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Opinion

Conceptualizing ecosystem services using social–ecological networks

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Social–ecological networks (SENs) represent the complex relationships between ecological and social systems and are a useful tool for analyzing and managing ecosystem services. However, mainstreaming the application of SENs in ecosystem service research has been hindered by a lack of clarity about how to match research questions to ecosystem service conceptualizations in SEN (i.e., as nodes, links, attributes, or emergent properties). Building from different disciplines, we propose a typology to represent ecosystem service in SENs and identify opportunities and challenges of using SENs in ecosystem service research. Our typology provides guidance for this growing field to improve research design and increase the breadth of questions that can be addressed with SEN to understand human–nature interdependencies in a changing world.

Highlights

Social–ecological networks (SENs) provide a promising approach to represent the complex ecological, social, and social–ecological relationships that influence ecosystems service supply.

Ecosystem services can be represented in SENs as nodes, links, attributes, or as emergent properties of the network, each bringing distinct aspects of ecosystem services into focus to address different questions.

Applications of SENs in ecosystem service research can foster: (i) understanding of the social and ecological drivers of ecosystem services; (ii) forecasting of the impacts of stressors; (iii) investigation of trade-offs between ecosystem services; and (iv) assessment of the effects of alternative management options.

Ecosystem service research would benefit from a typology to conceptualize particular ecosystem services in SEN analyses and from greater clarity of when ecosystem service research can benefit from a SEN approach.

Ecosystem services as SENs

Ecosystem services (see Glossary) represent an interface between ecological and social systems, as the benefits people receive from nature [1]. Given the inherent dependencies between social and ecological systems, **SENs** have recently been proposed as a promising approach to conceptualize and manage ecosystem services [2–6]. SENs complement and enhance current approaches to ecosystem service research (Box 1), such as those focused on the spatial mapping or valuing of ecosystem services [7,8], by explicitly considering complex interactions, dependencies, and feedbacks between ecosystem services and their underlying social and ecological components [3,4].

Despite this growing interest, we still lack guidance on conceptualizing particular ecosystem services in SEN analyses and identifying contexts in which ecosystem service research could benefit the most from a SEN approach [9,10]. SENs are an extraordinarily flexible tool for studying ecosystem services, yet this flexibility raises questions about how to apply them. Ecosystem services have been explicitly represented as elements of networks: as attributes of social or ecological **nodes** [4], as nodes in a network together with ecological and/or social nodes [3,5,11–13], and as **links** between social and ecological nodes [9,14]. Alternatively, ecosystem services have been conceptualized as an implicit outcome or **emergent property** of the interactions in a network, rather than explicitly depicted in a SEN [15–18]. As a result, it remains unclear how different representations may support specific research questions or contexts and when they may lead to divergent conclusions. Furthermore, data to build SENs are often rare, siloed in particular disciplines (e.g., social or ecological studies) and can be difficult and costly to gather [19]. As a consequence, clear objectives and methodological understanding are needed to reconcile

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Box 1. How can SENs complement other approaches to ecosystem service research?

Ecosystem service research can benefit from integration with SEN applications. For example, in tandem with economic valuation methods [80,81] SENs could be used to investigate changes in people's preferences and values when they are aware of social–ecological connections [2]. Incorporating SENs into spatial ecosystem-service mapping can provide information about: the direct or indirect role of stakeholders in influencing ecosystem services through conservation and management practices [82]; information flows [83]; cross-scale interactions among social actors [37] and ecosystem services [39]; and long-distance connections through telecoupling [24,50–52]. When ecosystem services transcend local scales (e.g., climate regulation), SENs can assess whether collaborations across multiple spatial scales [84] match the scale of the ecological processes underpinning ecosystem services [19,20,85].

Building on Dee *et al.* [3], we argue that important information can be missed in ecosystem service studies that analyze only social or ecological networks rather than an integrated SEN [19,86,87], such as the role of social relationships in shaping management actions that affect the ecological network [88,89] or the complex ecological interactions underlying ecosystem service supply [5]. SENs can complement other integrated modeling frameworks (e.g., [90,91]) that acknowledge linkages between, and complexities within, both social and ecological layers. Accounting for these interdependencies is fundamental to the advancement of ecosystem service research, as ecosystem services directly represent the connection between social and ecological systems [3].

For instance, a question that remains open in ecosystem service science [92] is: how do multiple ecosystem services interact and what are the consequences of those interactions for their management? An existing approach has been to map areas supplying multiple ecosystem services [93,94]. In turn, an ecological network approach could predict how management affects species providing ecosystem services by using simulations [13], while a social network analysis approach would identify policy actors associated with a particular ecosystem service to assess management coordination [95]. However, with a SEN a researcher could identify both the underlying ecological processes that connect ecosystem services mechanistically, using the ES-links approach, and how they connect to beneficiaries, using the ES-nodes approach.

these diverse conceptualizations and identify the best SEN representation for different research questions and contexts and to guide future data collection efforts.

Here, we synthesize and align research on SEN approaches for ecosystem service research. To do so, we bring together perspectives from an interdisciplinary group of researchers working with **social networks**, **ecological networks**, SENs, and ecosystem services. Specifically, we provide a typology to represent ecosystem services using SENs. Our perspective aims to support future studies addressing the remaining challenges to a full realization of the potential of SENs in ecosystem service research. Furthermore, our typology provides guidance for this growing body of work, including consideration of the diverse ways in which ecosystem services can be represented in a SEN and the benefits of each. Together, this typology can help to improve research designs by aligning specific SEN conceptualizations and research questions.

Representing ecosystem services in SENs

Building on examples from the literature (Table 1), we identified four main approaches to the representation and analysis of ecosystem services as part of SENs: ecosystem services as links, nodes, **node attributes**, or emergent properties of the network (Figure 1; see Figure S1 in the supplemental information online for a terrestrial example). We propose that the choice of representation ought to be guided by the research question and context, rather than suggesting a single 'best' representation. Thus, we provide examples of key questions that each approach can answer and identify associated applications and data requirements (Table 1).

In all representations, we describe a basic conceptualization of the study system as a network comprising two node categories: social (e.g., diver, farmer) and ecological (e.g., fish, coral). Nodes within each category can be linked to create a layer of social or ecological interactions. Links between social nodes can represent information or resource exchange, while links between ecological nodes can represent trophic interactions or competition. In turn, a SEN can constitute

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a **multilayer network** with three interaction types: those between social nodes, between ecological nodes, and between social and ecological nodes, where the latter can represent, for example, the management of an ecological node [14,20]. Other concepts such as drivers of change or stressors (e.g., deforestation, overfishing) can also be represented as nodes [3,12,21].

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Ecosystem services as links (ES-links)

In the ES-links (Figure 1A) approach, directed links from ecological nodes to social nodes represent the **ecosystem service flow** [10,14]. Links can be weighted to indicate the amount of service provided. Links from a species to a beneficiary could represent the supply of ecosystem services such as aesthetic value or food, while links from an actor to a species could indicate attachment (e.g., symbolic value) or management (e.g., conservation) affecting the nodes [15,17]. Utilizing the three interaction types of a SEN, it is possible to ask questions about the role of ecological interactions in ecosystem service supply (e.g., how do fish–coral relationships affect fisheries yields and the aesthetic values of coral reefs?) or how ecosystem services flow through the social system (e.g., who sells fish to whom or who benefits from tourism?) [22].

Table 1. Key research questions for ecosystem services (ES) and their corresponding conceptualization in SENs. We provide examples of key questions that each approach in our typology can answer and identify applications and data requirements of each.

Type of approach	Key research questions appropriate for this representation	Application in ES research	Data requirement
ES as links representing flows (Figure 1A)	• What is the role of ecological interactions in ES supply? • How do ES flow through the social system? • How do changes in one node affect the flow of ES? • How does managing social or ecological nodes affect the flow of ES?	• Identify interdependencies between systems affected by ES flows, including telecoupling [24,50–52] • Forecast impacts of stressors such as global change [3,53] • Predict potential threat propagation (e.g., drought, fires, disease, invasions) [16]	• Detailed information on either ecological or social networks • Dependent on the level of detail: trade-off between exhaustive (amount) versus precise (quality) information
ES as nodes representing natural capital stocks (Figure 1B)	• How do drivers (e.g., invasive species, species losses) impact ES? • How does direct or indirect management of ES impact the rest of the system, including other ES? • How does the structure of the governance network (i.e., the involvement of different types of actors) drive effective ES management? • Who are the beneficiaries of ES?	• Relationships within multiple ES or between ES and other social or ecological nodes [19] • Studies on supply, demand, and governance of ES [31] • Trade-offs between multiple ES [32,33] • Equity and justice in access to ES or distribution of ES [35–37] • Use of Bayesian belief networks [28–30,54] • Incorporation of ES in social–ecological fit analyses [55] • When primary data for ES are not available [3,12,31] • When multiple species provide a single ES to different beneficiaries [13] • When an ES depends on multiple ecosystem functions or species [11]	• Information on social and/or ecological networks (ES can represent the ecological or social underlying network, summarizing complex ecological or social interactions)
ES as node attribute (Figure 1C)	• What are the values attached to a particular species or landscape area? • How do management actions taken by an actor affecting some species or landscape area impact ES supply?	• Existence of multiple layers of information or multiple values associated with a node (e.g., economic or cultural value, management actions) • Defined ES providers or ES attached to a species (i.e., the species that delivers the ES is a node), such as a harvestable fish population or individual [4] • ES estimated from higher spatial scales (e.g., a forest patch is a node) [40] • Integration of decision-making with existing management units [20]	• Abundant information for each of the nodes in the network • Additional covariates of interest (social and ecological data that are relevant to the research question can be captured as node attributes)
ES as emergent property of the network (Figure 1D)	• What social and ecological elements are related to a particular ES? • What are the ES outcomes of coordinated landscape management?	• Uncover the ES outcomes of network structure. • Conceptualize relational values as SEN [46]. • Analyze ES co-production as SEN [56,57] • Identify power dynamics between actors related to ES [15,45] • When ES cannot be managed directly or management of ecological nodes is decentralized	• Identification of the many actors and connections • No requirement on quantification of ES or links from ES to particular actors • Generally not appropriate for large networks

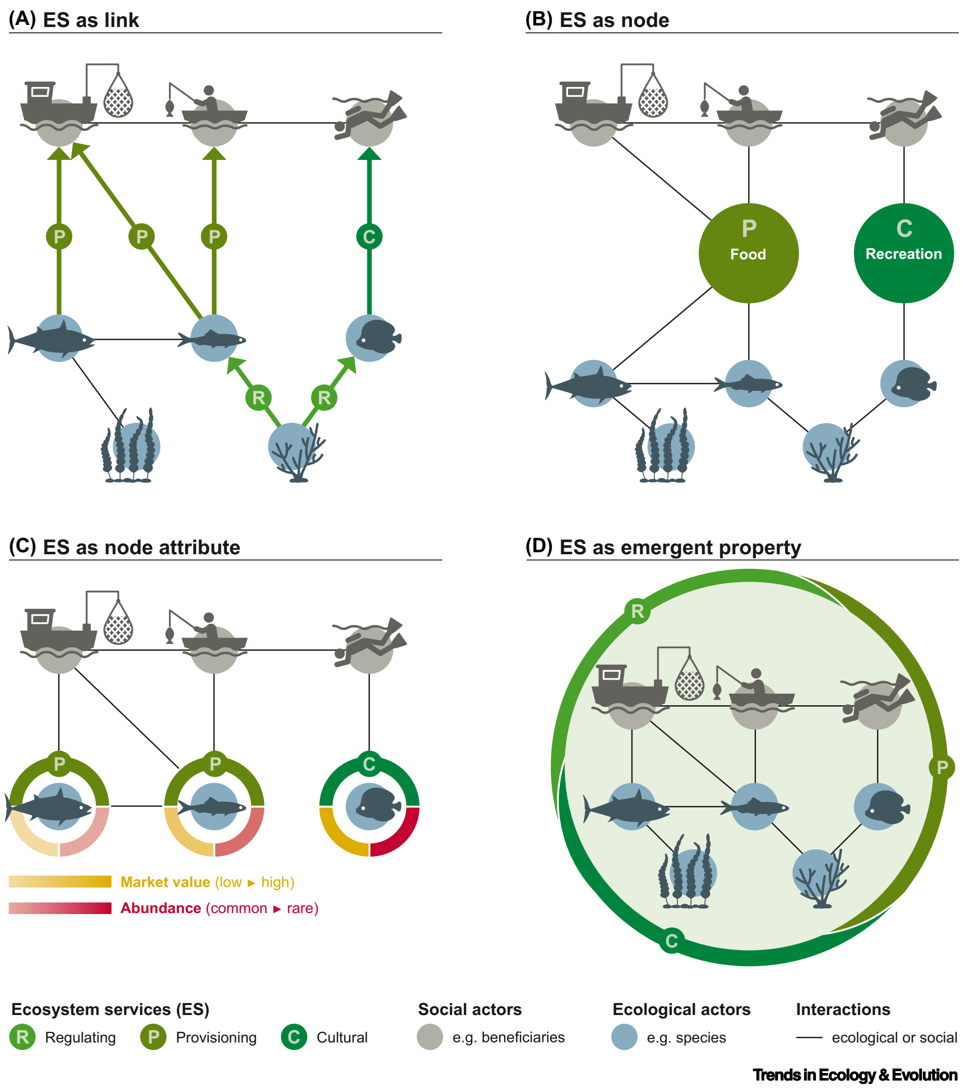

Figure 1. Typology of approaches to conceptualize ecosystem services (ES) in social–ecological networks of social actors (gray), ecological entities (blue), and ES (green). (A) ES as links: ES are directed links from sources to beneficiaries, where nodes are entities of the social–ecological system. (B) ES as nodes: ES are nodes together with the social and ecological entities they are related to by links. (C) ES as node attribute: ES are one attribute of each fish species, where nodes are both social and ecological entities. (D) ES as an emergent property: ES are represented as a circle surrounding the network, as they emerge as a property resulting from the interplay between different entities of the social–ecological system, which are represented as nodes. In all types, interactions between nodes could be positive (e.g., collaboration, influence, dependence, facilitation), antagonistic (e.g., competence, predation), formal (e.g., contractual, kinship), or informal (e.g., friendship) relationships. (See also Figure S1 in the supplemental information online.)

The ES-links approach focuses on identifying how the different nodes are connected to deliver or manage ecosystem services, which requires detailed information on both the ecological and social layers or subnetworks. As a result, this representation is best suited for analyzing how loss or change in one node can affect the supply or management of ecosystem services in other parts of the system (Table 1). Therefore, the ES-links approach can, for example, contribute to forecasting the impacts of stressors such as climate change and how these impacts may propagate through a SEN [13,23]. This approach can also be applied to understand interdependencies

Glossary

Ecological network: network depicting ecological entities, such as species, functional groups, or patches, and the processes that connect them (e.g., species interactions, connectivity through dispersal).

Ecosystem service: material or immaterial benefits people receive from nature. They are often classified as provisioning (e.g., food, water), cultural (e.g., learning, inspiration, aesthetic value), and regulating (e.g., carbon sequestration, water purification). The Nature Contributions to People [1] concept can also be used.

Ecosystem service flow: rate at which people use ecosystem services derived from a stock (for provisioning and cultural services) or regulating services derived from species interactions (e.g., predation).

Emergent property: an overall outcome, or property of the network, which results from the interactions between network components.

Link: connection between two nodes (e.g., dispersal between patches, resource exchange between actors); synonyms are arc, edge, interaction, and tie.

Multilayer networks and associated concepts: a family of networks that model multiple layers of information. Multilevel networks include multiple types of nodes (called multipartite), as in Figure 1. Multilayer (or multirelational) networks allow multiple kinds of links between nodes. Certain multilevel approaches (called multiplex networks) incorporate multiple link types (e.g., trophic and mutualistic interactions [72]) between nodes of the same kind. Here, we loosely use the term 'multilayer; to refer to all of these networks. Related concepts include multinetworks and networks of networks.

Network approach: a system of connected entities (nodes) and their pattern of interactions conceptualized and/or analyzed to understand how relations between entities of interest affect specific outcomes and/or are the results of specific underlying processes.

Node: an identifiable component of a network (e.g., user, beneficiary, species); synonyms are actor, alter, ego, entity, and vertex.

Node attribute: a characteristic of a node (e.g., market price of a fish; Figure 1).

in the system due to ecosystem services flowing from sources to their beneficiaries over long distances (i.e., telecoupling) [24,25].

Ecosystem services as nodes (ES-nodes)

The ES-nodes (Figure 1B) approach represents ecosystem services as nodes, together with social, ecological, or both types of nodes. This is a multilayer **network approach** that is convenient for representing relationships between an ecosystem service and the social and/or ecological system (see [3]). Ecological nodes can be included to indicate ecological entities that together deliver an ecosystem service (e.g., trophic networks, landscape features). Ecological interactions may be included if the research question is about the impacts of ecosystem service management on biodiversity or ecosystem functions or vice versa [3]. Social nodes can be added to indicate people who manage or benefit from ecosystem services to explore direct or indirect trade-offs between beneficiaries. For example, if the social node is a beneficiary of ecosystem services, the link could indicate whether this benefit flows directly from the ecological node or indirectly through other nodes. If the node is an actor involved in the management or governance of the ecosystem, a link between service and actor can represent the kind of management action (e.g., restoration, invasive species control, harvest quotas). In both cases, weights of links can represent the frequency or intensity of the relationship. In addition, it is possible to distinguish between positive (mutually supporting) and negative (antagonistic) relationships between nodes to analyze, for instance, how interactions in the social system, such as collaborations, impact ecosystem services through coordinated management actions [14,20,26,27]. The flexibility of the ES-nodes approach allows SENs to be constructed as Bayesian belief networks, where the states of social, ecological, and management or policy nodes can have a causal impact on ecosystem service nodes (i.e., with links representing causal relationships) [28–30].

The focus of the ES-nodes approach is on the existence or persistence of an ecosystem service rather than on the rate or amount of delivery that flows to people. Thus, it can be applied when there is no primary data on the magnitude or per-species contribution to ecosystem services but an indicator of ecosystem service supply. This is particularly useful given that per-species data are often lacking and difficult to obtain for most ecosystems and services [13]. The ES-nodes approach can help to assess how ecosystem services and network structure respond to drivers of change, such as species losses [13], climate change, or invasive species [3,12], and changes in governance structures [14,31] (see examples in Table 1). Representing ecosystem services as nodes instead of links can also facilitate an understanding of the relationships between multiple ecosystem services and between services and other social or ecological nodes [19]. Trade-offs between the management of multiple ecosystem services and their potential users are then easier to detect [32,33]. An ES-nodes approach can describe multiple species providing a single service to different beneficiaries (e.g., multiple species pollinating crops) [34] or a service depending on multiple ecosystem functions or species (e.g., provisioning services associated with biodiversity and ecosystem functions at low land-use-intensity levels) [3,11]. Another application of the ES-nodes approach is to assess how a service is affected by multiple stressors or threats [13]. For example, Rocha *et al.* [21] used a tripartite network to represent how stressors (e.g., deforestation and overfishing) lead to regime shifts in ecological systems that ultimately affect different ecosystem services. Keyes *et al.* [13] simulated direct and indirect consequences of species losses (e.g., from climate change) for multiple ecosystem services in coastal systems. Finally, the ES-nodes approach can contribute to studies on equity in the distribution of ecosystem services, including issues of procedural and distributive justice. For example, this can be analyzed using a multilayer network to identify which actors are more dependent on a predefined set of ecosystem services [35,36] and those with the greatest ability to manage or control services at different spatial scales [37], which is fundamental to multiscale power dynamics.

Social–ecological network (SEN): a network that considers connections within and between the social and ecological layers (i.e., a fully articulated [2] or type III [9] network), in contrast to ecological networks or social networks, which account only for interactions within one of these layers. For simplicity, we also consider as SENs those networks that only include the interactions between social and ecological nodes (i.e., partially articulated [2] or type II [9] networks).

Social network: network depicting interactions (e.g., knowledge exchange, trust, collaboration, resource sharing) between social actors (e.g., individuals, communities, organizations).

Ecosystem services as attributes of social or ecological nodes (ES-attributes)

The ES-attributes (Figure 1C) approach represents ecosystem services as attributes of nodes, indicating whether and how the node is related to the ecosystem service [4]. Other social and ecological information about the node (e.g., type of social actors, species richness) can also be added as a node attribute. The ecological nodes shown in Figure 1C, for example, have three attributes: abundance (from common to rare), economic value (from low to high), and the ecosystem service attached to it (the provisioning service – food; or the cultural service – the aesthetic value of an aquarium fish). Attributes of social nodes can also include ecosystem services to represent perceived values or management actions associated with them (not shown). For example, the attribute could represent the perceived ecosystem services received from the fish or natural resource that an individual is connected to or the ecosystem services impacted by the management actions of a manager or governance actor [37,38].

The ES-attributes approach is helpful when the social or ecological nodes or their links are central to the research question, such as interactions between users or managers, or interactions between species (Table 1). This type permits a single-layer representation when the research question is focused on one category of node (i.e., social or ecological), as the ecosystem service is captured by the node attributes. The ES-attributes approach may be useful when providers of ecosystem services are identifiable entities (e.g., harvestable fish stocks, seed varieties) [4] or when services are estimated from higher spatial scales, such as land-cover maps (e.g., with habitat patches [39] or municipal boundaries [40] represented as a nodes). When nodes represent existing management units, such as a farmers' union or a forest patch, this approach may be particularly useful for decision-making by integration with current management strategies. However, it would not be appropriate when existing management units are not properly designed to enhance ecosystem services [39] and could oversimplify the system by assuming that ecosystem services can be estimated from land-use/land-cover maps without testing those assumptions.

Ecosystem services as an emergent property of the network (ES-emergent)

In the ES-emergent (Figure 1D) approach, ecosystem services are not explicitly depicted in the network because they result from overall interactions in the network as an emergent property of the system [41,42]. An example is farmers' cooperatives organized around water temples to maximize rice production in Bali [42] (Figure S1 in the supplemental information online). In this example, each cooperative (node) is connected to other cooperatives by irrigation canals (link) through their paddy fields (node), in which they grow different rice varieties (node attribute). Biological pest control emerges as an ecosystem service from the interactions between farmers that coordinate water management and rice varieties. In this case, both the provisioning service (rice yield) and the regulating services (water supply and biological pest control) are quantifiable but not represented in the network; instead, authors consider these services as emergent properties of the network. Similarly, in Figure 1, the cultural service of recreation results from the interplay of all actors that maintain adequate fish and coral populations, water quality, and a safe swimming environment [43]. Other cases where ecosystem services can be conceived of as emergent properties of habitat networks include those with dependence on particular species [e.g., a sufficiently connected habitat underlies seed dispersal by ring-tailed lemurs (*Lemur catta*)] [101].

The main focus of the ES-emergent approach is to represent relevant management units to the ecosystem service of interest (e.g., species, habitats, society, industry) and their connections rather than to identify or quantify links between specific actors and services (Table 1). For example, power dynamics between actors related to ecosystem services are often visualized as links, without explicit representation of ecosystem services [15,41,45]. The ES-emergent approach also applies to relational values that people have with nature and others [46,47] and which are tightly connected to experiences of cultural ecosystem services [48]. As another example, co-produced ecosystem services result from the combination of both natural processes and different types of anthropogenic contributions [44,49]. In this case, human actions can directly influence the individual ecological or social nodes, indirectly affecting the emergent ecosystem service. Coordinated management of different ecological nodes can lead to sustained supply of multiple ecosystem services at the landscape scale through the persistence of wildlife populations that provide services [20,25].

Remaining challenges and opportunities in the use of SENs for ecosystem service research

In this section, we identify key challenges and opportunities in the application of SENs that can help ecosystem service research to advance knowledge and fully leverage SEN approaches. In addition, we highlight the need for coordinated approaches to data collection in interdisciplinary research to generalize insights in Box 2.

Mechanistic trade-offs in space and time

SEN can help to identify potential trade-offs in ecosystem services through direct and indirect paths connecting services with antagonistic interactions. For example, take two competitor species that provide two different ecosystem services. Favoring the abundance of one to increase the ecosystem services provided by it can reduce the abundance and correspondingly the ecosystem services stemming from the other species (Figure 1A). Transformations of Lotka–Volterra equations can be used to obtain competition coefficients from trophic interactions [58], while genetic algorithms can be used in multilayer networks to minimize trade-offs between ecosystem services associated to management practices [59].

Box 2. A call for coordinated research and data collection for generalizing insights

A standardized approach to measuring ecosystem services, together with key metrics for comparing studies using SENs, is needed to address sustainability challenges (see Table 1 in main text). The development and application of protocols for social–ecological system analyses [96] will allow us to infer SEN patterns from case studies. This effort would enable us to generalize the increasing knowledge available from local, place-based research [97] and to develop SEN theory [2,53,84] and predictions about changes in ecosystem service supply. Additionally, uniform data collection could enable the parametrization of system models by extending parameters from similar case studies rather than collecting new data [98]. Collecting empirical data to link quantities of ecosystem services to particular individuals or species requires substantial time and resources that are often limited, especially in data-scarce regions. When extensive data are unavailable, researchers can use simpler SEN representations with ecosystem services as a surrogate of complex social–ecological interactions (i.e., the ES-nodes approach; Table 1).

In an effort to overcome outstanding challenges and to enable generalization and comparability across cases we provide four suggestions for future studies.

(i) Choose appropriate and consistent indicators. Ecosystem service indicators should match the relevant social and ecological nodes connected to the services (i.e., it is critical to consider diverse types of services and their interactions). Some types of ecosystem services, particularly cultural and regulating services, are often ignored in SEN representations.
(ii) Select comparable levels of complexity and use coordinated protocols. Our examples show how the research question can guide the level of detail and type of SEN representation. Advances in this field could be made by sharing and following similar data collection and compilation protocols to facilitate comparisons and synthesis.
(iii) Expand data continuity and scope. Expanding spatial coverage and continuous time-series data will foster the development of dynamic SEN models that incorporate ecosystem services dynamics, e.g. for analyses of time-lagged or spillover effects of management on ecosystem service demand and use [99,100].
(iv) Leverage existing data. Large scale initiatives, such as LTSER platforms and national-level projects (e.g., https://www.nsercresnet.ca) could support SEN data needs. Existing databases, such as those on trade (https://comtrade.un.org/; https://trase.earth/) or social–ecological regime shifts (https://regimeshifts.org/) offer great potential to leverage existing data and contribute to this endeavor.

Second-order effects

SEN can also detect time-lag responses of the ecological systems and/or the governance process. Predicting impacts on ecosystem services requires an understanding of how shocks propagate through SENs, such as the identification of direct and indirect effects [3]. These can be represented using multilayer networks and hypergraphs and analyzed using a variety of methods (see following text) including Bayesian belief network approaches [29,30]. In addition, identifying the functional form of relationships between nodes related to ecosystem services [60] and simplifying networks into functional groups [61] has considerable promise to identify second-order effects and potential time lags for the management of ecosystem services [62].

Incorporating feedback and dynamics

Ecosystem service management rarely accounts for multiple interactions and feedback loops. SEN analysis is an interdisciplinary tool that could contribute to advancing this knowledge frontier; for example, by using network models that analyze structural change over time [63,64]. As time-series data become increasingly available, dynamic SEN models can be built on a common network structure to understand the determinants of network dynamics [64,65]. For example, dynamic stochastic block models can be used to understand the evolution of node groups through time [63,66]. Stochastic actor-oriented models can be used to test competing explanations for network change and to calculate the relative effect of different factors influencing changes in the network [67].

Communal interactions

Networks typically only represent pairwise relationships between nodes, which might not be sufficient when ecosystem services stem from a common pool or are obtained through communal actions and cannot be reduced to a series of pairwise interactions. For instance, animals use group behavior to protect individuals against predators. Similarly, 'work parties' for agricultural tasks result in services obtained at group level among the Duupa in sub-Sahelian Cameroon [68]. Recently, such communal interactions have been represented as simplicial complexes or hypergraphs [69–71]. Future research should investigate how to meaningfully approximate communal interactions in SEN and which pieces of information would otherwise be overlooked. For example, while individual ecosystem service benefits can be represented using our ES-links type (Figure 1A), community-level benefits could be better captured using the ES-nodes (Figure 1B) or ES-emergent (Figure 1D) types.

Weighted networks

Links between nodes can be weighted according to their strength (e.g., governance effectiveness, feeding rate), while nodes can be sized reflecting their state (e.g., population size, magnitude of service supplied). Such weighted networks can be used to compare ecosystem service outcomes from alternative management or governance scenarios. Modeling approaches able to integrate different types of weighted links in a multilayer network would contribute to advance these analyses but remain rare [72,73].

Methods to analyze multilayer networks

New methods from network theory have been developed for the analysis of multilayer networks [74,75], including methods to assess global properties (e.g., centralization [15], clustering [76]) and node-level properties (e.g., degree [74], hub score [11]). For example, multiplex network centrality has been used to assess the contribution of multiple ecosystem services to landscape resilience [39]. Further, these methods have been applied in a fully articulated SEN (*sensu* Sayles *et al.* [2]) showing that centralization in the multilayer network negatively correlates with collaboration productivity in watershed restoration [15]. Analyzing ecosystem services with multilayer networks can lead to results countering intuition developed from single-layer networks. For example, clustering in multilayer networks has been related to a reduction in SES robustness to disturbance [77], while the opposite is often hinted at by single-layer network analysis [78]. To further test hypothesized relationships between structure and outcomes in SEN, and to understand the implications of structure for ecosystem service flows, methods for structural statistics of multilayer networks need to be improved through interdisciplinary efforts and the iteration of modeling with case studies and experimentation [2,19,74].

Concluding remarks

SENs bridge social and ecological systems to represent the complex relationships that exist within and between them, enabling combined analyses of both synergistic and antagonistic relationships such as collaboration and conflict. While previous studies have investigated how SENs can be used in environmental management, here we specifically focus on ecosystem services (also applicable to Nature Contributions to People [1]) in SENs. We show four ways in which ecosystem services can be integrated in SENs depending on the research focus. Importantly, neither the focal type of service (e.g., regulating versus provisioning services) nor the spatiotemporal scale of interest are a determinant for a particular conceptualization of ecosystem services in SEN. Instead, choosing a representation fundamentally depends on the research question addressed [18] and is constrained by the availability of data (Table 1). Because ecosystem services can be represented as part of a SEN in multiple ways, alternative SEN approaches allow us to capture different aspects of ecosystem services according to the question at hand (Table 1). For example, to focus on ecosystem service flows or interactions we recommend representing services as links, while to focus on the entities constituting the system a node attribute representation fits better. If the system is very complex, representing ecosystem services as nodes is a good way to simplify the number of nodes, while all elements of the system could be explicitly represented in the network of less complex systems, and ecosystem services can be taken as the overall result of their interactions (emergent property) without being explicitly depicted.

We present a typology of ecosystem service representations in SENs to advance ecosystem service research and tackle complex social–ecological system management challenges. By disentangling which representation best fits different research contexts and delineating the data needed to answer some key ecosystem service questions, along with examples, we provide guidance for complex-systems thinking via network analyses for ecosystem service research (Table 1). These conceptualizations of ecosystem services in SENs enable new joint research avenues for many disciplines, including social sciences, geography, and ecology (see Outstanding questions) and support the exploration of new aspects of ecosystem services and interactions within systems not evident through other approaches [79]. Acknowledging the multiple representations of ecosystem services in SENs can reveal additional applications of ecosystem service research to address complex human–nature interdependencies and help to develop informed management and policy options in a changing world.

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Outstanding questions

What network characteristics (i.e., structures) and dynamics are most relevant to managing and enhancing ecosystem services supply and resilience at different scales?

How does the scale of management determine the influence of ecological variation on social outcomes, social variation on ecological outcomes, and joint variation on ecosystem services?

How can variation in network structures be linked to outcomes for ecosystem services (e.g., total amount of pest control or fished biomass) with a causal interpretation?

Which interaction types are most relevant for studies of ecosystem services and in which contexts? How will conclusions from SEN analyses vary based on the focal interactions?

How can we derive and standardize data and metrics to apply a SEN approach to ecosystem service research and at what scales and resolutions?

What is the potential of coordinated monitoring of SENs to inform ecosystem service management? How can data from Long-Term Social-Ecological Research (LTSER) platforms be used for comparative SEN analyses?

When will a SEN approach be most effective in adding value to existing knowledge of the system?

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Declaration of interests

No interests are declared.

Supplemental Information

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