**Linking network ecology and ecosystem services to benefit people**

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**Abstract**

1. Ecosystems are rapidly degraded by anthropogenic pressures, affecting the provision of ecosystem services. Therefore, it is increasingly important that we can quantify and manage ecosystem services to maintain human well-being.
2. Many ecosystem services are underpinned by ecosystem functions and processes that are driven by interspecific ecological interactions. Humans then benefit from ecosystem services through socio-ecological interactions. Therefore, interaction network approaches can provide a unique understanding of ecosystem service flows.
3. In this paper, we assess the current interface between network ecology and ecosystem services, before exploring how work linking these two fields could be enhanced.
4. We emphasize the value of network approaches and explore network methods to improve the assessment and management of ecosystem services. Within this, we highlight the role of local and indigenous knowledge in operationalising network approaches in a useful ecosystem service context.

**Keywords:**

Ecosystem services, interactions, interdisciplinary, local and indigenous knowledge, network ecology, network models

**Main Text**

1. **Introduction**

Ecosystems and the services that they provide are increasingly under stress due to anthropogenic environmental changes worldwide, with anthropogenic land degradation reducing productivity in 23% of the global terrestrial area that supports human livelihoods and well-being (Balvanera et al., 2019; IPBES, 2019). Ecosystem services are defined as the benefits that nature contributes to people (Costanza et al., 1998; Box 1), provided through stages from biophysical structures performing functions, to ecosystem services valued by humans (i.e. ecosystem service flows; see Potschin-Young et al., 2018; Box 1; Fig. 1). Therefore, declines in ecosystem service provisioning under ecosystem degradation can have negative impacts on human well-being (Díaz et al., 2018; IPBES, 2019). Both social and ecological factors are key to providing ecosystem services, and both social and ecological dimensions have been incorporated into different perspectives in ecosystem service science (Chan & Satterfield, 2020; Davies et al., 2015; Díaz et al., 2018), including the idea of nature’s contributions to people. The idea of nature’s contributions to people expands existing ecosystem service concepts by recognising and operationalising the central role of culture and local and indigenous knowledge in defining and understanding how nature and people interact (Brauman et al., 2020; Díaz et al., 2018; IPBES, 2022).

Decision and policy makers must understand how changes in an ecosystem will affect the delivery of benefits to people (Lindborg et al., 2017). To manage the delivery of benefits, an in-depth understanding of how different ecosystem services are provided at different scales (e.g., local to landscape, seasonal to decadal) is required (Lindborg et al., 2017; Moreno-Mateos et al., 2020). Many benefits nature provides to humans depend on interspecific biotic interactions (La Notte et al., 2017; Melton et al., 2016; Montoya & Raffaelli, 2010; Villamagna et al., 2013; Box 1; Fig. 1). This can include benefits for humans that directly rely on species interactions, such as crop pollination or zoochorous seed dispersal of raw materials. This can also include interactions that are less directly beneficial to humans but are fundamental to ecosystem processes, such as the role of trophic interactions amongst soil biota that underpin terrestrial nutrient cycling and soil carbon storage (Morriën et al., 2017). When ecosystem functions and processes underpinning ecosystem services are driven by relevant and quantifiable interspecific biotic interactions, such as trophic predation in fisheries or between natural pests and predators, network approaches can provide unique understanding of how ecological and socio-ecological interactions directly and indirectly contribute to the provisioning of ecosystem services at varying scales (Harvey et al., 2017; Fig. 1). It is also important to note that not all stages of ecosystem service flows will fit nicely into a network framework. For example, carbon storage is fundamentally underpinned by seed dispersal interactions maintaining large-seeded tree populations (Bello et al., 2015). However, the benefits that humans gain from carbon storage, such as climate regulation, are difficult to quantify in the sense of directly measurable interactions between humans and nature and may be more suited to alternative assessments such as economic valuation (Bello et al., 2021). There has been emerging interest in using interaction networks to understand ecosystem service provisioning, resulting in a number of frameworks exploring how to effectively use network approaches in ecosystem service contexts (Bohan et al., 2013; Dee et al., 2017; Gonzalez et al., 2017; Hines et al., 2015; Marini et al., 2019; Samways et al., 2010; Timberlake et al., 2022; Tixier et al., 2013; Van Kleunen et al., 2023; Xiao et al., 2018). However, the link between ecosystem services and network ecology has been underutilised in applied contexts (Dee et al., 2017; Marini et al., 2019), particularly operationalising network methods to monitor and manage ecosystem services to benefit people (The QUINTESSENCE Consortium, 2016).

**Box 1: Glossary of key terms relevant to ecosystem services.**

**Ecosystem services:** Benefits provided by nature to people. These benefits are a subset of existing ecosystem functions or processes which become a service once valued by humans. Ecosystem services are categorised into provisioning (e.g. food, raw materials, medicinal resources, fresh water), regulating (e.g. air quality regulation, climate regulation, water regulation, erosion control, disease and pest regulation, pollination, water purification), cultural (e.g. mental and physical health, recreation, spiritual and religious values), and supporting (e.g. nutrient cycling, photosynthesis, soil formation) services.

**Ecosystem service flow:** The provision of an ecosystem service through a system via stages from natural capital (e.g. biodiversity) carrying out ecosystem functions and processes (e.g. biodiversity interacting), becoming ecosystem services that benefit humans (see Fig. 1 and Potschin-Young et al., 2018).

**Ecosystem functions and processes:** Complex interactions between organisms that transfer energy and materials through ecosystems and underpin ecosystem services e.g. interactions between crops and pollinators drive pollination function that underpins food as an ecosystem service.

**Natural capital:** Biophysical structures (e.g. plants, animals, parasites, soil) and ecosystem characteristics (e.g. stored carbon, groundwater flux, habitat type) that provide ecosystem functions and processes and subsequent ecosystem services.

**Beneficiaries:** Those who benefit from ecosystem services, e.g. a coastal community benefiting from protection from sand dunes.

**Box 2: Glossary of key terms relevant to networks.**

**Ecological networks:** Systems of functional interactions between ecological units. These interactions can range in scale from between individual organisms to entire populations, and from community scale to landscape or even continental scale with dispersal of organisms between habitats. In most cases, studies focus on **interspecific** interactions, i.e. interactions between different types of ecological units (e.g. frugivore fruit interactions). However, **intraspecific** interactions may also be included in ecological networks, i.e. interactions between the same type of ecological unit (e.g. wind pollination between plants of the same species in different habitat patches). These interactions can be **mutualistic** where both partners benefit (e.g. seed dispersal, plant pollination), or **antagonistic** where one partner benefits at the expense of the other (e.g. parasitism, predation). Whilst the majority of ecological network studies use explicit interactions between organisms or habitats (i.e. empirically observed), some rely on implicit interactions (i.e. co-occurrence).

**Link:** Also known as **edges**, these represent interactions within networks between nodes, e.g. a pollination interaction (link) between a plant and a pollinator (nodes). These links can be directed (e.g. transfer of energy from node to another) or undirected (e.g. symmetrical relationship).

**Node:** Also known as **vertices**, these are components of networks, e.g. species, habitats, humans. These are connected by interactions (links).

**Multilayer network**: Network containing multiple layers of different types of interactions (i.e. intralayer interactions) connected by interlayer interactions. Each layer can represent different types of interactions (e.g. pollination interactions and seed dispersal interactions) or spatial (e.g. habitat patches) or temporal units (e.g. sampling years). Layers can have different sets of nodes and links or connect the same set of nodes partaking in different interactions (known as **multiplex networks**) e.g. frugivorous and nectivorous bird species moving between seed dispersal and pollination interactions. Layers can be node-aligned with all interlayer links between all nodes, or diagonally coupled with interlayer links between only those nodes appearing in different layers (see Fig. 2 and Fig. 3).

**Spatial ecological network:** Networks whereby habitats, either represented as nodes or layers of interactions in multi-layer networks, are linked by species’ foraging and dispersal between patches (see Fig. 2b).

**Socio-ecological networks:** Networks incorporating both ecological and social factors. These can include both social and ecological nodes (e.g. farmers and crops) and social (e.g. information sharing) and ecological links (e.g. predation) (see Fig. 3).

Here, we present a perspective piece supported by a selection of relevant recent literature (Table S1). We synthesise current efforts to use network ecology approaches in ecosystem service contexts, before considering how we could better use network approaches in ecosystem service assessment and management to benefit a wider range of users.

1. **Current network approaches in ecosystem service studies**

Interdisciplinary approaches to ecosystem service science have generally been tackled from a broad socio-ecological perspective, with many ecosystem service studies integrating both biophysical characterisations and forms of sociocultural or economic valuations (Chan & Satterfield, 2020). There has been a growing body of work taking such interdisciplinary approaches and introducing frameworks for employing ecological, social, and socio-ecological interaction network approaches in ecosystem service assessment (Bohan et al., 2013; Dee et al., 2017; Felipe-Lucia et al., 2020, 2022; Gonzalez et al., 2017; Hines et al., 2015; Keyes et al., 2021; Marini et al., 2019; Samways et al., 2010; Timberlake et al., 2022; Tixier et al., 2013; Van Kleunen et al., 2023; Windsor et al., 2022; Xiao et al., 2018; Table S1). For instance, Windsor et al. (2022) present a conceptual network framework to better understand and restore coexisting ecological processes in agroecosystems, whilst Felipe-Lucia et al. (2022) present a typology to incorporate ecosystem services directly into socio-ecological networks of social actors, ecological entities and ecosystem services. This existing body of work has laid the theoretical foundation for integrating network approaches into ecosystem service science. The next step involves the wider operationalization of applied network approaches, integrating ecological and social factors into one network, and using network analytical tools to assess and manage ecosystem service supply to benefit people (Dee et al., 2017; Felipe-Lucia et al., 2022; Timberlake et al., 2022).

1. **Using network approaches in ecosystem service assessment and management**

Network approaches allow for a unique understanding of how interspecific interactions facilitate the flow of ecosystem services (Harvey et al., 2017; Windsor et al., 2022). Here, we explore how network ecology can be used in ecosystem service assessment, allowing quantification of the entire flow of ecosystem services at various scales to better inform management.

**3.1 Ecosystem-scale networks and models**

Many ecosystem services are connected within landscapes (Gregr et al., 2020; Lowe et al., 2022), with the impact of changes cascading through multiple ecological functions and socio-ecological systems (Gregr et al., 2020; Keyes et al., 2021; Potschin-Young et al., 2018; Walsh et al., 2016). For example, in salt marshes a range of species both directly provide and support ecosystem services such as shoreline stabilisation, water filtration, carbon sequestration, fisheries, and birdwatching in a complex and interconnected system vulnerable to cascading species losses (Keyes et al., 2021). Therefore, considering all ecological and social stages of ecosystem service flows is particularly important in applied contexts (Potschin-Young et al., 2018). Doing so allows management decisions to be informed by understanding both direct and indirect drivers of ecosystem service provisioning, as well as trade-offs and synergies between them that are highlighted by the structure and dynamics of ecological and socio-ecological interactions underpinning ecosystem services (Rullens et al., 2019). Ecosystem-scale networks and models provide holistic assessments of ecosystem services and can include multiple types of ecosystem services and interactions (Gray et al., 2021; Hervías-Parejo et al., 2020; Fig. 2a), capture network structure and dynamics at a range of spatial and temporal scales (Lindborg et al., 2017; Fig. 2b), and increase insight into whole ecosystem service flows (Potschin-Young et al., 2018). Network analytical tools can then be used in ecosystem-scale networks and models, providing useful outputs for assessing current and future states of ecosystem service provisioning and informing management.

* + 1. **Working across scales**

Different ecosystem services are used and experienced on different spatial and temporal scales, ranging from site level to across landscapes and regions and over multiple seasons or years (Lindborg et al., 2017; Peh et al., 2013). However, network boundaries are often defined by site and time scale and restricted to specific taxa or type of interaction, missing the wider context in which these interactions occur. This limits the scope and detail of networks and subsequent meaningful analysis in the context of ecosystem service flows (Fortin et al., 2021). Furthermore, ecosystem service management decisions are often made based at site level (Peh et al., 2013; Windsor et al., 2022). Structural and analytical insights from ecosystem-scale networks and models can allow for more effective decision making by accounting for ecosystem service flows beyond site level, with the scale of information acquired from ecological interactions reflecting the scale of management needed (Lindborg et al., 2017; Marini et al., 2019). A useful approach to describe and analyse ecosystem-scale interspecific interactions is the use of multilayer networks (Pilosof et al., 2017).

* + 1. **Multilayer ecological networks**

Multilayer networks are increasingly being used across a range of disciplines, from sociology and transportation systems to biomedicine and ecology, with the aim of extracting more information than studying monolayer networks in isolation (Bianconi, 2018; Boccaletti et al., 2014; Pilosof et al., 2017). As the name suggests, multilayer ecological networks consist of more than one network ‘layer’, with different types of intralayer interactions, ecosystem services, and spatial and temporal units incorporated into one network as separate layers and connected by interlayer links (Felipe-Lucia et al., 2022; Pilosof et al., 2017; Windsor et al., 2022; Fig. 2; Box 2). Multilayer ecological networks move beyond confined representations of specific types of taxa, interactions, or locations within systems, providing opportunities to connect different spatial or temporal stages of ecosystem service flows across habitats or seasons (Gilarranz et al., 2015; Pilosof et al., 2017; Fig. 2b), as well as multiple different ecosystem services (Felipe-Lucia et al., 2022; Gray et al., 2021; Hervías-Parejo et al., 2020; Pilosof et al., 2017; Windsor et al., 2022; Fig. 2a). This holistic approach makes multilayer networks ideal structures for ecosystem-scale networks and models (Dee et al., 2017; Felipe-Lucia et al., 2022; Pilosof et al., 2017; Fig. 2).

Different types of interactions that drive ecosystem functions underpinning ecosystem services can be incorporated as different layers in multilayer networks, connected by various (‘diagonally coupled’; Pilosof et al., 2017) or all (‘node-aligned’; Kéfi et al., 2016; Pilosof et al., 2017) species. In the Galápagos Islands, for example, separate pollination and seed dispersal ecosystem functions were connected in a multilayer ecological network by interlayer links between bird species acting as both pollinators and seed-dispersers (Hervías-Parejo et al., 2020). We generally have a good understanding of species-specific contributions to ecosystem services through the harvest of species and direct dependence on species’ behaviour or function, for example fisheries, pollinator species, or carbon sequestering plants (Costanza et al., 1998). However, there is a gap in our understanding of the indirect contributions of species to ecosystem services, such as the cascading effects of species extinctions (Keyes et al., 2021). Multilayer ecological networks enable a more comprehensive understanding of the role of species directly and indirectly contributing to individual and multiple ecosystem services through their contribution to network structure and dynamics (Gray et al., 2021; Montoya & Raffaelli, 2010; Pilosof et al., 2017; Timóteo et al., 2023). Using multilayer network analysis, we can calculate how many species contribute to providing and connecting individual and multiple ecosystem services (i.e. network redundancy), enabling us to quantify the stability (Sauve et al., 2016) and robustness of individual and multiple ecosystem service provisioning (Keyes et al., 2021; Radicchi & Bianconi, 2017). Multilayer network analysis can also determine the importance of different species. Multilayer node centrality (i.e., strength) metrics such as eigenvector centrality or PageRank (Bianconi, 2018; Boccaletti et al., 2014; De Domenico et al., 2015) can be calculated to understand the importance of species within each layer, for example, for specific ecosystem functions or within different habitats, and for overall multilayer structure, such as dual-function key species contributing to multifunctionality of different ecosystem services (Hervías-Parejo et al., 2020; Timóteo et al., 2023). This information can then inform management decisions, such as prioritising protection of dual-function key species for wider ecosystem functioning (Felipe-Lucia et al., 2022).

Multilayer ecological networks also allow us to identify the role that functional diversity within the community plays in mediating ecosystem functions, thus underpinning different or multiple ecosystem services (Albrecht et al., 2018; Gray et al., 2021; Hale et al., 2023; Harvey et al., 2017; Hevia et al., 2017; Keyes et al., 2021; Raimundo et al., 2018; Windsor et al., 2021, 2022). Incorporating functional traits or phylogenetic data into networks allows trait matching, highlighting the interaction niches of species (Albrecht et al., 2018; Hale et al., 2023). Understanding the interaction niches of species, combined with linking species with functional traits necessary to provide ecosystem services, such as floral reproductive traits essential for successful pollination (Lanuza et al., 2023), can determine the fraction of species loss that an ecosystem can tolerate before ecosystem service failure (i.e., the resilience of ecosystem service provisioning) (Raimundo et al., 2018; Ross et al., 2021). Understanding the role of functional traits in influencing species interactions improves the predictive power of multilayer ecological network models and subsequent management decision making, with a more detailed understanding of the impact of fluctuations in biodiversity on synergies and trade-offs across multiple ecosystem services (Raimundo et al., 2018; Van Kleunen et al., 2023).

Multilayer ecological networks can also provide useful tools for understanding how an ecosystem service is provided at different spatial or temporal scales (Pilosof et al., 2017). Network layers can represent different habitat patches, for example, linking plant and pollinator communities by species extinction and colonisation (Gilarranz et al., 2015; Fig. 2b), or different time-stamps linked through the presence of a species in an ecosystem over time (Carstensen et al., 2014; Poisot et al., 2015; Trøjelsgaard et al., 2015; Fig. 2b). This not only allows for a better understanding of the long-term or landscape-scale ecosystem functioning and consequential ecosystem service delivery, but also offers an opportunity to understand dynamic ecosystem service flows through changing landscapes, reflecting seasonal variation in habitats, for instance (Carstensen et al., 2014; Gonzalez et al., 2017; Kim & Park, 2020; Marini et al., 2019; Trøjelsgaard et al., 2015).

Multilayer ecological networks not only provide tools to quantify current ecosystem services, they can also be modelled, enabling ecosystem service robustness to changes to be quantified (Keyes et al., 2021) and future predictions to be incorporated into decision making (Raimundo et al., 2018). The network structure can be altered, with the purposeful addition or removal of nodes and links reflecting environmental changes and disturbances such as fluctuation or loss of biodiversity (Keyes et al., 2021; Timóteo et al., 2016; Van Kleunen et al., 2023) or changing land use and cover, for example, natural seasonal fluctuation in wetland surface water (Kim & Park, 2020), or anthropogenically driven resource extraction (Gonzalez et al., 2017; Raimundo et al., 2018; Valdovinos et al., 2023). The impact of different management styles can also be modelled, such as, removing nodes to reflect invasive species removal (Kaiser-Bunbury et al., 2017) or adding nodes or extra links to reflect a population boost or introduction of a species (Van Kleunen et al., 2023). The model outputs and multilayer network analytics can then be used to infer the cascading impacts of changes on the stability of ecosystem service provisioning (Pilosof et al., 2017), such as the secondary loss of an ecosystem service following primary (or cascading) losses of species reducing ecosystem service robustness (Keyes et al., 2021; Ross et al., 2021), further informing decision making.

* + 1. **Multilayer socio-ecological networks**

When ecosystem service provisioning can be directly linked to humans through consumptive or culturally valued quantifications, multilayer ecosystem-scale networks can incorporate both ecological and social factors as network components and network layers, providing more holistic characterisation of whole ecosystem service flows through a multilayer structure (Dee et al., 2017; Felipe-Lucia et al., 2022; Timberlake et al., 2022; Windsor et al., 2022). Connected network layers of ecological functions, such as seed dispersal, and socio-ecological functions, such as human plant consumption, reduce the disconnect that is often felt between ecological dynamics and the provision of benefits from nature to people (Dee et al., 2017; Dee & Keyes, 2022; Felipe-Lucia et al., 2022; Keyes et al., 2021; Timberlake et al., 2022; Xiao et al., 2018; Fig. 3). Using the seed dispersal of useful plants for humans as an example, intralayer network links within an ecological layer could represent mutualistic interactions between frugivorous birds and the plants whose seeds they disperse. Intralayer network links within a socio-ecological layer could represent consumptive interactions between useful plants and the humans that use them directly for food, medicinal or cultural purposes in a subsistence farming community (Fig. 3a). Alternatively, intralayer network links within a socio-ecological layer could connect each useful plant to the benefit they provide humans, again allowing multiple ecosystem services to be connected in one network (Fig. 3b). Socio-ecological intralayer links can also be weighted with contextually relevant information, for example, weighting links between plants and local farmers with yields, nutritional, labour, market, or cultural values (Timberlake et al., 2022) (although care should be taken when using varying link information within multilayer networks, see Windsor et al., 2022). The interlayer links could then connect plants dispersed by frugivorous birds and consumed by humans (Fig. 3).

Incorporating both ecological functions and the direct provision of benefits from nature into one multilayer socio-ecological network allows network analysis to highlight the role of species in connecting them (Dee et al., 2017; Felipe-Lucia et al., 2022; Timberlake et al., 2022; Windsor et al., 2022). In our example, plants with high node centrality scores (Bianconi, 2018; Boccaletti et al., 2014; De Domenico et al., 2015) may be important for both seed dispersal ecological functioning and supporting food security of local farmers (Fig. 3a). Understanding the role and importance of different network components across ecological and socio-ecological network layers provides useful information for directing management efforts.The network links can also be weighted to enhance the output of the network analysis. For example, weighting links between plants and farmers with nutritional value or market value (Timberlake et al., 2022) can better inform management decisions with context-specific and useful information. Multilayer network modelling through simulating changes to network architecture can then be used to predict the impact of ecological, social, or economic disturbances on ecosystem service flow, as well as unveiling mechanistic socio-ecological processes behind the impact of different management decisions on ecosystem service provisioning. It is important to note that, although we have used a subsistence farming system as an example here, this multilayer socio-ecological network approach can be relevant to a range of other socio-ecological systems and the ecosystem services that flow through them (see Fig. 1). Therefore, future work should focus on how we can incorporate multiple ecological and socio-ecological layers into multilayer networks, such as trophic fishery layers, fish-coral herbivory layers, and separate human consumption layers including large and small-scale food provisioning and recreational enjoyment of coral reefs (Felipe-Lucia et al., 2022). This expansion of multilayer networks will further broaden the scope of ecosystem-scale networks and models for the assessment and management of ecosystem services and increase the level of complexity captured in network analysis.

**4. Challenges in the use of network approaches in the assessment and management of ecosystem services to benefit people**

Network approaches can act as a gateway for ecologists and social scientists working from different perspectives to take advantage of a descriptive and analytical toolkit that can provide holistic understanding and management of ecosystem services at a system level. However, there are several challenges associated with network approaches that can limit the way ecological networks are used. First, a general challenge in network ecology is difficulty in empirically confirming interspecific interactions and the inherent need for proxies and cooccurrences to define interactions in network data (Kaiser-Bunbury et al., 2017; Morriën et al., 2017). The collection of data is also a significant challenge in itself, and difficulties in acquiring species interaction information limits the benefits that network theory can provide for ecosystem service assessment and management.

Many ecological interaction studies are based on intentional human observation of potential interactions. Collating suitable datasets to build networks for sufficient analyses requires extensive observations (many months to years), making data collection expensive and incredibly time and labour intensive (Chacoff et al., 2012; Hegland et al., 2010). Other methods, such as cameras or DNA analyses, are increasingly being used in place of traditional observation methods (Cuff et al., 2022; Pegoraro et al., 2020); however, these still require expertise, lengthy processing periods, and expensive infrastructure (Elbrecht et al., 2017). Therefore, we suggest adopting an approach to collecting information about ecological interactions that demands less time and resources, thus allowing for a broader participation to harness the outcomes of network analysis to quantify and manage ecosystem services, making the process more inclusive. Considering that we live under increasing pressure to address environmental destruction, accessible ecosystem service assessment and management that can be executed efficiently by those who make decisions and implement management must be considered. Therefore, practical and affordable approaches to collecting information about ecological interactions driving ecosystem services are key (Peh et al., 2013). One such approach is the identification of the ecological interactions underpinning the benefits that nature contributes to people through local and indigenous ecological knowledge (Brauman et al., 2020; Díaz et al., 2018; IPBES, 2022). This approach to understanding ecological interactions empowers and conserves local and indigenous knowledge (Copete et al., 2023; IPBES, 2022) and allows a broader participation to harness the outcomes of network analysis for quantifying and managing ecosystem services.

**5. Local and indigenous knowledge in networks**

A recent IPBES report highlighted the value and inherent importance of empowering local and indigenous knowledge in equitable and sustainable ecological monitoring and assessment (IPBES, 2022). In light of this inherent importance, local and indigenous knowledge is central to the objectives and execution of many studies on the benefits that nature contributes to people (Cámara-Leret et al., 2019; Coelho et al., 2021; Díaz et al., 2018; Hill et al., 2020; IPBES, 2022; Peh et al., 2013; Rau et al., 2020). Local and indigenous knowledge has also been channelled into network studies, for example, seed networks (Labeyrie et al., 2023) or plant ecosystem service knowledge networks (Cámara-Leret et al., 2019; Tengö et al., 2014). However, only a small number of studies have used local and indigenous ecological knowledge to construct species interactions networks (Durand-Bessart et al., 2023; Hawes & Peres, 2014; Ong et al., 2021; Pereyra et al., 2023), with none directly relating these ecological networks to the benefits they provide to the local or indigenous community.

Local and indigenous ecological knowledge can provide information about visible ecological interactions underpinning ecosystem services, such as pollination, frugivory, or predatory interactions, at much lower resource costs than typical ecological interaction sampling methods, with interviews and participatory workshops saving significant time and resources over extensive observations of species interactions (Ong et al., 2021; Pereyra et al., 2023). For example, in a recent study by Durand-Bessart et al. (2023) investigating frugivory networks in Gabon, 2382 interactions were identified by local communities over 41 days of interviews. This was comparable to a dataset founded on 41,234 days of fieldwork which contained 2666 interactions, requiring over 1000 times as many research hours for only 0.12% greater number of interactions (Durand-Bessart et al., 2023). The information provided by local and indigenous ecological knowledge can then identify critical components of networks that represent the flow of ecosystem services in a local context. Nodes can be populated by biological units identified by local participants, and links both identified and weighted with frequency of observation (i.e. the amount of times an interaction between biological units is identified by participants), reflecting how links are often weighted in ecological networks (i.e. visitation frequency) and providing standardised numerical metrics necessary for network analysis (Kaiser-Bunbury et al., 2017).

Insights from local and indigenous communities can specifically influence interaction network approaches by providing information on ecological interactions beyond the typical snapshot from observational data collection and increasing spatial and temporal variation in recorded interactions, such as interactions from further afield, seasonally variable interactions, or historical interactions from recently extinct species (Ong et al., 2021; Ward‐Fear et al., 2019). Knowledge from local and indigenous communities can also provide useful baselines of cooccurrences and interactions towards which limited resources for ecological interaction sampling can be directed, for example, identifying sites or seasons where different interactions are present (Ong et al., 2021). Local and indigenous knowledge can also provide contextually relevant information on how humans interact with biodiversity in an ecosystem, providing network components for multilayer socio-ecological networks, and contextually assessing the relative importance of socio-ecological links. Network analytical tools can then provide additional value by revealing direct and indirect effects of ecological and social nodes and links on the provision and resilience of ecosystem services within the socio-ecological system (see Section 3.1.4), thus informing management decisions at a lower cost for a wider range of users including communities that implement local-scale ecosystem service management.

Species interactions reported through local and indigenous ecological knowledge have been carefully observed, and those observations passed on through cultural practice, enhancing our knowledge of ecosystem functions (Durand-Bessart et al., 2023; Hawes & Peres, 2014; Ong et al., 2021; Pereyra et al., 2023). Nevertheless, it is important to consider that there may still be reporting bias toward cooccurrences and the most abundant or culturally valued species and the most pronounced interactions being observed most frequently (Ong et al., 2021), thus missing important information associated with rare interactions (Lyons et al., 2005; Pocock et al., 2012). Despite this, it is important to note that targeting the most frequent, and therefore likely most important, ecological interactions in a system is an accepted and often used proxy in ecological network studies (Kaiser-Bunbury et al., 2010). Furthermore, by focusing on the behaviour of species interacting, the relevance of ecological interactions reported and subsequent output for management decision making can be maximised, for example, referencing specific behaviours that infer successful seed dispersal when engaging with interview or workshop participants (see Ong et al., 2021). Local and indigenous ecological knowledge can also be combined with other data such as observations of subsets of interactions (Song et al., 2023) or existing datasets and literature to co-produce information to identify interaction network components and structure, potentially increasing the resolution of network output informing ecosystem service management (Copete et al., 2023; Durand-Bessart et al., 2023; Ong et al., 2021; Pereyra et al., 2023; Quintero et al., 2022; Tengö et al., 2014). Combining sampling techniques is known to affect network topology and structure, which may limit the effective incorporation of multiple types of data in interaction networks (Brimacombe et al., 2023; Durand-Bessart et al., 2023). However, studies are emerging that combine ecological interaction information from local and indigenous ecological knowledge with academic knowledge (mostly frugivory e.g. Durand-Bessart et al., 2023; Hawes & Peres, 2014; Ong et al., 2021). It is evident that this coproduction of information is complimentary and enhances the completeness of interaction networks (Copete et al., 2023; Durand-Bessart et al., 2023; Hawes & Peres, 2014; Ong et al., 2021; Quintero et al., 2022; Tengö et al., 2014), exemplified in Malaysia where 97% of frugivorous interactions identified by Orang Asli agreed with the literature and primary field data (Ong et al., 2021).

It is clear that local and indigenous knowledge can improve understanding of the flow of ecosystem services underpinned by visible interspecific biotic interactions. In the context of efficient and relevant ecosystem service management, this approach may make a wider range of users, including local communities, more likely to incorporate and benefit from outputs of network representation and analysis in their natural resource management. Moving forward, particular attention should be paid to developing equitable collaborations with local and indigenous communities to understand species interactions and conserve local and indigenous knowledge (Copete et al., 2023; Gewin, 2023; IPBES, 2022). Further, attention should be paid to the continuous assessment of ecological networks constructed under the co-production of information through ecological data collection methods and local and indigenous knowledge (Durand-Bessart et al., 2023; Ong et al., 2021; Quintero et al., 2022).

**6. Concluding remarks**

In a world under increasing pressure to meet environmental and human needs, developing and operationalising ecological and socio-ecological multilayer interaction networks will enable holistic ecosystem-scale assessment and management of the benefits that nature contributes to people. Network analytics and modelling outputs provide further insight into direct and indirect components and mechanisms driving ecosystem service provisioning under a range of disturbance and management scenarios. Evidence suggests that insights from local and indigenous knowledge can provide contextually relevant and useful information about interspecific ecological interactions within local ecosystems, providing network components and structure that complement and enhance the completeness of ecological interaction networks. Embracing local and indigenous knowledge in this way will allow a wider range of users to benefit from the outputs of network approaches, including communities employing local-scale ecosystem service management. Therefore, there is great potential in building equitable collaborations with local and indigenous communities to assess and manage the benefits that nature contributes through a socio-ecological network lens.

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**Conflict of interest**

The authors have no conflict of interest to declare that are relevant to the content of this article.

**Authors’ contributions**

Anna Stanworth, Kelvin S.-H. Peh and Rebecca .J. Morris conceived the ideas; Anna Stanworth led the writing of the manuscript and made the figures. All authors critically contributed to the drafts and gave their final approval for publication.

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No data was used in this perspective piece.

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No ethics approval was required for this perspective piece.

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**Supporting information**

Additional supporting information may be found in the online version of the article at the publisher’s website.

**Figures**

A diagram of different types of fish

Description automatically generated

**Figure 1: Examples of different ecosystem service flows through ecological and socio-ecological interactions.** Natural capital (in this case biodiversity) interacts through trophic or mutualistic biotic interactions, driving ecosystem functions and processes that underpin a range of ecosystem services. Benefits are then provided through socio-ecological interactions between biophysical structures and humans.

A screenshot of a computer

Description automatically generated

**Figure 2: Conceptual multilayer ecological networks.** a) Multilayer ecological network connecting layers of different types of interaction (pink, seed dispersal; orange, pollination) underpinning ecosystem services. Pollination and seed-dispersal interactions are connected by interlayer links connecting bird species that both pollinate and disperse seeds (adapted from Hervías-Parejo et al., 2020). Plants (green) are categorised by corolla depth, relating functional traits to pollination. b) Multilayer ecological network connecting layers representing different spatial or temporal units. Community-scale pollination interactions are connected through space or time through species foraging or colonisation or their presence across seasons.

A diagram of a diagram

Description automatically generated with medium confidence

**Figure 3: Conceptual multilayer socio-ecological networks representing a subsistence farming system.** a) Multilayer socio-ecological network connecting layers of ecological functions (pink, seed dispersal) and socio-ecological functions (purple, human plant consumption). Seed dispersal and human-plant consumption interactions are connected by interlayer links connecting plants whose seeds are dispersed by birds and that are used by local farmers. b) In this multilayer network, the socio-ecological function layer represents interactions between plants and their different uses, with benefits to humans included as nodes.

**Supplementary Information**

**Table S1**: Table of literature linking network ecology and ecosystem services.

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
| Reference | Objective | Network Type | Ecosystem Service | System | Location |
| Bohan et al. (2013) | Exploring how network metrics can be applied to understand and manage agroecosystems for the provision of sustainable ecosystem services. | A range of network types, including mutualistic and antagonistic ecological networks, and bipartite and multipartite ecological networks. | Provisioning:  Food  Regulating:  Pollination  Pest control  Supporting:  Nutrient cycling  Disservices:  Herbivory  Weed-crop competition  Disease transmission | Agroecosystem | N/A |
| Dee et al. (2017) | Framework to use integrated ecological and socioeconomic networks to assess the impact of drivers and management actions on ecosystem services. | Meta-networks integrating multiple types of ecological and socioeconomic networks with multiple types of nodes and interactions. | Regulating:  Coastal protection  Water quality  Climate regulation  Cultural:  Recreation | Floodplains | Australia |
| Dee & Keyes, (2022) | Data paper integrating ecological networks and ecosystem functions and services to directly link species and service provisioning. | Food webs with species and ecosystem services nodes, species-species links, and species-ecosystem services links. | Provisioning:  Fisheries  Regulating:  Wave attenuation  Shoreline stabilization  Carbon sequestration  Water filtration  Cultural:  Birdwatching  Waterfowl hunting | Salt marsh | California, USA  Baja, Mexico |
| Felipe-Lucia et al. (2020) | Applying network ecology approaches to understand the impact of land-use intensity on ecosystem services and trade-offs with biodiversity and ecosystem functions. | Tripartite ecological networks with biodiversity, ecosystem functions, and ecosystem services nodes, connected by their correlations. | Provisioning:  Timber  Food | Grasslands  Forest | Germany |
| Felipe-Lucia et al. (2022) | Presenting a typology to incorporate ecosystem services directly into social-ecological networks. | Conceptual social-ecological networks directly incorporating ecosystem services as nodes, links, attributes, and emergent properties. | References different types of ecosystem services e.g. provisioning, regulating, supporting, cultural. | N/A | N/A |
| Gonzalez et al. (2017) | Reviewing how spatial ecological networks (SENs) can be harnessed to sustain ecosystem services. | Habitat-habitat spatial ecological networks. Habitat nodes are connected by links representing flows of resources, energy, information or organisms. | N/A | N/A | N/A |
| Gray et al. (2021) | Using multilayer networks to understand co-variance between different but related ecosystem services. | Multilayer ecological networks linking seed regulation and predation interactions. | Regulating:  Weed seed regulation  Gastropod mollusc predation | Agroecosystem | UK |
| Harvey et al., (2017) | Commentary exploring challenges and a potential roadmap in focusing on interaction networks to ultimately conserve provision of ecosystem services. | Antagonistic food web. | Regulating:  Pest control  Water quality  Cultural:  Recreation e.g. fishing | Agricultural example. | N/A |
| Hines et al. (2015) | Reviewing conceptual parallels in biodiversity-ecosystem functioning and food web theory to evaluate trade-offs between multiple ecosystem services, ultimately influencing management decisions with network theory. | Antagonistic food web examples. | Provision:  Food  Regulating:  Pollination  Pest suppression  Carbon Sequestration | Agroecosystems  Fisheries  (Identified as best examples) | N/A |
| Keyes et al. (2021) | Applying network ecology approaches to explore the vulnerability of ecosystem services to species loss. | Food webs with species and ecosystem services nodes, species-species links, and species-ecosystem services links. | Provisioning:  Fisheries  Regulating:  Water filtration  Shoreline stabilisation  Carbon sequestration  Cultural:  Waterfowl hunting  Birdwatching | Estuarine | USA  Mexico |
| Kim & Park, (2020) | Applying a novel ecological network framework using dynamic nodes and links to understand the functions of wetlands to aid decision-making. | Habitat – habitat spatial ecological network incorporating dynamic processes. Habitat nodes are connected by species dispersal paths. | Provisioning:  Food  Habitat  Regulating:  Carbon sinks and/or sources  Flood control  Groundwater discharge | Wetlands | USA |
| Marini et al. (2019) | Commentary exploring the applied use of bipartite species-habitat networks to real-world problems, e.g. ecosystem services. | Bipartite species-habitat spatial ecological networks. | No focus on specific ecosystem services. | N/A | N/A |
| Martínez-Núñez et al. (2019) | Applying network ecology approaches to understand the interacting effects of landscape and land management on plant-solitary bee networks to make inferences about the provision of ecosystem services. | Pollen-solitary bee mutualistic ecological networks. | Regulating:  Pollination | Agroecosystem | Spain |
| Montoya & Raffaelli (2010) | Reviewing how climatic changes may affect biotic interactions and network properties and the ecosystem services linked to them. | Focus on predator-prey interactions in food web theory, extending to network theory. | Provisioning:  Fisheries nurseries  Regulating:  Coastal protection  Carbon sequestration  Soil erosion prevention  Flood risk alleviation  Water purification  Supporting:  Nutrient cycling  Soil respiration | N/A | N/A |
| Mulder et al. (2017) | Review of network approaches to understand the relationship between biodiversity, ecosystem functioning, and ecosystem services, to allow evaluation of the improvement of ecosystem services. | Various network types including bipartite and multipartite ecological networks. | Regulating  Provisioning  Supporting  Cultural | A range of examples of managed ecosystems. | A range of examples. |
| Philpott et al. (2020) | Using natural enemy-herbivore co-occurrence networks associated with a common crop to infer how pest control services are affected by management and landscape composition. | Bipartite antagonistic natural enemy – herbivore ecological interaction network. | Regulating:  Pest control | Urban agroecosystem | California, USA |
| The Quintessence Consortium (2016) | Proposed network approach to re-centre natural science in ecosystem service research. | Cross-discipline multi-networks (networks of networks) combining individual networks through links between entities in different economic, social, and ecological domains. | Provisioning:  Food  Regulating:  Weed regulation  Water quality  Cultural:  Traditional farming  Aesthetics | Agroecosystem | Somerset, UK  Cote d’Or, France |
| Ross et al. (2021) | Using network approaches to identify features of networks that link species to functions that they perform, in turn influencing the robustness of ecosystem service provisioning to species loss. | Bipartite ecological networks representing anemone-fish, host-parasite, plant-ant, plant-pollinator, and seed-disperser interactions. | Regulating:  Pollination  Seed dispersal  Parasitism (disservice)  Herbivory (disservice) | N/A | N/A |
| Samways et al. (2010) | Reviewing the use of habitat ecological networks in the provision of ecosystem services among plantations. | Habitat-habitat spatial ecological networks with nodes representing habitat areas connected by habitat corridors. | Provision:  Raw materials (timber, thatching grass)  Honey  Firewood  Grazing land  Regulation:  Biodiversity conservation  Pollination  Biocontrol  Water filtration  Firebreaks  Supporting:  Nutrient cycling | Forestry plantation  Grassland | South Africa |
| Stein et al. (2020) | Applying network ecology approaches to understand the impact of land-use intensity and climate seasonality on plant-bee communities. | Plant-bee mutualistic ecological networks. | Regulating:  Pollination | Savanna | Burkina Faso |
| Timberlake et al. (2022) | Presenting a framework using a network approach to quantify the value of ecosystem services in the context of smallholder nutrition security, ultimately influencing ecological intensification (i.e. managing ecosystem services to increase agricultural productivity). | Mulitpartite ecological network linking pollinators – crops – nutrients.  Multilayer social-ecological network linking agricultural ecological interactions with local community social interactions. | Provisioning:  Food  Regulating:  Pollination  Pest control  Water regulation  Supporting:  Nutrient cycling | Smallholder agroecosystem | Nepal |
| Tixier et al. (2013) | Exploring the use of network modelling to assess and enhance ecosystem services at different scales, in the context of pest regulation services in agroecosystems. | Food web network models, spatial network models, and decision interaction network models. | Regulating:  Pest regulation  Pollination  Supporting:  Primary production | Agroecosystem | N/A |
| Van Kleunen et al. (2023) | Presenting a framework using ecological networks to aid in decision-making in species introductions considering both biodiversity and ecosystem service objectives. | Ecological network models (e.g. Allometric Trophic Network model or Lotka-Volterra model) incorporating dynamic processes to predict impact of introducing species on population dynamics. | A range of ecosystem services referenced throughout with no focus on any specifically. | N/A | N/A |
| Windsor et al. (2021) | Applying network ecology approaches to intentionally maximise ecosystem service provisioning and understand trade-offs in ecosystem service provisioning associated with management practices. | Bipartite and multilayer ecological networks exhibiting trophic, mutualistic, and parasitic interactions to represent pollination and pest control ecosystem services, and herbivory disservices. | Provisioning:  Crop production  Regulating:  Pollination  Pest Control  Disservices:  Herbivory | Agroecosystem | UK |
| Windsor et al. (2022) | Present a framework that uses network approaches to manage agroecosystems for food security, accounting for interactions between biodiversity and ecosystem services. | Conceptual multilayer ecological network of antagonistic, competitive, and mutualistic intra-layer interactions, connected by inter-layer interactions of organisms.  Conceptual merged agricultural network of ecological, social, and economic nodes and interactions.  A range of network types (e.g. bipartite, multipartite, multilayer, meta, spatial) at a range of spatial and temporal scales (e.g. field-landscape-global). | Provisioning:  Food  Regulation:  Pollination  Pest control  Supporting:  Soil nutrient provision | Agroecosystem | N/A |
| Xiao et al. (2018) | Analysing trophic interactions between species to understand differences in outcomes when targeting biodiversity or ecosystem services in management approaches. | Predator-prey food webs including ecosystem service nodes, connected to species via links weighted with ecosystem service value in US dollars. | Provisioning:  Fisheries production  Regulating:  Carbon sequestration  Water filtration  Shoreline protection | Saltmarsh | California, USA |

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