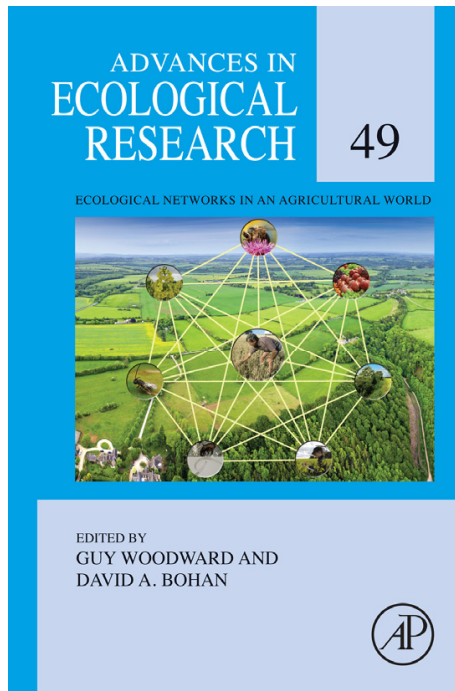


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Advances In Ecological Research, Vol. 49,
Amsterdam, The Netherlands: Academic Press, 2013, pp. 1-67.

ISBN: 978-0-12-420002-9

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Networking Agroecology: Integrating the Diversity of Agroecosystem Interactions

David A. Bohan^{*,1}, Alan Raybould[†], Christian Mulder[‡],
Guy Woodward[§], Alireza Tamaddoni-Nezhad[¶], Nico Bluthgen^{||},
Michael J.O. Pocock[#], Stephen Muggleton[¶], Darren M. Evans^{**},
Julia Astegiano^{††,‡‡}, François Massol^{††}, Nicolas Loeuille^{§§},
Sandrine Petit^{*}, Sarina Macfadyen^{¶¶}

^{*}UMR 1347 Agroécologie, AgroSup/UB/INRA, Pôle Ecologie des Communautés et Durabilité de Systèmes Agricoles, 21065 Dijon Cedex, France

[†]Product Safety, Syngenta, Jealott's Hill International Research Centre, Bracknell, Berks, United Kingdom

[‡]Department for Environmental Effects and Ecosystems, Centre for Sustainability, Environment and Health (DMG), National Institute for Public Health and the Environment (RIVM), Bilthoven, The Netherlands

[§]Imperial College London, Silwood Park Campus, Ascot, Berkshire, United Kingdom

[¶]Computational Bioinformatics Laboratory, Department of Computing, Imperial College London, London, United Kingdom

^{||}Ecological Networks, Biology, Technische Universität Darmstadt, Darmstadt, Germany

[#]Centre for Ecology & Hydrology, Wallingford, Oxfordshire, United Kingdom

^{**}School of Biological, Biomedical and Environmental Sciences, University of Hull, Hull, United Kingdom

^{††}UMR 5175 CEFE – Centre d'Ecologie Fonctionnelle et Evolutive (CNRS), Montpellier Cedex 05, France

^{‡‡}Departamento de Ecologia, Instituto de Biociências, Universidade de São Paulo (USP), São Paulo, Brazil

^{§§}Université Pierre et Marie Curie, Laboratoire Ecologie et Evolution, UMR 7625 Ecologie des populations et communautés (USC2031, INRA), Paris Cedex 05, France

^{¶¶}CSIRO Ecosystem Sciences, Canberra, ACT, Australia

¹Corresponding author: e-mail address: David.Bohan@dijon.inra.fr

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Abstract

Worldwide demand for food will increase dramatically in the future as global human population grows. Increasing efficiency of crop production is unlikely to be sufficient to meet the demand, presenting a long-term threat to humanity's 'well-being'. Knowledge of the system-level behaviour of agroecosystems, however, remains surprisingly limited, reflecting the agricultural focus on particular species. This is starting to change towards an ecosystem and network-based approach, following the recent revolution in thinking about resource use and sustainability in our other global food production industry: commercial fisheries.

Agroecosystems appear to retain plasticity of ecological processes that might be manipulated for productivity and sustainability. Network structure and dynamics have substantial impacts on ecosystem performance, but evidence from agroecosystems lags behind network theory. Here, we provide an introduction to network theory and application in agroecosystems, identify network metrics for management and environmental change, and, finally, we highlight gaps in our current knowledge and key research themes. These themes include: is the structure of agroecological networks affected by sampling; how do ecosystem services 'emerge' empirically from ecological organization, function and network properties; how do spatial and temporal scale and resolution influence system performance; and, can network agroecology be used to design systems that maximize ecosystem services?



1. INTRODUCTION

Conceptually, agroecosystems have typically been treated as crop monocultures, with a few associated plant and invertebrate species, residing in a single field. In reality, though, these systems are far more diverse: a

myriad of ecological interactions occur between individuals in populations, between species, within and between communities and functional groups, and across the cropped fields and other natural and semi-natural habitats in the agricultural landscape, and these produce the emergent structure and dynamics of agricultural ecosystems (Fig. 1.1). If we are to develop a predictive, 'sustainably intensive' agriculture, which satisfies our future societal needs, we will need to take account of these interactions because emergent behaviour often associated with complex ecological networks implies that the performance of the agricultural system is very much more than just the sum of the individuals parts (Cohen et al., 2009). This will mean broadening the scope of current agroecology research, to include network-based approaches. We propose, in this chapter, a large-scale, integrative agroecology built upon network theory and ecology. As has been seen in other exploitative ecosystems, such as commercial fisheries, network theory and

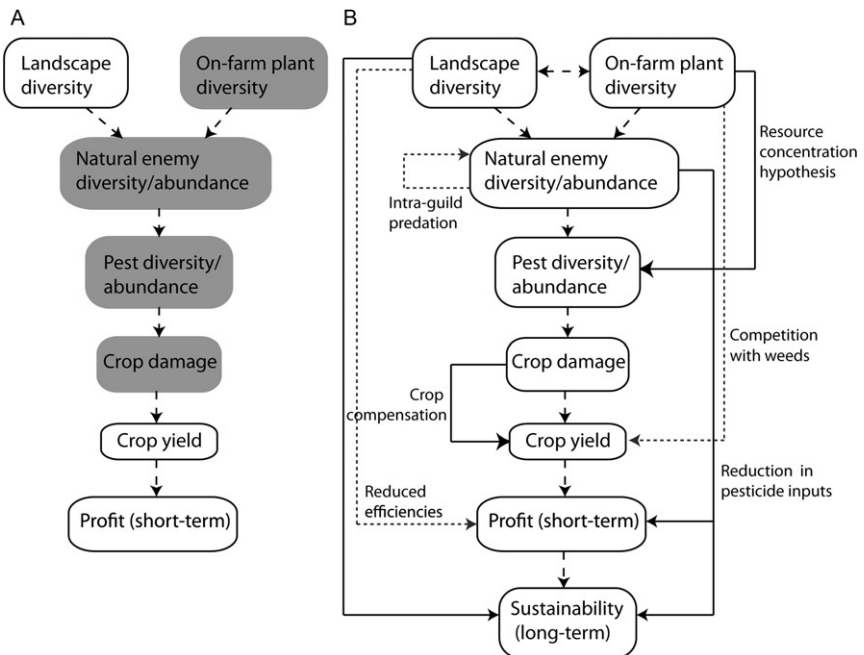


Figure 1.1 The traditional simplified view of the relationships between biotic components of agroecosystems (A) generally ignores some of the complex feedback loops (solid and dashed grey lines) and interactions between species that make up more realistic agroecosystems (B). Network studies to date have focussed on a narrow set of relationships, usually between plants, pest arthropods and their natural enemies (shaded grey on A).

approaches would provide a more holistic, system-based view of natural systems that could be employed in solving some of the problems that are being faced in current systems of intensive agriculture, as well as for anticipating potential future scenarios.

1.1. Current issues in agriculture

The worldwide demand for food will increase for at least the next 40 years owing to continuing population growth (Godfray et al., 2010). There is some potential to address the shortfall by reducing waste and altering consumer dietary demands (Godfray et al., 2010; Tschamtkke et al., 2012), but this will not be sufficient. We will therefore need to increase both the amount and the efficiency of food production. This clear challenge for agriculture is also set against global environmental changes and increasing pressure on natural ecosystems, some of which are driven by agriculture itself (e.g. forest clearance and reduced carbon sequestration capacity). Degradation of land and ecological processes, in turn, creates potentially dangerous feedbacks (e.g. desertification; salinization) and presents a long-term threat to agricultural production, human well-being on local scales and humanity's safe operating space on a global scale (Millennium Ecosystem Assessment 2005; Rockström et al., 2009).

Crop yields may be increased through better agronomy (e.g. Mueller et al., 2012) or improving crop genetics (e.g. Tester and Langridge, 2010), but this comes at the cost of increased risk from pests and disease. Oerke and Dehne (2004) estimated that in the eight major global crops, average loss of yield to fungi, bacteria, viruses, animal pests and weeds totalled 32% between 1996 and 1998; and without pest control, losses would have been 67%. While the 'conventional' management of pests and disease has benefits for crop yield, it is not without problems; for example, indiscriminate use of synthetic insecticides can affect non-target organisms and lead to outbreaks of secondary pests owing to loss of biological control (e.g. Metcalf, 1980; Newsom, 1967). Technological control measures that target pests, and leave non-target organisms unharmed, are feasible; such as the example of genetically modified (GM) cotton producing an insecticidal protein from *Bacillus thuringiensis* (*Bt*) that controls lepidopteran pests, like the cotton bollworm, *Helicoverpa armigera*, very effectively in cotton fields (Lu et al., 2012). In China, the abundance of biological control organisms in and around the *Bt* cotton fields was higher than that under the conventional management regime, highlighting that they provide a useful pest

management service (Lu et al., 2012). Just as broad-spectrum insecticides can lead to secondary pest outbreaks because of loss of biological control, narrow-spectrum insecticides like *Bt* can also lead to outbreaks of secondary pests, because these are unaffected by the insecticide and can expand into the 'niche' vacated by the primary pest: *Bt* cotton sometimes suffers from secondary infestations by mirid bugs (Li et al., 2011). This example is a specific case of more general pest management regimes, which effectively manipulate apparent rates and prey targets of predation among the guild of predators. This combination of direct and indirect effects demonstrates the need to take a wider, network-based perspective of all the interactions occurring in the food web in and around the crop fields, as many of these effects cannot be measured, understood or predicted without this wider view: focusing solely on the crop and its immediate pests misses the bigger economic and ecologically important picture.

Observations of pest regulation by control agents and outbreaks of pests, mediated by the action of pesticides, suggests that agroecosystems retain at least some plasticity in their ecological processes that might be manipulated to provide more effective ecosystem services. This is essential if we are to deliver an agriculture that is productive, sustainable, and has less environmental impact in the long term. The ecological functions provided by biodiversity in its broad sense (e.g. the diversity of species and interactions in the food web) have been put at the core of what is increasingly called 'sustainable agricultural intensification', that is, artificially intensifying the use of natural functions. Achieving these goals means that agroecosystems will need to change from their current states, ideally through rational, hypothesis-based design, and any changes made to the system therefore need to be evaluated in terms of the biodiversity, functioning and ecosystem services that are sought.

1.2. Learning from nature

The expectation that natural ecosystems can provide sources of inspiration for designing agroecological production systems is widespread (Altieri, 1999; Scherr and McNeely, 2008). In practice, however, there have been only a few attempts to design agroecosystems from nature, mostly because the services associated with natural systems are not targeted at achieving particular goals, such as biological control at economic thresholds. Faithful mimicry of natural systems is not expected to provide the yields obtained in modern agriculture, and the ecological concepts that are key in natural systems such as resilience, stability and capacity for self-organization are

not necessarily readily transferable or relevant to agroecosystems (Malézieux, 2011). There are, however, some key ecological principles that should hold in agroecosystems, such as maintaining diverse complementary functional traits in species assemblages, whether for sustaining the 'predictable' assembly of communities of species around a crop or for the management of the microbial, plant and animal species naturally present in the system.

The estimated economic value provided by biodiversity-derived ecosystem services is huge, and many of these are provided by interactions within ecological networks of multiple species, such as the benefits accrued from pollination, pest control and nutrient cycling (Zhang et al., 2007). Pest herbivory of crops, weed-crop competition and disease transmission, in contrast, provide a disservice in agriculture (Zhang et al., 2007). Attempts at maximizing a single ecosystem service, such as productivity, are expected to reduce the provision of others or to increase disservices (Seppert et al., 2013). New technologies, such as *Bt* crops (Lu et al., 2012) or selective herbicides, may reduce the side effects of pest management; however, decisions about managing trade-offs between ecosystems services are unavoidable (Chifflet et al., 2011).

1.3. Agricultural ecosystems are intrinsically linked to human society and our goals and ideals

There are few regulatory controls that mandate sustainability in intensive terrestrial food and fibre production systems. No 'maximum sustainable yield' concept as used in the fisheries industry, or 'allowable limits of take for trade' as used in the trade of wild species, or 'bag limits' as used in hunting, exist. Rather, the goal is to use the available light, water and soil resources to maximize the harvest for minimum input, so a farmer is really limited only by the costs associated with those inputs. Prior to the development of cheap pesticides and inorganic fertilizers, this was a fairly sustainable and closed process (i.e. the costs associated with these inputs were high, especially if they came from far away). The only exceptions are for some very recent technological crop innovations, such as the mandatory use of refuge crops (with no *Bt*) grown with transgenic (*Bt*) cotton to reduce the risk of resistance developing in the target lepidopteran pests (Baker and Tann, 2013).

In recent years, society's expectations about food and fibre production have changed, with environmental degradation becoming less acceptable, and unsustainable practices more closely scrutinized (Raffaelli and White, 2013). There is, however, little agreement on (or clear understanding of)

the best practices for reversing declines in species richness in agricultural landscapes, let alone how networks of interacting species might be restored (but see [Pocock et al., 2012](#)). Simply reversing some of the processes of intensification, by reducing inputs, increasing landscape diversity and increasing on-farm plant diversity, might not be enough. For example, in a grassland experiment, plant diversity in plots that received high rates of nitrogen for 10 years had not recovered to control levels 20 years after nitrogen supplements had ceased ([Isbell et al., 2013](#)). This might suggest that ‘turning back the clock’ to the more benign practices of the past, even where that is feasible, might not achieve these goals. There is increasing evidence that the structure and dynamics of networks modulates the trajectory and rate of change in response to the imposition and also the alleviation of stressors, with time-lags arising due to ecological inertia in the food web. This has been suggested as the reason for the lack of or slow recovery in commercial marine fisheries following reduced fishing effort, in freshwaters that have exhibited chemical but not biological recovery from acidification ([Layer et al., 2010, 2011](#)), and in eutrophied shallow lakes after reductions in nutrient loadings ([Scheffer et al., 2001](#)). Given the scope for network structure to alter the trajectory and rate of recovery, novel management regimes will likely be necessary in agroecosystems: simply reducing the impact might not suffice.

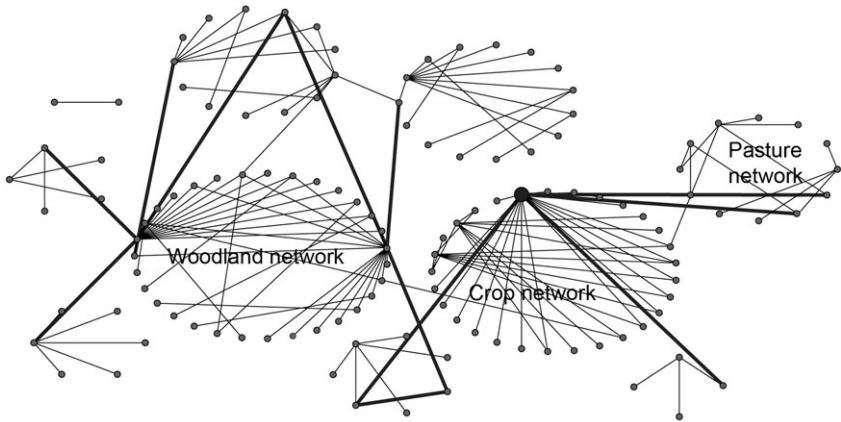
1.4. Assessing and predicting change in agriculture

Biodiversity assessment is often based on the *a priori* choice of specific indicator groups of animal or plant species. Indicator groups should be chosen to reflect particular protection goals (endpoints), such as agricultural sustainability ([Doré et al., 2011](#)), or ecological processes or functions ([Storkey et al., 2008](#)), or cultural service ([Gibbons et al., 2006](#)). In practice, these choices are often difficult to justify and the impacts of management on these species groups are not necessarily well-documented or understood ([Bond et al., 2011](#); [Braband et al., 2003](#); [Makowski et al., 2009](#); [Sadok et al., 2009](#)). ‘Tests’ of change among these groups of indicators often fail a basic requirement of being predictable. To compare across conditions, crops and ecosystem types, differences between observation and expectation for particular management and ecological combinations must be testable. Treatment effects, or the ratio of observed to expected values of each indicator group, can be used to infer ecological impact. A similar effect ratio, between species groups, implies the same ecological impact—no matter what type of

crop, management, or ecosystem is involved (Breure et al., 2005; Firbank et al., 2003). The accumulation of indices across many taxa can provide a more complete and objective evaluation of impact, which can also integrate physical and chemical variables (Ellenberg et al., 1992) and related ecosystem services (Schouten et al., 2004). This type of biodiversity impact testing, however, provides only a snapshot of the status of the system without providing information on the underlying processes. Recently, functionally based assessments have been advocated that more directly measure impacts on ecological process. These have included functionality—based on groups of organisms such as pollinators, natural enemies living in the soil or flying around fields (Bohan et al., 2007; Hawes et al., 2009; Pelzer et al., 2012), changes in performance (functional properties), diversity (structural properties), coherence (degree of interaction between components) and connect-edness (interactions with adjacent systems)—of agroecosystems (Groot and Pacini, 2010).

These approaches would be relatively straightforward if agroecosystems were simple and limited to a crop monoculture and a few associated species residing in a single field. In reality, cropped fields contain ecological networks of interacting species (e.g. food webs, plant–pollinator webs) that are themselves linked to one another in a spatial network of natural and semi-natural habitats via species movement and management across the landscape (Evans et al., 2013; Hagen et al., 2012; Macfadyen et al., 2011; Pocock et al., 2012; Fig. 1.2). Many beneficial species are highly mobile and are supported by ancillary species residing outside the cropped area (Kremen et al., 2007). Parasitoids, which are natural enemies of many crop pests and provide a valuable regulation ecosystem service, use host plants in adjacent habitats as food and shelter. These differing habitat requirements of species, and the plethora of interactions that occur among species, across functional groups and ecosystem services, produce outcomes that are often explicable only after the fact. This *post hoc* rationalization needs to be superseded by a more predictive agroecology, ideally based on first principles rather than contingent, phenomenological approaches. One important step towards this goal is to develop a large-scale, integrative agroecology built upon network theory and ecology. Modifying existing network theories to meet the needs of agroecology would produce fundamentally new understanding of how agroecosystems function and deliver services. This could give us general management rules that hold in a range of contexts and the knowledge to ‘tweak’ the rules to solve problems of relevance to local farming communities.

A



B

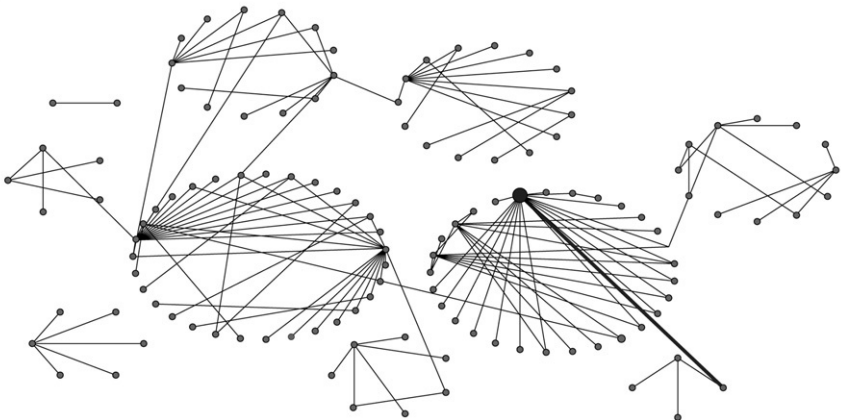


Figure 1.2 The impact of a disturbance on two hypothetical farm networks with high (A) and low (B) levels of connectivity between subunits. Each node represents a species and a line between two nodes indicates those two species interact in some way. Each subunit approximately corresponds to a habitat on the farm. In (A) a disturbance event (e.g. the spraying of an insecticide to control the species in the crop network) cascades through all other subunits of the network (thick black lines); in (B) the impacts are restricted to two subunits. *Figures adapted from Macfadyen et al. (2011).*

1.5. Networking agroecology

A critical question that faces ecologists seeking to apply network theory to practical real-world problems, such as agricultural production, is how informative is a network approach? We have some expectations as to how networks might change in response to environmental stressors, such as

agricultural intensification (Albrecht et al., 2007; Tylianakis et al., 2007), and we possess various network metrics that are ecologically meaningful (Tylianakis et al., 2010; Woodward et al., 2010a), yet predicting *a priori* exactly how a particular metric will change in response to a specific environmental change is still difficult (Heleno et al., 2012). There have been theoretical modelling advances in how traits of network properties, such as modularity, nestedness and connectance, affect the network itself (Bascompte et al., 2003; Thébault and Fontaine, 2010) and the species within it (Bascompte et al., 2003; Saavedra et al., 2011). What has been missing, however, is an understanding of how network structure relates to ‘emergent’ ecosystem functions (Thompson et al., 2012) and, hence, ecosystem services (or disservices) in agriculture. Network approaches have allowed us to assess the functional overlap of species (O’Gorman et al., 2011), which could help us to assign value to diversity and its associated function in ecosystem service provision (Perrings et al., 2010). Network theory suggests that even if the provision of a specific ecosystem services may be maximized through the abundance of functionally important species (Gaston, 2010), such as honey bees as pollinators (Calderone, 2012; Hagen et al., 2012), wider system resilience and ecosystem service provision relies directly on species diversity and functioning (Naeem et al., 2009).

Network theory and approaches could play a significant role in solving the problems that face current systems of intensive agriculture, just as they have been successfully employed to provide a more holistic system-based view of natural systems and agriculture’s sister industry, commercial fisheries. In this chapter, our principal aims are to: (i) introduce agroecosystems, in general, from the standpoint of network approaches; (ii) describe what networks are, supported by a Glossary of common terms, and what their analysis could achieve in agroecosystems; (iii) identify robust metrics for agroecological networks undergoing likely management and environmental change; and (iv) conclude by identifying the major gaps in our current knowledge and key research themes that need to be addressed in the future.



2. WHAT IS A NETWORK?

Networks describe interactions as links or ‘edges’ among the component ‘nodes’ of a given system. These links can have different properties that depend on the type of ecological interaction, with food webs, which describe the network of trophic interactions within a community, being one of the most familiar examples. A link can be directed, to describe energy

flowing from a prey species into a predator species or the strength of top-down control exerted by a predator on its prey for example, or a link can be undirected, describing a simple connection between a consumer and resource. Links can be weighted, by biomass flux or per capita interaction strength, or unweighted, as simple link presence/absence. Mathematically, networks can always be described by a matrix: in a food web, for instance, consumers may be shown in the columns of the matrix and resources as rows, with the intersection of a row and column defining the trophic link (or its absence) between two species.

The general goal of ecological network theory is to understand how network metrics and structure (the properties of the network) relate to the ecological system; for instance, how modularity, nestedness and connectance might impact the stability of interaction networks (Allesina and Tang, 2012; James et al., 2012; Thébault and Fontaine, 2010) and the emergent functions of the ecosystem (Thompson et al., 2012). One key finding, of general importance, is that networks are more than the sum of their parts, in the sense that studying each of the species populations in isolation would not enable the behaviour of the system as a whole to be predicted, as often emergent or counterintuitive effects (e.g. predators increasing prey abundance; prey suppressing one another's abundance through competition for enemy-free space; trophic cascades whereby top predators affect basal resources without consuming them directly) can arise from the myriad of pathways of interactions. These indirect interactions can have important effects in natural systems (e.g. Montoya et al., 2009), and a predictive understanding will be key for successful pest management and the avoidance of catastrophic human interventions in agroecosystems, such as have occurred repeatedly by focusing solely on the target species. Network-based perspectives, which consider the prey and predator spectrum (and trophic plasticity) of particular invasive or introduced species, might be used to avert considerable ecological and economic damage (Doody et al., 2013; Henneman and Memmott, 2001).

There are a wide variety of different types of ecological network, depending on the nature of the entity of interest (e.g. individuals, populations, species or habitat patches). The most familiar are antagonistic food webs and host–parasitoid webs, where the nodes and links refer to species populations and consumer–resource interactions, respectively (Ings et al., 2009). There are also mutualistic networks, including plant–pollinator and plant–frugivore systems, which have increasingly appeared in the literature in recent years. Such species-averaged, antagonistic and mutualistic

webs still dominate the literature, in both natural and agricultural systems, more than 100 years since the first representations of natural systems as networks (e.g. Camerano, 1880; Cohen and Briand, 1984; Fontaine et al., 2009, 2011; Kéfi et al., 2012; Pimm, 1982).

Where more resolved data are available and components are individuals, a network may be used to describe social interactions (Wasserman and Faust, 1994), clustering (Dupont et al., 2011), or evolutionary dynamics (Le Galliard et al., 2005; Ohtsuki et al., 2006; Zhong et al., 2013), as well as viewing the species-based food web as grouping by size class, irrespective of taxonomy (e.g. Gilljam et al., 2011; Woodward et al., 2010b). The latter can be very useful in size-structured networks where taxonomy is poorly resolved—as is likely to be the case in many agroecosystems. When components are populations of the same species, living in different spatial patches or fields, networks can be used to describe the metapopulation exchange of migrants (e.g. Economo and Keitt, 2008). While the idea of a ‘trophic species’, with species that occupy a similar position in a food web grouped together, has been criticized (Ings et al., 2009; Polis, 1991), it may be appropriate to apply it to aggregated resources, such as detritus in detritivore food webs and when assessing broad patterns of energy flow through systems.

2.1. Interactions among network nodes

Network approaches have generally been used to describe how species from different trophic levels interact (Cagnolo et al., 2011; Hall and Raffaelli, 1993; Ings et al., 2009; Tylianakis et al., 2007; Woodward et al., 2005). These studies have revealed unexpected, indirect effects, such as apparent competition via shared predators (Carvalho et al., 2008), arising from particular structures of network interactions. Mutualistic networks among flowering plants and their pollinators or seed dispersers (Bascompte and Jordano, 2007; Vázquez et al., 2009a,b), and floral or extra-floral nectar-bearing plants and ants (Blüthgen et al., 2004; Dáttilo et al., 2013; Guimarães et al., 2006) are less well studied, but our knowledge of the effects of facilitative interactions among plants has improved dramatically by studying the plant community from a network perspective (Verdú et al., 2010). Such effects, including when seedling growth and/or survival are promoted by another plant species, may be very important in agricultural situations. Leguminous plants which fix nitrogen are widely used in agriculture to promote soil fertility, in place of inorganic nitrogen application, but these plants also impact wider diversity (Viketoft et al., 2009). A combination of

facilitative and antagonistic networks analyses have also been advocated as a means to better understand how plants and their seed predators interact (Brooks et al., 2012; Lewis and Gripenberg, 2008; Prado and Lewinsohn, 2004) and how this impacts on the resultant ecosystem services of weed control (Bohan et al., 2011b).

Interspecific interaction networks have only relatively rarely incorporated the ontogenetic shifts that can occur within a species life cycle (Olesen et al., 2010). Resource provision by species can also vary among species (Bohan et al., 2011a; Evans et al., 2011; Pocock et al., 2012) and over time: granivorous birds switch to being insectivorous during the breeding season (Wilson et al., 1999), and insects that undergo complete metamorphosis can have dramatic dietary niche shifts, resulting in both direct and indirect impacts (Wäckers et al., 2007). For example, over their life cycle: plants experience herbivory, seed predation, pollination (Lundin et al., 2013), dispersal and protection from herbivores; butterflies may act as herbivores when larvae and as pollinators when adult (e.g. Altermatt and Pearse, 2011; Bronstein, 2001); hoverflies act as aphid predators as larvae and pollinators as adults (Gilbert, 2005). Each of these temporal stages could be represented by a particular network, and such shifts between link types can have seemingly unexpected effects, particularly when species are lost or introduced (see Pocock et al., 2012). There have been a few studies that have explicitly integrated different interaction types such as predation and parasitism (Lafferty et al., 2006, 2008), herbivory and parasitism (Cagnolo et al., 2011), pollination, dispersal and herbivory (Melián et al., 2009), and a recent example that includes 11 different groups of animal occurring within an agroecosystem network (Pocock et al., 2012).

Pocock et al. (2012) examined what is known as the 'optimist's scenario', in which the management of one ecosystem service, for improved outcomes, benefits the outcomes of all ecosystem services (Fig. 1.3). The specific dependencies of one service on any other are still poorly understood and the validity of this scenario at system-relevant scales can only be guessed at. Using antagonistic and mutualistic networks for 11 groups of animals from UK agriculture, considerable linkage was evident between services, with particular plant and invertebrate species and links being disproportionately represented (Pocock et al., 2012). Managing, and therefore changing, the abundance or presence of certain species for the benefits of one service, such as pollination, would not necessarily benefit other services, such as biocontrol of aphids. The optimist's scenario could not be maintained for this ecosystem, exemplifying some of the problems of trying to manage multiple, often-competing,

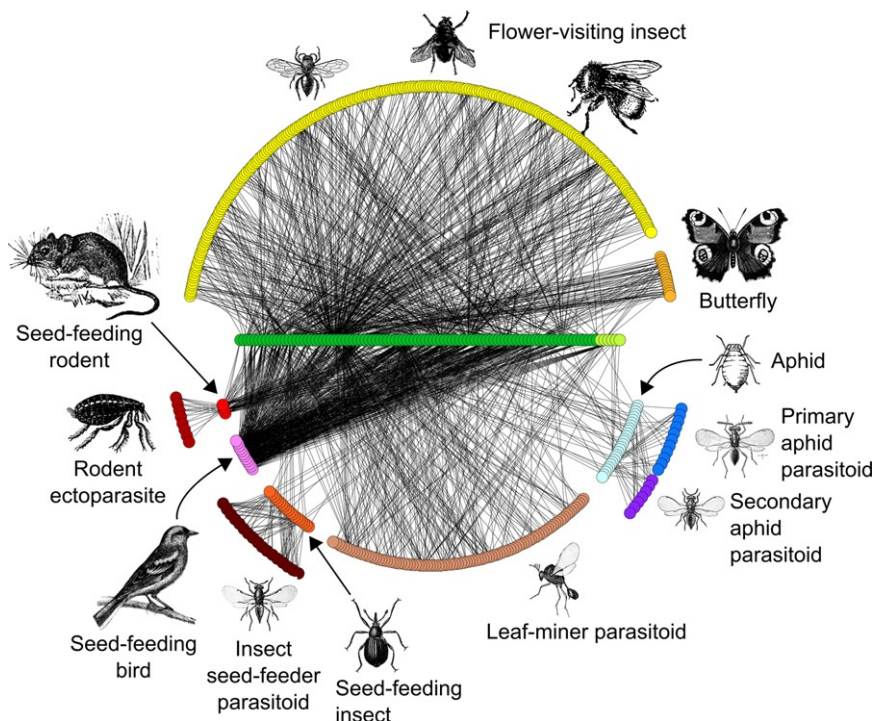


Figure 1.3 Species interaction networks at Norwood Farm, Somerset, UK (revised from Pocock et al. (2012) and used with permission). Each species is represented by a circle and each interaction is represented by a line. Plants are shown by green circles in the centre of the network, with crops being shown in light green. Interaction strengths are not shown in this diagram but were quantified during the study. See Pocock et al. (2012) for full details. The illustrations are used under license from ClipartETC and the network was drawn with Pajek (see Appendix B for full acknowledgements).

outcomes. Based upon this clear, but currently unique example in agriculture, the multi-network approach shows great promise for understanding how biodiversity change affects different agroecosystem networks, and the services provided by them (Memmott, 2009; Pocock et al., 2012).

Multi-network approaches clearly have benefits, but they may also have drawbacks, and these depend upon the questions being asked, the complexity of data and the differences in link type, all of which can blur the interpretation of multi-network results. For some authors, the separate interactions in each network, both positive and negative, are considered first, then the relationships between the interactions; multi-network

approaches are hence avoided. For others, the benefits of asking particular types of questions in a multi-network analysis outweigh the logistical and analytical difficulties. For instance, the identification of keystone species that need protection, in order to assure system performance and behaviour, is an important topic in ecosystem research (Barua, 2011) and may be crucially important in agriculture.

2.2. What structural information can we gain for agroecosystems using node-based metrics?

There are numerous metrics for condensing information from networks (see Costa et al., 2007), many of which have been applied to ecological networks (Bersier et al., 2002; Blüthgen et al., 2008; Ings et al., 2009; Thompson et al., 2012; Tylisanakis et al., 2010; Vázquez et al., 2009a). Here, we consider those most obviously relevant to agroecology, and assess the problems that the incompleteness of ecological datasets may pose for their use and interpretation. Thus, metrics that are 'more' robust to sampling biases resulting from rarity (e.g. Banašek-Richter et al., 2004; Blüthgen, 2010; Chacoff et al., 2012; Gibson et al., 2011; Vázquez et al., 2009a) and other 'quality-of-data'-related problems (Chacoff et al., 2012; Rivera-Hutinel et al., 2012) will be our main focus.

2.2.1 Network topology: connectance, degree distribution, nestedness and modularity

Possibly the simplest metric of the level of connection among the nodes (e.g. individuals, populations, species) is connectance, which measures the number of observed links as a proportion of all possible links. It can be viewed as the mean number of links that can be expected per node. However, connectivity may vary markedly among nodes (e.g. Bascompte et al., 2006; Jordano, 1987; Montoya et al., 2006). Thus, the 'degree' or cumulative frequency distribution of the number of interaction links per node gives more information on the probability of finding highly connected or very isolated nodes and can help to identify highly connected or potential 'keystone' species (Ledger et al., 2012, 2013; Montoya et al., 2009).

Both connectance and degree distributions are especially useful for characterizing relatively complete networks, where only a few realized links are believed to be missing from the data. This situation may apply to food webs based on exhaustive sampling and/or compiled external knowledge about trophic links between the taxa (Layer et al., 2010; Lurgi et al., 2012; Pockock et al., 2012), and it might also be achieved through models used

to infer links based on information about the nodes (Bohan et al., 2011a; Milns et al., 2010; Tamaddoni-Nezhad et al., 2013). However, in most ecological networks built using direct observation, there are typically problems related to sampling effort; some species may be represented by many observations, but many species by only few or even only a single record. This variation in total number of records alone, often a product of the log-normal abundance distribution of species (see Chacoff et al., 2012), constrains connectance to low values and might explain most of the variation apparently observed in degree distribution within networks (Blüthgen, 2010; Vázquez, 2005). Thus, the application of connectance and degree metrics without standardization, particularly where those networks have extreme distributions (such as in agriculture), should be treated with some caution, given that their value may better reflect observed network size and the underlying species' frequency distribution and not ecological specialization or generalization (Ings et al., 2009).

In extreme cases, randomly constructed networks of interactions, following particular frequency distributions, can display the entire range of reported values (Blüthgen et al., 2008). Practically, the exploration of patterns in sampling-limited interaction networks should therefore include correction, such as rarefaction, used in the characterization of diversity, or the frequency of observations as a covariate. For bipartite interaction networks, null model analyses that explicitly address the observation frequencies per species have also been advocated (Blüthgen et al., 2006; Dormann et al., 2009). Given that the frequency distributions of all species are then controlled, at least with respect to those of their interacting partner species, these approaches extend network analysis beyond the simple variation in total sampling intensity per network (Nielsen and Bascompte, 2007) or null models that maintain the number of links (Bascompte et al., 2003). However, using null models incorporate frequency distributions requires independent estimates of species abundance, which are generally unavailable for existing datasets. Moreover, how interspecific differences in sampling effort affect network properties is still a matter for debate (e.g. Chacoff et al., 2012; Rivera-Hutinel et al., 2012). Potential sampling biases may be gauged in directly observed networks via the use of yield-effort curves for the detection of both nodes and links, as has been done for some aquatic food webs (Gilljam et al., 2011; Woodward et al., 2005, 2010b): adopting comparable techniques, combined with modelling and/or literature searches to fill in the 'missing' links, could help produce more complete agroecosystems networks in the future.

The alternative to expending considerable resources on the diminishing returns that come with focusing effort on maximizing completeness in binary networks is to concentrate on quantifying just the main species and links. By using quantitative approaches it is possible to investigate how the frequency of interactions among nodes is distributed within a network, to determine, for instance, the relative impact of each node on other nodes. This has motivated the development of information-theoretical network metrics based on Shannon diversity, where links are weighted by their relative frequency (Bersier et al., 2002; Blüthgen et al., 2006; Ledger et al., 2013) or other weighted indices (Poisot et al., 2012). For sampling-limited interaction networks, standardized, weighted metrics are available that also correct for variation in total number of records per species and for the likelihoods of recording links with different partners (d' and H_2' , Blüthgen et al., 2006, 2007). The potential drawback of such metrics is their relatively high complexity compared with a simple metric based on the number or diversity of links, such as connectance and degree (Blüthgen, 2010; Schleuning et al., 2012). Asymmetric interactions, where a relatively rarely observed species specializes on a common partner species, may go undetected because they would be indistinguishable from neutrality (Blüthgen, 2010). However, except for situations where sampling efficiency is significantly biased, then using quantitative metrics of the whole network, with weighted links would help to account for variation due to sampling biases because it reduces the influence of the rare, and seemingly less-important interactions (e.g. Ledger et al., 2013).

Once the distribution of interactions among nodes is known, we will likely be interested in visualizing/examining how these interactions are organized. The emergence of particular interaction patterns among nodes has been widely documented for ecological networks (Ings et al., 2009; Lewinsohn et al., 2006). For instance, a 'modular' structure, where groups of nodes interact among themselves more frequently than with other nodes, has been reported for antagonistic networks, such as predator-prey food webs (Fig. 1.4). 'Nested' structure, in contrast, has often emerged from mutualistic networks, like plant-pollinator webs (Fig. 1.4; Thébault and Fontaine, 2010). This association between certain types of network structure and interaction types and structure might, however, simply reflect biases due to the incomplete search for all possible structure types (Lewinsohn et al., 2006); recently, both a modular structure in mutualistic networks (Olesen et al., 2007) and a nested structure in antagonistic networks (Cagnolo et al., 2011) have been reported.

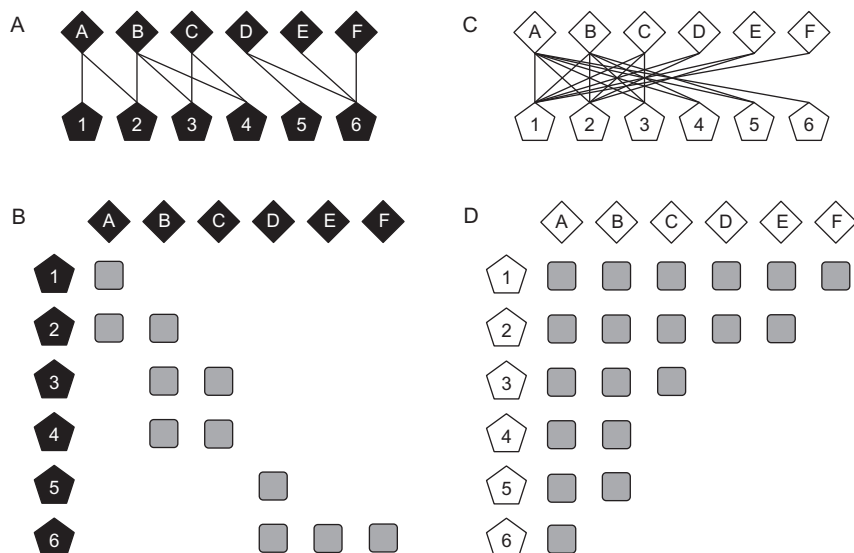


Figure 1.4 Schematic representation of ecological interactions across two types of network: (A) modular or compartmentalized interactions for an antagonistic network of stylized predators and their prey as closed symbols (predator species enumerated A–F and prey species enumerated 1–6); (B) tabular representation of the antagonistic predator–prey interactions where each edge, or link is denoted by the presence of a grey square; (C) nested interactions amongst a stylized group of mutualistic species represented by open symbols (pollinator species enumerated A–F and plant species enumerated 1–6); and (D) tabular representation of the mutual pollinator–plant interactions where each edge or link is denoted by the presence of a grey square. Note, the difference in form between the tabular representations of the ‘nested’ (B) and ‘modular’ (D) networks that are characteristic.

Nestedness (Bascompte et al., 2003) and its quantitative sister ‘dependence asymmetry’ (Bascompte and Jordano, 2007) both describe scenarios where nodes with few connections tend to be linked to a subset of nodes interacting with more connected nodes. Consequently, in nested networks, most interactions appear asymmetric and are organized around a core of highly interconnected nodes. It is worth emphasizing that this pattern may be a by-product of the typical variation in number of total records per species in sampling-limited interaction networks (Blüthgen et al., 2008). For example, profound nestedness has been observed in randomly generated networks, and thus should not necessarily be taken as evidence for specialization asymmetries, as is frequently suggested. Arguably, ‘dependence asymmetry’ may just be a statistical inevitability in incomplete networks with some common and many rare species (Blüthgen, 2010; Blüthgen et al., 2007).

For networks that are compartmentalized, with highly modular groups, such as the small but abundant organisms in soil ecosystems that dominate energy transfer—versus the large but rare habitat engineers (e.g. earthworms)—connectivity and structure could provide important insights into network dynamics (Mulder, 2006). Composition of the modules and the distribution of ‘redundant’ links among modules could also be used to gauge the likelihood of cascade effects, whereby changes in one module or network either constrain or release the next in a ‘domino-like’ manner. Such information would certainly help managers to maintain diversity in agroecosystems by preserving key groups of taxa that determine network persistence.

2.2.2 Obtaining information on the topological importance of nodes and functional groups

The topological position of nodes, or groups of nodes sharing common biological traits, can be used to identify those that contribute most to network structure and, by extension, network dynamics and stability. By characterizing their position and role in a network, keystone species or functional groups can be identified (Bauer et al., 2010; Estrada, 2007; Genini et al., 2010; Jordán, 2009; Martín González et al., 2010; Pocock et al., 2012; Sazima et al., 2010). These approaches could become fundamental to agroecology, as they could allow us to determine the importance of both our managed species and of other species or functional groups (e.g. populations of natural enemies that control pest species).

The importance of particular nodes varies with network structure (e.g. Guimera and Amaral, 2005; Olesen et al., 2007). The ‘centrality’ of each node can be assessed by examining how much it contributes to within- and among-module connectivity, as extended to mutualistic networks by Olesen et al. (2007), after Guimera and Amaral (2005). A range of different measures of node centrality such as ‘betweenness centrality’, or the extent to which a species lies on the shortest paths among other pairs of species, and ‘closeness centrality’, or how close a focal node i is to all other nodes of the network, can be calculated and compared among species and networks (Freeman, 1978; Jordán, 2009; Pocock et al., 2011; Sazima et al., 2010). Comparing unweighted and weighted options of these indices may also provide valuable information about keystone nodes, and the sensitivity to potential sampling biases arising from binary data (Pocock et al., 2011; Scotti et al., 2007). By measuring how network metrics change after eliminating each node or functional group of nodes their importance to network structure can be determined, in turn (e.g. Genini et al., 2010).

Measuring the proportion of species that remain in the network after sequentially eliminating species according to different criteria (e.g. in order of degree or body-mass or abundance) has been used to identify keystone species that confer robustness on the network: thus, cascading secondary extinctions can amplify the effects of primary species loss—for instance, as consumers are left without resources and thus go extinct themselves, and so on (Memmott et al., 2004; Montoya et al., 2006; Poccock et al., 2012).

In addition to simulated species deletions, network stability has also been assessed using population dynamic models (e.g. Layer et al., 2010, 2011). It has been suggested, for instance, that nested patterns might stabilize communities (Bastolla et al., 2009), though this approach has faced criticism of its underlying metrics (Blüthgen, 2010) and model assumptions, particularly those related to functional responses (see Holland et al., 2006) and interspecific competition (Benadi et al., 2012). More recently, James et al. (2012) have shown that connectance, rather than nestedness, best explains variation in stability. Despite this ongoing debate, the underlying logic is identical to that proposed in the ‘insurance hypothesis’ of positive biodiversity effects (Loreau et al., 2001). More links represent higher diversity, which may dampen the functional consequences of stochastic variations or loss of one or a few species (Reiss et al., 2009; Tilman et al., 2006). Network metrics of diversity and functional redundancy, such as connectance or generality or H_2' , may be good indicators of the robustness of the ecosystem function or service provided by that network in response to perturbations (Blüthgen, 2010). Moreover, since different links may contribute to each service in a complementary way, these diversity-related metrics might also correlate with overall network functional performance (Blüthgen and Klein, 2011). Apart from diversity-related or niche-based interpretations of networks, differences in densities of each species across sites or environmental conditions are also important but often ignored in network analyses, although these are key features of ecological effects and estimation of *per capita* interaction strengths (Blüthgen, 2010; Vázquez et al., 2005; Wootton and Emmerson, 2005). Most current networks have remarkably low levels of replication.



3. THE AGRICULTURAL LANDSCAPE AS A NETWORK OF AGRICULTURAL, SEMI-NATURAL AND NATURAL HABITATS

Strictly agricultural habitats, such as that of the cropped area of a wheat field, are, by definition, heavily managed by humans. Considered in

isolation, these habitats may appear to have little in common with truly natural, or even semi-natural, habitats. However, current agroecological thinking and legislation place these highly managed areas into a wider landscape context that consists of a mix of managed, semi-natural and natural areas, terrestrial components placed alongside aquatic components, including water courses and lakes, and above- and below-ground compartments. This much richer description of a diverse agricultural system means the key question we need to answer is not simply 'do agroecosystems operate differently from other systems?' but 'how do we incorporate this diversity of system operation into a network description of the agricultural landscape?'

Agricultural areas differ from natural ecosystems in several key ways (see [Gliessman \(2007\)](#) and [Nicholls and Altieri \(2007\)](#) for a full description), which vary with the type, location and intensity of the production system. At one extreme these are highly mechanized and intensive large-scale annual cropping systems, where most of the energy leaves the system as 'yield' at harvest ([Gliessman, 2007](#)), nutrient recycling is minimal and many nutrients are lost due to leaching, species diversity is greatly reduced to maximize yield, and the most abundant species (i.e. crop plants) are under artificial selection ([Nicholls and Altieri, 2007](#)). This system is inherently unstable in that it only persists due to constant management and external inputs. At the other extreme there are far more diverse agroecosystems; these often contain both annual and perennial vegetation ([Gliessman, 2007](#)) and high landscape complexity ([Deheuvels et al., 2012](#)). In many of these systems there may be one or a few crops for which yield has been optimized, there are many other species that are used by farmers, landholders and the broader community ([Qi et al., 2013](#)). These may include utilizing fertility building legume plants or plants that support pollinators, to support some of the wider goals for agriculture. Mixed agricultural systems also provide a landscape that is a complex habitat mosaic, which supports ecosystem service provider species that are mobile and have diverse food and/or habitat needs ([Kremen et al., 2007](#)). Such species associations with habitat introduce a further layer of interactions ([Evans et al., 2013](#)), and the landscape of agriculture has been described as a (spatial) network of (trophic) networks ([Hagen et al., 2012](#)).

In addition to these spatial interconnections among similar habitat types (e.g. wheat field–wheat field connections), there is also a network of links to other, often very different habitats across the landscape, which can act as sources of food or natural enemies of pest species (e.g. predatory dragonflies from neighbouring freshwaters that forage for crop pests across fields). A significant component of the pesticide safety legislation, for instance, as applied in farmland, has explicitly linked terrestrial and aquatic farmland

habitats in order to protect water bodies from perceived threats from agricultural activity. Leaching of chemicals into water bodies significantly affects the aquatic communities (Rasmussen et al., 2012). The realization that freshwaters are vulnerable 'islands in a terrestrial sea' has long been recognized in both pure ecology (e.g. Hynes, 1975) and environmental legislation (Friberg et al., 2011). However, it has become increasingly apparent that these aquatic communities receive resource subsidies in the form of invertebrate food items and basal resources from surrounding farmland (e.g. Hladysz et al., 2011a,b), and reciprocal subsidies between terrestrial and aquatic habitats have been unearthed in recent years. The extent of the interdependency of agroecosystems and neighbouring habitats is only now being appreciated.

3.1. Network regulation and diversity

Top-down, regulatory forces are evident in many ecosystems (Strong, 1992). In agriculture these can work through management and harvesting (e.g. overfishing, extensive management and destructive foraging) and through native, natural enemies. Such top-down regulation can lead to trophic cascades, whereby exploitation by the farmer or predators regulates the abundance of a prey resource, thus releasing the next trophic level down from regulation and potentially promoting instability in the system. Trophic cascades are often viewed as being especially prevalent in relatively low-diversity situations (Strong, 1992; but see Shurin et al., 2006), such as occur in many agricultural systems. This might suggest, echoing some of the ideas of the earliest ecologists, such as Elton (1927) and MacArthur (1955), that simple systems such as crop monocultures would be especially prone to collapse and pest outbreaks. In contrast, later modelling work of May (1973) and others raised an intriguing possibility that agroecosystems might in fact be more stable in their most simple form (for a given level of average interaction strength). A key question, for agriculture, is therefore whether there is a clear relationship between diversity and stability. However, it seems increasingly unlikely that there is a simple relationship in natural ecosystems, and there is evidence of complex yet seemingly stable systems, as well as stable, simple systems. Rather, it seems stability may be related not just to complexity and interaction strength but also to the particular configuration and pattern of interaction (Emmerson et al., 2005; Montoya et al., 2005, 2009; Neutel et al., 2002).

Alongside top-down effects, bottom-up regulation may be extremely important in agroecosystems, given the superabundance of crop plants

(Bohan et al., 2007; Scherber et al., 2010). Crop plant biomass is the major source of energy produced in agricultural systems and might be expected to drive both above- and below-ground processes. Links between above-ground vegetation and soil organisms have been recognized in natural systems (see some extensive reviews in Wolters et al., 2000 and Wardle, 2002). There is seemingly contrasting evidence for top-down or bottom-up regulation, leading to strong variation in cascade effects among agricultural systems, and the debate about the importance of bottom-up effects in soil is ongoing (Mulder et al., 2013). For instance, Wardle et al. (2004) linked the dominance of fungi in soils to N-poor litter, yet often the opposite is the case, at least for fungal diversity and spore production (Mulder et al., 2003; but also see Jansa et al., 2002 and Wardle, 1995 for soil tillage). Bottom-up effects, though, are widely reported in the literature and supported by laboratory evidence for extremely effective competition between microbes and plants for the N-uptake (Laakso et al., 2000; Setälä et al., 1998). In a replicated system of oilseed rape fields, Bohan et al. (2007) estimated that weed plant abundance explained about 5% of the variation in herbivore abundance; a statistically significant, yet relatively small amount. This increased to 32% when the presence of herbivore predators and parasitoids were included as covariates, leading Bohan et al. (2007) to conclude that these natural enemies exerted important top-down effects on the herbivores, but only after the weed plants had supported the herbivores in a qualitative, bottom-up manner.

Concepts of bottom-up and top-down control have yet to be integrated into a more formal network-based approach, particularly in agriculture where biomass is systematically removed as yield, causing disturbance. 'Stable states' exist primarily as conceptual conservation and management targets discussed by agricultural policymakers, rather than as empirically demonstrated phenomena, but combining network and top-down/bottom-up control theories holds great promise for understanding and manipulating network resilience and stability in agricultural situations.

3.2. The role of natural, semi-natural and 'agricultural' element composition

Natural systems are subjected to a myriad of stochastic, environmental factors that are moderated in agroecosystems by farmers making decisions to impose management, which may be the key driver of change in agriculture. Indeed, historically, the loss of species diversity that results from management activity has been considered a justifiable trade-off for agricultural production. Incorporating human decision-making into ecological network analysis could

therefore provide an especially fruitful avenue of future research. Recent approaches have attempted to incorporate social and ecological systems, particularly in the context of understanding the resilience of systems to perturbation (Walker et al., 2004). However, to our knowledge, there have been no attempts to explicitly integrate or quantify the impacts of human decision-making on ecological network analysis. Human 'nodes' have been included in ecological networks of the dynamics of exchange networks among farmers, where the relevant components may be information, propagules, or even whole groups of organisms (Pautasso et al., 2013). In principle, such networks are very similar to ecological networks of populations exchanging migrants. In that sense, it is the farm management nodes (farmers, research facilities, NGOs, etc.) that exchange planting material (seeds, cuttings, etc.) in varying quantities and in an essentially directional fashion. At the moment, this is an underdeveloped side of the use of networks in agroecology (Pautasso et al., 2013; Thomas et al., 2011), but it may hold the key to understanding the persistence of many different traditional crops and crop varieties in the face of considerable pressure towards crop homogeneity. It could also help to understand how diseases are propagated among agroecosystems, such as the rapid farm-to-farm spread of foot-and-mouth disease across the United Kingdom during the 2001 outbreak, and for anticipating other such human-propagated epidemics in the future.

In homogeneous agricultural landscapes, dominated by a handful of crops each of which may be represented by only a few varieties, considerable research effort has been devoted to species for which a lack of landscape connectivity is a problem, especially those of conservation concern. However, the ramifications of high connectivity, linked to homogeneity, for pest and disease spread have only been considered much more recently (Plantegenest et al., 2007). Margosian et al. (2009) used a network approach to show that maize and soybean crops are highly connected across the United States, potentially facilitating the rapid spread of pests or disease. At the farm-scale, large fields are generally more profitable and easier to manage in highly mechanized systems, so there has been a concerted move to consolidate multiple smaller fields into single, large fields. This is further exacerbated by 'block-cropping' the same crop-type in space, mainly to improve the efficiencies of planting, applying agrichemicals and harvesting. Large, block-cropped fields do have some positive effects on weed density within-fields, and reduce harvest impurities (Colbach, 2009; Petit et al., 2013), but they could also be riskier, promoting and propagating pest outbreaks and disease, especially at larger scales in time and space.

Management practices can also create corridors for movement and the spread of pests and diseases. [Plantegenest et al. \(2007\)](#) highlight the example of wider adoption of irrigation in Africa creating corridors for viruses to spread by encouraging populations of host plants in both cultivated and uncultivated areas. The functional connectivity of a landscape is often species specific, such that corridor features for one species can dissect the landscape and decrease connectivity for another. For example, [Avelino et al. \(2012\)](#) concluded that fragmenting coffee farms at small scales would reduce movements of the coffee berry borer between coffee plots, but could increase coffee leaf rust epidemics because open spaces facilitate pathogen movement. Interspersing coffee farms with forest corridors may give multiple positive benefits if it reduces borer movement while not favouring leaf rust dispersal.

Heterogeneous farm landscapes could be key for maintaining biodiversity ([Benton et al., 2003](#)), yet most ecological network studies within agroecosystems have focussed on antagonistic networks of trophic interactions, largely ignoring habitat attributes essential for other population processes, such as roosting, overwintering and breeding sites. Incorporating these non-feeding interactions into ecological network analysis is a crucial research priority for the future ([Hagen et al., 2012](#); [Ings et al., 2009](#)).

The impact of temporal connectivity on trophic interactions is only really now starting to be explored ([Hagen et al., 2012](#); [Ings et al., 2009](#); [Olesen et al., 2010](#)). [Vinatier et al. \(2012\)](#) used a landscape model to investigate the impact of management practices through time on the *Meligethes aeneus* beetle (a pest of oilseed rape) and an associated parasitoid. They found biological regulation declined with longer crop rotation sequences that had a lower proportion of oilseed rape, with the resulting reduction in temporal connectivity between suitable oilseed rape crops affecting the parasitoid more than the beetle. In most network studies, however, temporal resolution is often traded for increased spatial replication (but see [McLaughlin et al., 2013](#)), especially in agroecosystems. However, when [Gagic et al. \(2012\)](#) collected time-series of aphid–parasitoid–hyperparasitoid food webs in cereal fields, it was found that species diversity and food web structure changed most with time, in intensively farmed fields.

Clearly, there is a need to understand the functional connectivity of landscapes in space and time not just for simple, single-species interactions but also from complex networks of interacting species ([Hagen et al., 2012](#); [Loeuille et al., 2013](#)). [Macfadyen et al. \(2011\)](#) discovered a relationship between subunits in plant–herbivore–parasitoid food webs and landscape

structure, suggesting that just a few interactions may connect species in different habitat patches. Habitat-association networks have also revealed the impact of habitat loss on whole food webs (Evans et al., 2013), indicating that farmed system management, where decisions are often taken at the level of habitats, such as the removal of hedgerows and permanent pastures in temperate farming systems, could have marked impacts on system performance.



4. LINKING STRUCTURE, FUNCTIONING AND SERVICES

4.1. Understanding network structure, functioning and services

The structure and functioning of ecological networks are intimately coupled, because both are driven by a combination of demography, dispersal and evolution. Dispersal affects ecological structures, by introducing new individuals and species (Morton and Law, 1997), and thus modifies local population abundance (Pulliam, 1988). It also affects functioning, by modifying the overall distribution of energy and nutrient across the 'metaecosystem' (Loreau et al., 2003b, 2013). Demographic effects vary both with the conditions of the environment and the local interactions among species in the community, but can change the structure of the community through extinction and invasion events, and by increasing variation in species abundance (McGill et al., 2007). For a population to increase, there is a need for nutrient and energy and demographic and dispersal effects constantly redistribute these resources, affecting the structure, dynamics and functioning of the ecosystem as a whole. Finally, evolutionary dynamics have a large role in determining which interspecific interactions occur and, therefore, network structure (Caldarelli et al., 1998; Loeuille and Loreau, 2005; Rossberg et al., 2006), leading to a coupling of structural and functional properties of the ecosystem that are usually treated in isolation (Loeuille and Loreau, 2006; Loeuille et al., 2013; Urban et al., 2008). These processes can interact in complex ways: for instance, dispersal is often intimately linked to local population density (Clutton-Brock et al., 2006; Morris et al., 2004), and this constrains evolution by modifying gene flow (Bohonak and Jenkins, 2003; Dawson et al., 2010; Garant et al., 2005).

4.1.1 Diversity

Over the past two decades, biodiversity has been found to have a generally positive effect on ecosystem functioning (Cardinale et al., 2006; Hector

et al., 1999; Reiss et al., 2009; Tilman et al., 2006; Worm et al., 2002). Standing biomass or productivity tends to be higher in diverse ('speciose') plant systems (Hector et al., 1999; Loreau and Hector, 2001; Tilman et al., 2001). However, because diversity is relatively low in some agricultural systems (Robinson and Sutherland, 2002; Vigouroux et al., 2011), ecosystem functioning may be severely degraded (at least, without significant anthropogenic management and subsidies). Consequently, it has been hypothesized that yield could be improved by using more diverse suites of crop and companion plants, in contrast to current intensive, essentially monocultural agricultural systems (Macfadyen and Bohan, 2010; Meyer et al., 2012; Vigouroux et al., 2011). The positive link between yield and diversity has been explained by two mechanisms. First, highly productive species are more likely to be sampled from a diverse species pool. Such 'sampling effects' have analogies in artificial selection and GM modification in modern agriculture, producing highly productive species. Sampling effects may, however, be less important than 'complementarity effects', which explain a positive link between diversity and yield (Loreau and Hector, 2001) as a difference in species resource requirements. Some species exploit resources more efficiently, and across a diverse pool of species resource exploitation increases.

Diversity has also been linked positively to the stability of systems (Haddad et al., 2011; Loreau and de Mazancourt, 2013; Tilman et al., 2006), although this is not necessarily expected for any given local species population (May, 1973). This is an emergent, system-level property (e.g. low variations of total biomass or productivity in time) that can arise from the sampling effect and complementarity. As with marine fisheries, the traditional preoccupation in agriculture has been on one or two focal species, but this focus can miss the bigger network-level picture. Interacting species react in different ways to external disturbances: some benefit, others do not. There are parallels with economics here, where the price of a portfolio of stocks is much more stable than the price fluctuations in the individual stocks, due to an averaging effect. Similarly, stability across the portfolio of species is preserved in the face of variation in high-diversity systems (for the portfolio effect or insurance hypothesis, see Loreau et al., 2003a; Yachi and Loreau, 1999). Low-diversity agroecosystems may lack such statistical stability, suggesting that more diverse systems may improve overall agricultural sustainability and the reliability of ecosystem services.

The mathematical product of the number of nodes and connectance gives a measure of network complexity (May, 1973). In general,

connectance appears to decline with increasing diversity (Beckerman et al., 2006). Should agricultural systems follow similar rules, low-diversity networks may have high connectance, possibly reflecting sampling effects (Section 2, Heleno et al., 2012). Agricultural management modifies the species abundance distribution within the community: crops dominate, while other species become rare or are lost. Such a skew in species abundance distributions might favour specialist strategies through density-dependent effects, thereby decreasing network connectance (Loeuille et al., 2013). Therefore, while ecological, community-scale constraints suggest that connectance may increase, evolutionary or assembly processes under agricultural selective pressures may decrease connectance. As far as we know, levels of connectance in agricultural networks do not appear to differ markedly from other ecosystems (Mulder et al., 2006).

4.1.2 *Connectance*

Higher connectance is expected to decrease stability, at least in models of randomly assembled networks with strong pairwise interactions (May 1973), although this trend may be reversed if consumers are sufficiently plastic in their feeding behaviour (Kondoh, 2003; Loeuille, 2010). Within highly connected networks, indirect effects may propagate along many links and many species may ultimately be affected (Montoya et al., 2009). Consumer species tend to have higher numbers of linked resources, and so are probably less vulnerable to the extinction of any one prey species (Dunne et al., 2002). How such effects might operate in agricultural systems will require rigorous examination and experiment. The form of biodiversity–ecosystem functioning and complexity–stability relationships will remain topics of some debate in agriculture (Mulder et al., 2012), but ultimately, they will likely depend on a blend of behavioural, ecological and evolutionary processes.

While diversity and connectance set the coarse structure of the network, the interactions can be distributed in a variety of ways within it, and this has important dynamical and topological consequences. As we have seen, the network can be nested or modular (Fontaine et al., 2011; Krause et al., 2003; Thébault and Fontaine, 2010), but where connectance is sufficiently high, nestedness may become more prevalent (Bascompte et al., 2003). It seems, though, that agriculture most often produces compartmentalized food webs (Macfadyen et al., 2011). This could enhance the overall stability of the system (Fig. 1.2), because external disturbances are restricted to a given compartment, rather than rippling through the rest of the network. For mutualistic networks, nestedness might also increase stability (Thébault

and Fontaine, 2010) and maintain diversity (Bascompte et al., 2006), thereby enhancing overall sustainability. How agricultural management influences the modularity or nestedness of networks and if this might offset otherwise destabilizing network properties is, as yet, unclear.

4.1.3 Networks of metapopulations

When describing populations exchanging migrants, the network of intraspecific links can be visualized in spatial graphs that show the physical distances between the populations (Dale and Fortin, 2010). Spatially implicit migration networks may also contain information on the relative distance between populations, through weighted migration coefficients (Economato and Keitt, 2008). Population networks have already been used in community ecology to understand the role of the spatial arrangement of patches in shaping biodiversity patterns (Economato and Keitt, 2008; Muneeppeerakul et al., 2007, 2008) and habitat loss (Economato, 2011). Where intra-population rates exceed migration, colonization–extinction dynamics can be studied in network metapopulations (Adler and Nuernberger, 1994; Gilarranz and Bascompte, 2012; Hanski and Ovaskainen, 2000), which have clear parallels with the epidemiology of how contagious processes persist in contact networks (Chakrabarti et al., 2008; Harris, 1974; Meyers, 2007; Peyrard et al., 2008; Volz et al., 2011). In spatial metapopulation networks, where populations residing in different habitats exchange individuals, the metapopulation exists in tension between the processes of local population growth and dispersal between populations, which can lead to pest populations that fluctuate asynchronously. More recently, metapopulation theory has been extended to local assemblages of multiple species linked by dispersal to form a metacommunity. Some of these metacommunity concepts have proved useful for understanding and predicting food web structure and dynamics (Baiser et al., 2013; Hagen et al., 2012; Pillai et al., 2011) and might now be applied to agroecosystems (Massol and Petit, 2013).

4.1.4 Ecosystem services

Changes in diversity, connectance and interaction patterns are expected to influence the functioning of ecosystems. Given that future sustainable agricultural management goals emphasize ecosystem services (Doré et al., 2011; Malézieux, 2011), it is now imperative that we understand and can predict how these might be impacted by changes in network structure. The theory of biological control posits that natural (although not necessarily native) enemies of agricultural pests may be used to limit pest densities below economic

thresholds (Costanza et al., 1997). If achieved, such regulation should allow pesticide inputs to be reduced and system resilience and sustainability to be enhanced. It is, therefore, instructive to ask ‘under what conditions do we expect biological control to be effective, and in what type of network structure?’, drawing on the considerable body of literature in ecology.

For biological control to occur, natural enemies must suppress the biomass (or abundance) of the target species. Numerous models have investigated the conditions required for such ‘top-down control’, and one important structural property is the length of food chains. Pests associated with the crop are primary consumers and their top-down control requires a minimum of three trophic levels of crop-pest-natural enemy (Hairston et al., 1960; Oksanen et al., 1981; Oksanen and Oksanen, 2000). The efficiency of biological control might therefore depend on the number of trophic ‘levels’ in the agricultural network.

Diversity within trophic levels has possibly the most important structural effect on biological control. Within the natural enemies’ trophic level, higher diversity may increase overall predator efficiency, via complementarity and sampling effects, leading to improved biological control (Crowder et al., 2010), as observed in non-agricultural systems (Frank et al., 2006; Sinclair et al., 2003). However, should the natural enemies include competitive, omnivorous species, then additional intraguild predation effects, whereby where predators feed on other predators, could decrease system stability and performance (Bruno and O’Connor, 2005).

Diversity within the primary consumer assemblage is also important. Where pest species coexist with other primary consumers, diversity can dilute the action of natural enemy predators, decreasing top-down control (Duffy, 2002; Polis et al., 2000). It also poses an interesting problem: although it is often seen to be desirable to encourage biodiversity in agroecosystems, at the primary consumer level it may incur a cost by making biological control more diffuse. One possible solution, which has been adopted in classical biological control, is to use specialist predators as biological control agents that target specific prey pest species, limiting the influence of alternative prey. The efficacy of more generalist predators that consume a broader range of prey, which comes with the possible cost of diffuse control or even intra-guild predation, has been long debated (Flaherty, 1969; Symondson et al., 2002), although it is a cornerstone of conservation biological control. Multispecies approaches have been applied implicitly in biological control, but without the formal structure that network ecology could provide.

4.2. Can system service properties, such as yield or inputs, be brought into network approaches?

Understanding the link between network structure and functioning is an important research need (Reiss et al., 2009; Thompson et al., 2012), and a natural development from understanding classical biodiversity–ecosystem functioning relationships (Naeem et al., 2009). Human management of habitats can have different impacts on multiple ecosystem services (Fiedler et al., 2008; Olson and Wäckers, 2007) and, although only recently placed in the context of agroecosystem networks, the multi-network approach adopted by Poccock et al. (2012) has successfully illustrated this (Fig. 1.3). Many studies have examined the relationship between biodiversity *per se* (either plant genetic diversity or plant species diversity) and provisioning services, such as crop yield (Cardinale et al., 2012). Far fewer have explored the underlying mechanism, and how loss of diversity leads to reduced yields. Yield has been incorporated into crop growth models and agricultural production system simulators (e.g. McCown et al., 2002), for some time, but simulations are usually run with the assumption of efficient application of inputs and no other limiting factors, such as pest damage. Despite these simplifications, such models can be useful for demonstrating the potential benefits to farmers of altering pest management strategies (Nguyen Thi My et al., 2013). Some empirical network studies have quantified the diversity and complexity of species in agroecosystems, though they have not linked these with production practices or crop growth (e.g. Schoenly et al., 1996). For instance, Lohaus et al. (2013) measured the size of potato plants, *Solanum tuberosum*, as a proxy for herbivory under organic management practices, but they did not measure productivity gains. In pollinator network studies, the links to crop yield are being increasingly incorporated, however, and there is no reason why this should not also happen in pest control studies. It will require more empirical research, examining, for example, how management and environmental change affect ecological networks that include crops, mutualists, antagonists and possible indirect interactions from species at higher trophic levels (e.g. Knight et al., 2006; Van Veen et al., 2008).

Plant quantity, such as yield, and quality can have strong bottom-up effects on herbivores like aphids and their natural enemies (Bohan et al., 2007; Bukovinszky et al., 2008; Lohaus et al., 2013). Mulder et al. (2012) and Lavorel et al. (2013) examined the diversity of species and top-down/bottom-up interactions, in terms of traits such as body-size and elemental content (Fig. 1.5.). Higher nitrogen and phosphorus content in plant tissues

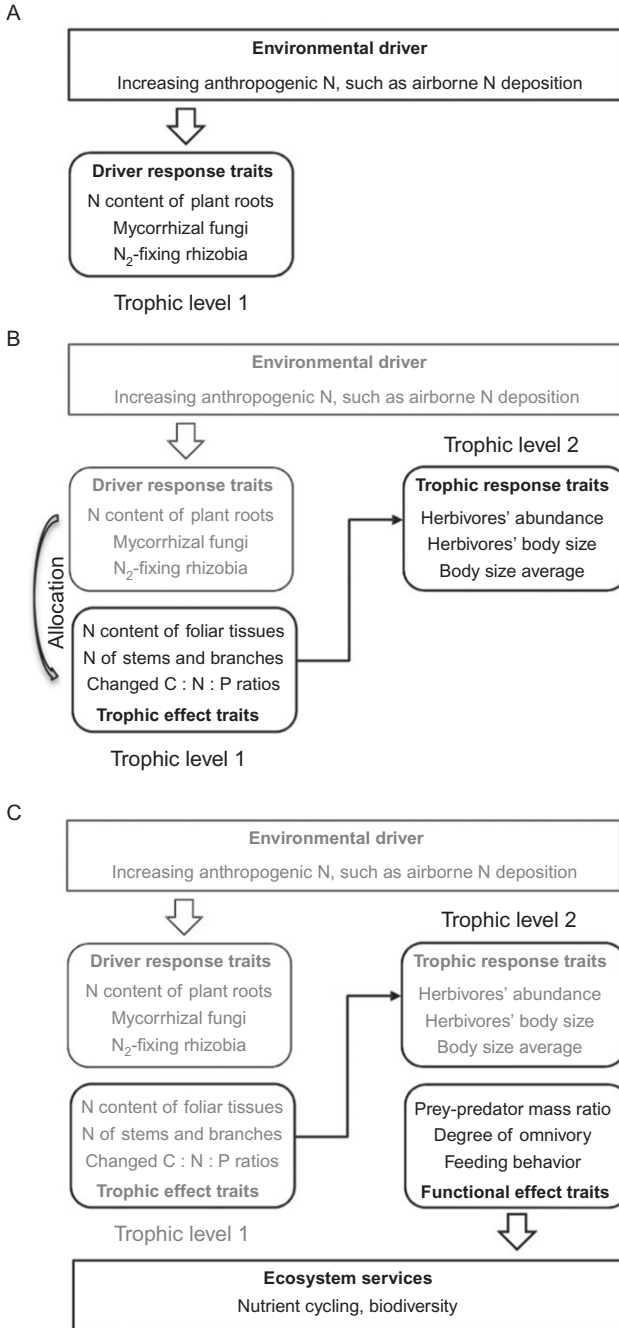


Figure 1.5—See legend on next page.

were found to favour larger grasshopper herbivores. Given that body size determines consumption, the herbivores could influence supporting ecosystem services related to litter breakdown rates, such as nutrient cycling. Intensified grassland mowing, which drives the system in a bottom-up manner, could enhance 'fodder production' by increasing foliar nitrogen content, leading to larger herbivore invertebrates; concurrent predation by spiders may control these herbivores, indirectly promoting plant growth (Lavorel et al., 2013; Moretti et al., 2013; Schmitz, 2008). Such trait-based, network approaches to investigating interactions can help to elucidate seemingly complex outcomes, which are constrained by stoichiometry and/or allometry (Elser et al., 2000; Mulder and Elser, 2009, Mulder et al., 2013; Scherber et al., 2010).



5. EVALUATING AND PREDICTING ECOSYSTEM CHANGE

5.1. Measuring disbenefit

In the absence of predictive frameworks, such as those advocated by Nienstedt et al. (2012), the evaluation of the risks of management choices for agricultural landscapes and ecosystems have used classical field survey methods and autecological approaches. Where risk assessments have been carried out prior to a new technology being released, these have tended to focus on a few iconic non-target taxa, such as honeybees and birds. The broad swathe of species that deliver important ecosystem services are generally not considered and many changes in management practices have effectively evaded a comprehensive risk assessment. Some management changes (e.g. no-till or reduced tillage) are implemented because they provide some direct economic benefit to the farmer, such as easier weed management and better water-use-efficiency, but can also change the risk of other outcomes in the wider agroecosystem; there is an increased risk of snail and slug damage to crops under minimum tillage, for example (Glen and

Figure 1.5 Framework articulating functional responses and effects within and across two adjacent trophic levels (Lavorel et al., 2013; Mulder et al., 2012). (A) Identifies response traits for each of the trophic levels to the elemental factor (environmental driver) or the climatological factor of interest, where the response of (part of) organisms can be related to particular functional traits (here, below-ground plant traits); (B) identifies the *effect traits* of a basal trophic level with expected cascading effects at higher trophic level(s), and the corresponding *response traits* of the adjacent trophic level; and (C) defines the identity of the *functional effect traits* contributing to one or more specific ecosystem services.

Symondson, 2003). Management and land-use change can have great impacts on ecosystem services, such as pest control. For example, the greater planting of corn to support biofuels reduced biocontrol services in soybean by 24% in some US states, possibly by reducing landscape diversity (Landis et al., 2008). Wider disbenefits, such as the loss of ecosystem services as a result of current agricultural chemical practices, have been acknowledged (e.g. Geiger et al., 2010) but have yet to make a substantial impact on how we manage agricultural production. However, there is some evidence that this change is starting to occur. For example, the recent EU ban on neonicotinoids was driven by concern about declines in bees and associated pollination services, and the consequent effects on the wider ecosystem.

5.2. Current regulation practice for agrochemicals

As part of regulatory decision-making to protect the environment, the ecological risks posed by the use of crop protection chemicals or GM crops are assessed using a set of nested assessment protocols called a 'tiered assessment' (e.g. Garcia-Alonso et al., 2006; Touart and Maciorowski, 1997). At low tiers, relatively simple laboratory ecotoxicology studies are used, whereby various 'model' organisms are continuously exposed to test substances under conditions where contact is unavoidable: essentially investigating the network one node at a time and in isolation. For crop protection chemicals, the test substance may be the active ingredient or formulated product, and for GM crops the test substance may be the active ingredient (e.g. a pesticidal protein) or tissue of the GM crop. The responses of the organisms are then used to estimate measures of effect, such as the concentration of a substance that is lethal to 50% of the test population (LC_{50}), or the highest concentration that has no observed adverse effect on the test population (NOAEC).

The species tested are intended to represent the wide variety of organisms that may be exposed to the product under the intended pattern of use. 'Representativeness' is the extent to which the effect on the species in the study predicts the effect, or perhaps more importantly absence of effects, on valued species in the field. Representative species may be chosen based on their high sensitivity to chemicals, their taxonomy, or their ecological role (Candolfi et al., 1999; Romeis et al., 2013). The measures of effects are then divided by the estimate of exposure to give a toxicity:exposure ratio (TER), which if low enough enables the agrochemical to proceed to higher tier studies that may expose the organisms to the test substance under more

realistic conditions, refined assessments of exposure using data not worst-case assumptions, or both. Again, toxicity and exposure are compared, and decisions are made based on the TER.

The relationships between values of TERs and the size of adverse ecological effects in the field are, however, not clear. First, definitions of what is regarded as adverse may be lacking or expressed in terms of reductions in the population size of certain organisms (e.g. [Ankley et al., 2010](#)) and not as harm to ecosystem functioning or services. Secondly, the TER cannot be converted easily into a predicted change in the population size of a particular organism. However, in general, tiered risk assessment appears to be conservative ([Campbell et al., 2000](#); [Duan et al., 2010](#)). Ideally, it would use the results of laboratory ecotoxicology studies and worse-case exposure assessments to predict the likely effects of agricultural management on multi-species networks and their associated ecosystem services. [Nienstedt et al. \(2012\)](#) have proposed that policy objectives of pesticide regulation in the European Union could be interpreted in terms of ecosystem service delivery; thus, it is foreseeable that adverse ecological effects could be defined functionally. This poses the question: 'how might simple, lower-tier studies be used to predict the effects of agricultural management on higher-level functions?'

5.3. Predicting agrochemical impact using networks

The theoretical and conceptual framework supporting tiered assessment has been developed over the last 20 years. While there have been problems during this period, such as the possible interaction between neonicotinoid pesticides and pollination services provided by bees ([Whitehorn et al., 2012](#)), the assessment methods appear to provide some meaningful level of environmental protection. This process deals with individual species, however, which leaves it open to criticism that it may fail to predict the emergent properties of ecosystem services that result from multispecies interactions within a network. [Raybould et al. \(2011\)](#) illustrated how ecosystem modelling, simulating a food web of interacting species or groups, might be used to extend the current ecotoxicological effects framework to changes in ecological functioning. Following [Caron-Lormier et al. \(2009, 2011\)](#), they modelled the yield loss from a crop subjected to attack by pest aphids. When an aphid predator, parameterized to be similar to a green lacewing, was introduced into the system, yield loss caused by the aphids was reduced. The difference between the yield with and without

predation of aphids was termed the biological control function. Further simulations were run in which the survival, growth or reproduction of the lacewing were systematically reduced, to mimic the potential adverse effects of a pesticidal molecule, such as an insecticidal protein produced in a GM crop. The simulations showed that reducing survival, growth or reproduction separately by up to 50% reduced the biological control function by less than 20%. Reducing all three parameters by 50% led to about a 60% reduction in biological control. Introduction of a second aphid predator, parameterized as a ladybird, reduced the loss of biological control caused by adverse effects on the lacewing: only about 10% biological control was lost when its survival, growth and reproduction were all reduced by 50%.

This kind of network modelling could be used far more widely in risk assessment to simulate the size of the adverse effects predators that would have to occur for that amount of biological control to be lost, and laboratory ecotoxicology studies could be targeted more efficiently to test for these effects. Network ecological approaches might, therefore, eventually be developed to simulate highly complex systems with numerous pests and their predators. Such simulations might be able to integrate ecotoxicology data from multiple species, to give far more sensitive and robust predictions of changes in ecosystem services, following pesticide use, than those based on laboratory data alone: similar approaches to modelling networks are considered in more detail by [Tixier et al. \(2013\)](#).

5.4. Predicting the effects of future change using networks

Empirical network studies have been used to assess past changes in management in agricultural landscapes. For example, [Tylianakis et al. \(2007\)](#) examined how a land-use intensity gradient (forest, coffee agroforestry, pasture and rice) modified host–parasitoid food webs, with the rice and pastures showing little change in species richness, but a huge increase in the skew of interaction strengths, with both systems being dominated by just a few interactions. The effect of organic farming on food web structure has also been assessed at the field ([Lohaus et al., 2013](#)) and farm level ([Macfadyen et al., 2009](#)), and the impact of GM organisms in terms of the movement of transgenic DNA has been examined in soil food webs ([Hart et al., 2009](#); [Powell et al., 2009](#)) and predator assemblages ([Peterson et al., 2009](#)). [Cohen et al. \(1994\)](#) used a food web approach to evaluate the effect of insecticide applications on insect assemblages in rice paddies.

An understanding of how network metrics describe impacts on the resilience of the system will be critical of predicting future agricultural system performance. [Figure 1.2](#), for example, illustrates an example of an agricultural disturbance effect, the application of an insecticide to control a pest, moving through a species community in a hypothetical, modular farm network. In this example, the communities with the fewest links to other subunits may be better protected from the indirect effects of the disturbance: that is, the expected effects are confined to the species immediately associated with the crop, whereas species in the semi-natural components of the network are less affected. What we cannot yet predict with certainty is what changes in structure, such as modularity or nestedness, will mean for the impact of disturbance on agroecological networks in general, or if any particular configuration makes farm communities more resilient to disturbance.

Thus, although the empirical evidence base for agroecological networks is growing, all these studies involved networks that were sampled independently from systems of different states, rather than across time as an agricultural system moves between states. Space-for-time substitution is still the *de rigueur* approach in ecology for assessing responses to stressors in multi-species systems (e.g. [Meerhoff et al., 2012](#)), including ecological networks (e.g. [Layer et al., 2010](#)), but it has its detractors, as the different states may already represent (different) equilibrium conditions, rather than exhibiting the transient dynamics of systems responding to environmental change (but see [Layer et al., 2010, 2011](#); [McLaughlin et al., 2013](#)). The latter may be ecologically very different from the former, especially where networks are experiencing biodiversity loss or invasions that can skew their linkage and size-structure (e.g. [Cohen and Havlin, 2003](#); [Layer et al., 2011](#); [Woodward and Hildrew, 2001](#)). [Gagic et al. \(2012\)](#) examined temporal change over a season, but not the transition between ‘treatments’ of high agricultural intensification to low agricultural intensification (also see [Lohaus et al. \(2013\)](#) who examined different crop growth stages). Characterizing the ‘baseline’ network properties of current farming systems and their associated management practices is crucial for gauging responses to future environmental changes. Given that the species composition of agroecosystems changes markedly among crops ([Hawes et al., 2009](#); [Smith et al., 2008](#)), it is still unclear what level of additional change might be ascribed to shifting environmental conditions. Whilst classical observation methods may be too labour intensive for constructing fully characterized and temporally resolved networks for formal risk assessment processes, including key species interactions and ecosystem services is not: thus, network-based proxies could provide useful indicators, just as

the size-spectrum or trophic height are now being adopted to gauge overexploitation of food webs in marine fisheries (Jennings and Warr, 2003; Jennings et al., 2007).

5.4.1 Would larger empirical networks support agricultural decision-making?

Agroecosystem ecology is a multidisciplinary science that involves microbial, plant and animal ecologists, as well as those that work in above- and below-ground systems in both agricultural and natural/semi-natural contexts. All these protagonists use discipline-specific protocols, so networks tend to be carved up and dealt with piecemeal rather than as a whole, and how the components are interlinked over time and space is still poorly understood. Understanding the structure and dynamics of ecological networks that incorporate a wide range of interaction types is a growing area in ecology, partly driven by advances in computer modelling (Evans et al., 2013; Lafferty et al., 2008; Pocock et al., 2012) and novel molecular approaches (Derocles et al., 2012a,b; Roy and Handley, 2012; Traugott et al., 2013), but ultimately by the desire to understand the real threat of biodiversity loss to ecosystem services and functioning (Evans et al., 2013; Macfadyen et al., 2009, 2011; Memmott et al., 2007, 2010; Pocock et al., 2012). Much of the recent work in this area has been in agroecosystems.

For example, Pocock et al. (2012) linked plants with 11 groups of animals on an intensively studied organic farm in England, focussing on animals feeding on plants (butterflies and other flower-visitors, aphids, seed-feeding insects and granivorous birds and mammals; Fig. 1.3) and their parasitic dependants (primary and secondary aphid parasitoids, leaf-miner parasitoids, endoparasitoids of seed-feeding insects and ectoparasitoids of rodents). This study inevitably encompassed a wide taxonomic and functional range, which included animals regarded as bioindicators and as ecosystem service providers. Although this was just a subset of species interactions at the farm scale, the study was unique in attempting to connect multiple species-interaction networks, which have traditionally been studied in isolation (Fontaine et al., 2011). By examining topological 'robustness' as a measure of the tolerance of the network to species extinctions (Dunne et al., 2002; Memmott et al., 2004), Pocock et al. (2012) found that some networks (e.g. the plant-pollinator network) were far more fragile than others (e.g. the bird-seed-feeder network). They also found that robustness did not co-vary among them, suggesting that targeted management of one group

will not necessarily benefit others. The study also used robustness values to compare the relative importance of plant species to the network's overall stability, and found that species such as thistles (*Cirsium* spp.), buttercups (*Ranunculus* spp.) and clover (*Trifolium* spp.) occurred in most habitats and were highly connected to many other species on the farm.

Evans et al. (2013) subsequently extended this approach to examine the effects of simulated habitat loss on the same spatial network of ecological networks. Habitat destruction is a primary cause of biodiversity loss (Pimm and Raven, 2000) and the impacts of management, such as habitat addition, loss and change, are likely to have large effects within ecological networks, as they will simultaneously affect multiple species across trophic levels (see Hagen et al., 2012; Tylianakis et al., 2008 for reviews). Evans et al. (2013) used 12 habitats (six managed and six non-managed) on the same organic farm to create multiple species–interaction networks for each habitat and then simulated sequential habitat loss under three scenarios: (a) random, (b) based on human decisions and (c) with a genetic algorithm to identify best- and worst-case permutations. Overall, the plant and animal groups exhibited high robustness, largely because habitats tended to have similar species composition and few unique interactions, despite considerable variation in management intensity and disturbance between habitats. Additionally, many of the animal groups (e.g. flower-visitors, birds and mammals) operated at spatial scales that integrated several habitats. These results suggest that the loss of a particular habitat may have little impact on animals, so long as suitable resources are available elsewhere. The models assumed that with the loss of a habitat-specific food source or host, animals could switch to alternate food sources in different habitats, but for some species this may not always be feasible. The models also assumed that the entire possible host range was observed: an observation likely to be affected by sampling bias (e.g. Chacoff et al., 2012; Cohen et al., 1993; Goldwasser and Roughgarden, 1997). Despite these potential caveats, such novel analyses that incorporate environmental variation into the network clearly have considerable potential for predictive agroecosystem management and restoration.

5.5. Could we learn, *in silico*, larger and greater numbers of networks?

The multi-network approaches of Poccock et al. (2012) and Evans et al. (2013) can be used to simulate the effects of species and habitat change on large networks of interacting species. These approaches typically rely on direct

observation, from field surveys and sampling, and/or information on species diet from the literature to construct networks. Collating such information is extremely labour intensive and this can hinder the use of predictive multi-network approaches in all but the simplest systems. In addition, many (trophic) interactions (e.g. nocturnal feeding and sectorial predation) cannot readily be observed and are under-represented in the literature. There are, however, computational approaches that can help here, by 'learning' interaction networks from existing empirical data.

Machine-learning approaches have been used in molecular and systems biology to learn the structure or annotations of genetic and biochemical networks from empirical data. For example, Bayesian approaches have been widely used to reconstruct gene regulatory networks from gene expression data (e.g. [Friedman et al., 2000](#)). Similarly, causal protein signalling networks have been derived using Bayesian networks ([Sachs et al., 2005](#)) and metabolic network inhibitions have been learned from temporal NMR data using logic-based machine learning ([Tamaddoni-Nezhad et al., 2007](#)). Computational approaches, and in particular data mining and machine learning, clearly have the potential to transform ecology, just as they have with molecular biology. This potential has been recognized in the computer science and artificial intelligence community ([Dietterich, 2009](#)), and the advantages of machine-learning approaches over the statistical approaches normally used by ecologists have been demonstrated and discussed in [Hochachka et al. \(2007\)](#). It has also been recently demonstrated that bioinformatics tools, such as Bayesian network approaches, can readily be adapted to ecological applications ([Tucker and Duplisea, 2012](#)). Nevertheless, machine learning of ecological networks from large scale and diverse data sets remains a challenge for future research.

Logic-based and relational approaches, such as Abductive/Inductive Logic Programming (Abductive ILP; [Tamaddoni-Nezhad et al., 2006](#)), could be especially useful because: (i) links or interactions can be viewed as 'relations', and networks as a set of relations which can be naturally represented as logical relationships in ILP; (ii) the already known ecological information about any network or system, the 'given background knowledge', is typically incomplete; and (iii) ILP can learn 'cause and effect' relationship from agroecological data where there are many different types of data to juggle with. For instance, qualitative hypothetical link data types can be learned from quantitative observational data on species abundance. Most importantly, Abductive ILP can integrate these diverse data and background knowledge into a single network model ([Sternberg et al., 2013](#)).

Such an approach was recently used by [Bohan et al. \(2011a\)](#) to hypothesize a probabilistic network of trophic interactions from national-scale, farmland data. [Figure 1.6](#) shows a food web which was ‘learned from scratch’ using this machine-learning approach, and then evaluated by cross-validation on unseen test data. The results suggested a predictive accuracy of the network of $73.67 \pm 2.55\%$, measured as the proportion of correctly predicted test data, significantly higher than the default accuracy ($\sim 51.7\%$). The initial food web hypothesized by machine learning was also examined against the literature, which corroborated many of the learned trophic links. In particular, links ascribed with high probability by machine learning corresponded well with those most frequently reported in the literature. In some cases, potential novel links were suggested, which can then be tested in the real world: for instance, spiders were hypothesized to reside at the base of the food web as prey ([Bohan et al., 2011a](#); [Tammadoni-Nezhad et al., 2012](#)). While these animals are small, they are obligate predators and at least at face value this trophic position seems strange; however, this hypothesized position was correct according to subsequent empirical work, at least for part of the agricultural season ([Davey et al., 2013](#); [Tammadoni-Nezhad et al., 2013](#)).

[Bohan et al. \(2011a\)](#) and [Tamaddoni-Nezhad et al. \(2012, 2013\)](#) have highlighted the potential of computational approaches for generating plausible and testable networks from field sample data. This could be especially useful for dealing with large networks, such as those used in multi-network approaches ([Pocock et al., 2012](#)), because the full set of subsystems operating in the wider agroecosystem need to be considered in order to predict future changes. Interactions between many different entities in different conditions (protocols, crops, seasonal conditions, etc.) will need to be taken on-board even though they cannot always be directly observed. Exploiting readily available historical and experimental data could be used as a means of overcoming this bottleneck, by recovering or ‘learning’ the structure of network from which to generate network hypotheses for future testing.



6. CONCLUSION

We have attempted to cover some of the major current issues in agricultural research and how network ecology might support these goals. Agriculture needs to remain productive, but at less of a cost to the environment, so natural biodiversity in agroecosystems will need to be more effectively employed in the future. We need agricultural biodiversity to work harder

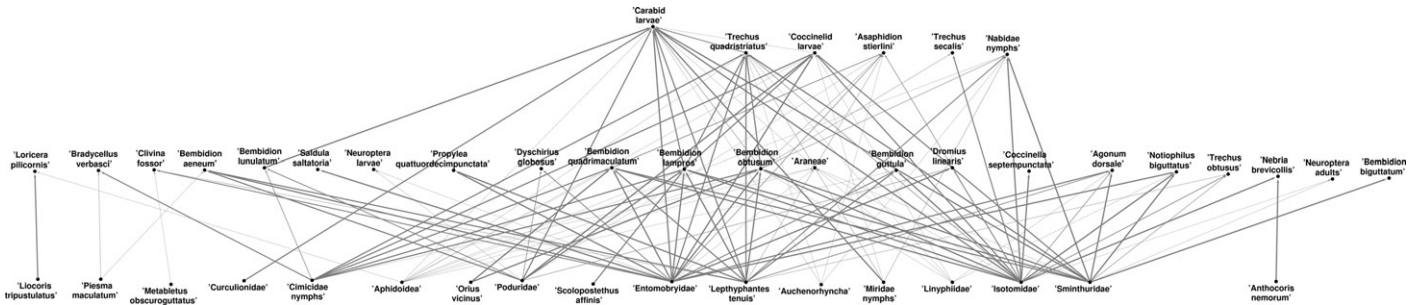


Figure 1.6 Hypothetical trophic network constructed by machine learning from Vortis suction sample data from the Farm Scale Evaluations data (Bohan et al., 2011a). The thickness of the trophic links represents probabilities, which are estimated from the frequency of hypothesis occurrence (Tamaddoni-Nezhad et al., 2012).

for us, ideally by augmenting the ecosystems services that naturally present diversity provides. It may be that provision of specific ecosystem services will be maximized through functionally important species (Gaston, 2010), such as honey bee pollinators (Calderone, 2012), but the *a priori* expectation is that maintaining resilient ecosystem services will require biodiversity to support ecosystem functioning (Naeem et al., 2009). It is here, by facilitating understanding and making predictions across the spectrum of individual traits—populations—species—communities—functions—ecosystem services, that network ecology will have its greatest impact on agriculture.

The network structure of agroecosystems can be evaluated using numerous metrics, and two broad groupings seem to emerge from different forms of network: modularity appears to be associated with antagonistic networks, while nestedness appears to be more common in mutualistic networks. Whether these different structures are real or are simply the consequence of sampling artefacts is still a point of discussion. This debate is important because many aspects of the expected performance of networks, whether measured as productivity or stability or resilience, are related to their structure. At present this is an area of network ecology where observation and empirical evidence still lag behind the available theory.

Agriculture's primary role is to deliver better crop yields, yet, except for a few notable studies in pollinator–plant networks, this measure is signally lacking from most agricultural network studies, and this shortcoming clearly needs to be addressed in future work. Management in agriculture is increasingly coming under scrutiny in an attempt to avoid perceived and real negative impacts on the environment. The current regulatory framework for 'plant protection products' offers clear scope for embedding network approaches in decision-making from the outset. The predictive aspect of these potential regulatory approaches also resonates with the wider need for more predictive network approaches. The benefits that these could bring to agriculture are exemplified by the multi-network approaches of Pocock et al. (2012) and Evans et al. (2013). They found that management and habitat influenced multiple ecosystem services simultaneously but differently, via the agricultural network, leading to the optimist's scenario of positive correlations among services being rejected.

Large-scale agroecological prediction is currently still limited by the number of networks available from different systems, due to financial and logistic constraints, although new methods of abstracting or learning agricultural networks from already available data could help to circumvent this problem. 'Network agroecology' clearly has a lot to offer at both practical

and philosophical levels. By bringing together people with different skills from across ecology, agriculture and other applied sciences, it offers an approach that is inherently much richer and more multidisciplinary than the classical autecological approach to agriculture. New research areas will inevitably open up as this emerging field matures and engages with critical agricultural questions, including: how are agroecological networks structured relative to their natural counterparts; how do ecosystem services 'emerge' from ecological functions within the network; how does network performance change with scales in time and space; and can networks be used predictively, to design systems that maximize pest control or crop yield? There is much to be learned by working more closely with general ecology and other network-based disciplines, but agroecology can also offer fundamental new insights in return: after all, agriculture itself is the longest-running and largest ecological experiment on the planet.



APPENDIX A. MIGRATION AND INTERACTIONS AMONG POPULATIONS

Spatial networks of populations offer us an opportunity to introduce network-related definitions in a practical context. First, let us consider a metapopulation network defined by a symmetric adjacency matrix \mathbf{A} , a colonization rate c and an extinction rate e . The probability that patch i is occupied is defined by time-dependent variable p_i and the probability that patches i and j are occupied at the same time is q_{ij} . In general, the dynamics of p_i are described by:

$$\frac{dp_i}{dt} = c \sum_j a_{ij} [p_j - q_{ij}] - ep_i \quad (\text{A1})$$

q_{ij} can be construed as the sum $p_i p_j + k_{ij}$ where k_{ij} is the covariance between the occupancies of patches i and j . Under the mean-field approximation (i.e. assuming zero correlations between neighbouring patch states) and when the species is rare at the metapopulation scale, Eq. (A1) yields the following criterion for persistence (Adler and Nuernberger, 1994; Gilarranz and Bascompte, 2012; Hanski and Ovaskainen, 2000):

$$c\lambda_{\mathbf{A}} - e > 0 \quad (\text{A2})$$

where $\lambda_{\mathbf{A}}$ is the dominant eigenvalue of the adjacency matrix.

Second, when describing a spatially structured population of a given species through its local stock in patch i as N_i , if the intra-population dynamics in patch i are described by growth function r_i , the dynamics of population i are given by:

$$\frac{dN_i}{dt} = r_i[N_i]N_i + \sum_{j \in \Delta_i} d_{ij}N_j - \left(\sum_{j \in \Delta_i} d_{ji} \right) N_i \quad (\text{A3})$$

where d_{ij} describes the diffusion rate from patch j to patch i , and Δ_i denotes the set of all patches connected to patch i through migration. If we note \mathbf{D} the diffusion matrix, \mathbf{R} the diagonal matrix such that $r_{ii} = r_i$, and \mathbf{B} the diagonal matrix defined by $b_{ii} = \sum_{j \in \Delta_i} d_{ji}$, then the matrix-form equivalent of

Eq. (A3) is given by:

$$\frac{d\mathbf{N}}{dt} = \mathbf{R} \cdot \mathbf{N} + \mathbf{D} \cdot \mathbf{N} - \mathbf{B} \cdot \mathbf{N} \quad (\text{A4})$$

Introducing the Laplacian matrix of the network as $\mathbf{L} = \mathbf{B} - \mathbf{D}$, this can be simplified to:

$$\frac{d\mathbf{N}}{dt} + \mathbf{L} \cdot \mathbf{N} = \mathbf{R} \cdot \mathbf{N} \quad (\text{A5})$$

which is the equivalent, in a discrete, network world of the classical diffusion partial differential equation in a continuous world, for example, in one dimension:

$$\frac{\partial n}{\partial t} + D \frac{\partial^2 n}{\partial x^2} = m \quad (\text{A6})$$

where D is the diffusion rate.



APPENDIX B. REFERENCES FOR FIG. 1.3

The network was drawn with Pajek (Batagelj, V. & Mrvar, A. *Pajek—Program for Large Network Analysis*. <http://vlado.fmf.uni-lj.si/pub/networks/pajek/>).

Drawings of animals in Fig. 1.3 are solely for illustration and not intended to be specific species that were identified. Drawings were used under a ClipArt ETC Paid Commercial License (<http://etc.usf.edu/clipart>). The source of each image (numbered anti-clockwise from the mouse) is:

1, 13: Chambers, W. & Chambers, R. (1881) *Encyclopaedia—A Dictionary of Universal Knowledge for the People* (Philadelphia, PA: J. B. Lippincott & Co.)

2: Cuppy, H.A., ed. (1895) *Beauties and Wonders of Land and Sea* (Springfield, OH: Mast, Crowell & Kirkpatrick)

3: Figuier, L. (1869) *Reptiles and Birds* (London: Cassell, Petter and Galpin)

4–8, 11: Whitney, W.D. (1911) *The Century Dictionary: An Encyclopedic Lexicon of the English Language* (New York, NY: The Century Co.)

9: Emmet S. Goff and D.D. Mayne, *First Principles of Agriculture* (New York: American Book Company, 1904)

10: Goodrich, S.G. (1859) *Animal Kingdom Illustrated Vol. 2* (New York, NY: Derby & Jackson)

11: Mathews, F.S. (1902) *Field Book of American Wild Flowers* (New York, NY: G. P. Putnam's Sons)

12: Smith, J.B. (1896) *Economic Entomology* (Philadelphia and London: J.B. Lippincott Co)

GLOSSARY

Basics

Bipartite and tripartite networks A network is said to be bipartite if nodes can be put in two disjoint groups so that edges only connect nodes from different groups (i.e. there is no within-group links). It is tripartite if there are three disjoint groups. For instance, a plant–pollinator network is bipartite, while a plant–herbivore–parasitoid network is tripartite. Analysis of bipartite networks is well developed, especially within ecology. Analysis of tripartite networks is less well developed and usually is done on the individual, stacked bipartite networks.

Connected components A group of nodes is connected if every node can be attained from every other node within the group through existing paths. Connected components of a network are the maximal sub-networks that are still connected.

Connectedness web A graphical form of food web based on three variables: the number of species, the average interaction strength and the connectedness according to binary interacting elements (either $C=0$, no interaction, or $C=1$, interaction).

Edge/link An edge or link connects two nodes in a network. An edge can be undirected (the connection goes both ways) or directed (one way). In the case of energy pathways, directed links represent the elemental flux; in the case of mutualistic networks, a pair of directed links represents an interaction with mutual benefit, such as in the case of plant–pollination syndromes; in the case of classical (i.e. trophic) food webs, directed links go from the prey/resource to the predator/consumer.

Loop A loop is an edge connecting one node with itself. An unweighted undirected graph without loops is said to be a simple graph.

Motifs Motifs refer to patterns of edges among a given number of nodes. For example, dyadic motifs refer to the set of all possible arrangement of directed (or undirected) edges between two nodes. Motifs are most often studied in directed networks (e.g. triadic motifs in food webs; [Stouffer et al., 2007](#)).

Node/vertex A node or vertex represents an individual component of a graph, for example, a species in a species–species interaction network such as a food web or a plant–pollinator network.

Path A path is a set of successive edges connecting one node to another one.

Unipartite network A network is said to be unipartite if nodes cannot be put in disjoint groups within which there is no interaction. For instance, a classical (multi-trophic) food web is often treated as being unipartite, although if trophic levels are distinct and the number of them is low, then they are often treated as stacked bipartite networks. Much of network analysis outside of ecology is based on unipartite networks.

Weighted and unweighted A network can either be unweighted, in which the links are present or absent, or weighted, in which the links are weighted by some measure of interaction strength (often interaction frequency). Using network metrics that specifically take account of the weighted nature of the links can be less susceptible to sampling biases, for example, because they put emphasis on the frequent interactions.

Ecology

Ecological amplitude The maximal range of environmental conditions within which a certain kind of organisms or taxa may occur.

Functional web A description or analysis of a food web focused on the potential to process energy by prey and predators. This food web focuses on the actual extent of functional differences among all the species occurring in a community. Functional diversity is mostly inferred from the number of functional groups, a set of organisms similar in their contribution to a specific process, activity or property of a given ecosystem.

Interaction strength Once a trophic link between two species has been established, the interaction strength has to be assigned from a specified distribution. Strong interactions (and an increased connectedness) are typical for a small community but are rare, as the most widespread interactions in nature are weak. Weaker interactions permit a much greater number of species to coexist in space. Therefore, it is difficult to estimate the interaction strengths of species in space and time, especially in the case of mutualistic networks. Food webs that include interaction strength in their algorithm show compartmentalization.

Predator–prey ratio Also known as consumer–resource ratio, is used in very different ways. Although the predator–prey body–mass ratio is the most used index, other indices, such as the predator–prey body–size ratio, the numerical abundance ratio, the biomass ratio and the diversity ratio (the latter in the case of lumped, i.e. size-structured nodes with more taxa with similar body mass) are used as well, but less frequently than the body–mass ratio.

Preferential species Organisms whose abundance strongly fluctuates although they show a greater deal of vigour under a given management regime, in a certain type of soil or within specific elemental (C:N:P) stoichiometric ranges.

Prey preference We have chosen for the assumption that every kind of predator has a constant, independent probability of feeding on every kind of prey in a given food web. If this parameter is not kept constant, the resulting model predicts the prey preference for a

given species in that food web. When a predator shares a common resource with its prey, an intraguild predation occurs.

Redundancy A measure of the extent to which species occurring within a given functional group or ecosystem are (partially) substitutable.

Resilience The speed at which a given ecosystem returns to its original state after a disturbance and the degree to which the ecosystem is capable of self-organization. More generally, when applied to ecosystem services, it is the speed at which a given ecosystem returns to a state with a similar level of functioning (even though species composition may have changed). Care needs to be applied because 'resilience' has also been used to refer to what is defined as 'resistance' (see below).

Resistance The extent to which a given ecosystem keeps its original state during an external disturbance. In the case of an unstable ecosystem, this measure of ability can be seen through time as persistence.

Trophic cascades These occur where predators in a food web regulate or control the abundance or traits of their prey, thereby releasing in turn the organisms at the next trophic level down from predation or herbivory.

Edge-wise properties

Edge betweenness The betweenness of an edge is defined as the sum, over all pairs of nodes i, j in a connected component, of the ratio of the number of shortest paths between nodes i and j that pass through the focal edge to the total number of shortest paths linking these two nodes (Freeman, 1978). This is an index that goes from 0 (nearly no nodes on one side of the edge) to 1 (two nodes only).

Matrices

Adjacency matrix A network can be represented through an adjacency matrix \mathbf{A} . The individual element a_{ij} of the adjacency matrix represents either: (i) in unweighted networks, $a_{ij}=1$ if there is a link going from node j to node i , or 0 if there is no such link; (ii) in weighted networks, a_{ij} is the weight associated with the link going from node j to node i . A network is undirected if and only if its adjacency matrix is symmetric.

Incidence matrix In bipartite undirected graphs, nodes can be put in two sets S_1 and S_2 . The incidence matrix is a simplified matrix representation of the adjacency matrix that accounts for the fact that $a_{ij}=0$ whenever i and j are drawn from the same S_k . The incidence matrix \mathbf{Z} is thus a $|S_1| \times |S_2|$ matrix defined implicitly by the representation of the adjacency matrix when elements are reordered so that the first $|S_1|$ elements are in $|S_1|$ and the remaining $|S_2|$ elements are in $|S_2|$:

$$\mathbf{A} = \begin{pmatrix} \mathbf{0} & \mathbf{Z} \\ \mathbf{Z}^T & \mathbf{0} \end{pmatrix} \quad (1)$$

Laplacian matrix In simple graphs, Laplacians (or Laplacian matrices) are matrix representation of a diffusive process along a given network. If matrix \mathbf{B} is the diagonal matrix of the degrees of each node, the Laplacian matrix \mathbf{L} is simply:

$$\mathbf{L} = \mathbf{B} - \mathbf{A} \quad (2)$$

The generalization of this definition to directed graphs uses out-degrees as matrix \mathbf{B} (see Appendix A, Eqs (A3)–(A5)).

Network-wise properties

Assortativity When nodes are labelled or valued with a categorical or continuous variable, assortativity is a measure of the similarity in labels/values between connected nodes (Newman, 2003). A natural discrete variable to measure assortativity onto is the degree of the nodes (Newman, 2002). Assortativity is in general measured through a correlation coefficient based on the probabilities that edges connect different categories, or nodes with different values (Newman, 2003).

Connectance/density Connectance (or density) measures the proportion of edges that exist in relation to the number of edges that can potentially exist (Wasserman and Faust, 1994). For obvious reasons, connectance is not well defined for weighted networks.

Global clustering coefficient The global clustering coefficient is simply the average of the clustering coefficient of all nodes within the network.

Modularity The grouping of nodes in the network into modules. Modules are defined as consisting of nodes that are well connected to other nodes within modules, but less well connected to nodes in other modules. Given the knowledge of a network's modules (i.e. some groups of nodes), modularity Q is a score that is based on the density of links within modules when compared to their expectation under a random assignment of links (Newman, 2004, 2006; Newman and Girvan, 2004; White and Smyth, 2005):

$$Q = \frac{\sum_i \sum_j \left[a_{ij} - \frac{\left(\sum_k a_{ik} \right) \left(\sum_k a_{kj} \right)}{\sum_k \sum_l a_{kl}} \right] \delta_{ij}}{\sum_i \sum_j a_{ij}} \quad (3)$$

where $\delta_{ij} = 1$ if and only if nodes i and j belong to the same module. This definition can even be extended to graphs that have negative edge weights (Traag and Bruggeman, 2009).

Nestedness A network is said to be perfectly nested if there is some reordering of vertices complying with the fact that node $i + 1$ can be connected to node j only if node i is connected to node j . Such a reordering must follow an ordering of vertices by decreasing degree. In bipartite networks, many different indices has been proposed to measure nestedness (Almeida-Neto et al., 2008; Atmar and Patterson, 1993; Baselga, 2012; Carvalho et al., 2012; Fortuna et al., 2010; Podani and Schmera, 2012; Ulrich and Gotelli, 2007; Ulrich et al., 2009), but the lack of formal definition of the concept makes it difficult to agree on a good general measure of nestedness. Recently, Staniczenko et al. (2013) have proposed that the spectral radius of the adjacency matrix could be used as a good proxy for nestedness.

Radius The radius of a graph is the minimum eccentricity among its nodes.

Scale-free network A network is said to be scale-free if its degree distribution follows a power law. Scale-free networks are 'ultrasmall', that is, they have typical path lengths even shorter than expected under the small-world property (Cohen and Havlin, 2003).

Small-world network A network is said to be a 'small-world' network if the expected path length between two random nodes is proportional to the logarithm of the total number of nodes in the network (Watts and Strogatz, 1998).

Node-wise properties

Centrality A general term that refers to one of various measures of the ‘importance’ of the node within the network. See ‘Eigenvector centrality’, ‘Closeness centrality’ and ‘Betweenness centrality’.

Clustering coefficient In unweighted graphs, for a node of degree k , its clustering coefficient is defined as the proportion of the $k(k-1)/2$ nearby edges (between two nodes that are connected with the focal node) that actually exist (Watts and Strogatz, 1998). A generalization of this formula for weighted graphs does exist (Barrat et al., 2004). The definition of clustering is ambiguous when the network has loops.

Closeness Closeness, or closeness centrality, is a measure of a node centrality given by the inverse of its average distance to other nodes within the graph (Freeman, 1978; Sabidussi, 1966).

Connectivity/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.

Eccentricity The eccentricity of a given node is the maximum value of the length of a shortest path to another node within the same connected component. In other words, eccentricity measures the distance between a given node and the node farthest to it.

Eigenvector centrality In an undirected graph, the eigenvector centrality of a node is defined by the corresponding element of the scaled eigenvector associated with the dominant eigenvalue of the adjacency matrix. This eigenvector has only nonnegative components (thanks to Perron–Frobenius theorem). In directed graphs, two alternative measures of centrality as being ‘a passage point’ for information to flow through the network have been designed. Kleinberg (1999) has defined the notions of hubs and authorities as the equivalent of eigenvector centrality for $\mathbf{A} \cdot \mathbf{A}^T$ and $\mathbf{A}^T \cdot \mathbf{A}$. By contrast, Bonacich and Lloyd (2001) have defined α -centrality as the vector \mathbf{x} that solves

$$\mathbf{x} = \alpha \mathbf{A} \mathbf{x} + \mathbf{e} \quad (4)$$

where α quantifies the balance between endogeneous and exogeneous processes in the determination of centrality and the vector \mathbf{e} is the vector of externally supplied centrality.

Node betweenness The betweenness of a node k is defined as the sum, over all pairs of nodes i, j in a connected component, different from the focal node ($i \neq j \neq k$), of the ratio of the number of shortest paths between nodes i and j that pass through the focal node to the total number of shortest paths linking these two nodes (Freeman, 1978). Betweenness takes values between 0 and 1.

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