

The Interdisciplinary Research Process

Any interdisciplinary research that does not resolve the balance across disciplines will, as we argue, make limited progress. This is particularly true when working across the natural and social sciences where different epistemologies and research traditions pose significant barriers to fruitful collaboration. One desirable feature of the network-centric approach is that it provides a common language, an argument made by Janssen *et al.* [4] and more recently by Bohan *et al.* [1]. Further, network science is not strongly tied to either the social or natural sciences, thus proving a neutral and common ground for integration across disciplines. Bohan *et al.* [1] and Dee *et al.* [2] certainly make important arguments. Whether focused on ecosystem services specifically, or on human–nature (social–ecological) interactions more broadly, our view is that their contribution would be strengthened by greater engagement across disciplines where their thinking couples tightly with a growing interdisciplinary research field.

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Letter

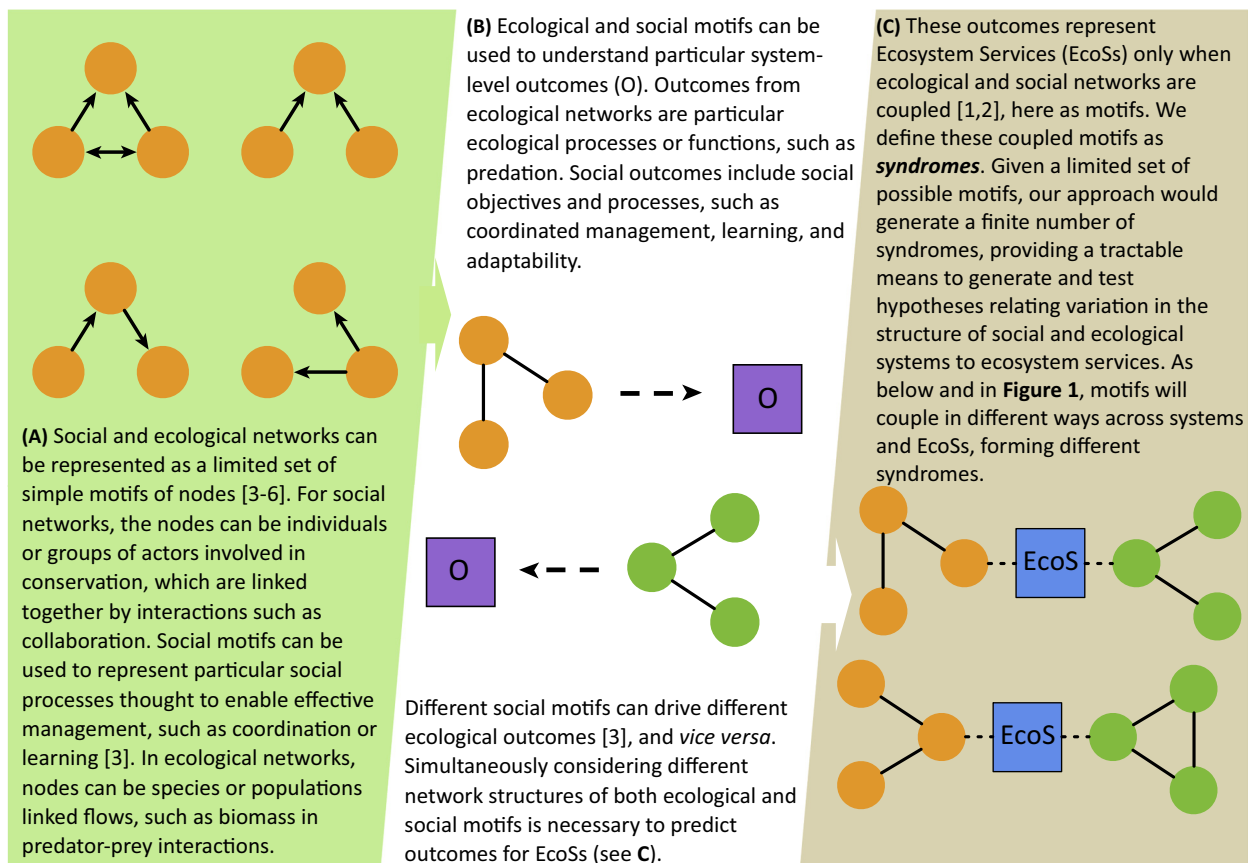
Do Social–Ecological Syndromes Predict Ecosystem Services? – a Reply to Bodin *et al.*

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Sustaining ecosystem services (EcoSs) involves managing interactions within

and between complex social and ecological systems. In two recent *TREE* papers, we described how network approaches, commonly used in sociology and ecology, can transcend these disciplines and help assess and manage EcoSs [1,2]. In reply to these papers, Bodin *et al.* [3] advocated that network approaches for EcoSs present an exciting opportunity but need to connect with existing literature on social–ecological systems (SESs) that use networks, particularly on environmental governance. We all agree that networks provide a way to generate interdisciplinary theory for EcoSs; to this end, Bodin *et al.* described how core subparts, known as configurations or motifs, of SES networks can be used to generate empirically testable hypotheses. To date, studies using motifs in social–ecological network approaches have largely focused on the effectiveness of different environmental governance arrangements given interdependencies between social and ecological systems [3,4]. Motifs have not been applied to represent EcoS delivery, for which different outcomes depend on the network structure in both social and ecological systems (Box 1). However, network motifs are used in ecology [5,6] and have been proposed as a means of linking ecological interactions to EcoSs [7]. Building on [3,7,12], we advocate applying motif analyses simultaneously to social and ecological systems to identify a set of syndromes that could lead to different ecosystem service outcomes (Box 1). We define a syndrome as social motifs and ecological motifs that co-occur and are linked by an EcoS of interest (Box 1). In addition to social complexity and some interdependencies between social and ecological systems described in [3], this proposed approach would also account for the ecological complexity (i.e., different patterns of ecological interactions) associated with different EcoS outcomes (Figure 1). Next, we identify two key interdisciplinary directions for future research on EcoSs and SES networks.

Box 1. Building Syndromes for EcoSs That Simultaneously Consider Variation in Social and Ecological Motifs



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Social–Ecological Syndromes: How Do They Vary by Service Type?

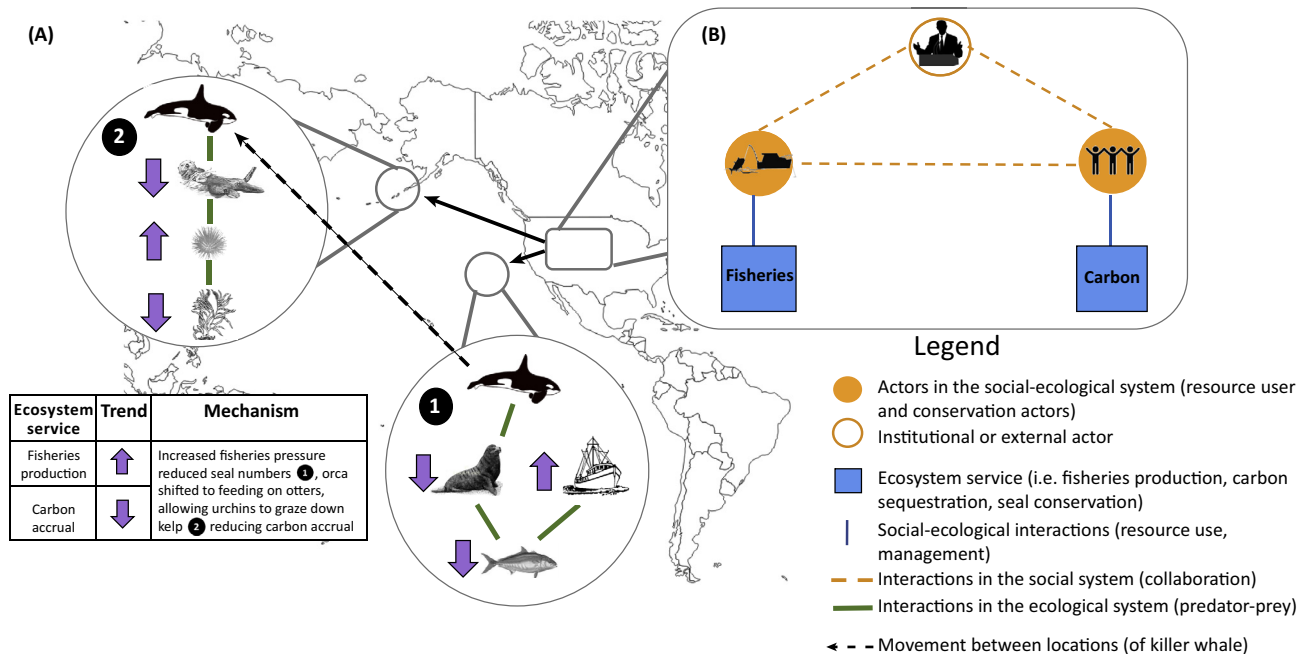
First, we suggest connecting both social and ecological motifs to understand how different network structures in one could drive outcomes for the other, and for EcoSs (Box 1 and Figure 1). EcoSs link social and ecological networks, acting as a common node in both types of network [2]. Particular motifs are characteristic of both social and ecological networks [3,5], but how these motifs couple to form syndromes (Box 1) and whether they drive particular EcoS outcomes is largely untested. Social motifs (e.g., cooperative versus uncoordinated management of a common-pool resource) can drive ecological outcomes [3]. Similarly, although not yet addressed in the SES literature,

change in ecological motifs can affect social outcomes and EcoSs (Figure 1). Different patterns of ecological interactions can increase the likelihood of particular EcoS outcomes and therefore require different management arrangements (see Figure 1 for an example). We propose that the next steps should address how syndromes differ with the EcoS considered and whether they predict EcoS outcomes.

Diverse Interactions between People and Nature: Where Are Key Links Missing?

Second, we need to better understand how humans interact with ecosystems in diverse ways that influence EcoSs, their diverse value, and which management interventions will improve outcomes. For

some services, who interacts with an EcoS and how is clearer (fish production) than for others (carbon sequestration). Importantly, the people who benefit from an EcoS may not be the same as those involved in governance of the ecosystem producing it [8]. For example, urban populations who benefit from recreational opportunities in rivers do not decide how much water is taken from rivers for irrigation on farms. Constructing network syndromes that connect user- to manager-groups around an EcoS node can identify key (sometimes indirect) stakeholders and potential trade-offs. With this knowledge, management outcomes can be improved by establishing links between these different groups [9]. For instance, upstream land uses impact downstream water quality. Payment-for-



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Figure 1. Social-Ecological Syndromes Can Drive Different Outcomes for Ecosystem Service (EcoS). Different ecological motifs will drive EcoS outcomes and require different management arrangements (social motifs) to achieve multiple EcoS objectives, as illustrated by this Northeast Pacific and Aleutian Islands food web based on [11]. The ecological motifs represent apparent competition between pelagic Pacific sea lions and Aleutian sea otters; both eaten by killer whales. (A) Sea lions and seals have declined due to increased harvesting of the fish species that they eat (along with other causes). In response, killer whales have shifted their feeding patterns, changing the ecological motif along the Aleutian coast, which reduced sea otters, increased herbivory of kelp by sea urchins, and ultimately reduced carbon accrual [11]. Syndrome approaches could be applied to this or other systems to evaluate, or predict, the socioeconomic motifs that will be more likely to produce sustainable EcoS outcomes across observed ecological motifs. Tests of these predictions can examine whether the required networks of collaboration between actors exists, in order to achieve multiple EcoS objectives (i.e., fisheries production, carbon sequestration, and sea lion conservation). (B) Collaboration between social actors, or the presence of an institutional or external actor that can facilitate cross-scale cooperation, is needed to ensure multiple EcoSs are maintained.

ecosystem service mechanisms allow downstream water users to pay upstream land users to take actions that improve their water quality [10], creating a link between these groups. Syndrome approaches would go beyond governance methods in [3] by considering that several possible ecological motifs can produce high water quality and therefore mediate links between groups of people. We hope this research area will expand to consider beneficiaries in syndromes and how they interact with services and groups managing services.

Conclusions and Outstanding Questions

We agree with [3] that social-ecological network motif approaches offer great promise for EcoS research and that

connecting with research on environmental governance is a valuable first step. However, the next step is to include variation that occurs simultaneously in the coupled social and ecological networks, implicit in EcoSs [1,2], to predict EcoS outcomes. We suggest considering the set of possible ecological motifs alongside motifs for different types of interactions between people and nature, thus including but extending beyond governance of shared resources. We advocate that future research could identify whether syndromes (i) lead to predictable EcoS delivery, or (ii) inform where different management interventions are needed to better achieve EcoS objectives. Such research could lead to a predictive understanding of EcoSs and

the management structures that deliver sustainable outcomes for them.

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Forum

Reshaping Darwin's Tree: Impact of the Symbiome

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Much of the undescribed biodiversity on Earth is microbial, often in mutualistic or pathogenic associations. Physically associated and coevolving life forms comprise a

symbiome. We propose that systematics research can accelerate progress in science by introducing a new framework for phylogenetic analysis of symbiomes, here termed SYMPHY (symbiome phylogenetics).

An Unfolding Revolution: The Symbiome in Systematics Research

An expanded symbiome [1,2] or holobiont [3] perspective embraces the following challenges: (i) the need to better account for, and provide robust phylogenies, taxonomies, and nomenclatures for, all individual biota on Earth, and (ii) the need to integrate these biota as coevolving units into the broader picture of organismal and ecosystem evolution. Despite a revolution in the documentation and description of the vast microbial world, systematics has not kept pace. Current phylogenetic tree analysis fails to recognize and depict coevolving symbiomes. Instead, systematics is primarily focused on individual species despite clear evidence that the symbiome comprises several to many individual units (i.e., species) that coevolve [4,5]. Thus, a new era in the understanding of microbial diversity has emerged without a clear path to portraying the impacts of microbes across the tree of life. Phylogenetic theory and practices should advance further and, eventually, new taxonomies and nomenclatural systems should follow suit. This contribution is

intended to serve as a forum for exploring these ideas. How precisely they should be implemented and ultimately manifested in phylogenetic practices is a task of great magnitude that requires an interdisciplinary approach to apply knowledge that spans the viral to multicellular animal, fungal, and plant worlds [4].

Defining the Symbiome

Although the terms 'symbiome' and 'holobiont' have often been used interchangeably, we here focus on the symbiome, which means the colocalized and coevolving taxa (i.e., under selection) comprising a given consortium. By contrast, holobiont includes all physically associated taxa, including those that are not coevolving or codependent. Current phylogenetic practices treat individual units, which rarely if ever evolve in isolation, and thus do not address processes that generate biodiversity for which we seek an accurate phylogenetic understanding. We believe that modern systematics is ready for such a sweeping change because the *status quo* does not accommodate the overwhelming evidence of evolving symbiomes [4,5]. In **Box 1** and **Figure 1** we provide some examples of symbiomes from the natural world.

Reshaping Darwin's Tree: Integrated Phylogenies for Symbiomes

The tree of life portrayed by Darwin [6] some 150 years ago has served well as a

Box 1. Examples of the Symbiome

Examples of symbiomes are shown **Figure 1** and include plant–fungus interactions (**Figure 1A**). Over 90% of fungal biodiversity on Earth remains to be discovered and the underlying principles of fungal diversification in varied habitats are poorly developed. The diversity of fungi recruited by plants in mycorrhizal symbiomes include poorly understood groups such as the Mucoromycotina, which appear not only to interact with ancestral plant lineages such as liverworts but also provide insights into the impact of atmospheric carbon concentration on evolution of plant–fungus interactions. Other symbiomes include plant–cyanobacteria interactions (**Figure 1B**) that not only support extant plant distributions and ecologies but also impact on their long-term success due to exchange of genes via horizontal gene transfer. Fungus–alga interactions such as in the lichen symbiome (**Figure 1C**) are more complex than previously thought, and the long-held dogma of a 'one alga, one fungus' partnership was upended by the application of high-throughput sequencing approaches and phylogenetic methods. Other symbiomes include insect–microbe interactions that facilitate the digestion and detoxification of food, and provide defense against pathogens and parasites, and virus–host interactions that are the driving force for the adaptation of viruses to new hosts and the evolution of new viral species.