PLOS COMPLEX SYSTEMS

RESEARCH ARTICLE

A systematic review of ecosystem services analysis and network theory

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Abstract

Managing ecosystems to sustain ecosystem services amidst global change presents a significant challenge for scientists and policymakers. Predicting how management strategies and fluctuating environmental conditions affect ecosystem services is challenging due to the complex nature of the interactions and the intrinsic dynamics within ecological and social systems. Overlooking these interactions can result in missed opportunities to secure ecosystem services, which are crucial for the well-being of both human societies and ecological communities. Given the nature of these interactions, complex systems in general and network theory in particular provide a framework for exploring their complexities. This study reviews the main scientific literature investigating ecosystem services using network theory. We systematically selected studies that combine complex network analysis with ecosystem service research. A total of 152 published papers were fully read and analyzed to investigate their temporal and spatial distributions, spatial scales, topics of study, network metrics, and the types of network models used in case studies. We aim to report on how ecosystems and their services are modeled and analyzed, identifying methods that could potentially advance the research field. The findings reveal that research tends to rely on a limited set of network metrics and models. By shedding light on existing practices and potential avenues for advancement, our review contributes to the ongoing dialogue on harnessing complex network analysis for effective ecosystem services management in a rapidly changing world.

Author summary

From the beginning, humans have always interacted with nature. These exchanges were and still are necessary for human survival and evolution in this world. Starting with their scientific recognition in the late 1990s, ecosystem services have been evaluated, measured, visually mapped, and discussed by scientists and policy-makers. There is a

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significant need to preserve and protect nature, which, in its social dimension, entails ensuring the sustainability of ecosystem services. Because ecosystem services are conceptualized as the exchanges between ecosystems and social parts, network theory can help in studying their properties. As such, we conducted a literature review to understand how networks are currently used and could help the development of this research field. We found that 152 papers analyzed ecosystem services using network approaches or discussed their applications. We found that there is a lack of studies in many areas of the world and that some network models and topics are still uncommon, meaning that there are ample possibilities for researchers to create new research projects. Our research provides material and guidelines for anyone interested in applications of complex networks for socio-environmental problems.

Introduction

Ecosystem services (ES) are the benefits people receive from nature and capture the dynamic interface between ecological and social systems [1]. They can be distinguished into direct and indirect benefits to human well-being, derived from ecosystems and their functions [2]. Direct ecosystem benefits are tangible and quantifiable contributions to people, whereas indirect benefits support the health and functioning of ecosystems. The ecosystems that provide services to society are occasionally denoted as 'natural capital' [3] and refer to the stock of natural resources. Manufactured and social services support flows of material, energy, and information from the natural capital to produce welfare [4]. In particular, abiotic flows refer to contributions to benefits from the environment that are not underpinned by, or reliant on, ecological characteristics and processes, for example, geophysical processes and the extraction of natural resources [5].

The state of the art identifies different ecosystem service types and functions [5,6]. Ref [6] classified 17 ecosystem services, categorizing them into provisioning, regulating, cultural, and supporting services. Provisioning services provide natural resources to people (e.g., food production, water supply). Regulating services control the regular functioning of ecosystems (e.g., flood control, pest control, pollination). Cultural services comprise all those non-material and symbolic flows that provide intellectual and emotional values to people (e.g., recreation, sense of place, aesthetics, scientific knowledge). Supporting services are the basic formation processes occurring in ecosystems and sustaining the provisioning, regulating, and cultural services (e.g., soil formation, nutrient cycling, provision of habitats). Ref [6] mentioned that studies may replace this last category with 'Habitat Services' to highlight the importance of ecosystems in providing habitat for migratory species and gene-pool areas.

With the increase of anthropogenic pressure on the environment, pressing goals have emerged to create better plans for managing ecosystem services and, ultimately, achieving harmonious coexistence between the social domain and the environment. The existing ES types and functions arise from the current distribution of social and environmental resources. Global and local environmental changes may modify the equilibrium of ecosystems and, as a consequence, their services. Moreover, social systems are not static. People's and communities' lives are influenced at local scales by policies, economies, pandemics, and wars. As a consequence, their needs and vulnerabilities vary over time and space. Changing environmental and social factors make ES dynamic complex systems that may be transformed by new development pathways.

Since the 1990s, frameworks have aimed to evaluate present functions, monitor changes over time, and inform future planning, conservation, and restoration of ecosystem services [7,8]. Modeling techniques used in ES analysis include qualitative models (e.g., participatory mapping, sociocultural methods, and surveys); matrix-based methods; spatial mapping techniques (e.g., hot-spot mapping, biophysical models, integrated mapping modeling approaches, and land-use scoring approaches); statistical techniques (e.g., regressions, correlations, multivariate analyses); data-driven approaches (e.g., machine learning); integration techniques (e.g., semantic meta-modeling); and monetary evaluation techniques [9–11]. In recent years, data-driven approaches with spatial data have been used to enhance the governance of ecosystem services [12]. Those have been made publicly available by models developed by the Integrated Valuation of Ecosystem Services and Tradeoffs (InVEST) software [13] and the Artificial Intelligence for Ecosystem Services (ARIES) modeling platform [14,15]. Research has focused on mapping ES under different scenarios to identify synergies and trade-offs between different services and the allocation of land or other natural resources [16]. Spatial mapping identifies and evaluates areas of ES demand, and questionnaires or surveys are generally integrated into the analysis to gather additional information [11]. The effects of scale on ES estimates have also been discussed as an important factor in providing greater accuracy and reliability in the analyses [16].

Since ES emerge from the interchanges between people and the environment, they can be understood within a broader socio-ecological systems framework. Specifically, socio-ecological systems refer to coupled human-environment interactions, forming integrated systems characterized by strong connections and feedback within and between social and ecological components [17]. Over the past two decades, research has increasingly focused on the sustainability and resilience of these complex systems [18–20]. One core challenge was to identify and analyze relationships between components across multiple levels and spatiotemporal scales, to account for complexity and avoid oversimplification of socio-ecological problems [18].

In addressing this challenge, network theory has emerged as a powerful tool for analyzing ecosystem services. By modeling relationships among components, networks enable us to explore the intrinsic interconnectedness and structural properties of socio-ecological systems. Although a few reviews have explored network-based approaches to studying ecosystem services and socio-ecological systems, the literature remains limited. Current studies span various fields and topics, including network ecology in ecosystem service assessment and management [21], social-ecological systems [22,23], habitat management for spatially structured populations [24], drivers and management actions influencing ecosystem services outcomes [25], and agroecological services [26]. Notably, only one paper has reviewed Bayesian Belief Networks in the context of ecosystem services [27], leaving opportunities to explore their applicability in future ecosystem service research.

This study reviews the literature concerning analyses of ecosystem services and network theory. The aims are, first, to summarize how and for what network approaches are used in ecosystem service research, and second, to create new guidelines for future research development.

Our work encompasses a range of interactions among components, without limiting a priori what possible kind of network interactions should be analyzed. Therefore, this review also includes studies that analyze social and ecological phenomena separately. Because ecosystem flows are supported by infrastructures to supply services, we collected contributions analyzing, by others, blue-green infrastructures and nature-based solutions.

Materials and methods

Collection and screening

This study reviewed the main literature investigating ecosystem services using network theory. First, we selected keywords that intersect network analyses and ecosystem service research; for the latter, "complex network", "graph", and "network-based approaches", "spatial network" and "social-ecological network"; for the former, "human-environment" interactions, to acknowledge the interplay between social and environmental components proper of ecosystem services, "natural capital" resources, the features and states of ecosystems (e.g., population size, sediment retention, stored soil carbon) that underpin the provision and distribution of ecosystem services (see [25], and "green infrastructures" and "nature-based solutions", as 'strategically planned networks of natural and semi-natural areas with other environmental features designed and managed to deliver a wide range of ES [28,29]. We used Scopus as a peer-reviewed literature database and conducted a keyword search on abstract texts with the following sequence: ("complex network*" OR "spatial network*" OR "graph" OR "network-based approach" OR "network approach" OR "social-ecological network") AND ("ecosystem servic*" OR "green infrastruct*" OR "nature-based solutions" OR "human-environment*" OR "natural capital").

Articles were included in the final collection if they met a set of eligibility criteria. Specifically, papers should:

- primarily use or discuss networks as a model for analyses of ecosystem services,
- be accessible on the web,
- be written in English, and
- use network theory to infer or build networks and/or to characterize topological or dynamical properties.

We screened papers by following two steps. First, we read titles and abstracts of each paper and checked if they were accessible. Second, we accessed the article and read the full text to selected the articles that fulfill the eligibility criteria. In total, two authors screened the papers by working independently, using a shared Excel file to record information and coordinate the screening process.

As a result of the screening, we collected quantitative documents, which applied methods to analyze case studies, and conceptual documents, which discussed frameworks and aspects related to ecosystem services and networks. Including conceptual papers was important because, in a developing field of research, new ideas may not meet the full data availability needed to be pursued. Moreover, we hypothesized that emerging research might initially be discussed in theory, rather than showcasing case studies.

We reviewed 152 documents (127 quantitative papers, 18 conceptual papers, and 7 reviews). Initially, we downloaded 323 papers (accessed on the 17th of September 2024), and after the screening, we selected 142 papers. Papers were excluded because they did not respect at least one of the eligibility criteria. For example, at least 30 documents were inaccessible because they referred to conference proceedings or were not available on the Web. Some articles were written in foreign languages; for instance, 10 were written in Chinese, 2 in Spanish, and 1 in Czech. Additionally, we found that around 23 papers were off-topic because they belonged to the fields of robotics or autonomous navigation. We want to emphasize that terms like 'complexity' and 'network' are commonly used in different research fields to describe characteristics of social or biological systems. Consequently, some screened studies were off-topic, as they used the chosen keywords but did not focus on network analysis. In the

Supplementary Information, we report the reasons for rejections for the screened papers (S1 Table).

Afterward, we searched for additional documents through a snowballing search, a method shown to be useful for extending a systematic literature study (see [30]). We followed the PRISMA 2020 protocol checklist (S1 Checklist) to provide better transparency in the systematic review reporting [31]; (see Fig 1).

Review and analysis

After applying the eligibility criteria and selecting the articles, we analyzed the body of literature by fully reading the papers. For each document, one reviewer selected key information, like title, authors, year of publication, the purpose of the study, place of the case study, the network metric used, the feature modeled as nodes, the types of interactions modeled as edges, and the type of network model. Those were all recorded in Excel and Word files (S2 Table). If papers did not report specific information, it was marked as missing. To prevent errors, two authors double-checked if information was not reported clearly in the paper. Our analyses primarily focused on five aspects. First, temporal distributions were intended to identify the popularity of analyses related to ES and network concepts over time. We expected that network theory would have gained more popularity in the analyses of ecosystem services. Therefore, we obtained the annual publication trends. Additionally, we evaluated the relative ratios in the number of publications on complex networks for ecosystem services to the total number of ecosystem services publications each year. We obtained the

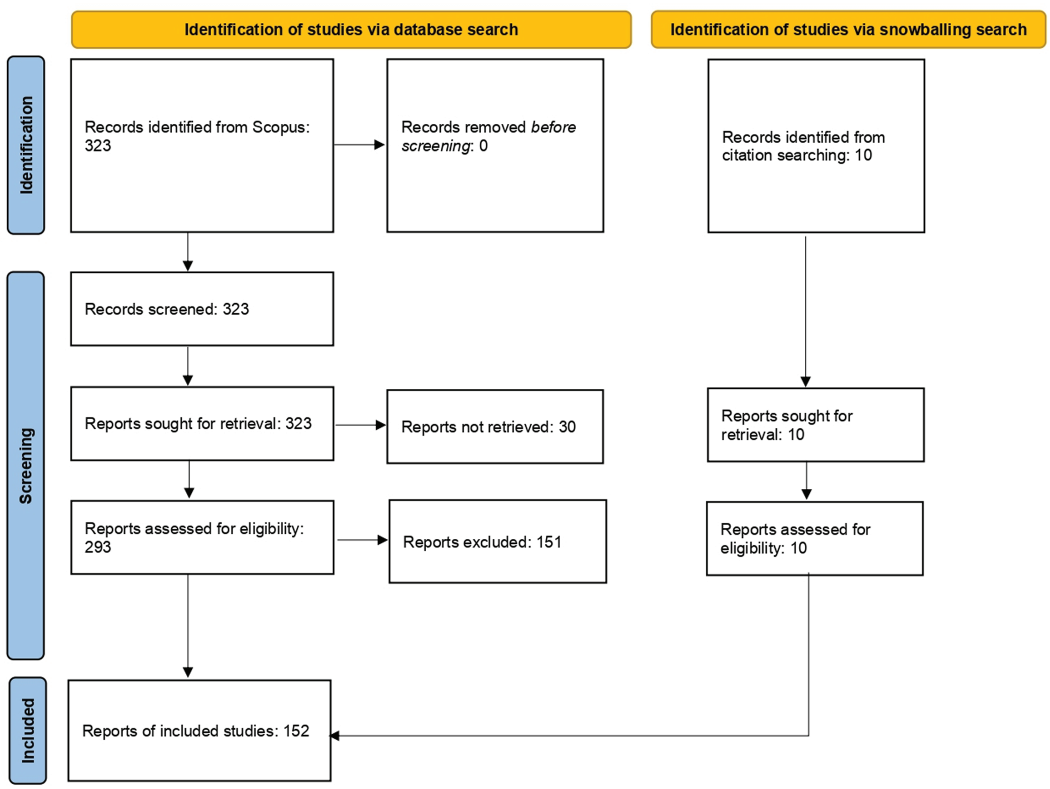

Fig 1. PRISMA protocol flowchart through the different phases of our systematic review, based on Ref [31].

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number of ecosystem services publications by searching the keyword "ecosystem servic*" in abstracts and keywords on Scopus. Second, spatial distributions detected the locations of case studies and their spatial scales. For locations, we selected the countries of case studies and we identified the most studied ones. We expected that there would be no homogeneous spatial distribution of investigations. We looked at the number of nodes and the spatial extension of the spatial scales. The relative size of nodes on areal extension measures the extent or range of network models. In this way, we investigated their spatial approximation. Third, we identified categories of studies based on four types of relationships: ecology, management, nature's contribution to people, and social. We selected these categories based on three interaction types that can occur between social and ecological systems; those between social components only, between ecological components, and between social and ecological components, where the latter represents nature's contribution to people and management of ecosystems and their services (see [1]). Studies on nature's contribution to people primarily analyze the distribution of natural resources and ecosystem benefits to social components. Conversely, management studies analyze the impacts and effects of society on the environment. Because we classified studies based on the interactions modeled, each study fits into one category. For example, ecology studies and social studies looked at relationships within ecological and social characteristics separately. Whereas, management and nature's contribution to people study relationships between the social and environmental domains. When studies modeled ecosystem services as nodes, we labeled them as environmental components as they represent the natural contribution provided to society. Additionally, we examined the topics studied to show the scope of the analysis and investigations developed. Analyses of topics help to identify emerging topics and possible missing gaps in research fields. We selected the topics based on the type of component or interaction the work focused on. For ecology studies, we also categorized them based on the aim of the analysis reported by the authors. This distinction was made because the main difference between some ecology studies lay in the scope of the investigation. Fourth, we investigated the methods. In particular, we looked at the network metrics, kinds of network models, and types of node features and edges used in case studies. In this way, we shed light on how systems were represented and commonly analyzed, looking for methods that improve the state of the art. Fifth, we summarized the topics covered in conceptual papers in chronological order of publication to illustrate how ideas have emerged over time. For the analyses, we first counted the information recorded in columns on the Excel files, and second, we used ArcGIS and Python to analyze and display the collected information. For spatial analyses, we created a map using a shapefile of countries polygons by manually editing the number of papers for each feature in the attribute table.

Results

We reviewed 152 documents. Of these, 127 were quantitative papers, 18 were conceptual papers, and 7 reviews.

Temporal and spatial distributions

The use of complex networks to represent and analyze ecosystem services has attracted increasing interest as reflected by the growth of the number of papers published in recent years (see Fig 2). Out of the total number of papers, 96% were published after 2010, with 68% released from 2020 onward. The growth of the number of papers follows an exponential shape (R^2=0.27). Fitting only data after 2010, the growth slope is 0.2 (R^2=0.86). To understand how the study of complex networks in ecosystem services is increasing compared to the growth of ecosystem services field in general, we looked at the ratios between the number of publications on complex networks in ecosystem services and the total ecosystem services publications in each year. The ratios grew from 0.08% in 2011 to 0.46% in 2024. Among the 127 quantitative studies - excluding conceptual or review papers - 95% (121 papers) provided information about their case study locations. Of these, 6 covered case studies across multiple continents, and 3 spanned different countries. Specifically, case studies were distributed as follows: 48% (61 papers) in Asia, 22% (28 papers) in Europe, 11% (14 papers) in North America, 6% (8 papers) in South America, 2% (3 papers) in the Middle East, and 2% (2 papers) each in Africa and Oceania. Notably, 51 case studies were conducted in China, and 12 in the USA (Fig 2).

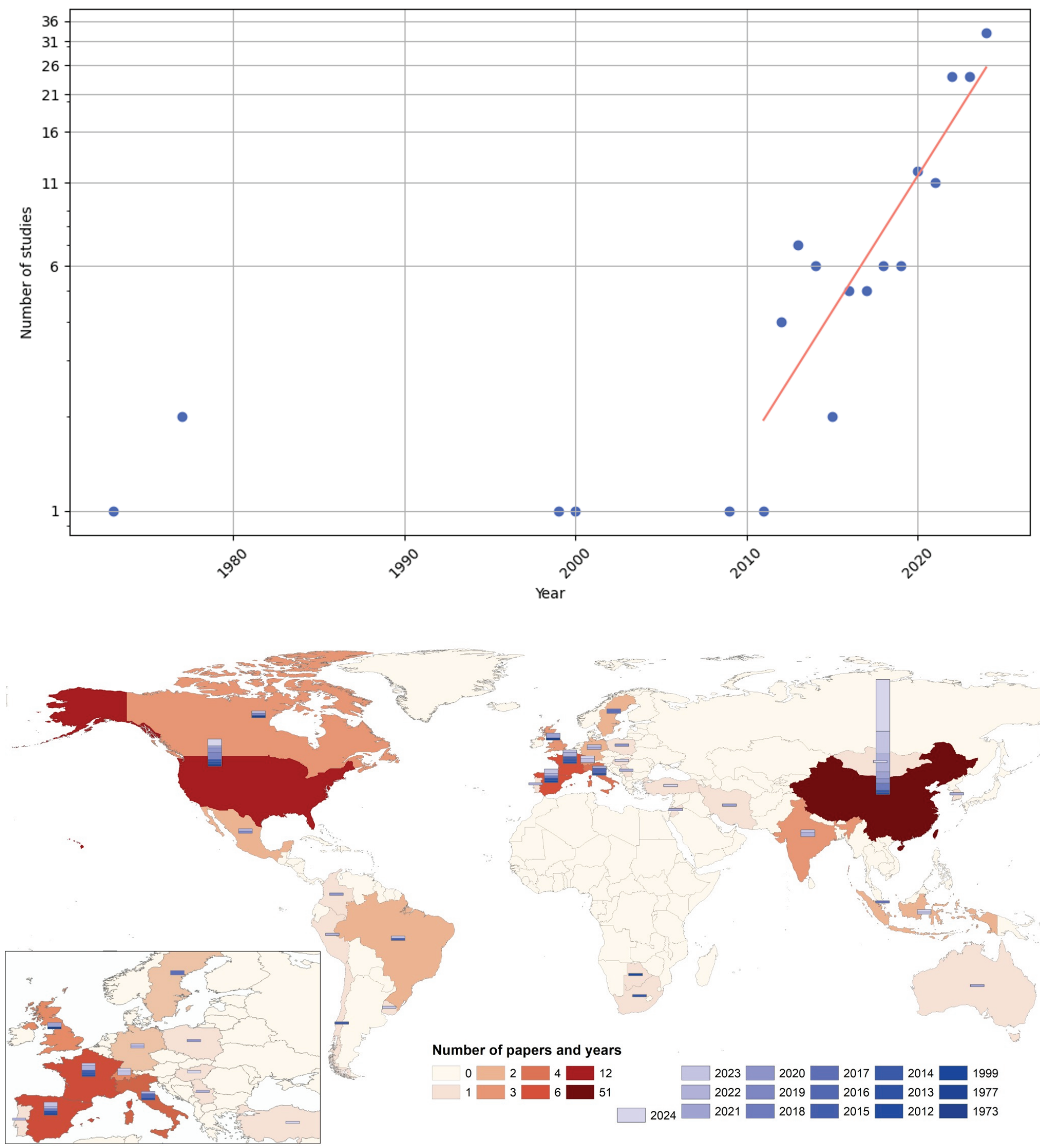

Fig 2. Temporal (top) and spatial (bottom) distribution of publications. The world map was provided by https://public.opendatasoft.com/explore/dataset/world-administrative-boundaries/export/, under an Open Government Licence v3.0.

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Spatial scale

The spatial scale of the studies ranges from a few square kilometers in urban areas to national scales encompassing millions of square kilometers. To represent this large spatial scale, networks comprised from a few hundred nodes to tens of thousands of nodes. Fig 3 shows the scatter plot of the number of nodes and area size identified in this literature review. There is no linear correlation between the number of nodes and the areas.

Two main groups of studies were identified depending on the average ratio of nodes to area. The first group used a limited number of nodes across **extensive areas**, while the second employed a substantial number of nodes within more **confined areas**. Extensive areas generally refer to national scales, whereas confined areas pertain to urban scales, such as cities and neighborhoods. Studies focusing on fewer nodes in extensive areas predominantly investigated ecological connectivity over large basins in China, like the Yellow River [32–35] and the Pearl River Basin [36], as well as forest habitat connectivity across mainland Spain [37]. The largest areal extension investigated ecological corridors across the entire Chinese mainland, using selected ecological patches as nodes [38,39].

In contrast, studies with a high number of nodes in confined areas focused on urbanized contexts. For example, on how to improve green infrastructure connectivity in the highly urbanized Padan Plain of Northern Italy [28] and the Ruhr Metropolitan Area in Germany [40], as well as strategies for prioritizing urban grassland in Wrocław, Poland [41]. The fragmentation of landscapes caused by urban development often increases the granularity of spatial data analyses, allowing for a greater number of areas available as nodes. Studies with the highest number of nodes analyzed green patches in the Parisian region, assessing how green roofs can improve connectivity in neighborhoods [42] and the impact of local businesses on green spaces [43].

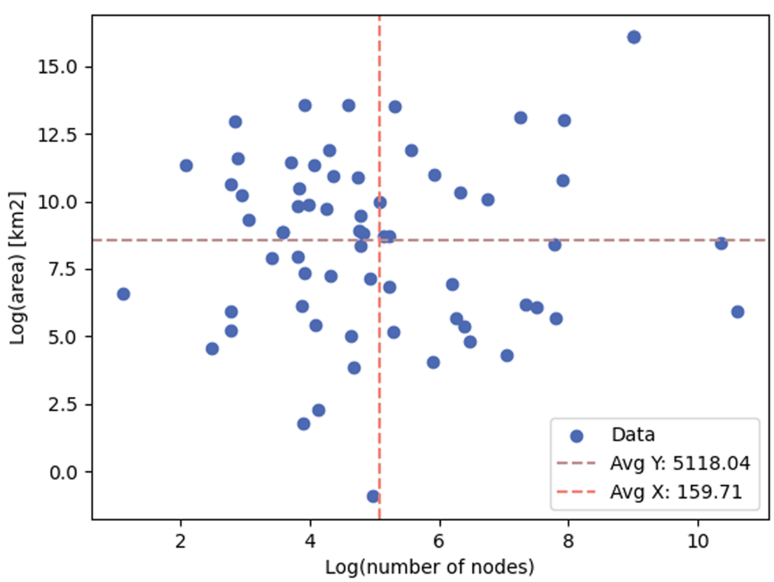

Fig 3. Relationship between the areal extensions (km^2) and the number of network nodes used to represent the system for each study area.

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We investigated which papers analyzed multiscale networks. We found that only Ref [36] studied grain ecosystem service across three different scales, classified according to administrative levels (e.g., town, city, and county).

Categories of studies

We classified the quantitative papers into four main categories, namely ecology, management, nature's contribution to people, and social. We selected these categories based on the interaction types that can occur between ecological and social components (see Ref [1]. 69% of the papers were in the ecology category (88 papers out of 127), 17% were in management (22 papers), 8% were about nature's contribution to people (10 papers), and 6% in the social category (7 papers). We will explore in detail the main topics within these categories of studies in the following sections (see Fig 4). In contrast to the main category groups, where studies fit

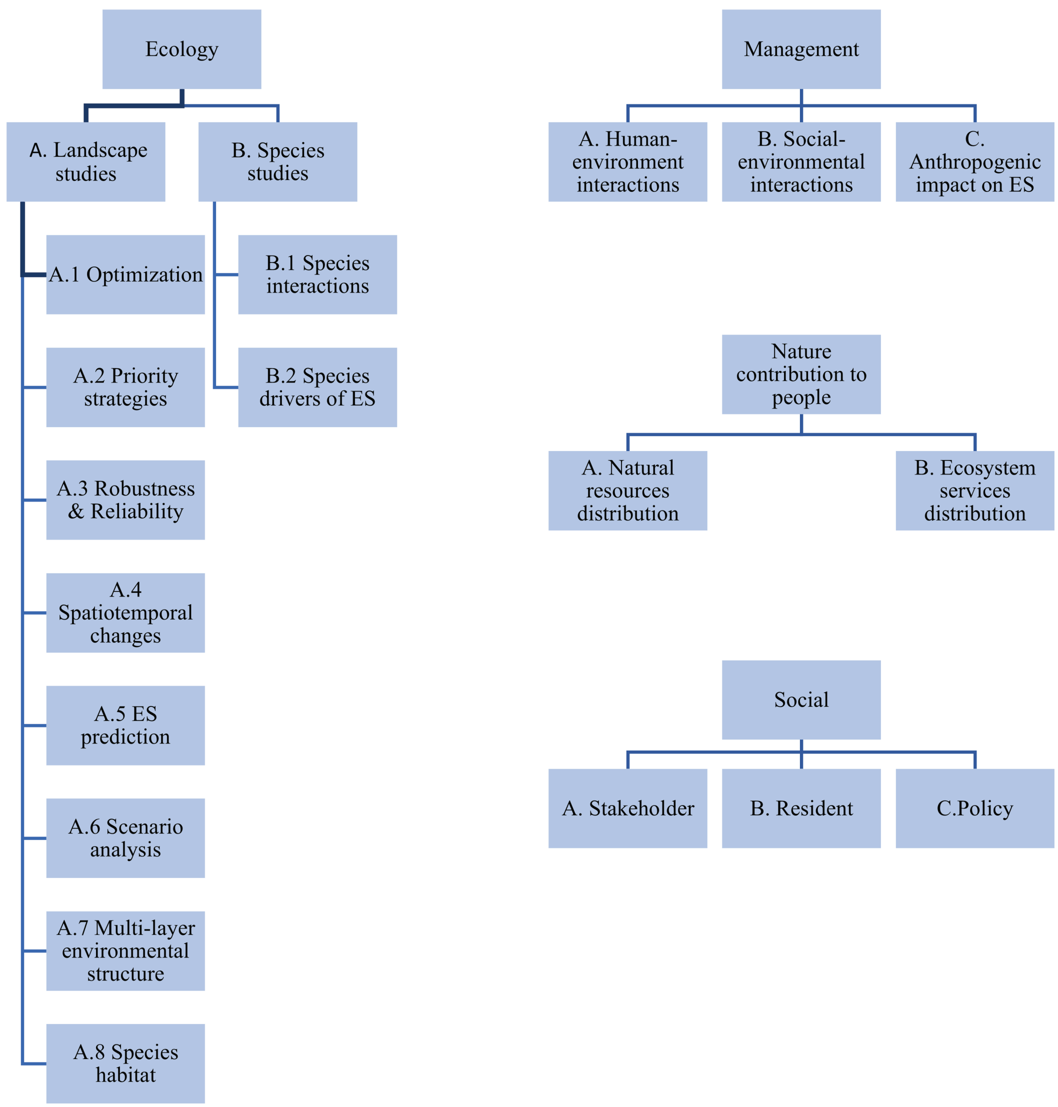

Fig 4. Categories of studies found in 127 papers that computationally analyzed case studies.

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into only one category based on the type of relationship between components modeled, studies could investigate multiple topics. This is because different analyses can be conducted using the same case study. We therefore reported those studies in different topic groups. We found that studies investigated different topics under the ecology group (see [32,33,39,44–56]).

Ecology. papers primarily examined natural ecological components and their characteristics. We classified them into two subgroups: A) landscape studies, which focused on landscape elements, and B) species studies, which concentrated on biotic components.

A. **Landscape** studies focus on the spatial distributions of landscape elements, such as habitat patches or ecological sources. Connectivity is examined through two main lenses: structural connectivity, which assesses the spatial arrangement of landscape elements, and functional connectivity, which reflects how organisms respond behaviorally to these structures [57]. Most studies in this area employ spatial network models to identify ecological patches and connect them via ecological corridors. These connections are often mapped using methods like circuit theory [32,49,58] or the minimal cumulative resistance (MCR) model [33,38,39,52], with some studies utilizing both approaches [45,46,59–61].

We identified eight topics within landscape studies: A.1 optimization, A.2 priority strategies, A.3 robustness and reliability, A.4 spatiotemporal changes, A.5 ecosystem services prediction, A.6 scenario analysis, A.7 multi-layer environmental structure, and A.8 species habitat.

A.1 **Optimization** studies focused on identifying the most effective spatial arrangement of landscape elements. By optimizing corridors between patches, the goal was to pinpoint ecological barriers and pinch points to enhance ecological conservation and protection [46,60–62]. The synergies between different ecosystem services and the topological structure were studied in the context of optimizing their ecospatial configuration [32,35,38,39,45,47]. Additionally, one study optimized the ecological network by analyzing correlations between the topological properties of source patches, climate, and ES under climate scenarios [44]. Other studies used the k-edge augmentation problem to investigate optimal landscape ecological networks under various [54] and generated alternative network designs [56]. To address carbon neutrality goals, several studies investigated the coupling between carbon sequestration capacity and topological structure [33,34,58]. Efforts to improve runoff control included optimizing green infrastructures [52,63] and land use scenarios that increase hydrological connectivity [51]. Finally, ecological networks were optimized in the context of various economic growth rates to assess how economic growth influences urban ecological risk [53].

A.2 Studies on **priority strategies** assessed conservation and protection interventions for landscapes. Conservation and restoration areas were identified as critical for maintaining regional ecological security [59], selecting priority connectors between forests [37], enhancing patch connectivity for habitat conservation and regeneration [48,64], and facilitating ecological restoration of mined areas [65,66]. For blue-green infrastructure planning, priority interventions were identified by analyzing tree canopy connectivity to revitalize brownfields [67], urban grasslands connectivity to improve plant richness [41], corridors between parks, gardens, and lakes for stormwater management [68], and tree canopy connectivity for enhancing socio-ecological functionalities [69]. Additionally, natural areas were targeted to improve urban-rural landscape cohesion [70], while green riparian zones and protected areas were prioritized to strengthen structural connectivity [28]. Two studies specifically addressed green roof implementations to increase urban green connectivity [42] and the ecosystem service benefits of tree canopies [71]. Only one study evaluated priority strategies within river networks to ensure a sustainable water provision services [72].

A.3 **Robustness** was mainly assessed to evaluate the resilience and stability of optimized ecological networks [32,33,39,44–47,52,53,55] and to analyze habitat connectivity in regeneration programs [48]. Only one study investigated spatiotemporal changes in robustness to identify critical ecological land [49]. Network **reliability** was studied in the context of habitat fragmentation [73]. Focusing on cascading failures, one study analyzed the land-use network over time to understand the cascading effects of land transfer networks under different attack intensities [50].

A.4 **Spatiotemporal changes** studies have delved into how landscapes vary over space and time. Related to blue-green infrastructures, studies looked at the influence of stormwater ponds on the connectivity of wet landscapes [74] and at the development of green infrastructure connectivity in urban agglomerations [40,75]. Similarly, a study focused on hydrological connectivity changes of lake wetlands [76]. Focusing on urbanization processes, studies analyzed the impact on the vulnerability of the land system [77], the ecological functional vulnerability from stock and flow changes of ES values caused by land use change [78], decreases in landscape connectivity [79], and the effects of business sites on urban green spaces [43]. Focusing on vulnerabilities, a study investigated the spatiotemporal changes of critical ecological lands in regional woodlands and cultivated land [49], and another one evaluated the impact of land-use transformation on ecological vulnerability [50]. Regarding ecosystem service alterations driven by land use, two studies investigated the change of ecosystem service value [80] and of bioenergy ecosystem service [81].

A.5 **ES prediction** studies tested whether landscape configuration affects trade-offs and synergies among ecosystem services using Bayesian Belief Networks [82,83].

A.6 **Scenario analysis** studies have been conducted to examine scenarios of land use and land cover development. These include examining hydrological connectivity [51], analyzing the impacts of various land cover types on forest connectivity [84], evaluating the effects of land cover restorations on watershed services [85], studying climate changes in the ecological spatial networks and ecosystem services [44], analyzing multi-scenario connectivity construction of landscape ecological network under different objectives [54], analyzing network configurations based on the distribution of nodes [56], and studying the ecological network under risk scenarios associated with protection efficiency levels of ecological areas [55]. Only one study compared past and future land use scenarios to enhance natural water retention through green infrastructures, aiming to offer clearer policy directions [86]. Another study focused on constructing urban ecological network scenarios with a decision-making process [87].

A.7 **Multi-layer environmental structure** studies explored different interconnected geographical layers. An initial study introduced a method for assessing connectivity between water provision, flow, and landscape aesthetic and environmental systems [88]. To facilitate the allocation of green infrastructure for water balance, a study analyzed the multilayer network structure linking the terrain's structural lines and the road infrastructure [89]. In planning for a networked ecological–cultural spatial system, ecological corridors were extracted along cultural sites [90].

A.8 **Species habitat** papers analyzed landscapes as habitats for specific species. Mainly, research has leveraged population data to investigate the movements of fauna species across habitat patches. Key areas of focus include bird migration analysis [91–93], potential habitat corridors for both migratory and non-migratory birds [94], amphibian distributions in ponds [95], habitat suitability assessments for deer, hares, toads and pollinators [96–98], habitat connectivity assessments for bee flight [99], the dynamics of soybean aphid and predators fluxes [100], and quantifying the importance of habitats for multispecies migrations of deer, ducks, and butterflies [101]. Connectivity priority areas were identified for amphibian species in wetlands [102] and in blue-green infrastructure corridors [103], and for plant distribution in saltmarsh landscape [104]. Only one paper analyzed how native and invasive plant species are spatially distributed [105].

B. **Species studies** investigated how specific species interact with or act as drivers of ecosystem services. Since species are the main focus of the analyses, these studies modeled species or functional groups as nodes.

B.1 **Species interactions** studies investigated relationships between species. For **flora** analyses, the first application of graph theory to the interspecific association of vegetation species was conducted to test the homogeneity of phytosociological tables [106]. Studies later detected plant species interactions in temperate forests [107], and developed models of the potential distribution of alpine vegetation communities to reveal ecological niches based on the co-occurrence of species [108]. For **fauna** analyses, topological analyses were suggested to study interspecies interactions and affinities [109]. Co-occurrence networks showed nutrient cycling processes driven by soil fungi and bacterial relationships [110], the potential of biological control related to the Odonata and mosquito species interactions [111], the effects of agricultural activities on arthropod communities [112], the impact of mangrove restoration projects on macrobenthic biodiversity [113], and the impacts of vegetation restoration on soil carbon-fixing functional bacteria [114]. Biological control services were also analyzed by studying the interactions between communities of predatory arthropods and prey in cotton systems [115] and herbivores and parasitoid interactions in farms [116]. Only one study analyzed the network of **flora and fauna** species together to study the response of bat-fruit interactions to habitat changes [117].

B.2 In the **species drivers of ecosystem services** category, research focused on the impacts of species on ecosystem services. One study investigated the vulnerability of ecosystem service supply to species loss [118]. Another study analyzed the recovery pathways and potential recovery debts following disturbances in coral reef ecosystems [119]. Only one study examined the ecosystem services provided by plant species [120].

Management. research has examined the influence of social systems on the environment and their ecosystem services.

A. **Human-environment interactions** articles explored the interactions between human behavior and the environment. For better planning of urban green infrastructures, some studies investigated **areas of human activity** that detected the locations where it is expected most of the human interaction with the environmental space [121–123]. Other studies looked at **touristic visits** to understand the distribution of socio-ecological systems interactions and attractiveness of places [124,125]. Examining spatially the **human-ecological resources security index**, a study investigated the management of the peri-urban forest by social-ecological network analysis [126]. One study also examined the relationships among ecosystem services to investigate how human activities affect water-related ES [127].

B. **Social-environmental interactions** used networks to model the relationships between social systems and environmental components. Studies investigated the interactions between **socioeconomic, management, and ecological systems**. One study evaluated sustainable urban development over time [128], one assessed management actions in coastal marine protected areas [129], and one analyzed the connections between actions and services and the influence of services to community well-being [130]. Studies analyzed the relationships between **stakeholders and ecosystem services** by studying their perspectives on managing coastal marine protected areas [131], the decision-making process concerning Southern Ocean ecosystem services [132], future planning of transhumance [133], land and water management under climate change [134], the influence of resource governance on coastal and marine cultural ecosystem services [135], and the role of expert opinions in prioritizing ES using the Analytic Network Process (ANP) method [136,137].

C. Papers focused on the **anthropogenic impact on ES**. Management can have negative effects on the environment, and, consequently, on ES. Studies investigated broader effects of trace metal contamination (pollution) on ecosystem services [138], the influence of drivers in lake ecosystem services over time [139], cause-effect relationships between drivers, system properties, and ES in coastal management scenarios by using Bayesian networks [140,141], and the relationship among ES stressors [142].

Nature's contribution to people. studies' overarching goal is to assess how natural resources and ecosystem services are distributed to societal needs.

A. **Natural resources distribution** studies analyzed the distribution of natural resources. Authors looked at the transportation of resources from forests, in particular examining timber transportation [143] and the transportation and consumption of wood-based bioenergy [144]. Studies analyzed the **supply-demand flows**, focusing on the spatiotemporal patterns of grain provision [36], and the increases of freshwater supply driven by urbanization over time [145]. Similarly, a study analyzed and optimized the ecological network and its ecological supply and demand to residents in cities [146]. Only a single study investigated the social-ecological benefit and the coupling coordination related to grain production over time [147].

B. **Ecosystem services distribution** studies focused on the spatial distribution of ecosystem services to people. Authors quantified the accessibility to residents of urban parks' cooling effect [148], detected cultural ecosystem services provision by social media networks [149], analyzed the spatiotemporal evolution process of supply-demand of ecosystem services based on the ecological networks [150], and studied the distribution flow of leisure and recreation services from urban ecological patches to residents [151].

Social. studies focus on the social components that deal with ecosystem services. We distinguished papers based on whether they focused on stakeholder interactions or residents living in geographic areas. Additionally, we include studies analyzing policy as social products in this category.

A. **Stakeholder** studies analyzed the organization and interaction of local functional groups and institutions. One study investigated the role of social capital in enhancing the resilience of mariculture businesses in response to El Niño climatic events [152]. A study examined factors that shape the social networks of organizations involved in implementing blue-green infrastructure [153].

B. **Resident** studies analyzed the characteristics and priorities of communities residing in specific areas. One study investigated how ecological restoration projects influenced the cognitive structure of communities by examining the perception networks of residents, linking users, resource systems, resource units, and governance systems [154]. The resilience of rural communities to cope with droughts and economic crises was analyzed within household characteristics [155]. The effects of land use incentive payments for ecosystem services were detected with Bayesian belief networks [156]. Only one study looked at the human perception of cultural services by examining crowdsourced descriptions (lemmas) of everyday lived landscapes [157].

C. **Policy** studies investigated characteristics of environmental policies. Only one study examined the transmission flow of ecological and environmental protection policies between cities [158].

Network approaches

This section examines the network models and metrics. Network models aim to conceptualize the components of a system and their relationships to capture the system's structure, while network metrics characterize its properties and functions.

Network models. When studying social-ecological systems, it is important to discuss how different social and environmental components and interdependencies are modeled [22]. As such, we first looked at the kinds of feature that were selected as nodes. Most of the papers conceptualized nodes with spatial landscape features. As a result, spatial networks were the predominant class of networks studied in the literature. In particular, 57% of the quantitative papers modeled nodes as spatial patches, sites, ecological sources or habitats (72 papers). These landscape features were grouped together because they share the same characteristics: to have a spatial attribute (coordinates) and refer to terrestrial ecological areas. Additionally related to landscape features, 6% of the quantitative studies modeled nodes as landscape measures and characteristics (8 papers), 6% as watersheds, ponds, or water stream points (8 papers), 3% as transport infrastructure points (4 papers), and 2% as land use or land cover types (3 papers). 13% of the quantitative papers conceptualized nodes as species (17 papers), 14% as ecosystem services and functions (18 papers), 6% as administrative areas (e.g., counties, cities) (7 papers), 6% as policy and human interventions (8 papers), and 6% as drivers of change or external pressures to ES (7 papers). For the social component, 9% of the papers modeled nodes as social entities (11 papers), which represent stakeholder groups, 2% selected nodes in correspondence to spatial census statistics (2 papers), and 1% as household units (see [155]. However, sometimes studies used administrative areas to represent the social component (see for example [126], or used household information [156]. Other minor nodes refer to linguistic elements, such as lemmas and hashtags from social media and crowdsourced data (see [149,157], human wellbeing attributes [130], and business sites [125]. Only [124] used social media data to map the interactions between tourism activities and ecological sites.

It was then important to understand how studies linked the social and/or ecological components to form networks. We identified different types of edges, which exhibit significant heterogeneity due to the diverse relationships between components. Tables 1 and 2 report all types of interactions reviewed. We divided the edges based on whether they represented observations or inferences from the data. Physical environment relationships refer to edges embedded in geographical space; flows represent mutual exchange of information and travel; one-way influences refer to unidirectional effects; and linguistic relationships include lexical and semantic connections. For the inferred connections, proximity refers to edges approximating spatial connections, associations to linkages between the social and environmental components based on stakeholders' evaluations. Additionally, Fig 5 illustrates some network models found in the literature. Depending on the types of interactions, networks capture diverse component properties and processes embedded in ecosystem service dynamics (see also [159].

Second, we examined the types of network models chosen by authors when studying ecosystem services. We found that papers mostly used the same set of nodes within a single layer, such as in not-partitioned and one-layer networks. Multipartite and multilayer networks were used in 15% of the quantitative studies (19 papers). Specifically, 11 papers used multipartite networks and 8 multilayer networks. Additionally, 5 papers used Bayesian Belief networks. Bipartite networks were mainly adopted to distinguish relationships between two components, represented by separate sets of nodes. These models have been found to represent species interactions or exchange of information between components of socio-ecological

Table 1. Edge types identified in the revised studies, number of papers reporting them, and references: observed connections.

Edges			
	Description	**Count**	**Reference**
Observed connections			
Physical environment relationships	- ecological corridors between patches or ecological sources	50	e.g., [59]
	- functional connectivity of ecological corridors	5	[94,96,97,102,103]
	- road segments or transport routes	4	e.g., [89]
	- water channels	4	e.g., [63]
	- conversion between land types	3	e.g., [50]
	- presence of plants in sites	1	[105]
	- overlaps in space	1	[88]
Flows	- interspecific interactions	13	e.g. [117]
	- habitat connections based on tracked bird movements	2	[92,93]
	- relationships between social organizations	2	[152,153]
	- bioenergy flux between land units	1	[81]
	- bird migratory routes	1	[91]
	- tourist visits to sites	1	[125]
	- travels	1	[151]
	- collaborations between business	1	[125]
	- social exchanges between households	1	[155]
	- policy transmission between cities	1	[158]
	- interaction between user's place of residence and sites	1	[124]
	- potential for species movement (based on survival and transition probabilities)	1	[101]
One-way influences	- utilization and management of forest resources	1	[126]
	- species - functional trait - ecosystem service linkages based on presence-absence configurations	1	[118]
	- connection between plant species to provided ES	1	[120]
	- logic chain from pollution to ES impact	1	[138]
Linguistic relationships	- syntactic relations connecting terms	1	[157]
	- connections between hashtags	1	[149]

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systems. For species interactions, bipartite models have been useful to study spatial site-plant interactions by detecting unweighted species presence-absence matrices [105], arthropods predator-prey interactions [115], species of plants and their ecosystem services provision [120], and bat-fruit interactions, where the weights measure the plant seeds in the fecal samples of bat species [117]. Interactions were mapped between herbivores and parasitoids in field experiments [116]. Co-occurrence network models identified interactions between mosquito-odonate [111], soil bacterial and fungal communities [110], mangrove macrobenthos [113], and carbon-fixing functional bacteria [114]. Alternatively, species-traits and species-ecosystem services presences or absences were modeled with a Boolean (binary) network model to test the ecosystem service supply to biodiversity loss [118]. A multipartite network was used to analyze an eco-decisional network by selecting nodes as actions, services, or domains of human well-being and linking them by weighted influence derived from stakeholder input [130].

Multilayer networks were discussed and showcased to develop spatially explicit network models between multiple ecosystem services across landscapes [88]. Looking at the city

Table 2. (cont.) Edge types identified in the revised studies, number of papers reporting them, and references: inferred connections.

Edges			
	Description	**Count**	**Reference**
Inferred connections			
Proximity	- Euclidean distances between patches	4	e.g., [64]
	- dispersal connectivity between patches	3	[98,100,104]
	- Euclidean distance between zoning units	1	[80]
	- Euclidean connections based on frog dispersal capacities between ponds	1	[95]
	- connections between cities based on hierarchical administrative levels	1	[126]
	- intervisible distances between patches for pollinators' movement	1	[99]
	- Euclidean sightlines from viewpoints	1	[88]
	- connections between grain supply and demand locations	1	[36]
Associations	- influences among ES identified by decision-makers	2	[136,137]
	- influences from trade-offs to synergies and sites	2	[82,83]
	- relationships between ecological components, ecosystem functions, social actors, human interventions and environmental stressors	2	[129,135]
	- similarities between sites collected from surveys	1	[125]
	- influence links among drivers, ES, and social groups	1	[133]
	- synergies among ES	1	[127]
	- impact among ES stressors	1	[142]
	- relationship among ES and landscape	1	[141]
	- relationship among drivers and ES	1	[139]
	- relationship among actions and drivers to change	1	[134]
	- relationship among activities and ES	1	[140]
	- influence of stakeholders to ES	1	[132]
	- relationships among ES, biodiversity features and uses prioritized by stakeholders	1	[131]
	- relationships among society, economy, and environment	1	[128]
	- relationships between policy, environmental change, ecological conservation goal, resource systems, governance	1	[154]
	- connections between ES, actions and domains of human well-being	1	[130]
	- dependencies between household characteristics and land-use characteristics	1	[156]
	- coupling coordination between counties	1	[147]

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context, the stream channels and street networks were spatially analyzed to extract the urban multilayered network structure [89]. Among socio-ecological systems representations, multilayer models have been applied to study specifically supply-demand between spatial locations. For instance, they have been used to analyze grain supply-demand sites for distribution grain flow analysis [36], and ecological supply-demand sources [146,150]. In these models, supply nodes refer to ecological spatial sources, while demand sources were modeled by calculating the ecological scarcity, represented by per capita ecosystem service value, to

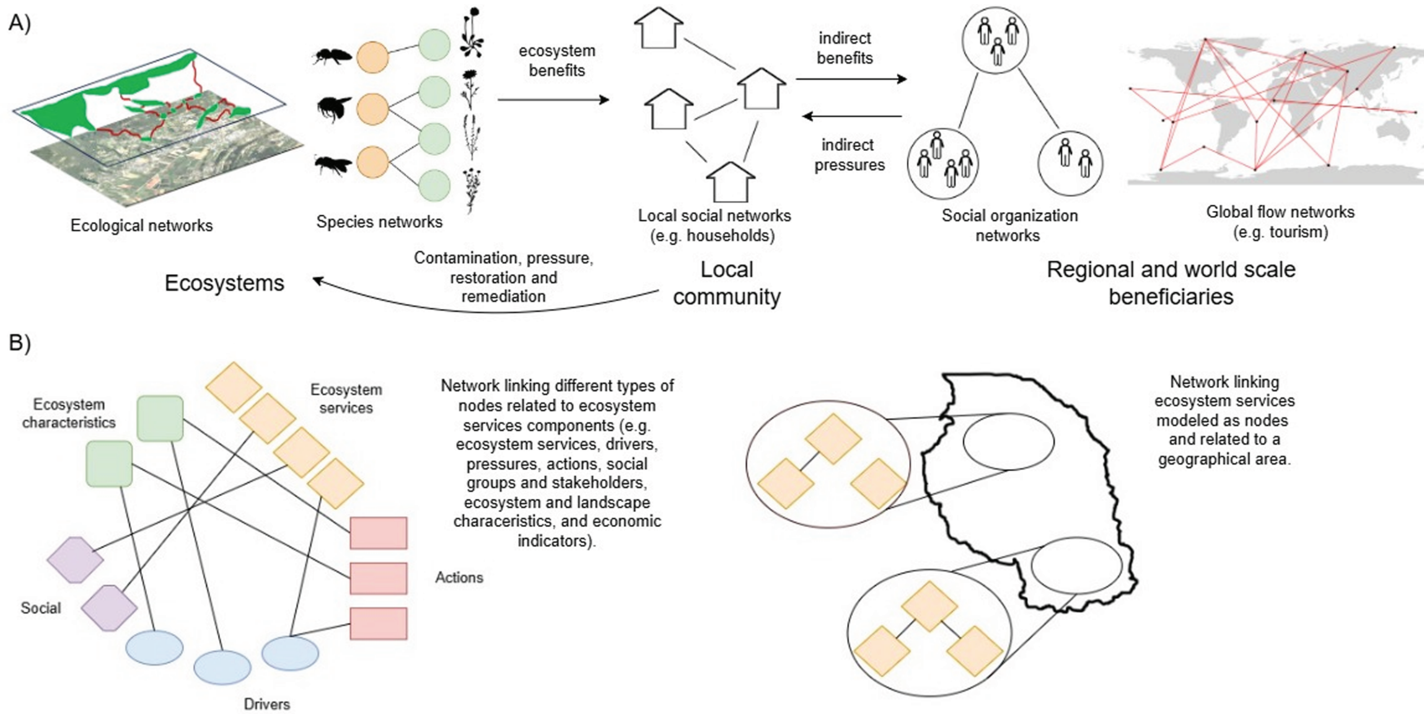

Fig 5. Networks can represent different types of interactions. (A) We illustrate how certain network models are embedded in the analysis of ecosystem services dynamics, which were displayed in Ref [159]. (B) We display two examples of networks in which nodes represent ecosystem services themselves. For the left figure, see also Ref [25]; for the right figure, see for example Ref [127]. All images used to create this figure are covered by open data licenses and provided by Regione Veneto (L.R. n. 28/76 Formazione della Carta Tecnica Regionale), PhyloPic, Publicdomainvector.org, and Natural Earth Vector Data.

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measure the scarcity relative to urban population [146], and by identifying human settlements [150]. Moreover, a multilayer network was studied for modeling the supply and demand of ecosystem services in urban systems, by selecting residential units as demand nodes and ecological sources as supply nodes [151]. Another use of multilayer networks in socio-ecological systems has been to model interactions between scuba diving businesses and coral reefs by accounting for the number of diver visits [125], as well as relationships between peri-urban forest sources and cities [87].

Other works used Bayesian Belief networks to define the relationship between network components, as such, models mapped interactions between threats and management activities on ecosystem services [140,141] or to map structural characteristics of the landscape with ecosystem services [82,83] or map inferences between land-use policies and local land-use outcomes [156].

Networks are not only structural representations of systems, but rather their structure is based on the information exchanged. Therefore, it is important to understand how studies model exchanges among system components. Third, we looked at how studies modeled interactions between nodes. We identified the gravity model and flow analyses as methods to include these aspects in investigations.

The gravity model is mainly used to study the interaction relationship between two objects or locations. Based on gravity model, studies evaluated the strength of the interactions between ecological sources [38,53], prioritized the most suitable corridors between sources based on the interactions [68,69], extracted and classified ecological corridors favorable to

Table 3. Metrics used in the literature of network studies for ecosystem services. To differentiate categories of studies, we labeled ecology as (E), social as (S), management as (M), and natural contributions to people as (NCP).

Metric	Reference	Count
A. **Centrality**		
Betweenness centrality	E: [32,33,35,38,42,44–53,55,58,59,72,75,77,88,89,92,95,103,109,110,114,117]	36
	S: [155]	
	M: [128,129,131]	
	NCP: [147,151]	
Closeness centrality	E: [32,34,35,44–49,55,58,59,110,117]	17
	M: [128,135]	
	NCP: [147]	
Eigenvector centrality	E: [34,35,44,46–48,55,58,59,110]	13
	M: [129,135]	
	NCP: [149]	
Strength	E: [77,93]	3
	S: [154]	
PageRank	E: [38,53]	2
Hub-Authority	E: [49,58]	2
Harmonic centrality	E: [48]	1
Polarity	M: [123]	1
Coreness	E: [33]	1
Centralization	S: [153]	1
B. **Landscape Connectivity metrics**		
Probability of Connectivity (PC)	E: [37,40,42,43,47,48,61,62,64–66,71,76,79,84,86,98,104]	21
	M: [123]	
	NCP: [146,150]	
Importance Percentage (dPC)	E: [35,37,40,43,47,61,62,64–67,74,76,84,86,104]	18
	NCP: [146,150]	
Integral Index of Connectivity (IIC)	E: [28,40,41,48,51,61,62,64,69,79,92,104]	13
	NCP: [146]	
Importance of the Integral Index of connectivity (dIIC)	E: [40,41,51,61,62,64,79,98]	9
	NCP: [146]	
dPCintra, dPCflux, and dPCconnector	E: [43,67,74,84]	4
Equivalent connectivity (EC)	E: [40,72,76,102]	4
dIICintra, dIICflux, and dIICconnector	E: [41,79],	2
Landscape Coincidence Probability (LCP), Importance of landscape coincidence probability (dLCP)	E: [64]	1

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species migration and diffusion [65]. The model was used also to calculate the weights between ecological sources without existing corridors connecting them [54]. Moreover, it evaluated the coupling coordination correlation in grain cropland areas [147].

Moreover, 12 papers studied flows. Some studies calculated flows, while others evaluated flow properties using metrics as proxies. They measured the changes in water supply-demand [145], ES values stock and flow [78], supply-demand of grain provision [36], policy transmission [158], decisional influence flow [130], trophic flow [119], dispersal and migratory fluxes of animal populations [100,101], and dispersion capacities between ecological elements [42,104]. Looking at supply-demand between social and ecological components, an evaluation index was proposed to evaluate the supply-demand relationships [150], and a methodology was proposed for constructing socio-ecological network based on mobility attributes (travels) [151]. Some of these studies used flow-related metrics listed in Tables 3-6 (see Network metrics section).

Table 4. (cont.) Metrics used in the literature of network studies for ecosystem services. To differentiate categories of studies, we labeled ecology as (E), social as (S), management as (M), and natural contributions to people as (NCP).

Metric	Reference	Count
C. **Robustness and fragmentation metrics**		
Connection Robustness	E: [32,39,44,46–49,52,53]	10
	NCP: [146]	
Node recovery robustness	E: [33,39,44,46–48,52]	7
Edge recovery robustness	E: [33,39,44,46–48,52]	7
Largest connected subgraph	E: [55]	2
	NCP: [146]	
Reliability	E: [73]	1
Network Robustness-fragility	E: [118]	1
Resilience degree	E: [55]	1
Cut-nodes, cut-edges	E: [103]	1
Point connectivity	E: [39]	1
D. **Networkwide metrics**		
I) **Based on number of nodes and edges**		
Degree	E: [32–35,38,39,44–50,52,53,58,75,77,93,103,106,107,110,112,113,117,120]	36
	M: [125,128,129,135]	
	NCP: [146,151]	
	S: [152,155,158]	
Network Density	E: [93,109,112]	10
	M: [125,127,131,135]	
	NCP: [147]	
	S: [153,158]	
Gamma index	E: [35,56,60,61,69,72]	7
	NCP: [150]	
Beta index	E: [35,56,60,61,69,72]	7
	NCP: [150]	
Edge density (per unit area)	E: [94]	1
Cost ratio	E; [56]	1
II) **Edge weights statistics**		
Average (edge) weight	E: [38]	3
	M: [64,130]	
Weight distribution difference	E: [38]	1

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Network metrics. We review the network metrics employed in quantitative studies of ecosystem services (see Tables 3-6. The network metrics can be organized in groups depending on the methodology and/or purpose. Notably, metrics used in more than five studies include centrality metrics (betweenness, closeness, eigenvector), landscape connectivity metrics (probability of connectivity, importance percentage, integral index of connectivity, importance of the integral index of connectivity), a robustness and fragmentation metric (connection robustness), networkwide metrics (degree, network density, alpha, beta and gamma indices, clustering coefficient, average path length), and a community structure metric (modularity). The overlap among study categories, network metrics and models is shown in Fig 6.

A. **Centrality metrics.** The most commonly used centrality metrics were betweenness centrality, closeness centrality, and eigenvector centrality. Most studies focused on closeness and eigenvector centrality in conjunction with betweenness centrality, indicating that betweenness centrality is the most frequently utilized metric in terms of both occurrence and analytical application.

A.1. **Betweenness centrality** (BC) is the number of shortest paths that pass through a node, divided by the total number of shortest paths. The metric served four main purposes.

Table 5. (cont.) Metrics used in the literature of network studies for ecosystem services. To differentiate categories of studies, we labeled ecology as (E), social as (S), management as (M), and natural contributions to people as (NCP).

Metric	Reference	Count
III) **Based on cycles**		
Clustering coefficient	E: [33,35,38,39,44,46–48,50,58,59,77,103,112,113]	18
	M: [128]	
	NCP: [146,151]	
Alpha index	E: [35,56,60,61,72]	6
	NCP: [150]	
Triangle numbers	E: [48,58]	3
	NCP: [146]	
Length of cycles	E: [107]	1
Transitivity	S: [153]	1
IV) **Based on geodesic distance**		
Average path length	E: [38,39,48,50,77,109,112,119]	12
	M: [125,128]	
	NCP: [146,151]	
Diameter	E: [48,103,109,112]	5
	M: [125]	
Global Efficiency	E: [45,55,72,77]	5
	NCP: [146]	
Minimum Spanning Trees	E: [54,80,103]	3
Eccentricity	E: [58]	1
Realized network roles (sets of paths)	M: [130]	1
V) **Based on connected components and degree distribution**		
Entropy and Shannon's Evenness Index	E: [50,78,94]	5
	M: [124]	
	S: [154]	
Assortativity	E: [93,114]	2
Edge connectivity	E: [54]	1
Reachability	M: [142]	1
Complementary Specialization (standardized two-dimensional Shannon entropy)	E: [117]	1
Overlap	M: [124]	1
Nestedness	E: [117]	1
Compartmentalisation	E: [103]	1

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First, it evaluated the characteristics of network elements; specifically, network elements' roles in information exchange [128,129,131], complexity in species connections [114,117], location significance for connectivity [38,42,46,51,59,75,155], the landscape structural connection with ecosystem services [48], multi-layer networks connectivity [88], connectivity between social-ecological elements [151], the interaction role between counties [147], location ranking [89], and connectivity for animal dispersion [92,95,103,109]. Second, BC quantified the importance of network elements by creating composite metrics that incorporated other topological measures, such as degree, closeness, hubs-authorities scores, eigenvector centrality [50,53,77,110]. Third, BC-guided optimization and prioritization strategies by adding edges based on BC-value rankings [52,58,72]. This optimization was further explored through correlations between ecosystem services values and topological metrics, including betweenness centrality [32,35,38,44,47]. Fourth, BC tested network robustness by informing strategies for targeted attacks on high BC-value nodes [33,55] or through the use of composite metrics [32,45,49].

Table 6. (cont.) Metrics used in the literature of network studies for ecosystem services. To differentiate categories of studies, we labeled ecology as (E), social as (S), management as (M), and natural contributions to people as (NCP).

Metric	Reference	Count
E. **Community structure metrics**		
Modularity	E: [48,93,110,112,113,117]	6
Hierarchical clustering	M: [125,139]	2
Core-periphery	S: [158]	1
Infomap (module detection algorithm)	E: [108]	1
Participation coefficient	E: [108]	1
Module degree	E: [108]	1
F. **Flow-related metrics**		
Flux ($\exp^{-kd_{ij}}$)	E: [42,100]	2
Static surplus of supply-demand nodes	NCP: [36,145]	2
Metapopulation capacity (MC) ($\exp^{-kd_{ij}} a_i a_j$) and Modified Metapopulation capacity (MMC)	E: [104]	1
Efficiency Cumulated Indicator	E: [119]	1
Total System Throughput (total flow)	E: [119]	1
Per-capita contribution metric	E: [101]	1
Flow intensity	NCP: [36]	1
Dynamic surplus of supply-demand nodes	NCP: [145]	1
Supply-demand value ratio	NCP: [36]	1
Supply-demand degree ratio	NCP: [150]	1
Ascendancy	M: [130]	1

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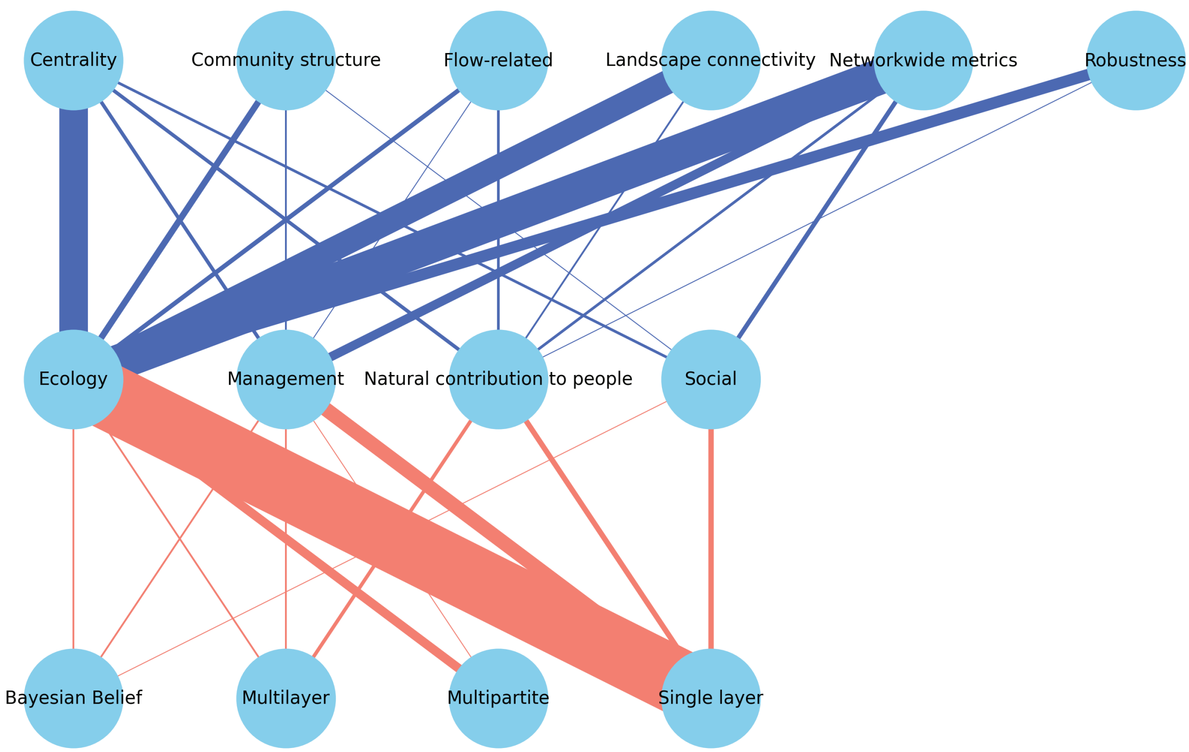

Fig 6. Multilayer network displaying the overlap of papers across categories of studies, network metrics, and network approaches. The edge width is proportional to the number of papers.

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A.2. **Closeness centrality** measures the inverse of the sum of the shortest path distances from one node to all other nodes representing closeness centrality. Studies used closeness centrality to characterize properties of nodes in the network [34,46,48,55,58,59,110,117,128,135,147]. Other studies studied the correlation of closeness centrality with ecosystem services values to study optimization problems [32,35,44,47]. Other studies used composite metrics of closeness centrality with other topological metrics to test robustness [32,45,49].

A.3. **Eigenvector centrality** calculates a node's importance depending on its neighbors' number and importance. It assigns scores to nodes based on their connections to high-scoring nodes. While investigating the structural properties of networks, studies used eigenvector centrality with other topology metrics mainly to identify important nodes [46,48,55,58,59,129,149] and a measure of influence and connectedness to other network components [34,110,135]. Other studies studied the correlation of eigenvector centrality with ecosystem services values to study optimization problems [35,44,47].

B. **Landscape Connectivity metrics: PC, dPC, IIC, dIIC.** Studies mainly adopted the probability of connectivity (PC), the integral index connectivity (IIC), and their derived importance metrics (dPC, dIIC), which are the most established in landscape connectivity studies. Less common metrics were the equivalent connectivity (EC) and the landscape coincidence probability (LCP). However, EC was developed from the PC metric to avoid the limitations related to the use of the study area in the calculations (see [160], therefore it highly correlates to PC. Additionally, LCP uses the ratio of areas within connected components of patches over the total study area. Unlike other landscape metrics, it does not use information from the edges between patches, focusing on components rather than individual patches.

B.1. The **probability of connectivity** (PC) was introduced to quantify functional graph connectivity and evaluates the probability that two random points in the landscape are located within interconnected habitats [161]. The *importance percentage of PC* (dPC) calculates the importance of each landscape element after removing it from the landscape network. Studies used the probability of connectivity (PC) and its importance percentage (dPC) to identify landscape elements contribution to the overall connectivity [35,37,42,47,65,66,71,76,84,86,123,150]. Other studies decomposed dPC into three components (*dPCintra, dPCflux, and dPCconnector*) to assess the internal connectivity of the patch, the role of each patch in connecting to surrounding patches, and the role of a patch as a stepping stone [43,67,74,84]. The *Integral Index of Connectivity* (IIC) was introduced to calculate the landscape network connectivity based on the rate of areal habitat occupancy, such that when IIC=1 it means that all the landscape is occupied by habitat (see [162]. Similarly to PC and the related metrics, metrics like Integral Index of Connectivity (IIC), the *importance of the Integral Index of connectivity* (dIIC), and its components (*dIICintra, dIICflux, and dIICconnector*) were used to measure the importance of maintaining the overall connectivity of any landscape element or combination of landscape elements [28,41,51,69,92]. Despite applying PC, IIC and the related metrics separately, we found that studies often used a compound of all connectivity metrics to analyze landscape connectivity and patches importance [40,48,61,62,64,79,98,104,146].

C. **Robustness and fragmentation metrics.** There are several approaches to characterize the capacity of a system to cope with different types of disruptions. Robustness characterizes the remaining system performance as a function of disruption magnitudes [163]. Most studies analyzed network robustness by removing edges mimicking random and targeted attacks. Targeted attacks remove edges based on the selection criteria of nodes, and consequently, edges. In the revised literature, studies mostly targeted nodes based on the ranking of degree and centrality values. To measure the overall robustness of systems, studies used the **connection robustness** metric that calculates the maximum connected subgraph of the network over the remaining number of nodes [32,39,44,46–49,52,53,146]. In addition to connection robustness, some studies also looked at the **node and edge recovery robustness**, which quantifies the number of recoverable nodes or edges after attacks [33,39,44,46–48,52]. Robustness is often studied concerning optimization problems in landscapes, with studies testing it as a way to evaluate the stability performance in optimized networks [39,44,47,52,146].

D. **Networkwide metrics.** Among the various metrics listed, the degree, clustering coefficient, average path length, network density, and alpha, beta, and gamma indices were used by more than five papers. We found that authors primarily study them to investigate the structural properties of systems.

D.1. **degree** of a node is the number of edges linked to that node. Average degree and distribution of (in- and out-) degree values were used to characterize network properties [35,38,44,46–48,58,103,112,113,125,128,129], and specifically, as a centrality metric to indicate connectivity importance [32,34,75,93,110,117,120,135,151,152,155,158]. To measure the importance of network components composite metrics formed by node degree and other topological metrics were calculated [50,53,77]. Degree distributions were tested by [106,107]. Robustness analyses were developed by attacking nodes with high degrees [33,52] or by measuring composite metrics of node degree and other topological metrics [45,49]. Optimization strategies were formed by evaluating degree values and adding edges respectively [39,52,53,146].

D.2. **Network density** is the proportion of realized potential connections and represents network-scale connectivity. Studies used it mainly to evaluate the structure of networks together with other topological metrics, which were mostly centrality metrics [93,109,112,125,127,131,135,147,153,158].

D.3. **Alpha, beta, gamma indices.** Studies mostly evaluated *alpha*, *beta*, *gamma indices* all together [35,56,60,61,72,150], and it is uncommon to select a few of them [69]. This set of metrics evaluates the connectivity of networks. The alpha index characterizes the connectivity of a network as the ratio between the observed number of cycles and the maximum number of cycles. The beta index, describing network complexity, is the ratio of the number of edges to the number of nodes. The gamma index represents the ratio between the observed number of edges and the maximum number of edges. Overall, these metrics were used to assess the connectivity of spatial ecological networks with planar characteristics.

D.4. The **clustering coefficient** measures the degree to which the nodes in a network tend to be more closely related. The global clustering coefficient is the fraction of the number of closed triplets over the sum of all open and closed triplets. Studies in ecosystem services and network analyses used it to characterize the tendency of nodes to be connected [35,44,47,58,59,77,112,113]. Moreover, studies detected stability patterns [33,39,46,48,128,146], with high clustering coefficients indicating more stable networks, heterogeneity among ecological sources [38], facility in species dispersal [103], shifts in land ecosystem transformations [50], and small-world characteristics [151].

D.5. The **average path length** is the average distance between any two nodes in a network. In particular, studies evaluated the average path length, along with other topological metrics, to measure the efficiency in the transfer of information through ecological corridors [38,39], to quantify the overall connectivity between habitats [48,146], to analyze the internal structural stability of land systems [50,77], to detect the stability of society-economy-environment system complex networks [128], to test small-world properties in social-ecological network

[151], to describe species interactions [109,112], to measure the average number of functional groups through which each trophic inflow passes [119], and to detect the connectivity of the socio-ecological bipartite network [125].

E. **Community structure metrics. Modularity** is defined as the number of edges falling within groups minus the expected number in an equivalent network with edges placed at random. Studies investigated modularity to identify communities of species [110,112,113], to detect habitat site fidelity from species [93], to detect structures of species interactions in fragmented and changing landscapes [117], and to analyze the structural properties of habitat fragmentation [48]. Specifically, modules represented subcommunities of species or taxa, while edges were relationships between them [110,112,113,117], they also represented aggregations of spatial patches, with edges accounting for bird movement connections [93], and groups of ecological sources, where edges functioned as ecological corridors in landscapes [48]. The reported algorithms used to calculate modularity were the hierarchical agglomeration algorithm [93,110] and the QuanBiMo algorithm [117].

Contributions from conceptual studies

This review comprised 18 conceptual papers. They covered different aspects of ecosystem services research, spanning from methods to the purposes of analyses. Here, we presented them in chronological order of publication. As the first conceptual studies, [164] suggested networks to study interaction patterns between plant species in communities. Ref [165] discussed how network and thermodynamic theories can compare functionalities of natural and socio-economic systems. Ecosystems are presented as systems that show long-time evolutionary trends with relatively low reactivity. Those are possibly optimized to evolve in a direction that increases utility and synergism. In comparison, society predominantly shows short-term evolution and fast reactivity. Ref [166] suggested Bayesian Belief Networks and actor-based modeling supporting transdisciplinary research by participatory scenario development, especially for land and water management. Ref [167] proposed a participatory framework to study ecosystem services in the transhumance cultural landscapes, where networks are used to identify initially socio-ecological components. Looking for a method to analyze all the range of ecosystem services, [168] introduced a framework to analyze ecosystem services flow using agent-based modeling. The framework suggested using spatially explicit information divided into source, sink, and use regions. Looking at agroecosystems, [169] discussed the role of temporal dynamics in driving predator–prey interactions, which form networks. Ecological dynamics in crop fields routinely behave as periodic oscillations or cycles, that should be studied to understand synchrony between interacting biological elements. Ref [170] proposed a multi-layer network approach for social-ecological systems. The social and economic networks are built upon the ecological network, within a series of layers that formalize the scales of the ecosystem under consideration and allow between-layer network analyses. The approach identifies the core group of nodes in an ecological network that is important in interactions between ecosystem functions and, in turn, can be managed by social and economic needs. [171] discussed the need to use network approaches for studying managed ecosystems, linking the human, biotic, and the abiotic factors that drive agricultural production on one hand, with the landscape properties. For managing forest resilience to global change, [172] looked at a functional complex network approach. Network theory is suggested to evaluate where and how silvicultural interventions should be carried out within the landscape to enhance connectivity, centrality, and modularity. The network approach models species-trait information at the forest stand level representing diversity within forests. Focusing on dynamic urban landscapes, [173] highlighted the importance of social-ecological connectivity to explain the interdependence and feedback between the movement of people and ecological actors in time and space. As urban populations increase, and demographics and physical structures change, it becomes important to assess how green spaces and people are connected across dynamic landscapes, and how this relates to ecosystem service provision. Looking at the conservation of marine biodiversity, [174] introduced a conceptual multi-layered network approach to understanding how ecosystem services supported by biodiversity drive service provision. Multi-layer network approach aims to provide an integrated analysis of impacts on biodiversity and ecosystem services while identifying ecosystem-specific signatures in the functioning of biodiversity, and cross-ecosystem general patterns. To study socio-ecological systems, [175] proposed a process graph, which is a kind of bipartite graph. Looking at governance interventions, [176] discussed how supply-demand nodes help to model ecosystem services provision. Ref [177] suggested that multi-layer networks should be developed to investigate different interaction types among wild species, crops, and people on smallholder farms. Ref [1] proposed a typology to represent ecosystem service in socio-ecological networks. Ecosystem services can be modeled as links from sources to beneficiaries and nodes are entities of the social-ecological system, or ES can be modeled as nodes together with the social and ecological nodes, or as node attributes of social and ecological entities, or as emergent properties that result from the interplay between different entities of the social-ecological system. For modeling agroforestry systems, [178] introduced a framework that uses combinatorial maps and can manage multiple scales by aggregating individual plants at lower scales and adding a positive or negative impact at higher scales. Focusing on urban areas and green infrastructures, [179] suggested spatial networks as a tool for planning. Ref [180] discussed how to expand activities across separated research fields by facilitating actions and discussions through social-ecological networks.

Discussion

Our review outlined the main results for temporal evolution, spatial distribution, spatial scale, categories of studies, network models and metrics.

Increasing interest. The number of publications analyzing or discussing network approaches in ecosystem services research has grown exponentially in recent years. This trend highlights the increasing interest in using network models to study ecosystem services [11,16]. Although spatial mapping has become a well-established method for analyzing ecosystem services and for communicating with society to support decision-making, this approach shows shortcomings in implementation of ES due to the complexity of analyzing the flow between supply areas and demand areas by different types of social actors (see [181]). Future research has called for a deeper exploration of the theoretical connections between mapping techniques and the underlying socio-ecological processes [16]. Compared to spatial mapping, complex networks have the advantage of modeling the relationships between socio-ecological components that spatial mapping alone lacks. This is because maps-based analyses look at the spatial distribution of values and do not identify relationships between the components of a system. Therefore, network theory can play a key role in addressing the gaps in ecosystem services research by advancing the analyses of socio-environmental systems.

Spatial distribution. Most case studies are concentrated in China, Europe, and the USA, while many regions in Africa, Southeast Asia, Central Asia, the Middle East, and Oceania, remain largely unstudied. These findings partially align with those of [182], who observed that urban ecosystem services research is predominantly focused on the USA and China. This geographic division leaves significant areas of the world understudied. The lack of research on ecosystem services in vast regions hampers the development of scientific knowledge regarding the socio-environmental processes that drive change, with potential political implications. This is especially critical for climate-related risks, where comprehensive strategies for conservation, restoration, and resource management are essential to strengthen resilience against regime shifts. Similarly, [183] identified disparities in the application of machine learning with spatial data, emphasizing the scarcity of accessible data from certain regions. The need of information presents an opportunity to advance data integration methods and technologies to improve information availability in data-poor areas. Recent progresses have been made in developing platforms that offer interoperable and accessible data and models for ecosystem services. For instance, ARIES (Artificial Intelligence for Environment & Sustainability) provides spatial data and ecosystem accounting models across continents, including Africa [14,184]. Additionally, our review showed that analyzing multiple case studies, particularly those conducted across different countries and continents, is uncommon. This means that research tends to focus mostly on regional perspectives of socio-ecological issues, rather than having a global view. As a consequence, global phenomena and dependencies are lacking in studies, which hinders the investigation of problems such as carbon sequestration and climate regulation. Network models have the potential to advance the field by modeling the relationships across different geographic locations of the world, broadening the perspective on these challenges. Moreover, developing analyses that compare studies across different regions of the world would still offer a comprehensive understanding of region-specific changes and challenges.

Future research should broaden case studies in understudied regions, particularly in Africa, Southeast Asia, the Indian subcontinent, the Middle East, South America, and Oceania, to address knowledge and methodological gaps. Additionally, future research can expand the state of the art by developing more analyses across different geographical regions to assess how ecosystem services and socio-environmental dynamics vary both locally and globally.

Spatial scale. The average ratio of the number of nodes to areal extension revealed two main categories of spatial analyses. The first group used a limited number of nodes across extensive areas, while the second group employed a large number of nodes within smaller areas. In terms of analytical purpose, the first group focused on urban analyses to inform planning outcomes, whereas the second group examined large ecological regions to assess connectivity within extensive ecosystems (e.g., China, Spain). Notably, the analytical results can vary with different spatial scales [16]. In the context of spatial network analyses, this variation implies that results can change based on the granularity chosen at the node level. Future research would benefit from comparing the effects of different granularities in node selection through case studies. Such comparisons would stimulate discussion on the spatial representation of network models and their implications for ecosystem service modeling. Previous analyses have already compared spatial mapping in ecosystem services research [16]. Furthermore, discussions of spatial scales within network studies are often lacking in the reviewed papers. To enhance our understanding of these systems and improve modeling, it is crucial to address both node selection and spatial scales (e.g., defining hypotheses and assumptions) along with the analyses.

In socio-ecological systems modeling, the importance of scale is paramount for effectively integrating coupled social and environmental systems [185,186]. Panarchy theory emphasizes cross-scale linkages, where processes at one scale affect those at other scales to influence the overall dynamics of the system [187]. This approach requires advancements in upscaling and downscaling methodologies [186,188]. However, this review revealed a lack of multi-scale analyses of ecosystem services, particularly in the modeling of socio-environmental components. The predominant approach involves selecting a set of nodes (see also network model results) at a single spatial scale, which aligns with the findings of [189], who found that multi-scale approaches in network analyses of ecosystem models are uncommon. Given that multiscale approaches are crucial for studying emergent phenomena across micro to macro scales in socio-ecological systems [186], neglecting them may impede our understanding of the complex interactions between environmental and social domains.

Aligning social and environmental scales presents a significant challenge that requires robust statistical methods. As highlighted by [186], the choice of which social scale to match with a specific environmental scale depends on the empirical research problem, complicating matters since social components can vary along the gradient of environmental scales. For network models, this opens the door for future studies to explore how nodes can represent different scales and how these nodes are linked to different social components. Environmental models use spatial boundaries to develop analyses but the nature of those spatial limits is often unclear. Servicesheds, i.e., the geographical areas that provide an ecosystem service to a specific group of beneficiaries [190], are often independent of administrative boundaries, as seen in watersheds or in the context of pollination and recreation services. In such cases, servicesheds should be identified and computed at the appropriate scale, with larger servicesheds required for ecosystem services that connect more distant ecosystems and their beneficiaries. Network analyses should investigate their accurate delineation to ensure that ecosystem service models reflect both ecological realities and human needs over time and space.

Moreover, some ecological studies identified nodes based on the results of spatial models. For instance, morphological spatial pattern analysis (MSPA) was used to measure structural connectivity and pinpoint important habitat patches as nodes [33]. Nodes have also been determined at the centroids of ecological sources, derived from assessing the significance of patches using landscape variables [52]. Other studies have employed the Minimum Cumulative Resistance (MCR) model [191] to select ecological nodes by calculating resistance surface values [46]. It is essential to discuss the implications of these model selections also for a robust spatial representation of nodes.

There is a need to discuss spatial scales in studies using spatial network models, compare various spatial scales to examine their effects on results, and analyze the rationale behind the selection of spatial models used to identify nodes within these networks. Addressing these aspects will enhance our understanding of spatial dynamics and improve the robustness of network analyses. Network analyses can study servicesheds and ecological-social interactions across scales to advance ecosystem service research.

Topics of studies. Most of the reviewed publications focused on ecology (69% of papers), with fewer addressing management (17% of papers) and even fewer exploring nature's contributions to people (8% of papers) and social studies (6% of papers). These findings are consistent with those of [182], who noted that a minority of urban ecosystem services research engages with all components of ecosystem services. Specifically, research rarely distinguishes between ecological structures, processes, and services to humans, and predominantly emphasizes the ecological perspective. To address this gap, future studies should look more at the social dimensions of ecosystem services. In particular, the social domain is studied mainly from organizational and residential perspectives. When examining the topics investigated in the social, nature's contribution to people, and management categories of studies - which were the ones integrating the most the social dimensions - there is a limited exploration of topics such as the accessibility of ecosystem services to people and social inequalities, the health and wellness impacts of ecosystem services distributions, or the social impact on environmental sustainability due to ecosystem service distribution. The ecosystem serviceshed concept is promising for aligning conservation investments with the local needs of beneficiary groups to ensure equity (see [190]. It delineates the scale and dynamics of the connections between ecosystems that provide services and the human beneficiaries, which can vary significantly depending on the type of service and the systems involved. Since the study of servicesheds is based on these connections, network analysis can significantly contribute to ecosystem service research through its investigation (see also the 'Spatial scale' paragraph).

Overall, topics of environmental sustainability and socioecological resilience offer vast possibilities for future studies (see [192–194]). When looking at management studies specifically, some key topics related to sustainability were overlooked. For example, only one paper addressed pollution [138]. Moreover, a few studies looked at drivers of pressures to ES changes [139,140], and examined ecosystem service trade-offs between management options [131–134]. Ref [195] also recommended that future research explore the trade-offs and synergies between services over time. To contribute to identifying strategies for sustainable management, future studies should address pollution and drivers of natural capital decline, and their impacts on ecosystem services, as well as expand the case studies on trade-offs involved in ecosystem service management.

Traditionally, ecosystem services research has investigated the economic value of ecosystem services. As [6] stated, being more explicit about the value of ecosystem services and natural capital can help society make better decisions in the cases where trade-offs exist. We have not found any study analyzing the societal values of ES with networks, which calculate the benefits to society. New research can propose methods to explore how to assign values to ES depending on network models, for example, by relating values with the supply-demand exchanges of socio-ecological components. Future research can also quantify how disrupting network connections, will impact the societal values of ES, giving so a numerical quantification if they are lost.

Notably, cultural services were limited from any social perspective. Ref [88] suggested measuring the aesthetic of the landscape through spatial networks of landscape elements, [90] examined networks of ecological and cultural sites, and [157] investigated human perceptions of cultural services. Thus, future works should propose frameworks to investigate cultural services within the ecosystem services paradigm.

In the ecology domain, there are some less studied topics, including ES predictions from landscape configuration [82,83], species drivers of ES [118–120], and multi-layer structure of landscape studies [88–90]. Further research is needed in these areas, particularly concerning multi-layer structures that connect different ecosystems and their functions in landscapes (see also network models). These layers represent exchanges of various natural resources and ecological information, and studying them could enhance our understanding of the relationships between landscape elements. Given the scarcity of publications using the multi-layer network approach, future studies should propose frameworks to analyze ES interactions through this lens, shedding light on how ecological components depend on one another to provide ecosystem services.

We found that 17 papers looked at temporal dynamics and 12 papers studied flows (see also network models). Considering that ecosystem service systems are dynamic, we expected more studies to address the temporal dimension and flows. Our findings align with those of [196], who noted that the temporal aspects of ecosystem services have received limited attention in research. Temporal variations are crucial for understanding how socio-ecological components respond to and co-evolve with external changes. Past studies have shown the impacts of urban expansion and population growth on ecosystem services [195], with most temporal analyses focusing on urbanization processes and land-use changes. Sustainability and resilience are critical factors to explore when preparing for future urban transformations [197]. Our review revealed that studies assessed the robustness of ecological landscapes over time by removing network components (e.g., [49]), while others examined the connectivity of land systems to evaluate vulnerability over time [77,78]. Robustness and vulnerability are key properties of resilient social-ecological systems (see [19,198]. Studies aiming for better characterization of resilient systems should also examine system functions and feedback mechanisms during crises. Those are factors that still depend on spatio-temporal variations. Moreover, beyond urbanization and land-use changes, other drivers - such as climate-related events (e.g., storms, floods, droughts) - can cause significant changes in ecosystem services. These dynamic processes can help inform better planning and policies, especially in response to climate change. Future research should expand the analyses of spatiotemporal changes resulting from environmental and climatic shifts.

Not all research questions are well-suited to network theory approaches. As [22] noted, questions that are not rooted in relationships may require alternative methodologies. Moreover, when using network topology to detect priorities and strategies, factors in the environmental conditions might prevent a linear solution as analyzed by network properties only. For example, [33] highlighted how soil salinization can limit network optimization strategies in landscapes, illustrating that evaluating network topology alone has limits in addressing environmental questions. Small changes in environmental conditions can cause large, unstable shifts in a system's status that research using network analyses should be aware of.

To advance the field, future research should analyze the social components of ecosystem services, including issues such as resource accessibility, health and wellness, environmental and climate justice, cultural services, and the societal values (benefit) of ecosystem services. Network analyses can significantly contribute to the field by investigating servicesheds. Additionally, studies should focus on multi-layer structures of ecosystems and their functions in landscapes, as well as spatio-temporal dynamics of change. It is still important to investigate sustainability and resilience in response to urbanization, environmental and climate change, pollution, and the depletion of natural capital, while also considering the trade-offs involved in managing ecosystem services.

Network models. Most papers used information regarding spatial patches, sites, and habitats, with 57% of papers modeling them as nodes. This highlights the importance of accessing and using spatial data for ecosystem services analysis. Other socio-ecological components can also inform ecosystem services studies and be modeled as nodes. For instance, network nodes can represent ecosystem services, social entities, policies, human interventions, and drivers of change. Our review found that social nodes typically represented groups of stakeholders, organizations, while rarely representing individuals. Only [124] and [149] used social media data, while [157] used crowd-sourced data to extract information about perception of people. Moreover, [155] modeled nodes as individual households, and [130] included the human wellbeing as a dimension of their analyses. These findings partially corroborate the results of Ref [22]: in social-ecological networks, most papers conceptualize social nodes as collective social entities (e.g., organizations, clans, fishers, and ecosystem service beneficiaries), while individual and household representation are rare. Ref [25] discussed the possible representations of network nodes in ecosystem service research, highlighting that representing a service as a node is particularly useful when multiple species provide a single service (e.g., multiple species pollinating crops) or when a service depends on several ecosystem functions. They proposed an integrated model that builds a network around management objectives, where the ecosystem service node is linked to the species, functional groups, or ecosystem processes that directly provide it. When examining the types of connections, we observed that edges could also represent a diverse range of relationships between components. Our review found no consensus on the best network model for ecosystem services research, with model choices typically driven by the specific research problem and availability of data, suggesting no definitive guidelines for selecting nodes and edges in modeling.

Multipartite and multilayer networks were used by 19 quantitative studies, and 5 papers used Bayesian Belief Networks. This suggests that the majority of studies used simple network models, with a single layer and with the same set of nodes. Ref [88] proposed modeling ecosystem services with a multilayer network to improve the evaluation of connectivity and resilience, and [22] advocated for fully articulated social-ecological network research that explores multidimensional and multiplex networks to represent different relationships among various types of nodes. Conceptual papers also suggested multilayer network approaches for diverse applications [170,174,177]. These modeling approaches offer more detailed analysis of places, organizations, and structures of social and ecological components. We recommend further exploration of these models in future studies. Regarding Bayesian Belief Networks, we anticipated more publications employing them, especially for participatory scenario development, a topic discussed as early as [166].

Despite these advances, limitations remain in integrated network modeling. Resolving integrated networks can be resource-intensive, requiring substantial information to account for dynamics or spatial heterogeneity [25]. Additionally, collecting meaningful data to yield actionable insights for policymakers is crucial. We agree with [25] that a research frontier lies in determining how much system models can be simplified and generalized while still delivering useful results. Flow analyses within networks for socio-ecological issues remain uncommon in the literature, despite the fact that ecosystem services are a result of dynamics between socio-ecological systems. For example, [168] proposed using agent-based modeling to simulate the flow of an ecosystem service from sources to users.

Future research should focus on expanding the analysis of complex interactions in systems using multipartite and multilayer networks, as well as Bayesian Belief Networks and flow analyses between socio-ecological components. Moreover, it is essential to evaluate the extent to which models can be generalized and simplified while still providing valuable outcomes for decision-makers and planners.

Network metrics. The most commonly studied metrics were centrality metrics (betweenness, closeness, eigenvector), landscape connectivity metrics (probability of connectivity (PC), importance percentage (dPC), integral index of connectivity (IIC), importance of the integral index of connectivity (dIIC)), networkwide metrics (degree, network density, alpha, beta, and gamma indices, clustering coefficient, average path length), a robustness and fragmentation metric (connection robustness), and a community structure metric (modularity). However, many less predominant metrics were also used in the literature (see Tables 3–6). We found that topological metrics are extensively adopted to evaluate the structural properties of systems. They are often used to study properties of individual components, like connectivity. For example, PC and IIC metrics, developed in the ecology field, are extensively used to study the importance of single patches for connectivity in landscapes, and also betweenness centrality often served for this purpose. We recommend that future research clearly explain the rationale for selecting certain metrics in their studies; otherwise, there is a risk of using them because of their popularity.

When studying network robustness, studies evaluated disrupted networks by random and targeted attacks. When targeting nodes, most of the studies identify them based on degree and centrality. We agree with [199], who discuss how it is also relevant to examine algorithms that seek to identify the sets of nodes or edges that, if removed, lead to the largest impacts. This is because it is possible that no node or edge centrality measure can reliably identify such sets [199]. Moreover, they also concluded that when no information about function or dynamics is available, it is difficult to obtain meaningful insights into a system's robustness by using metrics in simple graphs [199]. Looking in particular at environmental systems, those are under threat because of the human pressure on ecosystems and climate change. Disconnections of socio-ecological or only environmental components might be caused by hazards (e.g., drought, floods), anthropic impact (e.g., development plans), and environmental crises (e.g., biodiversity decline). Some of those can be characterized by return periods (e.g., floods), while others instead show more unexpected dynamics. Mimicking crises and calculating them by performance metrics based on total randomness or rankings of centrality serves as a way to mark the boundaries for more complex phenomena. However, to have a more realistic representation of systems' crises, research should propose new ways to measure them based on more realistic dynamics.

As guidelines for advancing applications of network metrics in future research, studies can improve their use of network metrics by leveraging specific domain knowledge in ecology, environmental and social science, with topological analyses.

Conclusion

This study reviewed 152 scientific publications drawn from ecosystem services and network theory research. Our aims were twofold: first, to summarize how and for what purposes network approaches are used in ES research; and second, to propose new frontiers for future research. Our analyses investigated the temporal and spatial distributions, spatial scales, topics of study, network metrics, and the types of network models used in case studies.

We found seven main results. First, the number of publications, analyzing or discussing network approaches for ecosystem services research, has been growing exponentially in past years. Second, most case studies are located in China, Europe, and the USA. In contrast, there are countries without any investigation, especially in Africa, Southeast Asia, Central Asia, the Middle East, and Oceania. Third, the average ratio of the number of nodes and areal extension identified two main groups of spatial analyses. Fourth, publications focused mostly on ecological studies and less on social ones. Fifth, most papers used information regarding spatial patches, sites, and habitats. Moreover, 57% of papers modeled them as nodes. This means that spatial data is important information to acquire for ecosystem service analysis. Sixth, multipartite and multilayer networks were used in 15% of quantitative studies. Seventh, betweenness centrality, closeness centrality, eigenvector centrality, degree, alpha, beta, gamma indices, landscape connectivity metrics, clustering coefficient, average path length, network density, modularity, and connection robustness were the most analyzed metrics in papers.

This study has implications for researchers and policymakers. Researchers can find research suggestions in the discussion section. Those can help develop network models, metrics, and spatial analyses further to advance state-of-the-art in ecosystem service research. Vice versa, ecosystem service research offers complex and meaningful problems for science. Policymakers can use this review to understand how data-driven modeling in general and network theory specifically can contribute to better evaluations, and so planning, of ES.

This study has limitations. While systematic reviews are meant to select most studies in a field by limiting biases, they can still produce errors. For this study, our search used a set of words linked to ecosystem services, nature-based solutions, green infrastructures, human-environment, natural capital, and social-ecological networks. If using another set of words, results would change. Additionally, consider that in emergent fields of research, new terms might become popular in a short time. Moreover, our categorization of quantitative works depends on what network components and their relationships studies focus on. Especially, our work is based on a synthesis of textual documents. Other researchers may interpret studies using different criteria. Other categorizations of studies based on different perspectives (e.g., based on ecosystem services classes) are still possible but not analyzed here. Therefore, we want to emphasize that researchers, particularly those proposing new approaches, should not view our classification as a strict imposition on their ES work, but rather as a way to provide an organized summary of the numerous studies developed over the past years.

Supporting information

S1 Checklist. PRISMA 2020 checklist for the present systematic review.
(PDF)

S1 Table. List of all documents identified in the literature search. The Source column indicates whether each document was retrieved from Scopus or through snowballing search. We reported the reasons for rejection and classified each document as quantitative, conceptual, or review.
(PDF)

S2 Table. Data extracted from quantitative papers used in the systematic review. Data extracted from quantitative papers used in the systematic review. The data were extracted by Ylenia Casali in 2024, and the table was compiled on April 7th, 2025. Network type description provides a brief summary of the network models, while Edges and Node descriptions specify the types of nodes and edges used. Since the study focused on the spatial scale of networks, we included information on the number of nodes and the areal extent of the case studies. When the area was not reported in the original paper, we searched for it using Wikipedia or Google and labeled it as "searched." For details on the network metrics extracted from the literature, refer to S2 Table for the complete list of metrics and references.
(PDF)

Author contributions

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