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### ► To cite this version:

María Felipe-Lucia, Angela Guerrero, Steven Alexander, Jaime Ashander, Jacopo Baggio, et al..  
Conceptualizing ecosystem services using social–ecological networks. *Trends in Ecology & Evolution*,  
2022, 37 (3), pp.211-222. 10.1016/j.tree.2021.11.012 . hal-03836772

**HAL Id: hal-03836772**

**<https://hal.science/hal-03836772>**

Submitted on 2 Nov 2022

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63 **Abstract**

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

73 **Keywords:** multilayer networks, multiplex network, complex systems, social-ecological  
74 interactions, coupled human and natural systems, nature contributions to people

75

76

77 **Ecosystem services as social-ecological networks**

78

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

87

88 Despite this growing interest, we still lack guidance for conceptualizing particular ecosystem  
89 services in SEN analyses and identifying contexts in which ecosystem service research could benefit  
90 the most from a SEN approach [9,10]. SENs are an extraordinarily flexible tool for studying  
91 ecosystem services, yet this flexibility also raises questions about how to apply them. Ecosystem  
92 services have been explicitly represented as elements of networks: as an **attribute** of social or  
93 ecological **nodes** [4], as **nodes** in a network together with ecological and/or social nodes [3,5,11–  
94 13], and as **links** between social and ecological nodes [9,14]. Alternatively, ecosystem services have  
95 been conceptualized as an implicit outcome or **emergent property** of the interactions in a  
96 network, rather than explicitly depicted in a SEN [15–18]. As a result, it remains unclear how  
97 different representations may support specific research questions or contexts, and when they may  
98 lead to divergent conclusions. Furthermore, data to build SENs are often rare, siloed in particular  
99 disciplines (e.g., social or ecological studies), and can be difficult and costly to gather [19]. As a  
100 consequence, clear objectives and methodological understanding are needed to reconcile these  
101 diverse conceptualizations and identify the best SEN representation for different research  
102 questions and contexts and to guide future data collection efforts.

103

104 Here, we synthesize and align research on SEN approaches for ecosystem service research. To do  
105 so, we bring together perspectives from an interdisciplinary group of researchers working with

106 social, ecological, social-ecological networks, and ecosystem services. Specifically, we provide a  
107 typology for representing ecosystem services using SENs. Our perspective aims to support future  
108 studies addressing the remaining challenges to fully realize the potential of SENs in ecosystem  
109 service research. Furthermore, our typology provides guidance for this growing body of work,  
110 including consideration of the diverse ways in which ecosystem services can be represented in a  
111 SEN and the benefits of each. Together, this typology can help improve research designs by aligning  
112 specific SEN conceptualizations and research questions.

113

## 114 **Representing ecosystem services in social-ecological networks**

115 Building on examples from the literature (see Table 1), we identified four main approaches for  
116 representing and analyzing ecosystem services as part of SENs: ecosystem services as links, nodes,  
117 node attributes, or as emergent properties of the network (Figure 1; see Supplementary Figure 1  
118 for a terrestrial example). We propose that the choice of representation ought to be guided by the  
119 research question and context – rather than suggesting a single “best” representation. Thus, we  
120 provide examples of key questions each approach can answer and identify associated applications  
121 and data requirements (Table 1).

122

123 In all representations, we describe a basic conceptualization of the study system as a network  
124 composed of two node categories: social (e.g., diver, farmer) and ecological (e.g., fish, coral). Nodes  
125 within each category can be linked to create a layer of social or ecological interactions. Links  
126 between social nodes can represent information or resource exchange, while links between  
127 ecological nodes can represent trophic interactions or competition. In turn, a SEN can constitute a  
128 **multilayer** network with three interaction types: those between social nodes, between ecological  
129 nodes, and between social and ecological nodes, where the latter can represent e.g., management of  
130 an ecological node [14,20]. Other concepts such as drivers of change or stressors (e.g.,  
131 deforestation, overfishing) can also be represented as nodes [3,12,21].

132

### 133 *Ecosystem services as links* (ES-links; Figure 1A)

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

143

144 The ES-links approach focuses on identifying how the different nodes are connected to deliver or  
145 manage ecosystem services, which requires detailed information on both the ecological and social  
146 layers or subnetworks. As a result, this representation is best suited for analyzing how loss or  
147 change in one node can affect supply or management of ecosystem services in other parts of the  
148 system (Table 1). Therefore, the ES-links approach can, for example, contribute to forecasting

149 impacts of stressors such as climate change, and how these impacts may propagate through a SEN  
150 [13,23]. This approach can also be applied to understand interdependencies in the system due to  
151 ecosystem services flowing from sources to their beneficiaries over long distances (i.e.,  
152 telecoupling) [24,25].

153

154 *Ecosystem services as nodes* (ES-nodes; Figure 1B)

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

175 The focus of the ES-nodes approach is on the existence or persistence of an ecosystem service  
176 rather than on the rate or amount of delivery that flows to people. Thus, it can be applied when  
177 there is no primary data on the magnitude or per-species contribution to ecosystem services, but an  
178 indicator of ecosystem service supply. This is particularly useful given that per-species data are  
179 often lacking and difficult to obtain for most ecosystems and services [13]. The ES-nodes approach  
180 can help assess how ecosystem services and network structure respond to drivers of change, such  
181 as species losses [13], climate change, or invasive species [3,12], and changes in governance  
182 structures [14,31] (see examples in Table 1). Representing ES as nodes instead of links can also  
183 facilitate an understanding of the relationships between multiple ecosystem services, and between  
184 services and other social or ecological nodes [19]. Trade-offs between the management of multiple  
185 ecosystem services and their potential users are then easier to detect [32,33]. An ES-nodes  
186 approach can describe multiple species providing a single service to different beneficiaries (e.g.,  
187 multiple species pollinating crops) [34], or a service depending on multiple ecosystem functions or  
188 species (e.g., provisioning services associated with biodiversity and ecosystem functions at low  
189 land-use intensity levels) [3,11]. Another application of the ES-nodes approach is to assess how a  
190 service is affected by multiple stressors or threats [13]. For example, Rocha et al. [21] used a  
191 tripartite network to represent how stressors (e.g., deforestation and overfishing) lead to regime

192 shifts in ecological systems that ultimately affect different ecosystem services. Keyes et al. [13]  
193 simulated direct and indirect consequences of species losses (e.g., from climate change) for multiple  
194 ecosystem services in coastal systems. Finally, the ES-nodes approach can contribute to studies on  
195 equity in the distribution of ecosystem services, including issues of procedural and distributive  
196 justice. For example, this can be analyzed using a multilayer network to identify which actors are  
197 more dependent on a predefined set of ecosystem services [35,36], and those with the greatest  
198 ability to manage or control services at different spatial scales [37], which is fundamental to  
199 multiscale power dynamics.

200

201 *Ecosystem services as attributes of social or ecological nodes* (ES-attributes; Figure 1C)

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

213

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

227

228 *Ecosystem services as an emergent property of the network* (ES-emergent; Figure 1D)

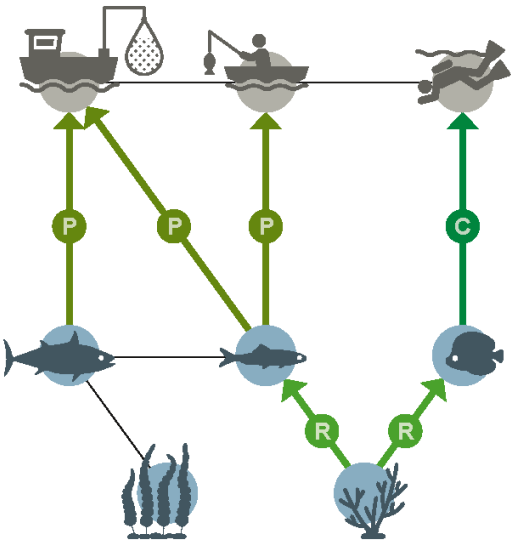
229 In the ES-emergent approach, ecosystem services are not explicitly depicted in the network because  
230 they result from overall interactions in the network as an emergent property of the system [41,42].  
231 An example is farmers' cooperatives organized around water temples to maximize rice production  
232 in Bali [42] (see Supplementary Figure 1). In this example, each cooperative (node) is connected to  
233 other cooperatives by irrigation canals (link) through their paddy fields (node), in which they grow  
234 different rice varieties (node attribute). Biological pest control emerges as an ecosystem service

235 from the interactions between farmers that coordinate water management and rice varieties. In this  
236 case, both the provisioning service (rice yield) and the regulating services (water supply and  
237 biological pest control) are quantifiable but not represented in the network; instead, authors  
238 consider these services as emergent properties of the network. Similarly, in Figure 1, the cultural  
239 service of recreation results from the interplay of all actors that maintain adequate fish and coral  
240 populations, water quality, and a safe swimming environment [43]. Other cases where ecosystem  
241 services can be conceived of as emergent properties of habitat networks include those with  
242 dependence on particular species (e.g., a sufficiently connected habitat underlies seed dispersal by  
243 ring-tailed lemurs (*Lemur catta*) [48]).

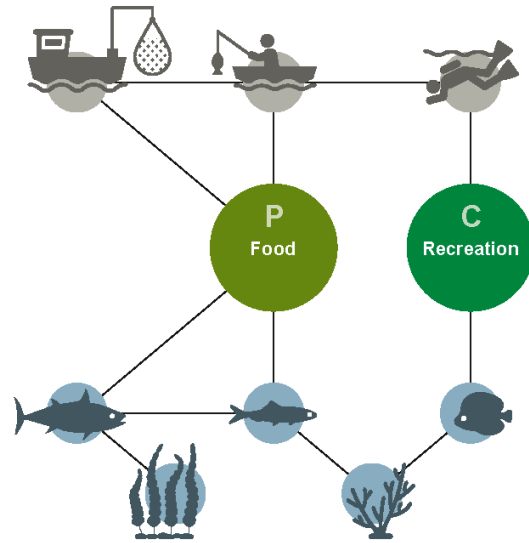
244  
245 The main focus of the ES-emergent approach is to represent relevant management units to the  
246 ecosystem service of interest (e.g., species, habitats, society, industry) and their connections, rather  
247 than identify or quantify links between specific actors and services (Table 1). For example, power  
248 dynamics between actors related to ecosystem services are often visualized as links, without  
249 explicit representation of ecosystem services [15,41,44]. The ES-emergent approach also applies to  
250 relational values that people have with nature and others [45,46], and which are tightly connected  
251 to experiences of cultural ecosystem services [47]. As another example, co-produced ecosystem  
252 services result from the combination of both natural processes and different types of anthropogenic  
253 contributions [48,49]. In this case, human actions can directly influence the individual ecological or  
254 social nodes, indirectly affecting the emergent ecosystem service. Coordinated management of  
255 different ecological nodes can lead to sustained supply of multiple ecosystem services at the  
256 landscape scale through persistence of wildlife populations that provide services [20,25].  
257



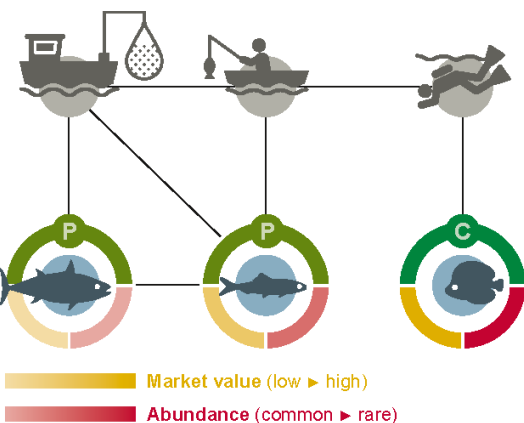
**A ES as link**



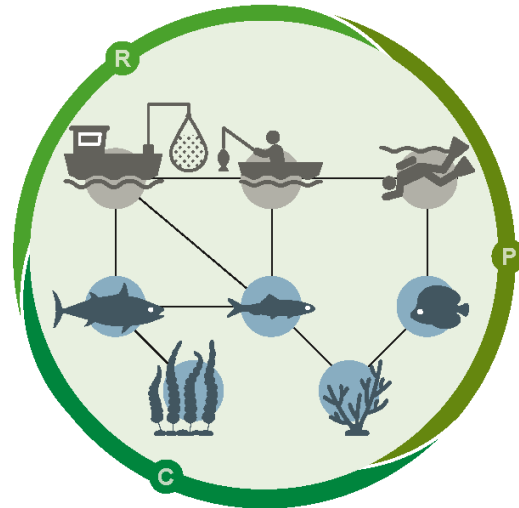
**B ES as node**



**C ES as node attribute**



**D ES as emergent property**



**Ecosystem Services (ES)**  
**R** Regulating   **P** Provisioning   **C** Cultural

**Social actors**   **Ecological actors**   **Interactions**  
 ● e.g. beneficiaries   ● e.g. species   — ecological or social

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**Figure 1. Typology of approaches for conceptualizing ecosystem services in social-ecological networks of social actors (grey), ecological entities (blue), and ecosystem services (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 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,

268 dependence, facilitation), antagonistic (e.g., competence, predation), formal (e.g., contractual,  
269 kinship) or informal (e.g., friendship) relationships. See also Online Supplemental Information  
270 Figure S1.

271 **Table 1. Key research questions for ecosystem services (ES) and their corresponding conceptualization in social-ecological**  
 272 **networks.** We provide examples of key questions each approach in our typology can answer and identify applications and data  
 273 requirements of each.  
 274

<b>Type of approach</b>	<b>Key research questions appropriate for this representation</b>	<b>Applications in ES research</b>	<b>Data requirements</b>
ES as <b>links</b> representing flows (Figure 1A)	<ul style="list-style-type: none"> <li>● What is the role of ecological interactions in ES supply?</li> <li>● How do ES flow through the social system?</li> <li>● How do changes in one node affect the flow of ecosystem services?</li> <li>● How does managing social or ecological nodes affect the flow of ES?</li> </ul>	<ul style="list-style-type: none"> <li>● Identify interdependencies between systems affected by ES flows, including telecoupling [24,50–52].</li> <li>● Forecast impacts of stressors such as global change [3,53].</li> <li>● Predict potential threat propagation (e.g., drought, fires, disease, invasions) [16].</li> </ul>	<ul style="list-style-type: none"> <li>● Detailed information on either ecological or social networks.</li> <li>● Dependent on the level of detail: trade-off between exhaustive (amount) versus precise (quality) information.</li> </ul>
ES as <b>nodes</b> representing natural capital stocks (Figure 1B)	<ul style="list-style-type: none"> <li>● How do drivers (e.g. invasive species or species losses) impact ES?</li> <li>● How does directly or indirectly managing ES impact the rest of the system, including other ES?</li> <li>● How does the structure of the governance network (i.e., the involvement of different types of actors) drive effective ES management?</li> <li>● Who are the beneficiaries of ES?</li> </ul>	<ul style="list-style-type: none"> <li>● Relationships within multiple ES or between ES and other social or ecological nodes [19].</li> <li>● Studies on supply, demand, and governance of ES [31].</li> <li>● Trade-offs between multiple ES [32,33].</li> <li>● Equity and justice in access to ES or distribution of ES [35–37].</li> <li>● Use of Bayesian Belief Networks [28–30,54].</li> <li>● Incorporating ES in social-ecological</li> </ul>	<ul style="list-style-type: none"> <li>● Information on social and/or ecological networks (ES can represent the ecological or social underlying network, summarizing complex ecological or social interactions).</li> </ul>

		<p>fit analyses [55].</p> <ul style="list-style-type: none"> <li>• When primary data for ES are not available [3,12,31].</li> <li>• When multiple species provide a single ES to different beneficiaries [13].</li> <li>• When ES depends on multiple ecosystem functions or species [11].</li> </ul>	
<p>ES as <b>node attribute</b> (Figure 1C)</p>	<ul style="list-style-type: none"> <li>• What are the values attached to a particular species or landscape area?</li> <li>• How do management actions taken by an actor affecting some species or landscape area impact ES supply?</li> </ul>	<ul style="list-style-type: none"> <li>• Existence of multiple layers of information or multiple values associated to a node (e.g., economic or cultural value, management actions).</li> <li>• Defined ES providers or ES attached to a species (i.e., the species that delivers ES is a node), such as a harvestable fish population or individual [4].</li> <li>• ES estimated from higher spatial scales (e.g., a forest patch is a node) [40].</li> <li>• Integration of decision-making with existing management units [20].</li> </ul>	<ul style="list-style-type: none"> <li>• Abundant information for each of the nodes in the network.</li> <li>• Additional covariates of interest (social and ecological data that is relevant to the research question can be captured as a node attribute).</li> </ul>
<p>ES as <b>emergent property</b> of the network (Figure 1D)</p>	<ul style="list-style-type: none"> <li>• What social and ecological elements are related to a particular ES?</li> <li>• What are the ES outcomes of coordinated landscape management?</li> </ul>	<ul style="list-style-type: none"> <li>• Uncover the ES outcomes of network structure.</li> <li>• Conceptualize relational values as SEN [45].</li> <li>• Analyze ES co-production as SEN [56,57].</li> </ul>	<ul style="list-style-type: none"> <li>• Identification of the many actors and connections.</li> <li>• No requirement on quantification of ES or links from ES to particular actors.</li> <li>• Generally not appropriate for large</li> </ul>

		<ul style="list-style-type: none"><li>• Identify power dynamics between actors related to ES [15,44].</li><li>• When ES cannot be managed directly or management of ecological nodes is decentralized.</li></ul>	networks.
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## 275 **Remaining challenges and opportunities in the use of SENs for ecosystem service research**

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

280

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

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

297 *Incorporating feedback and dynamics.* Ecosystem service management rarely accounts for multiple  
298 interactions and feedback loops. SEN analysis is an interdisciplinary tool that could contribute to  
299 advancing this knowledge frontier, for example, by using network models that analyze structural  
300 change over time [63,64]. As time-series data become increasingly available, dynamic SEN models  
301 can be built on a common network structure to understand the determinants of network dynamics  
302 [64,65]. For example, dynamic stochastic block models can be used to understand evolution of  
303 node groups through time [63,66]. Stochastic actor-oriented models can be used to test competing  
304 explanations for network change and to calculate the relative effect of different factors influencing  
305 changes in the network [67].

306 *Communal interactions.* Networks typically only represent pairwise relationships between nodes,  
307 which might not be sufficient when ecosystem services stem from a common pool or are obtained  
308 through communal actions and cannot be reduced to a series of pairwise interactions. For instance,  
309 animals use group behavior to protect individuals against predators. Similarly, “work parties” for  
310 agricultural tasks result in services obtained at group level among the Duupa in sub-Saharan  
311 Cameroon [68]. Recently, such communal interactions have been represented as simplicial  
312 complexes or hypergraphs [69–71]. Future research should investigate how to meaningfully  
313 approximate communal interactions in SEN, and which pieces of information would otherwise be  
314 overlooked. For example, while individual ecosystem service benefits can be represented using our

315 ES-links type (Figure 1A), community level benefits could be better captured using the ES-nodes  
316 (Figure 1B) or ES-emergent types (Figure 1D).

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

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

### 337 **Concluding Remarks**

338 SENs bridge social and ecological systems to represent the complex relationships that exist within  
339 and between them, enabling combined analyses of both synergistic and antagonistic relationships  
340 such as collaboration and conflict. While previous studies have investigated how SENs can be used  
341 in environmental management, here we specifically focus on ecosystem services (also applicable to  
342 Nature Contributions to People [1]) in SENs. We show four ways in which ecosystem services can  
343 be integrated in SENs depending on the research focus. Importantly, neither the focal type of  
344 service (e.g., regulating versus provisioning services) nor the spatiotemporal scale of interest are a  
345 determinant for a particular conceptualization of ecosystem services in SEN. Instead, choosing a  
346 representation fundamentally depends on the research question addressed [18] and is constrained  
347 by the availability of data (Table 1). Because ecosystem services can be represented as part of a SEN  
348 in multiple ways, alternative SEN approaches allow us to capture different aspects of ecosystem  
349 services according to the question at hand (Table 1). For example, to focus on ecosystem service  
350 flows or interactions we recommend representing services as links, while to focus on the entities  
351 composing the system a node attribute representation fits better. If the system is very complex,  
352 representing ecosystem services as nodes is a good way to simplify the number of nodes, while all  
353 elements of the system could be explicitly represented in the network of less complex systems, and

354 ecosystem services can be taken as the overall result of their interactions (emergent property)  
355 without being explicitly depicted.

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

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

371 Ecosystem services research can benefit from integration with SEN applications. For example, in  
372 tandem with economic valuation methods [80,81] SENs could be used to investigate changes in  
373 people's preferences and values when they are aware of social-ecological connections [2].  
374 Incorporating SEN into spatial ecosystem service mapping can provide information about: the  
375 direct or indirect role of stakeholders in influencing ecosystem services through conservation and  
376 management practices [82], information flows [83], cross-scale interactions among social actors  
377 [37] and ecosystem services [39], and long-distance connections through telecoupling [24,50–52].  
378 When ecosystem services transcend local scales (e.g., climate regulation), SENs can assess whether  
379 collaborations across multiple spatial scales [84] match the scale of the ecological processes  
380 underpinning ecosystem services [19,20,85].

381

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

390

391 For instance, a question that remains open in ecosystem service science [92] is: *How do multiple*  
392 *ecosystem services interact, and what are the consequences of those interactions for their*  
393 *management?* An existing approach has been to map areas supplying multiple ecosystem services



394 [93,94]. In turn, an ecological network approach could predict how management affects species  
395 providing ecosystem services by using simulations [13], while a social network analysis approach  
396 would identify policy actors associated with a particular ecosystem services to assess management  
397 coordination [95]. Yet, with a SEN, a researcher could identify *both* the underlying ecological  
398 processes that connect ecosystem services mechanistically – using the ES-links approach – and how  
399 they connect to beneficiaries – using the ES-nodes approach.

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## 402 **Box 2. A Call for Coordinated Research and Data Collection for Generalizing Insights.**

403 A standardized approach to measuring ecosystem services, together with key metrics for  
404 comparing studies using SEN, could contribute to answer key ecosystem service research questions  
405 to address sustainability challenges (Table 1). Developing and applying protocols for social-  
406 ecological system analyses [96] will allow us to infer SEN patterns from case studies. This effort  
407 would enable us to generalize increasing knowledge available from local, place-based research [97]  
408 and can contribute to the development of SEN theory [2,53,84] and predictions about changes in  
409 ecosystem service supply. Additionally, uniform data collection could enable the parametrization of  
410 system models by extending parameters from similar case studies rather than collecting new data  
411 [98]. Collecting empirical data to link quantities of ecosystem services to particular individuals or  
412 species requires substantial time and resources that are often limited, especially in data-scarce  
413 regions. When extensive data is not available, researchers can use simpler SEN representations  
414 with ecosystem services as a surrogate of complex social-ecological interactions (i.e., ES-nodes  
415 approach, see Table 1).

416

417 In an effort to overcome outstanding challenges and to enable generalization and comparability  
418 across cases we conclude with the following four suggestions for future studies:

419 1) *Choose appropriate and consistent indicators.* Ecosystem service indicators should match the  
420 relevant social and ecological nodes connected to the services, i.e., it is critical to consider diverse  
421 types of services and their interactions. Some types of ecosystem services, particularly cultural and  
422 regulating services, are often ignored in SEN representations.

423 2) *Select comparable levels of complexity and use coordinated protocols.* Our examples show how the  
424 research question can guide the level of detail and type of SEN representation. Advances in this field  
425 could be made by sharing and following similar data collection and compilation protocols to  
426 facilitate comparisons and synthesis.

427 3) *Expand data continuity and scope.* Analysis of time-lagged or spillover effects of management on  
428 ecosystem service demand and use requires continuous data over time and space, yet these data  
429 are rarely available [99]. Lack of spatial coverage and time-series data hinders the development of  
430 dynamic SEN models that incorporate ecosystem services dynamics [99,100].

431 4) *Leverage existing data.* Large scale initiatives, such as LTSER (Long-Term Social-Ecological  
432 Research) platforms and national-level projects (e.g., [www.nsercresnet.ca](http://www.nsercresnet.ca)) could support SEN data  
433 needs. Existing databases, such as those on trade (<https://comtrade.un.org/>; <https://trase.earth/>)  
434 or social-ecological regime shifts (<https://regimeshifts.org/>) offer great potential to leverage  
435 existing data and contribute to this endeavor.

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<b>Glossary</b>	
<b>Ecological network</b>	Network depicting ecological entities, such as species, functional groups, or patches, and the processes that connect them (e.g., species interactions, connectivity through dispersal).
<b>Ecosystem service</b>	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 employed.
<b>Ecosystem service flow</b>	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).
<b>Emergent property</b>	Overall outcome, or property of the network, which results from the interactions between network components.
<b>Link</b>	Connection between two nodes (e.g., dispersal between patches or resource exchange between actors). <i>Synonyms: arc, edge, interaction, tie.</i>
<b>Multilayer networks and associated concepts</b>	A family of networks that model multiple layers of information. <b>Multilevel networks</b> include multiple types of nodes (called multipartite), as in Figure 1. <b>Multilayer (or multi-relational)</b> networks allow for multiple kinds of links between nodes. Certain multilevel approaches (called <b>multiplex networks</b> ) 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 these networks. Related concepts include <b>multi-networks</b> and <b>networks of networks</b> .
<b>Network approach</b>	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.
<b>Node</b>	An identifiable component of a network (e.g., user, beneficiary, species). <i>Synonyms: actor, alter, ego, entity, vertex.</i>
<b>Node attribute</b>	A characteristic of a node (e.g., market price of a fish, see Figure 1).
<b>Social network</b>	Network depicting interactions (e.g., knowledge exchange, trust, collaboration, resource sharing) between social actors (e.g., individuals, communities, organizations).
<b>Social-Ecological Network (SEN)</b>	A network that considers connections <i>within</i> and <i>between</i> the social and ecological layers (i.e., a fully articulated [2] or Type III [9] networks), in contrast to ecological networks or social networks which only account for interactions <i>within</i> one of these layers. For simplicity, we also consider as SENs those networks that only

	include the interactions <i>between</i> social and ecological nodes (i.e., partially articulated [2] or Type II [9] networks).
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## 441 Acknowledgments

442 We are thankful to Editor A.E. A. Stephens and two anonymous reviewers for insightful comments  
443 on an earlier version of the article. We acknowledge funding from the National Socio-  
444 Environmental Synthesis Center (SESYNC) to L.E. Dee, A.M. Guerrero, R. Friedman for funding a  
445 workshop that developed this research, under funding received from the National Science  
446 Foundation (NSF) DBI-1639145. We thank other participants of the workshop for fruitful  
447 discussions, as well as G. Rada and S. Bernhardt from iDiv Media and Communications for creating  
448 the figures. J. Ashander and J. Gephart also acknowledge SESYNC for support. A. Bonn and M. R.  
449 Felipe-Lucia gratefully acknowledge the support of iDiv funded by the Deutsche  
450 Forschungsgemeinschaft (DFG-FZT 118, 202548816) and members of the ESS lab for insightful  
451 comments. M.L. Barnes acknowledges support from the Australian Research Council (grant no.  
452 DE190101583 and CE140100020). Ö. Bodin acknowledge support from the research council  
453 FORMAS through grant 2020-01551. L.E. Dee acknowledges support from NSF OCE-2049360. M.-J.  
454 Fortin acknowledges support from NSERC Discovery Grant and Canada Research Chair in Spatial  
455 Ecology. K.J. Helmstedt acknowledges support from the Australian Research Council Fellowship  
456 DE200101791. J.S. Sayles was supported by an appointment to the U.S. Environmental Protection  
457 Agency (EPA) Research Participation Program administered by the Oak Ridge Institute for Science  
458 and Education (ORISE) through an interagency agreement between the U.S. Department of Energy  
459 (DOE) and the EPA. ORISE is managed by ORAU under DOE contract number DE-SC0014664. S.A.  
460 Wood was supported by a Data Science Environments project award from the Gordon and Betty  
461 Moore Foundation (Award 2013-10-29) and the Alfred P. Sloan Foundation (Award 3835) to the  
462 University of Washington eScience Institute. All opinions expressed in this paper are the author's  
463 and do not necessarily reflect the policies and views of US EPA, DOE, or ORAU/ORISE.

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