A systems perspective: How social-ecological networks can improve our understanding and management of biological invasions

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Abstract

Reversing biodiversity loss and the sustainability crisis requires approaches that explicitly consider human-nature interdependencies. Social-ecological networks (SENs), which incorporate social and ecological actors and entities as well as their interactions, provide such an approach. SENs have been applied to a range of complex issues, including sustainable resource use, management of ecosystem (dis-)services, and collective action. However, the application of SENs to the field of invasion science remains limited so far, despite their clear potential for studying human contributions to introduction pathways of non-native species, invasion success, direct and indirect impacts, and their management. Here, we (1) review past applications of SENs to biological invasions, (2) provide guidance on how to construct and analyze such networks, and (3) outline future opportunities when using SENs in invasion science. Our overview aims to inform and inspire the applications of SENs to improve our ability to meet the diverse challenges facing invasion science.

Keywords: impacts of non-native species, invasive alien species (IAS), management of biological invasions, social-ecological network (SEN), social-ecological system

1. Introduction

Anthropogenic impacts on biodiversity, such as species extinctions or functional degradation, also include the intentional and unintentional transport of species to regions where they would not naturally occur; such species are termed “non-native” or “alien”. A subset of these species may become invasive if they spread beyond the places where they have been introduced and have negative or deleterious impacts on native biodiversity (Roy et al. 2024). Invasive species are recognized as driving forces of the ongoing global biodiversity loss (IPBES 2019; Turbelin et al. 2023; Roy et al. 2024). Their impacts on native species can be devastating, both directly, for instance through predation, parasitism or hybridization, and indirectly, for instance by transmitting pathogens and disrupting well-established predator-prey interactions (Blackburn et al. 2014; Vilà et al. 2011; Linders et al. 2019; Kumschick et al. 2020), as well as causing ecosystem-scale changes, for example through the alteration of community composition, trophic cascades, or ecosystem engineering (Pyšek et al. 2020; Bacher et al. 2024, Roy et al. 2024). Invasive species also lead to substantial financial costs through damage and management, affecting many economic sectors (Diagne et al. 2020; Novoa et al. 2021). They affect human health and wellbeing (Mazza and Tricarico 2018), as they can spread diseases (Zhang et al. 2022) or cause allergies (Bernard-Verdier et al. 2022), be venomous or toxic (Nentwig et al. 2017), or disrupt recreational activities and other social and cultural practices (Pyšek et al. 2020; Bacher et al. 2024). However, not all non-native species (NNS) are invasive, and both invasive and non-invasive NNS can have positive or beneficial ecological or socio-economic effects (Vimercati et al. 2020). For example, NNS can fulfil the functional role of a (locally) extinct native species (Vizentin-Bugoni et al. 2019), provide ecosystem services like improving water quality (Reynolds and Aldridge 2021; Neves et al. 2020), or stabilize fisheries revenues (Van Rijn et al.

2020). Due to myriad concurrent anthropogenic impacts, prioritization and choice of conservation efforts demands a holistic understanding contingent on environmental and social contexts, as well as different geographic scales (Corlett 2015; Bellard et al. 2022).

Several tools have been developed to assess impacts of invasive species with standardized and evidence-based approaches (for an overview, see González-Moreno et al. 2019; Vilà et al. 2019). For example, the IUCN Environmental Impact Classification for Alien Taxa (EICAT) is a protocol for assessing deleterious ecological impacts of NNS on native biodiversity (Blackburn et al. 2014; IUCN 2020). Similarly, the EICAT+ protocol guides assessments of beneficial ecological impacts (Vimercati et al. 2022), while the SEICAT protocol focuses on deleterious socio-economic impacts on human well-being (Bacher et al. 2018). Other approaches to assess NNS impacts have been developed, for instance by estimating monetary costs (InvaCost; Diagne et al. 2020) or exploring functional and numerical response parameters in consumer-resource interactions (Dick et al. 2014; Dickey et al. 2020), or the Dispersal-Origin-Status-Impact (DOSI) framework which incorporates dispersal mechanisms, species origin, population status, and addresses a range of impacts such as ecological, economic, cultural, or health-related (Soto et al. 2024). Assessments of future risks associated with biological invasions include horizon scanning techniques (Verbrugge et al. 2010; Srėbalienė et al. 2019). However, none of these approaches capture how different types of impacts are inter-related (Leung et al. 2012).

A broad understanding of the full range of NNS impacts, synergies and conflicts is important to make informed management decisions (Vilà and Hulme 2017; Stevenson et al. 2023; Roura-Pascual et al. 2024). Deciding which of the many existing management options to apply (Robertson et al. 2020; Roy et al. 2024) requires weighing their social and ecological costs and benefits in a given context. Invasive species and their impacts can be negatively perceived by some stakeholders, but positively by others, and may shift over time and space (Simberloff et al. 2013; Cottet et al. 2015). For example, fish species such as rainbow trout (*Oncorhynchus mykiss*) or brown trout (*Salmo trutta*) have been introduced to many ecosystems to increase the recreational value for anglers, but they have negatively affected native taxa that in turn be important to other fisheries (Jeschke et al. 2022). Likewise, nuisance caused by invasive aquatic macrophytes may be perceived as more problematic by residents than by visitors (Thiemer et al. 2023). Invasive trees can be aesthetically pleasing (Vaz et al. 2018), while simultaneously eliminating suitable habitat for native insects (Litt et al. 2024), birds (Grzędzicka and Reif 2020) or plants (Sádlo et al. 2017), or radically altering ecosystem services (Romero-Blanco et al. 2023; van Wilgen et al. 2022). Similarly, an environmental non-governmental organisation might favor eradication of an invasive plant, aiming to reduce its impacts on native flora, while local farmers would rather plant it to increase soil quality (Benediktsson 2015; Lojeski and Plante 2021). Incorporating active stakeholder engagement, such as participatory workshops or citizen science initiatives, is vital for developing effective management strategies by fostering collaborative knowledge production and integrating diverse perspectives into decision-making (Novoa et al. 2018; Nuñez et al. 2022). Since invasion management is an adaptive process requiring a governance structure, legal framework, and typically public support, it is crucial to study biological invasions as part of a social-ecological system (Richardson 2011; Frost et al. 2019; Hui and Richardson 2019; Heger et al. 2021; Groom et al. 2021).

Social-ecological systems are complex adaptive systems comprising humans and nature as well as their relationships (IPBES 2019). They are dynamic and open (i.e., they change in reaction to external drivers through time) as well as being context-dependent and producing emergent phenomena (i.e., characteristics that exist due to the interplay of the system components) (Preiser et al. 2021). Social-ecological networks (SENs) (see Glossary, Supplement 1) are one method used to understand relations (i.e. interactions) between entities, next to social-ecological system frameworks (e.g. common pool resource governance (Ostrom 2009)), which take a more qualitative approach, and system dynamic models (e.g. Stella (iseesystems.com)), which model causal relationships between variables. SENs can incorporate both qualitative and quantitative data in a structured way. They can disentangle direct and indirect connectivity and interdependencies between human-nature interfaces and can inform management initiatives at multiple scales (Bodin 2017; Beever et al. 2019; Kluger et al. 2019; Sayles et al. 2019; Kluger et al. 2020; Felipe-Lucia et al. 2022). SENs have been applied in the context of biological invasions (Table 1) and, for example, have identified management actions required to ensure a functioning ecosystem (e.g. Ortiz et al. 2015).

However, there is a lack of guidance on how to apply SENs in a standardized manner to enhance our understanding of biological invasions and advancing their wider application. Here, we explore how SENs can clarify and synthesize the various impacts and related processes associated with invasive species. We introduce networks and their applications (section 2), illustrate key aspects for constructing and analyzing SENs in an invasion context (section 3), and discuss the most promising opportunities this methodology presents to invasion science (section 4). We demonstrate that SENs provide an exciting avenue for future work that allows for holistic analysis of complex interdependencies surrounding the impacts and management options of invasive species as well as having the potential to give new insights into key questions within the field of invasion science (Musseau et al. 2024).

2. A brief overview of (social-ecological) networks

Since Euler's solution to the seven bridges of the Königsberg problem (Euler 1741), graph theory (see Glossary, Supplement 1), which forms the basis of structural network analysis, has evolved from the mathematical study of pairwise relations to the study of complex interactions. Network approaches have been applied across multiple disciplines, from mathematics to engineering and the humanities (Boccaletti et al. 2006). In its simplest form, a network (also commonly termed a "graph") consists of nodes (alternatively termed "vertices") (see Glossary) that are connected by links (also termed "edges" or "ties") (see Glossary). Networks can be found everywhere, for example transportation networks, such as train stations (nodes) connected by tracks (links), or the animal nervous system in which neurons (nodes) are connected through synapses (links). More abstract semantic networks show theoretical concepts (nodes) and the relations between them (links), while co-authorship networks show scientists (nodes) and their scientific collaborations (links). We can distinguish between networks that aim to analyze topological structures, how they came to be or what effects these have, based on graph theory, and those that represent causalities or ontologies. In this paper, we will refer to the former as interaction networks, where causal relationships are not explicitly depicted (although they can be implicitly included, e.g. in the case of food webs).

Social network analysis evolved as a discipline in the early 20th century, to investigate the structure of relationships among individuals. It is used to understand social structures and hierarchies, information flows, influence and power dynamics, and other aspects within social systems (McLevey et al. 2024). It is an important methodology for understanding how and why humans behave the way they do, and therefore how phenomena such as social norms, collective action, and self-organization emerge in different contexts (Bodin 2017; Teodoro et al. 2021). Social network analysis has also been applied to other animal species, for example to study the composition and dynamics of bird groups (Silk et al. 2014), the invasibility of fish assemblages (Beyer et al. 2010), or cultural behavior of dolphins (Mann et al. 2012).

In invasion science, ecological network analysis has been applied to assess the impacts of invasive species on biotic interactions such as pollination (Vilà et al. 2009), community assembly (Strong and Leroux 2014; David et al. 2017), and modelling the spread of invasive species across discrete habitats (Woodford et al. 2013; Ferrari et al. 2014). The strength and frequency of interactions among network components have been shown to affect the invasion success and impact of NNS, and a network's stability (see Glossary, Supplement 1) can give insights into the invasibility of a system (Frost et al. 2019; Groom et al. 2021; Hui and Richardson 2022, p. 209). Stability is the ability of the system to move towards or stay close to an equilibrium (see Glossary), i.e. the system's ability to recover from change (Biggs et al. 2021; Frost et al. 2019; Hui and Richardson 2022). More specifically, we can talk about demographic stability as in population numbers and structural stability as in interactions between system components, such as in a food web (Hui and Richardson 2022, p. 209). If demographic stability ceases, the population will crash and die out, whereas if trophic linkages in a food web are lost (such as between producers and consumers), the entire system ceases to function.

Networks have many different topologies which can be defined via their nodes, links, layers (see Glossary, Supplement 1), and temporal scales (e.g., bipartite, directed, dynamic, see Fig. 1a). There are also specific networks from different disciplines (e.g. food webs or sociograms). Unipartite, bipartite, and multipartite networks (see Glossary) refer to the number of node types within the network. Directed (as opposed to undirected) (see Glossary) networks have links coming from and going to specific nodes (e.g. food webs), and can include reciprocal links. Weighted networks (see Glossary) assign a value to the link (e.g. the amount of biomass being consumed or the number of times a pollinator visits a plant); and nested networks (see Glossary) are in essence networks within nodes of networks (e.g. food webs within connected ponds, Fig. 1a). These networks and topologies can be combined as layers (a layer corresponds to one network) in multilevel or multilayer networks (see Glossary). For example, a network can include layers of (i) different species interactions (e.g. antagonistic, mutualistic) that are linked to each other by species nodes (i.e., multiplex networks) and (ii) human interactions, such as communication between managers (within-layer link; Fig. 1b), and how humans interact with the different species (between-layer link; Fig. 1b).

Social-ecological networks (SENs) can thus use different combinations of the concepts above, but are, in essence, networks that integrate actors or entities (nodes) from both the social and ecological realms, interacting via social-social (SS), social-ecological (SE) and ecological-ecological (EE) links (*sensu* Bodin and Tengö 2012; see Fig. 1b for an example). SENs have been used to better understand nature's contributions to people (Dee et al. 2017; Felipe-Lucia et al. 2022), improve sustainable resource use (Barnes et al. 2019; Ortiz and Levins 2017; Zador et al. 2017), and inform measures for climate-change adaptation (Salgueiro-Otero et al. 2022).

We carried out a scoping literature review (see details in Supplement 2) and found 30 studies applying SENs to problems involving biological invasions. These studies applied a broad range of approaches to constructing and analyzing networks, stemming from different fields and theories. 18 studies (Table 1) used networks with interactions between actors (nodes), including biophysical and social entities, based on graph theory. The remaining 12 studies (see Supplement 2, Table 1) applied a range of tree graphs, causal influence diagrams (i.e. causal networks, see Glossary, Supplement 1), semantic networks, and decision-making diagrams, as well as five studies using Bayesian networks (see Glossary). Given the vast range of possible SEN approaches, we will in the following sections focus on those that seem most promising for invasion science.

3. Constructing and analyzing social-ecological networks in an invasion context

Step 1: Conceptualize the SEN

The start of every SEN is a clearly defined aim – a research question, hypothesis, or management goal. Based on this aim, the social-ecological system under study should be conceptualized and characterized in an iterative process (Fig. 2). Prior knowledge or sufficient time to investigate the social-ecological system is needed to identify and define the system boundaries and components. Ideally, this knowledge is co-produced with stakeholders within the system (Moallemi et al. 2023). The temporal and spatial limits of the study should be specified prior to data collection. Depending on data availability, however, these limits may need to be adjusted throughout the study. The different actors/entities and interactions within the system must be defined in terms of nodes and links (Fig. 1b). If relationships are causal (such as impacts), a causal influence diagram can be constructed. Non-causal relationships and interactions, such as movement or communication, are frequently included in SENs as directed or undirected links (Table 1). Alternatively, multilevel networks can help incorporate the many different interactions and actors; and for analyses based on graph theory, every layer in a SEN corresponds to one type of link (Fig. 1b). Identifying and defining the relevant system components can be aided with guiding questions (Fig. 2) and linked back to the aim.

With all their layers and components, SENs offer several ways to include invasive species (Fig. 1b): as nodes within the ecological network, as node attributes (see step 2 for details on attributes) of an invaded habitat node, or as links, for example if the research aims to model the spread of the invasive species across a landscape comprising discrete habitat patches serving as nodes. Invasive species can also be modelled as link attributes of an infected vector, which when made dynamic, models how invasive species can move through the network of interactions (as in a contagion network). All the above-described components can be contemplated conceptually, but a SEN should be simplified to an appropriate level of complexity considering the aim and available resources. In other words, beware the trap of complexity!

Step 2: Construct the SEN

Following conceptualization, the underlying data for the nodes and links must be gathered. Existing data from databases, impact assessments, or grey and scientific literature can be used, as can newly collected data. Interviews and surveys can provide valuable insights from stakeholders within the system under study. The data must then be organized in a network structure to allow for the subsequent analysis. Adjacency and incidence matrices (see Glossary, Supplement 1) are sometimes used, but we will focus on node and edge lists here (see Glossary). Node lists contain all node IDs as the first column (each row being one node) and the subsequent columns can contain different attributes of this node. Node attributes constitute any other relevant information or characteristic pertaining to the node, e.g. demographics for social nodes, population densities for species, or other quantitative or qualitative variables. The corresponding edge list contains the two involved nodes for each link in the first two columns (each row represents one link), and the subsequent columns can contain link attributes (i.e. any other relevant information one wishes to include). An example, with a focus on impacts of non-native vertebrates in Hawaii on native species and people (illustrated in Fig. 3) can be found in Supplement 3. Data analytics and AI tools can assist in integrating complex datasets from multiple sources, such as biodiversity databases, remote sensing platforms, or citizen science projects. These tools can help synthesize large amounts of information into actionable inputs for SENs.

Step 3: Analyze the SEN

Social-ecological interaction networks can be analyzed topologically by identifying different attributes and structures within the network. Centrality measures (see Glossary, Supplement 1), such as degree or closeness, inform on the relative importance of nodes. Diameter, density, (average) path length and transitivity are topological network metrics (see Glossary) that can be used to understand and compare network attributes. These metrics can be linked to different theories and frameworks in the social and natural sciences (e.g. see above; Hui and Richardson 2022; McLevey et al. 2024: Biggs et al. 2021). Finding groups in SENs can be done by applying algorithms like walk trap, page rank, or random walk (cf. Hashemi and Darabi 2022; Farine and Whitehead 2015) and dominator tree analysis can identify bottlenecks within directed networks (e.g. Kluger et al. 2019). Motifs (see Glossary) are specific recurring structures (subgraphs), consisting of the specific configuration of links among two, three or more nodes (Milo et al. 2002). They can inform on actors' abilities to manage shared resources (Bodin and Tengö 2012) and on social-ecological fit (Guerrero et al. 2015; Bodin et al. 2016; Epstein et al. 2015).

Motif analysis can be done by comparing the number of motifs in the SEN compared to a random network, or by using e.g. exponential random graph models where varying levels of “randomness” can be controlled for – and where node attributes can be accounted for (for a detailed description of how these models work and how they can be applied to analyzing networks, see McLevey et al. 2024). Such models can also be used to (i) analyze how the network structure arose (using the network as the response variable), (ii) understand how the network structure contributes to certain phenomena (using the network as a predictor variable), or (iii) how links are likely to emerge given the existing structure (like a simulation). Other types of models used for network analysis include contagion or diffusion models, where the spread of something (e.g., money, influence, an invasive species) across a network is analyzed (e.g. Haak et al. 2017). Block modelling looks at the position of structures within multi-relational (or multilevel or multilayer) networks (e.g. Harrer et al. 2013), whereas agent-based models (e.g. Baggio et al. 2016) permit analysis of multiple interrelated processes and can either be used to explain how a network was formed or create network-based scenarios.

A breadth of theories and frameworks from invasion science, social-ecological systems research and other disciplines can be applied in combination with the SEN methodology (Biggs et al. 2021; Hui and Richardson 2022). Next to insights already gained on how NNS affect food webs, the concept of social-ecological fit (see Glossary, Supplement 1), stemming from social-ecological systems research, seems particularly useful. It refers to analyzing whether the ecological interdependencies are mirrored or complimented by the managing social structures (e.g. Alexander et al. 2017). For example, if connected invaded habitats are managed by two different social actors, it is key that these actors at least communicate if not cooperate in order to match the ecological interdependencies. If no interaction between the social actors occur, it is likely that the management efforts will not be effective, as reinvasions from the respective habitat patches may occur, or different management actions counteract each other.

All network types, both causal and interaction networks, can be analyzed using path analysis, which explores how to get from point A to B in a network and gives insight into connectivity and indirect effects. Loop analysis (a specific type of path analysis, see Glossary, Supplement 1) is applicable to networks containing cycles, evaluating how one completes a loop from point A and back via other nodes and links in the network. Causal loop analysis can give insight into the stability of a system and the direct and indirect effects of external perturbations (stressors) (Levins 1974). More specifically, does a change in one state variable (node) increase, decrease, or have no effect on the other state variables in the system? The benefit of loop analysis is the relatively low resolution of data required (whether the effect of the interaction on the state variables is positive, negative, or neutral) and the ability to consider the system as a whole. In the context of biological invasions, causal loop analysis can be performed to understand whether NNS contribute to positive or negative feedback loops, what happens if interactions change (i.e. go from positive to negative or neutral, and vice versa) and with which changes in state variables (nodes) and interactions (links) the system loses stability (Scotti et al. 2020).

A multitude of software packages from different disciplines exist to analyze networks. Food-webs can, for example, be analyzed as mass-balanced models using Ecopath with Ecosim (Christensen and Pauly 1992; Christensen and Walters 2004); neural or genetic networks can be analyzed with software such as Cytoscape (https://cytoscape.org); and examples of software packages from the social sciences that help gather, organize, and analyze data are Gephi (https://gephi.org) and UCINET (Borgatti et al. 2002) with integrated NetDraw (Borgatti 2002). Alternatively, R provides many packages to visualize and analyze different network types, for example igraph (Csárdi et al. 2024), which allows the assembly of a network item based on node and edge lists as well as adjacency and incidence matrices, and many tools to characterize, quantify and visualize observed network structures. The ggraph package (Pedersen 2017) offers additional visualization options, based on ggplot2 (Wickham 2016). Many more options for network analysis across multiple formats exist, see the curated list of Awesome Network Analysis (Briatte et al. 2024).

4. Opportunities for social-ecological networks in invasion science

The SEN methodology enables insights into varying aspects of invasion science. In principle, one SEN (i.e. one model of a specific social-ecological system conceptualized as a network) can give insights into introduction pathways, invasion success, invasibility of a system, impacts, and management of invasive species (i.e. the major themes of invasion science, cf. Musseau et al. 2024), as these aspects are intrinsically linked to one another. Which specific aspects a given SEN addresses is based on how nodes and links are defined, and what data is included. In the following, we present particularly promising opportunities of the SEN methodology in invasion science.

Past, present, and future introduction pathways of NNS can be modelled using spatial networks, with nodes representing spatially discrete regions and links indicating human-mediated dispersal (Table 1). This has been done for trade networks to investigate pathways and thus possible introduction risks, e.g. for the pet trade (Sinclair et al. 2021) or for pest species associated with the cassava trade (Wyckhuys et al. 2018). It has also been done to identify possible dispersal hubs of marine invasive species based on ship movements (Letschert et al. 2021) or secondary introductions through, for example, angler movement between lakes (green highlights in Table 1). To better understand the conditions that lead to successful introductions, networks of the cultural and economic contexts of invasions can be constructed, such as by comparing non-native flora similarities across former empires in the context of colonialism (Lenzner et al. 2022). Therefore, links between locations could account for similarities, transport routes or many layers of relations in a multiplex network. Alternatively, node attributes of locations can reflect conditions of introduction in the above-described networks. This can facilitate the identification of factors that determine successful introductions of invasive species, ultimately serving as a suitable tool for risk assessment.

Location-specific SENs can inform on the invasion success of different species as well as the invasibility of the invaded social-ecological system. Nested networks allow modelling a specific SEN within each node of a spatially connected network (as described above). Building on Haak et al.'s (2017) food webs nested within lakes and expanding to larger spatial scales, movement between locations could be combined with a specific SEN for each location. For example, trophic interactions within a food web may give insight into the biotic resistance of a system, whilst additional interactions with humans (e.g. whether humans use the NNS, find it charismatic, or have any precautions against it) allow for a better understanding of the mechanisms surrounding invasion success and invasibility. Combining transport networks (which generate propagule pressure and thus increase invasion success, cf. Jeschke and Starzer 2018) with information about local systems and their context along the invasion stages into one cohesive network will allow for more holistic insights into the invasion process and what determines successful invasions, as well as informing risk assessment and management.

Mapping out and visualizing the interactions and effects of invasive species shows the cumulative, direct, and indirect invader impacts, and can be used as a communication tool to foster knowledge exchange, aid decision-making among stakeholders, and increase public awareness. As a case study, we used S/EICAT(+) assessments and similar relevant publications to create a SEN of non-native vertebrates in Hawai'i (Fig. 3). The direct and indirect beneficial and deleterious impacts are shown in a causal network of different groups of native and non-native species as well as stakeholders or social-economic concepts, such as culture or agriculture, and techno-physical entities, such as airports, as well as the different underlying mechanisms (Fig. 3; details on this case study are provided in Supplement 3). Predation is a common mechanism of a deleterious impact on biodiversity by NNS, leading to the reduction or loss of a native species, which in turn negatively impacts culture and recreation. The Hawaiian crow or 'Alalā, for example (Fig. 3b), is a native forest bird species that spreads the seeds of fruits – an important function for forest habitat maintenance and promoting biodiversity. It also has an important cultural role in Hawai'i as a spiritual family guardian and transporter of souls, and it is valued by bird watchers and wildlife enthusiasts. Two non-native predators (feral cats and mongooses), as well as habitat loss and other compounding factors, have caused the Hawaiian crow to become extinct in the wild, therefore posing losses to biodiversity, culture and recreation, affecting nature and people on Hawai'i in different, but connected ways. This is especially relevant as efforts to reestablish wild populations are ongoing (https://dlnr.hawaii.gov/alalaproject).

Networks can be used to simulate different future scenarios and make predictions that can inform policy and management. The efficiency of invasive species management under different scenarios has been assessed using agent-based models (Yletyinen et al. 2021), and how people will react to new environmental conditions has been modelled using scenario-based adaptation pathways (Salgueiro-Otero et al. 2022). Many more possibilities for network-based scenarios exist, such as causal influence diagrams for analyzing the impact of different changing environmental factors on Alaskan forests (Wolken et al. 2011) and predicting the impacts of people's perception on "nuisance" plant management using Bayesian belief networks (Thiemer et al. 2023). Interaction networks can be made dynamic with longitudinal data (i.e. different networks for different time points), thereby synthesizing historic development and supporting predictions of how the network may change in the future. This can also be done by specifically adding and removing nodes and links, for example adding an invasive species in the form of an additional node with its potential (i.e. biologically plausible) interactions (links) (cf. Penk et al. 2017; Fumero-Andreu et al. 2024) or removing impacted species to simulate extinctions and comparing the structural changes (i.e. network metrics). Alternatively, loop analysis can be utilized to simulate the knock-on changes within a network when interactions (links) and state variables (nodes) change.

Identifying the differences and similarities across different invaded social-ecological systems can give important insights into effective management along the invasion process. Network metrics enable the comparison of vastly different systems, assuming the network is similarly conceptualized and constructed using the same type of system components (nodes and links). This can be done to investigate (1) why an invasive species is or is not able to establish in different systems, (2) what governance structures lead to better management, and (3) why management of an invasive species in one region is more effective than in another (Alexander et al. 2015; Alexander et al. 2017; Sandström and Rova 2010). Other comparative methods include weighted topological overlap, which directly compares the structure of two networks, or clustering coefficients such as modularity and density (see Glossary, Supplement 1), which are just some of the network metrics that can give insight into how tightly connected a network is (Gysi and Nowick 2020). The frequency of specific motifs can also be compared across networks, however theory on what these motifs mean in an invasion context must be developed. Building on biotic resistance and theory on environmental governance, we can assess which SEN structures prevent or facilitate invasions, as well as which structures contribute to successful impact mitigation.

5. Conclusion

Given all the potential nodes and links that can be included in a network, from species to governing bodies, energy to causation, and a vast range of analysis methods already developed in different fields, the SEN methodology allows for comprehensive understanding of invasions. SENs that incorporate invasive species can inform on risk assessment and model future scenarios. They can be utilized as a synthesis tool as well as to communicate and engage with stakeholders to raise awareness and improve management. It is time to more fully explore the many opportunities of SEN analyses for biological invasions, as these pose great potential in tackling the complex interactions and impacts of NNS. The ability of networks to, in principle, incorporate all relevant system components, throughout different spatial and temporal scales, enables a holistic analysis of social and ecological interdependencies within real-world invaded systems, subject to multiple drivers of change.

While SENs offer numerous benefits, the approach also presents several challenges and needs for further development in areas with relevance to invasion science. Specifically, SENs require a considerable amount of (often complex) data, which implies that their extraction and subsequent analysis can be time-consuming. On the other hand, the advantage of networks is that they can be continuously expanded, making them dynamic and improving their accuracy over time and/or space. If the focal research question is sufficiently specific, the SEN can be of tractable complexity, enabling more sophisticated analyses of, for instance, well-defined subsystems. The data hunger of SENs is already becoming less problematic in the current age of big data. Large language models and other AI tools might provide additional support in this context, either by streamlining data collection from different sources or inferring interactions, based on traits and other relevant information, when these are unknown (e.g. Fricke et al. 2022). It is also important to realize that SENs can serve as powerful synthesis tools for integrating different data and information sources and extracting key insights relevant to researchers across disciplines and diverse stakeholder groups, thus facilitating inter- and transdisciplinary exchange. SENs explicitly facilitate the incorporation of different perspectives and are tools for turning data and information into knowledge (cf. Jeschke et al. 2019).

There is no single right way to construct and analyze SENs, but crucial decisions must be made on which system components to include and how to define network boundaries. Assumptions that one inevitably makes about the focal system should be based on prior knowledge of the system, ideally drawing on insights of actors that are part of the system, and by conducting participatory research. SENs force us to make our assumptions around the interactions within and across what were previously considered fundamentally different components of the human-nature relationships associated with invasive species. By connecting different disciplines, engaging with diverse stakeholders, and synthesizing knowledge across realms, SENs will support our efforts to better understand biological invasions and their impacts, as well as how to improve their management.

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AUTHOR CONTRIBUTIONS

FSR, FR and JMJ conceived the general ideas which were discussed and revised by all authors in a workshop in Berlin in November 2022. Additional online and personal exchanges in several meetings by FSR, FR, ÖB, TE, MSF, LCK, GL, BL, RLM and JMJ further refined the ideas. FSR carried out the scoping literature review and categorization of papers for the table with help from RLM. FSR and TE collected and assembled the data for the S/EICAT(+) case study, with input from JMJ. FSR created the figures, with input from JMJ and other authors. FSR led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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Table 1: Published studies of social-ecological networks that incorporate biological invasions (for an overview of the search protocol and inclusion criteria, see Supplement 2). In the column Research focus, *studies highlighted in yellow focus on biological invasions as opposed to studies that focus on other topics yet happen to include biological invasions. The column* Relevant theme(s) in invasion science *indicates which general theme(s) are addressed by each study, based on Musseau et al. (2024): pathways; invasion success, incl. spread, and invasibility; impact; or management. In the column* Nodes and links, *studies highlighted in purple indicate a focus on governance networks, and those in blue on spatially explicit networks of invasive species spread; also in this column, E and S refer to ecological and social nodes, respectively; thus, EE are ecological links, SS social links, and SE social-ecological links. In the column* SEN articulation *(sensu Kluger et al. 2020), type I refers to networks with only one type of link (either EE or SS), type II to networks with two types of links (either EE+SE or SS+SE), and type III to networks with all three types of links (SS, EE, and SE).*

Study(^{s} and ^{u} indicate if found with systematic or unsystematic search)	**Research focus**	**Relevant theme(s) in invasion science**	**Network type**	**Nodes (E, S) and links (EE, SS, SE)**	**SEN articu-lation**	**Invasive species**	**Data source(s)**	**Network analysis**	**Key findings in brief**
Alexander et al. (2017)^{s,u}	Governance networks in marine protected areas (MPAs); Social-ecological fit	Management, spread	Multilevel, directed	E - MPAs S - Governing organizations EE - Ecological connectivity SS - Information SS - Management SS - Collaboration SE – Management strategies	Type III	*Pterois miles* and *P. volitans* as node attribute	Sociometric survey, semi-structured interviews, legal documents	In-degree centrality, betweenness centrality, density.	Multilevel vertical ties (local–national) enhanced fit, addressing functional misfits (e.g. invasive lionfish removal).
Haak et al. (2017)^{s,u}	Angler movement data with ecosystem	Pathways, impact, management	Directed, weighted, nested	E - species E - lakes/reservoirs	Type II	*Bellamya chinensis*	Angler interviews	Contagion models (Angler movement)	Expanded on management implications, network

	models to evaluate the risks and impacts of species invasion			EE –trophic interactions SS – angler movement SE - fishing		as node, node and link attributes		Ecopath models (ecosystem trophic interactions)	structure, and ecosystem-level effects of the invasive species (*Bellamya chinensis*)
Fried et al. (2022)[s]	Fit between environmental governance and biophysical systems	Management	Bipartite, directed, weighted	E - water quality, invasive species S - managing actors EE – issue interdependencies SE - management actions by actors to address issues	Type II	Unspecified node	Text analysis, internet search	Bipartite exponential random graph models (ERGMS)	Addressing environmental problems holistically—by considering their interdependencies and leveraging specialized or regional actors—leads to better outcomes for governance and sustainability
Contesse et al. (2021)[s]	Non-human agency	Impact, management	Ego network	E – *Bagrada hilaris* S - stakeholders SE - interactions	Type II	*Bagrada hilaris* as node	Interviews	Qualitative	The study highlights how *Bagrada hilaris* acts as a non-human agent, catalyzing sustainability transitions by reshaping pest management networks
Sinclair et al. (2021)[s]	Introduction pathways via the pet trade, with attention to species transport dynamics and risk factors	Pathways	Directed network	S - Actors and entities involved in pet trade SE - Relationships and transactions in the pet trade (e.g. trade volumes, regulatory interactions)	Type I	Unspecific, vertebrate pet trade (fish, amphibians and reptiles) as links	Scientific literature, databases	Qualitative	This study highlights the importance of regulating pet trade pathways to mitigate invasion risks and emphasizes the interconnected

									roles of stakeholders in facilitating or preventing introductions
Ashander et al. (2022)[s]	Large-scale management of invasive species, control strategies, ecological information	Management, Pathways	Directed, weighted	E - lakes SS - boater movements	Type I	*Dreissena polymorpha* as node and link attributes	Boater movement data (2014–2017), zebra mussel infestation status	Metrics Degree, H+A, Betweenness centrality, ILP optimization	Network-based management using Degree and H+A centrality achieved near-optimal performance, especially under constrained budgets.
Drake et al. (2010)[s]	Modeling vector movement, angler activity	Pathways, spread	Directed, weighted	E - Angler origins/destinations (lakes) SS - Movements via road network	Type I	*Dreissena polymorpha* and *Neogobius melanostomus* as vectors (angler movements)	Surveys, road networks, lake attributes	Negative binomial and zero-inflated spatial interaction models; Least-cost routing; Distance-decay models GLM	Least-cost routing outperforms Euclidean models in explaining vector movements. Lake size and sportfish richness strongly influence destination attractiveness.
Escobar et al. (2019)[u]	Lake connectivity and risk analysis	Pathways, spread, management	Directed, weighted	E - lakes SS - angler movement SE - Watercraft movement	Type I	*Nitellopsis obtusa* as link attribute (vector as proxy)	Survey data from Lake Koronis (2013-2014)	In-degree scores	Identified "super receiver" lakes, like Rice Lake, based on watercraft flow; high connectivity increases invasion risk and proposed network guided management

Jentsch et al. (2020)[s,u]	Effectiveness of social incentives, direct interventions, and quarantines to mitigate the spread of invasive species	Pathways, management	directed	E - Campgrounds (with tree attributes) SS – camper movement	Type I	*Agrilus planipennis*, *Anoplophora glabripennis* as attributes in pest spread model	Campground reservation data	Pest spread model (mechanistic metapopulation model)	Social incentives (e.g. reducing firewood transport) are effective at slowing spread locally but less so for reducing total infestation.
Letschert et al. (2021)[u]	Risk assessment of invasive species dispersal through ship traffic in the GMR, biofouling	Spread, management	Directed, weighted	E - anchorages at port locations SS - ship routes	Type I	*Bugula neritina*, *Watersipora subtorquata* as link attribute (vector of fouling species as proxy)	Port and tourism data from Galapagos National Park (DPNG), ship movement from MarineTraffic website	Based on ship routes, WSA, and vessel types; dispersal model calculated cumulative DS	Identified highly connected hubs (e.g. Port Santa Cruz and Port Baltra) as key dispersal nodes; recreational and passenger vessels play dominant roles in non-native species spread;
Lubell et al. (2017)[s,u]	Management and governance of invasive species, stakeholder cooperation, trust	Management	Undirected	S – stakeholders SS – communication	Type I	*Spartina* sp. (hybrid population) as topic of network, not explicit	Survey, interviews	Centrality metrics, core-periphery analysis	Effective governance relies on coordinated research, consensus-building, and balancing conservation trade-offs.
McAllister et al. (2015)[s]	Management pest species and disease outbreak, governance	Management	Bipartite and multilevel	S - individuals, S – groups SS – communication SS - participation	Type I	*Mycosphaerella fijiensis* as topic of network	Surveys, interviews, reconstructed response network	Exponential Random Graph Models (ERGMs)	Local coordination drove success, but cross-scale interactions were limited, highlighting the

									reliance on informal networks
Nourani et al. (2018)[u]	Management, adaptive co-management, social learning	Management	Directed	S - Task force members (state/county/municipal staff, arborists, citizens, etc.) S - cooperation/ information	Type I	Emerald Ash Borer (EAB) as topic of network	Learning assessments (cognitive, normative, relational), network surveys, interviews, document analysis	In-/out-degree centrality, relational learning	Task forces improved learning and collaboration, with outcomes varying by local ecological and social contexts.
Omondiagbe et al. (2017)[u]	Management of invasive species, collective action	Management	Directed	S - Conservation groups S – government S – stakeholders SS - communication	Type I	*Rattus* *exulans*, *R. norvegicus*, *Mus musculus*, *Macropus* spp, *Erinaceus europaeus*, *Oryctolagus cuniculus*, *Felis catus* as topic of network	Survey	Organizational network analysis (ONA); centrality, density metrics	Conservation and ISM activities were networked but sparse; strong influence by central stakeholders.
Rebaudo et al. (2011)[s]	Modeling and educational intervention on invasive pest management	Management	Pest spread dynamics (based on ABM)	S – villages, farmers SS - human movement SE - Pest dispersal between villages via farmers	Type I	*Tecia solanivora* as link attribute (human-mediated long-distance dispersal as proxy)	Scientific studies, Simulation, GIS, participatory surveys	Agent-based model	Farmers' movements and pest control knowledge significantly influence pest spread speed

Wyckhuys et al. (2018)[s,u]	Biological control of invasive pests	Pathways, management	Dynamic, directed, weighted	S – countries SS - trade in Casava	Type I	*Phenacoccus manihoti* and *Anagyrus lopezi* as link attribute (vector as proxy)	Field surveys, trade data	Dynamic network analysis	Effective biological control using *A. lopezi* mitigated *P. manihoti* impacts on cassava production in SE Asia.
Martínez-Sastre et al. (2020)[s]	Farmers' perceptions and knowledge of natural enemies for biological control	Management	Directed, weighted	E - non-human species EE – trophic interactions SS - Perceptions of trophic interactions among natural enemies	Type I	*Cydia pomonella* as node	Surveys, questionnaires	Weighted degree & betweenness via Gephi and NodeXL, Spearmans rank correlation (rho)	Farmers valued natural enemies more for croplands in general than for cider-apple orchards. Education and farming experience influenced perceptions.
Ortiz et al. (2015)[s,u]	Management and control strategies for lionfish invasion	Management	Signed, directed	E – species, functional groups S - fishers EE – trophic interactions	Type I	*Pterois volitans* as node (predator and competitor)	Literature review, modelling	Qualitative loop analysis Stability criteria via Routh-Hurwitz and Levins' criteria	Coral restoration programs enhance ecosystem stability. Harvesting lionfish is sustainable if groupers (natural predators) are not exploited.

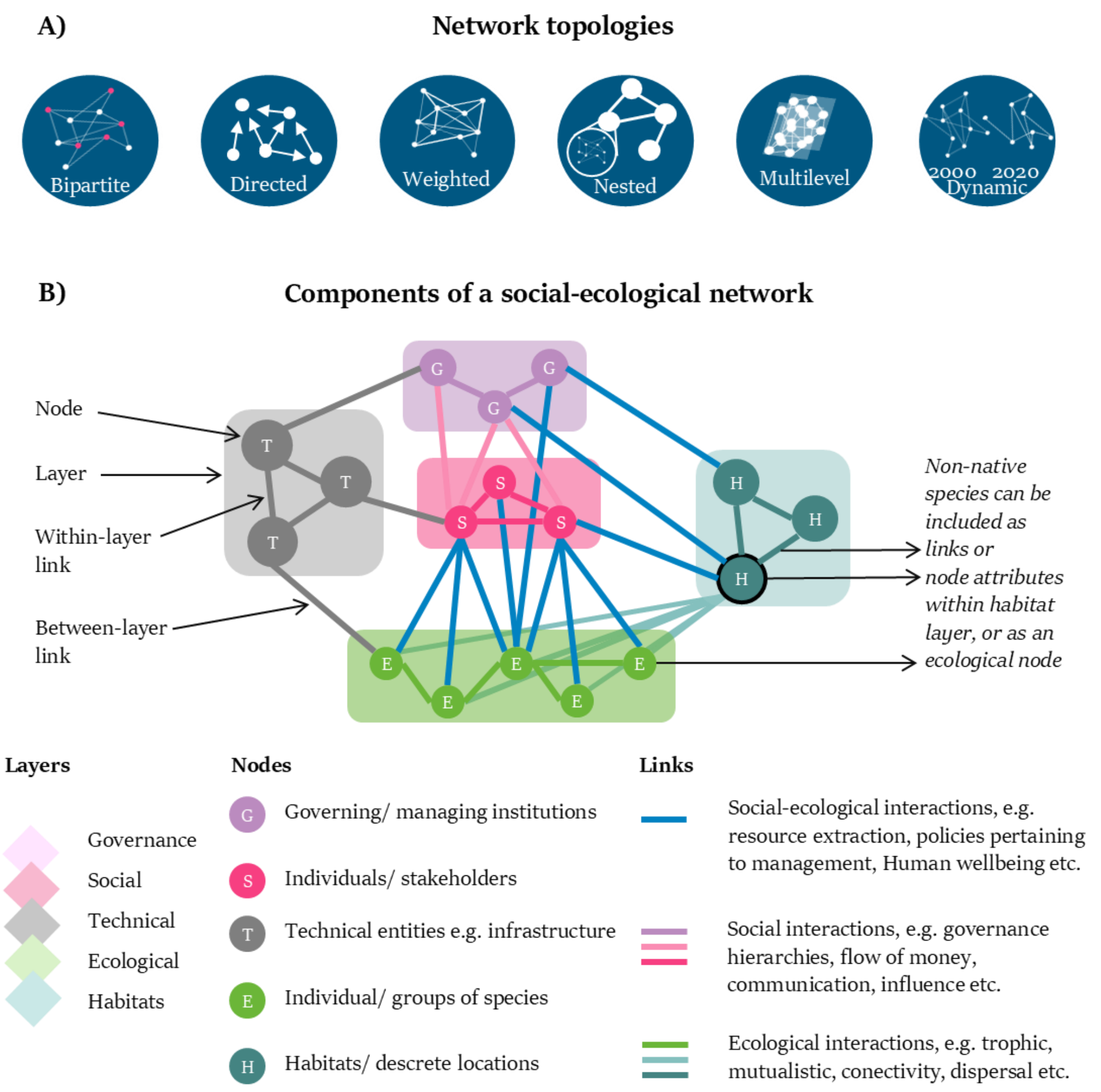
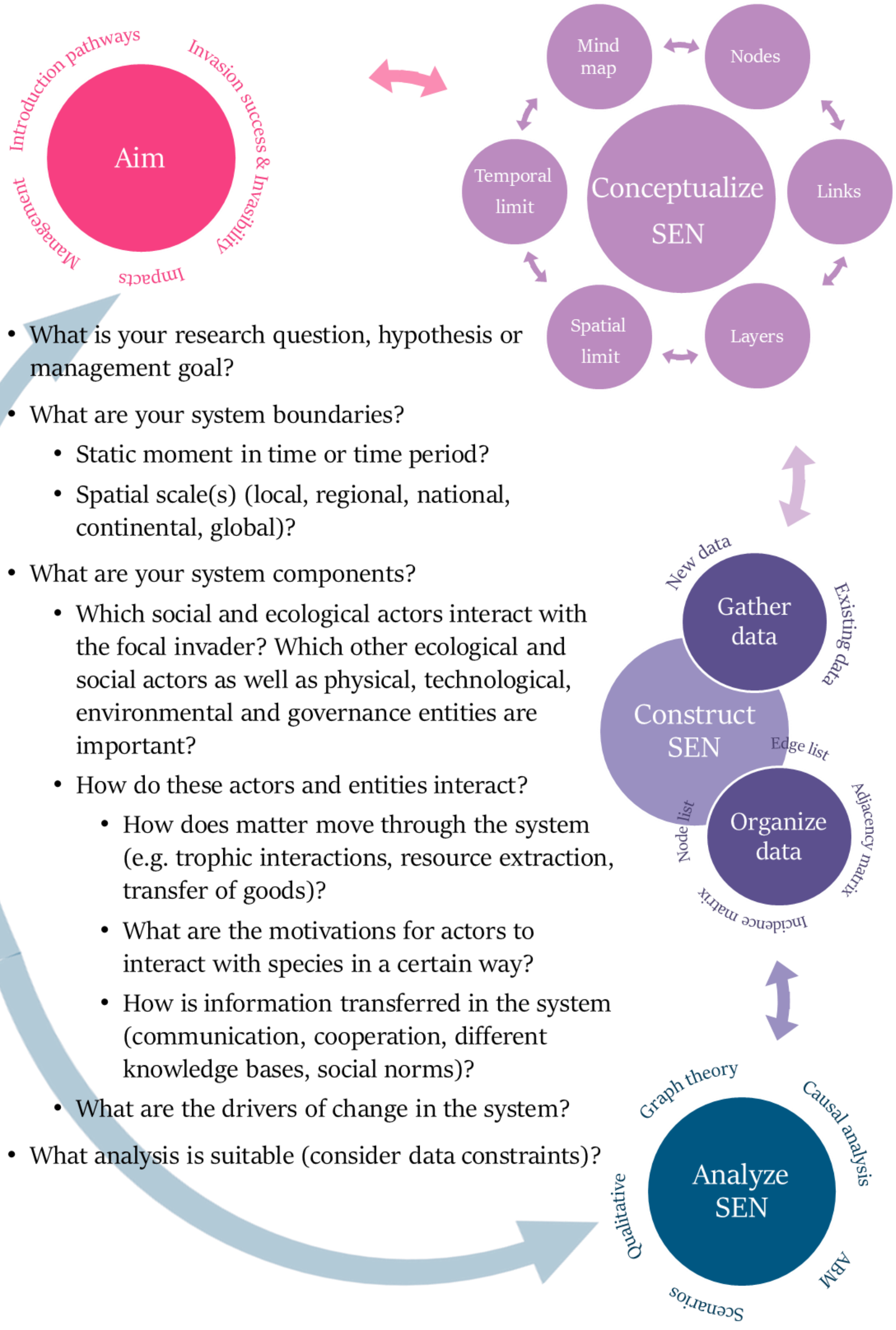


Figure 1: **A)** Illustrations of different simplified **network topologies**: *Bipartite:* a network where links only exist between two different node types. *Directed:* networks where links have a direction i.e. going from one node to another, including reciprocal relationships. *Weighted:* links have different strengths. *Nested:* networks within nodes of another network. *Multilevel:* multiple connected networks with a given node and link type per layer, with further links between the layers. *Dynamic:* Networks with a temporal component, e.g., the structure of the network may change at different points across time. **B)** Schematic representation of different **components of a social-**

ecological network with example layers and nodes as well as within- and between-layer links.



- What is your research question, hypothesis or management goal?
- What are your system boundaries?
  - Static moment in time or time period?
  - Spatial scale(s) (local, regional, national, continental, global)?
- What are your system components?
  - Which social and ecological actors interact with the focal invader? Which other ecological and social actors as well as physical, technological, environmental and governance entities are important?
  - How do these actors and entities interact?
    - How does matter move through the system (e.g. trophic interactions, resource extraction, transfer of goods)?
    - What are the motivations for actors to interact with species in a certain way?
    - How is information transferred in the system (communication, cooperation, different knowledge bases, social norms)?
  - What are the drivers of change in the system?
- What analysis is suitable (consider data constraints)?

Figure 2: A flowchart depicting the iterative steps involved in conceptualizing, constructing, and analyzing social-ecological networks (SENs) (from the top to the bottom), as well as guiding questions (center).

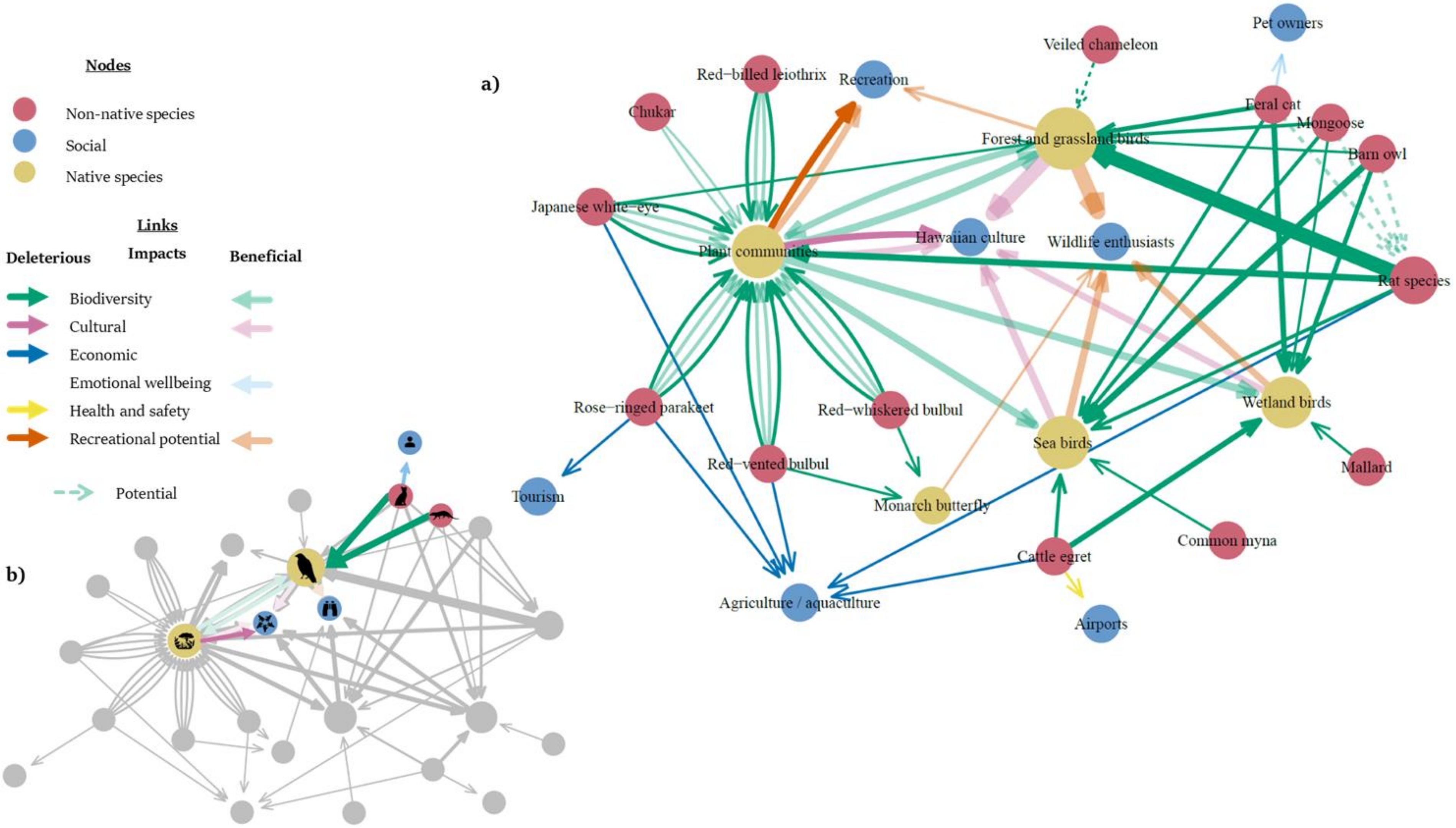

Nodes
Non-native species
Social
Native species
Links
Deleterious
Impacts
Beneficial
Biodiversity
Cultural
Economic
Emotional wellbeing
Health and safety
Recreational potential
Potential
a)
b)
Pet owners
Veiled chameleon
Red−billed leiothrix
Recreation
Chukar
Feral cat
Mongoose
Forest and grassland birds
Barn owl
Japanese white−eye
Hawaiian culture
Wildlife enthusiasts
Plant communities
Rat species
Rose−ringed parakeet
Red−whiskered bulbul
Wetland birds
Sea birds
Red−vented bulbul
Mallard
Tourism
Monarch butterfly
Common myna
Cattle egret
Agriculture / aquaculture
Airports

Figure 3: Case study illustrating the construction of a social-ecological network with a focus on impacts of non-native vertebrates in Hawaii (red nodes) on native species (yellow nodes; birds, selected invertebrates, plant communities) and people (blue nodes; including socio-economics), based on S/EICAT(+) assessments (see Supplement 3 for details). The full network **a) depicts beneficial and deleterious social-ecological impacts** (transparent lines indicate beneficial impacts), and **b) is a subset of impacts relating to the Hawaiian crow** ('Alalā) (*Corvus hawaiiensis*). The thickness of the links (width of connecting arrows) indicates the number of native species impacted. Several native species were aggregated into nodes (reflected by larger node size) representing taxonomic or functional groups; these nodes contain the following native species: Forest and grassland birds: Akikiki (*Oreomystis bairdi*), Hawai'i ʻakepa (*Loxops coccineus),* Hawai'i ʻelepaio (*Chasiempis sandwichensis*), Hawaiian short-eared owl (Pueo) (*Asio flammeus sandwichensis*), Palila (*Loxioides bailleui*), O'ahu ʻelepaio (*Chasiempis ibidis*), Hawai'i creeper (*Manucerthia mana*), ʻAkohekohe (*Palmeria dolei*), Kākāwahie (*Paroreomyza flammea*), O'ahu ʻalauahio (*Paroreomyza maculata*), Maui parrotbill (*Pseudonestor xanthophrys*), ʻŌʻū (*Psittirostra psittacea*), Laysan finch (*Telespiza cantans*), Hawaiian crow ('Alalā) (*Corvus hawaiiensis*); Sea birds: Brown noddy (*Anous stolidus*), Bulwer's petrel (*Bulweria bulwerii*), Hawaiian petrel ('Ua'u) (*Pterodroma sandwichensis*), Bonin petrel (*Pterodroma hypoleuca*), Newell's shearwater (ʻAʻo) (*Puffinus newelli),* Wedge-tailed shearwater *(Ardenna pacifica);* Wetland birds: Hawaiian common moorhen ('Alae 'ula) (*Gallinula chloropus sandvicensis*), Hawaiian coot ('Alae ke'oke'o) (*Fulica alai*), Hawaiian duck (Koloa) (*Anas wyvilliana*), Hawaiian goose (Nēnē) (*Branta sandvicensis*), Hawaiian stilt (Ae'o) (*Himantopus mexicanus knudseni*); Plant communities: ʻAla ʻala wai nui (*Peperomia subpetiolata*), Hawai'i cheesewood

(*Pittosporum hawaiiense*), Hō‘awa (*Pittosporum napaliense*), Pilo kea lau li'I (*Platydesma rostrata*), Hala pepe (*Pleomele fernaldii*), Opuhe (*Urera kaalae*).

Supplement 1: Glossary

Glossary containing key terms to the manuscript "A systems perspective: How social-ecological networks can improve our understanding and management of biological invasions" by Fiona Rickowski et al.

Adjacency matrix – a data structure for the construction and analysis of networks. The first row and column is a repetition of all nodes, and the spaces in-between can have binary, categorical or continues variables representing the links.

Agent-based models – a computational model where actors (agents) interact with other actors and the environment (patches) according to sets of rules.

Bayesian network – a specific type of network using Bayesian statistics to model probabilities as links between variables (nodes).

Bipartite network – network with two types of nodes and where links only exist between these different node types.

Causal network – a network depicting causalities (links) between variables (nodes).

Directed network – a network where links can be uni- or bidirectional.

Dynamic network – a network changing through time.

Equilibrium – a theoretical state to which the system strives.

Graph theory – the study of structures within a network of interactions), based on Euler (1741)'s mathematical solution to wanting to find a path over 7 the bridges within the then town of Königsberg, that leads across every bridge only once.

Incidence matrix - a data structure for the construction and analysis of bipartite networks or between-layer links. The first row and column are different node types, and the spaces in-between can have binary, categorical or continues variables as the links.

Layer – a sub-network of a multilayer or multilevel network consisting of one node and link type, linked to other layers in the network.

Link, edge or tie – the interaction or relationship between two nodes within a network.

Loop analysis – a type of path analysis that examines how to get from one node in a network via other nodes back again. The network must be directed and have information on whether the effects of the interactions (links) between two state variables (nodes) is positive or negative, so if it increases or decreases the other state variables.

Motifs – small building blocks within networks consisting of the links between three or more nodes (if node attributes are accounted for, or if directed links are used, the number of nodes could be less than two).

Multilayer network - a type of network consisting of multiple sub-networks (layers) that contain the same set or subset of nodes of the same type, but where each layer consists of a specific type of link. A specific subset of multilayer networks, which contain all nodes in all layers as opposed to only subsets of these, are called multiplex networks.

Multilevel network – a type of network consisting of multiple sub-networks (levels or layers) that are connected to each other (between-layer links), where each layer consists of a specific type of node and link, and the links between the layers are also of a specific type.

Multipartite network – network with multiple types of nodes.

Nested network – network conceptually embedded within the nodes of other networks.

Network metrics – descriptive variables of networks, such as:

- **Centrality measures –** indicate the potential importance of different nodes based on their location in the network, including degree centrality, closeness centrality and betweenness centrality which indicate the potential importance of different nodes based on their location in the network.
- **Density –** proportion of links compared to the maximum possible number of links.

- **Modularity –** number of groups of nodes in the network, based on the density of links between nodes.
- **Path length** is the number of steps from one node to the other along existing links.
- **Diameter –** the shortest path length of all the longest possible paths without repetition through the network.
- **Transitivity –** a measure of connectivity relating to the probability of adjacent nodes being connected.

Node or link attribute – characteristics of the entities or relationships included in the node and edge list respectively, such as demographic variables or contamination of vectors.

Node or vertex – an actor or entity within a network.

Social-ecological fit – a theory from environmental governance research on how ecological connectivity (ecological links) should be mirrored or matched by the cooperation (social links) between governing bodies (social nodes) that manage (social-ecological links) ecological entities (ecological node i.e. habitat patch), in order to sustainably manage social-ecological systems.

Social-ecological network (SEN) - a model of social (human) and ecological (nature) interactions, consisting of nodes and links.

Stability – a property of a system where the system continues to function despite external stressors (i.e. change) affecting it.

Unipartite network – network with one type of node.

Weighted network – a network where the strength/magnitude of the links is quantified.

Supplement 2: Scoping literature review

Methods, results and additional examples of papers utilizing causal social-ecological networks to study biological invasions by Fiona Rickowski et al.

A search in the Web of Science was conducted on 8 April 2024 with the following string, based on search strings applied by Evans et al. (2016) and Kluger et al. (2020):

> (ALL=(“introduced species” OR “invasive species” OR “invasive alien species” OR “IAS” OR “alien” OR “non-native” OR “non-indigenous” OR “invasive” OR “pest” OR “feral” OR “exotic”)) AND
>
> (ALL=(“social-ecological network” OR “socio-ecological network” OR “eco-social network”) OR ALL=(“ecological network” AND “social”) OR ALL=(“social network” AND “ecological”) OR ALL=(“social-ecological system” AND (“network approach” OR “network analysis” OR “network model”)) OR ALL=(“socio-ecological system” AND (“network approach” OR “network analysis” OR “network model”)) OR ALL=(“social-ecological” AND (“network approach” OR “network analysis” OR “network model”)) OR ALL=(“socio-ecological” AND (“network approach” OR “network analysis” OR “network model”)) OR ALL=(“eco-social” AND (“network approach” OR “network analysis” OR “network model”)) OR ALL=(“eco-social system” AND (“network approach” OR “network analysis” OR “network model)))

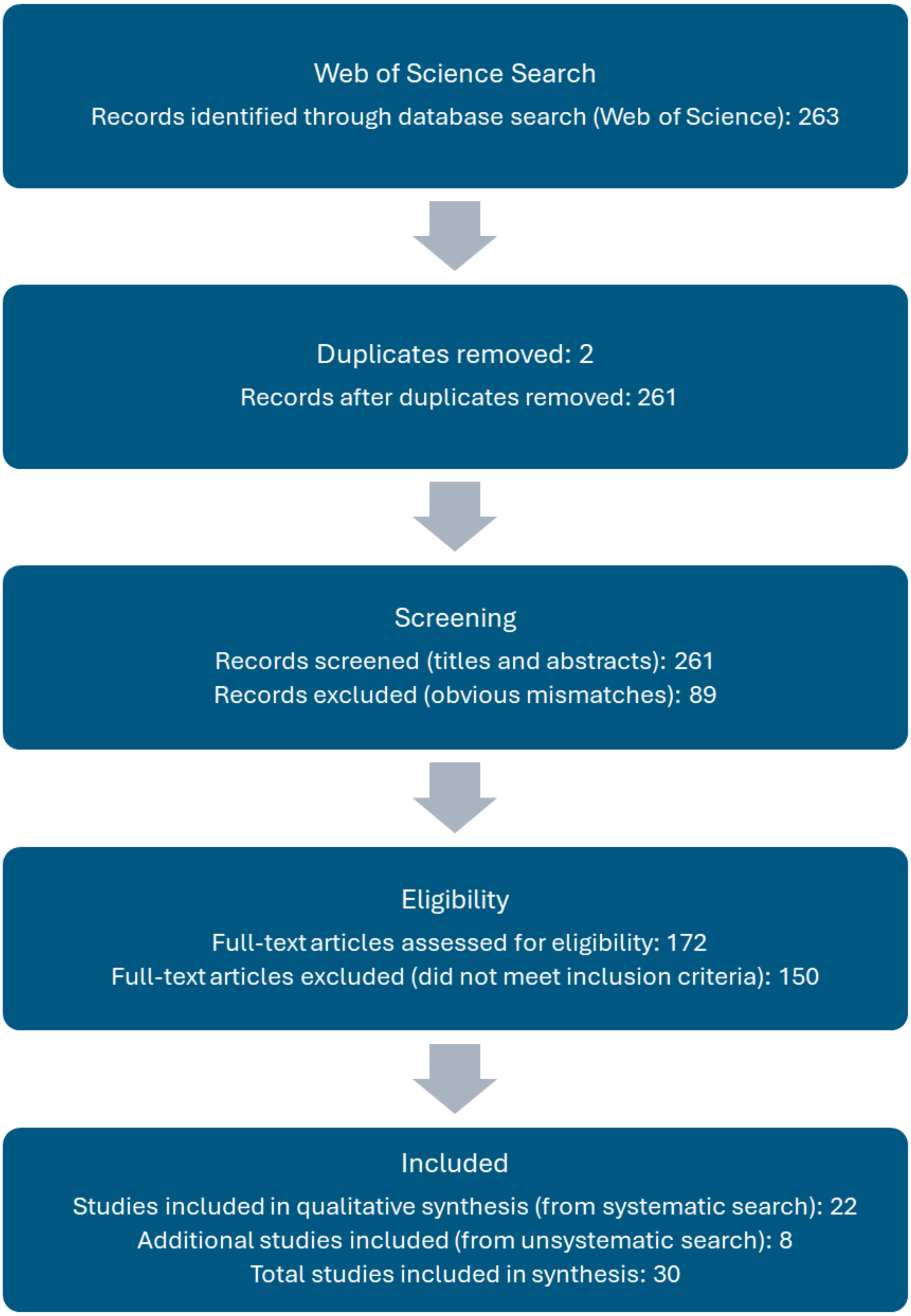
This search yielded 263 results which included two duplicates that were removed. The abstracts and titles of the remaining 261 publications were screened, and obvious mismatches were removed (e.g. papers on social interactions of ant colonies or router networks). The remaining 172 papers were checked extensively for the following criteria:

1) Non-native species explicitly as system component(s); AND
2) Relational data (qualitative or quantitative), either (a) explicitly defined as nodes, vertices or actors connected by links, edges or ties; or (b) visualized as a network; or (c) analyzed as a network (graph theory, etc.); AND
3) Both social and ecological system components, where social components can be humans or human-created entities and concepts, for example infrastructures,

> institutions, organizations or regulations; and ecological entities can be biophysical actors, entities or natural processes, for example non-human species, habitats or nutrient cycling.

This resulted in 22 studies, plus eight additional studies from an unsystematic search through google scholar, references within other papers and recommendations from colleagues over the period 2022-2024. These eight studies contained relevant examples, however due to keywords and the limitations of the Web of Science, they did not appear in the systematic search. Of these altogether 30 studies, 18 include graph theory based social-ecological networks examining interactions between actors. The remaining 12 studies examine causal effects and semantics, use Bayesian networks or classification trees and utilize visual benefits of networks (Supplementary 1, Table 1). While networks can be anything from a mind map, an ontology, a sociogram or the graphical depiction of causal relationships within a complex system, different disciplines use different terms and have developed different analysis techniques. Causal networks depict relationships between concepts and can be referred to as causal inference diagrams (CID), causal graphs or conceptual influence diagrams. Directed acyclic graphs (DAGs) are specific types of networks (or graphs) that have start- and endpoints as well as a direction and are frequently used for analyzing causality (Laubach et al. 2021).

Of the 18 studies applying a SEN analysis (Table 1, main manuscript), 13 focused on different aspects of invasive species whilst the remaining five studies included non-native species as secondary components related to other issues, such as alignment with institutional frameworks (two studies), management beyond invasive species control (two studies) and non-human agency (one study). The level of articulation i.e. how explicitly the social and ecological components are defined, sensu Kluger et al. 2020, ranged from one study including both ecological and social nodes as well as all links within and between these (articulation type III); to 10 studies including some, but not all social and ecological components and links (articulation type II); and seven studies considering social networks within an ecological context (six studies) or an ecological network based on stakeholders' knowledge (one study; both articulation type I). Although the types of networks constructed, the different nodes and links defined, and the analyses performed vary greatly (Table 1), the two most common applications of SENs to invasion science to date are: (1) the human-aided spread of invasive species across a geographic region (nine studies), where nodes are specific locations and links the vectors of spread; and (2) the investigation of governance networks surrounding invasive species (six studies).



Supplementary Figure 1: PRISMA flow diagram of scoping literature search for papers using social-ecological networks to study biological invasions.

Supplementary Table 1: Publications using other network approaches than social-ecological networks to study social-ecological relations involving invasive species (publications using social-ecological networks are included in Table 1 of the main article). Relevant selected themes in invasion science are based on Musseau et al. (2024; pathways; invasion success, incl. spread, and invasibility; impact; or management).

Study (s and u indicate if found with systematic or unsystematic search)	**Research focus**	**Relevant theme(s) in invasion science**	**Network type**	**Nodes and links**	**Invasive species**	**Data source(s)**	**Analysis**	**Key findings in brief**
Cidrás & González-Hidalgo 2022[u]	Management of invasive species through sociocultural and stakeholder perspectives	Management	Tree graph	Nodes: stakeholders' concepts of IAS Links: relations to category	*Eucalyptus globulus* Conceptual representations of invasive species as nodes in stakeholder networks	Survey; semi-structured interviews	Qualitative content analysis of survey and interview data	Activists in Galicia define *E. globulus* as invasive based on its non-native origin, rapid growth, poor forestry management, and its perceived cultural and landscape impacts
Drake et al. 2015[s]	Introductions of invasive species	Invasibility, management	Risky behavior classification tree	Nodes: risky behaviors Links: decisions	*Neogobius melanostomus*, *Bythotrephes longimanus*, and the viral hemorrhagic septicemia (VHS) virus Risky behaviors as nodes	Survey	Predictive models	Human behavior plays a crucial role in invasive species management, with prevention efforts hindered by persistent risky actions driven by misperceptions and external factors
Gonzalez et al. 2008[s]	Adaptive co-management, social-ecological systems	Pathways, invasibility	(Causal Influence Diagram), signed directed graphs	Nodes: source, producer, consumer, tank Links: influence	Unspecified; Invasive alien plants, insects, and native/endemic species as social-ecological components	Participatory workshop, resilience theory application	Causal systems, adaptive cycles, plausible scenarios	Resilience-building through integrative management, tourism as a key driver
Lebel et al. 2010[s]	Sustainable transition in shrimp aquaculture	Pathways, impact, management	Conceptual social-ecological network	Nodes: key events, farmers, policy Links: policy-environment interactions, impacts of species replacements	*Litopenaeus vannamei* as focus species as nodes in the transition framework	Databases, environmental indicators, interviews, grey literature (e.g., newspapers)	Qualitative analysis	Shift from black tiger to Pacific white shrimp improved resource efficiency but marginalized small producers, driven by disease management, global competitiveness, and certification
Luoma et al. 2021[s]	Biofouling management,	Management	Causal influence diagram	Nodes: decision, chance, utility	Unspecified, fouling species as nodes	Scientific and grey literature, interviews	Qualitative; Bayesian Networks or optimization models only	Trade-offs between hull coatings, in-water cleaning (IWC), and risks like NIS introduction and ecotoxicity.

				Links: conditional dependencies (effects)			suggested for future studies	
Wolken et al. 2011[s]	Climate change, , focusing on biophysical and social subsystem interactions	Management	Conceptual social-ecological interactions	Nodes: social-ecological system components Links: interactions between system components	*Dendroctonus rufipennis*, *Monsoma pulveratum*, *Eriocampa ovata*, *Alliaria petiolata*, *Caragana arborescens*, *Crepis tectorum*, *Fallopia* spp., *Hieracium aurantiacum*, *Melilotus alba*, *Prunus padus* as nodes	Literature, global climate models	Qualitative, conceptual framework	Increased wildfires, insect outbreaks, invasive species, and altered hydrology can cause region-specific impacts, with cascading ecological and societal consequences.
Yletyinen et al. 2021[u]	Management, stakeholder perceptions	Management	Decision-making diagram	Nodes: decision making, invasion dynamics, behavioral responses Links: influence	*Pinus nigra, P. contorta* as attribute in agent-based model	Survey	SEPIM (agent-based model), various management scenarios	Social and ecological processes interact dynamically, influencing control efficiency; early detection critical for success.
Bayliss et al. 2018[s]	Climate change adaptation and invasive species management	Management	Bayesian belief network	Nodes: social-ecological system components Links: positive and negative effects	*Sus scrofa*, *Urochloa mutica* as nodes	Scientific and grey literature, risk assessments	Bayesian belief network, management scenarios	Feral pigs and para grass threaten ecosystems, requiring adaptive, long-term management
Dutra et al. 2018[s]	Climate change adaptation and invasive species management	Management	Bayesian belief network	Nodes: social-ecological system components Links: positive and negative effects	Unspecified; feral and aquatic invasive species as nodes	Existing diagnostic frameworks, monitoring data, and participatory workshops	Bayesian belief network; management scenarios	Adaptive strategies combining soft barriers, participatory monitoring, and governance improve SES resilience under saltwater intrusion
Langmead et al. 2009[s]	Ecosystem management, eutrophication, social-ecological resilience	Management,	Bayesian belief network	Nodes: Socio-economic drivers, ecosystem components (abiotic and biotic) Links: effects	Unspecified planktonic and benthonic invasive species as nodes	Historical data, expert opinion, empirical time-series	Bayesian belief network; management scenarios	Socio-economic choices directly affect eutrophication, resilience, and recovery; adaptive policy integration is essential.
Salliou et al. 2017[s]	Ambiguity and stakeholder perspectives in	Management	Bayesian belief network	Nodes: stakeholder beliefs	*Cydia pomonella*, other pest species as nodes	Expert elicitation,	Bayesian belief network,	Stakeholders' beliefs about landscape effects on pests and ecosystem services

	social-ecological systems			(conceptual node), landscape complexity, pests, predators, apple production Links: interactions			participatory modeling	vary, highlighting the need for participatory approaches to resolve ambiguities.
Thiemer et al. 2023[u]	Stakeholder perception of macrophyte growth and its implications for management	Management	Bayesian belief network	Nodes: macrophyte species, growth levels, respondent types, recreation activities Links: conditional probabilities	*Egeria nuttallii* *Sagittaria sagittifolia* *Ludwigia* spp. *Pontederia crassipes* (formerly *Eichhornia crassipes*) *Juncus bulbosus* as nodes	Surveys	Bayesian modeling (decision support tool)	Perceived nuisance varies by respondent type, activity, and macrophyte species; management strategies should account for local user preferences and ecological consequences.

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Supplement 3: Illustrative example

A social-ecological network of Hawaii based on S/EICAT(+) assessments and other literature sources by Fiona Rickowski et al.

1. Study area & data (system boundaries)

The Pacific island state of Hawaii has, like many other (oceanic) islands, a high number of endemic species, mainly consisting of birds, fish, and invertebrates, with no native endemic reptiles or amphibians, and just three terrestrial or semi-terrestrial mammals (two bat species and the Hawaiian monk seal, *Neomonachus schauinslandi*) (Pratt et al. 2009; MMC 2024). Of the 1456 native species listed in the federal register to occur naturally in Hawaii, 32% (471 species) are endangered and many others have already gone extinct (U.S. Fish and Wildlife Service 2024). Out of the terrestrial birds, 98% are endemic to Hawaii. Hawai'ian people have a strong cultural connection to their rich biodiversity and native landscapes, reflected in their art, music, and use in traditional dress and practices (Anderson-Fung and May 2002). For example, feathers used in rituals as headdresses and as currency or native fauna feature in stories and legends and as spiritual guides or protectors (Pratt et al. 2009).

The decline of endemic species on Hawaii has several anthropogenic causes, one of which is the introduction of invasive species. They include, for example, several rat species (*Rattus* spp.) and the small Indian mongoose (*Urva auropunctata*) which prey on a range of native species, barn owls (*Tyto alba*) which prey on native birds, and Japanese white-eyes (*Zosterops japonicus*) which compete with native bird species and are implicated in the spread of avian malaria on the islands (Raine et al. 2019; Kaushik et al. 2018). These impacts have resulted in losses to ecosystem services provided by native species on Hawaii. For example, the islands have lost many native frugivorous birds that spread the seeds of native plants – resulting in negative environmental impacts (reduced habitat quality, although non-native bird species have partially taken over this ecosystem function; Vizentin-Bugoni et al. 2019) and cultural losses associated with the disappearance of these bird species which are a valued aspect of Hawaiian culture.

A large number of non-native species (NNS) are now established on Hawaii, including many birds and mammals, but also terrestrial reptiles and amphibians. The impacts they cause are widespread and diverse. Synthesizing them in a social-ecological network (SEN) will not only provide an integrative overview of these impacts but also reveal indirect effects and be an important basis for management decisions. Incorporating *all* impacts of NNS on biodiversity and culture in a SEN for Hawaii is challenging and beyond our scope. Here, as a proof of concept, we identified impacts associated with specific groups of native and non-native species creating a SEN for: (i) impacts on native birds that are caused by non-native vertebrate species, (ii) impacts affecting native species that are caused by non-native birds, and (iii) the wider positive and negative socio-economic impacts of these non-native vertebrates on Hawaii.

The biodiversity and socio-economic impacts of NNS (vertebrates and birds) were identified by reviewing literature reported in the IUCN Global Invasive Species Database (https://www.iucngisd.org/gisd/) and two global assessments of the environmental and socio-economic impacts of non-native birds (Evans et al. 2016, 2020) following the S/EICAT(+) framework (Blackburn et al. 2014; Bacher et al. 2018; IUCN 2020; Vimercati et al. 2022). Notice therefore that both deleterious and beneficial environmental impacts are included in the analysis. An additional online search for cultural and social-economic impacts was carried out using Google and Google Scholar from March to May 2024. The indirect impacts were explored by identifying the social-economic relevance of impacted native species. Impacts occurring between 1970 and present day were recorded.

2. Construction of node & edge list (system components)

As the aim of the network was to effectively visualize and communicate different cumulative impacts of invasive species, we chose to use node type to indicate the layers (so as not to visually overcomplicate the network). The layers and nodes therefore consist of native species, NNS, and social entities such as stakeholders and culture. Native species were aggregated into forest and grassland birds, sea birds, and wetland birds as well as plant communities. The nodes were assembled in a node list (Table 1), with columns containing the layer or node type, the name of the node and the individual species within the groups. Nodes not aggregated were given the value 1, and aggregated nodes the value of the respective number of species within that group. This was later used to scale the relative node sizes.

Table 1: Complete node list for the Hawaiian S/EICAT(+) SEN containing the different types of nodes (layers), the node names (node), the species contained within the nodes (species), and the respective sum (size).

Layer	**Node**	**Species**	**Taxa**	**Size**
Non-native spp.	Barn owl	Barn owl (*Tyto alba*)	Aves	1
Non-native spp.	Cattle egret	Cattle egret (*Bubulcus ibis*)	Aves	1
Non-native spp.	Japanese white-eye	Japanese white-eye (*Zosterops japonicus*)	Aves	1
Non-native spp.	Red-billed leiothrix	Red-billed leiothrix (*Leiothrix lutea*)	Aves	1
Non-native spp.	Red-vented bulbul	Red-vented bulbul (*Pycnonotus cafer*)	Aves	1
Non-native spp.	Red-whiskered bulbul	Red-whiskered bulbul (*Pycnonotus jocosus*)	Aves	1
Non-native spp.	Rose-ringed parakeet	Rose-ringed parakeet (*Alexandrinus krameri*)	Aves	1
Non-native spp.	Mallard	Mallard (*Anas platyrynchos*)	Aves	1
Non-native spp.	Common myna	Common myna (*Acridotheres tristis*)	Aves	1
Non-native spp.	Chukar	Chukar (*Alectoris chukar*)	Aves	1
Non-native spp.	Feral cat	Feral cat (*Felis catus*)	Mammalia	1
Non-native spp.	Mongoose	Small Indian mongoose (*Urva auropunctata*)	Mammalia	1
Non-native spp.	Rat species	Brown rat (*Rattus norvegicus*) Black rat (*Rattus rattus*) Polynesian rat (*Rattus exulans*)	Mammalia	3
Non-native spp.	Veiled chameleon	Veiled chameleon (*Chamaeleo calyptratus*)	Reptilia	1
Native spp.	Forest and grassland birds	Akikiki (*Oreomystis bairdi*) Hawaii akepa (*Loxops coccineus*) Hawaii elepaio (*Chasiempis sandwichensis*) Hawaiian short-eared owl (Pueo) (*Asio flammeus sandwichensis*) Palila (*Loxioides bailleui*) Oahu Elepaio (*Chasiempis ibidis*) Hawaii creeper (*Manucerthia mana*) Akohekohe (*Palmeria dolei*) Kakawahie (*Paroreomyza flammea*) Oahu Alauahio (*Paroreomyza maculata*) Maui parrotbill (*Pseudonestor xanthophrys*) Ou (*Psittirostra psittacea*) Laysan finch (*Telespiza cantans*) Hawaiian crow ('Alalā) (*Corvus hawaiiensis*)	Aves	14
Native spp.	Monarch butterfly	Monarch butterfly (*Danaus Plexippus*)	Invertebrata	1
Native spp.	Plant communities	‘Ala ‘ala wai nui (*Peperomia subpetiolata*) Hawai'i cheesewood (*Pittosporum hawaiiense*) Hōʻawa (*Pittosporum napaliense*) Pilo kea lau li'I (*Platydesma rostrata*) Hala pepe (*Pleomele fernaldii*) Opuhe (*Urera kaalae*)	Plantae	6
Native spp.	Sea birds	Brown noddy (*Anous stolidus*) Bulwer’s petrel (*Bulweria bulwerii*) Hawaiian petrel ('Ua'u) (*Pterodroma sandwichensis*) Bonin petrel (*Pterodroma hypoleuca*) Newell’s shearwater (‘A‘o) (*Puffinus newelli*) Wedge-tailed shearwater (*Ardenna pacifica*)	Aves	6
Native spp.	Wetland birds	Hawaiian common moorhen ('Alae 'ula) (*Gallinula chloropus sandvicensis*) Hawaiian coot ('Alae ke'oke'o) (*Fulica alai*) Hawaiian duck (Koloa) (*Anas wyvilliana*) Hawaiian goose (Nēnē) (*Branta sandvicensis*) Hawaiian stilt (Ae'o) (*Himantopus mexicanus knudseni*)	Aves	5
Social	Agriculture / aquaculture	Human	Mammalia	1
Social	Airports	Human	Mammalia	1
Social	Wildlife enthusiasts	Human	Mammalia	1
Social	Hawaiian culture	Human	Mammalia	1

Social	Pet owners	Human		Mammalia	1
Social	Recreation	Human		Mammalia	1
Social	Tourism	Human		Mammalia	1

The links were the different beneficial and deleterious impacts and underlying mechanisms of NNS as well as the indirect impacts of these. Nodes and links were transferred into an edge list (Table 2), including the node causing the impact, the node being impacted, the type of impact, its mechanism, the number of species impacted or causing the impact (*n*, i.e. the weight of the link), whether the impact and mechanisms were beneficial or deleterious to native species and valued aspects of Hawaiian culture, and whether the impact was actually observed (based on evidence included in previous S/EICAT(+) assessments and published studies) or potential (based on grey literature).

Table 2: Excerpt from the edge list of the Hawaiian S/EICAT(+) SEN, containing the starting node (from), end node (to), different link types (impact, mechanism), link weight (n), direction information for impact and mechanism (beneficial or deleterious), and status (observed or potential).

From	**To**	**Impact**	**Mechanism**	***n***	**Impact direction**	**Mechanism direction**	**Observed / potential**
Feral cat	Forest and grassland birds	Biodiversity	Predation	3	Deleterious	Deleterious	Observed
Feral cat	Rat species	Biodiversity	Predation	2	Beneficial	Beneficial	Potential
Plant communities	Forest and grassland birds	Biodiversity	Loss of native habitat	6	Beneficial	Deleterious	Observed
Forest and grassland birds	Hawaiian culture	Cultural	Loss of native species	13	Beneficial	Deleterious	Observed

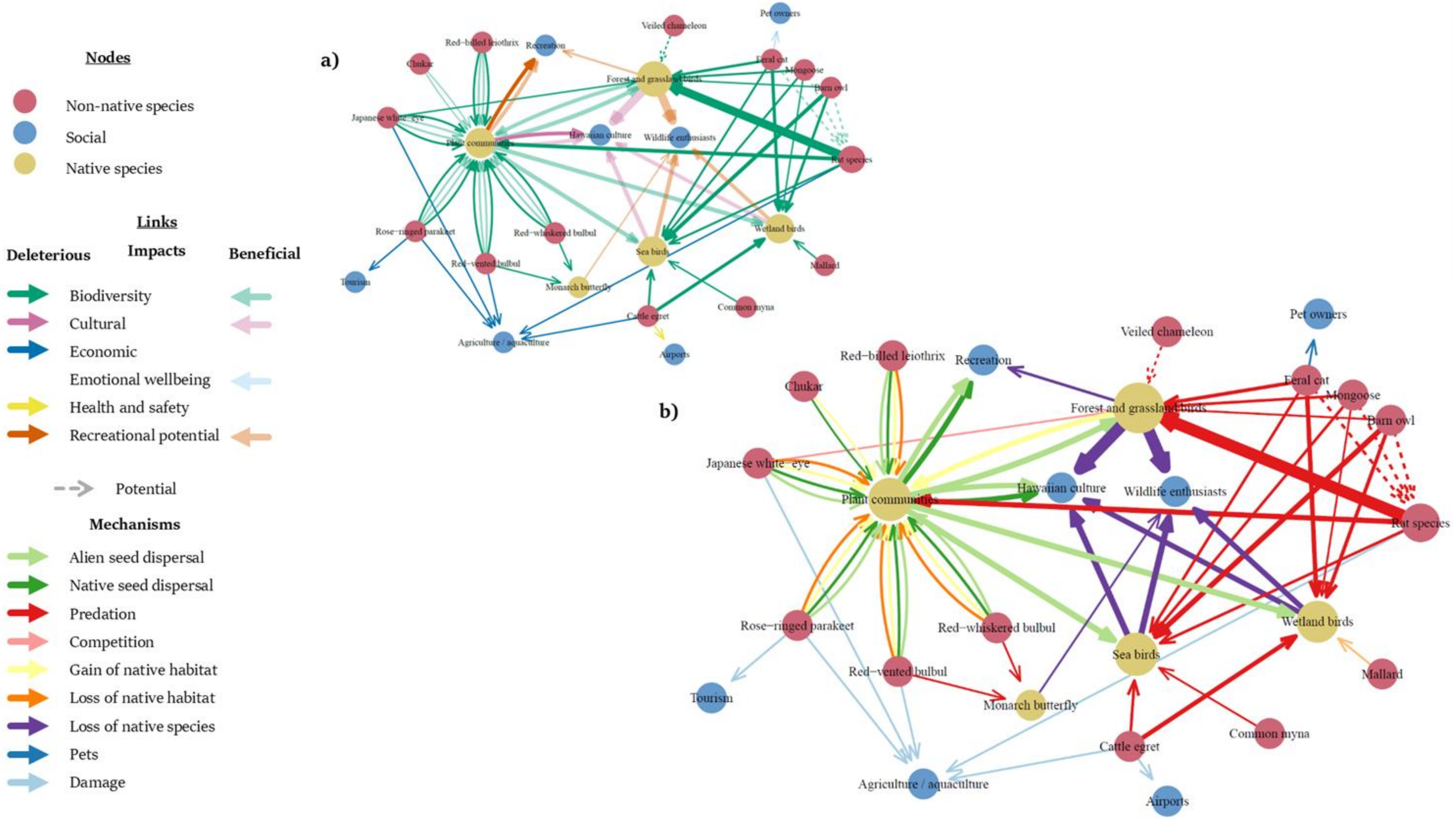
3. Visualization (analysis)

The network visualization was done with R version 4.3.2 (2023-10-31 ucrt) -- "Eye Holes". The R package *igraph* (Csardi & Nepusz 2006) was used to turn the edge and node list into a network item. The function *TKplot()* within *igraph* was used to manually lay out the network. The layout is an aesthetic attempt to visualize the network in a straightforward manner that is easy to interpret, without being based on an algorithm or framework. The *TKplot* layout was then used in a *ggraph()* plot using the packages *ggplot2* (Wickham 2016) and *ggraph* (Pedersen 2022). Additionally, nodes were colored according to type, and their relative sizes scaled according to how many species are aggregated in the group. Larger nodes therefore represent more species within that group for which impacts have been assessed. Two network plots were made, visualizing either the link being colored according to its impact or mechanism. The weights of the links (*n*) were visualized with the thickness of the line, representing the number of affected species. This shows, for example, the cumulative impacts of the loss of native bird species on Hawaiian culture that were caused, at least in part, by NNS. Beneficial impacts were visually displayed to be more transparent than negative impacts (with a lower alpha), so that they could be distinguished by the reader.

4. Results & Discussion

Supplementary Figure 2 shows direct beneficial and deleterious impacts of non-native vertebrates on native species and stakeholder groups as well as beneficial impacts of native species on human culture and recreation (see also Figure 3a in the main article). The deleterious impacts of NNS on native species indirectly negatively impact culture and recreation. This becomes evident when mapping the impacts and their mechanisms (Supplementary Figure 2).

This example should serve as a proof of concept about the potential of data collected for S/EICAT(+) and other NNS impact assessments to create SENs, which can be useful to identify indirect impacts of NNS that typical impact assessments can miss. Due to the proof-of-concept nature of this example, we acknowledge that the data we collected do not include all interactions within the Hawaiian social-ecological system. For example, there are likely feedbacks from wetland birds and seabirds to plant communities, for instance through the nutrient loads of seabird guano being released into the ecosystem.


Nodes
Non-native species
Social
Native species
Links
Deleterious
Impacts
Beneficial
Biodiversity
Cultural
Economic
Emotional wellbeing
Health and safety
Recreational potential
Potential
Mechanisms
Alien seed dispersal
Native seed dispersal
Predation
Competition
Gain of native habitat
Loss of native habitat
Loss of native species
Pets
Damage
a)
Veiled chameleon
Pet owners
Red−billed leiothrix
Recreation
Chukar
Forest and grassland birds
Feral cat
Mongoose
Barn owl
Japanese white−eye
Plant communities
Hawaiian culture
Wildlife enthusiasts
Rat species
Rose−ringed parakeet
Red−whiskered bulbul
Wetland birds
Sea birds
Red−vented bulbul
Mallard
Tourism
Monarch butterfly
Common myna
Cattle egret
Agriculture / aquaculture
Airports
b)
Veiled chameleon
Pet owners
Red−billed leiothrix
Recreation
Chukar
Feral cat
Mongoose
Forest and grassland birds
Barn owl
Japanese white−eye
Hawaiian culture
Wildlife enthusiasts
Plant communities
Rat species
Rose−ringed parakeet
Red−whiskered bulbul
Wetland birds
Sea birds
Red−vented bulbul
Mallard
Tourism
Monarch butterfly
Common myna
Cattle egret
Agriculture / aquaculture
Airports

Supplementary Figure 2: Case study: Hawaiian S/EICAT(+) SEN focusing on impacts and mechanisms of impact of non-native vertebrates on native birds, selected invertebrates, and plant communities. Network a) depicts positive and negative social-ecological impacts and b) depicts the underlying mechanisms causing the impacts. The thickness of the links indicates the number of native species impacted. Several native species were aggregated into nodes of species groups; these nodes contain the following native species: Forest and Grassland birds: Akikiki (*Oreomystis bairdi*), Hawaii akepa (*Loxops coccineus),* Hawaii elepaio (*Chasiempis sandwichensis*), Hawaiian short-eared owl (Pueo) (*Asio flammeus sandwichensis*), Palila (*Loxioides bailleui*), Oahu Elepaio (*Chasiempis ibidis*), Hawaii creeper (*Manucerthia mana*), Akohekohe (*Palmeria dolei*), Kakawahie (*Paroreomyza flammea*), Oahu Alauahio (*Paroreomyza maculata*), Maui parrotbill (*Pseudonestor xanthophrys*), Ou (*Psittirostra psittacea*), Laysan finch (*Telespiza cantans*), Hawaiian crow ('Alalā) (*Corvus hawaiiensis*); Sea birds: Brown noddy (*Anous stolidus*), Bulwer's petrel (*Bulweria bulwerii*), Hawaiian petrel ('Ua'u) (*Pterodroma sandwichensis*), Bonin petrel (*Pterodroma hypoleuca*), Newell's shearwater (‘A‘o) (*Puffinus newelli),* Wedge-tailed shearwater *(Ardenna pacifica);* Wetland birds: Hawaiian common moorhen ('Alae 'ula) (*Gallinula chloropus sandvicensis*), Hawaiian coot ('Alae ke'oke'o) (*Fulica alai*), Hawaiian duck (Koloa) (*Anas wyvilliana*), Hawaiian goose (Nēnē) (*Branta sandvicensis*), Hawaiian stilt (Ae'o) (*Himantopus mexicanus knudseni*); Plant communities: ‘Ala ‘ala wai nui (*Peperomia subpetiolata*), Hawai'i cheesewood (*Pittosporum hawaiiense*), Hōʻawa (*Pittosporum napaliense*), Pilo kea lau li'I (*Platydesma rostrata*), Hala pepe (*Pleomele fernaldii*), Opuhe (*Urera kaalae*).

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