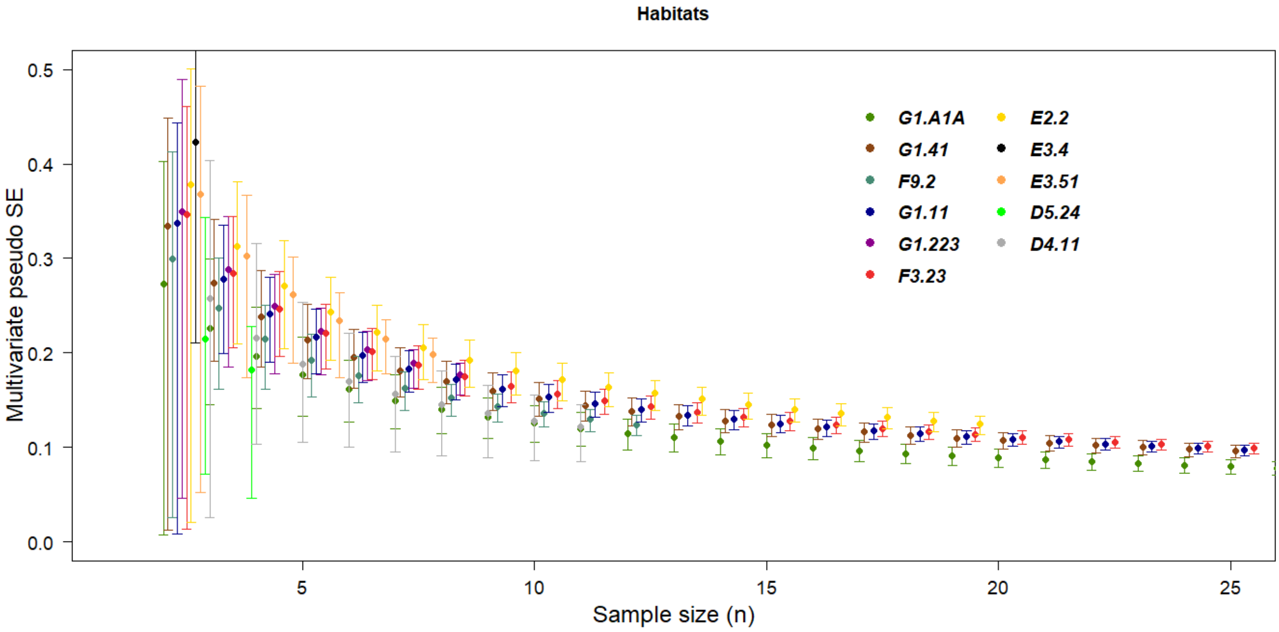

Figure 2.5: *MultSE* profile based on Bray–Curtis dissimilarity for each habitat within the ecological network. The white space on the left is due to a *MultSE* higher than 0.5 in the first plots.

In addition, our results proved to be robust when reducing the size of the dataset to the ones suggested by the previous analysis (i.e., 53 plots for HRS, 28 for ENRS) detecting similar patterns in terms of species richness and additive partitioning of diversity (Table 2.2, Table 2.3).

Table 2.2: Summary statistics of additive partitioning results showing the differences in species richness (α) at plot and habitat/node level vs. dissimilarity (β) at plot and network level derived from 999 stratified resampling of the original dataset based on the plot numbers given by the decay of habitats *MultSE* and from 999 random resampling of the original dataset based on the plot numbers given by the decay of whole EN *MultSE*.

Term	Distribution of values	α plot	Rate of Significance (% of permutations with $p < 0.05$)	β plot	Rate of Significance (% of permutations with $p < 0.05$)	α (habitat/node)	Rate of Significance (% of permutations with $p < 0.05$)	β network	Rate of Significance (% of permutations with $p < 0.05$)
Habitat	Min.	0.08	100%	0.16	100%	0.25	100%	0.70	100%
	1st quart.	0.09		0.18		0.27		0.72	
	Median	0.09		0.18		0.28		0.72	
	3rd quart.	0.10		0.19		0.28		0.73	
	Max.	0.10		0.20		0.30		0.75	
Node	Min.	0.10	100%	0.0000	60.2%	0.11	96.1%	0.80	96%
	1st quart.	0.11		0.02		0.14		0.85	
	Median	0.12		0.03		0.14		0.86	
	3rd quart.	0.12		0.03		0.15		0.86	
	Max.	0.14		0.06		0.20		0.89	

Table 2.3: Summary statistics of ANOVA results derived from 999 stratified resampling of the original dataset based on the plot numbers given by the decay of habitats *MultSE*. Fisher values (F) and measures of effect size (η^2) are shown along with the overall rate of significance of the tests.

Term	Distribution of values	F	η^2	Rate of Significance (% of permutations with $p < 0.05$)
Habitat	Min.	1.17	0.17	93.9%
	1st quart.	3.23	0.37	
	Median	4.14	0.43	
	3rd quart.	5.21	0.49	
	Max.	13.16	0.70	

DISCUSSION

Sampling diversity of plant communities, in terms of species richness and composition, allowed us to verify and update the distribution of the habitats within the nodes of the EN. In fact, the field survey can reach a higher level of detail than cartographic data, thus being able to capture and interpret the different aspects of plant mosaics and their dynamism over time, potentially caused by global change and/or anthropic pressure (Franklin et al. 2016). Moreover, this verification between ground and map data in EN planning should be required (Gippoliti and Battisti 2017) and it should be undertaken independently of the cartographic reference checks, which are completed during map drafting. In fact, these incongruences between maps and the observed environment can be a limit in the planning and design phase of the EN and in the application of indexes for connectivity analysis, where weight evaluation of the nodes is requested (i.e., probability of connectivity index). Moreover, it highlights once again the need for verification and monitoring of the modeled EN once implemented. This issue is well known in literature, and Foltete et al. (2020) recently highlighted the weakness of approaches based on landscape structure data, suggesting to not use landscape graphs in operational contexts without validating them beforehand with empirical data on species or communities.

As expected, the species richness and rarefaction curves for habitats and nodes (Figure 2.2, 2.3, S2.1, S2.2) described the high heterogeneity existing between nodes, in fact, the method used to identify the EN has been developed to cover the functional areas needed to host the highest number of different species (Sigura et al. 2017), assuming that the species and habitats used for modeling the EN stand as a proxy for many other species. Moreover, the SERs for habitats (Figure S2.1) showed an increasing species richness going from moist or wet grasslands and fens (D4.11, D5.24, E3.4), to shrublands and forests (F3.23, F9.2, G1.A1A, G1.11, G1.223, G1.41) and meadows (E2.2, E3.51). A similar trend was found by De Simone et al. (2016) studying patterns of biodiversity in cultivated landscapes, where meadows and woodlands proved to be hotspots of biodiversity. Furthermore, the habitat-based RC accumulated species less rapidly than the node-based RC (Figure 2.3) while the SER first displayed a trend similar to the node-based RC, and then to the habitat-based one. This feature indicated a higher similarity among habitats in terms of species composition, than nodes.

Nodes were also generally more extended than habitats and therefore they accumulated species more rapidly (Arrhenius 1921). Additionally, some of the nodes were often composed by more habitats, allowing for a faster accumulation of species.

These results pointed out that node-based RC accumulated more species than habitat-based RC, suggesting that a sampling design based on nodes is more efficient in capturing the EN heterogeneity: similar habitats, sharing similar species composition and structure (e.g., shrublands and forests shared numerous species: *Salix* spp., *Alnus glutinosa*, *Populus* spp., *Quercus robur*, *Fraxinus* spp., etc.), include indeed a high redundant composition of species that can be characterized with fewer sampling units. This is further corroborated by additive partition of diversity (Figure 2.4), which showed as nodes were more diverse between them than habitats themselves.

Regarding *MultSE* profiles, the number of plots required for characterizing habitats ranged from 4 to 8 (Figure 2.5 and Table S2.1). Grassland habitats needed fewer plots than woodland habitats, due to the lower degree of habitat complexity. Probably the applied plot size was too small for forest habitats due to the scale of the vegetation patchiness but, even though the plot size might not completely proper in every habitat, a uniform plot size was needed for the aims of this work and for further research concerning the EN under study. The number of plots required for nodes ranged from 2 to 10 (Figure S2.3), depending on the number of habitats present within the node. It is interesting to note that if we consider the whole dataset (Figure S2.4), 28 replicates (14.51% of the original dataset) are sufficient to maintain the same level of heterogeneity of the network as observed with all the sampling units. Indeed, the additive partitioning of diversity for the reduced dataset, showed a minimum variation of α plot, β plot and β (Table 2.2) thus the overall signal for the whole EN remained comparable to the original. This suggests that sampling all the nodes of the EN leads to a redundancy in the data, if the aim is to point out an overall plant diversity contained within the EN.

Conversely, the approach that allows for distinguishing best among plant communities is the habitat-based sampling design. Indeed, when considering the HRS' analysis (53 plots, 27.46% of the original dataset), we noticed that the significant difference between habitat composition remained constant (Table 2.3) and the partitioning of diversity underwent a slight variation (Table 2.2). In this case, the observed variation in the diversity partitioning was due to a lower redundancy of sampled species, in fact, oversampling habitats that had many species in common (e.g., shrublands and forests) led to a lower diversity between habitats (72.38% in the reduced dataset vs. 66.64% of the original dataset). Considering the results in their totality, the best approach between habitat-based and node-based depends on the aims of the research: in our study case the habitat-based approach gave us important information both on the heterogeneity of the network and on habitats' structure and composition, but a node-based approach can be a valid alternative when time and resources are scarce and the aim is to point out an overall richness for the studied EN.

It is worth noting that our results give a general indication on the adequate sampling effort that can be applied in similar contexts. It should be highlighted that our EN is predominantly wetlands based, so more studies would be needed if applied to other habitat types (e.g., an EN based primarily on grasslands would probably need more plots). Moreover, the proposed methodology can be useful for monitoring the ENs over time considering that ENs are never monitored after being implemented (Gippoliti and Battisti 2017). That is, starting with a sampling design proportional to the extent of the EN under study, it is possible to establish the minimum and sufficient number of sampling units to subsequently monitor diversity variation over time. Finally, our results on *MultSE* profiles, albeit applied in a completely different context, are consistent with previous studies (Anderson and Santana-Garcon 2015; Maccherini et al. 2020), thus confirming it to be a useful statistic for assessing sample-size adequacy in studies of ecological communities.

Since ENs are often modeled on the basis of species-habitat interactions and designed based on graph theory (Urban et al. 2009; Galpern et al. 2011), it is extremely important to join biological data in the graph's early construction stage (Foltete et al. 2020) to confirm the distribution of the habitats in the area and their composition in terms of plant communities, as they are the primary component for habitats determination (Devillers et al. 1991; Devillers and Devillers-Terschuren 1996; Davies et al. 2004; European Commission 2013) and the basis on which the interaction species-habitat are set up. As already acknowledged in literature, it is not recommended to analyze plant communities by preferential sampling (e.g., Diekmann et al. 2007; Lájer 2007) which may lead to biased results, and for this reason the sampling design must be probabilistic and replicates independent, and it is essential to establish a measure of sampling adequacy to exhaustively distinguish different plant communities. A final consideration regarding wetlands should be made. These environments are reported to be less studied in ENs’ literature (Foltete et al. 2020) and they are known to be vulnerable ecosystems extremely important for the maintenance of biodiversity, as they are peculiar environments extremely rich in both plant and animal diversity. More than 78% of the habitats within our EN were attributable to wetland habitats and 4 of those resulted to be rich of rare, protected, or endemic species. In particular, *Schoenus nigricans* dominated fens (D4.11) presented 7 species as well as *Molinia caerulea* meadows (E3.51), while Illyrian *Quercus robur-Carpinus betulus* forests (G1.A1A) and *Alnus glutinosa* swamp woods (G1.41) respectively 5 and 4 species. This result confirms that these habitats are particularly important for the conservation of biodiversity in this region (Poldini and Oriolo 2002; Wassen et al. 2005, Dybkjær et al. 2012, Natlandsmyr and Hjell 2016; Della Longa 2019) and should be paid particular attention.

CONCLUSIONS

In this study, we used an innovative integrated approach in order to estimate the adequate sample size to maintain the observed features of plant communities within the habitats and nodes of the EN. This integrated method helped to fill the gaps regarding the collection of biodiversity data before the definition of an EN as well as the monitoring of biodiversity content within existing ENs.

The importance of validating ENs obtained through graph analysis, based on land cover maps and/or habitat maps, is widely known (e.g., Foltete et al. 2020). It is fundamental to optimize sampling design to enhance temporal and economic resources and define the minimum effort to adequately represent the biodiversity content of the networks.

Overall, our results gave us important information on the biodiversity conserved within the EN, the composition of plant communities and the sufficient sampling effort. One of the future developments of this study could be to distinguish between different ecological roles (e.g., Deák et al. 2020) of plant species within the habitats for fine-tuning the methodology for applied practical conservation. In fact, the use of total biodiversity in our models is perfect for testing the integrated method but, in practical conservation planning, distinguish between different ecological roles would be better. However, this study represents a novel approach to be applied in the context of designing and monitoring ENs, and thus more tests are needed to validate its suitability in different habitats and organisms. In addition, we would recommend the use of this approach for conducting pilot studies on ENs, both for designing and monitoring, aiming at optimizing resources and in general for habitat monitoring.

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Chapter 2

Connectivity, landscape structure, and plant diversity across agricultural landscapes: novel insight into effective ecological network planning

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ABSTRACT

Natural habitats in rural and urban areas are increasingly fragmented and altered by human impacts that are limiting the animal and plant dispersal process. Fragmentation and isolation can be reversed by restoring landscape connectivity through effective Ecological Network (EN) planning. However, most of the studies analyzing the influence of connectivity and landscape structure on biodiversity are focused on animals, while the understanding of their interplaying role on plant diversity remains limited.

We studied the relationships between α and β diversity pattern and landscape structure and connectivity in the nodes of an EN developed in agricultural landscapes, as a part of regional landscape planning framework in Friuli Venezia Giulia region (North-East of Italy). As an innovation, the study aims at parsing the interacting effect of landscape structure, surrounding habitats and nodes, and structural connectivity on EN plant diversity at two specific scales of investigation i.e., the habitat and the node scale. The habitat was the basic ecological unit, while the node was the basic cartographical unit for the EN mapping (multi-habitat or mono-habitat nodes).

We found that high node connectivity leads to higher species richness (α-diversity) but also increases plant community similarity (i.e., low β-diversity) at both scales. The effect of landscape structure showed differing trends depending on the habitat. In general, landscape composition of semi-natural land cover (i.e., hedgerows, watercourses) showed a positive effect on species diversity as opposed to that of the configuration of anthropogenic elements on both scales. Our results provided crucial information on the landscape processes useful to improving biodiversity conservation by EN. Our findings suggest that i) improving connectivity within ENs favors α plant diversity ii) different habitats have different sensibility to landscape structure iii) semi-natural land cover around nodes improve plant diversity; iv) planning both mono-habitat and multi-habitats nodes, increases the biodiversity conserved therein; v) nodes with more compact shapes are to be preferred.

Keywords: connectivity metrics, landscape composition, landscape planning; Local Contributors of Beta Diversity; multi-scale analysis; multiple regressions; species richness

Abbreviation: AREAMN mean area (class natural land use); CCe Closeness centrality; Dg node degree; DsqrtA maximum distance to square root of area ratio; Ec eccentricity; ED edge density (class agricultural land use); EN ecological network; F flux; GLM Generalized Linear Models; GLMM Generalized Linear Mixed Models; GYRATEMN mean radius of gyration (class natural land use); HRA hedgerow area; IF interaction flux; LCBD Local Contributors of Beta Diversity; NOH number of habitats; NOLU number of land uses; TE total edge (class natural land use); WA watercourse area

INTRODUCTION

Biodiversity loss is one of the major concerns of our time, caused by many factors such as land use change, habitat fragmentation, pollution, natural resource exploitation, climate change, and biological invasion (Landi et al. 2018; IPBES 2019; EEA 2020). Among them, land use change is considered the major cause of natural habitat fragmentation and alteration due to the sprawl of rural and urban areas (Foltête et al. 2014). In these landscapes, natural patches and/or protected areas are often surrounded by an anthropogenic matrix that limits animal and plant dispersal process, increasing their functional isolation (Nowicki et al. 2014; Mossman et al. 2015). Fragmentation and isolation of natural habitats can be reversed by restoring landscape connectivity through an effective Ecological Network (EN) planning by implementing nodes, corridors, and steppingstones (Mossman et al. 2015). Connectivity is a key concept in landscape management as it encompasses all aspects affecting the displacement of an individual among resource or habitat patches within landscapes (Baguette and Van Dyck 2007). Many approaches based on spatial modeling have been proposed to estimate potential landscape connectivity, such as indices of landscape pattern (Cook 2002), least-cost modeling (Vuilleumier and Prélaz-Droux 2002; Adriaensen et al. 2003; Gurrutxaga et al. 2010; Théau et al. 2015), randomized shortest paths (Panzacchi et al. 2016), cost-benefit methods (Drielsma et al. 2007), circuit theory (McRae et al. 2008) and graph-theoretic methods (Urban and Keitt 2001; Urban et al. 2009). Among them, landscape graph modelling is a promising approach applied in different scenarios (Galpern et al. 2011; Foltete et al. 2020; Sahraoui et al. 2021).

ENs are increasingly accepted as proactive tools for preserving biodiversity by improving landscape connectivity (Gilbert-Norton et al. 2010; Damschen 2013; Modica et al. 2021). ENs represent also an effective approach integrating environmental management strategies and landscape planning and can be understood by different actors (De Montis et al. 2016; Keeley et al. 2018; Sahraoui et al. 2021). The practical implementation of EN planning depends on opportunities, the interest of landowner and other stakeholders, and costs (Bergsten and Zetterberg 2013; Mossman et al. 2015). Therefore, it is crucially important to provide practitioners with practical, field-tested advice for planning effective ENs to support biodiversity. On the other hand, landscape connectivity and conservation plans often rely solely on environmental and land cover data (Brooks et al. 2004): however, such a broad approach based on these heterogeneity surrogates, hardly can be used to conserve the real biodiversity content of a large area (Araujo et al. 2001; Schindler et al. 2013), and also raises criticism for the lack of validation and monitoring plans in addition to ignoring the community structure (Gippolitti and Battisti 2017; Luo et al. 2021).

EN models are typically based on nodes, such as a single or groups of habitat patches, identified to support the viability of many species, with different movement and dispersal capabilities, and hence expressing different connectivity requirements (Minor and Lookingbill 2010; Brodie et al. 2015). However, many of the studies analyzing the influence of landscape connectivity on biodiversity were studied for animal species, while the understanding of the role of EN connectivity on plants remains limited, especially at the community level (but see Uroy et al. 2019; McLeish et al. 2021). Plant communities are a primary component for habitat identification that has been adopted also in modern European habitat classifications (Devillers et al. 1991; Devillers and Devillers-Terschuren 1996; Davies et al. 2004; European Commission 2013; Maccherini et al. 2020). Plants support the life of most of the other ecosystem organisms, and they also regulate nutrient cycling and soil protection (Lieth 1973) and represent a large portion of landscape biodiversity. Landscape connectivity for plants is mainly linked to their ability to disperse between habitat patches via propagules. Their dispersal is only successful if habitat patches are sufficiently connected (Fahrig and Merriam 1985; Bowne and Bowers 2004) or if it is facilitated by suitable landscape features (Taylor et al. 1993). Moreover, the ability of plants to disperse in fragmented landscapes also depends on their dispersal strategy, only specialized species can profit by long-distance dispersal events (Vittoz and Engler 2007; Boscutti et al. 2018).

Landscape structure and connectivity often interplay generating complex interacting effects on biota (Uroy et al. 2019) that are poorly investigated especially in EN context. The effects of landscape structure (i.e., composition and configuration) on plant communities are still debated (Zambrano et al. 2019; Fahrig 2020) as are those regarding connectivity (Uroy et al. 2019; McLeish et al. 2021), and for this reason our understanding and ability to analyze the interaction between them on plant communities has yet to be improved.

This research integrates the study of both α and β plant diversity as a function of landscape structure and connectivity in an EN. As an innovation, it aims at parsing the interacting effect of landscape structure, surrounding habitats and nodes, and structural connectivity on EN plant diversity at two specific scales of investigation i.e., the habitat and the node scale. The habitat was the basic ecological unit, while the node was the basic cartographical unit for the EN mapping (multi-habitat or mono-habitat nodes).

We hypothesized that plant diversity (i.e., α and β) is related to landscape structure (i.e., composition and configuration) and EN connectivity, and their effect depends on habitat type and node complexity. The hypothesis was tested by exploring the plant diversity in the nodes of an EN developed as part of regional landscape planning framework in Friuli Venezia Giulia region (North-East of Italy). Our aim was to explore how landscape structure and EN connectivity characteristics influence the plant diversity of both habitats and EN nodes.

METHODS

Study site

This study was carried out in a local EN in the lowlands of the Friuli Venezia Giulia region (NE Italy; centroid coordinates: 45°48'13.4" N - 13°08'11.0" E; Figure 3.1). The study area has an extent of 298 km^2 including a large agricultural area embedded in two river systems (Stella and Corno, respectively). The landscape is characterized by a mixed mosaic of intensively and extensively cultivated areas, settlements, semi-natural and natural habitats. It includes eight Natura 2000 Special Area of Conservation (Habitats Directive 92/43/EEC) and nine regional protected sites (biotopes), mainly connecting remnants of wetland habitats and lowland forests.

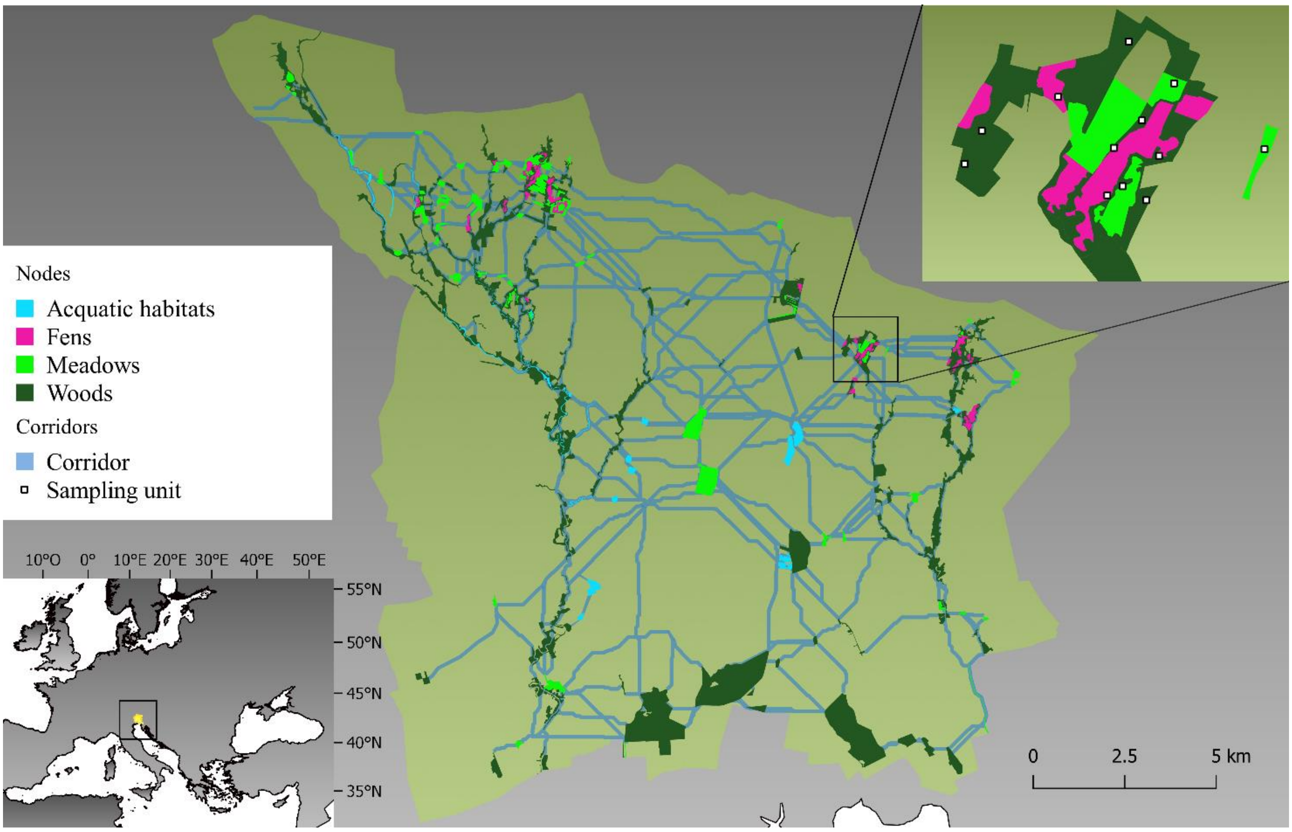


Figure 3.1: Study area location and ecological network representation. An example of the hierarchical sampling design in which each node was sampled stratified by habitat proportionally to habitat extension within the node is shown on the top right of the figure.

The soils of the area consist mainly of Quaternary sand, silt and silt-clay sediments formed by glacial fluvial transport during the Pleistocene and by alluvial deposition during the Holocene. The area is characterized by an average annual temperature of about 13°C and an average annual precipitation between 1100 and 1400 mm.

Ecological network model

The studied EN was designed using a habitat-species based model (considering flora and fauna) developed at the local scale (Figure 3.1) in the context of the regional landscape planning process (Sigura et al. 2017). The model was based on least-cost path analysis and graph theory, which were used to obtain species-specific ENs that were later merged into the final composite multi-species network. The nodes (target habitats), corridors and steppingstones (links between target habitats) were obtained for a set of 10 target animal species and 9 plant communities (assumed to be crucial for several plant species of conservation concern) to proxy favorable conditions for overall network biodiversity. Specifically, the EN was originally modeled using the regional habitat map based on the habitat classification European Nature Information System (EUNIS, Davies et al. 2004) and crossing costs for species were attributed by expert assessment and literature review data.

The entire EN is composed of 108 nodes and 17 different habitats (14 terrestrial and 3 aquatic), corresponding to a total extent of 5900 ha, of which 1700 ha represent nodes and 4200 ha ecological corridors. Nodes vary greatly in extent, ranging from less than 1 ha up to 432 ha, with an average of 22 ± 59 ha, in shape and habitat composition, as they can consist of a single habitat (mono-habitat) or many habitats (multi-habitat, Figure 3.1).

The lack of information on the actual distribution of species in the modelling process makes the assessment of biodiversity, within the nodes, extremely important for EN model reliability.

Sampling design and data collection

Plant diversity in all EN nodes composed of terrestrial habitats and bigger than 1 ha were sampled (i.e., 87 nodes). The sampling design chosen was hierarchical (e.g., Figure 3.1): each habitat type was sampled within each node proportional to the area occupied within the node (see Table S3.1). Sampling density in relation to habitat extent was chosen as follows: a random square plot of 100 m^2

for a habitat area < 5 ha, 2 plots for an area ≥ 5 and ≤ 10 ha, and finally 3 plots for an area > 10 ha. A total of 219 plots were randomly selected within the nodes of the EN, corresponding to an overall sampling density of 0.13 plot/ha. Presence and abundance (% visual cover estimate) of vascular plants rooted in each plot were recorded. Nomenclature and taxonomy of species followed Bartolucci et al. (2018) for native species and Galasso et al. (2018) for alien species. Data were collected in spring and summer 2019 and 2020.

The 14 habitats present in the EN were divided into 3 groups based on the similarity of their ecological characteristics (e.g., attributable by EUNIS habitat classification level) and differences in species richness resulting from previous chapter: 1. woods, 2. meadows, and 3. fens (see Table S3.1).

Analysis at the habitat scale

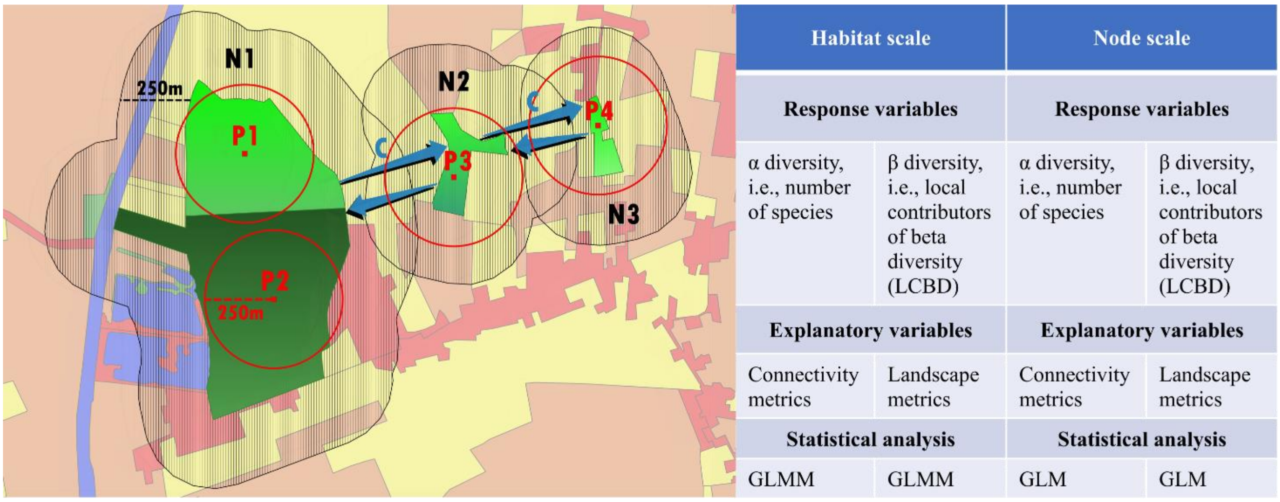
Response variables

We considered α diversity (i.e., species richness), and β diversity as response variables. The latter was examined by calculating Local Contributors of Beta Diversity (LCBD, Legendre and De Caceres 2013) in the R package "`adespatial`" (Dray et al. 2021). LCBDs represent comparative indicators specifying the degree by which each sampling unit contributes to β diversity compared to a site with an average species composition, thus assessing ecological uniqueness in terms of species composition for each sampling unit. LCBDs were obtained as sums of rows derived after centering and squaring each column of the composition matrix.

The relationships between α and β diversity values at the habitat scale were assessed to identify their respective trends.

Explanatory variables: landscape structure and connectivity metrics

Landscape composition and configuration around each plot was assessed using several landscape metrics (see Supplementary material) calculated on a circular buffer centered in the plot and with a radius of 250 m (Figure 3.2), which has been already proven to be a sensitive scale when analyzing plant diversity in similar landscapes (Kumar et al. 2006; Boscutti et al. 2018).



Habitat scale		Node scale	
Response variables		Response variables	
α diversity, i.e., number of species	β diversity, i.e., local contributors of beta diversity (LCBD)	α diversity, i.e., number of species	β diversity, i.e., local contributors of beta diversity (LCBD)
Explanatory variables		Explanatory variables	
Connectivity metrics	Landscape metrics	Connectivity metrics	Landscape metrics
Statistical analysis		Statistical analysis	
GLMM	GLMM	GLM	GLM

Figure 3.2: Schematization of the study: on the left the representation of the two scales of analysis, at the habitat scale (P, red diamonds) with a 250 m buffer around the plot and at the node scale (N, green polygons, different shades of green indicate different habitats) with a 250 m buffer around the node. Blue arrows (C) indicate connectivity between nodes. In the background, land use classes (red for urban land use, yellow for agricultural land use, blue for watercourses, and green for hedgerows). On the right, the diagram summarizing the materials and methods: the response variables (α and β diversity), the explanatory variables (connectivity metrics and landscape metrics), and the statistical analyses (GLMM at the habitat scale and GLM at the node scale).

All landscape metrics were calculated using the R package "`landscapemetrics`" (Hesselbarth et al. 2019). Connectivity within the modeled EN was assessed by 7 connectivity metrics (see Supplementary material) using Graphab software (Foltete et al. 2012a). These metrics were integrated into the final dataset by linking the value of the metric for a node to all the plots collected within that node. To reduce multicollinearity in the set of landscape and connectivity metrics, correlation analysis was performed in R (R Core Team 2021, see Supplementary material) estimating coefficients using non-parametric Spearman's ρ. A total of 29 variables were selected as not highly correlated (< |± 0.7|) (see Table S3.2) and used in the full models.

Model selection

Prior to model simplification, all quantitative variables were standardized (zero mean, unit variance) to obtain comparable coefficient values. A subsequent stepwise selection procedure based on AIC minimization criteria (Burnham and Anderson 2002), using the function "dredge" within the

“`MuMIn`” R package (Barton 2020), was run for both α and β diversity models. Finally, the Minimum Adequate Model (MAM) was obtained simplifying the resulting models by removing one-by-one the non-significant interaction terms or variables ($p > 0.1$) using a manual backward selection procedure. The overall final variables resulting in the two MAMs are reported in Table 3.1.

Table 3.1: Explanatory variables resulting from the MAMs at the habitat scale. For more details on formulas and meaning, see Foltete et al. (2012a) for connectivity metrics and the “`landscapemetrics`” package vignette (Hesselbarth et al. 2019) for landscape metrics. Connectivity formula terms: n_k = number of patches in the component k, N_i = all patches close to the patch i, d_{ij} = least-cost distance between the patches i and j, $e^{-\alpha d_{ij}}$ probability of movement between the patches i and j, α = brake on movement distance, β = exponent to weight more or less capacity. Landscape metric formula terms: e_{ik} = total edge length in meters, A = area in square meters, G = radius of gyration of each patch.

Connectivity metric	*Formula*	*Meaning*	*Reference*
Closeness centrality (CCe)	$CCe_i = \frac{1}{n_k - 1} \sum_{j=1}^{n_k} d_{ij}$ $j \neq i$	Mean distance from the patch i to all other patches of its component k.	Freeman 1978
Eccentricity (Ec)	$Ec_i = \max_{j} d_{ij}$	Maximum distance from the patch i to another patch of its component k.	Urban &Keitt 2001
Flux (F)	$F_i = \sum_{j=1}^{n} \alpha_j^{\beta} e^{-\alpha d_{ij}}$ $j \neq i$	For the focal patch i: sum of capacity of patches other than i and weighted according to their minimum distance to the focal patch through the graph. This sum is an indicator of the potential dispersion from the patch i or, conversely to the patch i.	Urban & Keitt 2001; Saura & Torné 2009; Foltete et al. 2012b
Interaction flux (IF)	$IF_i = \sum_{j=1}^{n} \alpha_i^{\beta} \alpha_j^{\beta} e^{-\alpha d_{ij}}$	Sum of products of the focal patch capacity with all the other patches, weighted by their interaction probability.	Foltete et al. 2014; Sahraoui et al. 2017
Node degree (Dg)	$Dg_i = N_i \vee$	Number of patches connected directly to the patch i.	Freeman 1978
Landscape metric	*Formula*	*Meaning*	*Reference*
Edge density (ED; class agricultural land use)	$ED = \frac{\sum_{k=1}^{m} e_{ik}}{A} * 10000$	The edge density equals the sum of all edges of class i in relation to the landscape area. The metric describes the configuration of the landscape.	McGarigal et al. 2012
Mean area (AREAMN; class natural land use)	$AREA_{MN} = mean(A[patch_{ij}])$	The metric summarizes each class as the mean of all patch areas belonging to class i. The metric describes the composition of the landscape.	McGarigal et al. 2012
Mean radius of gyration (GYRATEMN; class natural land use)	$GYRATE_{MN} = mean(G[patch_{ij}])$	The metric summarizes each class as the mean of the radius of gyration of all patches belonging to class i. It measures the distance from each cell to the patch centroid and is based on cell center-to-cell center distances. The metrics characterizes both the patch area and compactness.	Keitt et al. 1997; McGarigal et al. 2012
Total edge (TE; class natural land use)	$TE = \sum_{k=1}^{m} e_{ik}$	Sum of all edges between class i and all other classes k. It measures the configuration of the landscape because a highly fragmented landscape will have many edges.	McGarigal et al. 2012

The models were designed as follows: the effects of landscape structure and connectivity of the EN on α and β diversity were examined using two different Generalized Linear Mixed Models (GLMMs; Bolker et al. 2009) using a Penalized Quasi-likelihood (PQL) method by means of the "`MASS`" R package (Venables and Ripley 2002). The random effect in both models was the node to which the sampling unit belonged to. A quasi-Poisson distribution was used to model the error structure in the α diversity model, and a Gamma distribution in the β diversity model.

Analysis at the node scale

Response variables

The 219 plots used to survey the biodiversity of habitats were pooled by node obtaining 87 observations and then considering α diversity (i.e., species richness of the nodes), and β diversity (i.e., LCBD of the nodes) as response variables. Their relationship was then assessed to identify the respective trend and compare it to that at the habitat scale.

Explanatory variables: landscape structure and connectivity metrics

In contrast to the habitat scale where all areas around the sampled points have the same extent, the nodes have very different shapes and sizes, so we considered other variables for the landscape structure: i.e., node shape, number of habitats forming the node and type of land covers (natural and anthropogenic) surrounding the node. Various shapes indexes were calculated with QGIS (QGIS Development Team 2021) using the EN nodes as the main spatial unit (see Supplementary material). 18 landscape metrics were calculated on a buffer area of 250 m around each node (Figure 3.2) and are reported in Table S3.2. Connectivity within the EN was assessed using the same 7 metrics described above. To exclude multicollinear variables, correlation analysis was performed with the same specification as described above (see Supplementary material). A total of 18 variables were found to be uncorrelated (see Table S3.2) and used in the full models.

Model selection

The modeling procedure was the same as explained in the section on the habitat scale. The overall final variables resulting in the two MAMs are reported in Table 3.2.

Table 3.2: Explanatory variables resulting from the MAMs at the node scale. For more details on formulas and meaning, see Foltete et al. (2012a) for connectivity metrics and Forman and Godron (1986) and Lang and Blaschke (2007) for DsqrtA metric. Connectivity formula terms: n_k = number of patches in the component k, N_i = all patches close to the patch i, d_{ij} = least-cost distance between the patches i and j, $e^{-\alpha dij}$ probability of movement between the patches i and j, α = brake on movement distance, β = exponent to weight more or less capacity. Landscape formula terms: Dmax = maximum distance between two vertices of a polygon, A = area.

Connectivity metric	*Formula*	*Meaning*
Closeness centrality (CCe)	$CCe_i = \frac{1}{n_k - 1} \sum_{j=1}^{n_k} d_{ij}$ $j \neq i$	Mean distance from the patch i to all other patches of its component k.
Eccentricity (Ec)	$Ec_i = \max_j d_{ij}$	Maximum distance from the patch i to another patch of its component k.
Flux (F)	$F_i = \sum_{j=1}^{n} \alpha_j^{\beta} e^{-\alpha d_{ij}}$ $j \neq i$	For the focal patch i: sum of capacity of patches other than i and weighted according to their minimum distance to the focal patch through the graph. This sum is an indicator of the potential dispersion from the patch i or, conversely to the patch i.
Interaction flux (IF)	$IF_i = \sum_{j=1}^{n} \alpha_i^{\beta} \alpha_j^{\beta} e^{-\alpha d_{ij}}$	Sum of products of the focal patch capacity with all the other patches, weighted by their interaction probability.
Node degree (Dg)	$Dg_i = N_i \vee$	Number of patches connected directly to the patch i.
Landscape metric	*Formula*	*Meaning*
Hedgerow area (HRA)	$HRA = \sum \frac{A[hedgerow]}{TotalA}$	Percentage of hedgerows area.
Maximum distance to square root of area ratio (DsqrtA)	$DsqrtA = \frac{D_{max}}{\sqrt[2]{A}}$	Maximum distance between two polygon part's vertices divided by the square root of polygon's area. The minimum value of the metric corresponds to a circle, and the value increases as the shape becomes narrower.
Number of habitats (NOH)	$NOH = \sum HAB_i$	Sum of the number of different habitats present inside the node i.
Number of land uses (NOLU)	$NOLU = \sum LUSE_i$	Sum of the number of different land uses present around the node i.
Watercourse area (WA)	$WA = \sum \frac{A[watercourse]}{TotalA}$	Percentage of watercourse area.

The models were designed as follows: the effects of landscape structure and connectivity of the EN on total α and β diversity were examined using two different Generalized Linear Models (GLM). In the α diversity model a quasi-Poisson distribution was used to model the error structure while in the β diversity model a Gamma distribution was used.

RESULTS

α and β diversity pattern and relationship in the EN

A total of 443 plant species were recorded during the sampling activity, of which 47 were alien and 24 were classified as protected, rare, or endemic species according to the European, Italian, or regional Red Lists (see Table S3.3). The most frequent native species were *Rubus caesius* (present in 57.5% of the plots), *Cornus sanguinea* (54.3%), *Rubus ulmifolius* (53.9%), *Quercus robur* (53.4%), *Hedera helix* (51.1%), and *Salix alba* (45.2%). Among alien species, the most common were *Platanus hispanica* (27.9%), *Robinia pseudoacacia* (15.1%) and *Potentilla indica* (14.6%). Finally, the most frequent protected or endemic species were *Ruscus aculeatus* (Habitat Directive 92/43/CEE Annex V, 8.7%), *Centaurea jacea* subsp. *forojulensis* (endemic, 5.0%), and *Gladiolus palustris* (Habitat Directive 92/43/CEE Annex II, 4.6%).

The mean number of species per plot was 24.4 ± 7.7, per habitat was 14.9 ± 5.3 in fens, 23.3 ± 5.8 in woods, and 31.3 ± 8.8 in meadows, and finally per node it was 39.4 ± 29.6. Concerning β diversity, the mean LCBD value (*10^{-3}) per plot was 4.6 ± 0.9, per habitat was 5.6 ± 0.4 in fens, 4.1 ± 0.6 in woods, and 5.8 ± 0.4 in meadows, and finally per node it was 11.5 ± 3.0.

The relationships between α and β diversity values at the habitat and node scales showed significant contrasting relationships ($p < 0.05$; Figure 3.3). At the habitat scale, α diversity increased at high values of β diversity, whereas it was negatively related at the node scale.

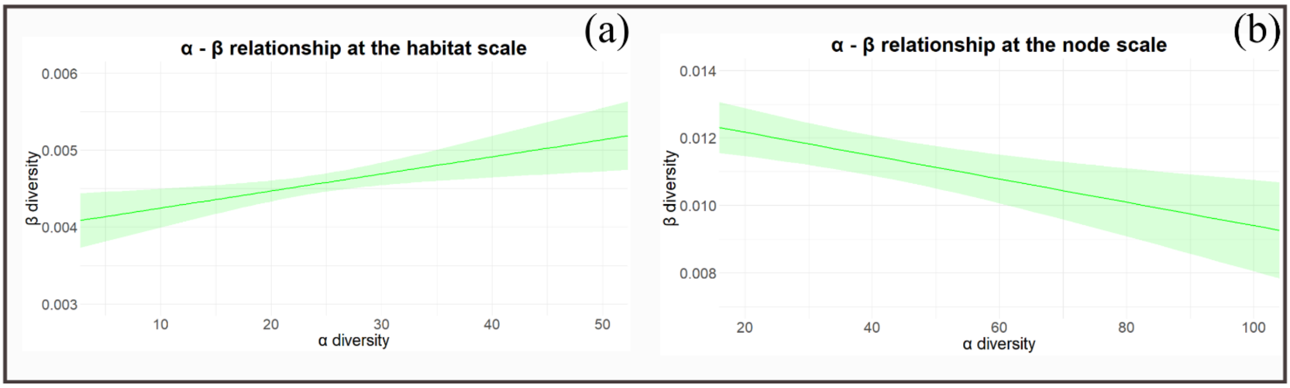


Figure 3.3: Observed relationships between α and β diversity values at the habitat scale (a), and at the node scale (b).

α and β diversity vs connectivity and landscape structure of the EN

Habitat scale

GLMMs showed that the habitat α and β diversity had consistent responses to both connectivity and landscape structure (Table 3.3).

Table 3.3: Results of the GLMM models testing the effects of landscape metrics and connectivity metrics on α diversity (species richness) and β diversity (LCBD) at the habitat scale.

α diversity at the habitat scale				
Coefficients	*Estimate*	*Std. Error*	*t-value*	*P-value*
Intercept	2.545	0.099	25.707	< 0.001 ***
Eccentricity (Ec)	0.041	0.023	1.779	0.079 .
Flux (F)	0.248	0.090	2.749	0.007 **
Closeness centrality (CCe)	0.286	0.144	1.982	0.051 .
Total edge of natural land use (TE)	0.178	0.076	2.328	0.021 *
Habitat	0.902	0.103	8.772	< 0.001 ***
CCe:Fens	-0.093	0.152	-0.610	0.543
CCe:Meadows	-0.389	0.151	-2.585	0.011 *
CCe:Woods	-0.322	0.145	-2.224	0.028 *
F:Fens	-0.117	0.096	-1.220	0.225
F:Meadows	-0.169	0.099	-1.698	0.092 .
F:Woods	-0.250	0.091	-2.751	0.007 **
TE:Fens	0.103	0.075	1.370	0.173
TE:Meadows	-0.256	0.080	-3.192	0.002 **
TE:Woods	-0.174	0.079	-2.190	0.030 *
β diversity at the habitat scale				
Coefficients	*Estimate*	*Std. Error*	*t-value*	*p-value*
Intercept	-5.152	0.029	-174.854	< 0.001 ***
Flux (F)	-0.020	0.010	-2.027	0.045 *
Interaction flux (IF)	0.048	0.029	1.664	0.099 .
Node degree (Dg)	-0.056	0.024	-2.332	0.022 *
Edge density of agricultural land use (ED)	-0.025	0.009	-2.802	0.006 **
Mean area of natural land use (AREAMN)	0.047	0.015	3.007	0.003 **
Mean radius of gyration of natural land use (GYRATEMN)	-0.039	0.014	-2.838	0.005 **
Habitat	-0.342	0.029	-11.682	< 0.001 ***

In particular, the MAM on α diversity ($R^2 = 0.57$, p = <0.001, Figure 3.4, Table 3.3) included the following predictive variables: Closeness centrality (CCe), Eccentricity (Ec), Flux (F), and Total Edge (TE) all with a significant interaction term with habitats except for Ec. The α diversity model showed a positive relationship with Ec, F in fens and meadows, CCe in fens, and TE in fens; in contrast it was negatively related to CCe in woods and meadows, and TE in meadows. No relationship was observed between species richness and F and TE in woods.

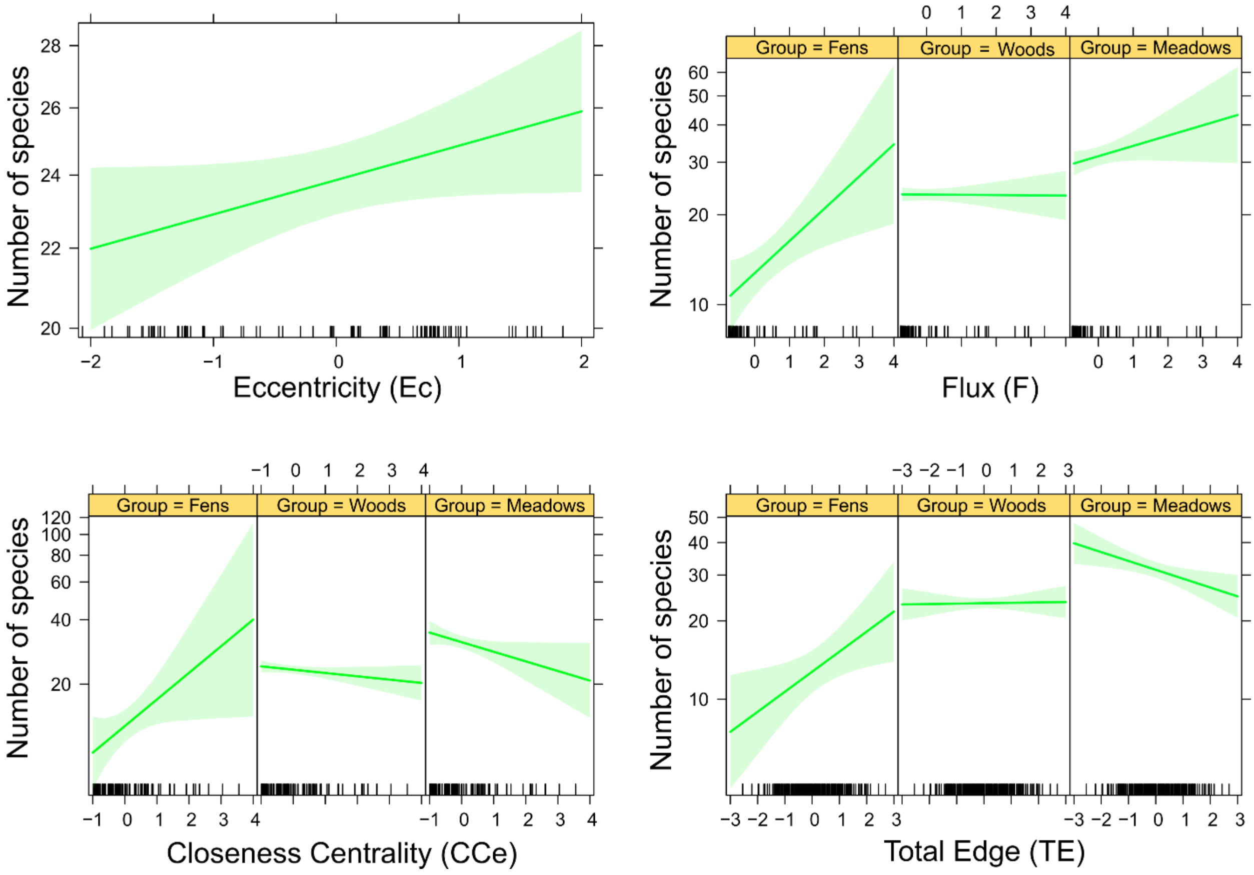


Figure 3.4: Effects on α diversity (i.e., species richness) of eccentricity; flux, closeness centrality and total edge with anthropic land uses in different habitats (fens, woods, and meadows) resulting from the GLMM at the habitat scale.

On the other side, the MAM developed to explain variation in β diversity ($R^2 = 0.76$, $p = <0.001$, Figure 3.5, Table 3.3) retained the following predictors: Flux (F), Interaction flux (IF), Node degree (Dg), Edge density of agricultural land use (ED), Mean area of natural land use (AREAMN), Mean radius of gyration of natural land use (GYRATEMN), and habitat without interaction, as no interaction between habitat and considered variables emerged. Overall, it was observed a positive relationship with IF, AREAMN, and a negative relationship with F, Dg, ED, GYRATEMN.

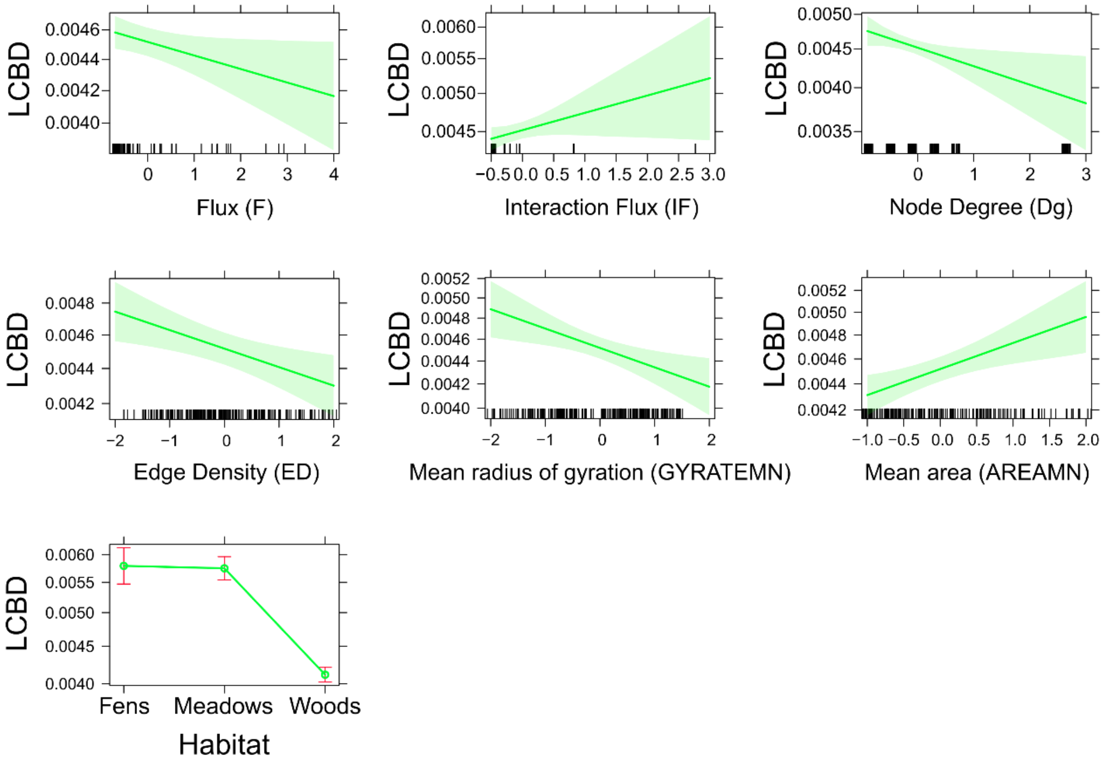


Figure 3.5: Effects on β diversity (i.e., LCBD) of flux, interaction flux, node degree, edge density of agricultural land use, mean radius of gyration of natural land use, and mean area of natural land use along with mean values of LCBD per habitat resulting from the GLMM at the habitat scale.

Node scale

The MAM for α diversity ($R^2 = 0.86$, p = <0.001, Figure 3.6, Table 3.4) included the following predictive variables: Closeness centrality (CCe), Eccentricity (Ec), Interaction flux (IF), Node degree (Dg), Maximum distance to square root of area ratio (DsqrtA), log transformed Hedgerow area (HRA), Number of habitats (NOH), and Watercourse area (WA). α diversity increased at the increase of Ec, Dg, HRA, NOH, and WA, but decreased in nodes with high CCe, IF, and DsqrtA.

The β diversity MAM at node scale ($R^2 = 0.57$, $p < 0.001$, Figure 3.7, Table 3.4) retained the following predictive variables: Flux (F), Node degree (Dg), Maximum distance to square root of area ratio (DsqrtA), Hedgerow area (HRA), Number of habitats (NOH), Number of land uses (NOLU), and Watercourse area (WA). It estimates a positive relationship with HRA and WA and a negative relationship with F, Dg, DsqrtA, NOH and NOLU.

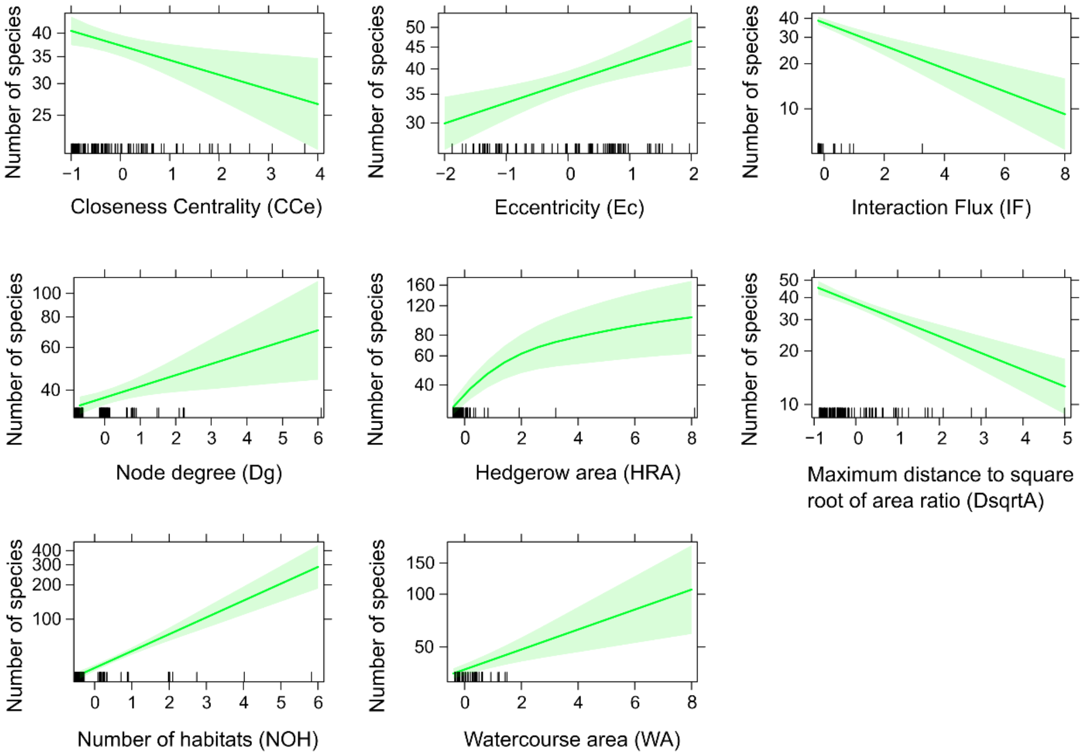


Figure 3.6: Effects on α diversity (i.e., species richness) of closeness centrality, eccentricity; interaction flux, node degree, hedgerow area, maximum distance to square root of area ratio, number of habitats, and watercourse area resulting from the GLM at the node scale.

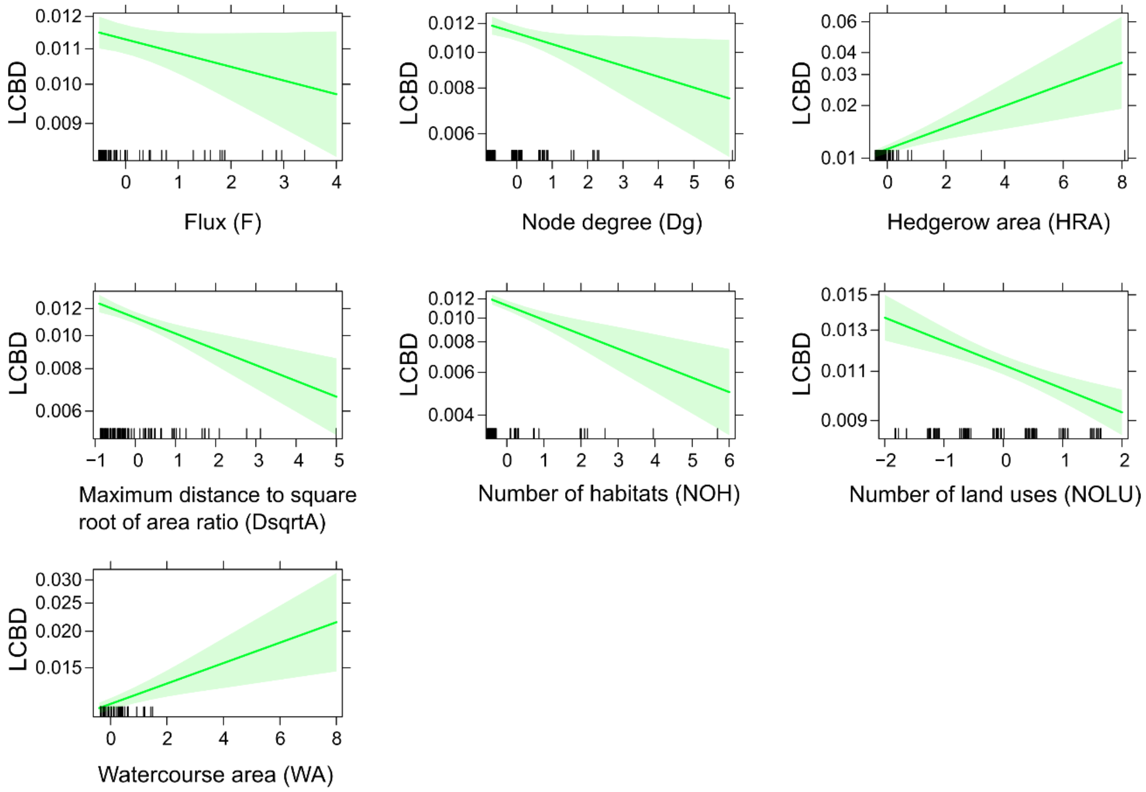


Figure 3.7: Effects on β diversity (i.e., LCBD) of flux, node degree, hedgerow area, maximum distance to square root of area ratio, number of habitats, number of land uses, and watercourse area resulting from the GLM at the node scale.

Table 3.4: Results of the GLM models testing the effects of landscape metrics and connectivity metrics on α diversity (species richness) and β diversity (LCBD) at the node scale.

α diversity at the node scale				
Coefficients	*Estimate*	*Std. Error*	*t-value*	*p-value*
Intercept	3.619	0.031	116.758	< 0.001 ***
Closeness centrality (CCe)	-0.084	0.031	-2.691	0.009 **
Eccentricity (Ec)	0.110	0.031	3.583	< 0.001 ***
Interaction flux (IF)	-0.175	0.034	-5.068	< 0.001 ***
Node degree (Dg)	0.106	0.039	2.716	0.008 **
log (Hedgerow area) (HRA)	0.459	0.109	4.211	< 0.001 ***
Maximum distance to square root of area ratio (DsqrtA)	-0.217	0.036	-6.038	< 0.001 ***
Number of habitats (NOH)	0.341	0.039	8.783	< 0.001 ***
Watercourse area (WA)	0.131	0.036	3.616	< 0.001 ***
β diversity at the node scale				
Coefficients	*Estimate*	*Std. Error*	*t-value*	*p-value*
Intercept	-4.485	0.019	-237.063	< 0.001 ***
Flux (F)	-0.037	0.021	-1.781	0.079 .
Node degree (Dg)	-0.068	0.031	-2.223	0.029 *
Hedgerow area (HRA)	0.142	0.038	3.734	< 0.001 ***
Maximum distance to square root of area ratio (DsqrtA)	-0.107	0.026	-4.126	< 0.001 ***
Number of habitats (NOH)	-0.136	0.034	-4.014	< 0.001 ***
Number of land uses (NOLU)	-0.096	0.021	-4.496	< 0.001 ***
Watercourse area (WA)	0.081	0.024	3.319	0.001 **

DISCUSSION

The present work integrates the study of both α and β plant diversity as a function of landscape structure and connectivity at two different scales of analysis (habitat and node) in an EN.

Landscape structure and connectivity play different roles on plant species depending on whether one considers species richness or community dissimilarity (Damschen et al.2006; Billeter et al. 2008; Concepcion et al. 2012; Thiele et al. 2018; Chisté et al. 2018; Uroy et al. 2019). Our findings showed contrasting trends when considering different scale of investigation (i.e., habitat or node). Based on the models (Tables 3.3, 3.4), connectivity had a more pronounced effect on α diversity while landscape structure on β diversity at both scales. In general, we found that improved connectivity leads to greater species richness but also to homogenization of communities. The landscape composition of semi-natural land covers (i.e., hedgerows, watercourses) showed a positive effect on species diversity as opposed to that of the configuration of anthropogenic elements.

Plant diversity: α and β contribution and relationships in the EN

The number of species (443) found within the EN was about 68.1% of the overall species richness of the study area (ca 650 taxa, Poldini 1991). When considering the percentage of the EN nodes extent on the overall study area (5.7%), the EN contribution in terms of total biodiversity is remarkable, confirming the high conservation potential of the areas that constitute ENs (e.g., Pryke et al. 2015; Xun et al. 2017).

The relationship between α and β diversity showed contrasting trends (Figure 3.3), highlighting a species composition homogenization as the species richness increases at the node scale (pools of habitat) while promoting β diversity in single habitat patches with high floristic richness. The scale dependence of biodiversity patterns is a well-known issue in ecology, where the effects of abiotic and biotic processes can only be detected at an appropriate investigation scale and can be masked by using large sample units that aggregate environmental heterogeneity (Huston 1999). In our study, the differences between communities belonging to different habitats were well detectable at the finest scale (habitat): habitat showing a high α diversity exhibited also a greater community heterogeneity (e.g., meadows). At the node scale, habitat pools into nodes resulted in richer communities in multi-habitat nodes but with low species variation compared to mono-habitat nodes that contributed more, in term of uniqueness, to the total EN plant diversity. What has been observed in the mono-habitat nodes could also be related to the presence of rare and/or specialist plant species that contribute to the uniqueness of those patches as recently found by Deák at al. (2020) in fragmented dry grassland.

α and β diversity vs connectivity and landscape structure

Habitat scale

Connectivity had different effects depending on the habitat: α diversity in meadows and woods (Figure 3.4) was higher when the belonging nodes were closer to each other (low CCe), but a higher structural probability of dispersion (high F) showed no effect on woods, suggesting that landscape connectivity might be linked to the species dispersion ability between communities (Fahrig and Merriam 1985; Bowne and Bowers 2004; Vittoz and Engler 2007; Boscutti et al. 2018).

Ec also showed a positive effect on α diversity, leading to the conclusion that habitats, belonging to the nodes of the EN, that were peripheral, most of the times were also well-connected. We expected that the most peripheral nodes were less rich because of the position in the graph, instead we have observed that the parameter affecting more species richness was the degree of connection. This suggests that the location of the nodes within the network is not as important as the degree of connectivity between them and confirm the importance of connections between patches for higher plant richness (Damschen et al. 2006; Uroy et al. 2019).

Total β diversity showed opposite trends in response to landscape connectivity (Figure 3.5) where habitats within nodes with more connections (high F and Dg) had lower community dissimilarity, as already pointed out by other studies (see Uroy et al. 2019). In contrast, it has been observed in other research (e.g., Mouquet and Loreau 2003; Tscharntke et al. 2012), that when connectivity decreases, landscapes may become highly heterogeneous, causing strong divergence in the composition of local communities due to reduced dispersal ability. Thus, rewarding species that have the ability to disperse over long distances and in anthropogenic landscapes (Boscutti et al. 2018).

Our results showed clear effects of landscape structure on α and β diversity in different habitats composing the EN nodes, although drivers of diversity are often difficult to identify at the fine scale and are more readable at a broader scale (Amici et al. 2015).

The effect of landscape configuration, related to the amount of margin (TE) between habitats and anthropogenic land use, on α diversity was shaped by habitat type response (Figure 3.4). Meadows showed to be more sensitive to the agricultural matrix displaying a lower species richness as TE increased, and this could be due to a reduction in specialist species that are more sensitive to landscape composition than generalists, as found for example by Miller et al. (2015) for glades, where specialists were observed to be generally poor dispersers and more sensitive to anthropogenic disturbance.

Woods appeared to be unaffected by landscape configuration, related to the amount of margin (TE), while in fens an increasing in TE resulted in higher species richness (Figure 3.4). This may be explained by ecological conditions of the habitat, characterized by water submersion and low nutrient availability. As a result, fens plant communities have low species richness in undisturbed landscapes while at the increase of landscape disturbance species richness tends to increase due to the ingression of generalist species (Mälson et al. 2008; Øien et al.2018).

Concerning β diversity, the effect of landscape structure was consistent in all habitats (not significant interaction) and showed that the contribution of sampling units to β diversity was the highest when natural patches were larger (high AREAMN), more compact (low GYRATEMN), and had a smaller shared boundary with agricultural land use (low ED, Figure 3.5). What was observed could be related to the amount of core area within the patches that is known to play a role in determining diversity: e.g., Hill et al. (2003) found that large forest patches contain the greatest local diversity as well as the greatest number of rare and shade-tolerant tree species, those species that certainly contribute more to the uniqueness of sampling units' composition.

Node scale

The nodes of the EN represent the hubs of biodiversity and are the basis for effective planning. Therefore, information on possible drivers that may influence the characteristics of communities within the nodes is critical. What emerged from the connectivity analysis is consistent with what was observed at the habitat scale and confirms that α diversity of nodes (Figure 3.6) was higher when the nodes were closer to each other (low CCe), with more connections (high Dg) and with β diversity values suggesting a homogenization of communities as connectivity increased (Figure 3.7). These trends were expected based on other studies (e.g., Damschen et al. 2006; Brudvig et al. 2009; Thiele et al. 2018). Even at the node scale, it can be seen that a decrease in connectivity leads to a decrease in the number of species in the nodes: a decrease in connectivity can in fact decrease species richness acting as a strong ecological filter and selecting for species that are able to disperse and survive in isolated patches (Uroy et al. 2019). Often those species with higher dispersal ability are generalists (Haddad and Tewksbury 2006) leading specialist species to be more affected by connectivity loss (Mouquet and Loreau 2003; Tscharntke et al. 2012; Miller et al. 2015; Boscutti et al. 2018). This decrease in response to the loss of structural connectivity was detected to be even stronger in grassland communities (Adriaens et al. 2006; Brückmann et al. 2010; Evju et al. 2015).

The effects of landscape structure on plant diversity at the node scale provide useful insights to EN planning, in particular our results (Figure 3.6) pointed out that α diversity is positively related to the amount of semi-natural land covers (HRA and WA) confirming their positive effects on species diversity in agricultural landscapes (Billeter et al. 2008). Moreover, we verified the importance of planning multi-habitat nodes (NOH variable) to increase species richness.

Considering the shape of the node that most contributes to α diversity, we observed that the greater and more regular the expansion along the maximum distance between two vertices (lower DsqrtA) the greater the α diversity. This is in contrast to other observations that state that more complex shapes have more species (e.g., Moser et al. 2002; Heegaard et al. 2007). However, in the first case the authors considered all patches in a landscape without distinguishing between natural and rural land uses; while in the latter they considered habitat patches individually, and unlike their study, in our case nodes often already contained multiple habitats and thus the dispersal ability of species within nodes probably contributed more to diversity than the contribution resulting from dispersal from the outer matrix, which, being predominantly agricultural, can be a source of weeds and/or alien species (Hulme 2005; Boscutti et al. 2018).

What we observed in the β diversity models (Figure 3.7) is consistent with what was noticed at the habitat scale: node contribution to total β diversity was higher when nodes had more compact shape (low DsqrtA), were surrounded by few land uses (low NOLU), and numerous semi-natural elements (high HRA and WA). The only exception is that mono habitat nodes promoted higher community differentiation (low NOH). The resulting signal of DsqrtA and NOLU confirms that different anthropogenic land uses shaping the boundary of natural patches promote homogenization of plant communities (Chisté et al. 2018).

The lesson we learned

In summary, the practical implementation of a connectivity plan depends on opportunities, the interest of landowners and other stakeholders, and cost (Bergsten and Zetterberg 2013; Mossman et al. 2015). Therefore, it is crucially important to provide practitioners with practical, field-tested advice for planning effective ENs to improve the viability of target species.

On the other hand, landscape connectivity and conservation planning often rely solely on environmental and land cover data (Brooks et al. 2004): however, such a broad approach based on these heterogeneity surrogates, can hardly be used to conserve the real biodiversity content of a large area (Araujo et al. 2001; Schindler et al. 2013).

EN planning should take into account which are the key drivers of biodiversity in the landscape and how they interact, rather than being based on untested assumptions, as also emphasized by Mossman et al. (2015). Our methodology used simple models to explore the relationships between plant diversity, landscape structure, and connectivity to provide guidance on how the EN should be structured and which elements are drivers of plant diversity.

Overall, our results provided important information about the plant diversity pattern within the EN, allowing us to highlight where action is needed to optimize the expression and conservation of biodiversity. To the best of our knowledge, our study is the first to test, by extensively sampling all nodes in the EN, the effectiveness of an EN model based on a habitat map and expert assessment of species movement to design the connectivity model. In addition, our work investigated the effects of connectivity and landscape structure on a multi-species connectivity model by considering two scales of investigation: the habitat scale, considering the single habitat patch, and the node scale considering all habitat patches forming the single node as a whole.

Our study contributes to an unresolved issue, about the multiplicity of factors that modulate the effects of landscape connectivity on plant communities (Uroy et al. 2019), adding a new element to an answer that likely cannot be unique.

In summary, based on our results, we can conclude that:

i) improving connectivity (e.g., planning habitat patches similar to the target), within ENs favors plant α diversity although it increases similarity of plant communities;

ii) different habitats have different requirements and imply different management. Forests were less sensitive to land use intensification (e.g., increase in anthropogenic land use edge) than meadows and fens. Specifically, the latter were observed to be very sensitive, and the disturbance favored the entry of generalist species;

iii) less land use intensity (ED, TE, NOLU) and semi-natural areas around nodes (HRA and WA) mitigates the effects of landscape structure, as seen at both scales for α and β diversity models;

iv) inclusion of nodes in ENs, both mono-habitat (higher β diversity, i.e., more unique community) and multi-habitats (higher α diversity, i.e., richer community), increases the plant diversity conserved therein as attested to by the plant diversity pattern at the node scale (Figure 3.3) and by the effect on α and β diversity of NOH in the models at the node scale (Figure 3.6, 3.7);

v) nodes that maximize compactness (low DsqrtA) are to be preferred, as they were observed increasing both α and β diversity.

CONCLUSIONS

In this study, we analyzed the relationships among plant diversity, landscape structure, and connectivity in an EN. From an applied perspective our methodology helped to fill the gaps regarding the knowledge on key-drivers related with landscape context and network pattern that influence plant diversity. Understanding the effects of surrounding landscape patterns and intrinsic properties of ENs on species diversity at different scales, could help promote effective environmental and conservation strategies and management practices of ENs. From our research, it was possible to highlight the role of connectivity and landscape structure in shaping plant diversity. It takes on different meanings depending on whether we consider species richness (α diversity) or dissimilarity among communities (β diversity). The role of connectivity in promoting greater species richness at both scales was evident and was in contrast to that of increasing similarity among communities. Landscape structure has shown different trends in different habitats and that can have a positive or negative effect depending on whether the patches considered are semi-natural or anthropogenic.

Our results provided important information about the behavior of plant communities within the EN, allowing us to highlight where action is needed to optimize the expression and conservation of biodiversity. Based on our results, we can conclude that i) improving connectivity within ENs favors α plant diversity ii) different habitats have different sensibility to landscape configuration iii) semi-natural buffer areas around nodes mitigate the effects of landscape structure; iv) planning nodes both mono-habitat and multi-habitats, increases the biodiversity conserved therein; v) nodes with more compact shapes are to be preferred.

Some weaknesses of the study might be that the animal component that is an integral part of the multi-species EN was not able to be included and that multiple buffers of different sizes on sampling units and nodes to observe the landscape structure effects at different scales was not able to be used. Thus, integrating these deficiencies for future studies aimed at EN design and management is suggested.

It is further suggested the use of these indications to support land-use planning decisions, particularly in prioritizing, modifying of existing ENs, and designing new ENs.

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Chapter 3

Use of remote sensing techniques to estimate plant diversity within ecological networks: a worked example

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ABSTRACT

As there is an urgent need to protect rapidly declining global diversity, it is important to identify methods to quickly estimate the diversity and heterogeneity of a region and effectively implement monitoring and conservation plans. The combination of remotely sensed and field-collected data, under the paradigm of the Spectral Variation Hypothesis (SVH), represents one of the most promising approaches to boost large scale and reliable biodiversity monitoring practices. Here, the potential of SVH to capture information on plant diversity at fine scale in an ecological network (EN) embedded in a complex landscape, has been tested using two new and promising methodological approaches, based on "`biodivMapR`" and "`rasterdiv`" R packages. The first estimates α and β spectral diversity and the latter ecosystem spectral heterogeneity expressed as Rao's Quadratic heterogeneity measure (Rao's Q). Our aims were to investigate if spectral diversity and heterogeneity provide reliable information to assess and/or monitor over time floristic diversity maintained in a EN selected as an example and located in North-East Italy. We analyzed and compared spectral and taxonomic α and β diversities and spectral and landscape heterogeneity, based on field-based plant data collection and remotely sensed data from Sentinel-2A, using different statistical approaches. We observed a positive relationship between taxonomic and spectral diversity and also between spectral heterogeneity, landscape heterogeneity, and the amount of alien species in relation to native ones. Our results confirmed the effectiveness of estimating and mapping α and β spectral diversity and ecosystem spectral heterogeneity using remotely sensed images. Moreover, we highlighted that spectral diversity values become more effective to identify biodiversity-rich areas, representing the most important diversity hotspots to be preserved. While the spectral heterogeneity index in anthropogenic landscapes could be a powerful method to identify those areas most at risk of biological invasion.

Keywords: biodiversity patterns, free and open-source algorithms, multispectral, satellite images, spectral diversity maps, spectral heterogeneity maps, vegetation plots

INTRODUCTION

As there is an urgent need to protect rapidly declining global diversity (IPBES 2019), it is important to identify methods to quickly estimate the diversity and heterogeneity of a region and effectively implement monitoring and conservation plans. It is well known that biodiversity assessment through field surveys has a very high cost both in terms of time and money. Economic limitations often cause the inability to implement monitoring programs based on large-scale fieldwork (Vihervaara et al. 2017). Biodiversity monitoring programs must be planned on a sound basis to obtain quality information and three aspects are considered particularly relevant, i.e., sampling design, sample size and type of statistical analysis (Yoccoz et al. 2001, Maccherini et al. 2020). These requirements make it complex to obtain statistically valid monitoring data for better understanding and modeling of biodiversity over space and time (Rocchini et al. 2021a). In contrast to traditional monitoring, earth observation based on airborne and satellite systems is particularly important for biodiversity monitoring, as it allows the observation of regions that may be easily accessible or even remote with a high spatial and temporal resolution, thus enabling the production of maps for modeling and monitoring diversity from local to global scales (Féret et al. 2017; Rocchini et al. 2016, 2018). Operational methods for detecting biodiversity patterns and ecosystem heterogeneity using remote-sensing data shall require minimum supervision and should not rely on extensive ground-based data collection, as they should be non-expensive and ready-to-use methods (Féret and de Boissieu 2020). From this point of view, the development of Free and Open-Source algorithms to measure and monitor biodiversity and/or ecosystem heterogeneity from space provide robust, reproducible, and standardized estimates of ecosystem functioning and services (Rocchini and Neteler 2012).

The combination of remotely sensed and field-collected data represents one of the most promising approaches to boost large scale and reliable biodiversity monitoring practices (Vihervaara et al. 2017). To date, much research has considered the relationships between remotely sensed and field sampled data (e.g., Palmer et al. 2002; Rocchini et al. 2015a; Lausch et al. 2020), under the paradigm of the Spectral Variation Hypothesis (SVH), proposed for the first time by Palmer et al. (2002) and further developed by Rocchini et al. (2004, 2010). This concept hypothesizes that the variability of the spectral response of a remotely sensed image could be used as a proxy to assess plant biodiversity. The ability of SVH to detect plant diversity was tested on several ecosystems covering large areas (e.g., Féret and Asner 2014; Heumann et al. 2015; Torresani et al. 2019), but few studies (e.g., Marzialetti et al. 2021) have investigated SVH application at a greater level of detail over small, complex, and heterogeneous areas.

Typically, in these studies, diversity is defined in term of α and β components (Whittaker 1960, 1972), accounting for taxonomic diversity in ground-based data as well as for spectral diversity in remotely sensed data. Specifically, α diversity represents local diversity or diversity within a community and β diversity represents compositional variation among communities. Furthermore, another often neglected component of ecological diversity is represented by ecosystem heterogeneity that is linked to a range of ecological processes and functions that, in addition to species diversity patterns and change (Rocchini et al. 2018), includes metapopulation dynamics (Fahrig 2007), population connectivity (Malanson and Cramer 1999) or gene flow (Lozier et al. 2013).

Here, we decided to test the potential of SVH to capture information on plant diversity at fine scale in a complex landscape, computing both traditional α and β components and ecosystem heterogeneity via remote sensing. Two new and promising methodological approaches for estimating α and β spectral diversity and ecosystem heterogeneity have been tested using the R packages "`biodivMapR`" (Féret and Asner 2014; Féret and de Boissieu 2020) and "`rasterdiv`" (Marcantonio et al. 2021; Rocchini et al. 2021b) respectively. Specifically, we investigated whether spectral diversity and heterogeneity can be used as proxies for taxonomic diversity and landscape heterogeneity. In more detail, i) we examined whether spectral diversity, considered as α and β diversity, can be compared with α and β taxonomic diversity and with what degree of relationship and ii) whether spectral heterogeneity (in pixel reflectance variation) is related to ecosystem, landscape heterogeneity and plant diversity in a complex landscape, where natural and anthropogenic elements interact, and thus whether this data can be used to assess and/or monitor plant diversity and its dynamics in an Ecological Network (EN) or more generally in natural environments over time.

We tested the reliability of the two methodological approaches on an EN in Friuli Venezia Giulia region (north-eastern Italy), which was developed at the local scale in the context of the Regional Environmental Landscape Plan (Sigura et al. 2017). The considered EN was modelled as a composite multi-species ecological network where the nodes (natural habitats), corridors (links between natural habitats) capture favorable conditions for biodiversity in an agricultural landscape matrix. Most of these natural habitats are wetlands which are vulnerable ecosystems extremely important for the maintenance of biodiversity and among the most exploited and impacted by human activity especially in Europe (Jones and Hughes 1993; European Commission 2007; Jantke et al. 2011). These environments are usually characterized by marked vegetation zonation, associated with the environmental gradients, determined primarily by hydrology (Liccari et al. 2020), which permits one to host numerous species, including rare and endemic ones.

METHODS

Study site

This study was carried out in the lowlands of the Friuli Venezia Giulia region (NE Italy; centroid coordinates: 45°48'13.4" N - 13°08'11.0" E; Figure 4.1). The study area has an extent of 298 km^2 including vast agricultural area bordered by two river systems (Stella and Corno, respectively). The landscape is characterized by a mixed mosaic of intensively and extensively cultivated areas, settlements, semi-natural and natural habitats, including eight Natura 2000 Special Area of Conservation (Habitats Directive 92/43/EEC) and nine regional protected sites (biotopes), mainly connecting wetland habitats.

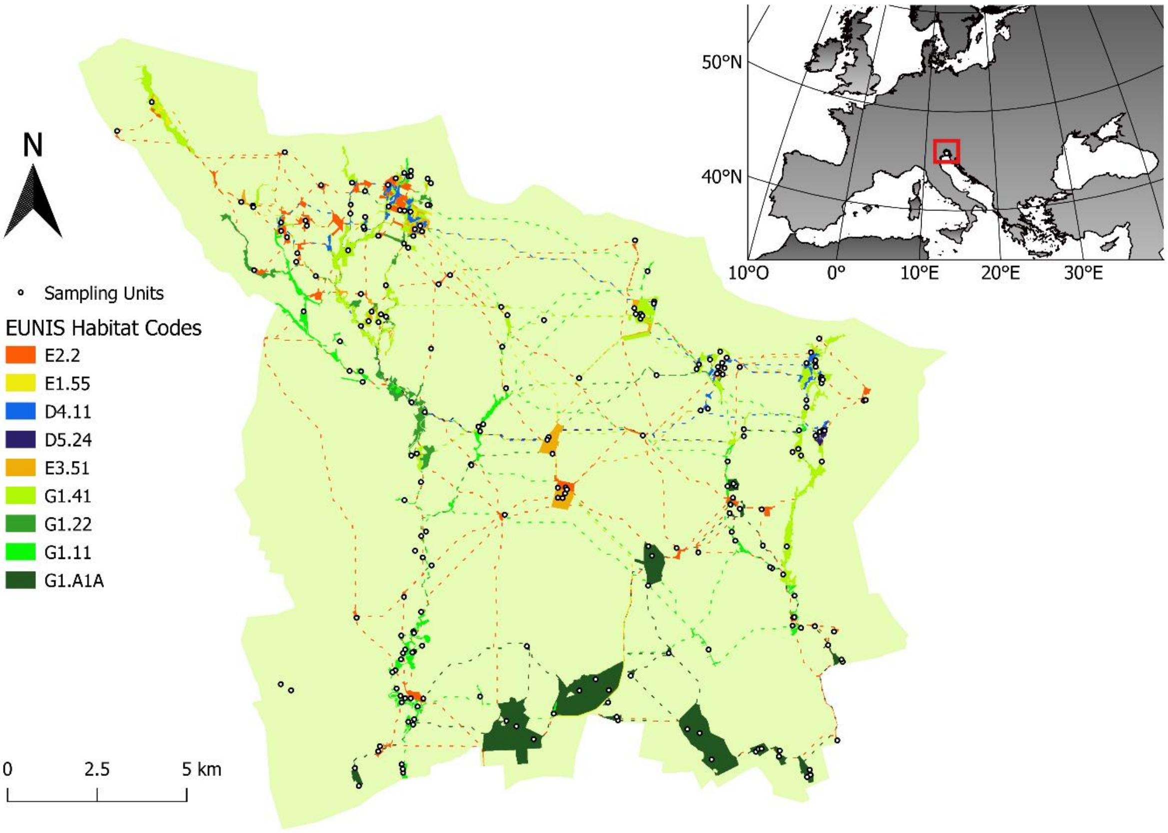

Figure 4.1: Study area, representation of the Ecological Network model with natural habitat patches as nodes (colored polygons) and corridors as links (dotted lines), and location of the sampling units.

The geology of the area consists mainly of Quaternary sand, silt and silt-clay sediments formed by glacial fluvial transport during the Pleistocene and by alluvial deposition during the Holocene. The area is characterized by an average annual temperature of about 13°C and an average annual precipitation between 1100 and 1400 mm.

The natural habitats of the area are woods, meadows and fens and have been classified following EUNIS habitat classification (Davies et al. 2004; Chytrý el al. 2020). Specifically part of the forests are dominated by *Carpinus betulus* and *Quercus robur* (EUNIS habitat codes G1.A1A) while the wet forests by *Alnus glutinosa*, *Fraxinus* spp., and *Salix* spp. (EUNIS habitat codes F3.23, F9.2, G1.11, G1.22, G1.41), dry meadows are characterized by *Arrhenatherum elatius*, *Brachypodium rupestre*, *Bromopsis erecta*, *Carex* spp., *Chrysopogon gryllus*, *Festuca rubra*, *Filipendula vulgaris*, *Lolium* spp., *Lotus* spp., , *Trifolium* spp. (EUNIS habitat codes E1.55, E2.2) while wet meadows by *Carex* spp., *Molinia* spp. and *Filipendula* ulmaria (EUNIS habitat codes E3.4, E3.51) and fens by *Armeria helodes* (endemic), *Cladium mariscus*, *Equisetum palustre*, *Frangula alnus*, *Lysimachia vulgaris*, *Molinia caerulea*, *Potentilla erecta*, *Salix cinerea*, *Scirpoides holoschoenus*, *Schoenus nigricans*, and *Senecio fontanicola* (endemic; EUNIS habitat codes D4.11, D5.24).

Data collection and analysis

Sampling units

Data on plant richness and composition have been collected during a field campaign realized to characterize plant diversity in the EN (see previous Chapters). All EN nodes with an area over 1 ha were sampled. The sampling design chosen was hierarchical, with each habitat type sampled within each node, proportional to habitat extent within the node (see Table S3.1 from Chapter 2). Sampling density in relation to habitat extent was chosen as follows: a square plot of 100 m^2 was randomly placed for a habitat area < 5 ha, 2 plots for an area ≥ 5 and ≤ 10 ha, and finally 3 plots for an area > 10 ha. A total of 219 plots were randomly selected within the EN, corresponding to an overall sampling density of 0.13 plot/ha. Presence and abundance (% visual cover estimate) of each vascular plant species rooted in each plot were recorded. Nomenclature and taxonomy of species followed Bartolucci et al. (2018) for native species and Galasso et al. (2018) for alien species. Data were collected in the spring and summer of 2019 (193 plots) and 2020 (26 plots).

Satellite data

The SVH has been tested using Sentinel-2 Level 2A (bottom of atmosphere, which is already atmospherically corrected) multispectral images with tile 33TUL for the year 2019, downloaded from Copernicus Open Access Hub (Copernicus Open Access Hub 2021). The reflectance signal of the vegetation was derived from the Sentinel-2A's multispectral instrument (MSI) on board, that measures the solar electromagnetic spectrum from 457 nm to 2280 nm with 13 bands.

The images were further processed using SNAP-ESA Sentinel Application Platform (ESA SNAP Homepage 2021) to select the bands of interest (bands: 2, 3, 4, 5, 6, 7, 8, 8A, 11, 12), scaling them all to 10 m x 10 m spatial pixel resolution using bilinear interpolation, and finally to crop the images with the extent of the study area. The selected bands were blue (B02, 458–523 nm), green (B03, 543–578 nm), red (B04, 650-680 nm), three red edges (B05, 698-713 nm; B06, 733-748 nm; B07, 773-793 nm), near infrared (B08, 785–899), near infrared narrow (B08A, 855-875 nm), and two short wave infrareds (B11, 1565-1655 nm; B12, 2100-2280 nm).

Spectral diversity estimation

We used the R package "`biodivMapR`" (Féret and Asner 2014; Féret and de Boissieu 2020) for estimating spectral α and β diversity. The estimation method is based on the SVH and takes advantage of high spatial resolution multispectral information to differentiate species or groups of species based on the optical traits corresponding to the reflectance of each pixel (Ustin and Gamon 2010; Homolová et al. 2013; Féret and de Boissieu 2020). We considered taxonomic diversity in ground-based data and spectral diversity in remotely sensed data. In general, α diversity, here taxonomic or spectral, summarizes the number of different elements (species or reflectance spectrum values) within sampling units and can be expressed as richness (i.e., the number of species) and evenness (i.e., their relative abundance) (Whitaker 1960, 1972; Féret and Asner 2014). To consider both richness and evenness and compare spectral and taxonomic diversity values, we computed species richness and Shannon diversity index (H', Shannon 1948), the latter varies from 0 in plots with one dominant species to an undetermined maximum in plots with equally abundant species.

β diversity, whether taxonomic or spectral, represents the variation among sampling units in both composition and abundance values (Whittaker 1960, 1972; Féret and Asner 2014). β diversity in remotely sensed and field data was analyzed using the Bray–Curtis (BC) dissimilarity index (Bray and Curtis 1957). This dissimilarity index is defined as the sum over the whole species of the ratio between the difference of abundance values and the sum of abundance values for each species, and it represents the vegetation plots (or spectral value of the pixels) pairwise differences using quantitative species abundance data. The BC dissimilarity index ranges between 0, when two plots share the same elements, to 1, when the two sampling units are totally different.

The package supports only one multispectral raster image at a time in its functions. Thus, we chose to use a satellite image taken on 03 June 2019, as it was the period with the most active green biomass and the most ground surveys carried out. The Sentinel 2 multi-spectral image was filtered to remove non-vegetated, shaded, and cloudy pixels as suggested by Féret and de Boissieu (2020). The applied thresholds were as follows: 1) Normalized Difference Vegetation Index (NDVI) higher than 0.4 to exclude non-vegetated/dry vegetation pixels, 2) NIR > 1500 to remove shaded areas as these are characterized by low overall reflectance, and 3) blue < 500 to ignore cloudy pixels as residuals from atmospheric corrections may lead to increased reflectance in the blue domain (Féret and de Boissieu 2020).

After the filtering, a Principal Component Analysis (PCA) was performed on a random sub-set (21% ca) of the image to ensure computational efficiency. The result of this PCA has been then applied to order the whole image. Subsequently, a second filtering based on PCs thresholding was applied discarding automatically the pixels showing values beyond the mean PC value ±3 standard deviations for any of the first five components and the mask was updated accordingly. Finally, the PCA preprocessing, including random pixel selection was applied a second time with the updated mask. Based on PCA results, relevant features for biodiversity mapping were selected considering the PCA outputs.

Spectral species mapping, based on k-means clustering of the components selected from the PCA, was performed setting number of clusters parameter to 50. This value was suggested by Féret and de

Boissieu (2020) for tropical forests, but it was also indicated that the number of clusters should be set according to the level of heterogeneity of the landscape under study, in our case quite high.

The α and β spectral diversity maps were produced through the computation of three indexes (i.e., species richness and H’ for α diversity and BC for β diversity), based on the distribution of clusters in the spectral species map for a window size set of 6 x 6 pixels over the whole image. The smaller the window, the more accurate the estimate, but small windows may not contain a sufficient number of pixels. For this reason, we decided to use a window of 6x6 pixels as a compromise. Finally, spectral diversity index values were extracted for the sampled plots (plots containing less than three pixels were discarded) in order to compare field inventories with diversity indices estimated by the “`biodivMapR`” package. We compared these values by linear regression, correlation analysis and using the R package “`Metrics`” (Hamner and Frasco 2018) that computes evaluation metrics (i.e., RMSE, bias) that are commonly used in supervised machine learning to compare actual and predicted values.

Spectral ecosystem heterogeneity estimation

The “`rasterdiv`” package (Marcantonio et al. 2021) provides a flow of functions based on information theory and generalized entropy, incorporating abundance information for each informative value but also on the relative numerical distance between these values (Rocchini et al. 2021b). We used this package for calculating the Rao's Quadratic heterogeneity measure (Rao's Q; Rao 1982). It can be defined as the expected difference in reflectance values between two pixels drawn randomly with replacement from the evaluated set of pixels. The 10 selected bands from the Sentinel image of 03 June 2019 were re-scaled to 8-bit radiometric resolution as suggested by the authors (Rocchini et al. 2021b) and a moving window of 9 × 9 pixels was used for calculating the index (Q_{multi}) and the weight for the distance matrix (alpha) was set to 1, 5 and infinite (see package vignette for more details, Marcantonio et al. 2021). A larger window was used here since in this case the larger the window the greater the accuracy of the heterogeneity index. For this reason, we decided to use a window of 9 x 9 pixels and not 6 x 6 as in the previous case.

In addition, we also calculated the Rao's Q on an NDVI time series (i.e., one image per month for the year 2019; Q_{NDVI}) rescaled to 8-bit radiometric resolution, with a moving window of 9 x 9 pixels and alpha set to 1, 5 and infinite. Here again, Rao's Q values were extracted for all the sampled plots and the relationships between spectral heterogeneity and field data were estimated using Generalized Additive Models (GAM) and transformation-based Redundancy Analysis (tb-RDA). We hypothesized that in a highly heterogeneous landscape, such as the one under study, relationships were to be sought between spectral heterogeneity, landscape heterogeneity, and the amount of native and alien species. For this reason, in the GAMs we considered Rao's Q values deriving from both NDVI time series (Q_{NDVI}) and multispectral single image (Q_{multi}) as response variables and ratio of alien to native species richness (RatioAN) and Shannon index for land use category (ShannonLU) calculated in an area of 250 m around the plots as predictive variables.

Six GAMs were considered, the response variables were alternatively $Q_{NDVI}1$, $Q_{NDVI}5$, $Q_{NDVI}Inf$, $Q_{multi}1$, $Q_{multi}5$, $Q_{multi}Inf$, and the predictive variables were always ShannonLU as smooth term and RatioAN as linear term.

Regarding β diversity, the contribution of previous variables (Q_{multi}, RatioAN and ShannonLU) with the addition of three other variables (i.e., native species richness, N.Nat; focal species richness, N.Foc; and habitat type) to the observed community composition, was considered using tb-RDA (Legendre and Gallagher 2001). Q_{NDVI} and alien species richness were not considered as they were highly collinear with Q_{multi} and RatioAN respectively. The tb-RDA was based on Hellinger (Legendre and Legendre 2012) pre-transformed species composition matrix. Species abundances were log transformed before Hellinger transformation was done. These transformations were made possible as tb-RDA supports the use of many data transformations to perform ordination, offering much more flexibility for the analysis of community data (Blanchet et al. 2014). Variation partitioning was then computed in order to assess which group of variables (habitat, land use and Rao's Q) contributed more to explain the variability in the community composition.

RESULTS

Comparison of α and β spectral diversity vs measured taxonomic diversity

The resulting α and β spectral diversity maps, obtained from the "`biodivMapR`" package, are shown in Figure 4.2.

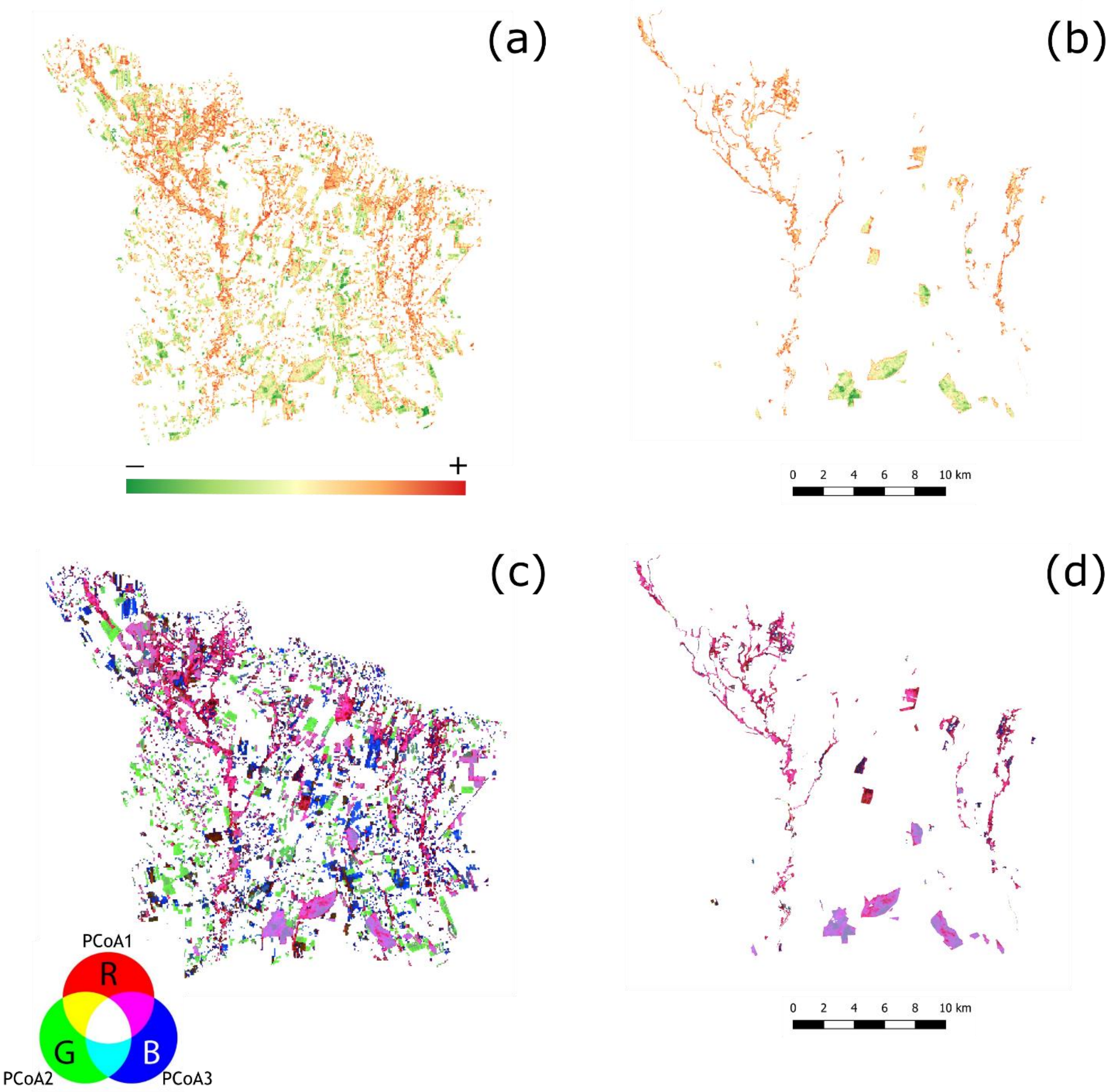

Figure 4.2: Spectral α diversity map, expressed as Shannon index, of the study area (a) and of the EN nodes (b). Spectral β diversity map, expressed as Bray-Curtis dissimilarity index, produced by the projection of the n × n dimensional space of the dissimilarity matrix into an n × 3 dimensional space (PCoAs), of the study area (c) and of the EN nodes (d).

The comparison between the observed values of α and β taxonomic diversity calculated from sampled plots and the ones remotely estimated via the "`biodivMapR`" are reported below.

The regression between observed taxonomic and estimated spectral species richness (Figure S4.1a) gave an RMSE = 16.68 and a bias = 15.15 that indicate a high underestimation of the number of species. We also computed the Pearson correlation between the observed species richness and the estimated one obtaining a value of 0.16 ($p = 0.03$). This result was partly expected considering the study of Féret and Asner (2014) where they observed an underestimation that could be explained by the limited number of spectral species compared to the maximum taxonomic diversity. However, as stated by Féret and Asner (2014), it can be easily corrected with a linear factor derived from the relationship obtained between field data and estimation (for example in our case by 0.4 Figure S4.1b). The regression between observed taxonomic and estimated spectral *H'* (Figure S4.2) yielded an RMSE = 0.39 in *H'* units and a bias = -0.01 that indicated a slight overestimation of *H'*. We also computed the Pearson correlation between the observed *H'* and the estimated *H'* obtaining a value of 0.53 ($p < 0.001$). The regression between observed taxonomic and estimated spectral BC (Figure S4.3) yielded an RMSE = 0.17 in BC units and a bias = 0.06 that indicated a slight underestimation of BC dissimilarity. Mantel correlation between the observed BC and the estimated one yielded a value of 0.48 ($p < 0.001$).

The spectral β diversity map, expressed as BC dissimilarity index, produced by the projection of the $n \times n$ dimensional space of the dissimilarity matrix into an $n \times 3$ dimensional space (PCoAs, Figure 4.2c,d), presents a good estimate of natural habitats, showing a distribution along the positive PCoA1 axis for 79% of the pixels contained in the nodes of the EN.

Spectral heterogeneity vs landscape heterogeneity and taxonomic plant diversity

The resulting Q_{NDVI}Inf and Q_{multi}Inf spectral heterogeneity maps, obtained from the "`rasterdiv`" package, are shown in Figure 4.3.

We observed significant relationships in all GAMs between spectral heterogeneity, land use diversity, and alien native species richness ratio, except for the term RatioAN in Q_{multi}1 GAM (Table 4.1, Figure S4.4). The adjusted R^2 increased as the weight for the distance matrix was higher for both Q_{NDVI} and

Q_{multi} GAMs. Comparing the models with the same distance weight, those with Q_{multi} had always a higher goodness-of-fit (Table 4.1).

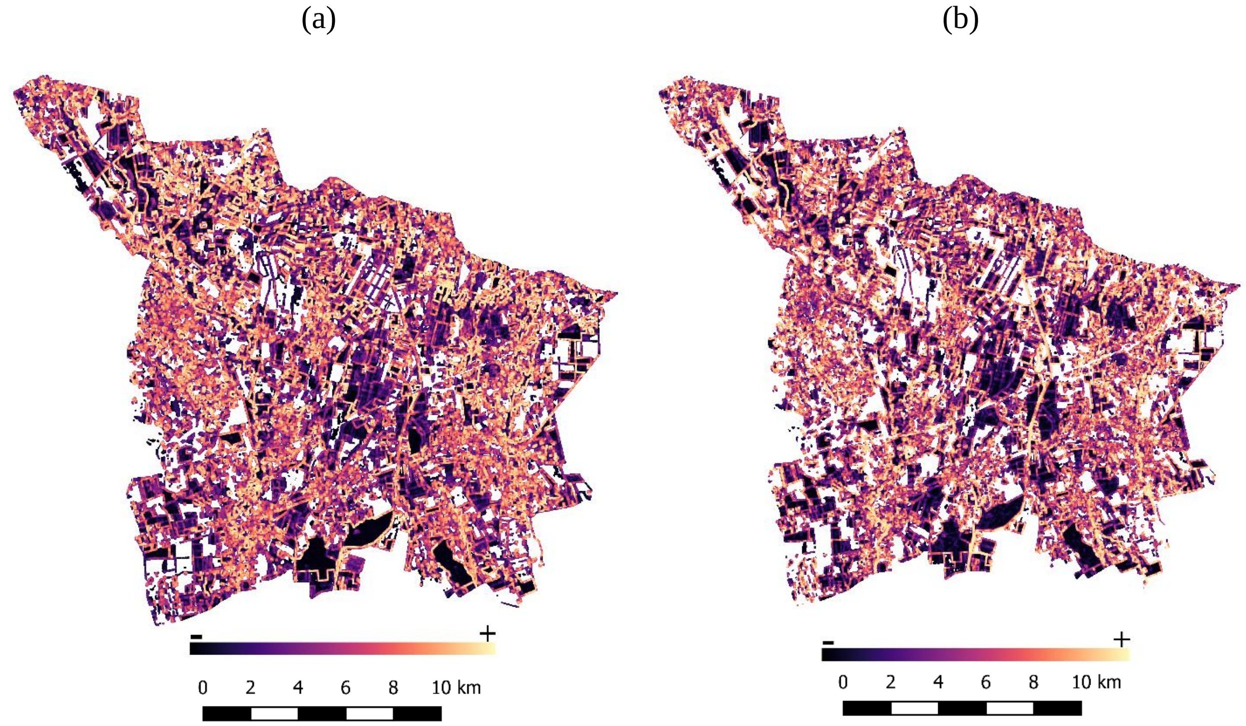

Figure 4.3: Rao's Q index, calculated from the NDVI time series covering the year 2019 (Q_{NDVI}) with the weight for the distance matrix set to infinite, for the study area (a). Rao's Q index, calculated from the 10 bands of the Sentinel 2 image of 03 June 2019 (Q_{multi}) with the weight for the distance matrix set to infinite, for the study area (b).

The best model ($R^2 = 0.43$) was the one using the Q_{multi} with the highest distance weight. The linear term RatioAN was always positive related to Rao's Q in all models, while the smooth term ShannonLU was more positively related to Rao's Q the greater the distance weight considered (Figure S4.4).

Table 4.1: Summary of generalized additive models (GAMs) for spectral heterogeneity (Rao's Q index calculated from NDVI timeseries (Q_{NDVI}) and from a multispectral image (Q_{multi}) with three different weights for the distance matrix (i.e., 1, 5, infinite) vs. alien native species richness ratio (RatioAN, linear term) and Shannon index calculated on land uses (ShannonLU, smooth term). Est. ± SE = estimate ± standard error; Edf = effective degrees of freedom.

$Q_{NDVI}1$ ~ RatioAN + s(ShannonLU)				**$R^2 = 0.21$**
Terms	**Est. ± SE**	**p-value**	**Edf**	**p-value**
Intercept	45.43 ± 1.95	< 0.001	-	-
RatioAN	51.82 ± 19.83	0.010	-	-

Smooth (ShannonLU)	-	-	2.25	< 0.001
$Q_{NDVI}5$ ~ RatioAN + s(ShannonLU)				**$R^2 = 0.25$**
Intercept	76.36 ± 3.49	< 0.001	-	-
RatioAN	99.34 ± 35.60	0.006	-	-
Smooth (ShannonLU)	-	-	3.37	< 0.001
$Q_{NDVI}Inf$ ~ RatioAN + s(ShannonLU)				**$R^2 = 0.27$**
Intercept	282.50 ± 12.34	< 0.001	-	-
RatioAN	347.65 ± 125.88	0.006	-	-
Smooth (ShannonLU)	-	-	3.67	< 0.001
$Q_{multi}1$ ~ RatioAN + s(ShannonLU)				**$R^2 = 0.25$**
Intercept	51.92 ± 1.59	< 0.001	-	-
RatioAN	18.02 ± 16.20	NS	-	-
Smooth (ShannonLU)	-	-	3.34	< 0.001
$Q_{multi}5$ ~ RatioAN + s(ShannonLU)				**$R^2 = 0.41$**
Intercept	92.52 ± 2.40	< 0.001	-	-
RatioAN	72.55 ± 24.55	0.003	-	-
Smooth (ShannonLU)	-	-	4.64	< 0.001
$Q_{multi}Inf$ ~ RatioAN + s(ShannonLU)				**$R^2 = 0.43$**
Intercept	368.62 ± 9.64	< 0.001	-	-
RatioAN	401.20 ± 98.43	< 0.001	-	-
Smooth (ShannonLU)	-	-	4.51	< 0.001

The tb-RDA ordination explained 36.20% of the variance, the first three axes accounting for 11.30%, 10.15% and 5.41% of the total explained variance, respectively (Figure 4.4). The first seven axes out of eighteen exceeded the threshold of statistical significance ($p < 0.05$). The first axis was correlated with native (N.Nat) and focal (N.Foc) species richness and ratio of alien to native species richness (RatioAN) and the second with land use diversity and spectral heterogeneity (ShannonLU and $Q_{multi}Inf$, Figure 4.4, S4.5). The axes from three to seven mainly described the difference between plant community composition in different habitats dictated by the presence of hygrophilous or xerophilous, woodland or grassland species. Forest habitats were mainly distributed along the second axis based on a gradient of spectral heterogeneity (RDA2 -0.54), land use diversity (RDA2 -0.44) and ratio of alien to native species richness (RDA2 -0.38) while fens and meadows were distributed on the first and third axes along a gradient of focal (RDA1 -0.40; RDA3 -0.38) and native species richness (RDA1 -0.37; RDA3 0.36). These gradients showed that higher values of Rao's Q spectral heterogeneity were more related to wet habitats, and with those habitats where the land use diversity of the surrounding landscape was higher, features that are also known to often promote plant invasion.

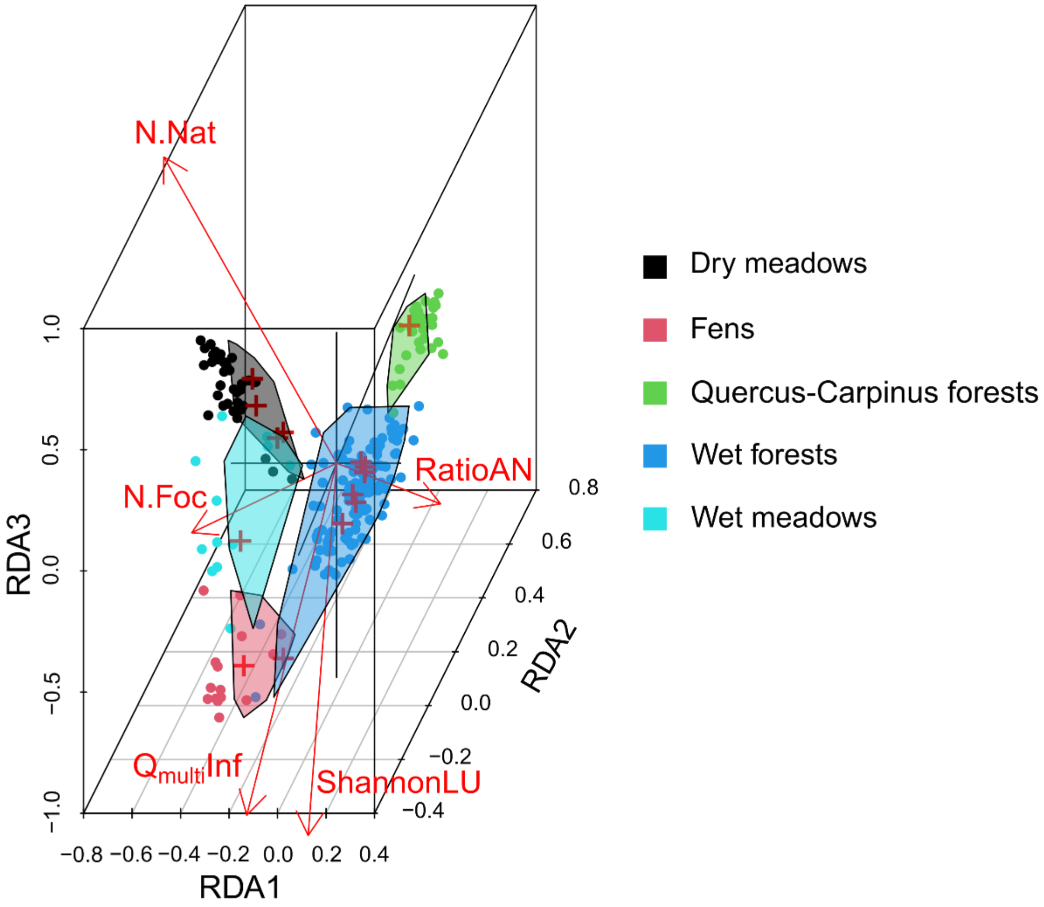

Figure 4.4: tb-RDA ordination based on Hellinger pre-transformed species composition matrix, with site grouped per habitat and displaying the following variables: focal species richness (N.Foc), native species richness (N.Nat), Rao's Q index, calculated from the 10 bands of the Sentinel 2 image of 03 June 2019 with the weight for the distance matrix set to infinite (Q_{multi}INF), and ratio of alien to native species richness (RatioAN), Shannon index on land use diversity (ShannonLU).

The variation partitioning on species composition data highlighted that habitat was the main explanatory factor, accounting for 29% of the total variation (Figure 4.5). Interestingly, spectral heterogeneity and land use diversity contributed only to 8% of total variation, with the latter almost completely negligible in explaining plant community variations.

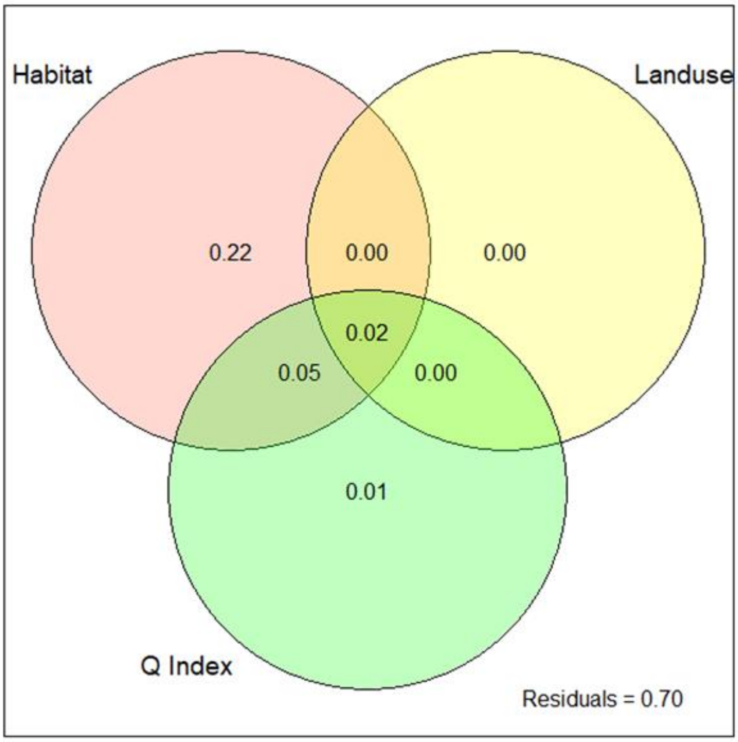

Figure 4.5: Partition of the variation of the community matrix according to the three explanatory variable groups, namely habitat, land use heterogeneity, and spectral heterogeneity (Rao’s Q index).

DISCUSSION

This research aimed at investigating the use of SVH in a complex and anthropogenic landscape, using two new and promising methodological approaches for estimating α and β spectral diversity and ecosystem heterogeneity. Their outputs differed but both gave important information on plant diversity expendable for planning data collection and monitoring campaigns for biodiversity conservation programs.

The relationships between floristic and spectral α and β diversity indices provided evidence of the potential, but also of the limits, of remote sensing data as proxies of plant diversity (Rocchini et al. 2021a). In particular, in our case study, in a heterogeneous and anthropogenic landscape, where natural habitat patches (the nodes of the EN) are embedded in an agricultural matrix, these relationships were slightly weaker in comparison with other studies in homogeneous natural habitats (Nagendra et al. 2010; Hall et al. 2012; Warren et al. 2014; Heumann et al. 2015; Arekhi et al. 2017; Mandosela et al. 2017; Torresani et al. 2019). For example, Féret and Asner (2014), in homogeneous natural forests, reported a weak relationship between observed taxonomic and estimated spectral species richness that could be easily corrected with a linear factor derived from the relationship obtained between field data and estimation, as we also noticed in our results. Moreover, Féret and Asner (2014) in tropical forests reported an underestimation of both α and β diversity indices but with high correlation rates (between 0.73 and 0.86 for α and between 0.61 and 0.75 for β). On the contrary, we observed an overestimation of α diversity (*H'*) and an underestimation of β diversity (BC) and both diversity indexes achieved lower correlation values between floristic and spectral values (i.e., 0.53 and 0.48 respectively). These lower correlation values observed may be determined by the plot dimension (10 x 10 m) in comparison with that of the window used to calculate the spectral species (60 x 60 m): in a highly heterogeneous landscape, such as the one under study, the signal can vary a lot moving away from the sampled plot due to plant community and land use variations, driven by many factor such as habitat type, anthropic pressure, and edge effect (Porensky and Young 2013; Amici et al. 2015). The effect of the grain size on the robustness in the relationship between spectral diversity and taxonomic diversity has been examined by different authors (e.g., Rocchini et al. 2004;

Oldeland et al. 2010) and all of them concluded that the increase of the spatial scale of analysis, from both field and remotely sensed data, increased correlation between spectral heterogeneity and species richness. This issue, defined Modifiable Areal Unit Problem (MAUP), is a well-known pattern in landscape ecology and has been exhaustively discussed and analyzed by Jelinski and Wu (1996). Nevertheless, in our case, the relationship between taxonomic and spectral diversity values became more accurate for high diversity values (Figure S4.1, S4.2, S4.3), thus highlighting that spectral diversity values become more reliable for biodiversity-rich areas that also represent the most important diversity hotspots to be monitored and preserved. In addition, the spectral maps in Figure 4.2 have given evidence of the real differences between plots both in terms of α and β diversity. In fact, taking into consideration the entire study area and the sorting of the β diversity values of the pixels on the three axes of the PCoA (Figure 4.2c,d), it was possible to observe that the majority of the pixels linked to the positive part of the first axis of the sorting, represented in red, corresponded to the forested nodes of the EN.

The results produced by “`rasterdiv`” package (Figure 4.3) highlighted the influence of the surrounding landscape composition and fragmentation on the values expressed by the Rao's Q heterogeneity index. In fact, the areas with higher values of spectral heterogeneity were not those that we would expect to be richer in biodiversity, but those that were characterized by more anthropogenic impact (high values of land use diversity) and so also to biological invasion (high values of alien to native species richness ratio). Remote sensing data can provide information on complex systems, which depend on the original radiometric and spectral resolution, giving different results and interpretations depending on the composition of the study area and the type of existing vegetation. Using an ecological parallelism, the spectral space defined by many bands is analogous to the Hutchinson’s hypervolume, defined by a set of n independent axes corresponding to those variables (abiotic and biotic) shaping species’ niches (Hutchinson 1959; Blonder 2018). In this case, spectral space was expected to be related to both species’ niches and their relative diversity (Thouverai at al. 2021), and this was the case, albeit with a relationship opposite to that expected. That is, greater spectral difference was found to be related to greater ratio of alien to native species richness rather than greater native or focal species richness (Figure 4.4). However, this result should not be neglected as it relates well to the use of remote sensing techniques for monitoring invasive alien plants across vast areas (Rocchini et al. 2015b). Many studies have demonstrated the capability of remote sensing approaches to detect invasive plant species and to map their distribution (Müllerová et al. 2016; Skowronek et al. 2017a, 2017b; Vaz et al. 2018; Lopatin et al. 2019; Ewald et al. 2020) and certainly the use of the Rao's Q heterogeneity index in anthropogenic landscapes could be a powerful method to identify those areas potentially more prone to biological invasion.

GAMs (Table 4.1, Figure S4.4) showed that the greater the weighting between the spectral distance of pixels, the greater the relationship between spectral heterogeneity, land use diversity, and ratio of alien to native richness. It was interesting to observe that Q_{multi} was better explained than Q_{NDVI} by the above-mentioned variables, probably because the amount of spectral information contained in the 10 bands used in Q_{multi} was greater than that contained in the two bands of Q_{NDVI}, albeit the latter was calculated over a longer time frame. Spectral heterogeneity analysis suggests that the indexes can be interpreted in the opposite way (e.g., - Q_{multi} or - Q_{NDVI}), in our case study, and could allow to identify a method to detect core areas within nodes (i.e., patches of natural habitats) of an EN. The core area is the inner part of a node that is less affected by the external impacts and to the edge effects, these latter are important ecological processes that are closely related to species habitat protection (Paton 1994), community dynamics (Fagan et al. 1999), and ecological restoration (Loveridge et al. 2010; An et al. 2021). The analysis of heterogeneity using Rao's Q, can thus represent a new tool to be integrated in the context of EN structure optimization.

Variation partitioning (Figure 4.5) pointed out that the variable contributing the most to explaining differences among communities was habitat while the contribution of land use diversity is completely negligible in this context. Instead, spectral heterogeneity contributes to nearly one-third of the explained variation. This shows that the Rao's Q in complex areas, not dominated by a single habitat, is unable to account for variation among different communities. However, this result also suggests, observing the forests in the ordination plot (Figure 4.4, S4.5), Rao's Q potential to explain variation in the composition of the community in environments dominated by forest habitats.

Our results highlighted the effectiveness of estimating and mapping α and β spectral diversity and ecosystem spectral heterogeneity using remotely sensed images. This is currently a key topic in ecology and could provide landscape managers with rapid and effective tools to estimate and monitor global change (Rocchini et al. 2021a). Moreover, this study confirms once again the robustness and importance of SVH for estimating and monitoring diversity in different habitats (Féret and Asner 2014; Warren et al. 2014; Arekhi et al. 2017; Mandosela et al. 2017; Torresani et al. 2019; Marzialetti et al. 2021). In addition, we suggest experimenting with spectral heterogeneity analysis in the field of landscape ecology (e.g., ENs structure analysis) as well as the use of spectral diversity maps as fast approach in data-poor settings as starting base.

The observed relationship between spectral and floristic diversity, in a complex and anthropogenic landscape, supports SVH as a method to quickly estimate α and β diversity and heterogeneity. Moreover, it is suggested to explore their variation across regions to effectively implement monitoring and conservation plans allowing the production of maps for modeling and monitoring diversity from local to global scales (Féret et al. 2017; Rocchini et al. 2016, 2018), considering also recent innovative contributions for the implementation of multi-temporal analysis with image composition optimization based on seasonal profiles (Praticò et al. 2021), on object or pixel-based techniques (Tassi et al. 2021), implemented on Google Earth engine (Gorelick et al. 2017) or on open-source workflow with combined use of optical and radar data (De Luca et al. 2022).

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General conclusions

Key findings and implications

The broad objective of this Thesis was to provide an insight for testing and monitoring diversity and the factors that influence it in the habitats and nodes of an EN. Specifically, the Thesis explored the plant diversity content present in an EN, evaluating the possible effects of the surrounding landscape on the communities studied and possible methods for monitoring vegetation within habitats and nodes over time.

One of the main conclusions achieved (Chapter 1) relates to reducing sampling effort to assess and monitor plant diversity hosted in the EN over time. The importance of validating ENs obtained through graph analysis, based on land cover maps and/or habitat maps, is widely known (e.g., Foltete et al. 2020). Moreover, the practical implementation of EN planning depends on opportunities, the interest of landowner and other stakeholders, and costs (Bergsten and Zetterberg 2013; Mossman et al. 2015). It is thus fundamental to optimize sampling design to enhance temporal and economic resources and define the minimum effort to adequately represent the biodiversity content of the ENs and in general natural habitats leading to an effective possibility to carry out projects related to biodiversity conservation and smart landscape management.

ENs are increasingly accepted as proactive tools for preserving biodiversity by improving landscape connectivity (Gilbert-Norton et al. 2010; Damschen 2013; Modica et al. 2021) and represent also an effective approach integrating environmental management strategies and landscape planning that can be understood by different actors (De Montis et al. 2016; Keeley et al. 2018; Sahraoui et al. 2021). Therefore, it is crucially important to provide practitioners with practical, field-tested advice for planning effective ENs to support biodiversity. However, plant diversity is often neglected when considering the influence of landscape connectivity on biodiversity (but see Uroy et al. 2019; McLeish et al. 2021). Another conclusion achieved in this Thesis (Chapter 2) relates precisely to the study of plant diversity as a function of landscape structure and connectivity considering two investigation scales, aiming at parsing the interacting effect of landscape structure, surrounding habitats and nodes, and structural connectivity on EN plant diversity. Important information about the plant diversity pattern within the EN was derived, i.e., i) improving connectivity within ENs favors α plant diversity ii) different habitats have different sensibility to landscape configuration iii) semi-natural buffer areas around nodes mitigate the effects of landscape structure; iv) planning nodes both mono-habitat and multi-habitats, increases the biodiversity conserved therein; v) nodes with more compact shapes are to be preferred. These indications highlight where action is needed to optimize the expression and conservation of biodiversity, contributing to an unresolved issue, about the multiplicity of factors that modulate the effects of landscape connectivity on plant communities (Uroy et al. 2019), adding a new element to an answer that likely cannot be unique.

In addition to traditional assessing/monitoring biodiversity methods, it is important to identify new approaches to quickly estimate the diversity and heterogeneity of a region and effectively implement monitoring and conservation plans. As mentioned above economic limitations often cause the inability to implement monitoring programs based on large-scale fieldwork (Vihervaara et al. 2017). In contrast to traditional monitoring, earth observation based on airborne and satellite systems is particularly important for biodiversity monitoring, as it allows the observation of regions that may be easily accessible or even remote with a high spatial and temporal resolution, thus enabling the production of maps for modeling and monitoring diversity from local to global scales (Féret et al. 2017; Rocchini et al. 2016, 2018). The combination of remotely sensed and field-collected data, under the paradigm of the SVH, represents one of the most promising approaches to boost large scale and reliable biodiversity monitoring practices. In the last part of the Thesis (Chapter 3) the potential of SVH to capture information on plant diversity at fine scale has been tested using two new and promising methodological approaches, based on "`biodivMapR`" (Féret and Asner 2014; Féret and de Boissieu 2020) and "`rasterdiv`" (Marcantonio et al. 2021) R packages. The first estimates α and β spectral diversity and the latter ecosystem spectral heterogeneity expressed as Rao's Q heterogeneity measure. I investigated if spectral diversity and heterogeneity provide reliable information to assess and/or monitor floristic diversity hosted in the EN, or in general in natural environments over time. The results showed a positive relationship between taxonomic and spectral diversity and also between spectral heterogeneity, landscape heterogeneity, and amount of alien species in relation to natives. Moreover, the results highlighted the effectiveness of estimating and mapping α and β spectral diversity and ecosystem spectral heterogeneity using remotely sensed images. In addition, it was also observed that spectral diversity values became more reliable for biodiversity-rich areas, representing the most important diversity hotspots to be preserved. While the spectral heterogeneity index in anthropogenic landscapes could be a powerful method to identify those areas most at risk of biological invasion.

Research outlook and future perspectives

Considering that ENs will increasingly represent tools with which to connect and protect the patch of natural habitats containing most of landscapes' biodiversity, it is necessary to study them thoroughly. In fact, the possibility of comparing field surveys in different ENs would lead to a better understanding and optimization of efforts to verify and monitor biodiversity. It would also allow a better understanding of the patterns of diversity in relation to connectivity, with the possibility to distinguish between different ecological roles of the species under study.

Another noteworthy approach is the use of remote sensed data to assess biodiversity, suggesting experimenting spectral diversity with different type of remote sensing instruments (e.g., LiDAR, SAR) and to explore their potential in different application fields such as conservation biology, landscape ecology, and many others. In conclusion, due to rapid biodiversity loss worldwide, identifying actions that can be implemented to reduce the degradation of biodiversity and simplification of landscapes has become crucial and a key topic in the field of landscape ecology and conservation biology. It is mandatory that research make steps forwards to limit and mitigate this irreversible biodiversity erosion.

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Article list

Papers related to this Thesis, published or prepared during the PhD

Liccari F, Sigura M, Tordoni E, Boscutti F, Bacaro G (2022) Determining plant diversity within interconnected natural habitat remnants (ecological network) in an agricultural landscape: a matter of sampling design? Diversity 14(1):12. https://doi.org/10.3390/d14010012

Liccari F, Boscutti F, Bacaro G, Sigura M. Connectivity, landscape structure, and plant diversity across agricultural landscapes: novel insight into effective ecological network planning. (*In prep*.)

Liccari F, Sigura M, Bacaro G. Use of remote sensing techniques to estimate plant diversity within ecological networks: a worked example (*In prep*.)

Side papers published during the PhD

Liccari F, Castello M, Poldini L, Altobelli A, Tordoni E, Sigura M, Bacaro G (2020) Do Habitats Show a Different Invasibility Pattern by Alien Plant Species? A Test on a Wetland Protected Area. Diversity 12(7):267. https://doi.org/10.3390/d12070267

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Supplementary materials to Chapter 1

Table S2.1: Estimated sample size for each habitat based on the slope change in the linear relation between *MultSE* and sample size. The value could not be estimated in habitats with 3 or less replicates (NA = Not assessed, see main text).

Habitat EUNIS	**Estimated sample size (± SE)**
G1.A1A - Illyrian *Quercus* - *Carpinus betulus* forests	8 ± 0.31
G1.41 - *Alnus* swamp woods not on acid peat	7 ± 0.31
F9.2 - *Salix* carr and fen scrub	5 ± 0.23
G1.11 - Riverine *Salix* woodland	8 ± 0.33
G1.223 - Southeast European *Fraxinus* - *Quercus* - *Alnus* forests	4 ± 0.22
G1.224 - Po *Quercus* - *Fraxinus* - *Alnus* forests	NA
F3.23 - Tyrrhenian sub-Mediterranean deciduous thickets	7 ± 0.29
E1.55 - Eastern sub-Mediterranean dry grassland	NA
E2.2 - Low and medium altitude hay meadows	6 ± 0.26
E3.4 - Moist or wet eutrophic and mesotrophic grassland	NA
E3.51 - *Molinia caerulea* meadows and related communities	4 ± 0.18
C3.21 - *Phragmites australis* beds	NA
D5.24 - Fen *Cladium mariscus* beds	NA
D4.11 - *Schoenus nigricans* fens	4 ± 0.21

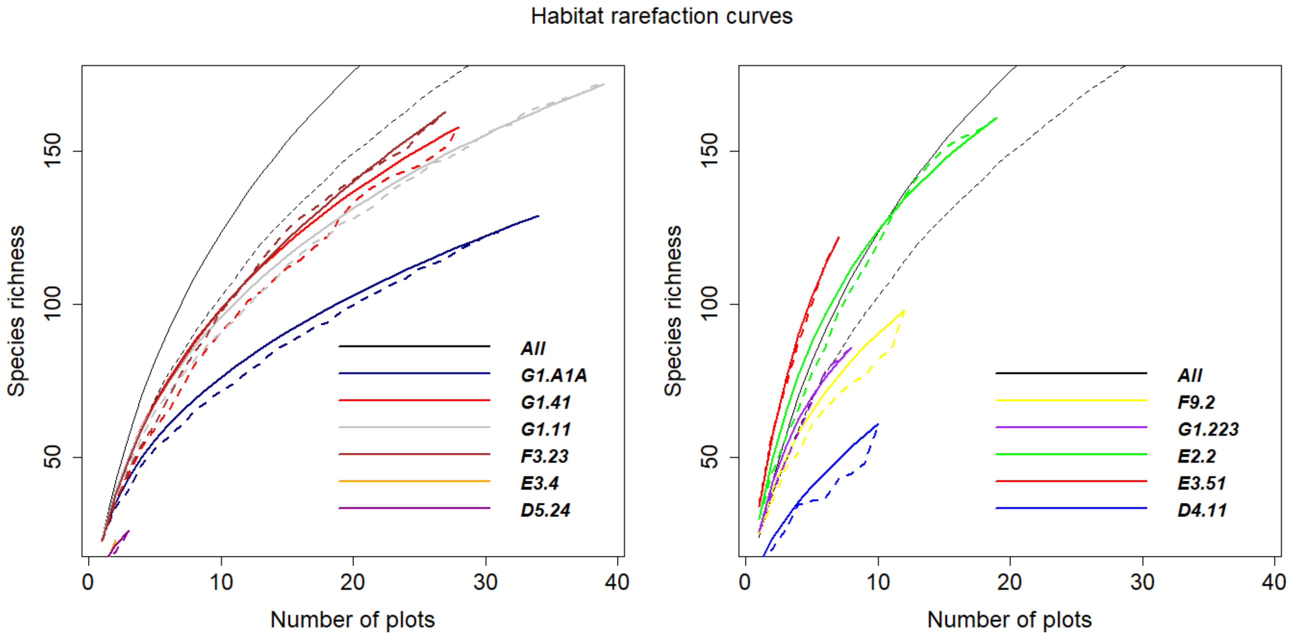


Figure S2.1: Spatially explicit rarefaction curves (SERs, dashed lines) and traditional rarefaction curves (RCs, solid lines) calculated for each habitat of the ecological network. The black solid line represents the RC calculated from the whole dataset.

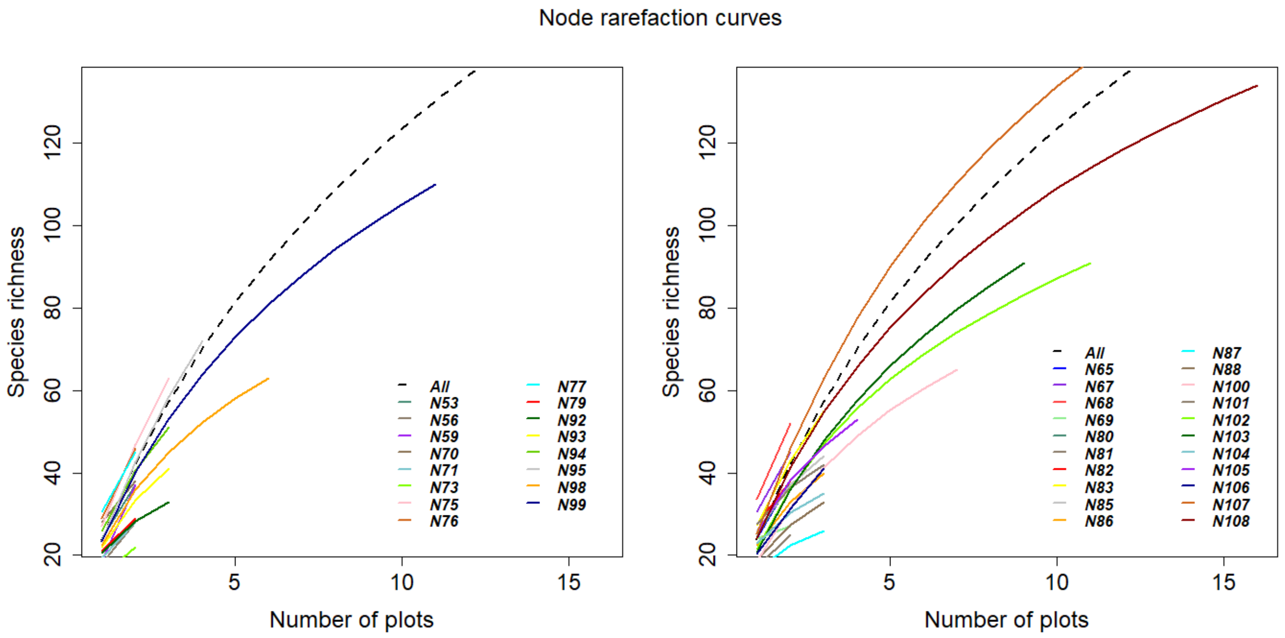


Figure S2.2: Classic rarefaction curves (RCs) calculated for each node of ecological network. The black dashed line represents the RC calculated from the whole dataset.

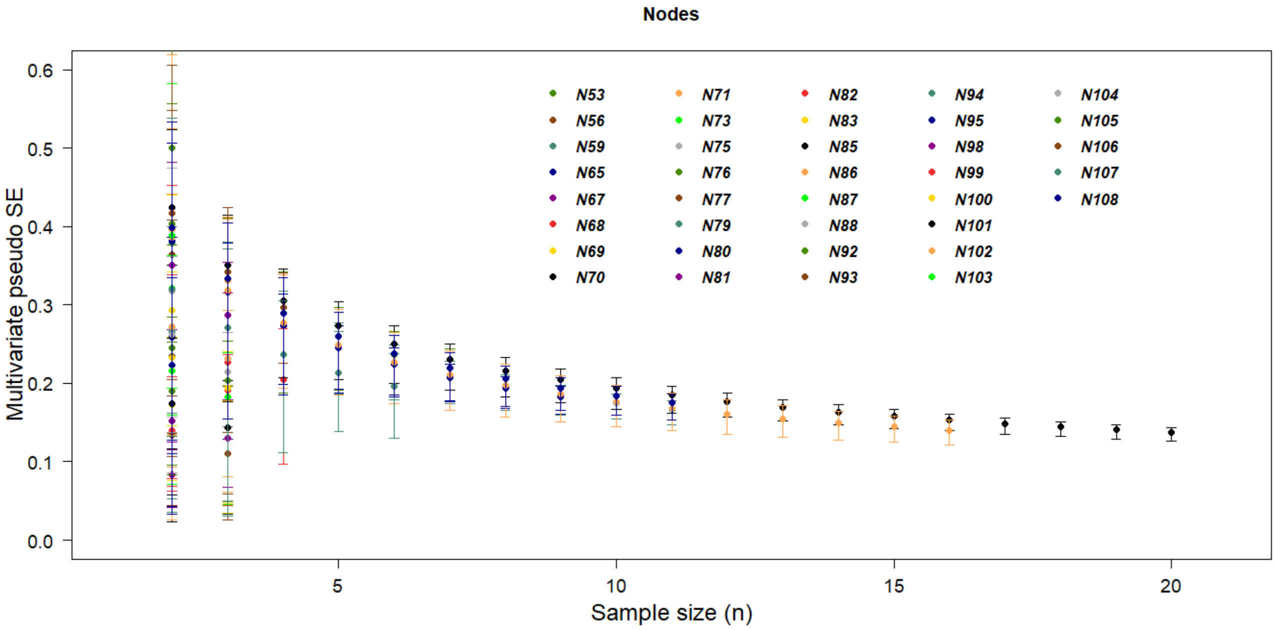


Figure S2.3: *MultSE* profile based on Bray–Curtis dissimilarity for each node within the ecological network.

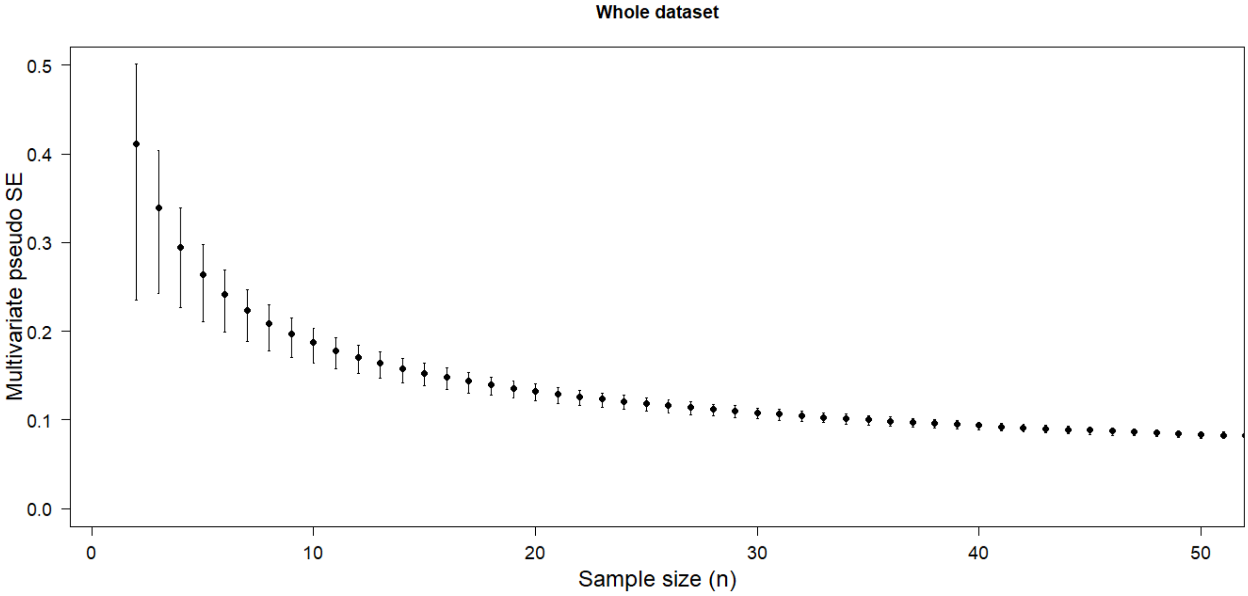


Figure S2.4: *MultSE* profile based on Bray–Curtis dissimilarity for the whole dataset within the ecological network.

Supplementary materials to Chapter 2

Metrics and correlation tables

Habitat scale

All class and landscape level metrics of "`landscapemetrics`" package (Hesselbarth et al. 2019) were used, except for the core area metrics. For more information see the package vignette at: https://cran.r-project.org/web/packages/landscapemetrics/landscapemetrics.pdf

The metrics with more than 25% of NA values were discarded.

Correlation analysis was executed using the R function cor(), estimating coefficients using non-parametric Spearman's ρ, and then the metrics were selected using the function findCorrelation() of the R package "`caret`" (Kuhn 2008) and setting the cutoff to ± 0.7.

Correlation values will be archived along with data supporting the results in an appropriate public repository and the data DOI will be included in the event of publication.

Seven connectivity metrics were calculated on Graphab (Foltete et al. 2012a): betweenness centrality (BC), closeness centrality (CCe), connectivity correlation (CCor), eccentricity (Ec), flux (F), interaction flux (IF) and node degree (Dg). Correlation analysis was executed using the R function cor(), estimating coefficients using non-parametric Spearman's ρ, and then the metrics were selected using the function findCorrelation() of the R package "`caret`" (Kuhn 2008) and setting the cutoff to ± 0.7.

Correlation values are reported in the table below.

	BC	***CCe***	***CCor***	***Ec***	***F***	***IF***	***Dg***
BC	1.00	-0.26	0.50	0.01	0.51	0.48	0.68
CCe	-0.26	1.00	-0.10	0.24	-0.29	-0.19	-0.25
CCor	0.50	-0.10	1.00	-0.07	0.09	0.39	0.82
Ec	0.01	0.24	-0.07	1.00	0.14	0.02	-0.05
F	0.51	-0.29	0.09	0.14	1.00	0.41	0.26

IF	0.48	-0.19	0.39	0.02	0.41	1.00	0.56
Dg	0.68	-0.25	0.82	-0.05	0.26	0.56	1.00

Node scale

All shapes indexes present in Polygon Shape Indices tool were calculated on QGIS (Quantum GIS Development Team 2021) using the EN nodes as the main spatial unit. Namely, perimeter divided by area, perimeter divided by square root of area, maximum distance between to vertices, maximum distance between to vertices divided by area, maximum distance between to vertices divided by square root of area, and shape index (Perimeter / (2 * Square Root (PI * Area))). All shape indexes are obviously interrelated, so we chose the unitless indexes and then the less correlated to the others.

	Per sqrt A	***D sqrt A***	***Shape index***
Per sqrt A	1.00	0.70	1.00
D sqrt A	0.70	1.00	0.70
Shape index	1.00	0.70	1.00

Landscape metrics were calculated for a buffer area of 250 m around each node, taking into accounts the number of land uses, watercourse area, woodland area, hedgerow area, semi-natural woodland area, permanent grassland, agricultural areas with residual natural elements, extensive crops, tree crops, intensive arable land, urban areas and the number of habitats within each node.

Correlation analysis was executed using the R function cor(), estimating coefficients using non-parametric Spearman’s ρ, and just woodland area was correlated with number of habitats and hedgerow area (cutoff ± 0.7).

Correlation values will be archived along with data supporting the results in an appropriate public repository and the data DOI will be included in the event of publication.

Seven connectivity metrics were calculated on Graphab (Foltete et al. 2012a): betweenness centrality (BC), closeness centrality (CCe), connectivity correlation (CCor), eccentricity (Ec), flux (F), interaction flux (IF) and node degree (Dg). Correlation analysis was executed using the R function cor(), estimating coefficients using non-parametric Spearman's ρ, and then the metrics were selected using the function findCorrelation() of the R package "`caret`" (Kuhn 2008) and setting the cutoff to ± 0.7.

Correlation values are reported in the table below.

	BC	***CCe***	***CCor***	***Ec***	***F***	***IF***	***Dg***
BC	1.00	-0.29	0.43	-0.33	0.22	0.29	0.63
CCe	-0.29	1.00	-0.18	0.33	-0.59	-0.35	-0.18
CCor	0.55	-0.18	1.00	-0.10	0.11	0.35	0.89
Ec	-0.33	0.33	-0.13	1.00	-0.18	-0.07	-0.29
F	0.22	-0.59	0.11	-0.18	1.00	0.59	0.03
IF	0.29	-0.35	0.23	-0.07	0.59	1.00	0.26
Dg	0.63	-0.18	0.89	-0.29	0.03	0.26	1.00

Table S3.1: Habitat of the area according to EUNIS habitat classification, belonging group in the models along with descriptive statistics of the study area (i.e., total area, mean area ± standard deviation, number of patches, number of plots and average total, native and alien richness).

EUNIS Habitat	**Group**	**Total area (ha)**	**Mean area ± SD (ha)**	**N. Patches**	**N. Plots**	**Average richness (± SD)**	**Average native richness (± SD)**	**Average alien richness (± SD)**
C3.21 - *Phragmites australis* beds	2. meadows	3.7	3.7	1	1	21.0	20.0	1.0
D4.11 - *Schoenus nigricans* fens	3. fens	77.5	2.8 ± 2.0	28	12	15.1 ± 5.7	15.0 ± 5.5	0.1 ± 0.3
D5.24 - Fen *Cladium mariscus* beds	3. fens	9.9	5.0 ± 5.6	2	3	14.3 ± 4.2	14.3 ± 4.2	0.0 ± 0.0
E1.55 - Eastern sub-Mediterranean dry grassland	2. meadows	33.6	11.2 ± 12.9	3	4	34.8 ± 7.3	34.8 ± 7.3	0.0 ± 0.0
E2.2 - Low and medium altitude hay meadows	2. meadows	149.2	3.7 ± 3.6	40	30	32.0 ± 7.7	29.7 ± 8.1	2.3 ± 1.5
E3.4 - Moist or wet eutrophic and mesotrophic grassland	2. meadows	8.5	4.3 ± 0.2	2	3	17.0 ± 13.2	17.0 ± 13.2	0.0 ± 0.0
E3.51 - *Molinia caerulea* meadows and related communities	2. meadows	50.4	3.7 ± 5.6	19	8	33.9 ± 7.4	33.5 ± 7.0	0.4 ± 0.5
F3.23 - Tyrrhenian sub-Mediterranean deciduous thickets	1. forests and shrublands	186.2	3.6 ± 3.4	46	30	22.4 ± 5.0	19.9 ± 5.2	2.5 ± 1.3
F9.2 - *Salix* carr and fen scrub	1. forests and shrublands	46.6	5.2 ± 4.9	9	12	25.0 ± 5.2	23.0 ± 4.9	2.0 ± 1.3

G1.A1A - Illyrian *Quercus* - *Carpinus betulus* forests	1. forests and shrublands	603.4	31.8 ± 56.2	19	36	23.2 ± 5.6	22.9 ± 5.7	0.3 ± 0.7
G1.11 - Riverine *Salix* woodland	1. forests and shrublands	199.2	6.0 ± 7.9	34	40	23.4 ± 6.9	20.7 ± 6.3	2.7 ± 1.3
G1.223 - Southeast European *Fraxinus* - *Quercus* - *Alnus* forests	1. forests and shrublands	112.5	5.6 ± 4.7	20	9	26.1 ± 4.6	23.0 ± 4.9	3.1 ± 2.5
G1.224 - Po *Quercus* - *Fraxinus* - *Alnus* forests	1. forests and shrublands	1.9	1.9	1	1	18.0	15.0	3.0
G1.41 - *Alnus* swamp woods not on acid peat	1. forests and shrublands	416.4	11.0 ± 15.2	38	30	22.6 ± 5.7	20.7 ± 5.7	1.9 ± 1.5

Table S3.2: Explanatory variables used to build the full models at the habitat and node scales and related references.

Connectivity metrics (both scales)	***References***
Betweenness centrality	Bodin & Saura 2010; Foltete et al. 2012a
Closeness centrality	Freeman 1979
Eccentricity	Urban &Keitt 2001
Flux	Urban & Keitt 2001; Saura & Torné 2009; Foltete et al. 2012b
Interaction flux	Foltete et al. 2014; Sahraoui et al. 2017
Node degree	Freeman 1979
Landscape metrics (habitat scale)	***References***
Coefficient of variation fractal dimension index	Mandelbrot 1977; McGarigal, et al. 2012
Coefficient of variation of patch area	McGarigal et al. 2012
Coefficient of variation perimeter-area ratio	McGarigal et al. 2012
Coefficient of variation of related circumscribing circle	Baker & Cai 1992; McGarigal et al. 2012
Edge density of agricultural land use	McGarigal et al. 2012
Mean area of natural patches	McGarigal et al. 2012
Mean fractal dimension index	Mandelbrot 1977; McGarigal, et al. 2012
Mean fractal dimension index of agricultural land use	Mandelbrot 1977; McGarigal, et al. 2012
Mean of related circumscribing circle of agricultural land use	Baker & Cai 1992; McGarigal et al. 2012
Mean radius of gyration of agricultural land use	Keitt et al. 1997; McGarigal et al. 2012
Mean radius of gyration of natural patches	Keitt et al. 1997; McGarigal et al. 2012
Mean shape index	Patton 1975; McGarigal et al. 2012
Mean shape index of agricultural land use	Patton 1975; McGarigal et al. 2012
Natural patch density	McGarigal et al. 2012
Normalized landscape shape index of agricultural land use	Patton 1975; McGarigal et al. 2012
Normalized landscape shape index of natural patches	Patton 1975; McGarigal et al. 2012
Patch richness	McGarigal et al. 2012
Patch richness density	McGarigal et al. 2012
Percentage of natural patches	McGarigal et al. 2012
Simpson’s diversity index	Simpson 1949; McGarigal et al. 2012
Total edge with anthropogenic land use	McGarigal et al. 2012
Landscape metrics (node scale)	***References***
Maximum distance to square root of area ratio	Forman & Godron 1986; Lang & Blaschke 2007
Agricultural areas with residual natural elements	/
Extensive crops	/
Hedgerow area	/
Intensive arable land	/
Number of habitats	/
Number of land uses	/

Permanent grassland	/
Semi-natural woodland areas	/
Tree crops	/
Urban areas	/
Watercourse area	/

Table S3.3: List of collected species. Type A=alien, N=native, PRE=protected, rare or endemic. % = percentage of occurrence. Protection HD=habitat directive, RRL=regional red list, NRL=national red list, R=rare, E=endemic

Species	Type	%	Protection	Species	Type	%	Protection
Acalypha virginica L.	A	3.20	-	**_Lactuca sativa_ L. subsp. _serriola_ (L.) Galasso, Banfi, Bartolucci & Ardenghi**	N	1.83	-
Acer campestre L.	N	30.14	-	**_Lamium galeobdolon_ (L.) L.**	N	1.83	-
Acer negundo L.	A	5.94	-	**_Lamium maculatum_ L.**	N	2.28	-
Acer pseudoplatanus L.	N	4.11	-	**_Lamium orvala_ L.**	N	6.39	-
Achillea millefolium aggr.	N	2.74	-	**_Lapsana communis_ L.**	N	0.91	-
Aegopodium podagraria L.	N	0.91	-	**_Lathyrus pratensis_ L.**	N	9.59	-
Agrimonia eupatoria L. subsp. _eupatoria_	N	1.83	-	**_Lathyrus venetus_ (Mill.) Wohlf.**	N	1.37	-
Agrostis capillaris L.	N	0.46	-	**_Lathyrus vernus_ (L.) Bernh.**	N	1.83	-
Agrostis gigantea Roth	N	1.83	-	**_Laurus nobilis_ L.**	N	5.02	-
Agrostis stolonifera L.	N	3.65	-	**_Lemna minor_ L.**	N	2.28	-
Ailanthus altissima (Mill.) Swingle	A	0.46	-	**_Leontodon hispidus_ L.**	N	1.37	-
Ajuga reptans L.	N	10.05	-	**_Leucanthemum ircutianum_ DC.**	N	5.02	-
Alisma plantago-aquatica L.	N	1.37	-	**_Leucanthemum platylepis_ Borbás**	PRE	0.46	R
Alliaria petiolata (Bieb.) Cavara & Grande	N	0.46	-	**_Leucojum aestivum_ L.**	N	1.83	-
Allium carinatum L.	N	1.37	-	**_Ligustrum lucidum_ W.T.Aiton**	A	5.94	-
Allium polyanthum Schult. & Schult.f.	N	0.46	-	**_Ligustrum sinense_ Lour.**	A	1.83	-
Allium scorodoprasum L.	A	0.46	-	**_Ligustrum vulgare_ L.**	N	41.10	-
Allium suaveolens Jacq.	PRE	1.37	NRL	**_Limniris pseudacorus_ (L.) Fuss**	N	16.44	-
Allium ursinum L.	N	7.31	-	**_Limniris sibirica_ (L.) Fuss**	PRE	1.37	NRL
Allium vineale L.	N	3.65	-	**_Linum tenuifolium_ L.**	N	0.46	-
Alnus glutinosa (L.) Gaertn.	N	39.27	-	**_Lolium arundinaceum_ (Schreb.) Darbysh. subsp. _arundinaceum_**	N	13.24	-
Alopecurus myosuroides Huds. subsp. _myosuroides_	N	0.46	-	**_Lolium multiflorum_ Lam.**	N	2.74	-
Alopecurus pratensis L. subsp. _pratensis_	N	0.91	-	**_Lolium perenne_ L.**	N	3.65	-
Amaranthus retroflexus L.	A	0.46	-	**_Loncomelos pyrenaicus_ (L.) L.D.Hrouda subsp. _pyrenaicus_**	N	4.11	-
Amorpha fruticosa L.	A	9.59	-	**_Lonicera caprifolium_ L.**	N	14.16	-
Anacamptis laxiflora (Lam.) R.M.Bateman, Pridgeon & M.W.Chase	PRE	0.46	RRL	**_Lonicera japonica_ Thunb.**	A	9.13	-
Anacamptis palustris (Jacq.) R.M. Bateman, Pridgeon & M.W. Chase	PRE	0.46	NRL	**_Lonicera xylosteum_ L.**	N	1.37	-

Anemonoides nemorosa (L.) Holub	N	14.16	-	**_Lotus corniculatus_ L. s.s.**	N	16.44	-
Angelica sylvestris L.	N	3.20	-	**_Lotus herbaceus_ (Vill.) Jauzein**	N	5.48	-
Anisantha sterilis (L.) Nevski	N	0.46	-	**_Lotus maritimus_ L.**	N	0.46	-
Anthericum ramosum L.	N	0.91	-	**_Luzula multiflora_ (Ehrh.) Lej.**	N	0.46	-
Anthoxanthum odoratum L. subsp. _odoratum_	N	4.57	-	**_Lychnis flos-cuculi_ L. subsp. _flos-cuculi_**	N	2.28	-
Anthriscus sylvestris (L.) Hoffm.	N	0.46	-	**_Lycopus europaeus_ L.**	N	5.02	-
Aphanes arvensis L.	N	0.46	-	**_Lysimachia arvensis_ (L.) U.Manns & Anderb.**	N	0.46	-
Arctium minus (Hill) Bernh.	N	0.91	-	**_Lysimachia nummularia_ L.**	N	5.02	-
Aristolochia clematitis L.	N	0.91	-	**_Lysimachia vulgaris_ L.**	N	18.72	-
Aristolochia rotunda L. subsp. _rotunda_	N	1.37	-	**_Lythrum salicaria_ L.**	N	34.25	-
Armeria helodes F.Martini & Poldini	PRE	1.83	HD	**_Malus sylvestris_ (L.) Mill.**	N	0.91	-
Arrhenatherum elatius (L.) P.Beauv. ex J.Presl & C.Presl	N	8.22	-	**_Medicago lupulina_ L.**	N	2.74	-
Artemisia verlotiorum Lamotte	A	0.46	-	**_Medicago sativa_ L.**	A	2.74	-
Artemisia vulgaris L.	N	0.46	-	**_Melica nutans_ L.**	N	0.46	-
Arundo donax L.	A	0.91	-	**_Melittis melissophyllum_ L.**	N	2.28	-
Asarum europaeum L.	N	0.46	-	**_Mentha aquatica_ L. subsp. _aquatica_**	N	6.39	-
Asparagus tenuifolius Lam.	N	9.59	-	**_Mentha longifolia_ (L.) L.**	N	0.46	-
Asperula cynanchica L.	N	0.46	-	**_Mentha spicata_ L.**	N	0.46	-
Asplenium scolopendrium L. subsp. _scolopendrium_	N	0.46	-	**_Mercurialis perennis_ L.**	N	0.46	-
Athyrium filix-foemina (L.) Roth	N	2.28	-	**_Molinia caerulea_ (L.) Moench (incl. _Molinia arundinacea_ Schrank)**	N	14.61	-
Avena barbata Pott. ex Link. subsp. _barbata_	N	3.65	-	**_Morus alba_ L.**	A	1.37	-
Avenula pubescens (Huds.) Dumort. subsp. _pubescens_	N	0.46	-	**_Myosotis ramosissima_ Rochel subsp. _ramosissima_**	N	0.46	-
Bellis perennis L.	N	3.65	-	**_Myosotis scorpioides_ L. subsp. _scorpioides_**	N	1.37	-
Bergenia crassifolia (L.) Fritsch	A	0.46	-	**_Nasturtium officinale_ R.Br.**	N	0.46	-
Berula erecta (Huds.) Coville	N	3.65	-	**_Neottia ovata_ (L.) Bluff & Fingerh.**	PRE	3.65	NRL
Betonica officinalis L.	N	5.48	-	**_Nuphar lutea_ (L.) Sm.**	PRE	0.46	RRL
Bidens frondosa L.	A	4.57	-	**_Oenothera biennis_ L.**	A	1.83	-
Blackstonia perfoliata (L.) Huds.	N	0.91	-	**_Oenothera glazioviana_ Micheli**	A	0.46	-
Bolboschoenus maritimus (L.) Palla	N	0.46	-	**_Ononis spinosa_ L.**	N	2.74	-
Brachypodium rupestre (Host) Roem. & Schult. subsp. _rupestre_	N	11.87	-	**_Oplismenus undulatifolius_ (Ard.) P. Beauv.**	PRE	0.46	NRL

Brachypodium sylvaticum* (Huds.) P.Beauv. subsp. *sylvaticum	N	44.75	-	***Oreoselinum nigrum* Delarbre**	N	1.37	-
***Briza media* L.**	N	2.74	-	***Orobanche gracilis* Sm.**	N	0.46	-
***Bromopsis erecta* (Huds.) Fourr.**	N	5.48	-	***Oxalis articulata* Savigny**	A	4.57	-
***Bromus hordeaceus* L.**	N	7.76	-	***Oxalis corniculata* L.**	N	6.39	-
***Bryonia dioica* Jacq.**	N	1.37	-	***Oxalis stricta* L.**	A	2.28	-
***Buphthalmum salicifolium* L.**	N	3.65	-	***Parietaria officinalis* L.**	N	5.02	-
Calamagrostis epigejos* (L.) Roth subsp. *epigejos	N	0.91	-	***Paris quadrifolia* L.**	N	1.37	-
***Callitriche stagnalis* Scop.**	N	0.46	-	***Parthenocissus quinquefolia* (L.) Planch.**	A	2.28	-
***Caltha palustris* L.**	PRE	2.28	RRL	***Paulownia tomentosa* (Thunb.) Steud.**	A	0.46	-
***Calystegia sepium* (L.) R. Br.**	N	12.33	-	***Pentanema hirtum* (L.) D. Gut.Larr., Santos-Vicente, Anderb., E. Rico & M.M. Mart.Ort.**	N	0.46	-
***Campanula glomerata* L.**	N	1.37	-	***Pentanema salicinum* (L.) D.Gut.Larr., Santos-Vicente, Anderb., E.Rico & M.M.Mart.Ort.**	N	1.83	-
***Carex acutiformis* Ehrh.**	N	5.48	-	***Persicaria lapathifolia* (L.) Delarbre**	N	0.46	-
***Carex caryophyllea* Latourr.**	N	0.46	-	***Persicaria maculosa* Gray**	N	9.13	-
***Carex davalliana* Sm.**	N	0.46	-	***Phalaris arundinacea* L.**	N	0.91	-
***Carex distans* L.**	N	7.31	-	***Phleum pratense* L.**	N	0.46	-
***Carex divulsa* Stokes**	N	6.39	-	***Phragmites australis* (Cav.) Trin. ex Steud.**	N	33.33	-
***Carex elata* All. subsp. elata**	N	2.28	-	***Phyllostachys aurea* Carrière ex Rivière & C.Rivière**	A	0.46	-
***Carex flacca* Schreb.**	N	22.83	-	***Picris hieracioides* L.**	N	1.37	-
***Carex flava* L.**	N	0.46	-	***Pilosella officinarum* Vaill.**	N	0.46	-
***Carex hirta* L.**	N	12.79	-	***Pilosella piloselloides* (Vill.) Soják**	N	0.46	-
***Carex hostiana* DC.**	N	0.46	-	***Pimpinella saxifraga* L.**	N	0.46	-
Carex lepidocarpa* Tausch subsp. *lepidocarpa	N	0.46	-	***Pinus pinaster* Aiton**	N	0.46	-
***Carex montana* L.**	N	0.46	-	***Plantago altissima* L.**	PRE	0.91	NRL
***Carex otrubae* Podp.**	N	4.57	-	***Plantago lanceolata* L.**	N	15.98	-
***Carex pairae* F.W.Schultz**	N	1.37	-	***Plantago major* L.**	N	0.91	-
***Carex pallescens* L.**	N	0.46	-	***Plantago media* L.**	N	0.46	-
***Carex panicea* L.**	N	1.37	-	***Platanthera bifolia* (L.) Rchb.**	PRE	0.46	NRL
***Carex pendula* Huds.**	N	31.51	-	***Platanus hispanica* Miller ex Münchh.**	A	28.77	-
***Carex pseudocyperus* L.**	N	2.28	-	***Poa annua* L.**	N	4.11	-
***Carex remota* L.**	N	12.79	-	***Poa compressa* L.**	N	0.91	-
***Carex riparia* Curtis**	N	2.28	-	***Poa palustris* L. subsp. *palustris***	N	0.46	-
***Carex spicata* Huds.**	N	3.20	-	***Poa pratensis* L.**	N	4.57	-
***Carex sylvatica* Huds.**	N	2.74	-	***Poa sylvicola* Guss.**	N	19.18	-

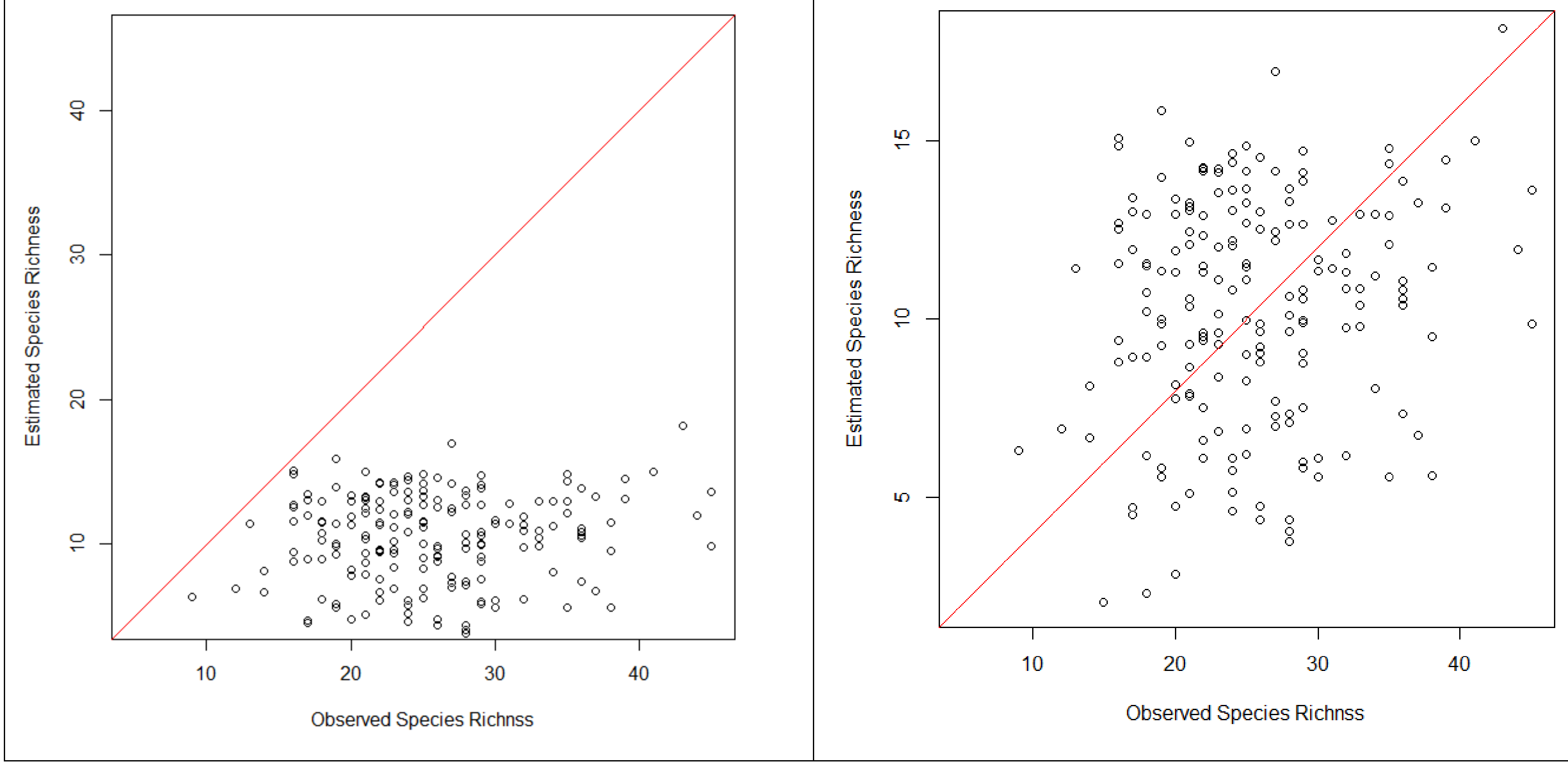
Carex tomentosa L.	N	0.46	-	**_Polygala comosa_ Schkuhr**	N	1.37	-
Carex umbrosa Host subsp. _umbrosa_	N	0.46	-	**_Polygala vulgaris_ L.**	N	0.46	-
Carex vesicaria L.	N	3.65	-	**_Polygonatum multiflorum_ (L.) All.**	N	11.87	-
Carex viridula Michx.	N	1.83	-	**_Polygonatum odoratum_ (Miller) Druce**	N	0.46	-
Carpinus betulus L.	N	16.44	-	**_Populus alba_ L.**	N	2.74	-
Celtis australis L. subsp. _australis_	N	0.46	-	**_Populus nigra_ L. subsp. _nigra_**	N	18.72	-
Centaurea jacea L. subsp. _forojulensis_ (Poldini) Greuter	PRE	5.02	NRL	**_Populus tremula_ L.**	N	0.46	-
Centaurea nigrescens Willd.	N	1.37	-	**_Potamogeton natans_ L.**	N	0.46	-
Centaurea scabiosa L.	N	0.91	-	**_Potentilla erecta_ (L.) Räuschel**	N	11.42	-
Centaurium erythraea Rafn	N	4.57	-	**_Potentilla indica_ (Jacks.) Th.Wolf**	A	14.61	-
Centaurium pulchellum (Sw.) Druce subsp. _pulchellum_	N	0.46	-	**_Potentilla reptans_ L.**	N	39.73	-
Cerastium brachypetalum Desportes & Pers.	N	1.83	-	**_Poterium sanguisorba_ L.**	N	0.91	-
Cerastium holosteoides Fr.	N	0.46	-	**_Primula vulgaris_ Huds.**	N	7.76	-
Cervaria rivini Gaertn.	N	2.28	-	**_Prunella grandiflora_ (L.) Scholler**	N	0.91	-
Chamaeiris graminea (L.) Medik.	N	0.46	-	**_Prunella laciniata_ (L.) L.**	N	0.91	-
Chelidonium majus L.	N	0.46	-	**_Prunella vulgaris_ L.**	N	2.28	-
Chenopodium album L.	N	1.37	-	**_Prunus avium_ L.**	N	5.48	-
Chrysopogon gryllus (L.) Trin.	N	3.65	-	**_Prunus cerasifera_ Ehrh.**	A	0.91	-
Cichorium intybus L.	N	2.74	-	**_Prunus domestica_ L.**	A	3.20	-
Circaea lutetiana L.	N	3.65	-	**_Prunus mahaleb_ L.**	N	0.46	-
Cirsium arvense (L.) Scop.	N	4.57	-	**_Prunus padus_ L. subsp. _padus_**	N	3.65	-
Cirsium canum (L.) All.	PRE	0.46	NRL	**_Prunus serotina_ Ehrh.**	A	1.37	-
Cirsium oleraceum (L.) Scop.	N	1.83	-	**_Prunus spinosa_ L.**	N	13.70	-
Cirsium palustre (L.) Scop.	N	3.65	-	**_Pulicaria dysenterica_ (L.) Bernh.**	N	0.46	-
Cirsium vulgare (Savi) Ten.	N	3.20	-	**_Pulmonaria officinalis_ L.**	N	5.94	-
Cladium mariscus (L.) Pohl	N	12.33	-	**_Pyracantha coccinea_ M. Roem.**	N	0.46	-
Clematis recta L.	N	2.74	-	**_Pyrus communis_ L.**	N	1.83	-
Clematis vitalba L.	N	17.35	-	**_Quercus robur_ L.**	N	53.42	-
Clematis viticella L.	N	10.96	-	**_Ranunculus acris_ L.**	N	9.59	-
Clinopodium vulgare L.	N	1.83	-	**_Ranunculus auricomus_ L. aggr.**	N	4.57	-
Colchicum autumnale L.	N	2.74	-	**_Ranunculus bulbosus_ L.**	N	1.83	-
Convolvulus arvensis L.	N	5.02	-	**_Ranunculus polyanthemophyllus_ W.Koch & H.E.Hess**	N	1.37	-
Cornus mas L.	N	3.20	-	**_Ranunculus repens_ L.**	N	0.91	-
Cornus sanguinea L.	N	54.34	-	**_Ranunculus sardous_ Crantz**	N	0.91	-

Corylus avellana L.	N	36.99	-	**_Raphanus raphanistrum_ L.**	N	0.46	-
Crataegus laevigata (Poir.) DC.	N	5.48	-	**_Rhamnus cathartica_ L.**	N	7.31	-
Crataegus monogyna Jacq.	N	20.55	-	**_Robinia pseudoacacia_ L.**	A	15.53	-
Crepis capillaris (L.) Wallr.	N	1.37	-	**_Rosa canina_ aggr.**	N	11.87	-
Crepis foetida subsp. _rhoeadifolia_ (M. Bieb.) Čelak.	A	1.37	-	**_Rubus caesius_ L.**	N	63.47	-
Crepis taraxacifolia Thuill.	N	2.74	-	**_Rubus ulmifolius_ Schott**	N	57.08	-
Crocus vernus (L.) Hill	N	0.91	-	**_Rudbeckia laciniata_ L.**	A	0.46	-
Cruciata glabra (L.) C.Bauhin ex Opiz	N	1.37	-	**_Rumex acetosa_ L. subsp. _acetosa_**	N	1.37	-
Cynodon dactylon (L.) Pers.	N	0.46	-	**_Rumex acetosella_ L.**	N	0.46	-
Cynosurus cristatus L.	N	0.46	-	**_Rumex conglomeratus_ Murray**	N	2.74	-
Cyperus esculentus L.	A	0.46	-	**_Rumex crispus_ L.**	N	5.48	-
Cyperus longus L.	N	0.46	-	**_Rumex obtusifolius_ L.**	N	2.74	-
Dactylis glomerata L.	N	25.11	-	**_Ruscus aculeatus_ L.**	PRE	8.68	HD
Danthonia decumbens (L.) DC.	N	0.91	-	**_Salix alba_ L.**	N	45.21	-
Daphne mezereum L.	N	0.46	-	**_Salix babylonica_ L.**	A	0.46	-
Daucus carota L.	N	11.87	-	**_Salix cinerea_ L.**	N	36.99	-
Deschampsia cespitosa (L.) P.Beauv.	N	3.65	-	**_Salix purpurea_ L.**	N	6.39	-
Dianthus hyssopifolius L.	N	0.46	-	**_Salvia pratensis_ L. subsp. _pratensis_**	N	1.37	-
Dioscorea communis (L.) Caddick & Wilkin	N	23.29	-	**_Sambucus ebulus_ L.**	N	0.46	-
Dipsacus fullonum L.	N	0.91	-	**_Sambucus nigra_ L.**	N	18.72	-
Drosera rotundifolia L.	PRE	0.46	RRL	**_Samolus valerandi_ L.**	N	0.91	-
Dryopteris filix-mas aggr.	N	3.20	-	**_Sanguisorba officinalis_ L.**	N	5.02	-
Echinochloa crus-galli (L.) P.Beauv.	N	0.46	-	**_Scabiosa triandra_ L.**	N	3.65	-
Elymus repens (L.) Gould subsp. _repens_	N	1.83	-	**_Schoenoplectus lacustris_ (L.) Palla**	N	0.91	-
Epilobium hirsutum L.	N	2.74	-	**_Schoenus nigricans_ L.**	N	9.13	-
Epilobium parviflorum Schreb.	N	1.37	-	**_Scirpoides holoschoenus_ (L.) Soják**	N	10.50	-
Epilobium tetragonum L.	N	0.91	-	**_Scrophularia canina_ L.**	N	0.46	-
Epipactis palustris (L.) Crantz	PRE	1.37	NRL	**_Scrophularia nodosa_ L.**	N	0.91	-
Equisetum arvense L.	N	10.96	-	**_Scrophularia umbrosa_ Dumort. subsp. _umbrosa_**	N	0.91	-
Equisetum palustre L.	N	9.13	-	**_Sechium edule_ (Jacq.) Sw.**	A	0.46	-
Equisetum ramosissimum Desf.	N	5.48	-	**_Senecio fontanicola_ Grulich & Hodálová**	PRE	2.74	NRL
Equisetum telmateia Ehrh.	N	22.37	-	**_Serratula tinctoria_ L. subsp. _tinctoria_**	N	3.20	-
Erigeron annuus (L.) Pers.	A	10.50	-	**_Sesleria uliginosa_ Opiz**	PRE	1.37	NRL
Erigeron canadensis L.	A	0.46	-	**_Setaria pumila_ (Poir.) Roem. & Schult.**	N	0.91	-
Erucastrum palustre (Pirona) Vis.	PRE	0.91	HD	**_Silene baccifera_ (L.) Durande**	N	0.46	-

Euonymus europaea L.	N	10.50	-	**_Silene latifolia_ Poir.**	N	0.46	-
Eupatorium cannabinum L.	N	13.70	-	**_Silene vulgaris_ (Moench) Garcke**	N	0.91	-
Euphorbia amygdaloides L.	N	1.37	-	**_Silphiodaucus prutenicus_ (L.) Spalik, Wojew., Banasiak, Piwczyński & Reduron**	N	0.46	-
Euphorbia cyparissias L.	N	0.46	-	**_Solanum dulcamara_ L.**	N	5.02	-
Euphorbia dulcis L.	N	3.65	-	**_Solidago canadensis_ L.**	A	0.46	-
Euphorbia illirica Lam.	PRE	0.46	R	**_Solidago gigantea_ Aiton**	A	4.57	-
Euphorbia nutans Lag.	A	0.91	-	**_Sonchus oleraceus_ L.**	N	0.46	-
Euphorbia palustris L.	N	0.46	-	**_Sorbus torminalis_ (L.) Crantz**	N	0.46	-
Euphorbia peplus L.	N	0.46	-	**_Sorghum halepense_ (L.) Pers.**	A	4.11	-
Euphorbia platyphyllos L.	N	0.91	-	**_Sparganium neglectum_ Beeby**	N	0.46	-
Euphorbia verrucosa L.	N	3.65	-	**_Stachys palustris_ L.**	N	0.91	-
Festuca heterophylla Lam.	N	0.46	-	**_Stachys sylvatica_ L.**	N	0.46	-
Festuca rubra L.	N	10.96	-	**_Stellaria aquatica_ (L.) Scop.**	N	0.46	-
Ficaria verna Huds.	N	0.91	-	**_Stellaria holostea_ L. subsp. _holostea_**	N	0.46	-
Ficus carica L.	N	1.83	-	**_Succisa pratensis_ Moench**	N	0.46	-
Filipendula ulmaria (L.) Maxim.	N	15.07	-	**_Symphytum officinale_ L.**	N	9.59	-
Filipendula vulgaris Moench	N	6.85	-	**_Symphytum tuberosum_ L. subsp. _angustifolium_ (A.Kern.) Nyman**	N	2.74	-
Fragaria vesca L.	N	10.50	-	**_Taraxacum_ sect. _Taraxacum_**	N	16.89	-
Frangula alnus Mill. subsp. _alnus_	N	19.63	-	**_Thalictrum aquilegiifolium_ L. subsp. _aquilegiifolium_**	N	3.20	-
Fraxinus angustifolia Vahl subsp. _oxycarpa_ (M.Bieb. ex Willd.) Franco & Rocha Afonso	N	18.72	-	**_Thalictrum lucidum_ L.**	N	5.02	-
Fraxinus excelsior L. subsp. _excelsior_	N	9.59	-	**_Thymus pulegioides_ L.**	N	2.28	-
Fraxinus ornus L. subsp. _ornus_	N	9.13	-	**_Tofieldia calyculata_ (L.) Wahlenb.**	N	0.46	-
Galega officinalis L.	A	0.46	-	**_Torilis arvensis_ (Huds.) Link**	N	2.28	-
Galeopsis pubescens Besser	N	0.46	-	**_Trachycarpus fortunei_ (Hooker) Wendl.**	A	4.57	-
Galium aparine L.	N	2.74	-	**_Tragopogon dubius_ Scop.**	N	1.37	-
Galium laevigatum L.	N	1.37	-	**_Tragopogon orientalis_ L.**	N	6.39	-
Galium mollugo L.	N	12.79	-	**_Trifolium campestre_ Schreb.**	N	3.20	-
Galium palustre L.	N	3.20	-	**_Trifolium fragiferum_ L. subsp. _fragiferum_**	N	0.46	-
Galium verum L.	N	9.59	-	**_Trifolium montanum_ L. subsp. _montanum_**	N	1.37	-
Genista tinctoria L	N	3.20	-	**_Trifolium pratense_ L.**	N	10.96	-
Geranium dissectum L.	N	4.11	-	**_Trifolium repens_ L.**	N	5.94	-
Geranium nodosum L.	N	0.46	-	**_Trifolium rubens_ L.**	N	1.83	-

Geranium pusillum L.	N	1.83	-	**_Trigonella alba_ (Medik.) Coulot & Rabaute**	N	0.91	-
Geum urbanum L.	N	20.09	-	**_Trisetaria flavescens_ (L.) Baumg. subsp. _flavescens_**	N	0.46	-
Gladiolus illyricus W.D.J.Koch	N	0.46	-	**_Tussilago farfara_ L.**	N	0.46	-
Gladiolus palustris Gaudin	PRE	4.57	HD	**_Ulmus minor_ Miller**	N	25.11	-
Glechoma hederacea L.	N	12.79	-	**_Urtica dioica_ L.**	N	17.81	-
Gleditsia triacanthos L.	A	0.46	-	**_Utricularia vulgaris_ L.**	N	0.46	-
Gratiola officinalis L.	N	0.91	-	**_Valeriana dioica_ L.**	N	1.37	-
Gymnadenia conopsea (L.) R.Br.	PRE	0.91	NRL	**_Valeriana officinalis_ L.**	N	29.68	-
Hedera helix L.	N	51.14	-	**_Verbena officinalis_ L.**	N	9.13	-
Helianthemum nummularium (L.) Mill.	N	0.91	-	**_Veronica arvensis_ L.**	N	1.37	-
Helminthotheca echioides (L.) Holub	N	1.37	-	**_Veronica beccabunga_ L.**	N	0.46	-
Heracleum sphondylium L. subsp. _sphondylium_	N	0.91	-	**_Veronica chamaedrys_ L. subsp. _chamaedrys_**	N	0.46	-
Holcus lanatus L.	N	22.83	-	**_Veronica officinalis_ L.**	N	0.46	-
Houttuynia cordata Thunb.	A	0.46	-	**_Veronica persica_ Poir.**	A	3.65	-
Humulus lupulus L.	N	26.94	-	**_Veronica serpyllifolia_ L.**	N	0.46	-
Hypericum perforatum L.	N	10.50	-	**_Viburnum lantana_ L.**	N	10.50	-
Hypericum tetrapterum Fr.	N	0.91	-	**_Viburnum opulus_ L.**	N	24.66	-
Hypochaeris maculata L.	N	0.91	-	**_Vicia cracca_ L.**	N	0.46	-
Hypochaeris radicata L.	N	0.91	-	**_Vicia sativa_ L.**	N	1.83	-
Impatiens glandulifera Royle	A	0.46	-	**_Vicia tenuifolia_ Roth**	N	0.46	-
Jacobaea vulgaris Gaertn.	N	0.46	-	**_Vicia villosa_ Roth**	N	1.37	-
Juglans nigra L.	A	1.83	-	**_Vinca major_ L. subsp. _major_**	N	1.37	-
Juglans regia L.	A	12.33	-	**_Vinca minor_ L.**	N	0.46	-
Juncus articulatus L. subsp. _articulatus_	N	6.85	-	**_Vincetoxicum hirundinaria_ Medik.**	N	8.22	-
Juncus compressus Jacq.	N	0.91	-	**_Viola hirta_ L.**	N	2.74	-
Juncus conglomeratus L.	N	0.91	-	**_Viola odorata_ L.**	N	4.57	-
Juncus effusus L. subsp. _effusus_	N	1.83	-	**_Viola reichenbachiana_ Jord. ex Boreau**	N	9.13	-
Juncus inflexus L. subsp. _inflexus_	N	0.46	-	**_Viola riviniana_ Rchb.**	N	0.46	-
Juncus subnodulosus Schrank	N	0.46	-	**_Vitis vinifera_ L.**	N	2.74	-
Knautia illyrica Beck	N	1.83	-	**_Xanthoselinum venetum_ (Spreng.) Soldano & Banfi**	N	1.37	-
Knautia ressmannii (Pacher) Briq.	PRE	1.37	E				

Supplementary materials to Chapter 3



(a) Observed vs estimated species richness

(b) Observed vs estimated species richness scaled by 0.4

Figure S4.1: Regression between observed taxonomic and estimated spectral species richness unscaled (a) and scaled by 0.4 (b).

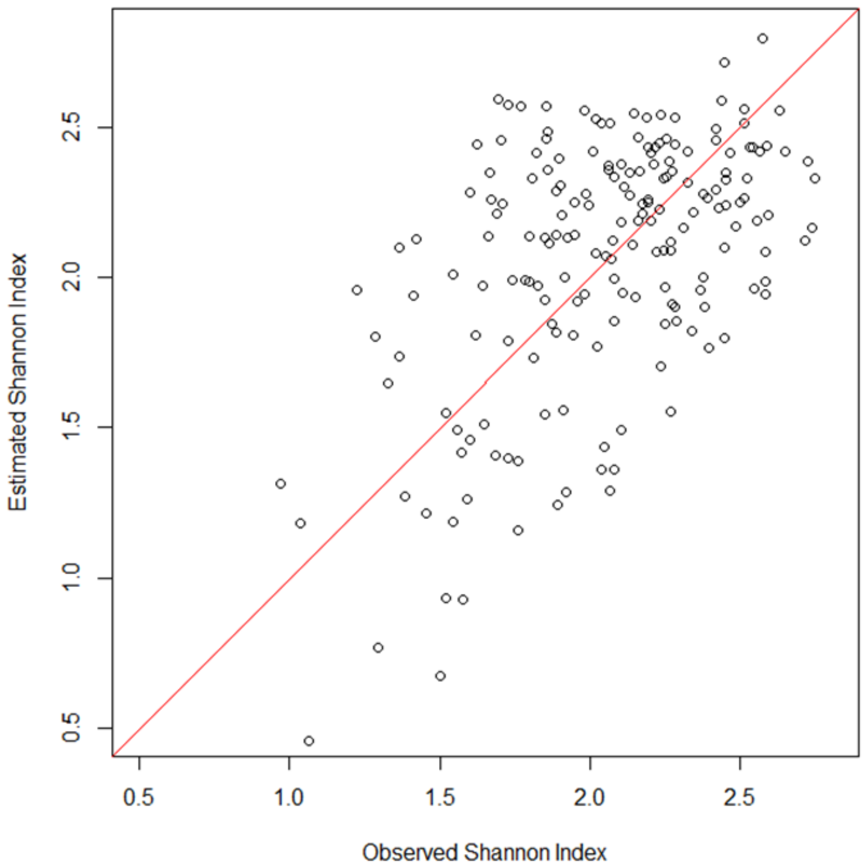


Figure S4.2: Regression between observed taxonomic Shannon index and estimated spectral Shannon index.

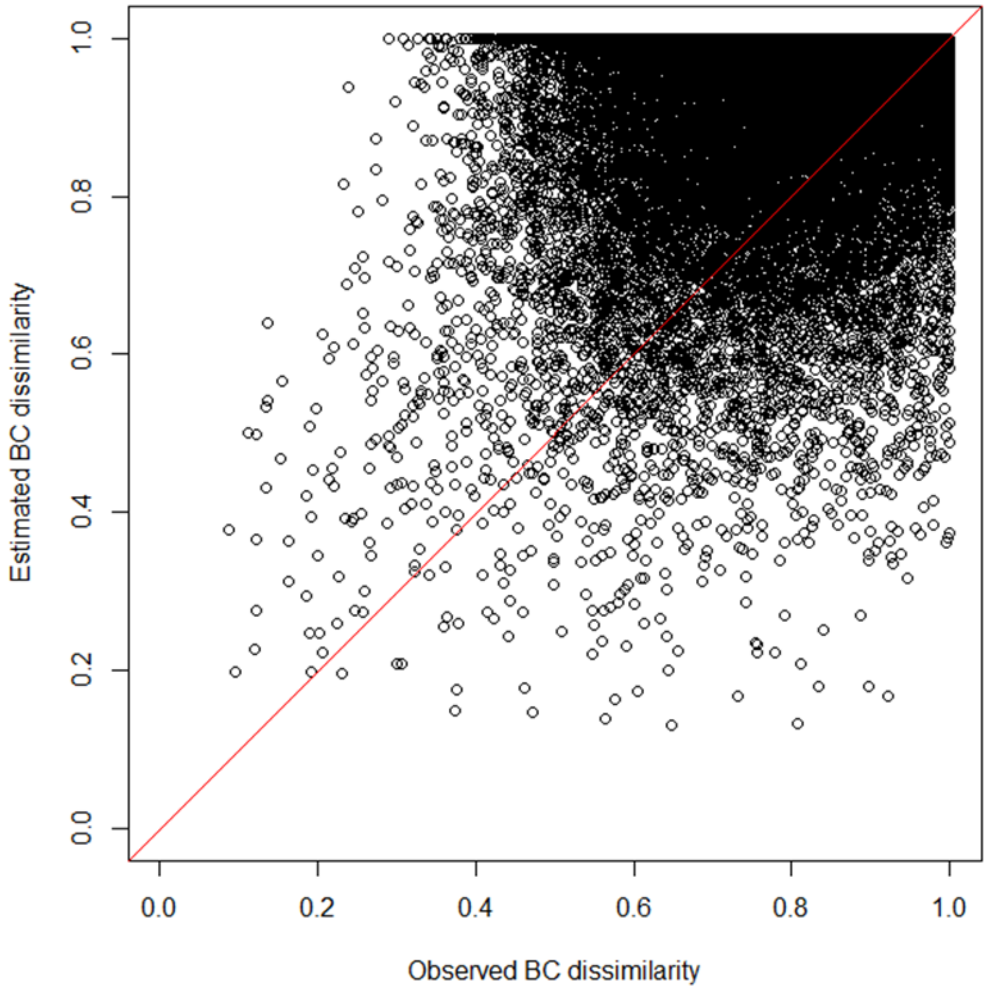
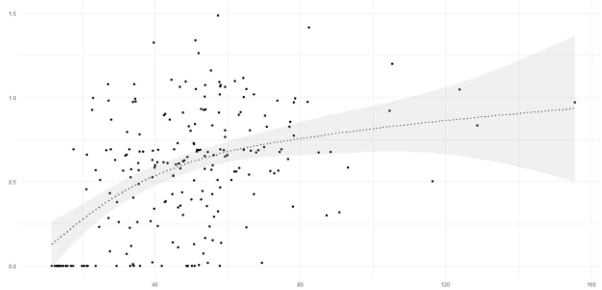
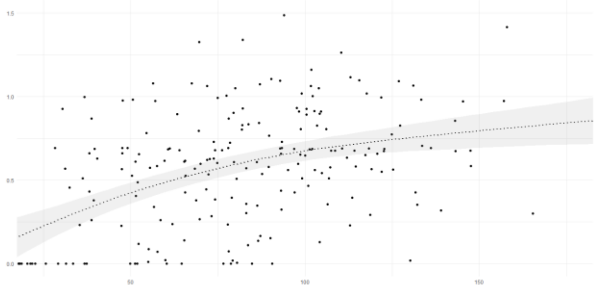


Figure S4.3: Regression between observed taxonomic Bray-Curtis dissimilarity index and estimated spectral Bray-Curtis dissimilarity index.

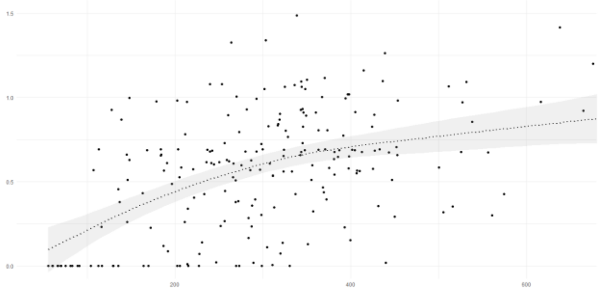
$Q_{NDVI}1$ ~ s(ShannonLU)



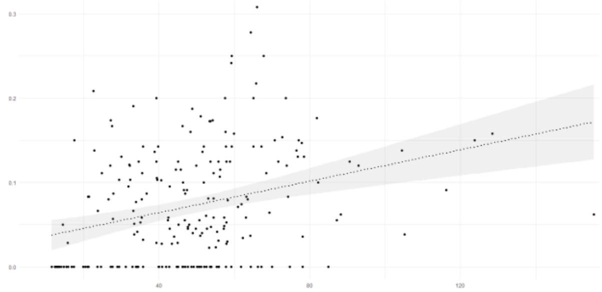
$Q_{NDVI}5$ ~ s(ShannonLU)



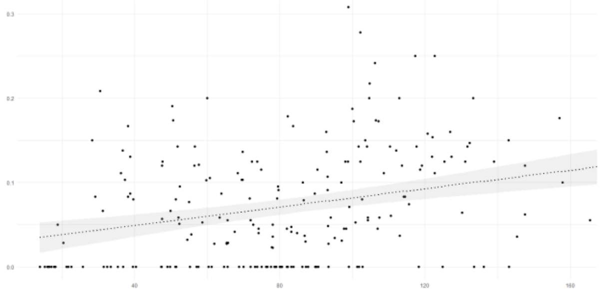
$Q_{NDVI}Inf$ ~ s(ShannonLU)



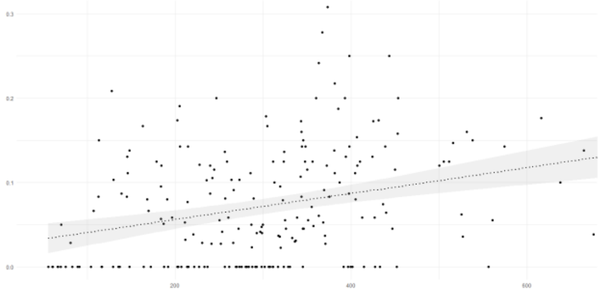
$Q_{NDVI}1$ ~ RatioAN



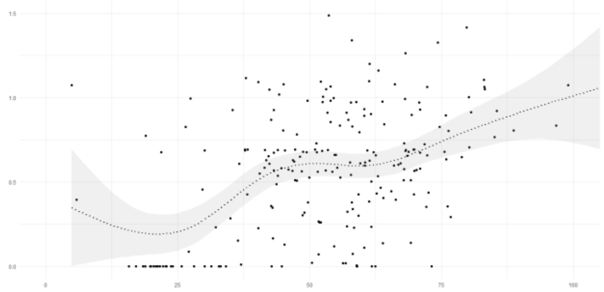
$Q_{NDVI}5$ ~ RatioAN



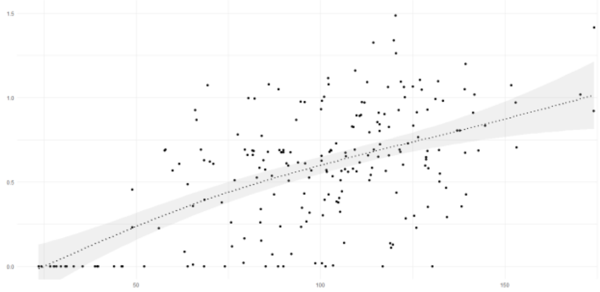
$Q_{NDVI}Inf$ ~ RatioAN



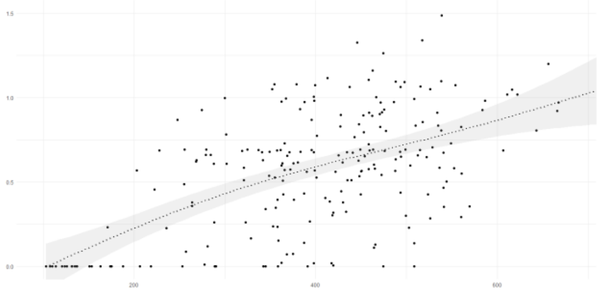
$Q_{multi}1$ ~ s(ShannonLU)

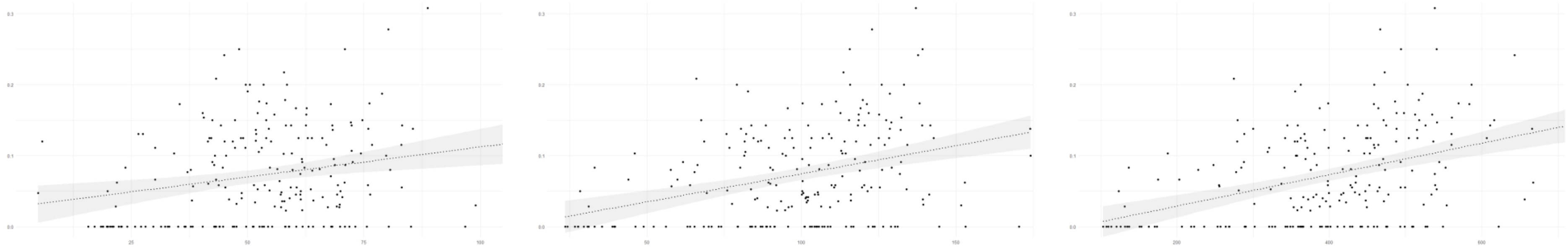


$Q_{multi}5$ ~ s(ShannonLU)



$Q_{multi}Inf$ ~ s(ShannonLU)





$Q_{multi}1$ ~ RatioAN **$Q_{multi}5$ ~ RatioAN** **$Q_{multi}Inf$ ~ RatioAN**

Figure S4.4: Relationships between spectral heterogeneity (Q), land use diversity (ShannonLU; smooth term), and alien to native species richness ratio (RatioAN; linear term), resulting from the six GAMs. Rao's Q values derived from the NDVI time series (Q_{NDVI}) and the multispectral single image (Q_{multi}) and the weight for the distance matrix was set to 1, 5 and infinite.

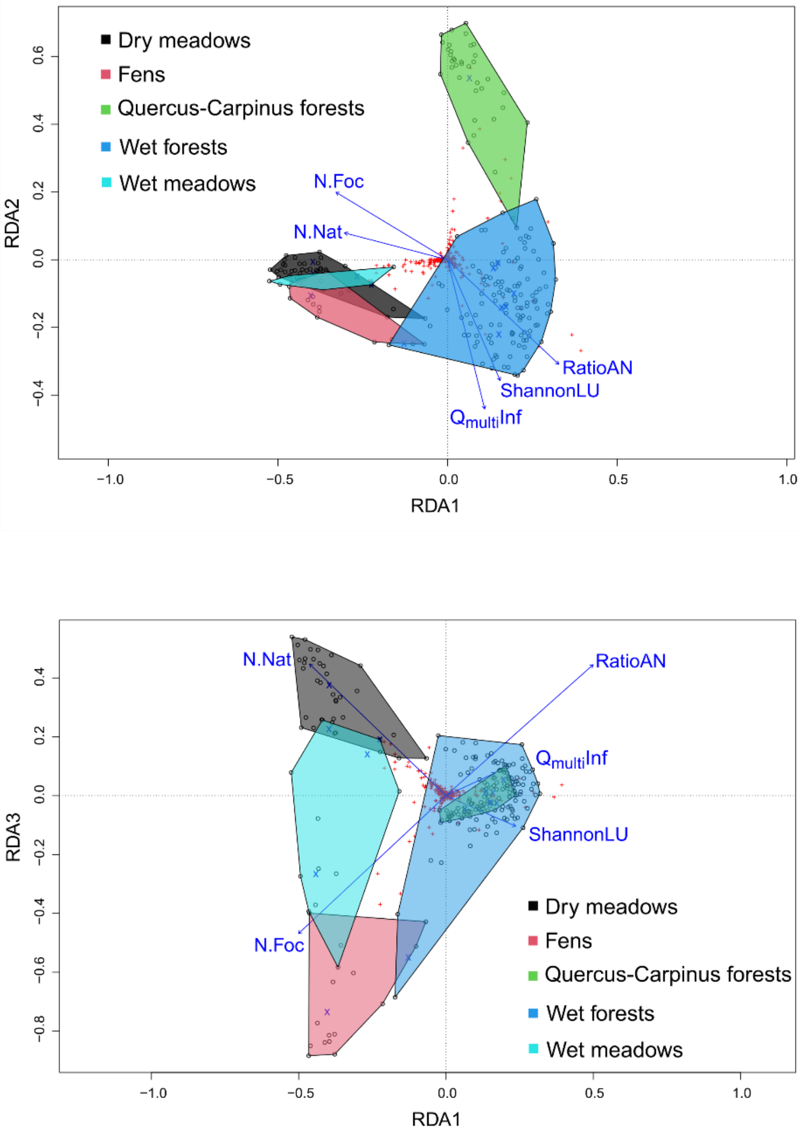


Figure S4.5: tb-RDA ordination based on Hellinger pre-transformed species composition matrix, with site grouped per habitat and displaying the following variables: focal species richness (N.Foc), native species richness (N.Nat), Rao's Q index, calculated from the 10 bands of the Sentinel 2 image of 03 June 2019 with the weight for the distance matrix set to infinite (Q_{multi}INF), and ratio of alien to native species richness (RatioAN), Shannon index on land use diversity (ShannonLU).