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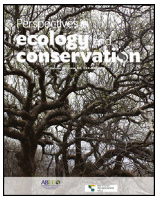

Essays and Perspectives

Network science: Applications for sustainable agroecosystems and food security

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HIGHLIGHTS

- We reviewed the use of network science in sustainable agriculture.
- Network science can be used to understand, harness and restore ecological processes in agricultural systems.
- Social, economic and ecological aspects of agriculture can be incorporated using novel methods.
- Agricultural systems can be managed using a network-based framework.

GRAPHICAL ABSTRACT

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ABSTRACT

The global challenge of feeding two billion more people by 2050, using more sustainable agricultural practices whilst dealing with uncertainties associated with environmental change, requires a transformation of food systems. We present a new perspective for how advances in network science can provide novel ways to better understand, harness, and restore multiple ecological processes in agricultural environments. We describe: (i) a network-focused framework for managing agro-ecosystems that accounts for the multiple interactions between biodiversity and associated ecosystem services; (ii) guidance for incorporating socio-economic factors into ecological networks; and (iii) the potential to upscale network methods to inform efforts to build resilience, including global food-supply chains. In doing so we aim to facilitate the application of network science as a systems-based way to tackle the challenges of securing an equitable distribution of food.

> "*The natural living world is arranged in very complex channels of supply that are known as food-chains. [. . .] But with land in cultivation, whether pastoral, ploughed, or gardened, the earnest desire of man has been to shorten food-chains, reduce their number, and substitute new ones for old. [. . .] The enormous problem still is to manage, control, and where necessary alter the pattern of food-chains in the world, without upsetting the balance of their populations. It is this last problem that has not by any means been solved.*" Charles Elton (1958)

Introduction

Over six billion people are directly dependent upon agriculture for their livelihoods worldwide (Food and Agriculture Organization of the United Nations, 2013), with one in ten people (690 million) undernourished and the majority of the world's hungry people living in developing countries (United Nations, 2020). Feeding nine billion people by 2050, using less environmentally damaging agricultural practices whilst also dealing with the uncertainties posed by climate change, is a significant undertaking (Godfray et al., 2010). The scenario is especially challenging if we consider that 52% of agricultural land is currently moderately or severely degraded as a result of intensive agricultural practices (Food and Agriculture Organization of the United Nations, 2019). The nexus between food demand and supply poses a major challenge to contemporary food systems that appear under-equipped to deal with future challenges. Ultimately they may lack resilience to potential perturbations and long-term changes (i.e., climate change), which threaten the integrity of global food production, food quality, environmental stability and human health (Cottrell et al., 2019).

Addressing these issues alongside '*bending the curve of biodiversity loss*' (Leclère et al., 2020) associated with the unsustainable intensive farming practices and inequitable distribution and consumption of food, requires a radical transformation of food systems from local to global scales (World Wide Fund for Nature, 2020). "*Bending the curve*" is now a major policy driver for many nations in the quest for sustainable agriculture (e.g., the European Union's Farm to Fork Strategy). However, the significant socio-ecological complexity in contemporary agriculture, coupled with the global movement of goods and labour, inequitable distribution of water and rapid changes in environmental conditions, means that future agricultural challenges are multifaceted, interconnected and require large amounts of information in order to succeed (Hazell and Wood, 2008). The United Nations Sustainable Development Goals (SDGs) were developed to address such interconnected challenges (Chaudhary et al., 2018) and the ecosystem services provided by agricultural systems depend on the strong interactions and feedbacks between humans, the environment, and food systems. Therefore, whole systems-based approaches are required to understand and effectively manage these layers of complexity and face the challenges imposed by the SDGs (McGowan et al., 2019). We contend that complexity science (Table 1), in particular advances in network science, can provide a systems-based framework within which the challenges to contemporary agricultural and food systems can be addressed at multiple spatial and temporal scales and using different information types.

Network science, when applied to the study of ecosystems, has been used to describe and understand the patterns of interactions in assemblages of interacting species, characterising the underlying structure of ecological communities. The network structure of ecological systems, combined with mathematical modelling, can enhance our understanding of ecological and evolutionary processes (e.g., co-evolution of antagonists and mutualists), energy and matter flow in ecosystems, the ecosystem services provided by biodiversity, and demographic dynamics in species, due to environmental change (Montoya et al., 2006). In recent decades, significant advances in our understanding of the structure and robustness of ecological networks have been derived from empirical studies conducted in agro-ecosystems, allowing us to better understand the relationships between the structure and function of complex ecosystems (Supplementary Table S1). In turn, this has enabled new guidance for the sustainable management and restoration of important and beneficial groups of organisms across agricultural regions (see below).

As well as proving useful for studying ecological dynamics, network-based thinking enables an understanding of the socio-ecological interactions present in agricultural environments (Bohan et al., 2013). This is particularly important for developing future management, conservation and restoration strategies to build resilience in both crop and non-crop habitats in agricultural regions (Bullock et al., 2017). By scaling-up further, the same network approaches can be developed to examine and improve the resilience of global food supply chains (Puma et al., 2015).

Here, we present a state-of-the-art for network science in agricultural systems, from species interaction networks in fields through to global trade networks. We highlight recent developments in the field, identify future advances required to build resilience into food systems and ultimately demonstrate how we can use networks predictively to generate efficient and sustainable agriculture. With a focus on a range of different terrestrial cropping systems (e.g., intensive to extensive management), our aims are fourfold: (i) to summarise the theory and application of network science in agro-ecosystems; (ii) to demonstrate the use of network approaches to understand and manage agro-ecosystems across scales; (iii) to identify important research themes in agricultural networks; and (iv) to elucidate future advances required to understand and develop resilience in agro-ecosystems across the globe.

Table 1
Glossary of terms relating to complexity and network science in agriculture.

Term	Description
General terms	
Complexity science	The study of complex systems, those composed of multiple components that may interact with one another to produce emergent properties, local conditions, non-linearity and adaptation, which shape the collective behaviours. Complexity is observed in a variety of systems.
Network science	The study of the interactions between discrete elements and their potential implications.
Network	A system of interconnected or linked elements, also called a 'graph' in mathematics.
Ecological network	A system of interconnected ecological units (e.g., individuals, populations, species) at a particular temporal and spatial scale (e.g., a habitat, a community, an ecosystem).
Network terms	
Nodes (or vertices)	Elements within a network. Nodes may be people, animals, plants, ideas, places, ecosystem services, habitats or a range of other discrete elements.
Links (or edges)	Interactions or relationships between two or more nodes within a network (see Ecological interaction). This could be weighted (e.g., visitation frequency of a pollinator or number of caterpillars attacked by parasitoids) or unweighted (e.g., present/absent). Furthermore, edges can be directed (i.e., from one node to the other) or undirected (i.e., where the relation between the two nodes is symmetrical).
Ecological interaction	A functional link (see Links) between two organisms (see Nodes) in an ecological network. This may be mutualistic (e.g., pollination, seed dispersal and endosymbiosis), competitive, antagonistic (e.g., predation and parasitism), commensalistic (e.g., some plants and arbuscular mycorrhizae) or amensalistic (e.g., trampling of plants and invertebrates by large animals). See Ecological terms for full definitions of different ecological interaction types.
Direct interactions	The effects of one node on another that are mediated by a link between these two nodes (e.g., exchange of goods, predation, parasitism).
Indirect interactions	The effects of one node on another which is mediated by one or more intermediary nodes.
Unipartite network	A network comprised of one set of nodes in which interactions occur between all nodes (e.g., food webs).
Bipartite network	A network comprised of two sets of nodes (e.g., plants and pollinators, herbivores and parasitoids or farmers and policy makers) in which interactions only occur between nodes of different sets.
Multilayer network	A network with multiple layers describing different types of links, nodes (e.g., mutualistic and antagonistic or social and ecological), or spatiotemporal variation in the system.
Network structure	The patterns of interaction of a given network (e.g., the arrangement of nodes and links).
Robustness	The tolerance of network structure to node extinctions.
Ecological terms	
Amensalism	An interaction in which one species is negatively affected, yet the other receives no cost or benefit (e.g., trampling of a plant by an animal).
Competition	An interaction between two species over a common resource that is in limited supply (e.g., two pollinators vying for nectar and pollen from the same flower).
Apparent competition	An indirect, interspecific interaction where the abundance of one species is reduced by the increase of other species abundance, without direct interaction occurring (e.g., abundance of one prey species is reduced through predation from a food-limited generalist predator shared with another organism, or abundance of one species is reduced in the presence of a parasite shared with a competitor species).
Mutualism	An interaction in which both partners benefit (e.g., plant-pollinator interactions).
Antagonism	An interaction in which one partner benefits at the expense of another (e.g., predator-prey, plant-herbivore and herbivore-parasitoid interactions).
Spillover effects	Ecological processes occurring in one habitat spill over into the neighbouring habitats (e.g., field margins enhance pollination in neighbouring arable fields).
Resilience	The amount of disturbance that an ecosystem can withstand without changing self-organised processes and structures (Holling, 1973)
Ecosystem functions	The ecological processes that regulate the transfers of energy and materials through an ecosystem.
Ecosystem services	The benefits provided by ecosystems to human wellbeing, i.e., Nature's contribution to people. There are four classes: provisioning (products, i.e., food, fresh water, fuel, wood), regulating (regulation of processes, i.e., climate, flood, disease, pollination), supporting (support other ecosystem services, i.e., nutrient cycling, soil formation, primary production) and cultural (non-material benefits, e.g., recreation, educational, cultural heritage).

Network applications for agriculture

Agro-ecosystems have typically been considered as crop monocultures with a few associated plant and invertebrate species residing in a single field, but they are clearly far more complex (Bohan et al., 2013). The relative contributions of biodiversity and species interactions in the provision of these services, however, remains under-appreciated in agro-ecosystems. Agricultural plants and animals are embedded in complex networks of above- and below-ground species interactions (including fungi, bacteria, viruses and a whole host of other organisms; Fig. 1), where organisms are co-dependent (de Vries and Wallenstein, 2017). These ecological interactions provide a wide range of ecosystem services, such as crop pollination by insects (Klein et al., 2007), natural pest control (Derocles et al., 2014) and beneficial effects of soil microbial activity (e.g., promotion of plant growth; Bennett et al., 2019). In this sense, a fundamental problem to solve is, how to characterise these services if they do not occur in isolation but rather affect each other through direct and indirect interactions between organisms.

Network science allows us to explore not just the direct and indirect interactions between biodiversity in crop and non-crop systems, but also incorporate human decision-making information by farmers, consumers, regulators and land managers from local, regional and global scales (Fig. 2). By exploring the direct and indirect interactions among the components of social-ecological systems, network science provides systems-based approaches that can characterise, analyse and potentially design sustainable food systems at different scales.

Field scale

Recent studies have provided a better understanding of the structure of mutualistic and antagonistic interactions in crop, non-crop and other habitats around the world. Collectively, this work has provided new insights into a number of ecological and evolutionary problems (e.g., community assembly and trait evolution) and has also indicated how to harness ecosystem services; mostly pollination and natural pest-control (Supplementary Table S1). In agro-ecosystems, the challenge ahead is to describe these systems

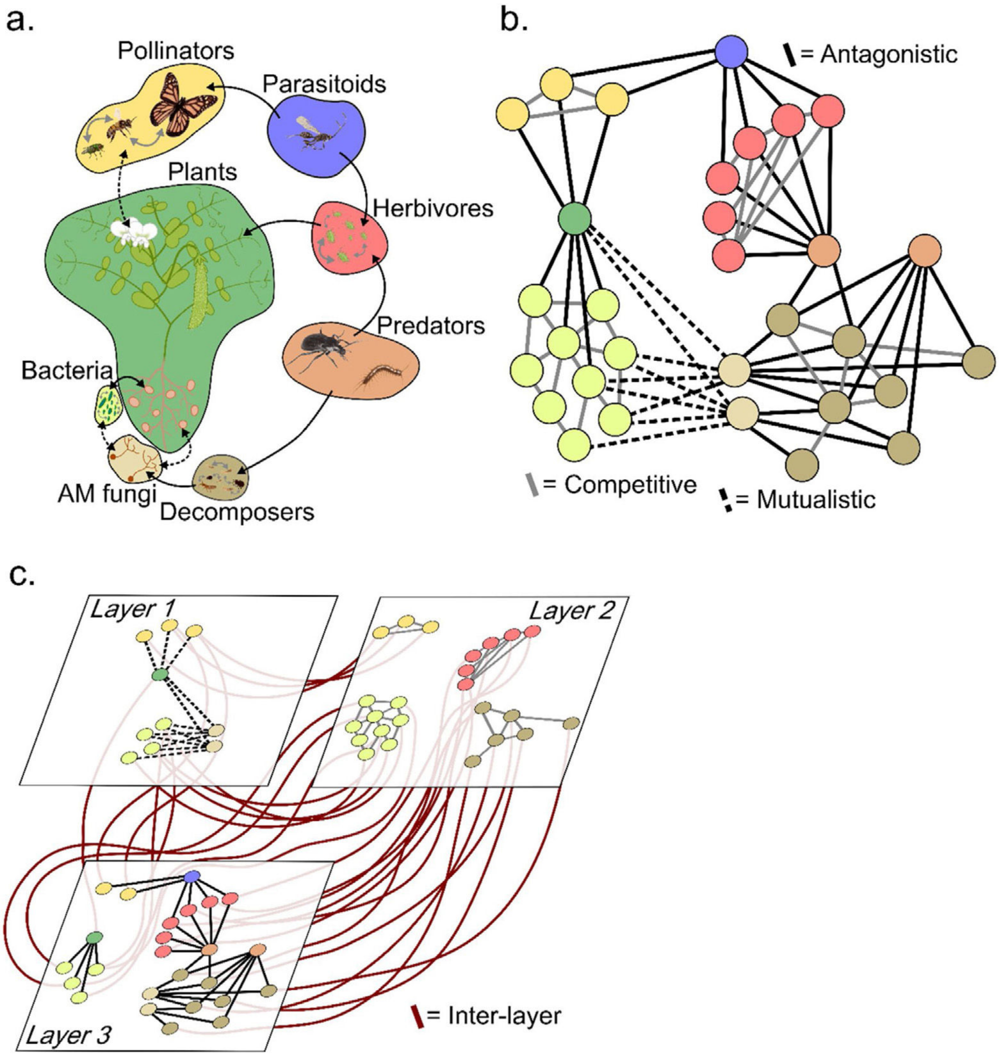

Fig. 1. Multilayer networks in agro-ecosystems. (a) A diagrammatic representation of a conceptual ecological network at a field scale. (b) A graphical representation of the network of multiple species interactions in (a), demonstrating how apparent intractable biological complexity can be systemised for mathematical analysis. (c) A multilayer representation of the network where intra-layer interactions are the same as in (b), yet inter-layer interactions are present connecting the same populations of organisms interacting across the multiple layers. The layers here represent different types of interaction. Layers, however, could also represent different fields, habitats, seasons, years or other discrete spatial or temporal units. Node colour indicates the role of the organisms within the network (e.g., symbiont, pathogen, pollinator, plant, herbivore, parasitoid, detritivore and predator). Link colours and line types represent different types of intra- and inter-layer interactions. Not all potential intra-layer interactions have been included in (a), (b) or (c) for illustrative purposes, for example antagonistic interactions between predators, parasitoids, pollinators and decomposers.

in ways that the full suite of important direct and indirect interactions that occur within the landscape are incorporated (Hutchinson et al., 2019). Indeed, current assessments of changes in farm management overlook important processes derived from interacting species, such as changes in trait distributions at the species-level may be compensated for at higher levels of biological organisation (Ma et al., 2019). Furthermore, a wide range of other interactions that may impact the design of agro-ecosystems have been less well studied, including spillover of pollination from non-crop to crop plant species and beneficial interactions between soil and plant communities. Although we can continue to obtain insights from studying these interactions in isolation, theory predicts that just a few links connecting elements may markedly change the dynamics of wider systems (Watts and Strogatz, 1998).

Conceptually, merging ecological networks of different interaction types is state-of-the-art. In an agricultural context, multiple direct and indirect interaction types with crops, both above and below-ground, can be quantified (Fig. 1). The simultaneous quantification of the multiple ecosystem services provided by biodiversity can provide insights on: (i) trade-offs in crop and non-crop management practices; and (ii) the often-unexpected dynamical consequences of coupling ecological interactions (e.g., emergent effects, indirect effects which transcend interaction networks and plasticity in the role of species within multilayer networks); both of which facilitate the task of improving sustainable yields. Pocock et al. (2012) were the first to show the usefulness of a '*network of ecological networks*' at a farm-scale by analysing how different interconnected groups of organisms respond to species loss. This work enhanced our understanding of the robustness and resilience of combined groups of plants and animals to environmental change, hence identifying vulnerable groups and demonstrating novel methods to restore ecosystem functioning based in identifying important plants and habitats.

Landscape scale

Networks at the field or habitat scale are inherently nested within a wider landscape of complex interactions (Evans et al., 2013). These networks connect habitats at a range of scales, with connections resulting either from the movement of individual

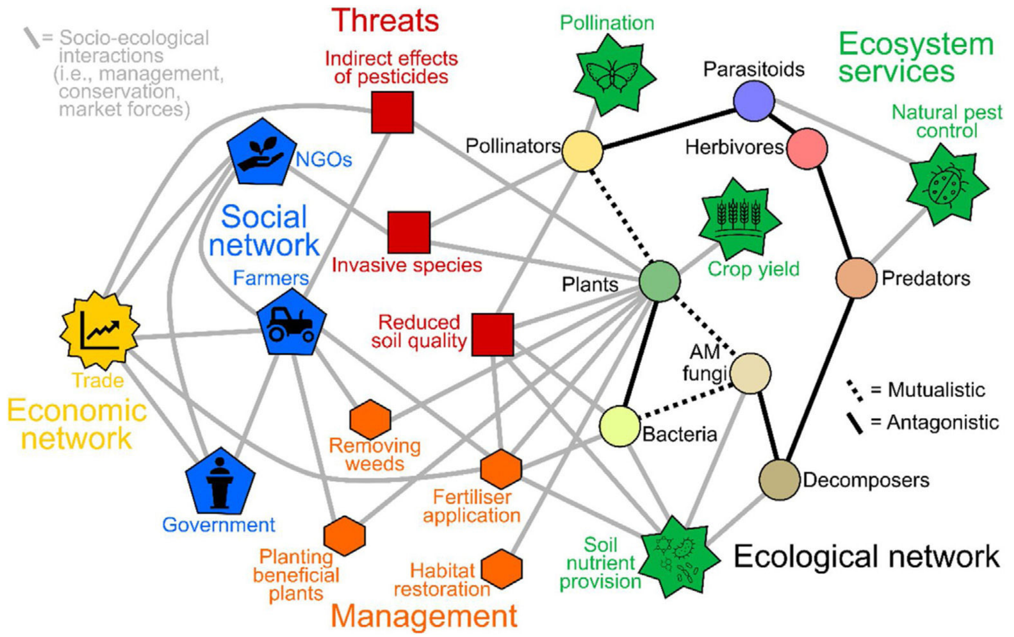

Fig. 2. An example of a merged agricultural network. Symbols represent threats to ecosystems (red squares), management interventions or actions (orange hexagons), social actors (blue pentagons), ecological networks (circles, where individual symbols represent individual species) and the ecosystem services (green stars) and economic compartments (yellow star). The figure covers only a subset of the potential social actors, economic pressures, threats, management actions and ecosystems services that are present in agricultural systems. Threats can directly link to ecosystem services, but also threaten their provision through ecological networks. Management can occur in response to threats and translates to ecosystem services through impacting the structure and function of the ecological network. Different types of interactions require different data, for example interactions between management and threats can be quantified by assessing the success of previous management interventions using monitoring.

organisms in space (i.e., the utilisation of multiple habitats by the same organism or long-distance dispersal among populations), by the use of different habitats by different populations of the same species, or by the transfer and flux of materials and energy across the landscape through existing networks of species (Massol and Petit, 2013). Research on meta-communities shows that, due to the inherent heterogeneity of ecological systems across space, the network of networks affects the response of both the overall network and its subnetworks to perturbations (Holyoak et al., 2005).

Several attempts have been made to understand the interactions between networks at the landscape scale in agriculture. These studies have looked at the shared interactions between habitats in order to understand the potential benefits of, for example, shared parasitoids of pest herbivores in both crop and non-crop habitats (Derocles et al., 2014). They draw on how concepts such as apparent competition, spillover effects, and top-down/bottom-up effects proliferate into crop systems, potentially improving yields. For instance, the potential of top-down effects, otherwise known as trophic cascades, to regulate pests may be achieved by manipulating habitat heterogeneity. Habitat heterogeneity causes changes in the feeding behaviour of generalist predators, leading to the presence of predators feeding on a greater number of prey taxa (Staudacher et al., 2018). Generalist predators, in turn, are known to shift ecosystem states through exerting predation pressure on pest species (e.g., fruit-eating birds in orchards), generating an increased productivity of plants in natural systems and crops (Shave et al., 2018).

There are a range of methods for linking and analysing these spatial networks in agricultural regions. The concept of meta-networks, an extension of previous meta-population, community and ecosystem theory, has recently been developed to link previously isolated habitat-specific networks (Emer et al., 2018). Furthermore, spatial networks including ecological, social and management systems, have been proposed (Dee et al., 2017). This field is developing rapidly, yet further advances are required before we fully understand how networks at intermediate, landscape scales interact with one another to affect ecological processes (Poisot et al., 2015). Initial studies constructing and investigating networks at broad geographical scales (e.g., Great Britain; Redhead et al., 2018) demonstrate the potential for constructing spatially connected networks at broad scales using combinations of methods, both new and existing. We explore some of the new developments and advances in this area of network ecology in subsequent sections (see *Connecting the agricultural landscape using networks*).

Global scale

Ecological networks are yet to be fully explored at the global scale, but there are efforts to collate international datasets to help answer macro-ecological questions. Nevertheless, advances in network science more generally are increasingly being applied to agricultural systems data, in particular the global trade of goods, services (Anderson, 2010) and ecosystem services (Silva et al., 2021). An appreciation of multiple scales is particularly important in agricultural systems, especially considering that the movement and trade of agricultural goods, as well as current and future global environmental changes and biological variation at broad scales, influence the agricultural processes occurring at smaller spatial scales (e.g., landscapes and fields). These studies are particularly important when considering the risks presented by economic and environmental shocks (Challinor et al., 2016). For example, an analysis of networks of trade in cereal crops from 1986 to 2013 showed that three entangled, time-invariant sub-networks were responsible for the majority of trade, but there were also transient subnetworks that displayed exponential growth over intermediate timescales (Dupas et al., 2019). Transient structures, although contributing relatively little to the total trade of cereals, may present a buffer against perturbations or shocks in the short-term. Little, however, is known about the resilience of these networks — a substantial gap in our understanding of agricultural networks and their ability to respond to future scenarios (but see Puma et al., 2015).

Attempts have also been made to link together agricultural trade and social networks. For example, a triadic analysis framework successfully classified countries based on their level of connectivity to trade partners and indicated a distinct development trajectory associated with an increase in the levels of global agricultural imports and exports for a country (Shutters and Muneepeerakul, 2012).

Much can be learned from other disciplines where network approaches have been used to examine a range of global phenomena, including banking systems (May and Arinaminpathy, 2010) and disease transmission (Pastor-Satorras et al., 2015). From an agricultural perspective it may be possible to link together processes at the global scale (i.e., trade and community) to those at field and landscape scales. For example, changes in the international trade of pesticides and fertilisers will affect access to these products by farmers, in turn enhancing or restricting their application at landscape and field scales, and thus altering the structure and function of ecological networks at local scales through the effects of either higher or lower levels of chemical application.

Including people in agricultural networks across scales

Humans are rarely included in agro-ecosystem networks. This is surprising given that: (i) people are the direct beneficiaries of agricultural outputs; and (ii) agricultural networks are characterised by top-down structuring, through a series of knowledge-exchange and decision-making networks in the human compartment of systems (Manson et al., 2016). Agricultural social networks combine a range of stakeholders involved in the management of the landscape, such as farmers, land managers, consumers and regulators (Jarosz, 2000). The interactions between these stakeholders (e.g., information and equipment sharing, co-management of landscapes and common responses to policy or legislation), and the land management decisions that arise, are a major influence on ecological networks in the agricultural environment (Nelson et al., 2009). Likewise, it is logical that changes to the ecological network (e.g., as a result of drought, pest outbreaks or pollinator declines) will affect decision making in social networks and this can propagate across spatial scales. We contend that merging social, economic and ecological networks has considerable scope for better understanding and management of human–ecosystem relationships and feedbacks. Merging such networks is a major challenge but now feasible, and the benefits for building resilience into food-systems are considerable (see *Merging social and ecological networks to understand how management decisions affect agro-ecosystems and vice versa*).

Advances required to operationalise network science in agriculture

Collecting more network data to enable a whole system understanding of agro-ecosystems

A greater volume of data on different agricultural networks is required across many different network types in agro-ecosystems, including ecological, sociological and economic. Here, we focus on ecological networks due to recent developments surrounding the collection of species-interaction data.

Comprehensive and detailed ecological networks can be constructed using a range of techniques. Yet recent advances in DNA-based network construction methods provide unprecedented opportunities to scale-up the construction of highly resolved ecological networks (Derocles et al., 2018; Evans et al., 2016; Srivathsan et al., 2021). These techniques are particularly applicable to network construction where interactions may be cryptic, infrequent, short-lived or difficult to observe (Vacher et al., 2016). Furthermore, they allow the inclusion of evolutionary information (e.g., phylogenetic data), that is particularly important in the context of using networks predictively for restoration purposes (Raimundo et al., 2018). Within agro-ecosystems, examples of potential applications of eco-evolutionary networks include: linking above- and below-ground networks (Toju and Baba, 2018), incorporating crop viruses and pathogens into ecological networks and investigating the role of intra-specific competition. Although DNA-based methods show great promise, with low per sample costs (<10 cents; Srivathsan et al., 2021) and the ability to process large numbers of samples rapidly, we recognise these methods have limitations (Cuff et al., 2022) and their accessibility varies geographically. A range of alternative methods for constructing networks exist and are suitable for creating agro-ecosystem networks. For a more comprehensive review of novel methods of constructing replicated species interaction networks over large spatial scales see sections in Windsor et al. (in revision).

An increase in the amount of available network data, combined with a focus on the functional implications of such interactions (e.g., understanding the wider role of soil microbiota in agro-ecosystems), will enable a better understanding of the responses of agricultural networks to natural or anthropogenic perturbations. Such knowledge provides options for management in extensive sustainable systems and/or building resilience into those food systems which appear at risk of negative effects (see below).

Making the most of existing agricultural data by inferring ecological interactions

Inference networks, constructed from co-occurrence data and/or existing information on species interactions (e.g., Pocock et al., 2020), provide a potentially valuable resource for investigating networks over broad spatial and temporal scales. Indeed, this method of network construction is gaining momentum when community data is generated using environmental DNA (eDNA) methods, although co-occurrence is not necessarily evidence of ecological interactions (Blanchet et al., 2020). These methods have numerous applications, including reconstruction of historical species interaction networks, construction of networks in remote regions with poor interaction datasets and development of networks across broad spatial and temporal scales that allow for testing global environmental change hypotheses. Furthermore, the potential application to existing long-term biomonitoring projects is an area of interest (Bohan et al., 2017), particularly in the context of examining pest and beneficial insect interactions in agro-ecosystems (Petsopoulos et al., 2021).

Linking above- and below-ground environments to create complete ecological networks in agro-ecosystems

We currently have limited knowledge regarding how biotic interactions between plants and below-ground micro-organisms influence ecosystem productivity and fluxes of matter and energy through trophic levels, limiting our ability to understand how agro-ecosystems respond to environmental change. Again, DNA-based methods combined with network analysis offer new ways to overcome some of the hitherto difficulties in studying more complex plant–microbe interactions (Bennett et al., 2019) and unearthing a range of ecosystem services that can be harnessed (e.g., arbuscular mycorrhizal fungi and other root symbionts for plant growth). Indeed, agricultural plants do not only rely on direct defences when attacked, but they can also recruit pest antagonists such as predators and parasitoids, both above and below-ground, mainly via the release of volatile organic compounds (i.e., indirect defences). However, from an ecological network perspective it is mechanistically unclear how changes in one trophic level (e.g., soil arthropods) affect interactions in another (e.g., insect pollinators), and vice versa (Fig. 2), nor the potential trade-offs for focal plants (e.g., crops). As such, we do not know what drives the multidirectional fluxes between the above- and below-ground components of the agricultural networks at multiple scales. This advance is required to understand how these components of the system interact to alter productivity and ecosystem services within the agricultural environment.

Using multilayer networks to identify key ecosystem services that spill over between crop and non-crop habitats

Using non-crop habitats, for example field margins, hedgerows, uncultivated land and woodland, to influence the network structure of plant–animal networks in arable agriculture is a common technique to enhance the provision of ecosystem services in some regions of the globe. Assessments and management interventions, however, do not often consider the simultaneous provisioning of multiple ecosystem services (Gaba et al., 2015). It is nevertheless important to consider the potential synergies and trade-offs associated with decisions surrounding agricultural systems, especially considering that different non-crop habitats enhance different ecosystem services in a context-dependent manner (Albrecht et al., 2020).

Developing methods that allow for an understanding and management of multiple ecosystem services is an important challenge that needs to be addressed. This advance can be achieved using an adaptation of current network methods for selecting optimal mixtures of organisms to maximise the abundance and/or species richness of interacting organisms. For example, it is possible to use machine learning algorithms applied to network data to identify species contributing to different ecosystem services across habitats and determine optimal mixes of species to provide simultaneous ecosystem service provision (Windsor et al., 2021).

Incorporating different aspects of agriculture in a multilayer framework through developing new tools

Although studies on multilayer networks are still in their infancy (Hutchinson et al., 2019), in agro-ecosystems there are several clearly defined ‘layers’ that can be incorporated into multilayer network frameworks. These include, but are not limited to; plant–herbivore, herbivore–parasitoid, herbivore–predator, plant–frugivore, plant–human (e.g., removal of weeds, diversifying plant species in field margins) and herbivore–human (e.g., pesticide use, enhancing the abundance of natural enemies of pest herbivores). Through incorporating this array of network types into one framework, we suggest that it is possible to gain a better understanding of the mechanistic processes through which management decisions at a range of scales alter the ecosystem services provided by the ecological networks embedded within the agricultural landscape. In turn, this would allow for an improved design of management strategies, incorporating all potential knock-on effects across the ecosystem and allowing for maximum ecosystem service provision whilst minimising environmental harm.

The current toolbox available for analysing ecological multilayer networks is limited to a small but growing number of analyses, such as qualitative measures of robustness (Pilosof et al., 2017). There are also challenges associated with linking together layers with different link information in a meaningful manner. For example, it is often not appropriate to combine individual weighted networks into a single weighted multilayer network as the methods used to collect data do not lend themselves to direct comparisons. There are also issues with linking large numbers of disparate layers in a parsimonious and computationally efficient way that fits within current mathematical frameworks. To address this challenge, we believe a bottom-up, plant-focused approach in cropped systems provides a suitable starting point to investigate the role of different interactions within agro-ecosystems. By altering plant communities there are a range of consequences that can influence even those organisms that are not directly connected to them in the network (Scherber et al., 2010). Leading on from this starting point, it would be possible to link in- and off-crop habitats as well as above- and below-ground components of the agricultural networks using multilayer networks. Doing so will allow for the development of management techniques that enhance the provision of ecosystem services through making use of ecological processes such as apparent competition (see *A roadmap for using networks predictively in agriculture*).

Applying adaptive and dynamic networks to provide new insights in agricultural systems

Most studies to date have analysed the structure of ecological networks (or a ‘snapshot’ of species interactions in time) and ignore important temporal dynamics. Yet the properties of ecological networks can vary drastically at a range of spatial and temporal scales (Poisot et al., 2015). To deal with the dynamic nature of ecological systems, a novel suite of network models has recently been developed, incorporating additional information on the phylogeny and traits of the organisms that comprise a given ecological network (Raimundo et al., 2018). These adaptive network models incorporate potential functional or co-evolutionary changes that might manifest themselves in response to changes in the wider network, adding greater detail — e.g., information on changes in the abundance and traits of organisms over time (Derocles et al., 2018). The aim of such methods is to allow for an improved understanding of how systems respond to extinctions and reductions, which is in stark contrast to classical approaches of robustness with a binary response of persistence or extinction based on whether all previously observed links are removed, e.g., complete disconnection. A remaining challenge surrounding adaptive networks, however, is that of parametrisation data which remains limited. DNA based methods may present a way forward providing an opportunity to gain information on the evolutionary history of organisms and useful information on potential interaction rewiring (see *Collecting more network data to enable a whole system understanding of agro-ecosystems*).

Further developing adaptive network models within agricultural systems provides significant potential, especially in research investigating how human management may affect other aspects of the agricultural system. Examples of potential research include understanding the response of network structure and function to pesticide resistance, climate change and reductions in pollinator diversity, as well as developing precision fertiliser application and investigating the optimal combinations of non-crop plants in organic agricultural systems. By developing these methods of analysis, we can gain more information about the ecological networks and suitable management practices can be developed to make use of eco-evolutionary principles (Loeuille et al., 2013). Ultimately this will allow adaptive networks to be used predictively for targeted management outcomes (Raimundo et al., 2018).

Developing spatial networks to connect the agricultural landscape and develop a broader picture

Currently, it is not possible to accurately identify, quantify and understand how management decisions at different scales affect the structure and dynamics of ecological and social networks, and thus how these processes impact upon agricultural productivity, sustainability and resilience, across the surrounding landscape (Massol and Petit, 2013). As such, a meta-network framework is required to understand the interactions between agricultural networks at the landscape scale. To date there are few studies investigating spatial meta-networks, yet this concept can be applied widely, across multiple network types (i.e., social and ecological), to understand how management or perturbations affect the provision of different ecosystem services at the agricultural landscape scale. Meta-network theory could provide a suitable framework within which agricultural questions at the landscape scale can be answered. This has been shown in previous work investigating plant–bumble bee interactions in forestry systems, which demonstrated the variable effects of habitat patch size and flight distances on the potential effectiveness of conservation and restoration strategies (Devoto et al., 2014).

Substantial field and laboratory work is required to upscale network assessments in agricultural environments to allow for an understanding of how spatial variation and heterogeneity in social and ecological processes alters the ecosystem services provided across the landscape. These efforts have started with theoretical models (Loeuille et al., 2013), but empirical (field-based and experimental) studies are now required to drive further advances in our understanding.

Merging social and ecological networks to understand how management decisions affect agro-ecosystems and vice versa

Agricultural systems are a combination of social and ecological networks (Fig. 2), with top-down effects of management altering the nature of ecological systems and networks (Lescourret et al., 2015). Yet, until recently these two interlinked networks have been analysed in relative isolation. New studies have sought to combine these (and multiple other) types of networks to provide insights into how the interface between management and biodiversity alters ecosystem functioning (Felipe-Lucia et al., 2021). These efforts have included agricultural environments (Hutchinson et al., 2019), and theory surrounding socio-ecological networks is sufficiently mature for actionable interdisciplinary research (Bodin et al., 2017). Putting multilayer networks to work in the context of agriculture may improve our understanding of the mechanistic basis through which management decisions translate to changes in production, or other services provided by the agro-ecosystems.

Examples at different scales demonstrate the importance of combining social and ecological networks in agriculture to understand where changes in social networks impact ecological networks, and vice versa. At the landscape scale, agricultural environments are composed of different types of farmers, ranging from family farmers through to intensive commercial farm managers, who form nodes within a farmer-biota network. In this example network, farmers are linked together through their effects on the wider biodiversity of the landscape, i.e., agricultural management by one farmer may affect biota at the landscape scale and in turn have impacts on other farmers. An example of this would be the application of pesticides reducing pollinator diversity and thus reducing the probability of pollination across other farms and crops — even those where pesticides are not applied. Across continental and global scales, ecological and social networks at local scales can be linked together through national and international trade networks, as has been the case in recent work investigating virtual pollination trade networks (Silva et al., 2021). In these networks, effects on pollinators at local scales will alter the yields of pollinator-dependent crops and thus have social and economic consequences in other regions of the globe with which those crops are traded. Linking together systems at large scales is particularly important (see *Furthering global agricultural network analyses to help enhance the resilience of food systems*).

Using the discourses surrounding ecosystem services and natural capital appears to have consolidated efforts linking social and ecological networks across other ecosystems. Such application has allowed for the fusion of information on management strategies and ecosystem service provision with detailed socio-ecological networks (Dee et al., 2017). For example, recent work that integrated ecosystem services into coastal salt marsh food webs found indirect risks to services through species loss, and that vulnerability across services was predictable (Keyes et al., 2021). Using an ecological network, this study links together social aspects of systems: (i) threats, the anthropogenic stressors imposed on the ecosystem by human actors (e.g., climate change or overexploitation of species); and (ii) ecosystem services, the human benefits derived from the natural world. We contend that a similar 'threats-network-ecosystem services' advance is a tangible starting point for operationalising work in agro-ecosystems (Fig. 2), building on a bottom-up species-interaction approach. Here, using robustness analyses, it would be possible to examine how agricultural management and/or threats to species interacting with plants propagate through the network to impact multiple ecosystem services, and thus socio-economic activities.

Going forward, a significant challenge for the integration of social and ecological networks surrounds the collection of appropriate data. Specifically, collecting and collating data of the right kind (i.e., weighted links with comparable or interactable units), at the correct resolution (e.g., seasonal management decisions and knowledge sharing by farmers). Many methods exist for generating social data to construct networks; however, current methods are qualitative (i.e., using ecosystem service as a node linked to species without a measure of the effects of a species on service provision) and/or collect data in an inappropriate spatial or temporal resolutions for integration with ecological networks (Felipe-Lucia et al., 2021).

There appear to be three options for combining social and ecological networks: (i) include social networks in the framing of ecological network questions (i.e., use research questions driven by social networks — for example decision making and/or land management at the landscape scale); (ii) reduce the resolution (i.e., level of detail) of both social and ecological networks and use an existing analytical framework (e.g., Bayesian networks and game theory have previously been applied to multi-agent ecosystem service modelling; Mulazzani et al., 2017); or (iii) develop a completely new method/framework to link social and ecological systems.

Furthering global agricultural network analyses to help enhance the resilience of food systems

Determining the resilience of global agriculture to perturbations, shocks and disturbances is crucial and a policy priority (Challinor et al., 2016), especially considering the global nature of agricultural food supply and the potential for future food shortages (Silva et al., 2021). Although data exist at the global scale, for example Food and Agriculture Organisation (FAO) crop and livestock products data (Food and Agriculture Organization of the United Nations, 2018), there remains limited network-based assessments of the global trade of agricultural products and research opportunities (Puma et al., 2015). Current data provide a strong basis for potential analyses as there is detailed information on the value of annual imports and exports of different agricultural products, as well as the quantity of products moving between countries. Using these data, understanding the robustness of the trade network, for example if a global health crisis prevents exports (Aday and Aday, 2020) or if climate conditions reduce production of agricultural goods within a geographic region, is a fruitful place to begin. Furthermore, building network-based analyses into current global and regional agricultural monitoring schemes (e.g., Group on Earth

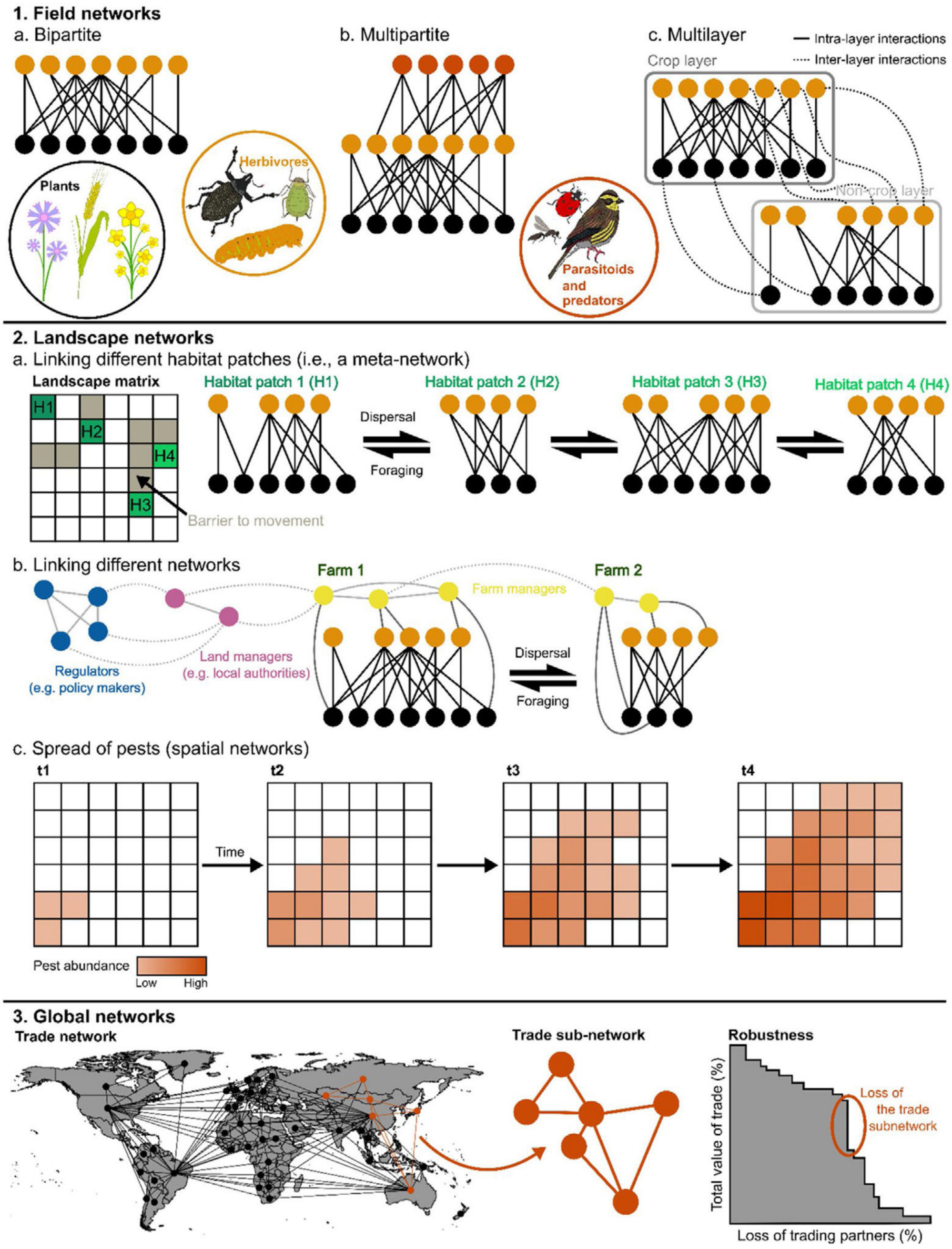

Fig. 3. Agricultural networks at different spatial and temporal scales. Each section of the figure summarises examples of network science applications at different scales. At the field scale (1) the colour of the nodes indicates the different taxonomic groups and trophic levels represented in the various networks. The networks at this scale can vary in their complexity from bipartite (interactions between two groups, i.e., plants and herbivores) through to multilayer or meta-network approaches which include either multiple habitats, networks through time (linked by the same organisms or populations of organisms) or multiple interaction types. Across landscapes (2) which can range in scale from multiple fields to entire regions, networks can take many forms and be represented by classic node and link diagrams (2a and 2b), or spatially using lattices representing space (2c). In the latter case, adjacent blocks directly interact with one another, and other blocks further afield may interact through indirect interactions. The spread of organisms across the landscape matrices can be estimated using a network of the blocks within the landscape and the direct and indirect interactions between them. At the global scale (3), networks are equally diverse, yet good examples exist for trade networks. Subnetworks of trade may be particularly important for agricultural goods and the loss of production in these subsets of nodes (countries) may lead to a loss of robustness in global agricultural trade. For specific terminology refer to the main text and Table 1. Examples of many networks in agriculture and associated processes are provided in Table S1.

Observations Global Agricultural Monitoring [GEOCLAM], Anomaly Hot Spots of Agricultural Production [ASAP], Global Information and Early Warning System [GIEWS] and Famine Early Warning Systems Network [FEWS NET]; Fritz et al., 2019), would further enhance the ability to provide an early-warning system for global food systems and promote enhanced food security.

A roadmap for using networks predictively in agriculture

Using networks predictively for specific management outcomes, such as building resilience to climate change, resistance to invasion from non-native species, or achieving greater crop yields whilst supporting increases in the levels of native biodiversity, could be achievable. However, using the principles of network ecology to predict the potential effects of farm management interventions

Table 2
Major research questions, applications or challenges, potential options for analytical methods and the intended outcomes associated with network thinking in agro-ecosystems.

Topic	Challenge	Potential methods	Intended outcome
Ecosystem functioning and services	Linking above- and below-ground ecological networks and biogeochemical fluxes/processes	DNA-based multilayer networks	Mechanistic knowledge of relationships between species interactions and biogeochemistry in crop systems
	Understanding the effects of non-crop habitats on crops and associated networks (and vice versa)	Meta-networks (linking crop and non-crop habitats)	Improved non-crop management strategies
	Quantifying trade-offs in ecosystems service provision resulting from management strategies	Machine learning algorithms	Management strategies that maximise the provision of ecosystem services whilst minimising disservices
Resilience and risk management	Determining the robustness and resilience of global agricultural trade networks	Robustness analysis	Areas of vulnerability in global trade and methods of creating more resilient global crop trade systems
	Describing knowledge transfer between agricultural actors and understanding effects on agro-ecosystems	Socio-ecological models	An understanding of the wide range of knock-on social and ecological effects of management decisions and strategies
	Evaluating how management at the landscape scale can reduce risk and increase resilience for individuals	Meta-networks (linking sites across the landscape)	Landscape scale management strategies that account for spatial ecological processes
Restoration	Identifying sets of species (or functional traits) to optimise the restoration of ecosystem processes and services in farmlands	Dynamic network models	Restoration strategies to promote long term recovery of degraded agricultural habitats
	Assess whether restoring degraded habitats can benefit crop production and other ecosystem services	Meta-networks (linking habitats)	An improved understanding of spillover from restoration activities
Integrating people and nature	Producing a methodological framework for merging social and ecological networks	Multilayer socio-ecological networks	Whole-system management strategies to promote environmental and societal benefits
	Quantifying interactions between social and ecological networks and the resulting novel network patterns	*No current methods*	Measurement methods and metrics for socio-ecological interactions
	Investigating the reciprocal interactions and the indirect effects between social and ecological networks	Dynamic socio-ecological network models	Methods for determining the social and environmental trade-offs and management strategies based on the data generated.
Scale dependence	Identifying the processes influencing the structure and dynamics of agricultural networks at different spatial and temporal scales	Dynamic network models	Linkages between scales (i.e., either species or processes) that affect structure, function and services at other scales.
	Evaluating the scale-dependence of network properties (e.g., stability, resilience and robustness)	Meta-networks	An understanding of how interventions at a given scale influence network properties at other scales.

is rare. Theoretical development of predictive network science, coupled with empirical testing in a range of farming and food security contexts, is thus a research priority before these approaches become mainstream.

A paradigm shift is required to enable accurate predictions and thus alter how agro-ecosystems are managed for the environment and humans. Using social- or socio-ecological network analysis (SEN) is a rapidly developing field of research that offers an opportunity to achieve this challenging goal (Felipe-Lucia et al., 2021). The development of SEN is comprehensively reviewed in Sayles et al. (2019). Briefly, SEN includes a range of methods, including: (i) “non-articulated”, having nodes with both social and ecological attributes, (ii) “partially articulated”, linking ecological to social nodes without links between social nodes, i.e., incorporating ecosystem services as nodes in the network (see Dee et al., 2017); and (iii) “fully articulated”, explicitly modelling social and ecological units and all of their relationships. Fully articulated methods have been successfully applied to investigate sustainability and management across multiple ecosystems. For example, finding suitable methods for managing urban wetlands based on social and ecological connectivity (Kininmonth et al., 2015) and assessing scale mismatches between governance and ecological systems in estuarine watershed restoration (Sayles and Baggio, 2017). There remains, however, a lack of examples of SEN in agro-ecosystems.

Developing SEN methods to understand and predict the social and ecological dynamics of agricultural environments would allow for predictions of the success of present or future management strategies. Furthermore, it would incorporate variation generated by individual and group decision-making in both social and ecological systems. These methods could be adapted to cover different ecosystems, agricultural environments and social systems, providing a framework for managing agro-ecosystems across scales. Predictions generated by SEN in agricultural systems would allow for the design and refinement of sustainable management programmes. This would drive the field forward in the pursuit of predictive methods for creating resilient agricultural systems through sustainable intensification.

Conclusions

Network thinking has advanced at a rapid pace over the past decade, providing enormous potential for sustainable agro-ecosystem management. Here we have shown the utility of these techniques for constructing and analysing agricultural systems at multiple scales (Fig. 3), highlighting the recent advances that now allow for a more complete evaluation of how networks influence the ecosystem services generated by the social and ecological components, and a roadmap for how this could be applied to the agricultural environment. However, research is needed within this field (Table 2), and further advances are likely to yield significant improvements in our understanding of agricultural ecosystems. Furthermore, through constructing and analysing social and ecological networks in agricultural regions there is the potential to use this information predictively to determine the resilience of these systems to future environmental changes — something which is necessary in the face of the global water-energy-food nexus.

Declaration of interests

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Author contributions

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Appendix A. Supplementary data

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