

1 **OPERATIONALIZING NETWORK THEORY FOR ECOSYSTEM SERVICE**

2 **ASSESSMENTS**

3

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33

34 ***Abstract***

35 Managing ecosystems to provide ecosystem services in the face of global change is a pressing
36 challenge for policy and science. Predicting how alternative management actions and changing
37 future conditions will alter services is complicated by interactions among components in
38 ecological and socioeconomic systems. Failure to understand those interactions can lead to
39 detrimental outcomes from management decisions. Network theory that integrates ecological
40 and socioeconomic systems may provide a path to meeting this challenge. While network theory
41 offers promising approaches to examine ecosystem services, few studies have identified how to

42 operationalize networks for managing and assessing diverse ecosystem services. We propose a
43 framework for how to use networks to assess how drivers and management actions will directly
44 and indirectly alter ecosystem services.

45 **PART I: REPRESENTING ECOSYSTEM SERVICES WITH NETWORKS**

46 Ecosystems contribute to human well-being by providing **ecosystem services** (*see*
47 *Glossary*) [1,2]. However, increasing pressures from human population growth, global change,
48 and land-use change are degrading natural resources and threatening ecosystem services [2],
49 driving a need for new tools to guide sustainable management of ecosystem services. Currently,
50 many assessments of ecosystem services primarily map services spatially – relating an average
51 value of an ecosystem service to a land cover type without considering the driving dynamics
52 within either the ecological or social systems [3–6]. This approach is an important step in
53 incorporating ecosystem services into policy decisions (e.g., for land-use management) but does
54 not provide a mechanistic understanding of how social-ecological systems provide multiple
55 benefits [7,8]. The lack of an underlying mechanistic framework limits the success of many
56 management actions, our ability to forecast how future conditions and policies will alter
57 ecosystem services [6,9], and our opportunity to efficiently identify which parts of a system are
58 most **vulnerable** to change. Making management decisions without such a mechanistic
59 understanding can lead to unexpected or perverse outcomes (Box 1).

60 An important step towards avoiding detrimental outcomes – and anticipating how
61 ecosystem services will respond to future changes – is considering interactions within and among
62 components of social-ecological systems [10]. Interactions influence both how ecosystems
63 produce ecosystem services and how people **value** these benefits [11]. First, the amount or
64 **supply** of a service is influenced by species that alter ecosystem functions or directly provide

65 ecosystem services and their interactions with other species (e.g., for food or habitat) [12,13].
66 Second, how people value ecosystem services depends on their social interactions that influence
67 preferences, and therefore, demand for ecosystem goods and services [14]. Third, most
68 ecosystem services are co-produced, meaning they arise from interactions between ecosystems
69 and anthropogenic assets (e.g., knowledge, technology, or built infrastructure), and are modified
70 by institutions [2,15]. Fourth, social attitudes that arise from social interactions can influence
71 resource managers' priorities and choices, and therefore which management actions are taken
72 [14,16].

73 Not considering interactions in management decisions has led to unintended
74 consequences of management actions and unmet policy objectives (Box 1). Because interactions
75 cause impacts on one part of a system to propagate to others, **drivers** and management actions
76 can alter ecosystem services in ways that are difficult to predict [10,13,17–19]. For instance, to
77 protect habitat for spotted owl in the Pacific northwest U.S.A., policies restricted logging in old
78 growth forests. These restrictions displaced and increased logging on other private lands [20].
79 Further, impacts can propagate through both bio-physical and socioeconomic pathways and
80 feedbacks [19]. For example, impacts from extreme storms spread through social-ecological
81 systems altering fisheries (e.g., [21]) and the carbon cycle [22]. To predict and avoid detrimental
82 outcomes, understanding links between **ecological networks** (i.e., species interaction) and
83 **socioeconomic networks** (i.e., stakeholders, their incentives, and management actions) is critical
84 (Box 1). However, to date, ecological and socioeconomic networks have largely been considered
85 in isolation from each other [23, *but see* 24] and from the drivers and management actions
86 affecting ecosystem services.

87 To aid forward-looking assessments and promote better management decisions, we
88 propose to model ecosystem services as a single **meta-network** (Fig. 1) to examine how
89 ecosystem services will respond to drivers and management actions. Network science, and the
90 diversity of theories developed therein, offers valuable approaches to construct and analyze
91 integrated networks for ecosystem services. In networks, **nodes** depict actors (e.g., species in
92 ecological networks and individuals or organizations in socioeconomic networks), while **links**
93 depict interactions (e.g., feeding relationships in ecological networks, information exchange or
94 friendship in social networks) [14,25–29]. Therefore, networks can represent a diversity of
95 interactions. Network science approaches from diverse fields include both one-mode (where all
96 nodes are of similar type) and multi-mode (where nodes are different types) networks. For
97 example, methods for identifying subgroups in networks [30,31] have a rich history in social
98 science [32,33], computer science [34] and increasingly in ecology [35]. Similarly, multi-mode
99 networks have been used to analyze clustering to gain insights in such diverse topics as
100 marketing, patterns in scientific publications [36], regime shifts in the sea [37] and to define
101 keystone actors in fisheries [38]. Therefore, a substantial library of tools is available to build and
102 analyze meta-networks representing ecosystem services (Fig. 1), prompting calls to use networks
103 in ecosystem service research [23,39,40].

104 While prior studies highlight the many potential benefits of using network approaches for
105 ecosystem services (e.g., linking natural and social sciences, bridging spatial scales, embracing
106 interactions – [23,40]), adoption of network approaches in ecosystem service science and
107 management has been limited. Here, we provide a starting point for operationalizing network
108 theory into management for ecosystem services, bridging the gap between conceptual
109 understanding and application. While previous studies propose to focus primarily on the

110 underlying ecological networks, with a secondary focus on services (e.g., [10,23,40]), we suggest
111 starting to build a network around the management objective – the ecosystem services of interest.
112 We outline ways to represent different classes of ecosystem services with networks, using an
113 integrated socioeconomic and ecological approach. In the following sections, we propose steps
114 for using meta-networks to represent ecosystem services (Fig. 1) for a key area of application: to
115 assess how drivers and management actions will impact ecosystem services directly and
116 indirectly (Box 2).

117 To construct a meta-network representing one or more ecosystem services, we suggest
118 starting with the management objective: the ecosystem service(s) of interest. The management
119 objective is often dictated by policy but can also be determined by consulting stakeholders to
120 determine their priorities [41]. Centered around the objective(s), we propose to use meta-
121 networks to identify how services are 1) provided by ecosystems, 2) used by different
122 beneficiaries, 3) impacted by drivers directly and indirectly by propagating through a system via
123 interactions, and 4) respond to management actions (Box 2). To represent ecosystem service
124 provision, the meta-network should integrate multiple types of nodes (e.g., species, people,
125 ecosystem services) and multiple types of interactions (e.g., trophic, friendship, information
126 exchange) that occur within and between network types (Fig. 1). Beyond the ecosystem service
127 of interest, deciding which types of nodes and interactions to include is a challenge, as for any
128 complex systems analysis, and should be determined by the study and management objective *a*
129 *priori* [14,42] (see [42] for a guide to selecting nodes and interactions). To assess direct and
130 indirect effects of management decisions, interactions within a network type, such as species
131 interactions in an ecological network and information exchange between organizations in
132 socioeconomic networks [14,23,29], can provide insights (e.g., [13,39]; Fig. 1 A). However, for

133 assessing ecosystem services, we emphasize that interactions between network types are
134 especially critical, including between species and ecosystem services, ecosystem services and
135 beneficiaries, as well as stakeholders and management actions (Fig. 1 B-D).

136 First, we propose to represent ecosystem services as either nodes that are **natural capital**
137 **stocks** [43] or links depicting the rates at which people use ecosystem services (**ecosystem**
138 **service flows**) [44]. Nodes representing natural capital stocks can be a population that directly
139 provide services (e.g., a harvestable fish for **provisioning services** like food production), or the
140 service in itself for **regulating** (e.g., climate regulation) or **cultural services** (e.g., a sense of
141 place). Representing a service as a node is particularly useful when multiple species provide a
142 single services (e.g., multiple species pollinating crops) and when a service depends on multiple
143 **ecosystem functions** [9]. For instance, vegetation in a salt marsh attenuates floodwater, reduces
144 wave energy, and stabilizes shorelines (ecosystem functions) that together protect coastlines and
145 reduce storm damages to coastal property (ecosystem services) [45]. We suggest representing an
146 ecosystem service flow, such as annual yields from harvesting a population, as a link between a
147 natural capital stock (e.g., a harvestable population like salmon) and a beneficiary node (e.g.,
148 fishers). Further, to represent co-production of ecosystem services [46], ecosystem service nodes
149 can be connected to both the ecological (e.g., crop species) and socioeconomic nodes (e.g.,
150 households providing labor) involved.

151 The second step of our proposed approach is using ecological networks to identify which
152 ecological components directly and indirectly contribute to ecosystem service provision. The
153 first step is to establish which nodes (species, functional groups, or their ecosystem functions)
154 are directly linked to the ecosystem service of interest (see Box 2). To identify indirectly critical
155 nodes, we propose to determine how nodes directly providing an ecosystem service rely on other

156 species using an ecological network (Fig. 1). Supporting species are indirectly critical for various
157 services, such as crop pollination where native vegetation supports pollinator populations [13]
158 and fisheries where harvested species eat other species [12]. Ecological networks help identify
159 critical dependencies that indirectly affect ecosystem services. Networks also elucidate how
160 species nodes indirectly contribute to ecosystem services by driving ecosystem functions (e.g.,
161 water filtration) that produce services (e.g., improved water quality or recreation).

162 Third, by building a network centered around the ecosystem services of interest,
163 networks can specify who benefits from an ecosystem service, which entities manage the
164 services, and how these individuals or organizations interact. Identifying the stakeholder groups
165 that benefit from each ecosystem service (Fig. 1 B) and the groups influencing management
166 actions is an important step in considering how management actions will influence service value
167 (Fig 1). Interactions within a socioeconomic network influence knowledge exchange between
168 different stakeholders involved in decisions, governance of natural resources [16,33], power
169 relations among resource users [47], and which policy objectives are pursued [48] (Box 1). In
170 turn, socioeconomic networks (and the institutions they create) determine how people value, use,
171 and demand different services, including via social norms and perceptions of amenity value (e.g.,
172 public parks) [49,50]. For example, in Madagascar, taboos about harvesting certain species
173 benefit efforts to conserve threatened species like the lemur, *Propithecus edwardsi*, and social
174 norms encourage sustainable harvesting practices for other species [51]. Further, social norms
175 arising from socioeconomic networks are especially critical to cultural services (e.g., sense of
176 place, aesthetic appreciation of landscapes, enjoyment of iconic species), as the benefits from
177 ecosystem services are only realized when people appreciate and demand them [46].

178 The next step is to determine how ecosystem services will respond to drivers, while
179 considering interactions. Patterns in pairwise interactions between nodes build a **meta-network**
180 **structure** that illuminates how an ecosystem service is provided and will respond to drivers.
181 Therefore, we suggest to first identify how drivers impact particular nodes (e.g., [37]), then to
182 evaluate how these impacts could spread through the network structure to affect services (Box 2;
183 Box 3; Fig. 1 K-P). Drivers impacting one or more nodes include human impacts to ecosystems
184 (e.g., eutrophication, harvesting), global change (e.g., warming will impact all nodes to different
185 extents), regulations, or market changes (e.g., changes in prices for clean water). By determining
186 how an impact to one node propagates to others and influences a system's dynamics, network
187 structure informs whether and how services will be vulnerable to different drivers (Box 3) [52].
188 For instance, the Lough Hyne marine reserve's meta-network structure influences how severe
189 storms might impact coastal protection and local tourism (Fig. 1 C). We emphasize that impacts
190 to services will depend on which drivers are present, which nodes are impacted, and the node's
191 vulnerability [53] (Box 3). Further, vulnerability will differ across services and locations,
192 because meta-network structures differ based on which species or stakeholders are present and
193 whether they interact. For instance, an ecological network is vulnerable when a single species is
194 impacted *and* provides a crucial link with little redundancy [54] (Box 3, Fig. 1 A).

195 The last step we propose is to identify management actions that mitigate the threats posed
196 by drivers impacting the system and evaluate the consequences of these actions (Box 2).
197 Management actions can be represented as nodes, e.g., building coastal defenses (Fig. 1 C),
198 allowing researchers to explicitly map how different actions interact with other types of nodes
199 (e.g., species, organizations). Actions can target species nodes in ecological networks (e.g.,
200 restoration or protection), nodes in socioeconomic networks (e.g., regulation, taxes), or drivers

201 (i.e., by mitigating threats) [44]. In turn, nodes in socioeconomic networks (individuals or
202 organizations) influence which management actions are chosen and which are available (e.g.,
203 due to financial, institutional, and legal constraints). Within a network of actions, different
204 actions interact positively, negatively, and often in non-linear ways [55]. Actions interact
205 negatively with each other when alternative management options compete for the same resources
206 (i.e., a constrained budget), such as floodwall construction versus floodplain regeneration. In the
207 next section, we highlight several approaches that can be used or extended to evaluate the
208 consequences of implementing management actions for ecosystem services, while considering
209 interactions.

210 **Part II. ASSESSING AND MANAGING ECOSYSTEM SERVICES USING NETWORKS**

211 Using networks to represent ecosystem services provides a way to consider direct and
212 indirect consequences of management interventions and drivers. In order to operationalize
213 network approaches for ecosystem services, we propose that the first step in any analyses is to
214 determine the study and management objective. This decision will determine the nodes and
215 interaction types that are appropriate to consider; therefore, this step will involve establishing the
216 analysis' scope and complexity that is needed for the context. A recurring challenge in studying
217 complex networks – and for meta-networks describing ecosystem services -- is defining the
218 nodes and links and deciding on level of complexity (i.e., which nodes and edges to include) in
219 the network to be analyzed [14,42]. After deciding on the scope and on how to represent the
220 ecosystem services as part of a meta-network, several options for analyses exist. Network
221 representations and their analyses range from qualitative to highly quantitative (Fig. 1 B),
222 spanning a gradient from low to high data needs. The management objective and decision
223 context should dictate the approach, and analyses can be done iteratively. Starting with

224 conceptual representations provides a framework for identifying knowledge gaps (Box 1) and for
225 integrating new knowledge in a systematic way, enabling development of more complex network
226 representations. For many management decisions, the most complex approach may not be
227 necessary to make a decision that improves the state of ecosystem services, or constructing a
228 highly quantitative network is not possible due difficulties quantifying interactions between
229 nodes.

230 The least complex approach to describing networks is drawing influence diagrams (e.g.,
231 Fig. 1 B) which provide a visual representation of mental models. Influence diagrams have been
232 applied in fisheries (e.g., [56]), water resource management (e.g., [57]) and species conservation
233 (e.g., [58]). They are most valuable for tracing cause and effect, including potential indirect
234 effects, and for visualizing relationships between bio-physical and socioeconomic systems
235 [23,33]. By considering interactions, influence diagrams can improve management outcomes
236 relative to the status quo.

237 Binary maps of interactions between nodes are the next simplest representation (Fig. 1 B
238 & C), in which interactions are defined by a link's presence or absence (assigned "1" if two
239 nodes interact and "0" if not) (Fig. 1 B & C). Binary networks have been applied to manage
240 ecosystems (e.g., [59]) and have a long history of use in food-web ecology (reviewed in [60])
241 and social network analysis (e.g., [61]), despite criticism [62]. Although they have not been used
242 widely in ecosystem service assessments, these network approaches can readily accommodate
243 different types of nodes and interactions. For instance, they can be used to visualize co-
244 occurrence and clustering between different types of nodes (e.g., [37]), like which households
245 benefit from which services (Fig. 1 B). They also generate metrics that characterize networks
246 properties (e.g., interaction evenness) [63,64], which previous studies propose to use to guide

247 management and conservation efforts [39,65,66]. However, understanding the empirical
248 relationship between these network attributes and variation in ecosystem services is a research
249 frontier [39,60].

250 Approaches of intermediate complexity require more information than a binary
251 representation but do not require quantifying system dynamics. Intermediate complexity
252 approaches include qualitative models, which require only knowledge about the sign of an
253 interaction between two nodes (positive or negative) [67]. Qualitative models have been used to
254 understand responses to management interventions, such as invasive species eradication on
255 Macquarie Island [68]. Another intermediate approach, weighted networks, incorporate the
256 strength of interactions between nodes [69] (e.g., how much information is exchanged between
257 people). Weighted networks have helped predict responses to drivers (Fig. 1 B), including how
258 biodiversity responds to dam management in the Colorado River [70]. Interactions between
259 nodes can be weighted using empirical [71] and qualitative information (e.g., Fuzzy Cognitive
260 Mapping; [56,72]). Further, probabilistic approaches, like Bayesian Belief Networks (BBN),
261 express interactions between nodes as probabilities and contingencies [73–76] and are being used
262 increasingly for ecosystem services (reviewed in [75]).

263 The most complex network analyses use dynamical system models (Fig. 1 B), where a set
264 of ordinary differential equations describes interactions between nodes and requires extensive
265 parameterization. For example, the steady-state model, ECOPATH [77], and its dynamic
266 counterpart ECOSIM [78] have been applied widely in fisheries management [78] and to a lesser
267 extent to restoration (e.g., [79]) and ecotoxicology (e.g., [80]). Both require numerous
268 parameters, including each species' biomass and diet. Another example is the Allometric Trophic
269 Network model [81], which defines species interactions with differential equations [82,83] and

270 has examined the ecosystem-level consequences of biodiversity loss [84] and warming
271 temperatures [85]. In an example that modeled social and ecological dynamics among fishers,
272 fish, and fishing, Lade et al [24] examined how social dynamics influenced the collapse of Baltic
273 cod, and how social versus ecological factors impacted the system's stability. These approaches
274 generate specific predictions but require expensive and time-consuming data collection to
275 characterize interactions.

276 We suggest that several of these approaches can be readily used or extended to assess
277 how ecosystem services will respond to drivers and management actions. In particular, BBN
278 approaches hold promise, because they leverage qualitative and quantitative data from diverse
279 sources for parameterization (e.g., expert opinion, surveys, and quantitative models) [75]. For
280 instance, BBNs have been used to model optimized pastures with mixtures of service-providing
281 trees, using data on both financial returns to farmers and tree functional traits [74]. BBNs also
282 capture uncertainty and allow for findings to be expressed in terms of risk [74]. In contrast, for
283 many ecosystem services and systems, more work is needed to use dynamic network models, in
284 part due to uncertainty over specifying and parameterizing dynamics in coupled social-ecological
285 systems.

286 When choosing a network method to guide ecosystem service management, it is critical
287 to assess trade-offs between information required to model a system, uncertainty associated with
288 that information, and the decision to be made [86]. For instance, if a decision needs to be made
289 quickly, then drawing an influence diagram could provide enough insight to improve decisions
290 and avoid detrimental outcomes. Resolving integrated networks can be costly and time
291 consuming, considering the information needed to characterize dynamics or spatial
292 heterogeneity. However, how much information is needed to inform management decisions and

293 achieve policy objectives? An important research frontier is determining the extent that systems
294 models can be generalized and simplified while still providing useful predictions [86], which is
295 also true for managing ecosystem services (Outstanding Questions Box).

296 We suggest using value of information (VOI) analysis, which requires an explicitly
297 defined objective, to guide the collection of new information about networks. Used widely in the
298 fields of health, economics, and environmental management, VOI approaches determine whether
299 reducing uncertainties will improve outcomes from decisions and identifying which information
300 is the most strategic to collect [87], given an objective. In some cases, new information will not
301 alter which management action best achieves an objective – or reducing uncertainty about
302 interactions might switch which management strategy is optimal (Box 1) [88]. To date, VOI
303 approaches have not been applied widely to network studies but offer a promising and systematic
304 way to decide how much complexity to include or new information to gather about a network.

305

306 **CONCLUSIONS**

307 Here we propose a starting point to operationalize networks for ecosystem service
308 management – to build a network around the management objective -- in order to consider how
309 ecosystem services will respond to drivers and alternative management options. This proposed
310 approach differs from previous work by emphasizing the importance of first identifying the
311 service of interest and then describing the network that influences that service, rather than
312 describing a whole network then superimposing services. Complementing existing strategies to
313 model services, network approaches can integrate existing qualitative and quantitative
314 information from disparate sources or disciplines (e.g., species interactions and household-level
315 socioeconomic data). Further, representing ecosystem services as part of an integrated network

316 enables approaches from network science to be transferred to study ecosystem services, which
317 are useful for evaluating alternate management actions while considering feedbacks. Therefore,
318 operationalizing network theory to study ecosystem services is one promising step towards more
319 predictive approaches to assess and manage ecosystem services – and to avoid undesirable
320 outcomes from management decisions.

321

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534

535 **FIGURES**

536

537 **Figure 1. Integrated networks for ecosystem services**

538 **Figure 1. A.** Using a network approach to assess and manage ecosystem services requires
539 integrating multiple types of networks (actions, ecological, socioeconomic, drivers, and
540 ecosystem services). Quantitative analysis of particular network types (e.g., an ecological food
541 web, social network, *etc.*) can provide important insights when analyzing ecosystem services
542 (e.g., governance or ecosystem-level consequences of fishing or climate change).

543

544 **Figure 1 B.** Nodes representing ecosystem services can be connected to an ecological network
545 (e.g., by establishing which species provide each ecosystem service) and with a socioeconomic
546 network (e.g., establishing which people or households benefit from a service, and which entities
547 manage the service). Analyzing two-mode networks (i.e., species-ecosystem services and
548 ecosystem-services here as an example) provides insight into patterns of service provision, such

549 as co-occurrence. These approaches could also be used to assess patterns in other two-mode
550 networks (e.g., connections between drivers and species; management actions and services; and
551 management actions and species).

552

553 **Figure 1. C.** An integrated network for ecosystem services should include interactions within
554 and across network types and, therefore, multiple types of nodes (e.g., species, people, ecosystem
555 services, actions, and drivers) and multiple types of interactions (e.g., trophic, information
556 exchange, flow of benefits). These **meta-networks** help identify how services are supplied by
557 populations of species, delivered to beneficiaries, and directly and indirectly impacted by drivers
558 and management actions. **C)** illustrates a range of approaches from network science to visualize
559 and model meta-networks of ecosystem services, with increasing complexity and data
560 requirements from left to right. These approaches range from influence diagrams (that do not
561 allow for feedbacks) to dynamical systems models. The management objective and context for
562 the assessment (e.g., time until a management decision must be made, available data) will
563 determine which approach to use.

564

565 **Figure 1. D.** Networks can help evaluate direct and indirect impacts of management actions and
566 drivers on ecosystem services. Here, we present a case study of the Lough Hyne marine reserve,
567 illustrating a decision about a management action: constructing coastal defenses to minimize
568 erosion and storm damages from extreme storms. For visual simplification, this example shows
569 only interactions between different types of networks, including actors that are part of a social
570 network (e.g., the tourism sector and the administrative bodies) and two species, *Laminaria*
571 *saccharina* (kelp) and *Chelidonichthys cuculus* (Red Gurnard), which are part of an ecological

572 network. This example identifies how coastal protection, recreation (supporting tourism), and
573 carbon sequestration (supporting climate regulation) are supplied by species; for instance, kelp
574 provides coastal protection, and Red gurnard supports ecotourism and recreational activities.
575 This meta-network also shows how these ecosystem services directly link to several beneficiaries
576 and management agencies, including the local community, tourism industry, and the Public
577 Administration, National Park & Wildlife Services. A key part of our proposed approach is
578 assessing impacts of drivers and management actions. Therefore, we show multiple drivers
579 (climate change, pollution, erosion, and invasive species) that impact this system. To reduce
580 these impacts, several management actions are available. We consider the potential “path of
581 impacts” (the interactions highlighted in black) that can result from a management decision to
582 construct coastal defences. For instance, constructing coastal defences directly benefits local
583 communities by protecting shorelines. Indirectly, coastal defences benefit tourism industries by
584 reducing erosion and improving kelp populations that support recreation.

585

586

587 **BOXES**

588 **Box 1. Case study: Conceptualizing environmental management in networks**

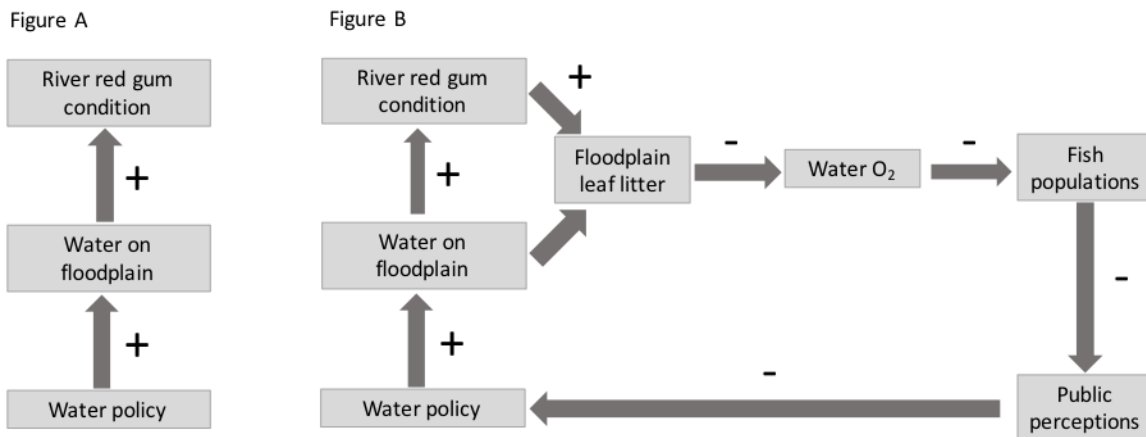
589 River red gum (*Eucalyptus camaldulensis*) is the dominant riparian tree
590 species along major rivers and floodplains in south eastern Australia,
591 occupying a critical role as a keystone species for riparian communities
592 [89] and as an icon of natural floodplain ecosystems [90]. The species
593 relies on periodic flooding and declined significantly due to a major
594 drought in the early 21st Century [90]. Over the same period, water policy
595 reforms caused water to return to the environment to support and restore ecosystem functions
596 and services, particularly river red gum condition that supports habitat provisioning and erosion
597 control [91].



598 An initial conceptual understanding of the relationship between river
599 red gum condition and water flow did not consider indirect effects and
600 feedbacks (**Figure I. A**). This led to water being added to floodplains in
601 mid-summer, inundating large amounts of organic matter that had
602 accumulated during the preceding drought. High water temperatures led to
603 the partial decomposition of the organic matter and to the overlying water
604 becoming deoxygenated. The return of water flows into the river's main channel generated a
605 2000 km long 'blackwater' event, which caused the death of many native fish [92]. The negative
606 social perceptions of this event provided political pressure to alter water policies on
607 environmental water flows. Conceptualizing this system as network provides a framework to
608 predict and manage the risk of perverse outcomes by incorporating second-order effects of
609 management interventions and potential feedbacks (**Figure I. B**).



611 **Box 1 Figure I.**



612

613 **Box 2. Developing integrated networks to assess management alternatives.**

614 Networks can help assess how socioeconomic-ecological systems provide ecosystem services
 615 (ES), determine their vulnerability to drivers, and systematically evaluate management options.

616 We propose several steps for this process:

617 **Step 1.** Identify the objective and management context for the assessment. The assessment’s goal
 618 will guide how many steps are needed (e.g., a goal to elucidate the causal chain of how ES are
 619 provided (step 2) versus to evaluate alternate management strategies (step 7)) and which node
 620 and interaction types to include in the analysis (see [42] for a guide).

621 **Step 2.** The ES(s) of interest can be represented as nodes, and a network for the system will be
 622 based around these nodes.

623 **Step 3:** An ES node can be linked to the node(s) (species, functional groups, or ecosystem
 624 processes) that directly provide it, for example by using binary or Bayesian categorical
 625 assignments (e.g., [35,76]). The nodes providing ES can then be linked to the species they

626 interact with (e.g., feeding, mutualism), thereby linking the ES to an ecological network. To
627 attribute ES to species nodes, a combination of field data and/or models with species- and
628 system-specific parameters should be used, if available, in addition to literature reviews and
629 expert knowledge from different social actors, including local knowledge.

630 **Step 4:** Determine the socio-economic network by identifying beneficiaries who receive the ESs
631 the entities that manage the ES, and then which actors (people, organizations) interact with these
632 nodes.

633 **Step 5:** Identify drivers that may impact the system and assign **vulnerability** to the nodes
634 impacted by the drivers (e.g., [53]). For example, for species nodes, information about extinction
635 risk or population status can be used to parameterize Bayesian Belief Networks [93].
636 Vulnerability can also be assessed by relating external threats to species responsiveness to those
637 threats based on their functional traits or characteristics (e.g., body size or trophic level) [94].

638 **Step 6:** Qualitatively or quantitatively assess vulnerability of service provision, in response to
639 drivers or management interventions. Section II and Fig. 1 C outline several approaches to assess
640 how drivers and management actions spread through networks via dependencies among nodes.

641 **Step 7:** Identify plausible management actions and evaluate alternative management strategies
642 by assessing *a priori* how management decisions will directly and indirectly impact ES provision
643 (e.g., controlling pests, restoring habitat).

644

645 **Box 3. Visualizing potential vulnerability of ecosystem services to drivers.**

646 Depending on network structure, the effects of a driver on a particular node (shown by red
647 arrows) can propagate or attenuate within a network resulting in different levels of vulnerability
648 for ecosystem services (represented as triangles). Using a stylized food web characterizing fish
649 production from a lake, we illustrate how visualizing impacts to nodes in a network provides
650 qualitative predictions about how vulnerable the services provided by populations are to drivers
651 (e.g., habitat destruction, eutrophication, overfishing). In Box 3 Fig. I below, black symbols
652 indicate the nodes (e.g., taxa and services) that are present, while white symbols indicate nodes
653 that are lost following an impact, and grey symbols indicate nodes decreasing in abundance or
654 amount following an impact.

655 The expected risk that drivers pose to ecosystem services depends on the vulnerability,
656 number, and position of impacted nodes in a network. An ecosystem service is particularly
657 vulnerable to a driver when a single node (e.g., one species) provides a service with no
658 redundancy, as in **(A)** versus in **(B)** and **(C)**. A service provided by a food web is also vulnerable
659 to degradation or loss when all node(s) providing the service depend on a single food resource
660 that is impacted greatly **(D)**, or where all food resources **(G)** or habitat **(J)** are impacted by the
661 driver **(J)**. In contrast, redundancy will lower vulnerability of service provision, if more
662 redundancy in pathways (e.g., energy flow in food webs) lowers the likelihood that drivers will
663 impact every pathway, as in **(H)** and **(I)**.

664 Features of network structure also influence vulnerability, including how connected **(K-**
665 **M)** and how modular (i.e., divided into less connected sub-networks) the network is (see **N-P**).
666 As shown in **K**, less connected networks might be more vulnerable to drivers than more
667 connected networks (as in **L** and **M**) [17], for instance due to less redundancy in food resources.
668 In a more connected network, if two services are strongly dependent on the same part of the

669 network, both may be vulnerable to the same perturbation (**N**). As networks become more
670 ‘modular,’ where the sub-networks providing services have fewer connections to other sub-
671 networks, network theory predicts that services will be less sensitive to drivers that propagate
672 through a network (as in **P** versus **N** and **O**) [95]. Notably, modularity does not reduce the threat
673 of localized effects that propagate within modules (i.e., **A** is nested within **P**).

674 **Box 3 Figure 1**

TYPE OF IMPACT ON BIODIVERSITY	IMPACT ON ECOSYSTEM SERVICE		
	HIGH	MODERATE	LOW
Impacts to a single node	A 	B 	C
	D 	E 	F
Impacts to multiple nodes	G 	H 	I
	J 		
Impacts mediated via network structure (from low to high connectance)	K 	L 	M
	Low ←		→ High
Impacts mediated via sub-network structure (from low to high modularity)	N 	O 	P
	Low ←		→ High
Key:	Driver Link lost Link unaffected	Node lost Node reduced Node unaffected	Service lost Service reduced Service unaffected

676 **GLOSSARY**

677 **Ecosystem services:** The contributions of ecosystems to human well-being, derived from
678 populations, processes, and functions in ecosystems.

679 **Value:** Ecosystems benefit human well-being, and people attach different values to benefits from
680 ecosystems, based on preferences or underlying ideals. Value does not need to be expressed in
681 monetary terms.

682 **Vulnerability:** The capacity for a system to cope with threats caused by **drivers**.

683 **Ecosystem functions:** The processes (e.g., nutrient cycling and biomass production) that benefit
684 humans indirectly when they underpin services (e.g., clean water and food) but do not directly
685 benefit humans.

686 **Driver(s):** A factor or set of factors impacting an ecosystem service, including human impacts
687 (e.g., land-use change), management decisions, or global change (e.g., climate change).

688 **Beneficiaries:** The people or groups of people receiving benefits from ecosystems.

689 **Ecosystem service supply:** The amount of a service that can be produced by an ecosystem (also
690 known as capacity), which is not equivalent to the amount of service used or demanded by
691 people.

692 **Natural capital stocks:** The ecosystem characteristics and states (e.g., population size, sediment
693 retention, stored soil carbon) that form the basis for ecosystem service supply and flow [43].

694 **Ecosystem service flow:** The use of an ecosystem service by people [96].

695 **Network:** A system of connected entities (nodes) and their pattern of interactions

696 **Ecological networks:** Network representing species interactions, in which links reflect who eats
697 who or other types of interactions (e.g., mutualism).

698 **Socioeconomic networks:** A network in which the nodes represent people, households, or
699 organizations, whereas links represent social (e.g., friendship) and/or economic (e.g., market
700 exchange) interactions that influence the behavior of individual nodes.

701 **Meta-network:** A network that include multiple types of nodes (e.g., species, people, ecosystem
702 services, organizations) and multiple types of interactions (e.g., trophic, friendship, labor
703 exchange).

704 **Node:** The fundamental components of a network (also known as vertices).

705 **Link:** The line connecting two nodes, representing an interaction (also known as edges).

706 **Provisioning services:** Material outputs produced by ecosystems including food, fiber, and
707 pharmaceuticals, with direct market value.

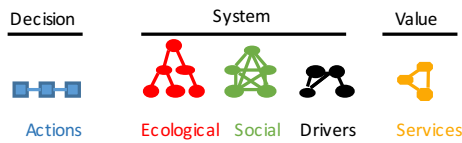
708 **Regulating services:** Benefits to humans that rely on ecosystem processes or the moderation of
709 extreme environmental events. Examples include climate regulation, natural hazard regulation,
710 water quality, and crop pollination.

711 **Cultural services:** Non-material benefits human receive from interacting with ecosystems,
712 including aesthetic enjoyment, spiritual enrichment, intellectual development, and recreation.

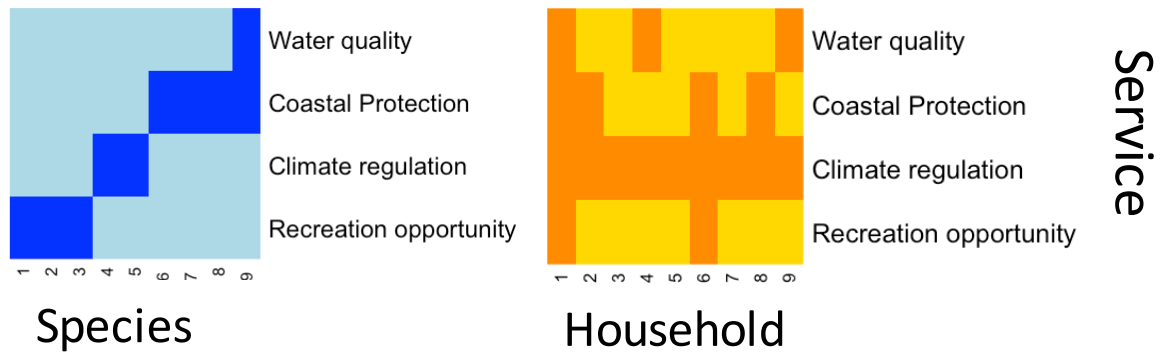
713 **Network structure:** Pattern of interactions between nodes.

Figure 1

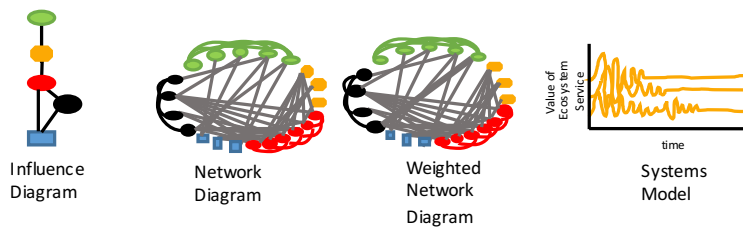
A



B

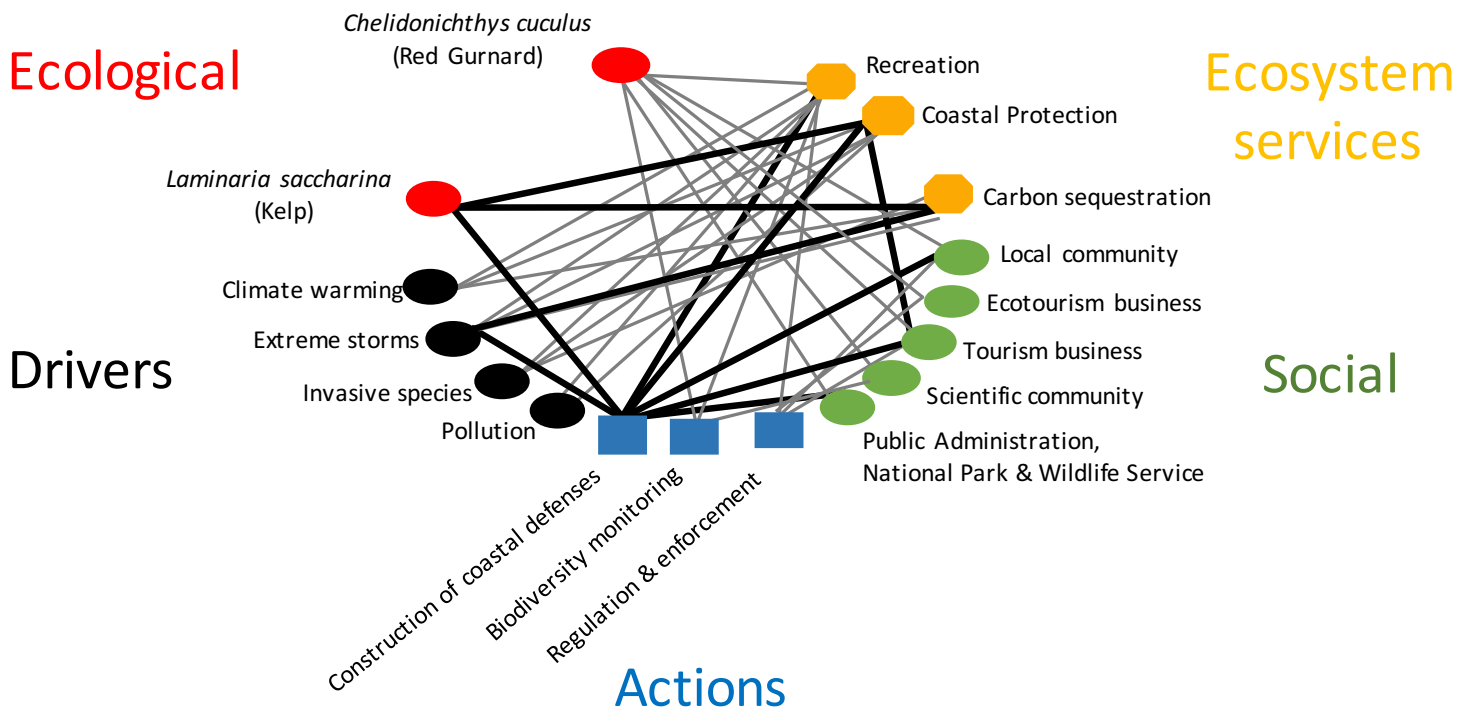


C



D

Lough Hyne Marine Reserve



Trends Box (890 characters)

Managing ecosystems to provide ecosystem services (ES) in the face of global change is a pressing challenge for both policy and science

Most ecosystem service studies do not consider interactions, limiting insight how future conditions will change ES. Failure to consider interactions among components of socioeconomic, ecological, management systems can lead to detrimental outcomes from management decisions.

Recent papers call to use network theory in ES research, yet adoption remains challenged by a gap between broad concepts and application

We suggest a starting point to operationalize networks for ES: build an integrated socioeconomic and ecological network around the management objective, the ES of interest. We outline steps to represent ES using networks and to analyze how drivers and management actions will impact ES directly and indirectly.

Operationalizing network theory for ES is a promising step towards more predictive approaches to assess and manage ES – and for avoiding unintended outcomes from management decisions.

OUTSTANDING QUESTIONS BOX

- What is the relative importance of socioeconomic versus ecological interactions in determining ecosystem service supply and value?
- How can network approaches be most effectively scaled up to larger systems?
- Which drivers and network structures create the most or least vulnerability for ecosystem services?
- Does integrating ecological, economic, and social network approaches improve assessments of ecosystem services vulnerability, or can simpler approaches or a focus on a single network type give approximately the same answer?
- How much money and time should be invested in learning network structure and dynamics for ecosystem service management? What is the value of this information, in terms of enhanced benefits from ecosystem services to people?