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Ramirez, K.S.; Geisen, S.; Morriën, E.; Snoek, B.L.; van der Putten, W.H.

DOI

[10.1016/j.tplants.2018.06.009](https://doi.org/10.1016/j.tplants.2018.06.009)

Publication date

2018

Document Version

Final published version

Published in

Trends in Plant Science

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[Link to publication](#)

Citation for published version (APA):

Ramirez, K. S., Geisen, S., Morriën, E., Snoek, B. L., & van der Putten, W. H. (2018). Network analyses can advance above-belowground ecology. *Trends in Plant Science*, 23(9), 759-768. <https://doi.org/10.1016/j.tplants.2018.06.009>

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Opinion

Network Analyses Can Advance Above-Belowground Ecology

Kelly S. Ramirez,^{1,*} Stefan Geisen,^{1,2} Elly Morriën,^{1,3}
Basten L. Snoek,^{1,2,4} and Wim H. van der Putten^{1,2}

An understanding of above-belowground (AG-BG) ecology is important for evaluating how plant interactions with enemies, symbionts, and decomposers affect species diversity and will respond to global changes. However, research questions and experiments often focus on only a limited number of interactions, creating an incomplete picture of how entire communities may be involved in AG-BG community ecology. Therefore, a pressing challenge is to formulate hypotheses of AG-BG interactions when considering communities in their full complexity. Here we discuss how network analyses can be a powerful tool to progress AG-BG research, link across scales from individual to community and ecosystem, visualize community interactions between the two (AG and BG) subsystems, and develop testable hypotheses.

Linking Across Scales in AG-BG Ecology

Terrestrial ecosystems are structured by the many interactions between AG and BG subsystems [1–3]. Plants are the link between the two subsystems, connecting herbivores, pathogens, mutualistic symbionts, and their natural antagonists to the soil and rhizosphere communities belowground. It is this myriad of linkages that altogether are expected to influence biodiversity and ecosystem functioning under current and future environmental conditions [4–8]. In the past, research was carried out with model species of herbivores and their antagonists. But research is now moving from known species interactions between a few species to many multiple species interactions where many species (especially microbial) remain unknown. In order to make progress, it will be important to observe species assemblages to which plants are exposed, both belowground and aboveground, in the field. These species assemblages may contain thousands of taxa and in order to advance the field we must assess how the composition of these assemblages may respond to environmental changes (e.g., CO₂, N deposition, climate warming, extreme events, land use changes, etc.). Here we argue that network approaches may be helpful in characterizing not only the composition of the assemblages, but also their structure.

For **AG-BG interactions** (see [Glossary](#)), the scale at which we study a system strongly determines how we view those interactions ([Figure 1A](#)). At the individual level, direct specific interactions are most often studied. For example, mutualistic symbiotic or antagonistic relationships are often studied in relatively simplified systems (e.g., where a single plant species is grown with a single or several AG and BG herbivores) [9,10]. Some studies have additionally manipulated aboveground tritrophic or multitrophic interactions and the soil community in the greenhouse [11,12] or used biocide experiments in the field [13]. From these small-scale, high-resolution experiments, much mechanistic knowledge has been gained on herbivory and plant defenses [14], herbivory and decomposition [15,16], and multitrophic interactions [12,17,18].

Highlights

In spite of the current proof of concept that aboveground and belowground (AG-BG) organisms interact, research questions and experiments often focus on only one level of interactions (e.g., individual, community, or ecosystem), creating an incomplete picture of how species between subsystems interact.

Advancing the field requires the ability to incorporate AG-BG linkages between all members and fluxes of a system into our knowledge of presence/absence, abundance, and community structure.

Networks analyses, which are used in both above and belowground systems, offer a way to link between the two subsystems.

These approaches are particularly relevant for linking the microbial and macrobial world; for assessing the functional consequences of AG-BG interactions in changing ecosystems; and for predicting effects of global changes.

¹Department of Terrestrial Ecology, Netherlands Institute of Ecology (NIOO-KNAW), P.O. Box 50, 6700 AB, Wageningen, The Netherlands

²Laboratory of Nematology, Wageningen University, P.O. Box 8123, 6700 ES, Wageningen, The Netherlands

³Institute of Biodiversity and Ecosystem Dynamics, Department of Ecosystem and Landscape Dynamics (IBED-ELD), University of Amsterdam, P.O. Box 94248, 1090 GE Amsterdam, The Netherlands

⁴Theoretical Biology and Bioinformatics, Utrecht University, Padualaan 8, 3584 CH Utrecht, The Netherlands

*Correspondence: k.ramirez@nioo.knaw.nl (K.S. Ramirez).

At the same time, community and ecosystem level approaches are more inclusive in scope. Studies at these levels can include species interactions, resource flows, functional traits, and large-scale processes that result from AG-BG interactions (e.g., carbon fluxes, nutrient cycling, and decomposition) [3,19,20]. These studies highlight the importance of AG-BG interactions for maintaining community structure and ecosystem functions, yet give little indication of the nature of the underlying interactions occurring at the individual species level. Along the path from individual to ecosystem-level study is a gradient of increasing system complexity (more interactions and players), yet a decreasing ability to discern mechanisms. While much knowledge has been gained from studying AG-BG interactions at individual [21], community [13,14], and ecosystem [22–24] levels independently, progress in the field has slowed. The combined knowledge is important for our basic understanding of terrestrial ecology and to predict variations due to the ongoing change in global climate [19,25,26] and other global changes in land use and species distribution patterns.

Network Analysis of AG-BG Interactions

There are a wide range of methods available to explore AG-BG interactions, and maybe the most difficult step is choosing an analysis that accommodates both the research questions and the data collected. **Network analysis** is only one type of analysis that allows for combining AG-BG information, but we highlight it here because its versatility with complex data has potential for advancing the field (Table 1). The most familiar **network types** used in terrestrial systems are flow networks (such as food webs) and structural equation models (SEMs). Food webs are used to show energy flows between individuals [27,28] while SEM-type networks are used to test the strength of predicted interactions [29]. Both flow and SEM networks are targeted approaches and have the ability to directly test relationships between organisms; they are stronger if interactions between species are known *a priori*.

One specific network type which has recently gained popularity in ecological studies is based on correlations [30,31]. Correlational networks are more flexible, allow for untargeted exploration of the data, are particularly good at exploring unknown organisms or unknown functions, and can accommodate many data points (such as molecular data from next-generation sequencing) and data types [32]. At an even finer resolution, there has been much advancement in using networks to study plant organization from the cell to the whole organism [33] and to evaluate gene coexpression [34]. The application of correlation network analyses at the interface of AG-BG research has the potential to identify species relevant to community composition and functioning, and to indicate ecosystem transitions. We see correlational networks as a new step in understanding species interactions from small to large scales. To illustrate this point, we constructed a series of correlation networks from a well-known study [35] (Box 1), but acknowledge that this could be illustrated with any number of datasets. For instance, this could be used to further assess herbivore and nematode interactions in Arctic systems [36,37] or to link ecosystem multifunctionality to network topology [38]. Overall correlational network analyses can be used as a tool to link the many types of AG-BG species data (morphological and molecular, relative and absolute abundance, taxonomic and functional data) with environmental (abiotic) and process measurements.

A number of other network analyses have been developed in fields outside of ecology and have potential to be applied to AG-BG interactions. For instance, stochastic networks explicitly include the variation of interactions, and we envision this can be used to describe how interactions between plants and soil biota change over the growing season. Bayesian networks, like SEM models, require *a priori* knowledge but have more predictive ability and make them ideal for understanding resource dependencies. This can be helpful in conservation or

Glossary

AG-BG interactions: relationships between two or more species from both the soil subsystem (e.g., microbes and soil animals) and aboveground subsystem (e.g., herbivores and pollinators) and are often mediated by the plant.

AG-BG network: representation of the biotic and abiotic interactions between both above and belowground taxa and relevant environmental variables, often centered around a plant species or community.

Edge: a connection (line) between two objects (nodes), describing a parameter such as correlation, similarity, or function. Can link within and between subsystems.

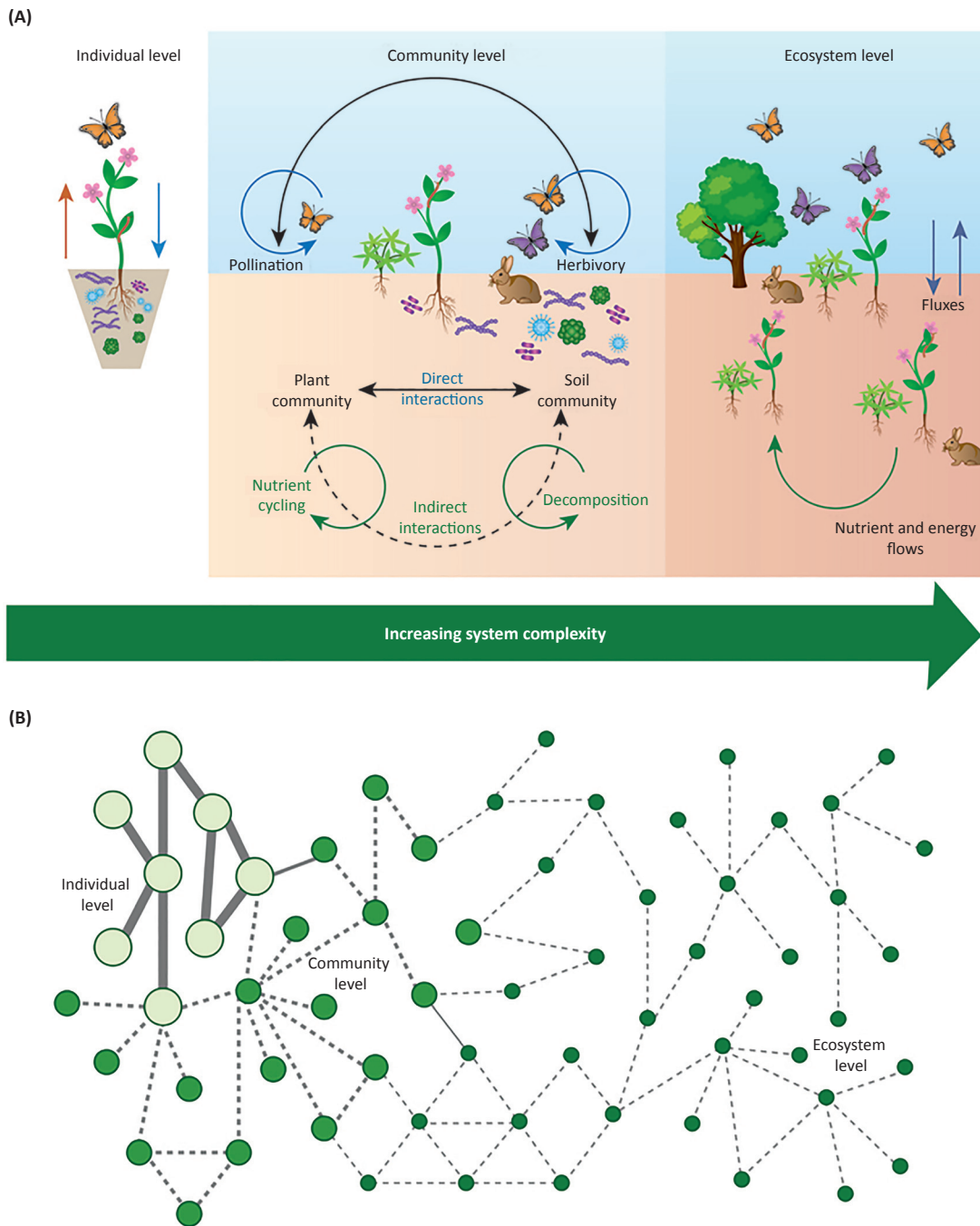
Network analysis: assessment of network structure. Can also be used to compare network structures to determine differences in entire systems.

Network structure (topology, clustering, nestedness, density, and connectedness): measures of the layout of objects (nodes and edges) in a network. Can be used to describe ecological parameters (i.e., stability), assess relatedness of groups/taxa, and describe species interactions. Often can provide a novel way to view AG-BG systems.

Network type: underlying mathematical models used to assess connections. This includes: flow, correlation, and SEM (see Table 1).

Network visualization: visualizing patterns in large data sets, by connecting objects (nodes) by their similarity (edges).

Node: an object in a network for which a relation with other objects is investigated (edges), such as an animal species, plant trait, abiotic factor, or sample site.



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Figure 1. Three Levels at Which Above-belowground (AG-BG) Interactions Can Be Studied. (A) There is often a tradeoff between what level AG-BG interactions are studied and the resolution of information acquired. At the individual level, focus is generally on targeted interactions between few organisms in a controlled study system; at the community level, studies are mostly more interested in many members of the community and interactions with the environment; and at the ecosystem level, changes in fluxes and processes are commonly studied in broad field studies. Along the path from individual- to ecosystem-level study is a gradient of increasing system complexity (more interactions and players), yet a decreasing ability to discern mechanisms, and it remains difficult to scale between these three levels of research. (B) Network analyses have the potential to link the many types of data across levels, resulting in nested knowledge relating individuals through community and ecosystems.

Table 1. Potential for Network Analyses in AG-BG Ecology^a

Network type	Description	Potential use in AG-BG ecology	Advantages/caveats	Refs
Correlation based	Correlation analyses based on a matrix of species abundances, diversity metrics, and/or measurements of other environmental variables.	To detect co-occurrences and to view connectivity in unknown AG-BG linkages.	Significance tested against randomized networks. Correlations are not necessarily biologically relevant.	[30,32,85]
Flow/transportation networks	A weighted directed graph in which the nodes are species, the edges are 'who eats whom' relationships, and the weights are rates of energy or nutrient transferred between species.	Can be used to show energy flows in food webs or nutrient transfers between AG and BG systems.	Suitable for energy and nutrient flows. Many replicates required.	[29,35,86]
Structural equation modelling (SEM)	The use of two or more structural [cause-effect] equations to model multiple processes operating in systems. Allows for an intuitive graphical representation of complex networks of relationships.	Can visualize how energy flows are structured within a food web.	Some SEM methods require many replicates.	[87–89]
Bayesian network	For reconstructing species interaction networks from observed field data. Enables robust inference of species interactions considering autocorrelation in species abundances and allows for variation in interactions across space.	To model environmental systems, conservation, and management when assessing influence of environmental parameters on species interactions. Could be highly relevant in AG-BG global change studies.	Ideal for modelling resource dependencies in a food web. However, they can only solve directed acyclic graphs.	[48,90,91]
Stochastic networks	When assessing network topology allows for inclusion of variation in known relationships.	Besides usage in metapopulation and metacommunity calculations, it has potential to include stochastic interactions and processes in AG-BG systems, such as mutualisms.	Can also be used for food web analyses with random dot-product graph models.	[27,54,92,93]

^aNetwork analyses can be applied in many AG-BG scenarios. Choosing a network should be based on research questions. Here we highlight a few key examples and indicate where the field can be developed. For example, there is much potential to use stochastic networks to predict how interactions change across space and time.

management of AG-BG systems as Bayesian methods can better predict how interactions might change. In all cases, network analyses are a tool to bridge spatial and temporal scales to assess species interactions, and this may be particularly relevant under climate change and other global change factors.

Opportunities and Possible Caveats

The utility and versatility of networks explains why 'network ecology' has increased fivefold over the past 20 years and is now a commonly applied technique in terrestrial ecology [39]. Network analyses and visualization can include many types of data sources, are flexible at scaling across space and time [40,41], and can accommodate the dynamic nature of biological interactions [42]. Arguably, major advances in ecology could not have been made without some creative uses of network analyses. For example network modularity was recently used in combination with targeted indicator analyses to search for interacting functional groups, such as plant pathogenic microorganisms [43]. Another emergent function is the use of network topology to assess ecosystem resilience and stability. As explained by Thébault and Fontaine [44], **network structure**, such as connectivity and nestedness, informs about community stability. While results between studies are inconsistent, valuable information has been gained regarding plant communities and nutrient use efficiency [41], as well as host-parasitoid relationships and system functioning [45]. Similarly, networks can be used to reassess well-known ecological concepts like species area relationships [46]. Networks can also be used to bridge disciplines, as shown in a recent innovative use, to simultaneously assess ecological and evolutionary

Box 1. The Versatility of Network Analyses

Here we visualize the data from Scherber *et al.* [35] using a nontargeted correlational network (Figure I). In that experiment, plots were sown for five diversity levels, with species richness of 1, 2, 4, 8, and 16 plant species per plot. Then a range of measurements were recorded, including abundance and diversity of both above- and belowground organisms, plant traits, abiotic factors, and biological processes. This dataset was kindly shared as a means to visualize possible network analyses that may be performed and is not intended as a reanalysis of the previous approach.

In AG-BG interactions where many unknowns persist, correlation networks are a potentially strong tool to explore connections in a system [94]. The AG-BG network analysis gives an overview of the data that can be used to create a *priori* hypotheses that are then tested with future experiments. A correlation network can also give evidence for known ecological patterns and supports the idea that **nodes** with more connections are worthwhile to investigate [40]. Another strength of this analysis is that we can clearly visualize gaps in data. For example, in this data we can see that there are many more measurements collected aboveground than belowground. Likewise, many species abundance and diversity measurements were collected, but much less data have been collected on plant traits, abiotic, or process measurements.

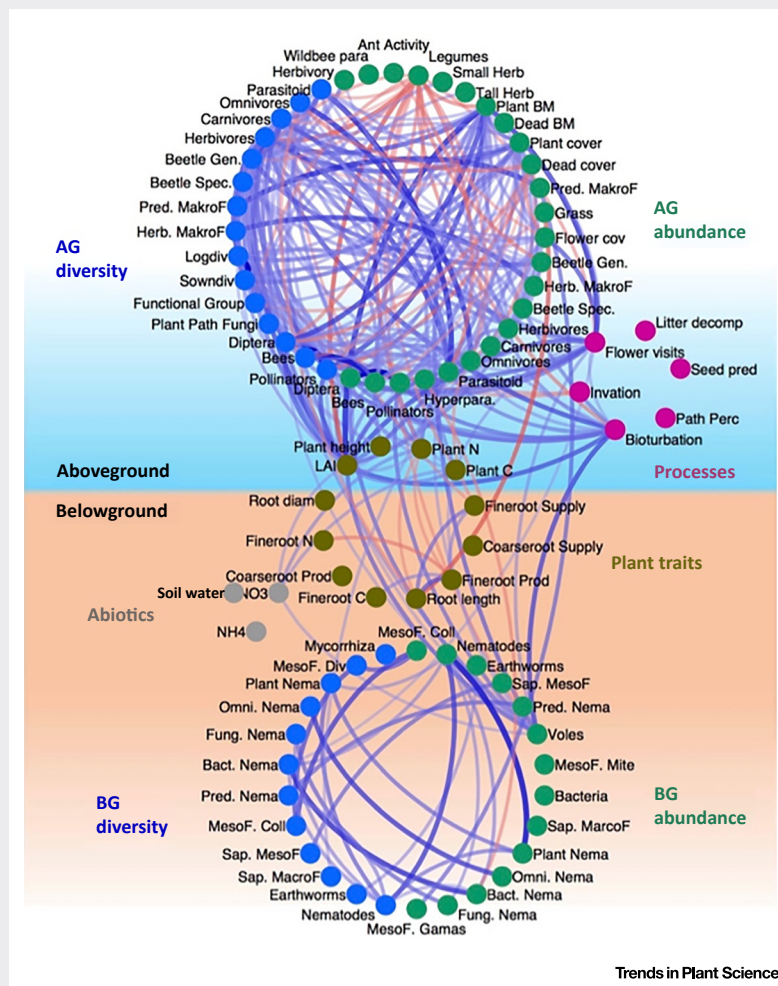


Figure I. Correlation Network for Visualizing Interactions between Above- and Belowground Systems. A visualization of relationships within and between above- and belowground subsystems, including species abundance and diversity, abiotic factors, plant traits, and other processes. Colored nodes represent the measurements taken in both the aboveground and belowground systems: species abundance (green) and diversity (blue), plant traits (brown), abiotic (grey), and process measurements (pink). The thickness and transparency of the edge designates the strength of the correlation (darker, thicker edges have higher correlation values). Positive correlations are colored blue, and negative correlations are red. Full names of parameters can be found in supplemental information online (Table S1).

As a secondary step, explored linkages between species of a known function and those of unknown functions (Figure II). Specifically, using the same Jena biodiversity data, we compared plots with ($n = 43$) and without legumes ($n = 39$) (Figure II). Legumes have long been known to have different physiological properties than other plants, such as grasses and therefore would also have different relationships with belowground communities [95] (and indeed in Scherber *et al.* [35], legumes were treated as a separate covariate). Here legumes provide an example of how the absence and presence of functionally different taxa can influence network connectivity.

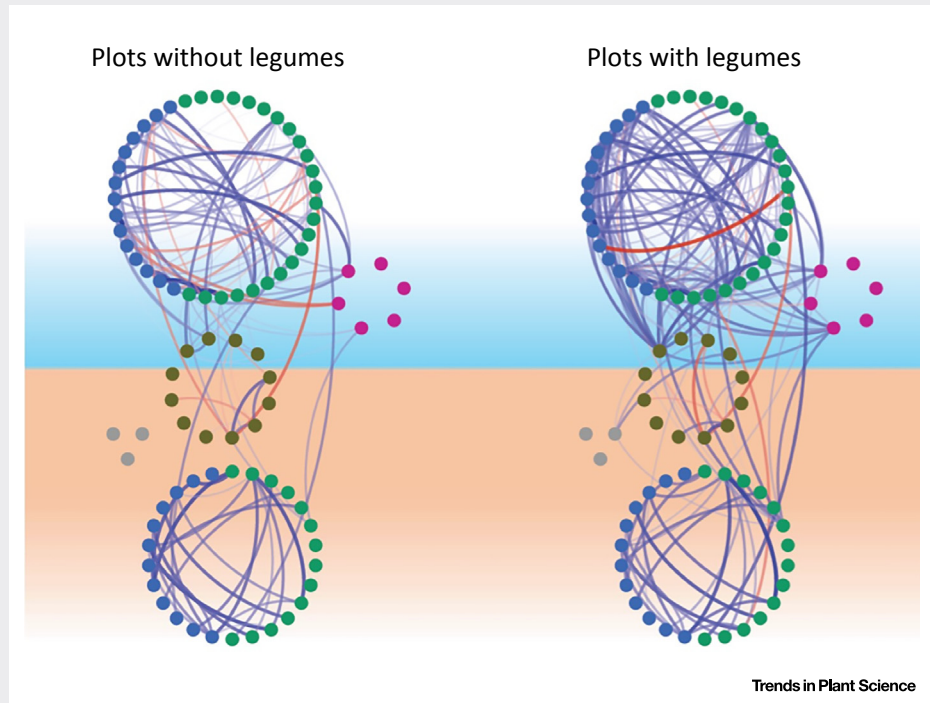


Figure II. Network Analyses for Exploring Function in Above-belowground (AG-BG) Interactions. Network visualization of plots with ($n = 43$) and without ($n = 39$) legumes. Plots with legumes have many more ground-AG-BG interactions when compared to plots with legumes. Plots without legumes had less connections (740 compared to 811), and perhaps more biologically interesting was that plots without legumes had many more negative connections than plots with legumes (without legumes, 254 negative out of 740; with legumes, 110 negative out of 811). As with Figure I, positive correlations are colored blue, and negative correlations are red. The thickness and transparency of the lines designate the degree of correlation (darker thicker lines have higher correlation values).

dynamics; by placing ecological and evolutionary information together in a single network, it can be possible to view real-time species dynamics [47,48]. Finally, networks will likely play a large role in management and sustainability of global systems. Most recently this was applied in agricultural systems, in which searching for valuable microbial communities linked to the growing plants [49].

While both AG and BG research disciplines are familiar with networks, analyses are rarely applied at the interface of AG-BG environments, with a few exceptions [35,50]. In aboveground systems, network analyses are frequently used to link across trophic levels, such as between predators and prey, or plants and pollinators [44,51,52]. For example, Valverde *et al.* [53] examined the temporal variation of pollinator communities using network topologies, and concluded that plant reproduction can be better understood when assessing their interactions with pollinators over the entire flowering season. Belowground, soil food webs may be the most recognizable network type [27,54], yet the strength of co-occurrence networks to explore community structure and functional potential of hyperdiverse communities has also been used to connect microorganisms [30,32,55–57].

As with most analyses, networks are not without caveats. For networks analyses, especially when large datasets are used, the number of significant linkages that can appear with the inclusion of many species can affect the structure of the network [58]. This will become a greater challenge as large molecular datasets are included [6,59]. Therefore, in addition to using informed, stringent cut-offs, networks are most suitable when compared between treatments or over environmental gradients, where the basic biodiversity is comparable while species assemblages, or correlations between species change. In those cases, comparisons between network topology may enable hypothesis generation on causes and consequences of differences in network properties. For a more complete review of ecological networks we recommend Pocock *et al.* [58] and Borrett *et al.* [39].

The Future of AG-BG Ecology

The future of AG-BG ecology research will involve large datasets collected from interdisciplinary research teams, will explore potential functional roles of known (and unknown) species, and will predict global change effects. When used properly, networks can be a powerful tool to scale between research approaches and advance research of AG-BG systems. Here we point out three areas where network ecology either has been used successfully or has potential to expand the field.

Big Data and the Phytobiome

Traditionally, the organisms of AG-BG systems have been studied with classical isolation and identification techniques such as extraction, culturing (in case of microbes) or rearing (in case of insects), followed by morphological identification. However, in the past decades a wide range of molecular techniques have been developed, most prominently high-throughput sequencing (HTS) [60,61], which have greatly advanced our knowledge of belowground species and genetic diversity both above- and belowground. For example, metabarcoding and other HTS sequence based 'omics' approaches are frequently used to characterize belowground microbial communities of bacteria, archaea, fungi, and protists [62–64]. While HTS is less frequently applied aboveground, there has also been a number of developments using molecular markers in insects [65] and the microbes of the phyllosphere [66,67]. Further, rapid developments in phytobiome research demonstrates advances can be made when data is merged across scales and subsystems [68]. Growth in novel molecular methods and large data will only continue [58–60]. Thus, advances in our understanding of AG-BG interactions must be interdisciplinary and must include input from many specialists in taxonomic groups and expertise across many ecological systems.

Functional Information

Regardless of the number of interactions research can uncover, without taking functional measurements these steps remain limited. Although few examples exist linking functional data across AG-BG systems, much work has been done on single subsystems or between individual plant and insect species [17] or plant and soils [69]. For example, in belowground systems labelled tracers have been used to quantify soil feeding relationships [70], and in aboveground systems, plant traits have been added to study pollinator networks [71]. If functional data cannot be collected, then it might be possible to use functional information already published and available, as done by García-Palacios *et al.* [72], who used plant traits to model decomposition rates. Belowground sequence information has been used to track traits and function [43,73]. Collection of functional data must be made a priority in future AG-BG studies, and then with network analyses it can be possible to link functions and known taxa to identify previously unknown functions associated with organisms.

Global Change

Data collected from both experimental and observational studies can be used to predict how changes will influence the spatial and temporal dynamics of a community, as well as consequences for AG-BG interactions and for ecosystem processes [74,75]. Networks can be used to indicate whether or not ecosystems are in transition [51,76,77] due to any number of global change effects: climate change, land use, or changes in species diversity. There is also potential scope for using network approaches for land management or for improving conservation or restoration efforts [78,79]. The applied value of networks might be best exemplified in agricultural systems where applied knowledge offer tangible outcomes like increased crop yield and improved ecosystem services [80,81]. For example, Macfadyen [82] and van der Heijden [83] observed differing network structures in organic versus conventional farming, suggesting that the stability of organic systems might be stronger and more resilient than conventional systems. Likewise, Pocock *et al.* [84] used a network approach to assess the fragility of pollinator systems and to give insight into the strength of different agricultural systems for restoration efforts. Networks will likely not provide linear solutions to the complex challenges facing our ecosystems, but instead can motivate hypotheses and direct research for predicting and responding to global changes.

Concluding Remarks

The integrity, stability, and functioning of terrestrial ecosystems is largely dependent on the myriad of interactions among and between species, and with the physical and chemical environment. Ecologists must walk a line between managing these large datasets and asking ecologically relevant questions. We see network analyses as a research tool to go across scale and time, connect organisms between aboveground and belowground subecosystems, to act as a bridge between microorganisms and macroorganisms. Network approaches enable exploring AB-BG interactions in their full complexity, thereby generating hypotheses that may be tested under specified controlled conditions. Beyond expanding primary research, we can use networks to explore and guide ecosystem restoration and sustainability, where a 'network' understanding will help to predict consequences of (human-induced) global changes and facilitate conservation and adaptation responses (see also Outstanding Questions).

Acknowledgments

The authors would like to thank Christoph Scherber and his colleagues from the Jena Experiment for use of the data to make the correlation networks. This study was supported by ERC Adv grant 26055290 (SPECIALS to W.H.v.d.P., and NWO-VENI grant to E.M.)

Supplemental Information

Supplemental information associated with this article can be found, in the online version, at <https://doi.org/10.1016/j.tplants.2018.06.009>.

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Outstanding Questions

What research developments must be made to increase functional knowledge of AG-BG interactions?

How can a better understanding of AG-BG interactions be used to improve agriculture?

Which fields outside ecology (e.g., genetics, engineering, and physics) can stimulate research of AG-BG interactions?

When can network analyses be used to predict global change scenarios?

How can we ensure network analyses are not used to overestimate interactions between species?

How can observed connections in hypercomplex and diverse systems be scaled from the population to the ecosystem level?

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