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Laura E. Dee, Stefano Allesina, Aletta Bonn, Anna Eklöf ...+7 more authors

Institutions: University of Minnesota, University of Chicago, Helmholtz Centre for Environmental Research - UFZ, Linköping University ...+5 more institutions

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OPERATIONALIZING NETWORK THEORY FOR ECOSYSTEM SERVICE ASSESSMENTS

Laura E. Dee, Institute on the Environment and Department of Forest Resources, University of Minnesota- Twin Cities, Minneapolis, MN 55108, USA

Stefano Allesina, Department of Ecology & Evolution and Computation Institute, University of Chicago, Chicago IL 60637, USA

Aletta Bonn, Department of Ecosystem Services, Helmholtz Centre for Environmental Research – UFZ, Leipzig, GERMANY; Friedrich-Schiller-University Jena, Jena, GERMANY; German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Leipzig, GERMANY

Anna Eklöf, Department of Physics, Chemistry and Biology, Linköping University, Linköping, SWEDEN

Steven D. Gaines, Bren School of Environmental Science & Management, University of California, Santa Barbara, Santa Barbara, CA 93117, USA

Jes Hines, German Center for Integrative Biodiversity Research (iDiv), Halle-Jena-Leipzig, Leipzig, Germany; Institute for Biology, University of Leipzig, Leipzig Germany

Ute Jacob, German Center for Integrative Biodiversity Research (iDiv), Halle-Jena-Leipzig, Leipzig, Germany; J.F. Blumenbach Institute of Zoology and Anthropology University of Goettingen Berliner Str. 28 37073 Goettingen

Eve McDonald-Madden, Centre for Biodiversity and Conservation Science, School of Geography Planning and Environmental Management, University of Queensland, St Lucia, Australia

Hugh Possingham, ARC Centre of Excellence for Environmental Decisions, School of Biological Sciences, University of Queensland, St Lucia, Australia

Matthias Schröter, Department of Ecosystem Services, Helmholtz Centre for Environmental Research – UFZ, Leipzig, GERMANY; German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Leipzig, Germany

Ross M. Thompson, Institute for Applied Ecology, University of Canberra, ACT, Australia

Corresponding author: Laura E. Dee, ledee@umn.edu

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Abstract

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

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

PART I: REPRESNTING ECOSYSTEM SERVICES WITH NETWORKS

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

An important step towards avoiding detrimental outcomes – and anticipating how ecosystem services will respond to future changes – is considering interactions within and among components of social-ecological systems [10]. Interactions influence both how ecosystems produce ecosystem services and how people **value** these benefits [11]. First, the amount or **supply** of a service is influenced by species that alter ecosystem functions or directly provide ecosystem services and their interactions with other species (e.g., for food or habitat) [12,13]. Second, how people value ecosystem services depends on their social interactions that influence preferences, and therefore, demand for ecosystem goods and services [14]. Third, most ecosystem services are co-produced, meaning they arise from interactions between ecosystems and anthropogenic assets (e.g., knowledge, technology, or built infrastructure), and are modified by institutions [2,15]. Fourth, social attitudes that arise from social interactions can influence resource managers' priorities and choices, and therefore which management actions are taken [14,16].

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

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

While prior studies highlight the many potential benefits of using network approaches for ecosystem services (e.g., linking natural and social sciences, bridging spatial scales, embracing interactions – [23,40]), adoption of network approaches in ecosystem service science and management has been limited. Here, we provide a starting point for operationalizing network theory into management for ecosystem services, bridging the gap between conceptual understanding and application. While previous studies propose to focus primarily on the underlying ecological networks, with a secondary focus on services (e.g., [10,23,40]), we suggest starting to build a network around the management objective – the ecosystem services of interest. We outline ways to represent different classes of ecosystem services with networks, using an integrated socioeconomic and ecological approach. In the following sections, we propose steps for using meta-networks to represent ecosystem services (Fig. 1) for a key area of application: to assess how drivers and management actions will impact ecosystem services directly and indirectly (Box 2).

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

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

The second step of our proposed approach is using ecological networks to identify which ecological components directly and indirectly contribute to ecosystem service provision. The first step is to establish which nodes (species, functional groups, or their ecosystem functions) are directly linked to the ecosystem service of interest (see Box 2). To identify indirectly critical nodes, we propose to determine how nodes directly providing an ecosystem service rely on other species using an ecological network (Fig. 1). Supporting species are indirectly critical for various services, such as crop pollination where native vegetation supports pollinator populations [13] and fisheries where harvested species eat other species [12]. Ecological networks help identify critical dependencies that indirectly affect ecosystem services. Networks also elucidate how species nodes indirectly contribute to ecosystem services by driving ecosystem functions (e.g., water filtration) that produce services (e.g., improved water quality or recreation).

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

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

The last step we propose is to identify management actions that mitigate the threats posed by drivers impacting the system and evaluate the consequences of these actions (Box 2). Management actions can be represented as nodes, e.g., building coastal defenses (Fig. 1 C), allowing researchers to explicitly map how different actions interact with other types of nodes (e.g., species, organizations). Actions can target species nodes in ecological networks (e.g., restoration or protection), nodes in socioeconomic networks (e.g., regulation, taxes), or drivers (i.e., by mitigating threats) [44]. In turn, nodes in socioeconomic networks (individuals or organizations) influence which management actions are chosen and which are available (e.g., due to financial, institutional, and legal constraints). Within a network of actions, different actions interact positively, negatively, and often in non-linear ways [55]. Actions interact negatively with each other when alternative management options compete for the same resources (i.e., a constrained budget), such as floodwall construction versus floodplain regeneration. In the next section, we highlight several approaches that can be used or extended to evaluate the consequences of implementing management actions for ecosystem services, while considering interactions.

Part II. ASSESSING AND MANAGING ECOSYSTEM SERVICES USING NETWORKS

Using networks to represent ecosystem services provides a way to consider direct and indirect consequences of management interventions and drivers. In order to operationalize network approaches for ecosystem services, we propose that the first step in any analyses is to determine the study and management objective. This decision will determine the nodes and interaction types that are appropriate to consider; therefore, this step will involve establishing the analysis' scope and complexity that is needed for the context. A recurring challenge in studying complex networks – and for meta-networks describing ecosystem services -- is defining the nodes and links and deciding on level of complexity (i.e., which nodes and edges to include) in the network to be analyzed [14,42]. After deciding on the scope and on how to represent the ecosystem services as part of a meta-network, several options for analyses exist. Network representations and their analyses range from qualitative to highly quantitative (Fig. 1 B), spanning a gradient from low to high data needs. The management objective and decision context should dictate the approach, and analyses can be done iteratively. Starting with conceptual representations provides a framework for identifying knowledge gaps (Box 1) and for integrating new knowledge in a systematic way, enabling development of more complex network representations. For many management decisions, the most complex approach may not be necessary to make a decision that improves the state of ecosystem services, or constructing a highly quantitative network is not possible due difficulties quantifying interactions between nodes.

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

Binary maps of interactions between nodes are the next simplest representation (Fig. 1 B & C), in which interactions are defined by a link's presence or absence (assigned "1" if two nodes interact and "0" if not) (Fig. 1 B & C). Binary networks have been applied to manage ecosystems (e.g., [59]) and have a long history of use in food-web ecology (reviewed in [60]) and social network analysis (e.g., [61]), despite criticism [62]. Although they have not been used widely in ecosystem service assessments, these network approaches can readily accommodate different types of nodes and interactions. For instance, they can be used to visualize co-occurrence and clustering between different types of nodes (e.g., [37]), like which households benefit from which services (Fig. 1 B). They also generate metrics that characterize networks properties (e.g., interaction evenness) [63,64], which previous studies propose to use to guide management and conservation efforts [39,65,66]. However, understanding the empirical relationship between these network attributes and variation in ecosystem services is a research frontier [39,60].

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

The most complex network analyses use dynamical system models (Fig. 1 B), where a set of ordinary differential equations describes interactions between nodes and requires extensive parameterization. For example, the steady-state model, ECOPATH [77], and its dynamic counterpart ECOSIM [78] have been applied widely in fisheries management [78] and to a lesser extent to restoration (e.g., [79]) and ecotoxicology (e.g., [80]). Both require numerous parameters, including each species' biomass and diet. Another example is the Allometric Trophic Network model [81], which defines species interactions with differential equations [82,83] and has examined the ecosystem-level consequences of biodiversity loss [84] and warming temperatures [85]. In an example that modeled social and ecological dynamics among fishers, fish, and fishing, Lade et al [24] examined how social dynamics influenced the collapse of Baltic cod, and how social versus ecological factors impacted the system's stability. These approaches generate specific predictions but require expensive and time-consuming data collection to characterize interactions.

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

When choosing a network method to guide ecosystem service management, it is critical to assess trade-offs between information required to model a system, uncertainty associated with that information, and the decision to be made [86]. For instance, if a decision needs to be made quickly, then drawing an influence diagram could provide enough insight to improve decisions and avoid detrimental outcomes. Resolving integrated networks can be costly and time consuming, considering the information needed to characterize dynamics or spatial heterogeneity. However, how much information is needed to inform management decisions and achieve policy objectives? An important research frontier is determining the extent that systems models can be generalized and simplified while still providing useful predictions [86], which is also true for managing ecosystem services (Outstanding Questions Box).

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

CONCLUSIONS

Here we propose a starting point to operationalize networks for ecosystem service management – to build a network around the management objective -- in order to consider how ecosystem services will respond to drivers and alternative management options. This proposed approach differs from previous work by emphasizing the importance of first identifying the service of interest and then describing the network that influences that service, rather than describing a whole network then superimposing services. Complementing existing strategies to model services, network approaches can integrate existing qualitative and quantitative information from disparate sources or disciplines (e.g., species interactions and household-level socioeconomic data). Further, representing ecosystem services as part of an integrated network enables approaches from network science to be transferred to study ecosystem services, which are useful for evaluating alternate management actions while considering feedbacks. Therefore, operationalizing network theory to study ecosystem services is one promising step towards more predictive approaches to assess and manage ecosystem services – and to avoid undesirable outcomes from management decisions.

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FIGURES

Figure 1. Integrated networks for ecosystem services

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

Figure 1 B. Nodes representing ecosystem services can be connected to an ecological network (e.g., by establishing which species provide each ecosystem service) and with a socioeconomic network (e.g., establishing which people or households benefit from a service, and which entities manage the service). Analyzing two-mode networks (i.e., species-ecosystem services and ecosystem-services here as an example) provides insight into patterns of service provision, such as co-occurrence. These approaches could also be used to assess patterns in other two-mode networks (e.g., connections between drivers and species; management actions and services; and management actions and species).

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

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

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

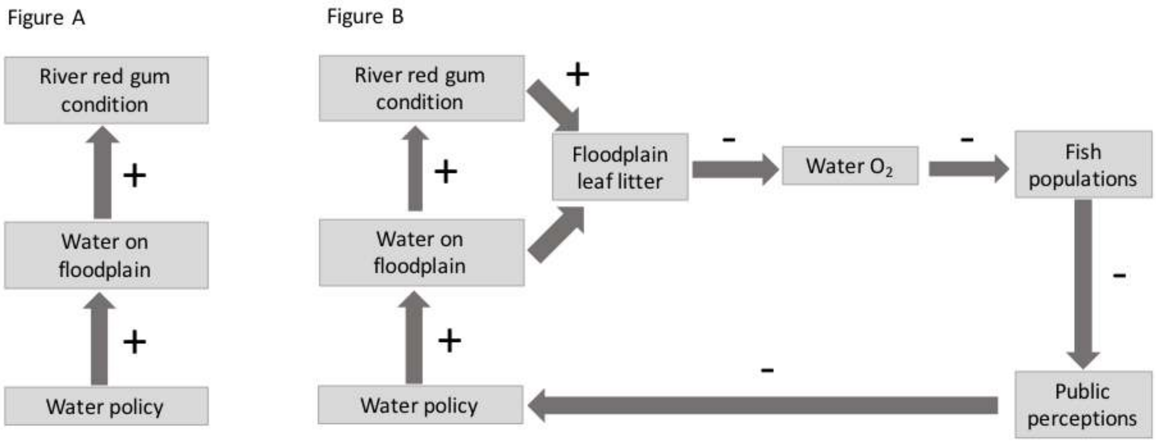
BOXES

Box 1. Case study: Conceptualizing environmental management in networks

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

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

Box 1 Figure I.



Box 2. Developing integrated networks to assess management alternatives.

Networks can help assess how socioeconomic-ecological systems provide ecosystem services (ES), determine their vulnerability to drivers, and systematically evaluate management options. We propose several steps for this process:

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

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

Step 3: An ES node can be linked to the node(s) (species, functional groups, or ecosystem processes) that directly provide it, for example by using binary or Bayesian categorical assignments (e.g., [35,76]). The nodes providing ES can then be linked to the species they interact with (e.g., feeding, mutualism), thereby linking the ES to an ecological network. To attribute ES to species nodes, a combination of field data and/or models with species- and system-specific parameters should be used, if available, in addition to literature reviews and expert knowledge from different social actors, including local knowledge.

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

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

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

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

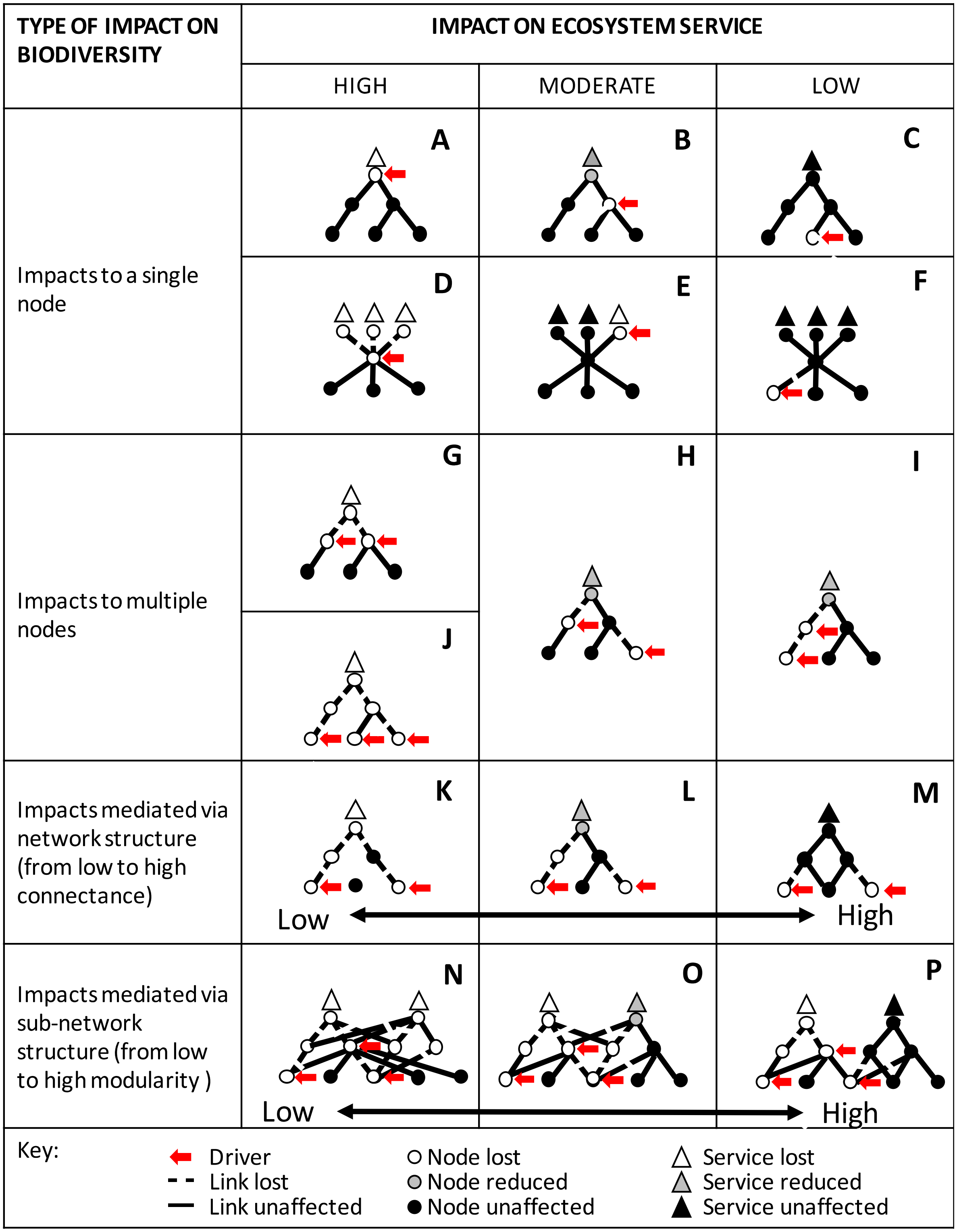
Box 3. Visualizing potential vulnerability of ecosystem services to drivers.

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

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

Features of network structure also influence vulnerability, including how connected (**K-M**) and how modular (i.e., divided into less connected sub-networks) the network is (see **N-P**). As shown in **K**, less connected networks might be more vulnerable to drivers than more connected networks (as in **L** and **M**) [17], for instance due to less redundancy in food resources. In a more connected network, if two services are strongly dependent on the same part of the network, both may be vulnerable to the same perturbation (**N**). As networks become more 'modular,' where the sub-networks providing services have fewer connections to other sub-networks, network theory predicts that services will be less sensitive to drivers that propagate through a network (as in **P** versus **N** and **O**) [95]. Notably, modularity does not reduce the threat of localized effects that propagate within modules (i.e., **A** is nested within **P**).

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

GLOSSARY

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

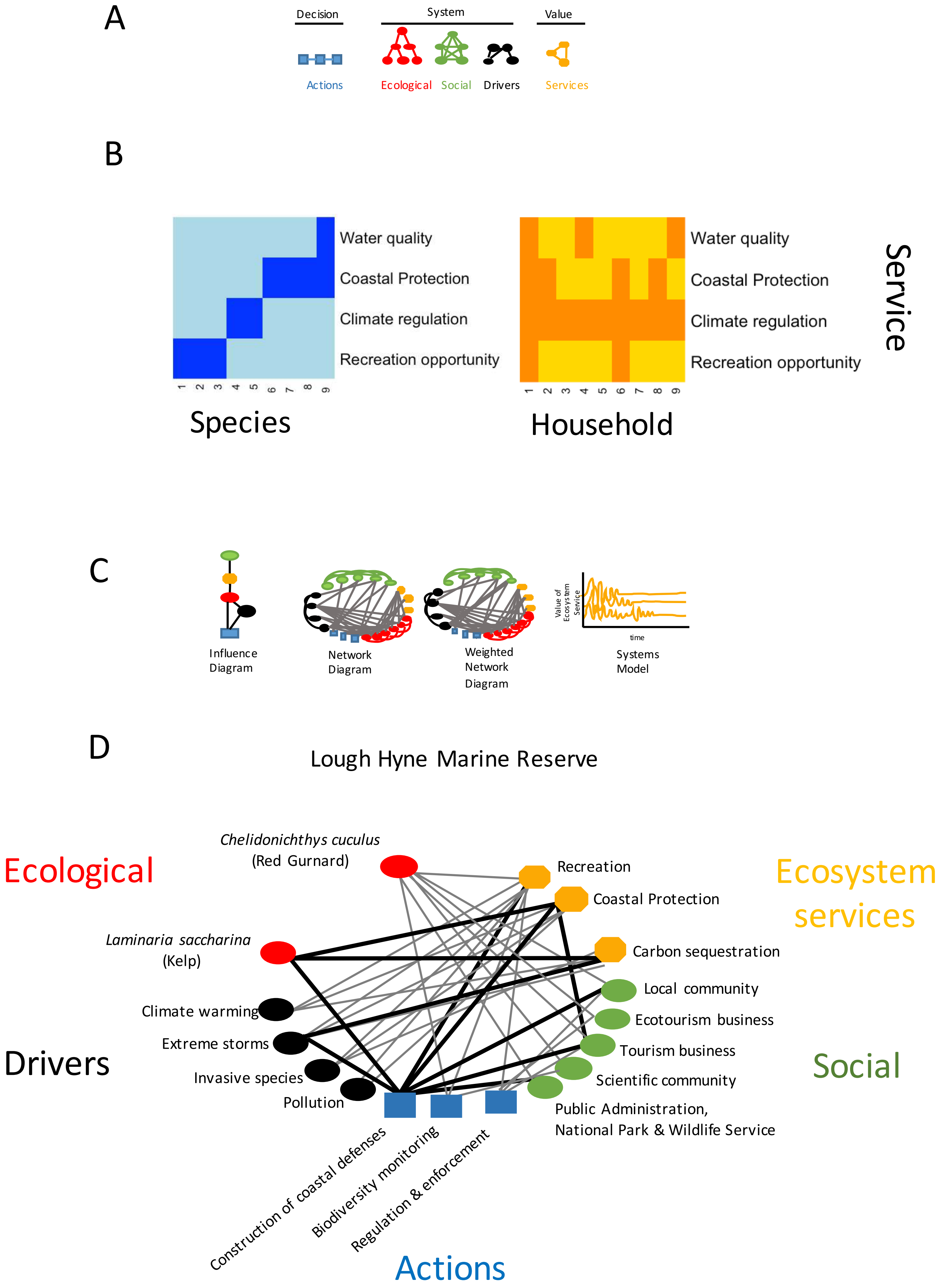
Provisioning services: Material outputs produced by ecosystems including food, fiber, and pharmaceuticals, with direct market value.

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

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

Network structure: Pattern of interactions between nodes.

Figure 1


A
Decision
System
Value
Actions
Ecological
Social
Drivers
Services
B
Water quality
Coastal Protection
Climate regulation
Recreation opportunity
1 2 3 4 5 6 7 8 9
Species
Water quality
Coastal Protection
Climate regulation
Recreation opportunity
1 2 3 4 5 6 7 8 9
Household
Service
C
Influence Diagram
Network Diagram
Weighted Network Diagram
Value of Ecosystem Service
time
Systems Model
D
Lough Hyne Marine Reserve
Ecological
Chelidonichthys cuculus (Red Gurnard)
Laminaria saccharina (Kelp)
Climate warming
Extreme storms
Invasive species
Pollution
Drivers
Recreation
Coastal Protection
Carbon sequestration
Ecosystem services
Local community
Ecotourism business
Tourism business
Scientific community
Public Administration, National Park & Wildlife Service
Social
Construction of coastal defenses
Biodiversity monitoring
Regulation & enforcement
Actions

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?