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A functional connectivity approach for exploring interactions of multiple ecosystem services in the context of agricultural landscapes in the Canadian prairies

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ABSTRACT

Land-use and land-cover patterns, including their spatial heterogeneity and configuration, are fundamental in shaping landscape-level ecological processes, functions, and services. Despite growing recognition of the importance of these patterns, gaps remain in our understanding of how they influence the functional connectivity of ecosystem services (ES)—a crucial aspect for ecosystem resilience and sustainability. This research aims to bridge this gap by investigating the functional connectivity among multiple ES, such as pollination, carbon storage, soil erosion control, wetland-based ES such as habitat provisioning and water storage capacity from marshes, swamps, and open water wetlands, and agricultural food production within a complex landscape. We define functional connectivity as the extent to which the landscape facilitates or impedes the interactions and interdependencies of ecological processes that combine to create distinct ecosystem services. This definition encompasses the dynamics within a spatially interconnected mosaic of land use and land cover, exemplified by connections such as those from pollination provisioning areas to croplands. The primary goal of this research is to develop an empirical framework that encapsulates 'network topological' interactions— essentially, the complex interplay among various components of the ecosystem — specific to agricultural landscapes and then to apply this framework to the Canadian prairies. Our methodology uses the spatial tools including InVEST, ARIES, and GIS to map diverse ES. An ecological network is then constructed for these ES at the landscape scale, designating network nodes based on high-value ES provisioning areas and defining links between pairs of ES according to their functional connections (overlapping and proximal in physical space). These functional connections effectively delineate areas of the landscape where the majority of ES flows occur. Mapping ES connectivity and network building revealed that around 29% of the studied landscape lies within functional connectivity zones for the selected ES, representing hotspots of significant ES interactions. Our findings reveal that although soil erosion-control spans just 1.36% of the total area, a substantial 72.59% of its spatial extent was identified as functionally connected. Land cover analysis in functional connectivity zones revealed that natural habitats such as shrublands, broadleaf forests, wetlands, and grasslands are vital mediators of ES. The variability in ES interconnectivity in the landscape was evident both in the intensity of interactions and observed connections. Our findings, informed by Ecological Network Analysis (ENA), emphasize the need for integrating connectivity and systems thinking in conservation sciences to achieve sustainability and ecosystem resilience. The insights offer a foundation to explore optimal ES provisioning scenarios at the landscape scale.

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1. Introduction

The term ecosystem services (ES) has gained increased recognition in recent years as a means of environmental management in diverse contexts, from the economic valuation of natural resources (Bockstael et al., 2000; Costanza, 2020; Loomisa et al., 2018) to mapping and modeling complex processes and functions of ecosystems (Burkhard et al., 2012; Burkhard and Maes, 2017; Tallis and Polasky, 2009). ES are the benefits that societies obtain from nature either directly or indirectly, such as food provisioning, climate regulation, wildlife habitat and recreational opportunities (Assessment, 2005; Braat and De Groot, 2012; Costanza et al., 1997; La Notte et al., 2017). Recognizing the importance of functional connectivity in understanding ecosystem service interactions marks a significant shift in environmental management. This concept, which highlights the complex interconnectedness and dynamic flow of services, offers a new perspective on how these services interact within and across different landscape contexts (Field and Parrott, 2022). Although the concept of ES has been explored for over two decades, its detailed application in analyzing complex biophysical and social system interactions has notably advanced in recent years (Agudelo et al., 2020; Bagstad et al., 2013; Bodin et al., 2019; Cord et al., 2017; Thierry,Parrott,and Robinson, 2021). However, despite advances in our perception of ES interactions and their importance to human society, much work needs to be done to better understand functional connections between different ES across a landscape, and how this connectivity varies across different contexts, scenarios, and scales. To capture how ESs change in response to multiple factors and how their interactions shape the complex mosaics of landscapes, we need modeling approaches that account for the functional connectivity of ES across the landscape. This research is a step forward in integrating concepts related to functional connectivity and ecosystem service dynamics for improving our understanding of interconnectivity at a landscape scale.

Estimating ES service provisioning is inherently challenging largely due to their dependence on spatial distribution and temporal dynamics of environmental conditions. This task requires an in-depth understanding of the interactions between biotic components and environmental factors across landscapes. Ecosystems, as complex systems, exhibit a web of interconnected services, each influenced by functional connections within the landscape (Anand et al., 2010; Field and Parrott, 2022; Metzger et al., 2021). The importance of the connectivity in ES provisioning and the interactions among different ES is highlighted in empirical studies. For instance, Rieb and Bennett (2020) demonstrated how the configuration of landscapes and the scales at which they are analyzed can significantly influence the patterns of ES interactions. To reach this conclusion, they utilized indicators of landscape fragmentation, such as diversity, connectivity, and distance to the edge, and conducted a pairwise correlation analysis of ES at two spatial scales (30 m and 1 km). Their results demonstrate the importance of considering both landscape configuration and scale in understanding and predicting the interactions of ES. This conclusion is further exemplified by MacQueen (2020) who studied the relationship between landscape structure and the crop pollination service, highlighting that foraging sites in croplands substantially impact pollination patterns across a landscape. Collectively, these studies emphasize that functional connectivity is not just about physical links in the landscape, but also about understanding how different services interact and coexist in the landscape.

Most ES-based frameworks that use the landscape composition as their input values to map ESs have applied statistical relationships to represent the ES associations (Lee and Lautenbach, 2016; Qiu et al., 2018; Schirpke et al., 2019; Zhang et al., 2021). However, there has recently been a paradigm shift from correlative analysis to modelling functional connectivity in the spatial representation of ES interactions (Field and Parrott, 2022; Jennings et al., 2021; Zeller et al., 2020). Functional connectivity refers to the interconnectedness of ecological systems that enables the flow of ecosystem services across a landscape, emphasizing the ecological processes and interactions that support the provisioning of these services, beyond merely the physical layout of habitats (Field and Parrott, 2022). This approach considers both the spatial and temporal patterns of service delivery, accounting for spatiotemporal lags that promote biodiversity conservation and create nutrient-rich environments at different times, fostering biodiversity (Fremier et al., 2013). Functional connectivity focuses on how resources flow within ecosystems and is mediated by landscape connectivity. In this context, landscape connectivity refers to how the landscape's composition and configuration facilitate or impede ecological processes that are critical for ecosystem service interactions. This concept is integral to our approach, which shifts from traditional statistical analyses to a more dynamic understanding of functional connectivity in modeling the spatial interplay of ecosystem services (Leitão et al., 2012). Although the application of functional connectivity in ES research is in its infancy, a few recent empirical studies have been developed to explore the different types of ES interactions that might be linked to functional connectivity. For instance, Karimi, Harris, and Corstanje (2021) have used Bayesian Belief Networks at a very fine spatial resolution (2 m) in an urban setting in the UK to analyze whether functional connectivity influences ES supply and triggers trade-offs and synergies among ES. They found that landscape connectivity affected the provisioning of multiple ES and the formation of ES bundles (Karimi et al., 2021). Field and Parrott (2022) present a novel application of functional connectivity to demonstrate spatial ES interactions at a regional scale in British Columbia, Canada. This study is significant because it provides a novel approach to mapping ES interactions on a regional landscape, highlighting where connectivity and interconnectivity of multiple ES is weak or strong, which can be used to guide environmental planning and conservation decisions at a landscape scale. As the above examples demonstrate, landscape connectivity research has been instrumental in helping us understand how changes in landscape structure can impact the production of both individual and multiple ES and illustrate how multiple ecosystem functions and services interact spatially.

In this paper, we developed an empirical framework that extends previous work on landscape connectivity and mapping functional connectivity of multiple ecosystem services (Field and Parrott, 2017, 2022) with an explicit focus on how the attributes of functional connectivity can promote or hinder multiple ES provision and their interaction at the landscape scale. Unlike previous methodologies, which typically apply correlative analysis of ES interactions at a broader ecological or administrative level, our approach considers ecosystem service interactions as functional processes among multiple services. This allows for a more granular and process-oriented understanding of how different services influence and are influenced by each other within the landscape. By providing this more nuanced perspective, we aim to enrich our understanding of ES dynamics and offer a valuable contribution to the complex domain of ES interactions in landscape ecology, ecosystem service, and conservation planning.

2. Methods

This research follows a three-step methodological approach with the ultimate goal of mapping ES interactions, focusing on the intra-connectivity of ES within a small-scale agricultural landscape. In the first stage, we assessed the spatial distribution of ES values for six selected ES (Table 1). Next, we implemented an ecological network approach, wherein nodes were delineated as areas with high ES provisioning values, and links were established based on functional connections (Table 2), which were determined through two distinct methods – overlapping connections and proximity connections in space. Notably, for pollination and agricultural food provisioning ES, we exclusively considered proximity connections. This decision was informed by the shortcomings of the node delineation approach, which fails to capture the true nature of pollination mechanisms at the landscape scale. Finally, we utilize the established network based approach on ecosystem service mapping for identifying connectivity of ecosystem service interactions on the landscape. Fig. 1 below demonstrates an overview of the research framework to establish a network of ecosystem service interaction using functional connectivity and ES assessment approaches.

2.1. Study area

The study area for this research is situated within a mixed agricultural landscape in the Canadian prairies, specifically in the central region of Alberta. The landscape, encompassing approximately 3750 km, is characterized by its predominance of grasslands, which cover about 35 % of the total area. Additionally, the region is interspersed with diverse natural cover types such as shrublands, wetlands, pasture, and broadleaf forest. The primary agricultural crops cultivated within this landscape are spring wheat, canola, and barley, which respectively account for 10.17 %, 7.54 %, and 5.04 % of the spatial coverage in the study area. The landscape is relatively flat, with elevation levels ranging from 541 m to a maximum of 924 m, resulting in an overall height variation of 383 m. An essential feature of the landscape is the presence of three distinct wetland types: swamps, marshes, and open water wetlands. The spatial configuration and heterogeneity of these various cover types contribute to the landscape richness in terms of ecosystem service provisioning. In this study, we identified and mapped six key ES that the landscape provides and supports. These services include pollination, carbon storage, soil erosion control, agricultural food provisioning, as well as wetland-based ES such as habitat provisioning and carbon storage in marshes and swamps, and water storage capacity in open water wetlands. The geographic focus of this research is visually represented in Fig. 2.

2.2. Ecosystem services mapping and quantification

ES mapping and quantification for the study area was done using spatially explicit modeling tools such as ARIES (Villa et al., 2014) and InVEST (Sharp et al., 2014) for pollination, carbon storage and soil erosion control. We used GIS tools to develop indices for wetland-based ES. In utilizing ARIES for pollination, we leveraged a process-based model specifically designed for the Canadian prairies. This model not only captures the complex dynamics of pollination but also includes a comprehensive global sensitivity analysis, highlighting the significant impact of key parameters. This approach allows for a nuanced understanding of pollination services, essential for accurate ecosystem service mapping in our study area (detailed further in Appendix 3: Mapping Pollination with ARIES). Table 1 provides an overview of the models and datasets used for ES mapping in this study. Detailed methodologies, including spatial quantification processes for ES mapping, are comprehensively described in Appendices 3 to 7 for each of the ES in Table 1.

2.3. Constructing the network of ecosystem services

We constructed an ecological network of multiple ecosystem services using the spatial distribution of ES provisioning areas, drawing on methods similar to those proposed by Field and Parrott (2022). First, we identified ES provisioning hotspots within the landscape based on a predetermined threshold value, derived from classifying ES model outputs, to determine areas of high ES provisioning capacity. These areas, recognized as nodes in our ecological network, correspond to high ES provision as classified by the model. Links between nodes are determined by the functional connections between pairs of ES, defined by overlapping connections of one ES supply area that flows to another, indicating areas where the provision of one service enhances another. In addition, we incorporated proximity connections between pollination service nodes and agricultural food production nodes, accounting for pollination flows from nearby natural and semi-natural habitats, hedgerows, and roadsides to croplands. Given the complexity of the ecosystem services under consideration, we employed an operationalized version of a functional connectivity framework, based on overlapping and proximity connections among multiple ecosystem services within the landscape.

2.3.1. Node delineation

Depending on the type of ES, different strategies were applied for node delineation. For wetland-based services and agricultural food production, the entire ES provisioning polygon was considered as a node without additional sub-division. For services such as pollination, carbon storage, and soil erosion regulation, we adopted service-specific contextual threshold values to define nodes. These thresholds were informed by a local sensitivity analysis and rooted in the ecological dynamics unique to each service type at the landscape. Specifically, we applied distinct threshold values to the raster outputs from ES mapping. For example, areas ranking in the top 50 % of pollination model values were classified as high pollination provisioning nodes. Similarly, regions within the top 95 % for soil erosion were identified as critical soil erosion nodes. The selection of these specific thresholds is further examined in the sensitivity analysis (see the sensitivity analysis section in Appendix 2 in the SI). Thresholds were chosen based on the ecological characteristics of the landscape. While this methodological approach is designed to approximate the spatial distribution and intensity of ES provisioning, it is essential to acknowledge that such classifications are informed estimates, contingent upon the inherent variability and complexity of ecological systems. The complexity in ecological systems stems from the interplay of various biotic and abiotic factors, which can lead to significant spatial and temporal differences in ecosystem service provisioning. Recognizing this, our node delineation approach incorporates service-specific thresholds, reflecting the unique ecological dynamics of each service within the landscape.

2.3.2. Defining functional Connectivity: Edges and weights

Edges, or links between nodes, were created to represent two types of connections: (1) spatially overlapping connections, where one ES supply area spatially intersects another, and (2) proximity connections, for services that influence surrounding areas such as the impact of pollination on agricultural areas. The complexity of functional interactions among ES necessitated this simplified, yet robust, approach (examples of functional connections provided in Appendix 1 in the supplementary information). Edge weights were assigned based on spatial analysis, specifically using zonal statistics to aggregate relevant attribute values within the overlapping areas of ES layers. This involved aggregating the summed raster values of ES mapping outputs, which represent various attributes such as carbon storage (tons/ha), soil erosion (tons per pixel), and pollination (a dimensionless unit). To ensure consistency and comparability across these diverse ES metrics, we normalized the values within a range of 0–1 using the min/max normalization method prior to network construction. This normalization process was crucial to convert the diverse units of ES into a common denominator. Subsequently, the normalized summed raster values were utilized as the weights of the links, quantifying the relative strengths of the functional connectivity within the ES network. These weights quantified the strength or intensity of interactions between connected nodes, thereby capturing at least some aspects of the functional connectivity of the ES network. The primary objective of our methodology was to identify functional connectivity zones through the spatial network construction, areas in the landscape that facilitate the provisioning of ES. While our approach allows for node-based analysis using various network metrics, such as centrality measures, our emphasis was on understanding the spatial arrangement and interconnectivity of ES. This spatial network analysis elucidated the patterns of connectivity in terms of the frequency and intensity of connections within the landscape, thereby revealing how these areas contribute to the effective provisioning of ES at a landscape scale.

By applying these computational methodologies, we synthesized a spatially explicit, weighted, and directed network of ecosystem services. Each node and link in this network were assigned quantitative

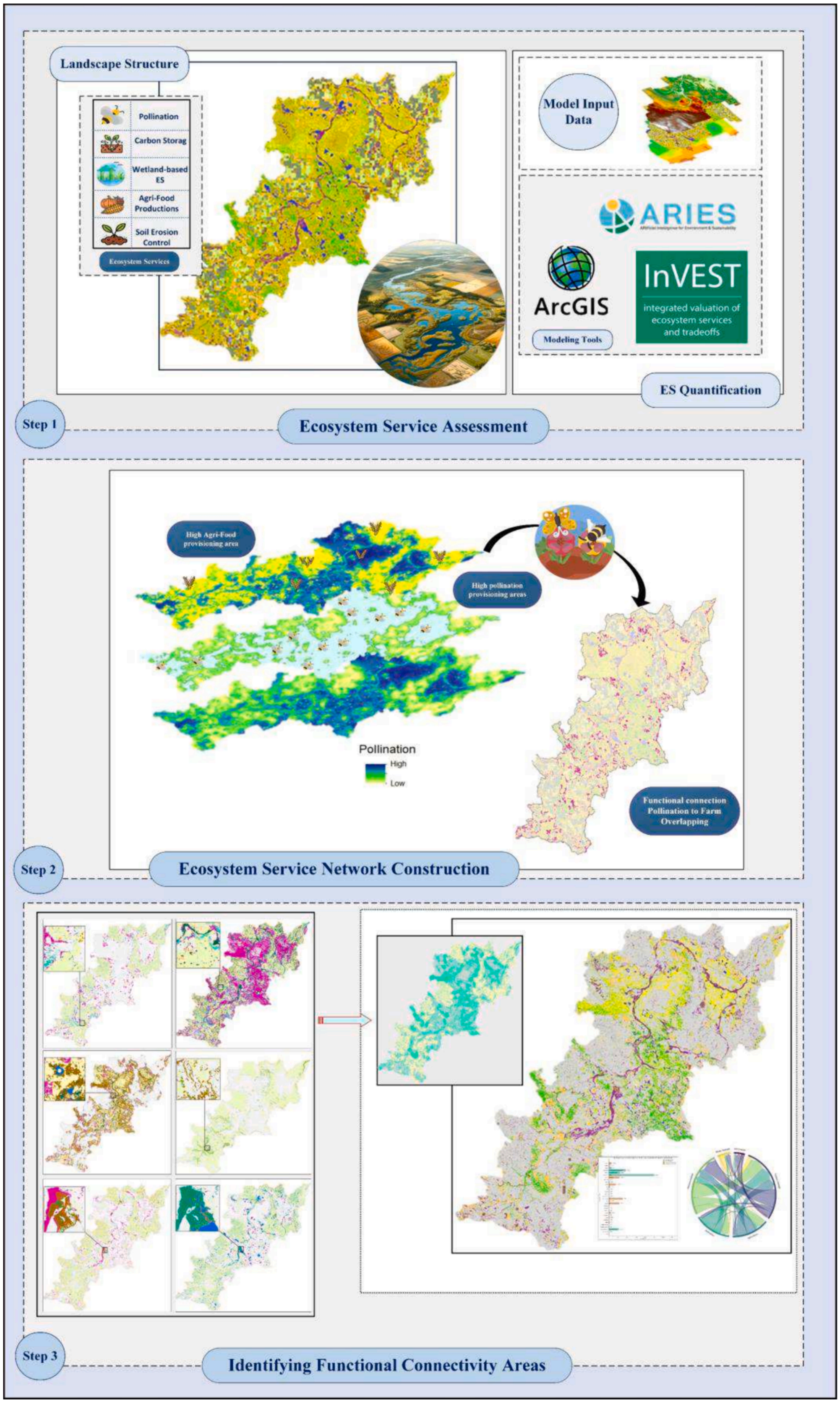


Fig. 1. Operational framework of ecosystem service interactions network at a landscape scale using ES assessment, functional connectivity and network analysis approach.

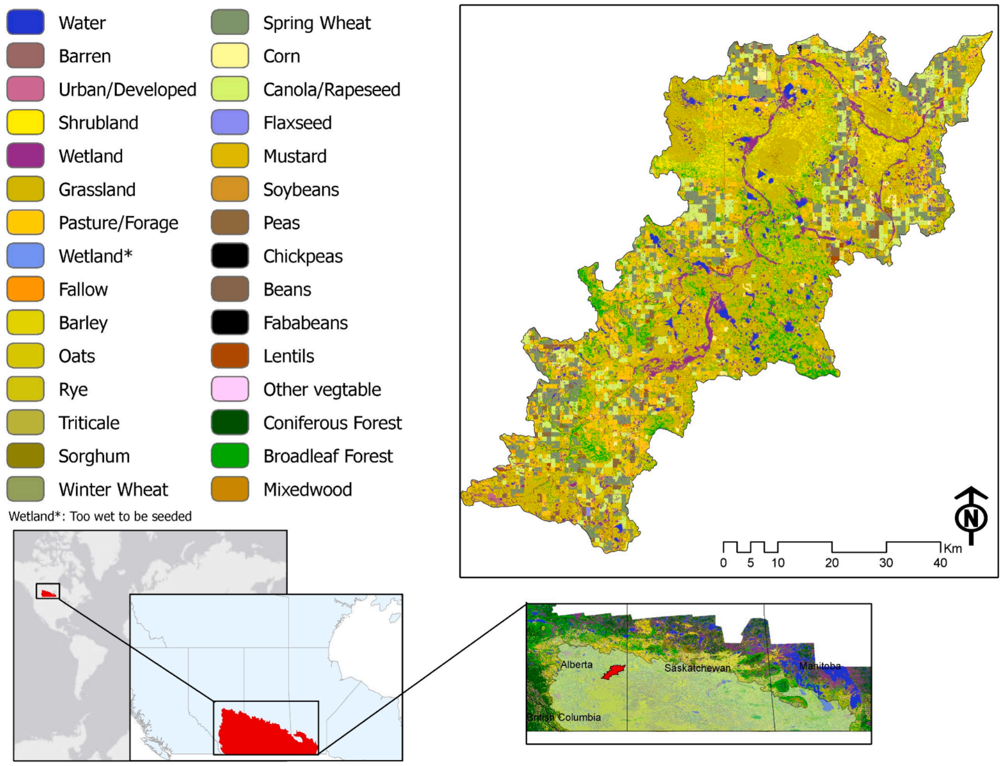


Fig. 2. The location of the study area in the Canadian prairies.

attributes, making the framework robust for subsequent topological and spatial network analyses. To build our network we used networkX package in Python (Hagberg et al., 2008). Our ES network was structured as a multi-layer network, where each ecosystem service was represented as a distinct layer. This structure allowed us to examine meticulously the functional connections, such as overlay and proximity links, between different ES layers. However, it is important to note that the establishment of these links is contingent upon both ecological relevance and the structural characteristics of the data we analyzed. A key objective of our approach was to distill these complex interactions into a more accessible, simplified conceptual framework. Table 2 below illustrates this simplification, with each row representing a different layer in our ES network. For instance, the first layer encompasses functional connections between pollination and various ES, including agricultural food production nodes, carbon storage, and wetland-based services. The method of linking – whether through geographical overlap or proximity – is central to understanding these interactions (see Table 2).

A value of 1 indicates the existence of a bidirectional relationship between pairs of ecosystem services (ES), while 0 denotes the absence of such a relationship. The first column of the table lists all the ES layers within our network, with each row representing a separate layer. For instance, the first row, corresponding to pollination, shows interactions of this service with carbon storage, agriculture, and wetland-based ES. However, it is noted that there is no functional relationship between pollination and soil erosion control, as reflected by 0. Appendix 1 in Supplementary Information (SI) provides examples of functional connections and how we established the connections among these ES.

3. Results

Fig. 3 depicts the spatial distribution of selected ES within the study area. The spatial distribution patterns of these ES are intrinsically linked to the land cover types—the key input for most of ES models applied in this study —present in the landscape. In panel A of Fig. 3, areas with high agricultural food production are visibly represented in dark blue, indicating the prominence of cropland within these regions. The pollination hotspots, on the other hand, are primarily located within natural and semi-natural habitats, including grassland and pastureland cover types. This pattern is confirmed by visual inspection of the map presented below. These hotspots can be seen in Panel B, particularly in the north-central part of the map. Soil erosion regulation, a function of factors such as rainfall erosivity, slope length gradient, and the presence of sediment-trapping vegetation, is another vital ecosystem service represented in our study. Panel C highlights the areas with high soil erosion regulation, which generally coincide with regions of significant vegetation cover and low slope gradients. Lastly, carbon storage, a crucial ecosystem service, is heavily influenced by the presence of wetlands and other natural habitats in the landscape. The spatial pattern of this service (Panel D) reflects this relationship. The wetland based ESs (Panel E and F) are only quantified within the limitation of wetland boundaries. As seen in the figure, the central regions of study area are identified as hotspots or habitat provisioning and carbon storage that comes mostly from marshes and swamps. Fig. 3, in fact illustrates where ES nodes and links in the landscape can be found, however, maps are shown in a scaled representation. The following section provides an in-depth representation of ES network established based on mapping output.

3.1. Multi-Layer ecosystem service network

The subsequent section provides a comprehensive examination of the functional connectivity among multiple ES within the study area. To structure our findings systematically as presented in the methodology, we employ a multi-layered ES network approach. In this representation, each layer corresponds to an individual ES type, along with its connections to other ES types, contingent on the existence of interrelationships based on Table 2.

Table 1
An overview of selected ecosystem services and mapping methods with data requirements and sources used in the study.

#	ES	ES model and platform	Data requirements	Data sources
1	*Carbon Storage*	InVEST carbon model (Sharp et al., 2014)	LULC Global aboveground & belowground biomass Carbon storage and distribution in terrestrial ecosystems of Canada	Annual crop inventory[1] ORNL DAAC[2] (Spawn et al., 2020) WWF Canada[3] (Sothe et al., 2022)
2	*Soil Erosion Control*	Sediment Delivery Ratio (SDR), InVEST (Sharp et al., 2014)	LULC, precipitation, evapotranspiration	Climate NA[4]
3	*Crop Pollination*	ARIES, a guild-based pollination model	LULC	Annual crop inventory
4	*Agricultural Food Production*	Spatial distribution of cropland and NDVI	LULC and NDVI	Annual crop inventory, Landsat satellite imageries
5	*Habitat provisioning and carbon storage*	InVEST carbon model and a developed index based on NDVI in GIS	LULC, Carbon model output, NDVI, wetland inventory	Annual crop inventory, Environment and Climate Change Canada, Landsat satellite imageries (USGS[5])
6	*Water storage capacity in open water wetlands*	Index based on DEM and NDWI	LULC, Canadian Wetland DEM	Annual crop inventory, Environment and Climate Change Canada[6]

[1]https://www.agr.gc.ca/atlas/apps/metrics/index-en.html?appid=aci-iac.
[2]https://daac.ornl.gov/VEGETATION/guides/Global_Maps_C_Density_2010.html.
[3]https://wwf.ca/carbonmap/.
[4]https://climatena.ca/.
[5]https://earthexplorer.usgs.gov/.
[6]https://open.canada.ca/data/en/dataset/5095a5e0-e574-4769-84d3-acaac529399b.

Table 2
Interaction matrix of ES relationships based on existence functional connections between pairs of ES considered.

Ecosystem Services	*P*	*C*	*S*	*A*	*W*	*H*
Pollination (P)	0	1	0	1	1	1
Carbon Storage (C)	1	0	1	1	1	1
Soil Erosion Regulation(S)	0	1	0	1	0	1
Agricultural Food Provisioning (A)	1	1	1	0	1	1
Water Storage Capacity in Wetlands (W)	1	1	0	1	0	0
Habitat and Carbon sequestration in Marshes & Swamps(H)	1	1	1	1	0	0

3.1.1. Pollination layer

As per our assumption, pollination, a naturally occurring ecological process, is widespread in the landscape. This leads to an overlapping relationship between pollination and all other selected ecosystem services, except for soil erosion regulation, and proximal connections between agricultural food production nodes. However, an indirect relationship does exist between pollination and soil erosion regulation, as both are heavily reliant on vegetation cover (see Appendix 1. Examples of functional connections in agricultural landscapes for more information). For the sake of analytical simplicity, we have chosen to exclude these indirect connections from the current study. A circular plot presents the network of pollination with other ES, highlighting the interconnected linkages among various ecosystem services (Fig. 4). Utilizing the node delineation approach, we identified 127 node patches that provide high pollination services within the landscape. Despite ranking last in terms of node quantity, pollination covers a substantial portion of the study area, specifically 57.37 % (2151.89 km^2). Out of 55,023 overlapping connections with other ES, areas of high carbon storage interact most frequently with pollination provisioning areas, accounting for 55.61 % (n = 30,597) of all connections. Wetland-based ES, particularly those derived from marshes and swamps, ranked second in terms of connection frequency with pollination, with a count of 14,878. Interestingly, our findings show a fewer number of connections between croplands and pollination, particularly when compared with wetland ecosystems and carbon storage areas. To address this limitation, we incorporated the concept of proximity connections into our ES network. This approach was particularly useful in the subsequent section where we identified functional connectivity zones, allowing for a more nuanced understanding of the spatial relationships and interactions within the network

3.1.2. Carbon storage Layer

The presence of carbon, similar to pollination, is evident across the landscape, as depicted in Fig. 3 (Spatial distribution of ecosystem services within the study area, Panel D) and Fig. 4 (Overlapping functional connections between carbon and other ESs). Despite this, it is noteworthy that regions characterized by high carbon storage are typically aligned with natural habitats, particularly wetland ecosystems (marsh and swamps), signifying their pivotal role in carbon storage. However, the landscape also contains certain areas, specifically within croplands, that act as significant carbon storage nodes (see the zoomed in map in Appendix 9, Fig. 6). The threshold definition-based identification of high carbon storage provisioning areas (carbon storage nodes) reveals a total of 47,753 nodes, covering an area of approximately 1071.25 km^2, or 28.56 % of the total landscape. These nodes demonstrate a significant number of overlapping connections (n = 77,980) with all other ecosystem services. The landscape covered by these intersections between carbon sequestration and other ecosystem services constitutes 33.22 % of the total area, approximately 363.37 km^2. Among the connections, pollination exhibits the highest frequency (n = 29,766, 38.17 %), while wetlands (marsh/swamps ecosystems) cover the largest area (45.33 %, equivalent to 164.75 km^2) associated with high carbon sequestration. This observation underscores the synergistic interactions between carbon storage areas and wetland ecosystems, reinforcing the significance of wetlands as potent reservoirs of carbon stock within the landscape.

3.1.3. Agricultural food production Layer

In the context of ES present in the study area and the Canadian prairies at large, agricultural food production—including crop yield, fodder, and animal products—plays a significant role. Our focus in this study, however, primarily lies with crop yield and its productivity, utilizing NDVI values as a link weight between cropland and other types of ES. The nodes representing agricultural food production depict the spatial distribution of cropland, as determined by the annual cropland inventory and NDVI calculations for the study area. We identified 15,610 such nodes, covering 37.38 % (or 1289.52 km^2) of the landscape. These nodes interact with all ES, establishing 34,714 overlapping connections—about 23 % (~298 km^2) of the cropland in the study area. Interestingly, the soil erosion regulation nodes hold the highest number of potential connections to croplands among all ES, with a count of 11,855. However, these connections only cover 3.98 % (or 51.13 km^2) of the agricultural food production areas. While carbon storage nodes rank second in terms of potential connections with agriculture (n = 8,926), the areas providing pollination services establish 6,941 connections

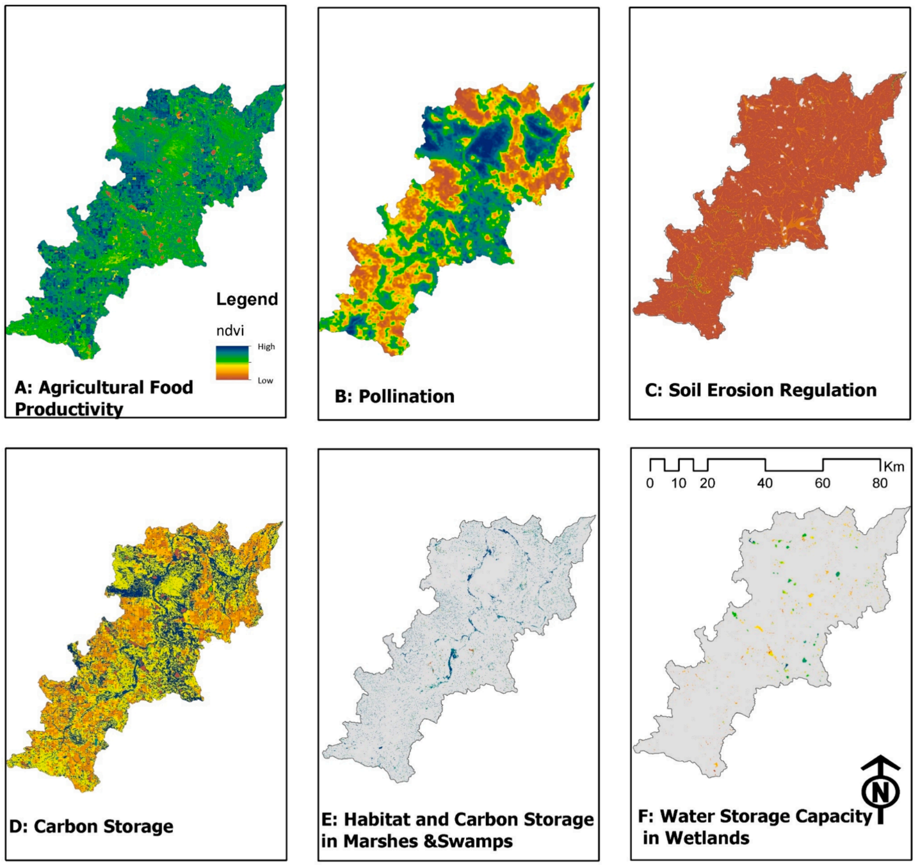
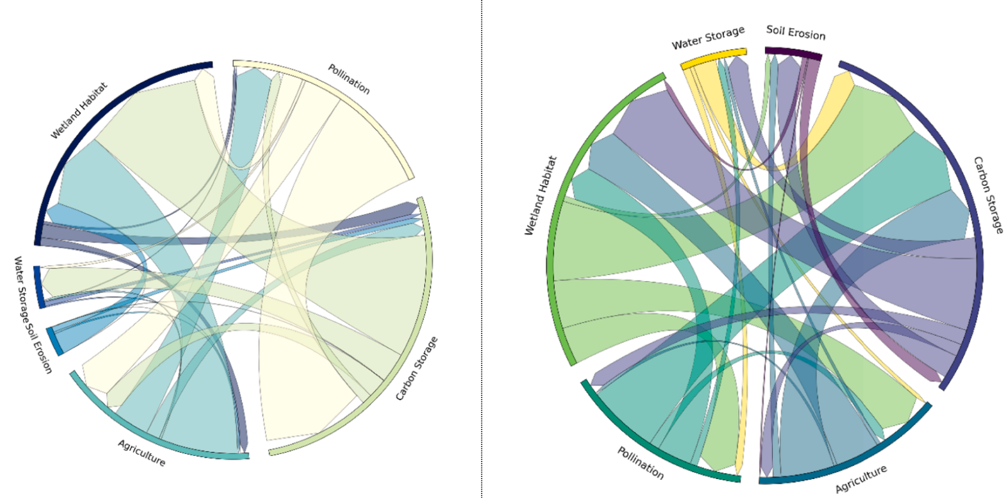


Fig.3. ES mapping output for the selected ES in the study area.



a. The interconnectivity of multiple ecosystem services at the landscape scale (based on aggregated link weights, considering overlapping and proximity connections)

b. Functional connectivity of ecosystem services based on overlapping connections (occurrence of connections) in the landscape

Fig. 4. Connectivity of ES nodes based on aggregated link weights and the amount of overlapping connections at the landscape scale.

with cropland nodes. Notably, the spatial coverage of pollination is seven times greater (160.85 km^2) than that of carbon storage nodes. Fig. 4 presents the landscape-scale connectivity of all ecosystem services including the interconnectivity of agricultural food production with other ES

3.1.4. Soil erosion regulation layer

The assessment of soil erosion is derived from the sediment delivery

Ratio model of InVEST. The generated mapping output identified 11,855 nodes indicative high value areas of this service. Despite the substantial number, the average node size is rather diminutive (n = 0.004 km^2), in contrast to the other ecosystem services within the study area (Table 4). The soil erosion regulation ecosystem service exhibits an interconnected functionality with wetland ecosystems (marsh/swamps), regions with high carbon sequestration, and croplands, demonstrating a total of 13,649 connections. This complex network of interactions among soil erosion regulation nodes spans an area constituting 72.59 % (37.12 km^2), marking it the second highest extent of overlap among all evaluated ecosystem services inside the high provisioning area (the portion of the high areas provisioning of the ES-node- that overlaps with other ESs). Carbon storage nodes stand out significantly in terms of both quantity and spatial extent within this overlap, exhibiting the highest contribution (connections = 8,759 and spatial coverage of avoided soil erosion = 32.28 km^2, 63.13 %) relative to the other ecosystem services. This underscores the crucial role that carbon storage nodes play in regulating soil erosion within the landscape. It hints at the existence of complex, dynamic interactions that evolve over time and space. These interactions may involve synergistic effects and feedback loops, where the processes of carbon sequestration and soil erosion regulation mutually reinforce each other, leading to cumulative benefits across the landscape

3.1.5. *Wetland-based ES layer*

Wetlands-based ES are significant in the functioning of agricultural landscapes and more specifically in the context of Canadian prairies as they are dominant natural elements in this landscape. Three wetland types including marshes, swamps, and open waters were considered in this study for multiple ES such as habitat provisioning and carbon storage from marshes/swamps and water storage capacity from open water wetlands. The wetlands layer consists of 42,711 nodes in overall with 81.46 % (n = 34,796) being marshes/swamps as an indicator for habitat provisioning and carbon storage, and open water wetlands considered for provisioning water for animal and cropland usage with 7915 nodes. Wetlands, despite constituting a minor fraction of the landscape, play a critical role in delivering various ecosystem services. Our study revealed a robust interrelation between wetland-based ES, particularly habitat provisioning and carbon storage from marshes and swamps, and other ES. Although marshes and swamps make up only 6.48 % of the studied area, their entire spatial extent (as illustrated in Table 3) was found to be interlinked with other ESs. Another key ecosystem service offered by wetlands is water storage, which is essential for the multifunctionality of the landscape. Open water wetlands span approximately 97.46 km^2 in the study area. Intriguingly, 61.14 % of this area is functionally linked with other ecosystem services. For habitat provisioning and carbon storage, the average node sizes are 0.007 km^2 in marshes and swamps and 0.012 km^2 in open-water wetlands

3.2. *Interconnectivity and occurrence patterns of ecosystem services*

The cord diagram below (Fig. 4) illustrates the ES network, focusing on the aggregated link weights and functional connections based the numbers of connection (incoming and out-going at each node level) to identify connectivity areas between different services. This diagram is instrumental in identifying areas of connectivity between different services, highlighting zones where ecosystem services interact most intensely. As reflected in the diagram and further detailed in the centrality metrics (Table 4), certain services, such as carbon storage, agricultural food production, and habitat provisioning, and pollination, exhibit the highest values for both in-degree and out-degree centrality at the landscape scale. These centrality measures indicate the prominence and influence of a given node (or service) within the network. However, it is essential to note that the spatial pattern of occurrence or events of interactions differs from the intensity of connectivity between these services (Fig. 4, panel b). All the ecosystem service nodes at the landscape scale demonstrate a relatively high degree of closeness centrality and a relatively low betweenness centrality. However, carbon and agricultural food production identified the highest in closeness centrality among others. This indicates that changes to these services can quickly affect all other services in the network due to their proximity. Closeness centrality suggests how close a node is to all other nodes in the network, reflecting the speed with which influence can spread from that node. Betweenness centrality measures the extent to which a node serves as a bridge between other nodes. In this context, the highest betweenness centrality, detected for carbon storage and agricultural food production (with a value of 0.116), may not seem particularly high. However, it still indicates the crucial role these services play in connecting various other ecosystem services. This could mean that these services have the potential to mediate synergies or trade-offs among other services, depending on the scenario. They could serve as leverage points for enhancing the overall provision of ecosystem services at the landscape scale.

Table 4
Centrality metrics of ES nodes.

Ecosystem Service nodes	*In-Degree Centrality*	*Out-Degree Centrality*	*Betweenness Centrality*	*Closeness Centrality*
Avoided Erosion Regulation	0.6	0.6	0.0	0.714
Carbon Storage	1.0	1.0	0.116	1.0
Agricultural food production	1.0	1.0	0.116	1.0
Pollination	0.8	0.8	0.033	0.833
Habitat provisioning and carbon storage in marsh/swamps	0.8	0.8	0.033	0.833
Wetland water storage capacity (open water)	0.6	0.6	0.0	0.714

Table 3
Landscape scale attributes of ES nodes and links and spatial coverage of nodes and functional link areas.

Ecosystem service	Numbers of Node	Extent of service provisioning areas in the landscape		Numbers of connections		Extent of connections in high service provisioning area		Average node extent (area, km^2)
		Area	%	Incoming	Outgoing	Area	%	
Pollination	127	2151.89	57.37	54,527	55,023	1107.36	51.46	16.94
Carbon storage	47,753	1071.25	28.56	82,778	77,980	363.37	33.92	0.02
Soil Erosion Regulation	11,855	51.13	1.36	22,360	13,649	37.12	72.59	0.004
Agricultural Food Production	15,610	1289.52	37.38	49,596	34,714	298.6	23.15	0.08
Habitat and carbon storage in wetlands (Marsh & Swamps)	34,796	243.09	6.48	75,088	62,337	243.09	100	0.007
Water Storage Capacity in wetlands (open water wetlands)	7915	97.46	2.6	8454	11,516	59.59	61.14	0.012
Landscape total		3750.45	–	–	255,219	1083.79	28.9	–

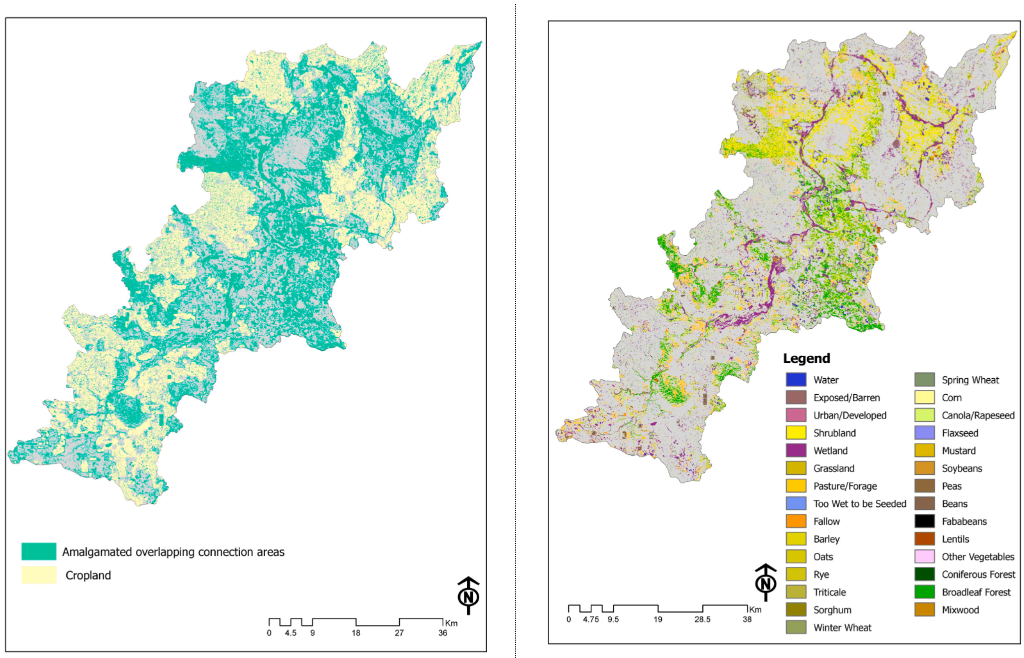
3.3. Identifying functionally connected zones

We integrated the interactions identified within each layer from the previous step to delineate distinct functional connectivity zones. Fig. 5 features an amalgamated map that illustrates these functionally connected zones, as well as the land cover types encompassed within them. In other words, functional connectivity map (Fig. 5, panel A) offers a spatial interpretation of the network's connectivity, as initially represented the circular diagram based on co-occurrence of the connections (Fig. 4). This interpretation specifically incorporates the analysis of proximity connections, highlighting the critical ecological linkages between areas providing pollination services and agricultural food production zones. Our analysis reveals that approximately 29 % of the landscape under study serves as functionally connected zones, as determined by spatial overlaps across all ES layers. While grasslands make up 35 % of the landscape, only 5.21 % of the grassland area falls within these functionally connected zones. In contrast, a significant proportion of natural land cover types such as forests, shrublands, and wetlands are located within these zones, representing 84.97 %, 83.25 %, and 75.68 % of their respective total areas within these specific cover types. Pastures are also notably represented, with 41.76 % of the total pasture area situated within these functionally connected zones. Among agricultural crops, canola, barley, and spring wheat are particularly prevalent within these zones, constituting 10.52 %, 10.24 %, and 7.78 % of their respective total areas within these specific cover types, as detailed in Fig. 5, Panel B and Fig. 6.

4. Discussion

Land-use and land-cover patterns, including their spatial heterogeneity and configuration, shape landscape-level ecological processes, functions, and services. Building on this foundation, our research introduced a comprehensive modeling framework that highlights the functional interrelations among multiple ES, particularly their overlapping and proximal connections. Our approach delves into the nuanced process of ES connectivity, deriving from spatial interaction such as spatial overlay and proximal connections. Using a conceptual framework and informed by existing literature (Felipe-Lucia et al., 2022; Field and Parrott, 2022; Mitchell et al., 2013; Obiang Ndong et al., 2020; Serna-Chavez et al., 2014; Snäll et al., 2021), we assert that these complex processes are inherent to the functional connectivity within landscapes, such as flows from pollination provisioning areas to croplands. Our exploration was primarily centered on spatial interactions within a specific, small-scale agricultural landscape in the Canadian prairies, as a means to demonstrate the utility of ES interactions through connectivity and ecological network analysis. While we recognize the presence of various other forms of connections among ES in this region, our focus was to exemplify these interactions through a spatial lens. Nevertheless, acknowledging the complexity of ecological processes, we highlight the importance of future research to encompass temporal fluctuations and delve into the nuanced, process-based interactions that underpin ES provision. Understanding the dynamics of ES requires examining how seasonal variability influences pollination dynamics and affects crop productivity, the impact of land-use changes on soil health, including composition and erosion patterns, and how landscape structure plays a crucial role in water regulation, affecting hydrological cycles and water quality. Additionally, exploring the effects of land management on carbon sequestration processes and the intricate balance of nutrient cycling, driven by microbial activity and organic matter decomposition, is vital.

In our methodology, node delineation is a fundamental step in constructing ecological networks of ecosystem services derived from mapping outputs. As such, when implementing the node and link delineation method across various contexts, nuanced judgment becomes



A.Amalgamated map of overlapping connectivity areas across the landscape

B.Spatial distribution of landcover types in functinally connected zones

Fig. 5. The identified functional connection areas and land cover types in these areas. Panel A represents the amalgamated map of overlapping functional connectivity areas (cyan-colored areas in the map), covering approximately 29% of the entire landscape. This map shows amalgamated functional corridors of ES where ES interactions happens based on overleaping and proximal connections. Panel B delves into the spatial distribution of various land cover types within these functionally connected zones. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

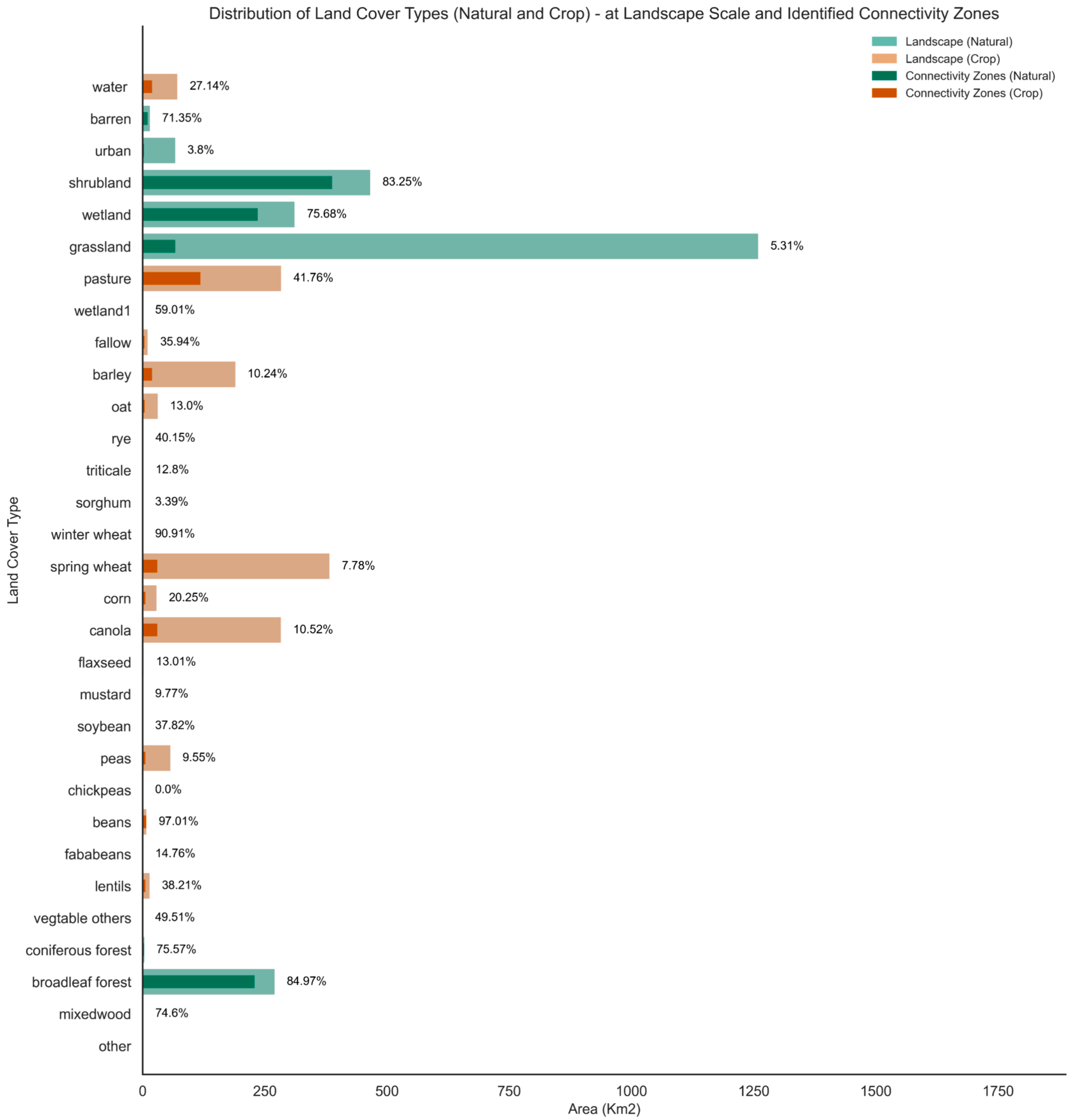


Fig. 6. Proportional representation of landcover types within the identified functional connectivity zones. The graph provides a quantitative breakdown, represented as a bar chart, of the proportion of each land cover type present in the connectivity areas. The bars in green and orange depict the distribution of natural and crop cover types, respectively, across the study area. Within each bar, the darker segment and accompanying percentage indicate the proportion of that specific cover type found within connectivity zones. These zones are key areas where ES interactions are most pronounced in the landscape, reflecting regions of heightened ecological interplay. The chart emphasizes that natural land cover types—such as shrublands, wetlands, forests, and grasslands, as well as select pastures—are predominant in connectivity zones. This underscores their critical role as key mediators in the provisioning of ecosystem services within the landscape. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

indispensable. The process of defining nodes, whether referred to as ES provisioning units or more commonly as ES hotspots (Akhtar et al., 2022; Bagstad et al., 2017; Li et al., 2017; Willemen et al., 2018) is closely tethered to both the underlying ecological characteristics of the landscape and the chosen classification algorithms. In our study, we used an area-based raster classification approach, targeting three distinct ESs: pollination, carbon storage, and soil erosion. Previous works, exemplified by Bagstad et al. (2017), indicate diverse spatial patterns emerging from different clustering methods for ES hotspot/coldspot delineation. Such methods as area-based and quantile classification utilize distinct high and low values, leading to varied spatial clustering outcomes. This observation highlights the potential limitations of a standardized approach. Similarly, Field and Parrott (2022) advocated for a universal threshold for all ES types in their node delineation within the ES network. Contrarily, our findings challenge this paradigm, suggesting that the nuances of each ES output demand tailored node thresholds. As evidenced by our sensitivity analysis, a heightened threshold for soil erosion regulation manifested in a greater number of smaller nodes. This trend starkly contrasted with carbon storage and pollination, where node count reduced.

The process of identifying connectivity zones in a landscape, based on the complex web of ES interactions can offer transformative insights into landscape ecology and management. Our approach, which integrates ES mapping with network analysis, illuminates these critical zones of functional connectivity on ES provisioning. The analysis of ES connectivity reveals that nearly a third (29 %) of the studied landscape functions as these connectivity zones, underlined by overlaps across all ES layers. This is significant fraction, and its implications for landscape management and conservation planning are manifold. Especially given that while grasslands constitute a major portion of the landscape, a meager 5.21 % of them are part of these functional zones, contrasting with the substantial representation of habitats like forest, shrublands and wetlands, which reinforce the critical role grassland play in enhancing ES-multifunctionality, both above and below ground (Tamburini et al., 2022). Such multifunctionality is notably higher in grasslands compared to crop field. This aligns with our observations and underscore the centrality of these natural and semi-natural habitats in the ES provisioning mechanism. In fact, this shows they are not just passive recipients of ecological benefits but are actively shaping the flows and connections of ecosystem services.

The salient role of managed landscapes (pastures) in the identified connectivity zones denotes potential synergies between anthropogenic activities and ES dynamics. Such findings build upon Donald and Evans (2006) premise of enhancing ES through agricultural modification. This hints at the possibility of designing pastoral and agricultural practices that are harmonized with the ecological rhythms and ES dynamics of the landscape. Additionally, the presence of certain agricultural crops like canola, barley, and spring wheat within these zones points to complex interactions between cultivated landscapes and ecosystem services, echoing Landis's (2017) call for redesigning agricultural landscapes for enhanced biodiversity-based ES. Such insight can guide agro-ecological practices that optimize both yield and ecological health of the landscape. Understanding the role of managed landscapes in ES connectivity zones offers essential insights for land use planning and conservation area strategy development. The insights gleaned from our research offer crucial information that could inform policy development, particularly in conserving ecosystems like grasslands and pasturelands. This information can assist decision-makers in considering the multifunctionality and connectivity of these landscapes, enabling the formulation of sustainable land-use strategies that effectively balance environmental conservation with agricultural productivity.

This research provides a novel approach in the operationalization of an ecological network of ecosystem services within a landscape by leveraging the spatial distribution of ES provisioning units. Drawing from the conceptualization by Felipe-Lucia et al. (2022), ES have been recognized not as isolated phenomena, but as dynamic, interlinked entities within ecological network. In our study, the ES provisioning units were extracted as nodes within the network, capturing the core areas of high ES provisioning capacity in the landscape. The functional relationships between these nodes, reflecting the flow and interplay of ES, were represented by the links or edges, while the intensity or strength of these connections was captured through link weights. This approach allowed us to appreciate the complex interdependencies among ES, and particularly underscored the crucial role of certain services, like pollination and carbon storage, in sustaining others. Such conceptual and methodological frameworks enhance our understanding of the landscape's complex ecological structure, function, and resilience; they also mitigate potential misinterpretations associated with these complexities (Fath, 2018; Kharrazi et al., 2018). For example, our methodology identifies functional connectivity zones—areas where ecosystem services (ES) interact most intensively. Recognizing these zones as critical to ES functioning enables targeted conservation efforts that bolster the landscape's integrity and resilience. Moreover, by translating abstract ecological relationships into tangible, spatially explicit networks, we pave the way for informed landscape management and conservation strategies that prioritize the holistic functionality and connectivity of ES. Recognizing ES as both nodes and links enables us to view landscapes not just as collections of separate services, but as complex systems where ES are both the attributes and emergent properties of the network (Turnbull et al., 2018).

Building upon this foundational exploration, there lies a vast potential for further study within ES network topology. Recognizing our investigation as an empirical pioneering endeavor, future research can immerse deeper into the nuanced interplays of the network, potentially unveiling cascading effects and emergent properties inherent to ES interactions and their connectivity. As Felipe-Lucas et. al (2022) conceptualization suggests, the interplay of ES extends beyond mere spatial connections. Although our focus is firmly planted in spatial dynamics, it is imperative for subsequent analyses to integrate temporal perspectives, deepening the understanding of the temporal evolution and potential shifts in ES networks. By advancing in this direction, we not only refine our grasp of the landscape's ecological subtleties but also equip stakeholders with the knowledge necessary for more informed landscape management and conservation strategies.

The conceptual and methodological frameworks developed in our study have practical applications in landscape management and conservation strategies. Land managers can utilize our findings to identify key areas for conservation or restoration, enhancing ecosystem service provisioning. By prioritizing these critical zones in landscape planning, we can create a mosaic of habitats that supports biodiversity, enhances carbon storage, and reduces soil erosion. This approach not only benefits ecological health but also supports sustainable land use, offering a model for integrating ecological insights into practical land management decisions.

5. Conclusion

In this study, we utilized a novel integrative methodology that combines ecosystem service mapping with network analysis to delineate functionally connected areas at a landscape scale. Our findings unravel the intricate dynamics that characterize interactions among various ecosystem services. Although traditional approaches such as bundling ES through correlation analysis between pairs of services provide insights into strong interdependencies and in some cases unexpected trade-offs among services, it is imperative to recognize that they might not encompass all indirect relationships between different ES. Through a novel integration of ecosystem service mapping and network analysis, this research highlights the important role of functional connectivity within diverse landscapes. Approximately 29 % of the study area emerges as vital connectivity zones, with key natural habitats serving as instrumental mediators in this complex web of ecological interactions. With the Ecological Network Approach (ENA) at its core, our framework paves the way for a deeper understanding of optimal ES provisioning scenarios at the landscape scale. Such nuanced comprehension of the ecosystem service interactions network is poised to inform strategic, targeted actions that leverage the inherent connectivity of the landscape to enhance ecosystem service provision and landscape resilience. We recommend further interdisciplinary research that combines ecological science with policy and land management to advance practical applications of ecosystem service networks. Future studies should explore how these frameworks can be implemented in diverse landscapes to inform decision-making processes and conservation strategies.

CRediT authorship contribution statement

Ehsan Pashanejad: Writing – review & editing, Writing – original draft, Visualization, Validation, Software, Resources, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Ali Kharrazi:** Writing – review & editing, Validation, Supervision. **Zuelclady M.F. Araujo-Gutierrez:** Writing – review & editing. **Brian E. Robinson:** Writing – review & editing, Validation, Funding acquisition. **Brian D. Fath:** Writing – review & editing, Validation, Supervision, Funding acquisition. **Lael Parrott:** Writing – review & editing, Validation, Supervision, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecoser.2024.101639.

References

Agudelo, César Augusto Ruiz, Sandra Liliana Hurtado Bustos, and Carmen Alicia Parrado Moreno. 2020. "Modeling Interactions among Multiple Ecosystem Services. A Critical Review." *Ecological Modelling* 429:109103. doi: https://doi.org/10.1016/j.ecolmodel.2020.109103.

Akhtar, M., Zhao, Y., Gao, G., Gulzar, Q., Hussain, A., 2022. Assessment of spatiotemporal variations of ecosystem service values and hotspots in a Dryland: a case-study in Pakistan. Land Degrad. Dev. 33 (9), 1383–1397. https://doi.org/10.1002/ldr.4245.

Anand, M., Gonzalez, A., Guichard, F., Kolasa, J., Parrott, L., 2010. Ecological systems as complex systems: challenges for an emerging science. Diversity 2 (3), 395–410. https://doi.org/10.3390/d2030395.

Assessment, Ecosystem, M., 2005. Ecosystems and Human Well-Being, Vol. 5. Island Press Washington, DC.

Bagstad, K.J., Johnson, G.W., Voigt, B., Villa, F., 2013. Spatial dynamics of ecosystem service flows: a comprehensive approach to quantifying actual services. Ecosyst. Serv. 4, 117–125. https://doi.org/10.1016/j.ecoser.2012.07.012.

Bagstad, K.J., Semmens, D.J., Ancona, Z.H., Sherrouse, B.C., 2017. Evaluating alternative methods for biophysical and cultural ecosystem services hotspot mapping in natural resource planning. Landsc. Ecol. 32 (1), 77–97. https://doi.org/10.1007/s10980-016-0430-6.

Bockstael, N.E., Myrick Freeman, A., Kopp, R.J., Portney, P.R., Kerry Smith, V., 2000. On measuring economic values for nature. Environ. Sci. Tech. 34 (8), 1384–11139. https://doi.org/10.1021/es990673l.

Bodin, Ö., Alexander, S.M., Baggio, J., Barnes, M.L., Berardo, R., Cumming, G.S., Dee, L. E., Fischer, A.P., Fischer, M., Mancilla Garcia, M., Guerrero, A.M., Hileman, J., Ingold, K., Matous, P., Morrison, T.H., Nohrstedt, D., Pittman, J., Robins, G., Sayles, J.S., 2019. Improving network approaches to the study of complex social-ecological interdependencies. Nat. Sustainability 2 (7), 551–559. https://doi.org/10.1038/s41893-019-0308-0.

Braat, L.C., De Groot, R., 2012. The ecosystem services agenda: bridging the worlds of natural science and economics, conservation and development, and public and private policy. Ecosyst. Serv. 1 (1), 4–15.

Burkhard, B., Kroll, F., Nedkov, S., Müller, F., 2012. Mapping ecosystem service supply, demand and budgets. Ecol. Ind. 21, 17–29. https://doi.org/10.1016/j.ecolind.2011.06.019.

Burkhard, B., Maes, J., 2017. Mapping Ecosystem Services, Vol. 1. Pensoft Publishers.

Cord, A.F., Bartkowski, B., Beckmann, M., Dittrich, A., Hermans-Neumann, K., Kaim, A., Lienhoop, N., Locher-Krause, K., Priess, J., Schröter-Schlaack, C., Schwarz, N., Seppelt, R., Strauch, M., Václavík, T., Volk, M., 2017. Towards systematic analyses of ecosystem service trade-offs and synergies: main concepts, methods and the road ahead. Ecosyst. Serv. 28, 264–272. https://doi.org/10.1016/j.ecoser.2017.07.012.

Costanza, R., 2020. Valuing natural capital and ecosystem services toward the goals of efficiency, fairness, and sustainability. Ecosyst. Serv. 43, 101096 https://doi.org/10.1016/j.ecoser.2020.101096.

Costanza, R., D'Arge, R., de Groot, R., Farber, S., Grasso, M., Hannon, B., Limburg, K., Naeem, S., O'Neill, R.V., Paruelo, J., Raskin, R.G., Sutton, P., van den Belt, M., 1997. The value of the world's ecosystem services and natural capital. Nature 387 (6630), 253–260. https://doi.org/10.1038/387253a0.

Donald, P.F., Evans, A.D., 2006. Habitat connectivity and matrix restoration: the wider implications of agri-environment schemes. J. Appl. Ecol. 43 (2), 209–218. https://doi.org/10.1111/j.1365-2664.2006.01146.x.

Fath, B.D., 2018. *Encyclopedia of ecology*. Elsevier.

Felipe-Lucia, M.R., Guerrero, A.M., Alexander, S.M., Ashander, J., Baggio, J.A., Barnes, M.L., Bodin, Ö., Bonn, A., Fortin, M.-J., Friedman, R.S., Gephart, J.A., Helmstedt, K.J., Keyes, A.A., Kroetz, K., Massol, F., Pocock, M.J.O., Sayles, J., Thompson, R.M., Wood, S.A., Dee, L.E., 2022. Conceptualizing ecosystem services using social-ecological networks. Trends Ecol. Evol. 37 (3), 211–222. https://doi.org/10.1016/j.tree.2021.11.012.

Field, R.D., Parrott, L., 2022. Mapping the functional connectivity of ecosystem services supply across a regional landscape. Elife 11. https://doi.org/10.7554/eLife.69395.

Fremier, A.K., DeClerck, F.A.J., Bosque-Pérez, N.A., Carmona, N.E., Hill, R., Joyal, T., Levi Keesecker, P., Klos, Z., Martínez-Salinas, A., Niemeyer, R., Sanfiorenzo, A., Welsh, K., Wulfhorst, J.D., 2013. Understanding spatiotemporal lags in ecosystem services to improve incentives. Bioscience 63 (6), 472–482. https://doi.org/10.1525/bio.2013.63.6.9.

Hagberg, A., Swart, P.J., Schult, D.A., 2008. Exploring Network Structure, Dynamics, and Function Using NetworkX. *Conference: SCIPY 08*.

Jennings, Megan K., Katherine A. Zeller, and Rebecca L. Lewison. 2021. "Dynamic Landscape Connectivity Special Issue Editorial." *Land* 10(6).

Karimi, J.D., Harris, J.A., Corstanje, R., 2021. Using Bayesian belief networks to assess the influence of landscape connectivity on ecosystem service trade-offs and synergies in urban landscapes in the UK. Landsc. Ecol. 36 (11), 3345–3363. https://doi.org/10.1007/s10980-021-01307-6.

Kharrazi, A., Kudo, S., Allasiw, D., 2018. Addressing misconceptions to the concept of resilience in environmental education. Sustainability 10 (12), 4682. https://doi.org/10.3390/su10124682.

Landis, D.A., 2017. Designing agricultural landscapes for biodiversity-based ecosystem services. Basic Appl. Ecol. 18, 1–12. https://doi.org/10.1016/j.baae.2016.07.005.

Lee, H., Lautenbach, S., 2016. A Quantitative review of relationships between ecosystem services. Ecol. Ind. 66, 340–351. https://doi.org/10.1016/j.ecolind.2016.02.004.

Leitão, A.B., Miller, J., Ahern, J., McGarigal, K., 2012. Measuring Landscapes: A Planner's Handbook. Island press.

Li, Y., Zhang, L., Yan, J., Wang, P., Ningke, Hu., Cheng, W., Bojie, Fu., 2017. Mapping the hotspots and coldspots of ecosystem services in conservation priority setting. J. Geog. Sci. 27 (6), 681–696. https://doi.org/10.1007/s11442-017-1400-x.

Loomisa, J., Kentb, P., Strangec, L., Fauschc, K., Covichc, A., 2018. Measuring the Total economic value of restoring ecosystem services in an impaired river basin: results from a contingent valuation survey. In: Economics of Water Resources. Routledge, pp. 77–91.

MacQueen, Sarah Anne. 2020. "Modelling the Effects of Landscape, Behaviour, and Population on Bumble Bee Crop Pollination Services.".

Metzger, J.P., Villarreal-Rosas, J., Suárez-Castro, A.F., López-Cubillos, S., González-Chaves, A., Runting, R.K., Hohlenwerger, C., Rhodes, J.R., 2021. Considering landscape-level processes in ecosystem service assessments. Sci. Total Environ. 796, 149028 https://doi.org/10.1016/J.SCITOTENV.2021.149028.

Mitchell, M.G.E., Bennett, E.M., Gonzalez, A., 2013. Linking landscape connectivity and ecosystem service provision: current knowledge and research gaps. Ecosystems 16 (5), 894–908. https://doi.org/10.1007/s10021-013-9647-2.

Ndong, O., Gregory, O.T., Cousin, I., 2020. Analysis of relationships between ecosystem services: a generic classification and review of the literature. Ecosyst. Serv. 43, 101120 https://doi.org/10.1016/j.ecoser.2020.101120.

Notte, La., Alessandra, D.D., Mäkinen, H., Paracchini, M.L., Liquete, C., Egoh, B., Geneletti, D., Crossman, N.D., 2017. Ecosystem services classification: a systems ecology perspective of the cascade framework. Ecol. Ind. 74, 392–402. https://doi.org/10.1016/j.ecolind.2016.11.030.

Qiu, J., Carpenter, S.R., Booth, E.G., Motew, M., Zipper, S.C., Kucharik, C.J., Loheide II, S.P., Turner, M.G., 2018. Understanding relationships among ecosystem services across spatial scales and over time. Environ. Res. Lett. 13 (5), 054020 https://doi.org/10.1088/1748-9326/aabb87.

Schirpke, U., Candiago, S., Vigl, L.E., Jäger, H., Labadini, A., Marsoner, T., Meisch, C., Tasser, E., Tappeiner, U., 2019. Integrating supply, flow and demand to enhance the understanding of interactions among multiple ecosystem services. Sci. Total Environ. 651, 928–941. https://doi.org/10.1016/j.scitotenv.2018.09.235.

Serna-Chavez, H.M., Schulp, C.J.E., van Bodegom, P.M., Bouten, W., Verburg, P.H., Davidson, M.D., 2014. A quantitative framework for assessing spatial flows of ecosystem services. Ecol. Ind. 39, 24–33. https://doi.org/10.1016/j.ecolind.2013.11.024.

Sharp, R., Tallis, H.T., Taylor Ricketts, A.D., Guerry, S.A., Wood, R.-K., Nelson, E., Ennaanay, D., Wolny, S., Olwero, N., 2014. InVEST User's Guide. The Natural Capital Project, Stanford.

Snäll, T., Triviño, M., Mair, L., Bengtsson, J., Moen, J., 2021. High rates of short-term dynamics of forest ecosystem services. Nat. Sustainability. https://doi.org/10.1038/s41893-021-00764-w.

Sothe, C., Gonsamo, A., Arabian, J., Kurz, W.A., Finkelstein, S.A., Snider, J., 2022. Large soil carbon storage in terrestrial ecosystems of Canada. Global Biogeochem. Cycles 36 (2). https://doi.org/10.1029/2021GB007213.

Spawn, S.A., Sullivan, C.C., Lark, T.J., Gibbs, H.K., 2020. Harmonized global maps of above and belowground biomass carbon density in the Year 2010. Sci. Data 7 (1), 112. https://doi.org/10.1038/s41597-020-0444-4.

Tallis, H., Polasky, S., 2009. Mapping and valuing ecosystem services as an approach for conservation and natural-resource management. Ann. N. Y. Acad. Sci. 1162 (1), 265–283. https://doi.org/10.1111/j.1749-6632.2009.04152.x.

Tamburini, G., Aguilera, G., Öckinger, E., 2022. Grasslands enhance ecosystem service multifunctionality above and below-ground in agricultural landscapes. J. Appl. Ecol. 59 (12), 3061–3071. https://doi.org/10.1111/1365-2664.14302.

Thierry, H., Parrott, L., Robinson, B., 2021. Next steps for ecosystem service models: integrating complex interactions and beneficiaries. FACETS 6, 1649–1669. https://doi.org/10.1139/facets-2020-0116.

Turnbull, L., Hütt, M.-T., Ioannides, A.A., Kininmonth, S., Poeppl, R., Tockner, K., Bracken, L.J., Keesstra, S., Liu, L., Masselink, R., Parsons, A.J., 2018. Connectivity and complex systems: learning from a multi-disciplinary perspective. Appl. Network Sci. 3 (1), 11. https://doi.org/10.1007/s41109-018-0067-2.

Villa, F., Bagstad, K.J., Voigt, B., Johnson, G.W., Portela, R., Honzák, M., Batker, D., 2014. A Methodology for Adaptable and Robust Ecosystem Services Assessment. PLoS One 9 (3), e91001.

Willemen, L., Crossman, N.D., Quatrini, S., Egoh, B., Kalaba, F.K., Mbilinyi, B., de Groot, R., 2018. Identifying ecosystem service hotspots for targeting land degradation neutrality investments in South-Eastern Africa. J. Arid Environ. 159, 75–86. https://doi.org/10.1016/j.jaridenv.2017.05.009.

Zeller, K.A., Lewison, R., Fletcher, R.J., Tulbure, M.G., Jennings, M.K., 2020. Understanding the importance of dynamic landscape connectivity. Land 9 (9).

Zhang, Y., Xiao, Lu., Liu, B., Dianting, Wu., Guo, Fu., Zhao, Y., Sun, P., 2021. Spatial relationships between ecosystem services and socioecological drivers across a large-scale region: a case study in the Yellow River Basin. Sci. Total Environ. 766, 142480 https://doi.org/10.1016/j.scitotenv.2020.142480.