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REVIEW

ECOLOGICAL NETWORKS IN AGROECOSYSTEMS: APPROACHES AND APPLICATIONS

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KEYWORDS

bipartite network, co-occurrence network, food web, network theory

HIGHLIGHTS

- Agricultural intensification reduced the complexity and connectance of soil food webs.
- Agricultural intensification impaired the robustness of pollination networks.
- High connectance in co-occurrence networks indicates efficient nutrient utilization.

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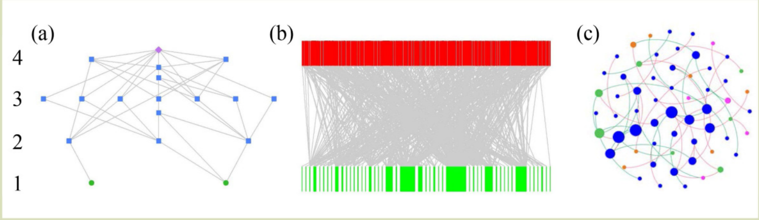
GRAPHICAL ABSTRACT



ABSTRACT

Complex network theory has been increasingly used in various research areas, including agroecosystems. This paper summarizes the basic concepts and approaches commonly used in complex network theory, and then reviews recent studies on the applications in agroecosystems of three types of common ecological networks, i.e., food webs, pollination networks and microbial co-occurrence networks. In general, agricultural intensification is considered to be a key driver of the change of agroecosystems. It causes the simplification of landscape, leads to the loss of biocontrol through cascading effect in food webs, and also reduces the complexity and connectance of soil food webs. For pollination networks, agricultural intensification impaired the robustness by reducing specialization and enhancing generality. The microbial co-occurrence networks with high connectance and low modularity generally corresponded to high efficiency in utilization of nutrients, and high resistance to crop pathogens. This review aims to show the readers the advances of ecological networks in agroecosystems and inspire the researchers to conduct their studies in a new network perspective.

1 INTRODUCTION

The productivity, stability and sustainability of agroecosystems is crucial in maintaining the growth and development of human societies[1]. The functions of agroecosystems are largely determined by their structures, which consist of large number of interspecific interactions. These interactions form complex networks are important in matter cycle and energy flow[2]. Therefore, studying the structure of ecological network can help us further understand how natural communities are assembled and maintained, and how ecosystem functions respond to global change by altering the structures[3]. For example, food webs describe the plant-herbivore or prey-predator interactions between species[4]. Pollination networks, which is one of the bipartite networks, describe the interactions between floral plants and pollinators[5]. Microbial co-occurrence networks describe the correlations between microorganisms[6]. To analyze the structures of these networks, we need to employ the complex network theory (or graph theory in mathematics). The studies of ecological networks can be traced back 50 or more years[7,8]. At the beginning of this century, the studies on complex network theory entered an outbreak period and involved many research areas, such as traffic networks[9], social networks[10] and even the dispersal networks for COVID-19[11]. With the development of the complex network theory, ecological networks have also been well studied[12–14]. In the context of ecological agriculture, the maintenance of species diversity and the application of biological interactions have received increasing attention, and many studies in agroecosystem research have begun to use network tools. There are certain differences between agricultural ecosystems and natural ecosystems. A timely summary of the application of the ecological networks in agriculture may help subsequent research to avoid problems discovered by predecessors and develop in new directions.

In this review, we firstly summarize the basic concepts and analyzing approaches used in complex network theory. Then we focus on three types of networks widely used in agroecosystems: food webs, pollination networks and microbial co-occurrence networks. We describe relevant construction methods and analysis tools. Finally, we review the applications of these three types of networks in agroecosystems. We expect our readers to be inspired by this work and gain new insights into agroecosystems at the view of networks.

2 BASIC CONCEPTS AND APPROACHES

Table 1 summarizes the basic concepts which are commonly used in network analyses. An adjacent matrix, which contains all the pairwise interactions, is the base of further analyses. In addition to an adjacent matrix, the other concepts can be divided into three groups: the network-level characteristics, the node-level characteristics, and the substructure characteristics.

Table 1 Summary table of the concepts in complex network theory

Concept	Equation	Description
Adjacent matrix	$A=\left[a_{ij}\right]$	A matrix describing a finite graph, in which its element a_{ij} indicates the relationship from the ith node to the jth node
Network size	S	Number of nodes in the network
Connectance*	$C=L/S^2$	The proportion of realized links over all possible links. L means the total number of links in the network
Nestedness	–	The tendency for nodes to interact with subsets of the interaction partners of better-connected nodes[15]
Robustness	R_{50}	The number of primary removel needed to attain 50% of node loss[16]
Modularity*	$Q=\frac{1}{4m}\sum_{ij}\left(a_{ij}-\frac{D_iD_j}{2m}\right)s_is_j$	The fraction of the edges that fall within the given groups minus the expected fraction if edges were distributed at random. Here m is the total number of edges. $s_i=1$ if the ith node belongs to group 1 and $s_i=-1$ if it belongs to group 2[17]
Centrality	–	A measure describing the importance of nodes, including degree centrality, betweenness centrality and closeness centrality
Degree	$D_i=\sum_j a_{ij}+\sum_j a_{ji}$	Number of links connected to the ith node
Closeness	$C_i=1/\sum_j d_{ji}$	A measure describing how close on average of the ith node to the other nodes. Here d_{ji} is the shortest path length from the jth node to the ith node
Betweenness	$B_i=\sum_{v\neq i\neq j}\frac{\sigma_{vj}(i)}{\sigma_{vj}}$	A measure describing the probability the ith node located in the shortest path from one node to another node. σ_{vj} is the number of shortest paths from the vth node to the jth node, and $\sigma_{vj}(i)$ is the number of shortest paths from the vth node to the jth node which go through the ith node
Motif	–	Simple patterns of interconnections from which networks are built[18]
Rich core	–	A subgroup of nodes which have high degree and are well-connected with each other[19]
Compartment	–	Also known as cluster, module or community in graph theory. Usually a network can be divided into several compartments, which are subgroups of nodes. Within compartments, nodes are well connected, and between compartments, nodes are rarely connected[20]

Notes: *, the corresponding equations for connectance and modularity in the table are used only for unipartite networks (such as food webs and co-occurrence networks), but not suitable for bipartite networks (e.g., pollination networks).

The network-level characteristics, includes network size, connectance, nestedness, robustness and modularity. Each of these describe an aspect of the whole network structure. Connectance measures the complexity of the network; nestedness measures how specialists interact with subsets of the species with whom generalists interact[15]; robustness measures how the network is robust to node loss[16], which is a kind of stability; and modularity measures the strength of division of a network into compartments[17].

The node-level characteristics are mostly about centrality, which is generally used in ranking nodes by their importance. Degree, closeness and betweenness are commonly used indices of centrality. To compare the efficiency of different centrality indices, numerical experiments of sequential node removal (e.g., from the node with the highest degree) need to be conducted to record the secondary node loss after each primary node removal. In this way, the robustness of a network resistance to sequential node loss can be calculated and compared. The sequence which leads to the lowest robustness should be the best indicator of node importance[16].

From local to global structure, we have listed three indices of substructure characteristics: motifs, compartments and rich-cores. Motifs are the basic blocks forming the whole network, including tritrophic food chains, exploitative competition, apparent competition and intraguild predation (Fig. 1(a))[18]. Compartments are subgroups of taxa in which strong interactions occur within the subgroups and few weak interactions occur between them. Rich core of a network describes a subgraph which shows high density of connections (Fig. 1(b)), which is important in maintaining ecosystem stability and functioning[4]. An example of compartmentalization of the food web in Chesapeake Bay ecosystem[21] is shown here (Fig. 1(c)). Modularity, as we have mentioned, is a measure of strength of compartmentalization.

There are three commonly used networks in agroecosystems: food webs, pollination networks, and co-occurrence networks. All these networks could be analyzed or visualized in R package “igraph”[22,23]. Food web is a directed network with its nodes as the species or taxon and its links as the predatory or consuming interactions. Qualitative food webs only define whether there are interactions between taxon whereas quantitative food webs contain the information of interaction strength, which could be consumption rate or matter/energy flow[16]. In analysis of food webs, some indices (e.g., modularity and nestedness) are related to food web stability, and are mainly used to identify the ecological niche of organisms. Indices, such as degree and other centrality indicators, are used to identify keystone species[24]. In addition to “igraph,” there are another two other R packages that could be useful: “cheddar”[25] and “enaR”[26]. Both were designed to analyze food webs, with the former focusing on food web structures, body size and abundance, and the latter on energy flow analysis. We provide an example of a soil food web in Lovinkhoeve Experimental Farm[27] visualized by “cheddar” in Fig. 2(a).

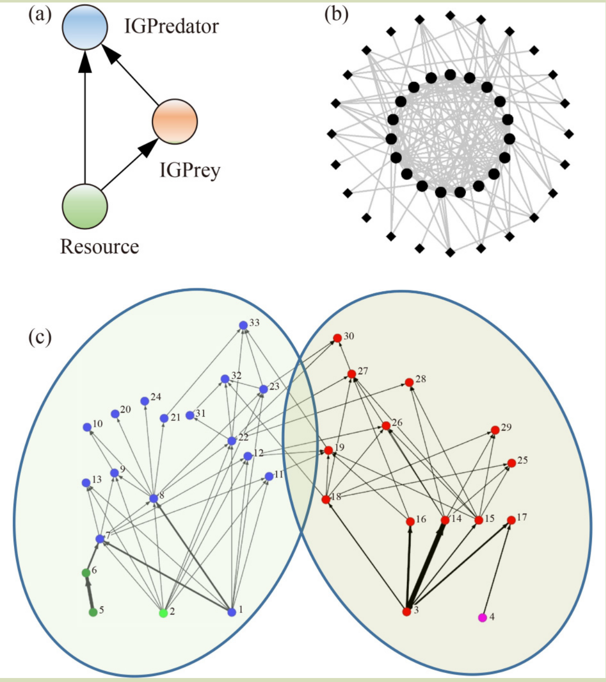


Fig. 1 Substructures of networks: (a) a special motif: intraguild predation; (b) the core-periphery structure; and (c) a network consists of two compartments.

Pollination network is a kind of bipartite network, which contain two types of entities. It is a reciprocal network which directly describes biological interactions between plants and their pollinators[28]. The stability and functioning of pollination networks can affect crop yields. Generally bipartite networks can be analyzed and visualized with R package “bipartite”[29], as shown for the pollination network in Norwood Farm[30] (Fig. 2(b)). In pollination networks, connectance can reflect the network generality. High connectance usually corresponds to high network generality. Nestedness, which describes the core of the interaction between plants and pollinators, is also interpreted as a niche attribute. It reflects the extent of specialists interacting with generalists. Interaction diversity describes the complexity of relationships in the system[31]. Degree distribution, nestedness and degree asymmetry are related to network size. Nestedness and degree asymmetry increase as the network size increases whereas the

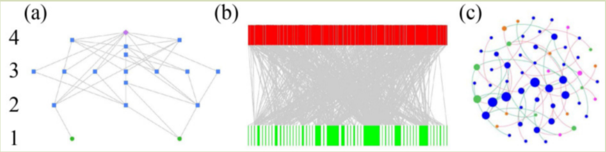


Fig. 2 Three types of networks: (a) a food web in which the green nodes indicating producers and detritus, the blue nodes indicating consumers, and the red node indicating the top predator; (b) a pollination network with the bottom level as plants and the top level as pollinators; and (c) a co-occurrence network with nodes as OTUs (different colors indicates different taxa) and links as correlations (red for positive ones and green for negative ones).

truncation of the degree distribution becomes more pronounced as the total number of species in the network and network core decreases[32].

The relationships of pairwise microorganisms are usually analyzed using co-occurrence network. To generate a co-occurrence network, the abundance of each species in many samples needs to be known. Then the pairwise correlation can be calculated based on these abundances. If a correlation between a pair of species is significant or its strength is higher than a threshold value, a link between these two species is made. If the process is repeated for all pairs, a co-occurrence network can be generated. We provide an example of fungus co-occurrence network sampled from Quzhou, China, visualized by Gephi program (Fig. 2(c)). In co-occurrence networks, centrality indicators were largely used to indicate the key nodes[33,34]. However, some studies argued the value of centrality indicators is exaggerated[24]. Modularity has been widely used to divide microbes into distinct groups[35]. Motifs frequently occur in gene metabolic networks and can be used to identify key regulatory factors[36]. The existence and function of motifs in microbial networks remains speculative, but studies have shown that they can be used at least as biomarkers[37].

The interspecific interactions directly affect the matter cycle and energy flow in the ecosystem, and the network structure largely determines ecosystem functions, including productivity, temporal stability, robustness and matter turnover. For example, primary production, as measured by the total nutrient uptake of a multitrophic community, is largely determined by vertical diversity of food webs[38]. The increase in network specialization and modularity of pollination networks is conducive to successful pollination[39]. The degree of specialization of plant-fruit-bird interaction networks drives large-scale seed dispersal processes[40]. Analysis of soil co-occurrence network showed that bacteria, rather than fungi, protists or invertebrates, were the hub nodes of the network (highly correlated with other nodes), and the richness of the hub nodes was positively correlated with various ecosystem functions such as nutrient cycling and plant productivity[41]. Soil multitrophic network complexity enhances soil biodiversity and enhances ecosystem function in agricultural systems[42]. The correlation network constructed based on structures and ecological functions, showed network vulnerability and modularity have great influence on community diversity, and average degree and link density largely influence ecological functions[43].

3 APPLICATIONS IN FOOD WEBS

Food webs provide an important research method that unify community structures and ecosystem functioning by combining multiple aspects such as species abundance, community composition, matter circle and energy flow[44]. Agroecosystems include two subsystems, the aboveground ecosystem and the belowground ecosystem. Aboveground food webs have an important impact on crop yield, quality and return of organic matter to field, and belowground food webs are responsible for important ecological processes such as decomposition, circulation and nutrient mineralization[45].

Aboveground food webs are mostly of concern for the biological control of pests, which are largely determined by some anthropogenic factors, such as farmland management and agricultural intensification. Increased intensity of farmland management leads to decline of seed biomass and energy, which further substantially decreased the potentially pest-controlling parasitoids through cascading effect in food webs[46]. The increase in non-crop plant diversity by habitat management in or around arable land, as well as plant phenology, had no effect on food web structures, but affected the parasitism rate of parasitic wasps to aphids, which in turn facilitated the conservation biological control of parasitoid populations[47]. Agricultural intensification could alter biological control by simplifying landscape and changing food web complexity. The simplification of landscape caused by agricultural intensification also led to the loss of biocontrol within agroecosystems, which further led to an increase in pest outbreaks[48]. A study of the response of cereal aphids and their natural enemy to landscape simplification using quantitative food webs found that with landscape simplification, the number of parasitic wasps increased and the number of ground predators decreased. The varied response of the three natural enemies may lead to large fluctuations in natural enemy-pest ratios, which disrupted the top-down control of natural predators[48]. A comparison of the complexity of aphid-parasitoid-hyperparasitoid food webs with different degrees of intensification showed that agricultural intensification simplified landscape structures, decreased parasitism rates, released top-down effect on aphids and increased complexity of aphid-parasitoid food webs, which leads to complex response in ecosystem functioning[49,50].

Belowground food webs have received much attention for their important function in many ecological processes. For example, soil food webs provide a large number of biological control services[51], affected the dynamics of carbon[52] and nitrogen[53] in soil, and largely affected soil health[54]. Interactions between organisms in soil food webs are a key determinant of soil functioning[55]. In soil food webs, the degree of omnivory is important for maintaining community stability[56]. Generally, agricultural intensification leads to a decrease in trophic group diversity, reduced the abundance of soil fauna such as earthworms and beetles, and reduces the complexity and connectance of soil interaction networks[57,58]. In an irrigated maize agroecosystem, the negative impact of long-term conventional agricultural management on the function and structure of soil food webs outweighed the impact of limited irrigation and short-term biochar amendment did not mitigate the negative impact of long-term agricultural management[59]. In semiarid agroecosystems, organic management did not perform better than standard management in terms of soil properties and soil food web structure[60]. However, under greenhouse conditions, organic management enhanced the biomass and complexity of soil food webs[61]. Other managements may also have substantial impact on soil food webs. For example, reducing tillage and covering crops had greater impact on soil food webs than organic matter input, pesticides, and mineral fertilizers[62,63].

Aboveground and belowground food webs are highly connected with each other. Belowground decomposers increased the nutrient supply and facilitated growth of plants as well as modulating the plant-herbivore interactions[64]. Active microbes and healthy soil food webs were important safeguards for crop yields[55]. Aboveground management (e.g., grazing) could also alter belowground communities. Aboveground grazing altered composition of plant species, and thereby altered the composition of belowground microbial/microfaunal communities and supported a longer belowground food chain[65]. Grazing reduced the associations between functional groups of soil food webs, weakening the correlation between soil food web and soil carbon and nitrogen mineralization[66]. Long-term grazing experiments have shown that even mild grazing had significant negative effects on plant communities and the composition of soil food webs, and the addition of nitrogen and water has an inconsistent effect on soil fauna and microorganisms[67]. For Tibetan Plateau meadows, moderate grazing increased the abundance and structural complexity of microbial food webs in soil, and increases herbivore and fungal abundance[68].

Many scholars have proposed that it is important to understand aboveground and underground ecology to evaluate how the interactions between plants and natural enemies, symbiotes and decomposers affect species diversity and response to global change. If network analysis is properly used, it can be a powerful tool to advance above-belowground research[69]. At present, studies on connections between aboveground and belowground systems have largely focused on the impact of aboveground plant change on belowground communities and the release of nutrients from the belowground food webs to promote plant growth. As a natural connector, plants are essential for the coupling of aboveground and belowground food webs. However, few studies have explored the coupling of these two types of food webs, especially for agroecosystems. However, it has been shown that agricultural intensification exerted influence on aboveground and belowground food webs separately, but it is still unclear whether the coupling of these would be undermined or strengthened by agricultural intensification or other anthropogenic activities. This should be a priority topic in future research.

4 APPLICATIONS IN POLLINATION NETWORKS

The research on pollination networks in agriculture study is mostly related to agricultural intensification[70–73], land use types[74–76], agricultural landscape restoration[77,78], biodiversity conservation[79] and the construction of agroecological networks[5,80].

As one of the most important anthropogenic disturbances to ecosystems, agricultural intensification has a clear impact on the structures and ecosystem functions of pollination networks. Reductions in habitat quality and landscape heterogeneity lead to species loss and reduction of network nestedness, and these structural changes reduce the robustness and resilience of plant-pollinator networks, thereby compromising plant reproductive success, biodiversity maintenance and stability of pollination services[81]. Many researchers consider that the transformation of biological habitats to agricultural land and the high-intensity management of intensive agriculture are not conducive to the robustness of pollination networks and the maintenance of biodiversity, which is caused by the reduction of the specialization level and the enhancement of the generality[76,79] and connectance[70,71,79] in pollination networks. For example, study of hummingbird-plant interaction networks in tropical regions have found that the transition of habitats to agricultural land leads to a decrease in the interaction diversity and species diversity and an increase in the level of generality[76]. Parra-Tabla et al.[79] suggested that agricultural pollination networks might be fundamentally different from natural pollination networks. They observed that agricultural pollination networks were highly connected and generalized, but not nested nor compartmentalized, and an increase of connectance could reduce robustness of the network[79].

However, some studies have also found agricultural land cover were positively correlated with generality and robustness to extinction in pollination networks. Reduction of plant species which are vulnerable to extinction and increase of pollinator generality promotes network robustness. In contrast, persistent features in agricultural landscape may be beneficial for resistance to disturbance[82]. Although some studies have drawn different conclusions on the stability of pollination networks due to agricultural intensification, most studies are more supportive of reducing the intensity of management of farmland for sustainable agricultural development[75].

Analyses of pollination networks could help in proposing suggestions on protecting pollinators. For example, wild bees are important for agroecosystems and need to be protected. Though some crops are highly dependent on domesticated bees, relying on single species makes ecosystem fragile and unstable. In fact, the pollination services provided by wild bees are sufficient to achieve high agricultural yields in many agroecosystems[75,83]. Therefore, crop planting structure should be adjusted to adapt to the local wild bee community to gain high-quality and sustainable yield. For this to be realized, the first step is to conduct an investigation and analysis of the local pollination network. For example, the analysis of pollination networks by Vilhena et al.[84] suggests that some non-crop plants that support wild bees should be planted near crops, and natural land should have enough nesting resources for bees to enhance their diversity. Also, Russo et al.[83] suggested that the matching of plant and pollinator phenological stages needs to be carefully considered.

Recent studies have analyzed hybrid networks to comprehensively explore the structure of both mutualistic and antagonistic networks[73,85]. Hybrid networks are a combination of pollination network and another type of network (e.g., prey-predator networks and parasitic networks). For example, the analysis on plant-pollinator-predator network shows that environmentally friendly practices maximize the representation of mutualistic and predation motifs whereas intensive agriculture favored generalist and intraguild predation interactions[73]. A study of 16 hybrid herbivore-plant-pollinator networks with over 15,000 interaction observations shows that agricultural intensification decreases modularity but increases nestedness and connectance, but counterintuitively an increase in connectance can led to a decline in hybrid network robustness[71]. Comparing mutualistic and antagonistic networks in response to anthropogenic disturbance, the mutualistic networks were consistently more nested whereas the antagonistic networks were consistently more modular. Also, interaction turnover in the mutualistic networks was largely caused by partner switching, and interaction turnover in the antagonistic networks largely contributed to species turnover[72].

In agricultural landscape restoration and biodiversity conservation, many researchers believe that increasing the abundance of plants is crucial in order to establish or restore pollination networks[74,75]. Subsequently it becomes possible to restore the diversity of corresponding pollinators[75], diversity of interactions[74], network size[74] and robustness of pollination networks[71], and to provide pollination services and other functioning of ecosystems. To restore plant abundance, first local generalized species should be chosen[78]. LaBar et al.[77] suggested that reintroduction of a group of highly-connected generalized species could efficiently restore species richness in mildly disturbed communities. However, for communities with severe biodiversity loss, the introduction of diverse species from outside that did not originally exist in the local community may be most effective in restoring species richness, though the restored community often shares few species with the original community[76]. A 10-year study on restored hedgerows and unrestored field margins within an intensive agricultural landscape showed that florally diverse sites and generalist, small-bodied bee species were most important for maintaining metacommunity connectance[80]. A study on the assembly of pollinator networks in agricultural landscapes found that the network locations of pollinator species were variable, inconsistent with the theory of preferential attachment, and more likely to be opportunistic attachment[5]. Theodorou et al.[86] suggested that providing rich floral resources in moderately urbanized areas could be beneficial for both bee richness and plant reproduction, because local land use markedly influenced plant and flying insect communities, and floral richness and bee richness were higher in urban compared to agricultural areas.

Overall, recent studies on pollination networks have largely focused on the response of topological structures to agricultural intensification, land use types and landscape restoration. A common conclusion is that disturbance would increase the generality and connectance of pollination networks, which increases the resistance of ecosystems to disturbance. Generalists are also crucial in the process of restoring local ecosystems. Recent studies extended the pollination networks into mutualistic-antagonistic networks, and analyzed the function of plants in pollinator-plant-herbivore network. This topic should be given priority in future research.

5 APPLICATIONS IN MICROBIAL CO-OCCURRENCE NETWORKS

With the in-depth study of various ecological problems, ecologists have gradually realized that many important interactions between plants occur underground. Plant roots, animals and microorganisms can determine where and how plant species grow. Soil microorganisms, including bacteria, actinomycetes, viruses, fungi, oomycetes and protozoa, are an important part of underground ecosystems. Their diversity is a key factor in regulating ecosystem functions[87], such as organic matter degradation and nutrient cycling[88]. Community structures of microorganisms are usually determined by interspecific relationships, however it is challenging to ascertain all interactions between species, considering the huge number of species in microbial communities and the complexity of relationships between them. With the widespread application of complex network theory, ecologists have begun to use networks to illustrate interspecies interactions, in which co-occurrence networks are often used to explore the interactions between species in microbial communities. Nodes in a microbial co-occurrence network usually represent microorganisms, and edges usually represent statistically significant associations between nodes[6]. Studies have found that modules in microbial co-occurrence networks can be related to habitat occupancy[89], and keystone species can be identified through the network analysis[90].

The importance of microorganisms in agroecosystems has received increasing attention. Soil microorganisms have a crucial function in the maintenance of productivity and soil health[91]. For crops, mycorrhizal and rhizosphere microorganisms can buffer the influence of pollutants and pathogens, and promote the absorption and utilization of nutrients[92]. Co-occurrence networks are a useful tool for revealing the mechanisms of structures affecting on functions in microbial communities.

Co-occurrence networks have been widely used in exploring the between-species relationship and the effect of crops on rhizosphere microorganisms. Analyses on co-occurrence networks found that fungi and bacteria in rhizosphere occupied different ecological niches, and the number of fungal modules was higher than that of bacteria[93]. Geographical distance was important for explaining the co-occurrence pattern of fungi, indicating the decisive role of dispersal limitation in the community assembly of fungi[93]. Different genotypes of lettuce had different co-occurrence networks of rhizosphere microorganisms, and most correlations were positive, indicating co-occurrence prevails over co-exclusion[94]. Compared with the co-occurrence networks of microbes in hazelnut root endospheres, the networks in rhizosphere soil had higher connectance and complexity and a more stable structure, although most relationships between the fungal community in root endospheres and rhizosphere soil were positive, indicating most fungi were mutually beneficial rather than competitive[95]. The modes of reproduction of plants can also affect rhizosphere microbial communities. Compared with the non-grafted grapes, the co-occurrence networks of rhizosphere microorganisms for grafted grapes showed higher complexity and stability, which may be beneficial to resist the stress of biotic or abiotic factors[96]. Comparing the rhizosphere microbial co-occurrence networks of inbred and hybrid maize, it was found that hybridization had a substantial impact on the rhizosphere microbial community structures[97].

Co-occurrence network analysis found that agricultural management patterns affected the community composition, structures, functions and potential resilience of rhizosphere fungi and bacteria[98]. For example, tillage patterns could affect the topological structures of rhizosphere microbial co-occurrence networks[99]. The number of connections between microorganisms decreased with the increase of the duration of monocropping (i.e., the interactions between microorganisms were weakened), and the number of nodes connecting different modules decreased, which might be an important reason for the problems of monocropping[99]. In a study comparing pea-wheat intercropping and monocropping, it was found that the rhizosphere microbial network for intercropping was more complex, but the elucidating the underlying mechanisms of the positive effect of increased complexity on plant growth and nutrient utilization needed further research[100]. In the cassava-peanut intercropping system, root exudates altered keystone species in the peanut rhizosphere microbial networks, restructured the networks and improved the availability of nutrients, which led to increased yield[101]. After the application of rhizobia, the degree of association between peanut rhizobacteria increased, and the hub taxa changed, which changed the composition and structure of the rhizosphere bacterial communities, and thereby affected the assembly of peanut rhizobacterial communities[102]. The colonization of rice endophytic fungi increased the abundance of beneficial microorganisms in rhizosphere, which in turn improved the transformation and utilization of soil nutrients by rice[103]. The combined application of organic amendments and mineral fertilizers can increase the number of links in rhizosphere microbial networks of crops, and increase the abundance of beneficial microorganisms, thereby improving nutrient use efficiency and increasing crop yield[104,105].

In exploring the function of rhizosphere microorganisms in resisting root pathogens, co-occurrence network analysis found that the high abundance of *Ralstonia solanacearum* decreased the diversity of tomato rhizosphere bacterial community as well as the connections of co-occurrence networks, and reduced resistance to pathogens[106]. Verticillium wilt of olive had similar effects, with pathogen infection decreasing node connectance and the abundance of beneficial microorganisms whereas it increased the distance between nodes, the modularity, and the number of negative interactions[107]. Co-occurrence network analysis is an important tool in revealing the role of microbiota in biotic stress tolerance.

The concepts of modularity and connectance have been widely used and well explained in the literature on co-occurrence networks. However, some other topological traits (e.g., nestedness) have not been as well applied, so this should stimulate some further research. Research on microorganisms in agroecosystems has largely focused on rhizosphere and root endosphere microorganisms, and microorganisms in other organs have seldom been studied, even though they could have crucial functions. For example, the hub taxa in the microbial networks in wheat leaves were involved in plant growth and fitness[108]. Further studies on integrated networks of soil, rhizosphere and plant microbes may reveal unidentified microbial mechanisms in plant growth with potential applications especially in nutrient cycling and utilization, and design of planting crop combinations.

6 CONCLUSIONS AND PERSPECTIVES

In this review, we have summarized the basic concepts and approaches in complex network theory, and recent advances of applying ecological networks in agroecosystems, including food webs, pollination network and microbial co-occurrence networks. In general, robust networks have high complexity and connectance, which can provide crucial ecological services (e.g., biological control, ecological restoration, and resistance to crop pathogens). However, network structures can be easily altered by anthropogenic activities, including agricultural intensification, landscape alteration and grazing. Considering that cascading effects can impact entire networks, it is important to treat the agroecosystems as a whole in agricultural practice and conduct research with a network perspective.

In general, most studies have focused on how network structures and functions change with agricultural drivers, such as landscape simplification and agricultural intensification, but have rarely explored how to improve or restore network structures to enhance biodiversity and functions in agroecosystems. This is partly because of the complexity of ecological networks which makes the whole network is difficult to manipulate. Therefor we recommend that biomanipulation measures should be attempted first on keystone nodes, which could then be detected using centrality indices using complex network tools. This would need well-designed experiments to test the function of keystone species by changing their abundance or even removing them. In this way, if could be possible to determine how these keystone species maintain the network structures and the agroecosystem functions.

Another question to be answered is how different types of networks combine with each other to reveal currently unidentified mechanisms in agroecosystems. For example, as we have described, some recent studies have combined pollination and herbivory networks to define mutualistic-antagonistic networks[85], which has led to some novel perspectives. Consequently, it could be informative to explore how altering of one type of network (e.g., a pollination network) affects the structure and functions of another type of networks (e.g., a food web). This is feasible because all types of networks occur in the same agroecosystem and some nodes overlap in different types of networks. For example, a pollination network and the soil food web may be linked through plants, and the combination of the two may help us understand the interaction between aboveground and underground ecosystems, which could provide a basis for improving agricultural production.

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Compliance with ethics guidelines

Ying Gong, Langqin Yu, and Lei Zhao declare that they have no conflicts of interest or financial conflicts to disclose. This article does not contain any studies with human or animal subjects performed by any of the authors.

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