

## Opinion

## Networking Our Way to Better Ecosystem Service Provision

The QUINTESSANCE Consortium<sup>‡,§</sup>

The ecosystem services (EcoS) concept is being used increasingly to attach values to natural systems and the multiple benefits they provide to human societies. Ecosystem processes or functions only become EcoS if they are shown to have social and/or economic value. This should assure an explicit connection between the natural and social sciences, but EcoS approaches have been criticized for retaining little natural science. Preserving the natural, ecological science context within EcoS research is challenging because the multiple disciplines involved have very different traditions and vocabularies (common-language challenge) and span many organizational levels and temporal and spatial scales (scale challenge) that define the relevant interacting entities (interaction challenge). We propose a network-based approach to transcend these discipline challenges and place the natural science context at the heart of EcoS research.

## Networks as Unifying Tools

EcoS [1–4] is a rapidly developing field that requires clear, unified interdisciplinary methods [5], but has been criticized on both philosophical and practical grounds [6,7]. Ecosystem processes or functions only become EcoS if they are shown to have social and economic value (Box 1). In seeking to pay for the services provided by ecosystems, many EcoS studies do not ‘get the science right’ owing to poor interdisciplinary coordination and communication [8], and often retain little natural science context despite EcoS being founded on ecological processes [6,8]. A network-based approach to EcoS built explicitly upon a foundation of ecological networks could help here. It would provide a consistent and common cross-disciplinary language and tools to deal with complex systems of interacting **nodes** (see *Glossary*) irrespective of whether these nodes are the species within an ecosystem or individual humans within a socioeconomic system. The approach would also naturally identify the organizational level and spatial/temporal **scales** of study through the appropriate definition of both the nodes and the relationships between nodes (**links**) within the network.

Network methods have proved to be key wherever interactions between multiple entities are important (Figure 1), resulting in complex, **nonlinear dynamics**. From the earliest work of Euler in 1735 on how to cross all the ‘Seven Bridges of Königsberg’ only once [9], networks have provided invaluable tools in disciplines from mathematics, physics, and engineering to biology [10,11]. In the social sciences [12–16] and ecology [17–22], networks are structuring concepts and startling commonalities in their properties have been found within and between disciplines [23,24], suggesting that they can act as useful bridges between disciplines and allow identification of the indirect effects and nonlinearities prevalent in complex multidisciplinary systems. Indeed, there is a history of promoting the use of networks across discipline boundaries [24], and considerable advances have been made across the divide between the social sciences and ecology [25–28]. Our contention, which mirrors calls made elsewhere (cf. [25,28,29]), is that

## Trends

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When formalized in a series of discipline-specific layers, network-based methods can be used in EcoS.

In layer 1, analysis of ecological networks identifies the crucial natural science context for EcoS research, which structures the overlying social science and economic layers, and thus limits the complexity of the problem.

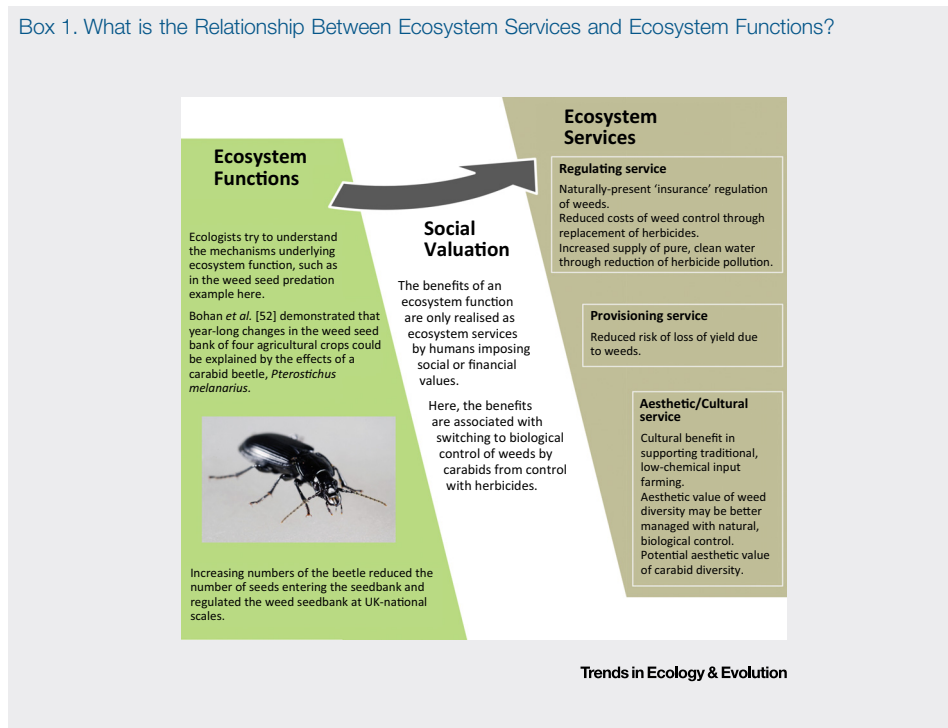
This brings a generic network-based language to EcoS and makes explicit the scales and interactions that connect the disciplines, fostering communication.

Network approaches are a promising method for interdisciplinary research aimed at understanding and predicting EcoS.

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## Box 1. What is the Relationship Between Ecosystem Services and Ecosystem Functions?



harnessing the benefits of these already established approaches to the explicitly interdisciplinary needs of EcoS research is simply the logical next step.

Despite their clear potential, network-based approaches in EcoS studies that simultaneously consider the economic, social, and ecological (**multi-networks**) still do not exist. This is because such approaches are data-rich, and guiding and simplifying principles need to be developed if the integration of networks across disciplines is not to very quickly become intractable. We use here examples of cross-discipline networks to develop and support our line of reasoning for the use of networks in EcoS. We do not advocate a crude one-size-fits-all approach, in which a prescriptive definition of network nodes and links is shoehorned into all types of study [30], nor do we suggest that economic, social, and ecological data must always be integrated into a single multi-network. Instead, we develop and advocate a tractable and flexible network-based approach that solves the common-language, scale, and interaction challenges, and places the natural, ecological sciences at the heart of EcoS research.

### The Common-Language Challenge

Scientists from different disciplines come to EcoS problems with specific vocabularies and analytical approaches. Similar terminology will be used for different things, while the same meaning may be ascribed to different terms. This may be effective for within-discipline communication, but it can hinder cooperation across disciplines and the interchange of results between EcoS studies [8,15,31]. Network science has a far stricter vocabulary, and comes with a ready-made lexicon and common set of tools that can be applied to any network problem. Thus, adopting a network approach could provide an EcoS 'language' that would greatly facilitate interdisciplinary communication, specifically, while retaining discipline-specific language and approaches where appropriate. Moreover, the precise terminology of networks would promote reuse of information between EcoS studies, potentially facilitating learning.

### Glossary

**Degree:** the degree (or connectivity) of a node is the number of edges connected to it. In directed networks, each node has an in-degree and an out-degree that respectively count the number of incoming and outgoing edges.

**Link:** a link, or edge, connects two nodes in a network. Information transacted across a link can be undirected (the flow goes both ways) or directed (one way). In the case of economic networks, directed links might represent the direction and amount of financial transactions. In mutualistic networks, a pair of directed links represents an interaction with mutual benefit, such as in the case of plant pollination. For classical food webs, directed links go from the prey/resource to the predator/consumer.

**Multi-networks (networks of networks):** combining individual networks through links between entities either in the same domain (e.g., pollinators and herbivores linked through shared plants) or in different domains, which is our proposal.

**Node:** a node, or vertex, represents an individual component of a network. These might be species in a species-species interaction network, such as a food web or a plant-pollinator network, or individuals interacting through sentiment or making financial transactions, respectively, in social and economic networks.

**Nonlinear network dynamics:** whether constructed using ecological, economic, or social data, the phrase 'more is different' can be fully applied to networks [53]. Networks, and their dynamical properties, are more than the sum of their interacting parts (*cf.* [54]), with intrinsically nonlinear dynamics. The combination of this nonlinearity and the multitude of possible interactions, both direct and indirect (i.e., those mediated by a third element), can produce highly non-intuitive effects when networks are subjected to perturbation, such as the importance of indirect effects for the maintenance of food-web complexity and biodiversity [55]. As a result, the dynamical properties of networks are not predictable through an additive, reductionist framework focused on the study on individual elements.

In a network, nodes (e.g., species, people, banks, etc.) are linked by flows (e.g., biomass flux, sentiment exchange, money, etc.) that can simply be treated as data to be analyzed: they are abstract. Analysis of these abstract nodes is discipline-independent and gives network metrics that can be used to describe groupings, structural complexity, **resilience**, and dynamics of information flow, with a strict network terminology that can then be mapped onto the (often less well defined) language used in each discipline, bringing both clarity and rigor.

A common language becomes particularly pertinent across the social and natural science divide. Whether due to genetic, friendship, or economic relationships, social groupings can value ecosystem functions very differently and thus affect the delivery of EcoS in complex ways. Understanding the effects of groupings is a basic goal of network analysis in engineering and social science, and is increasingly being used in ecology. New social metrics of substructure, such as the 'rich club' [32], are used to define groupings of important nodes for ecological network function and dynamics. Conversely, the 'keystone species' ecological concept is now routinely examined in studies of social and engineering network performance [20,33,34]. The transfer of network-based methods and language among disciplines is already underway, and could be extended to EcoS research.

A well-developed language for groupings, adopted from network science, would establish general rules for optimum group size, leadership, and maximizing fairness in EcoS use by stakeholders, such as governance of biodiversity in green areas in Stockholm [35] or a group-level competitive auction for the conservation of traditional quinoa varieties in the Andes [36]. Network approaches might also explain apparently 'emergent properties' of EcoS, such as why some groupings of quinoa farmers were self-policing, reducing cheating and potentially allowing reductions in the overhead for monitoring payments for EcoS [36].

### The Scale Challenge

Ecological data are typically collected on organisms that operate at local spatial scales and over the short term, of up to a few years [37,38]. Social scientists work with individuals or populations of humans at larger spatial scales and over the medium term, of annual to decadal timescales. Economists, meanwhile, work at scales up to the global economy and often over much longer time-periods. Although a gross simplification (*cf.* [39,40]), these examples illustrate that the scales at which the disciplines work often differ and, practically, this is an impediment to carrying out research across the disciplines [41,42].

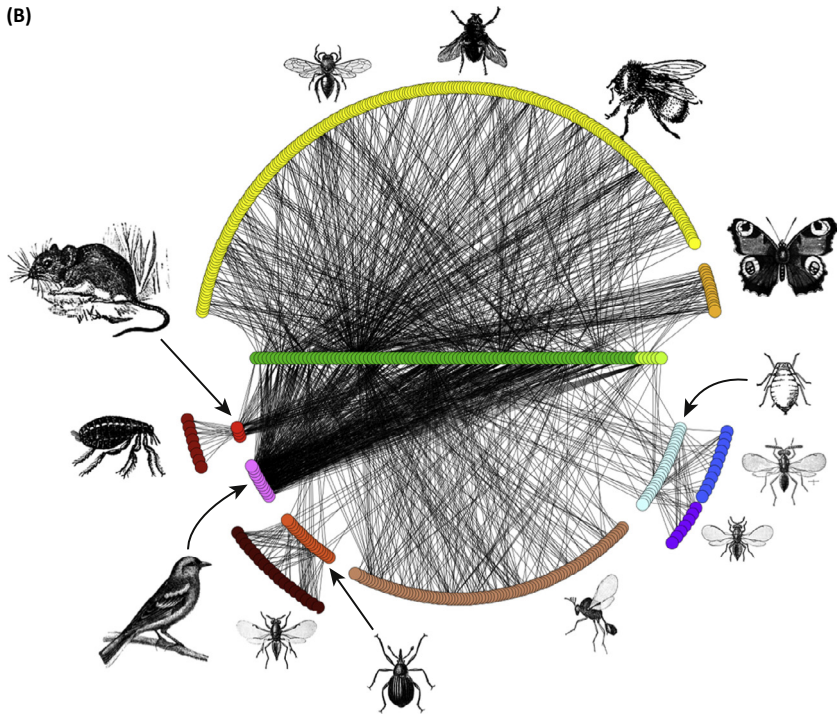
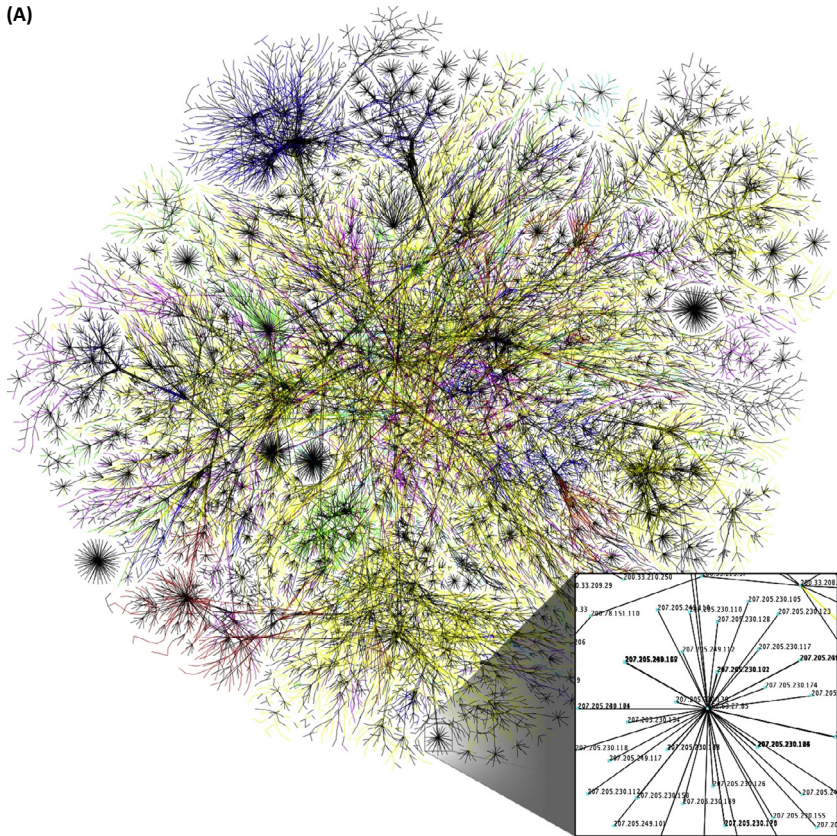
Network science offers methods and paradigms that can be adapted to cope with this scale disparity for EcoS (Figure 2). Computer and data networks such as the Internet can be treated as a complex of social, economic, and electronic elements that exist in a series of layers, each of which is discrete in terms of functionality and can be treated in isolation, but which also builds upon the layers below [43]. Thus, in the lowest layer, the engineering structure of the Internet is made up of individual computers as nodes physically linked together electronically. At higher levels, these engineering nodes are aggregated based upon economic criteria of response time and information flow that might have little relation to their physical distance; the computers might even be in different countries (Figure 1A). Higher layers again add social network information based upon the relationships between users of the Internet, which are in turn further aggregations of lower layers.

While it is possible to analyze any layer in isolation, and thus stay within a discipline, the tools exist to analyze across layers, scales, and disciplines, allowing the consideration of system-wide properties [44] such as how the engineering, economic, and social structure of the Internet can be managed to maximize information flow and resilience to disturbance and alterations in human

**Resilience:** in the strict mathematical sense, this is the rate at which a system returns to its original equilibrium following disturbances from it [56]. When applied to ecosystem functioning, it is the speed at which a given ecosystem returns to a state with a similar level of functioning. Another definition in common use is whether or not a system returns to its former equilibrium or to another one. This can be expanded to compare systems in terms of what range of disturbances a system can withstand before being shifted to the new equilibrium [57].

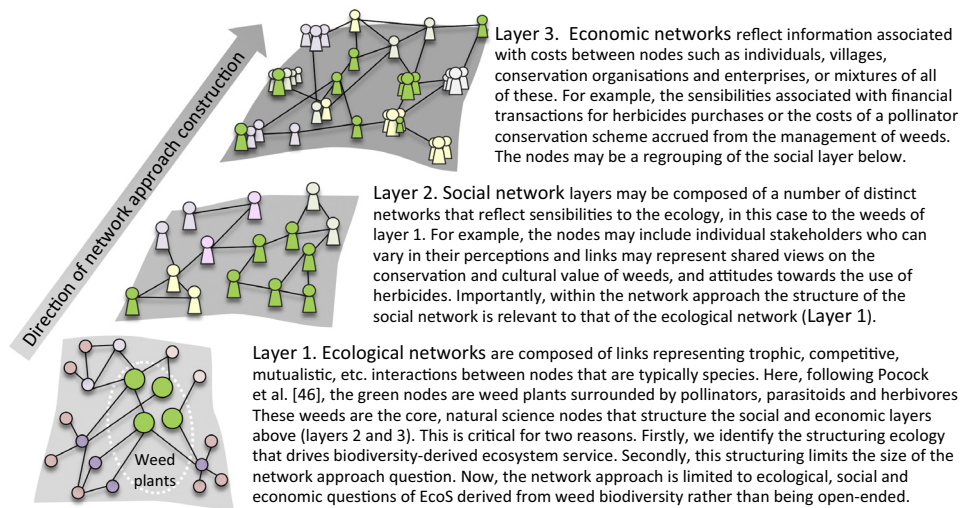
**Scale:** defines both the organizational level and the spatial and temporal dimensions of ecosystems, particularly because these can change between disciplines as we shift from ecological to anthropogenic representation of the ecosystem. The description of nodes and links naturally leads to the scale under consideration. If we consider a node to be an individual population of a species, we immediately define an organizational level based upon the population. The links, measured as the frequency and flow of information between the nodes, define the basic spatial and temporal dimensions of the network. Hence, at the organizational level of individual populations, trophic links are relevant to foraging patterns and frequency of feeding.





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Figure 1. Visualizations of Networks From Natural and Social Sciences and Engineering. (A) Map of the Internet, as of January 15th 2005. The link is drawn between nodes representing two distinct server IP addresses with color codes



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Figure 2. Illustration of the Layering of the Multi-Networks We Propose for EcoS, Using the Network of [46] as the Inspiration for the Ecological Network in Layer 1 (see also Figure 1B).

behavior [45]. It is these between-layer, cross-discipline properties of the system that resonate very strongly with the properties we might wish to evaluate and predict for EcoS.

### The Interaction Challenge

For practical purposes of time and cost, researchers have focused on a few groups or taxa that deliver simple EcoS. Such oversimplification to a single EcoS undermines the explicitly interactive nature of EcoS research [1,7]. Pocock *et al.* [46] investigated multiple interacting ecosystem functions, which underlie EcoS interactions, using an ecological network of species from arable agriculture (Figure 1B). They found that the different functions varied in their robustness, with pollinators being particularly fragile to loss of plant species, but there was no strong co-variation in function because the different functions in interaction were often in conflict. The structure of the Pocock *et al.* [46] network showed clearly why this was (Figure 1B): species interacted with one another through the diverse weed plants in the agricultural system, and some groups therefore profited by reducing the weeds at the expense of other groups.

By embracing the complexities of interaction, especially of nonlinearity and indirect effects, Pocock *et al.* [46] revealed robust and valuable ecological simplifications. There was no 'Optimist's Scenario' or 'win-win' conservation management that could benefit both biodiversity and multiple ecosystem functions in this agricultural system. More significantly, the network analysis demonstrated the central and crucial ecological role of the weeds in the provision of ecosystem functions, and thus identified a convincing natural science context for EcoS research in this system.

that denote the domain names of the server representing some combination of computer hardware, social use, and country of location (dark blue, .net, .ca, .us; green, .com, .org; red, .mil, .gov, .edu; yellow, .jp, .cn, .tw, .au, .de; magenta, .uk, .it, .pl, .fr; gold, .br, .kr, .nl; and white, unknown). The length of each link indicates an economic metric such as the response time between the nodes (used with permission of opte.org). (B) Species interaction networks (revised from [46] and used with permission). Each species is represented by a node that is a filled circle, and each trophic link is represented by a line. Weed plants are the green nodes in the centre, with crops in light green. Each type of consumer node has a unique color and associated indicative species in illustration.

### An EcoS Network Approach

To construct an EcoS network approach, we return to the layering paradigm and reimagine an EcoS network as being a multi-network of layers (Figure 2). Here, layer 1 is the natural science layer that structures all higher, social-science layers. For understanding EcoS in arable agriculture, layer 1 could be the ecological network of Pocock *et al.* [46], with the weeds as the core, natural science nodes that structure all interactions with the higher-layer social and economic networks. Building the social layers upon these core, natural science nodes gives context and makes tractable the analysis of the EcoS network. In place of potentially considering all social, economic, and ecological interactions linked to EcoS that might be imagined in arable farmland, layer 1 would here limit any analysis to the EcoS derived directly from weed biodiversity.

Few examples of ecological, social, and economic networks for the same system exist, however, and the ecological network of Pocock *et al.* [46] can only partially illustrate our line of reasoning. To detail more completely and extend the approach to the social sciences, we use a relatively small, ongoing study from French upland agriculture as a hypothetical case study (Box 2). The case study describes an EcoS network approach, with layer 1 being a field-scale ecological

#### Box 2. Case Study. Hypothetical Network Approach for the Adoption of Landscape Management To Support Multiple EcoS Delivered by Carabids

In upland Côte d'Or, France, farmers want to reduce herbicide and nitrogen use and stop ploughing to reduce soil erosion. They have begun to use a no-plough with cover plant system (NCP) that takes on some aspects of perennial systems, with low disturbance and a near year-round plant cover. After 4 years of adoption, NCP appears to reduce chemical inputs and supports EcoS, including pollination and weed seed regulation by carabids [58]. Farmers also report effects of 'well being' because local villagers value the flowering cover plants when fields would normally be bare. The first 3 years of NCP (<4 years) are critical, as slug and weed problems can increase pesticide use and limit adoption. Past research has shown that carabids can control weeds, via the seedbank [52], and slugs [59], where their numbers are high enough. We know from preliminary work that landscape management can increase carabid abundance in early NCP fields to late NCP field levels (Figure 1). Our question is whether it is possible to help farmers through adoption by increasing carabid abundance and using carabid-derived EcoS.

##### Layer 1. Ecological interactions

We begin with a quantitative trophic network of carabids, molluscs and weed seed species (Figure II). Each replicate of the network is from a given field, with parameters of crop and conditions, and an individual farmer. This network becomes layer 1 (see main text, Figure 2). The nodes structuring all higher layers are the carabids we wish to increase, tied to individual farmer information.

##### Layer 2. Social interactions

The network of social interactions between farmer nodes deals with landscape management to increase carabid number. In the Côte d'Or, the problem is that farms are not contiguous sets of fields. Using landscape management requires cooperation amongst farmers. Farmers, who trust one another through kinship or friendship, may show reciprocity and sow crops necessary to increase carabids in the landscape. Others will sow unilaterally. Inserting local villagers into the network, with the well being that they can bring, might modify decision making for or against adopting landscape management for carabids. A spatially explicit visualisation of the network might be used to persuade farmers of the benefits [49].

##### Layer 3. Economic interactions

The network in layer 3 is built around farmers and villagers and their assessments of the costs and benefits of managing the landscape for carabids. This might include the relative cost of growing a crop to aid neighbours over one that has a high commodity price. Interplay between layers 2 and 3 will directly modify the likelihood of adopting NCP.

##### Analysis

The analysis of this case study will be structured by the flow of aims in Box 3. We will, in principle, be able scale our questioning from any one layer all the way through to a full network approach using all layers simultaneously. Full approach questions might include whether: social and economic imperatives can bring about the conditions necessary for the regulation of slugs and/or weeds; the adoption of NCP requires group of farmers to work together in collective action; and, policy should be aimed at farmer group level? The goal is to identify the appropriate information for advocacy of NCP and the policy tools that might bring about adoption.

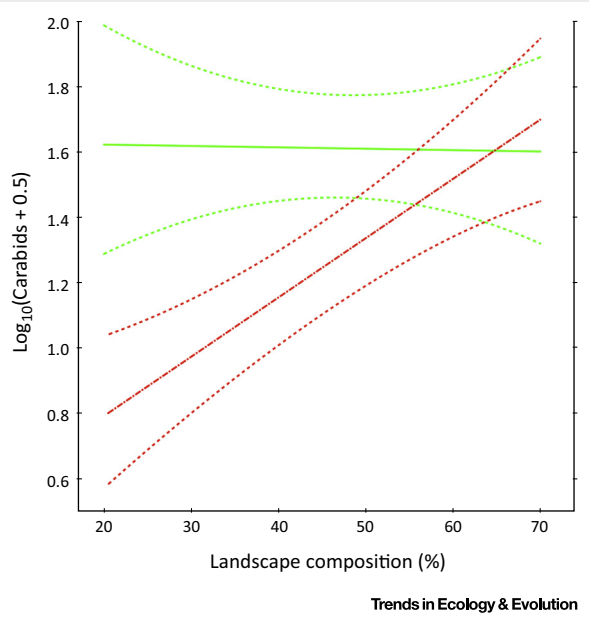


Figure I. Preliminary Data for the Change in Carabid Abundance in 60 NCP Fields, with Landscape Composition as the Percentage of Arable Fields in the Surrounding Landscape ( $\pm 95\%$  CIs). In late fields (green solid line), carabid numbers were high and independent of landscape. In the early fields (red dashed line), carabid numbers respond to landscape and appear to attain similar abundances to the late fields.

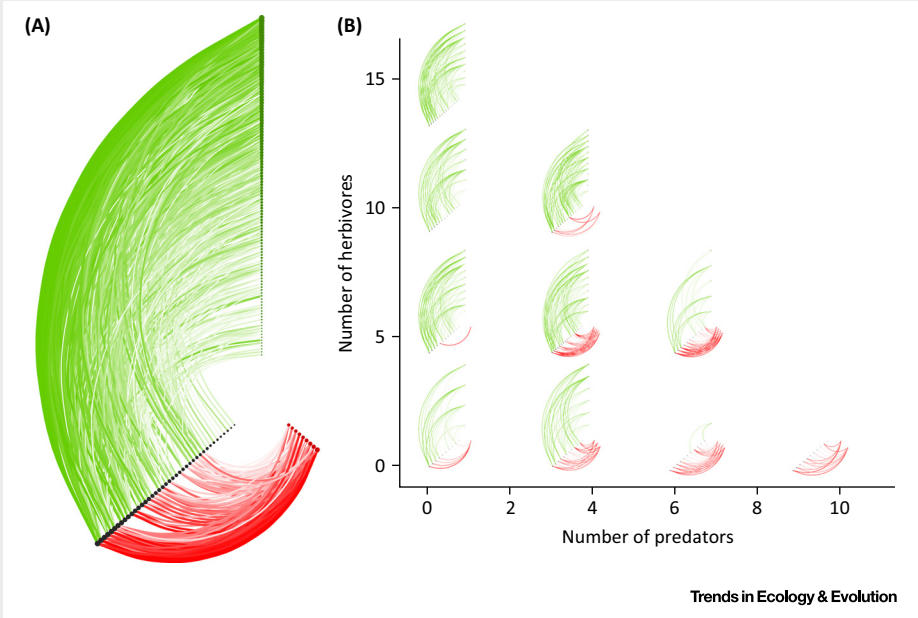
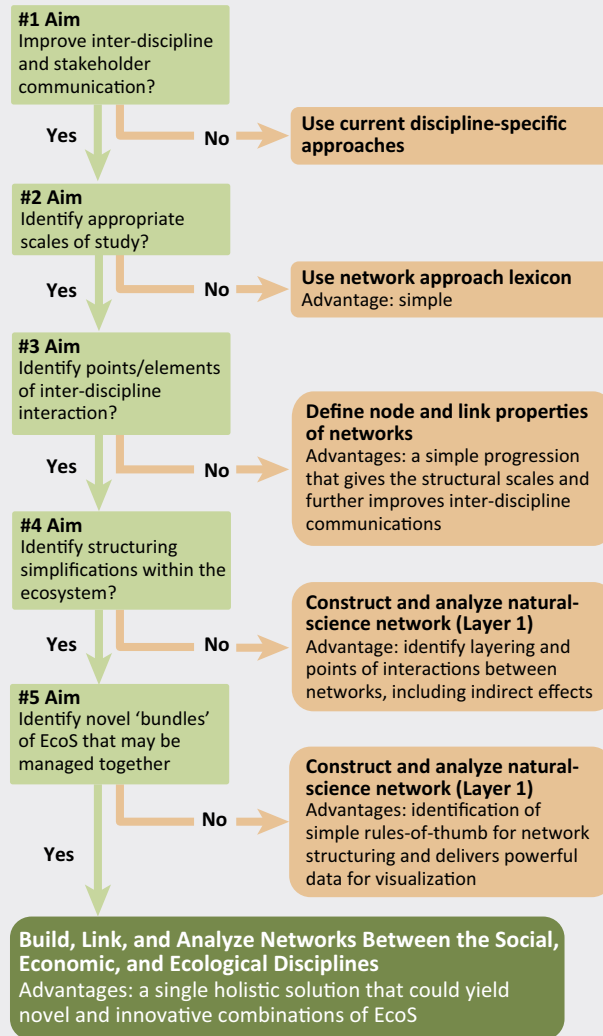


Figure II. Visualisations of a Trophic Network of Consumer Carabids (●), and Molluscs (●) and Weed Seeds (●) Resources. Each node represents a species, with the size of the node being its abundance. The links indicate trophic interactions between the predator and resources, with the width of the link reflecting the strength of the interaction. (A) The composite network aggregated across all sites. (B) Individual networks for sites with increasing numbers of carabid species playing the consumer roles of predator of molluscs and herbivore of weed seeds.



## Box 3. Decision-flow for Adopting a Network Approach to EcoS

Groups of researchers who are open to using networks for EcoS presumably either have data already available or are trying to specify the data requirements for the study. We imagine that they have in mind how deeply they would want to work with EcoS, ranging from simply facilitating inter-discipline communication all the way down to working with multi-networks. Given this, then working through the flow of text boxes, starting at Aim #1 below, would determine what would be required for their research question.



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network of two ecosystem functions, of weed seed and slug regulation, delivered by a common community of carabid beetle species. These beetle species nodes become the core nodes in the layer 1 network that structure the higher-layer social networks not only because they affect directly the ecosystem functions we want but also because the beetles can be managed, and their number and species richness increased, through choices for the agricultural landscape of fields made by stakeholders. Consequently, in layers 2 and 3 there are, respectively, networks of social and economic relationships between farmers and villagers that can modify choice in the management of the landscape and consequently the carabids in-field available to perform regulation services.



Thus, the EcoS network approach starts with the construction and analysis of a natural science network to identify a coherent set of nodes that drive interactions between ecosystem functions but, in turn, can also be manipulated through social and economic needs manifested in social networks at higher layers. This 'search' for a core group of nodes is very much reductionist in approach. Where several sets of nodes that each affect disparate functions are identified in a candidate network, for example, this suggests that the network should be broken up into smaller, simpler networks. Importantly, once identified, the coherent set of nodes donates to the EcoS network the suite of spatial and temporal scales applicable in the system. Layer 1 of our case study (Box 2) consists of networks for populations of species of weeds, slugs, and carabids at the field scale, with replication up to a landscape of fields. Layers 2 and 3 are made up of stakeholders, farmers, and villagers who reside within and have needs at the landscape scale, but can modify landscape management at the field scale. It is the language and tools of networks that ultimately tie the EcoS network approach together, facilitating analysis and communication within and between disciplines, to stakeholders, and between studies.

The utility of the approach, however, is not that it always requires full implementation but, instead, is adaptive and flexible (Box 3). At its simplest, the network vocabulary coexists with discipline-specific terminology, but serves the purpose of promoting communication between the disciplines. At intermediate levels of implementation, analysis of ecological networks already constructed can be used to help to identify the interactions that structure the system. Only with fullest implementation would the approach integrate networks from ecology, economics, and social science, tackling tractably the networks of interaction that exist within and between each of these disciplines, so as to deliver multiple EcoS.

### Conclusion and Perspectives

In this paper we propose a network-based methodology to develop more-rational, evidence-based decision-making that can be used to manage combinations (bundles) of EcoS simultaneously. The EcoS network approach begins by isolating the core group of nodes in an ecological network that are important in interactions between ecosystem functions and, in turn, can be managed by social and economic need. This identifies explicitly interactions between multiple functions and a point of contact between the natural and social science disciplines. The approach thereby establishes, from the outset, a strong natural science context for EcoS research, which through its absence is often identified as a weakness for the field [6–8,31], and makes the approach tractable by limiting the work to a core group of natural science nodes and their ecological and social interactions.

The EcoS network approach places the ecological network, and the social and economic networks that are built upon it, within a series of layers that formalize the scales of the ecosystem under consideration and allow between-layer network analyses to be conducted across the natural and social science divide. The strict language of networks can be applied to all network layers promoting communication between disciplines, potentially allowing learning by facilitating comparison between different studies that take the EcoS network approach. The EcoS network approach thus achieves our aims of solving the common-language, scale, and interaction challenges, transcending differences between the disciplines and placing the natural, ecological sciences at the heart of EcoS research.

Decision-making for EcoS requires that multiple stakeholders contribute via a feedback loop of advocacy that includes demonstration, consultation, learning, co-development, and engagement [47,48]. We believe that the EcoS network approach would play an important role here, ultimately providing a rigorous method to consider interaction between ecosystem functions and rendering them, through consideration of the social and economic sentiments of humans, into

### Outstanding Questions

We can see two types of outstanding questions. The first relates to EcoS network methodology, and how this might be developed. The second concerns the potential new research questions that an EcoS network approach might open up.

#### *EcoS Network Methodology Development*

*Scale Overlap.* While network analysis methods can cope with changes in scale (see text and Glossary), it would still be far simpler to find common, overlapping scales for EcoS analysis across all disciplines. Changing scale implies potentially important impacts on the types of information we can obtain from network analyses [52]. Future research should identify both compatible scales of research between disciplines and what the consequences of such common scaling would be: what information is lost; how does this affect network dynamics; and is this information loss worth the greater simplification that ensues?

*Layering.* The layering of networks, from the ecological through to social and economic layers, is a key element of the network approach for EcoS. With hindsight, the engineering, social, and economic layering used for electronic networks, which inspired the EcoS layering, would appear obvious, but this is not so with EcoS layering. There is an important research question of whether there exists a generalized layering, a common framework as it were, which would allow us to define *a priori* the layers that go into a network model of EcoS.

*Testing.* It seems to us that the possibility of carrying out the research necessary to examine the scale overlap and layering questions, and more importantly to evaluate the utility of a network approach to EcoS, is not too distant. For example, data probably exist across the different groups working on pollination or pest control to construct social and economic networks of stakeholder sentiment, which could be used with existing ecological networks to examine whether an EcoS network approach delivers the advantages expected from the decision-flow (Box 3).

EcoS for which trade-offs between needs can be examined. That networks are also explicitly graphical, visually attractive, and able to deliver complex information with often surprising clarity [49,50] can only help in further promoting their use in demonstration and engagement. We have immediate questions that we think need to be answered for this approach to 'prove its mettle', and we detail some of these in the Outstanding Questions. Ultimately, however, networks can be used to do more than simply analyze EcoS. Networks have proved to be very useful for understanding and also predicting complex patterns of behavior that are often described as 'emergent properties of the system'. Bundles of multiple, interlinked EcoS are such emergent properties that arise as a consequence of nonlinear and dynamic social and economic interactions with ecological functions. We expect, therefore, that the EcoS network approach will predict novel combinations of EcoS that can provide truly innovative management solutions beyond traditional ingrained expectations (cf. [51]).

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### Supplemental Information

Supplemental information associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.tree.2015.12.003>.

### References

1. Millennium Ecosystem Assessment (2005) *Ecosystems and Human Well Being: Synthesis*, Island Press
2. Carpenter, S.R. *et al.* (2009) Science for managing ecosystem services: beyond the Millennium Ecosystem Assessment. *Proc. Natl. Acad. Sci. U.S.A.* 106, 1305–1312
3. Daily, G.C. *et al.* (2009) Ecosystem services in decision making: time to deliver. *Front. Ecol. Environ.* 7, 21–28
4. Raudsepp-Heare, C. *et al.* (2010) Untangling the environmentalist's paradox: why is human well-being increasing as ecosystem services degrade? *BioScience* 60, 576–589
5. Intergovernmental Platform on Biodiversity and Ecosystem Services (2013) *IPBES Draft Work Programme 2014–2018*, IPBES
6. Silvertown, J. (2015) Have ecosystem services been oversold? *Trends Ecol. Evol.* 30, 641–648
7. Schröter, M. *et al.* (2014) Ecosystem services as a contested concept: a synthesis of critique and counter-arguments. *Cons. Lett.* 7, 514–523
8. Naeem, S. *et al.* (2015) Get the science right when paying for nature's services. *Science* 347, 1206–1207
9. Biggs, N. *et al.* (1986) *Graph Theory*, Oxford University Press
10. Mashaghi, A.R. *et al.* (2004) Investigation of a protein complex network. *EPJ B* 41, 113–121
11. Ideker, T. and Sharan, R. (2008) Protein networks in disease. *Genome Res.* 18, 644–652
12. Gardy, J.L. *et al.* (2011) Whole-genome sequencing and social-network analysis of a tuberculosis outbreak. *N. Engl. J. Med.* 364, 730–739
13. Valente, T.M. (1996) Social network thresholds in the diffusion of innovations. *Soc. Netw.* 18, 69–89
14. Acemoglu, D. *et al.* (2013) Opinion fluctuations and disagreement in social networks. *Math. Oper. Res.* 38, 1–27
15. Jackson, M.O. (2010) An overview of social networks and economic applications. In *The Handbook of Social Economics* (Benhabib, J. *et al.*, eds), pp. 511–585, Elsevier
16. Janssen, M.A. *et al.* (2006) Toward a network perspective of the study of resilience in social-ecological systems. *Ecol. Soc.* 11, 15
17. Woodward, G. *et al.* (2005) Body size in ecological networks. *Trends Ecol. Evol.* 20, 402–409
18. Mulder, C. and Elser, J.J. (2009) Soil acidity, ecological stoichiometry and allometric scaling in grassland food webs. *Glob. Chang. Biol.* 15, 2730–2738
19. Thompson, R.M. *et al.* (2012) Food webs: reconciling the structure and function of biodiversity. *Trends Ecol. Evol.* 27, 689–697
20. Montoya, J.M. *et al.* (2006) Ecological networks and their fragility. *Nature* 442, 259–264
21. Petchey, O.L. *et al.* (2008) Size, foraging, and food web structure. *Proc. Natl. Acad. Sci. U.S.A.* 105, 4191–4196
22. Reiss, J. *et al.* (2009) Emerging horizons in biodiversity and ecosystem functioning research. *Trends Ecol. Evol.* 24, 505–514
23. Barabasi, A.L. and Albert, R. (1999) Emergence of scaling in random networks. *Science* 286, 509–511
24. Harary, F. (1969) *Graph Theory*, Addison Wesley
25. Haines-Young, R. (2011) Exploring ecosystem service issues across diverse knowledge domains using Bayesian belief networks. *Prog. Phys. Geogr.* 35, 681–6992
26. Macfadyen, S. *et al.* (2009) Do differences in food web structure between organic and conventional farms affect the ecosystem service of pest control? *Ecol. Lett.* 12, 229–238
27. Rathwell, K.J. and Peterson, G.D. (2012) Connecting social networks with ecosystem services for watershed governance: a social ecological network perspective highlights the critical role of bridging organizations. *Ecol. Soc.* 17, 24
28. Costanza, R. and Kubiszewski, I. (2012) The authorship structure of 'ecosystem services' as a transdisciplinary field of scholarship. *Ecosyst. Serv.* 1, 16–25
29. Mulder, C. *et al.* (2015) 10 years later: revisiting priorities for science and society a decade after the Millennium Ecosystem Assessment. *Adv. Ecol. Res.* 53, 1–53
30. Tallis, H. *et al.* (2014) Working together: a call for inclusive conservation. *Nature* 515, 27–28
31. Tavoni, A. and Levin, S. (2014) Managing the climate commons at the nexus of ecology, behaviour and economics. *Nat. Clim. Cha.* 4, 1057–1063
32. Ma, A. and Mondragón, R.J. (2015) Rich-cores in networks. *PLoS ONE* 10, e0119678
33. Pascual, M. and Dunne, J.A. (2006) From small to large ecological networks in a dynamic world. In *Ecological Networks: Linking Structure to Dynamics in Food Webs* (Pascual, M. and Dunne, J.A., eds), pp. 3–24, Oxford University Press
34. Jordán, F. *et al.* (2009) Trophic field overlap: a new approach to quantify keystone species. *Ecol. Model.* 220, 2899–2907

### New Research Questions

*Nonlinearity and Indirect Effects on EcoS.* Nonlinearity and indirect effects have marked effects on network performance. Within the ecological layer, this can include effects on food-web stability and resilience [18,52]. How such 'higher-level' performance is affected by the addition of effects within and between the social and economic layers is as yet unclear. Whether this might lead to greater EcoS stability and resilience that might be promoted through 'payment for ecosystem services' schemes, or show that most domains of possible management would reduce stability and resilience of EcoS delivery, is clearly important to understand.

*Socioeconomic Feedback on Biodiversity-Ecosystem Function (B-EF).* A network approach to EcoS might be used to prioritize ecological and B-EF research. If we constrain part of the research in this area, through feedback from social and economic networks, which B-EF relationships become important and how do they vary under different scenarios of change?

*General Indicators and Rules-Of-Thumb.* Decision-making for EcoS would be greatly facilitated by the discovery of general, synthetic indicators or rules-of-thumb for the performance and behavior of EcoS networks. Future research should consider whether synthetic indicators, such as ecological traits considered at the node- and network-level, have predictive value.

35. Ernstson, H. *et al.* (2010) Scale-crossing brokers and network governance of urban ecosystem services: the case of stockholm. *Ecol. Soc.* 15, 28
36. Narloch, U. *et al.* (2013) How to achieve fairness in payments for ecosystem services? Insights from agrobiodiversity conservation auctions. *Land Use Policy* 35, 107–118
37. Hagen, M. *et al.* (2012) Biodiversity, species interactions and ecological networks in a fragmented world. *Adv. Ecol. Res.* 46, 89–120
38. Stewart, R.I.A. *et al.* (2013) Mesocosm experiments as a tool for ecological climate-change research. *Adv. Ecol. Res.* 48, 71–181
39. Shmida, A.V.I. and Wilson, M.V. (1985) Biological determinants of species diversity. *J. Biogeogr.* 12, 1–20
40. Palmer, M.A. *et al.* (2012) Socioenvironmental sustainability and actionable science. *BioScience* 62, 5–6
41. Mace, G.M. *et al.* (2012) Biodiversity and ecosystem services: a multilayered relationship. *Trends Ecol. Evol.* 27, 19–26
42. de Groot, R.S. *et al.* (2010) Challenges in integrating the concept of ecosystem services and values in landscape planning, management and decision making. *Ecol. Complex.* 7, 260–272
43. Zimmermann, H. (1980) OSI reference model – the ISO model of architecture for open systems interconnection. *IEEE T. Commun.* 28, 425–432
44. D'Agostino, G. and Scala, A., eds (2014) *Networks of Networks: The Last Frontier of Complexity*, Springer International Publishing
45. Albert, R. *et al.* (2000) Error and attack tolerance of complex networks. *Nature* 406, 378–382
46. Pocock, M.J.O. *et al.* (2012) The robustness and restoration of a network of ecological networks. *Science* 335, 973–977
47. Chan, K.M.A. *et al.* (2012) Where are cultural and social in ecosystem services? A framework for constructive engagement. *BioScience* 62, 744–756
48. Dicks, L.V. *et al.* (2014) A transparent process for 'evidence-informed' policy making. *Cons. Lett.* 7, 119–125
49. McInerney, G.J. *et al.* (2014) Information visualisation for science and policy: engaging users and avoiding bias. *Trends Ecol. Evol.* 29, 148–157
50. Pocock, M.J.O. *et al.* (2016) The visualisation of ecological networks, and their use as a tool for engagement, advocacy and management. *Adv. Ecol. Res.* 54 (in press)
51. Vespignani, A. (2009) Predicting the behavior of techno-social systems. *Science* 325, 425–428
52. Bohan, D.A. *et al.* (2011) National-scale regulation of the weed seedbank by carabid predators. *J. Appl. Ecol.* 48, 888–898
53. Anderson, P.W. (1972) More is different. *Science* 177, 393–396
54. Cohen, J.E. *et al.* (2009) Food webs are more than the sum of their trophic parts. *Proc. Natl. Acad. Sci. U.S.A.* 106, 22335–22340
55. Montoya, J.M. *et al.* (2009) Press perturbations and indirect effects in real food webs. *Ecology* 90, 2426–2433
56. Pimm, S.L. (1984) The complexity and stability of ecosystems. *Nature* 307, 321–326
57. Holling, C.S. (1973) Resilience and stability of ecological systems. *Annu. Rev. Ecol. Syst.* 4, 1–23
58. Trichard, A. *et al.* (2013) The relative effects of local management and landscape context on weed seed predation and carabid functional groups. *Basic Appl. Ecol.* 14, 235–254
59. Bohan, D.A. *et al.* (2000) Spatial dynamics of predation by carabid beetles on slugs. *J. Anim. Ecol.* 69, 367–379