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Network Analysis: A Systems Framework to Address Grand Challenges in Plant Pathology

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Abstract

Plant pathology must address a number of challenges, most of which are characterized by complexity. Network analysis offers useful tools for addressing complex systems and an opportunity for synthesis within plant pathology and between it and relevant disciplines such as in the social sciences. We discuss applications of network analysis, which ultimately may be integrated together into more synthetic analyses of how to optimize plant disease management systems. The analysis of microbiome networks and tripartite phytobiome networks of host-vector-pathogen interactions offers promise for identifying biocontrol strategies and anticipating disease emergence. Linking epidemic network analysis with social network analysis will support strategies for sustainable agricultural development and for scaling up solutions for disease management. Statistical tools for evaluating networks, such as Bayesian network analysis and exponential random

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graph models, have been underused in plant pathology and are promising for informing strategies. We conclude with research priorities for network analysis applications in plant pathology.

INTRODUCTION

Network analysis offers a useful new perspective on key aspects of plant pathology and provides tools to help plant pathology address major societal projects (**Figure 1**). Operational challenges that can keep plant pathology from effectively addressing these societal goals include resource limitations, system complexity, and global economic inequality. These challenges can make it difficult for many people to access good plant disease management strategies. Network analysis can

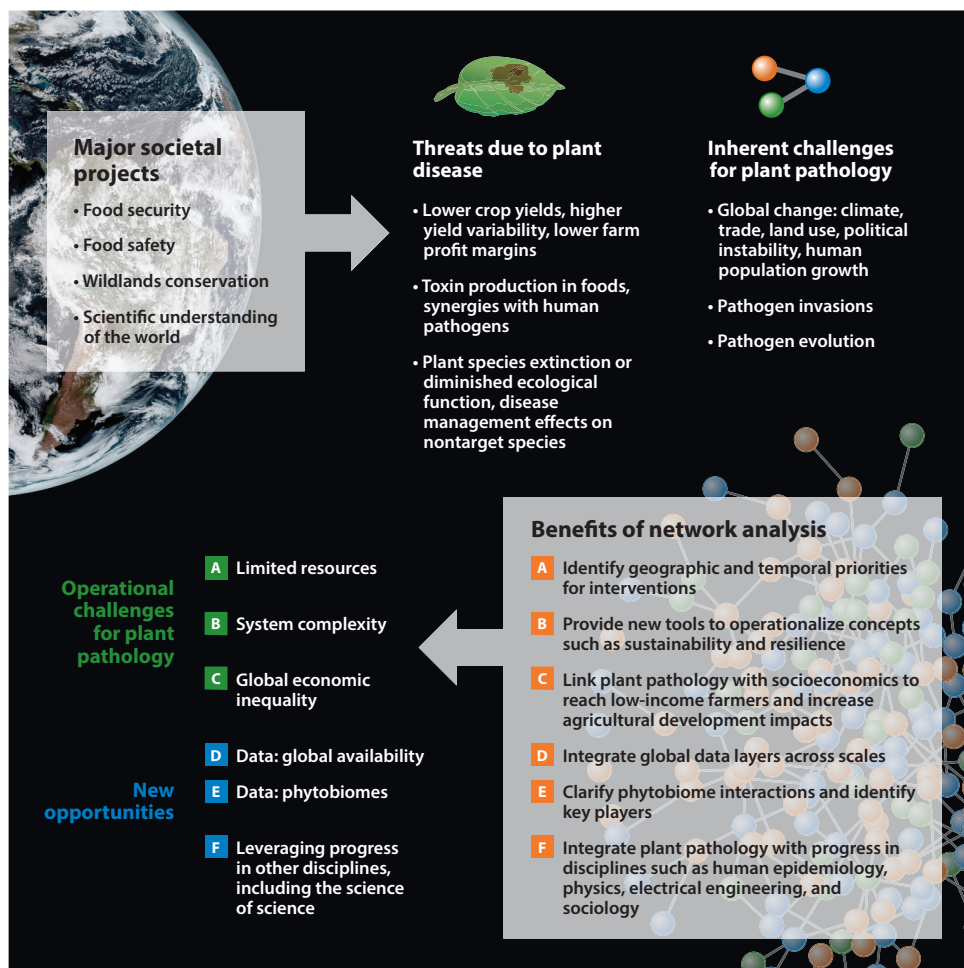


Figure 1

Challenges and opportunities for plant pathology and examples of how applications of network analysis in plant pathology can help address them. Image of the Earth courtesy of National Oceanic and Atmospheric Administration.

Table 1 Some networks important in plant pathology

Type of network	Nodes	Links	Example of questions that can be asked in analysis of this network
Gene	Putative genes	Associations, interactions, or upstream/downstream relationships	Which genes must be transcribed before others are transcribed?
Microbiome	Operational taxonomic units (OTUs)	Associations	Which OTUs have direct or indirect associations with important pathogens?
Host-vector-pathogen	Relevant host, vector, and pathogen species	Associations	What new diseases are likely to emerge in the region being characterized?
Epidemic	Plants, farms, and geographic areas	Potential movement of pathogens	Which nodes are key for epidemic management?
Collaborative	Scientists, extensionists, and farmers	Exchange of ideas and/or influence	Which people are inadequately linked to receive information through the network?
Trade	Businesses	Exchange of commercial materials and/or money	How can epidemic management be balanced with efficient trade?
Bayesian	Response and predictor variables	Association or predictive relationship	Which weather or other variables predict disease levels and yield loss?

address resource limitations by identifying key geographic locations for efficient implementation of sampling and mitigation. It can address system complexity by providing tools for operationalizing concepts such as system sustainability and resilience. And it can address global economic inequality by integrating socioeconomic network analyses with epidemic networks to support strategies for reaching farmers who are underserved by existing systems. Network analysis can also be used to help take advantage of new opportunities for plant pathology. It offers a suite of tools for making the most of new types of data, from microbiome data to multilayer global environmental and trade data. Excitement about networks in other disciplines is generating new tools and concepts that can benefit plant pathology, and network analysis is an attractive framework for developing synergies across subdisciplines within plant pathology, as we hope to demonstrate here.

Although the term network is often used casually to indicate a set of affiliated entities, here we discuss networks in the more formal sense of a group of nodes and the links between them. Nodes may represent entities ranging from genes to species to individual people to geographic locations (**Table 1**). Links may represent associations such as the tendency for species to occur together, communication between people, or potential pathogen spread between geographic locations. Nodes may be defined as more or less aggregated, depending on the goals of the study. For example, a node might represent a farm, a group of farms, all farms in a county, or all farms in a country, depending on the spatial resolution and spatial extent needed in a study (**Figure 2**).

The overall goal of this review is to introduce current applications of network analysis in plant pathology and the potential for new syntheses within plant pathology and among related disciplines. A number of stimulating reviews address network applications in plant pathology (e.g., 13, 102, 138, 160). Here, we focus on opportunities for understanding microbiome and phytobiome interactions, applications in epidemiology, agricultural development, systems such as seed networks, and methods for inference and scenario analysis.

HARNESSING NETWORKS OF INTERACTIONS

Species interactions are key to understanding and developing solutions for food security and food safety with reduced effects on nontarget species. New high-throughput sequencing technologies

Sustainability:

a system's ability to maintain a given state (such as a level of productivity) over time, usually considered in cases where the initial state is desirable

Resilience: a system's ability to return to a given state (such as a level of productivity) after perturbation, usually considered in cases where the initial state is desirable

Spatial resolution:

the number of pixels evaluated per spatial unit, where more pixels correspond to higher resolution

Spatial extent: the size of a spatial area being considered, often in terms of a bounding rectangle

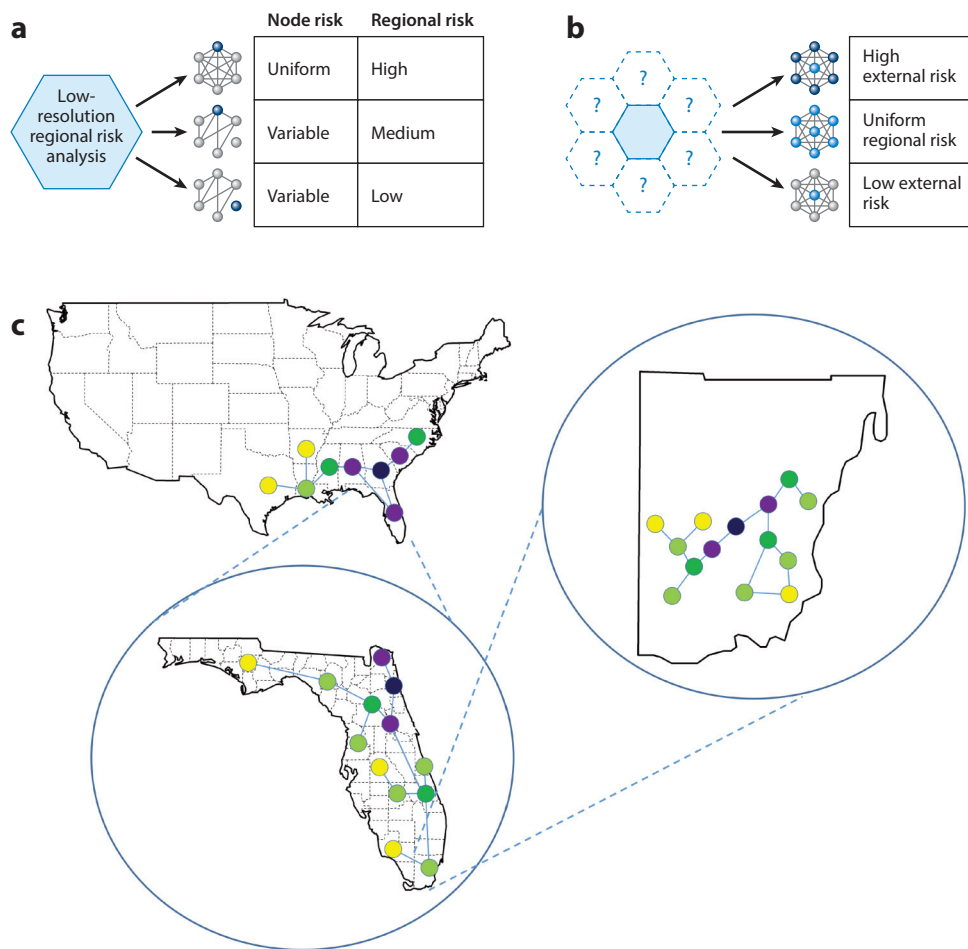


Figure 2

Potential benefits from increasing spatial resolution and spatial extent in network analyses. (a) In a low-resolution regional risk analysis for disease, an assessment of moderate risk (*homogeneous light blue hexagon*) provides some useful information. Higher-resolution understanding of the epidemic network structure can reveal how risk at specific locations within the region varies as a function of the network structure and the position of the point of introduction of a disease (*dark blue node*) within the network. Links represent a high probability of movement between nodes (geographic locations) within the region being analyzed. In this example, three different levels of regional risk may be revealed under a higher-resolution analysis. The risk to uninfected nodes (locations) is uniform when all nodes are linked but is variable when some nodes are more isolated from the initial infection. (b) Similarly, a small-extent (small geographic area) analysis of risk may be improved by understanding the larger network structure of which the region is a part. (c) Higher resolution and greater extent can be combined in multiscale networks, where networks at one scale are integrated into nodes at another scale. In this example, farms are nodes inside a county node, county nodes are inside a state node, and state nodes are observed across the southeastern United States. Darker shading of nodes indicates earlier infection during a pathogen invasion. This illustrates a hypothetical transmission route for the causal agent of laurel wilt, *Raffaelea lauricola*, at multiple scales (123).

are a major opportunity for understanding microbial interactions, although understanding of the functional roles of taxa lags behind. New microbial sequencing databases make it possible to consider microbial conservation, with all its challenges (62), and provide a baseline for understanding the effects of global change. These new types of data and associated analyses offer great opportunities for leveraging food web theories developed for macroflora and macrofauna and the risk of disease emergence (6), with the potential to incorporate genomic information to inform functional relationships.

Critical

transitioning: abrupt shift of a system from one state to a very different state

Microbiome Networks

The state of a microbiome is often evaluated in terms of diversity measures, as a proxy for processes and functional interactions (136). Microbiome networks capture more features of microbial systems, where network nodes represent taxa and links represent positive or negative associations between taxa across samples (**Table 1**). Microbiome network analyses include descriptions of general community structure (11, 45), host performance (139), host-microbe ecological interactions (32, 47), and identification of key nodes or topologies such as hub nodes, connectors, and module hubs (64, 159). Association-based network models have been applied to explore the mechanisms of host-microbe interactions, community structures, and microbial dynamics (1, 32, 60, 139). Understanding microbiome structures and their implications can enhance more broadly our understanding of coevolution (8, 79) and health (84).

Understanding plant-microbe network structures also offers promise for enhancing plant productivity and management of diseases, pests, and weeds. Understanding networks that include as nodes not only microbial taxa but also host responses (48, 125) can inform the design of disease-suppressive soils, plant microbiomes, and, potentially, communities to reduce food safety risks from mycotoxins (134). More progress in designing management will be made as empirical studies confirm the biological and ecological function of key taxon nodes (1). Incorporating community functionality, such as networks supporting bacterial quorum sensing (108), will expand possibilities for new types of disease management.

Challenges for translating the results of microbiome network analysis into disease management strategies include the inherent limitations of current sampling and sequencing approaches (125) and the potential for extreme variability across relevant scales (154). Recent microbiome analyses are often based on a single time point and location and thus do not represent many important dynamics of microbial interactions (48, 122). Multilayer networks, where layers represent time points or sample types, support richer analyses (122) (**Figure 3**). Ecological network theories developed in contexts such as food webs have the potential to provide insights into community structure, assembly, functions, and dynamics (43) and across nontrophic interactions such as mutualism, commensalism, amensalism, and antagonism (74, 106).

Key questions for understanding microbial communities, and for designing useful communities, revolve around how communities change. Analysis of microbiome networks has the potential to provide predictive power, on the basis of current observations of associations. What makes communities resilient in terms of continuing to provide desired ecosystem services? As an example, Wilmers et al. (164) found that the level of interaction (connectance) in a community was predictive of ecological stability and resilience. Abrupt shifts in the abundance of certain microbial clades may be signals of critical transitioning (83) from health to disease or vice versa. Shade et al. (137) suggest that many microbial communities are resilient to short-term stressors and are less likely to be resilient to long-term stressors. In resilient systems, changes could be transient and the community could return to the initial state (51, 72). Ultimately, it may be possible to design management to move communities, potentially including novel community structures, to the most beneficial states for ecosystem services.

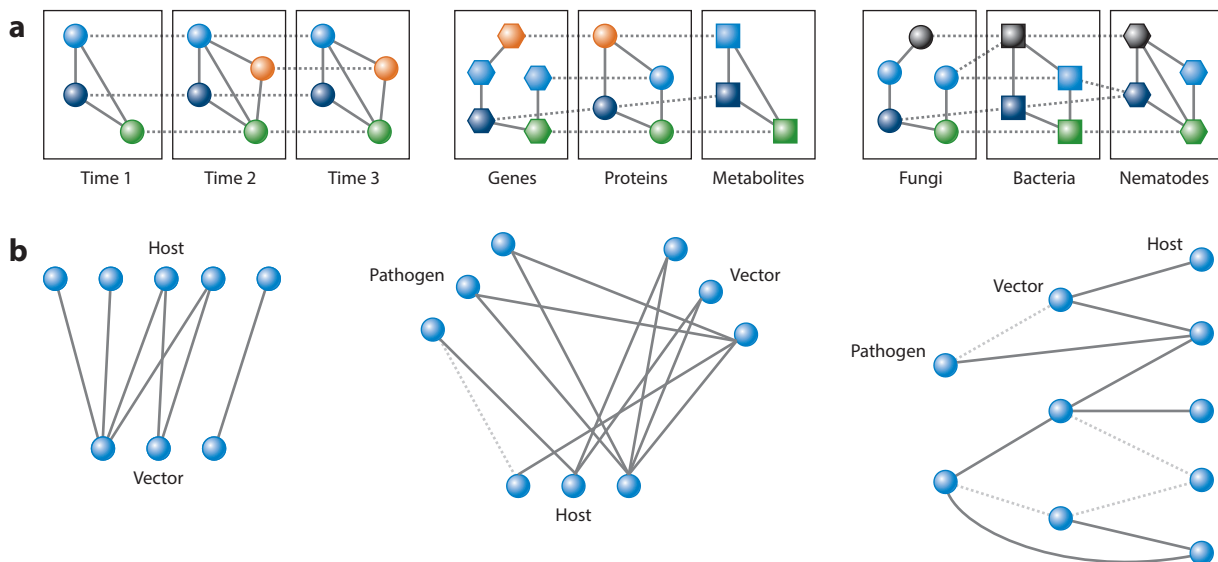


Figure 3

Multilayer networks and bipartite or tripartite networks can reveal structures driving phytobiomes. (a) In microbiome networks, nodes may represent taxa, genes, or molecules, with links indicating an association between pairs within layers (*solid lines*) or between layers (*dotted lines*). Layers might represent different time points, different molecules, or different types of organisms. (b) Left: a bipartite network indicating interactions between host and vector (or host and pathogen) species. Center: a tripartite network showing interactions among pathogen, vector, and host species. Note that for tripartite interactions, disease occurs for vector-dependent pathogens when a triangle is complete. When considered across many species, these networks may reveal the risk of new disease emergence, indicated by links that have not yet been observed but are likely on the basis of other observations, and would complete new triangles. Right: a schematic network indicates how new diseases may emerge. Solid lines indicate observed interactions, and dashed lines indicate interactions have not yet been observed but are likely.

Disease Emergence and Tripartite Networks of Phytobiome Interactions

Predicting the emergence of new diseases is a major challenge for plant pathology (6). Ultimately, the microbiome networks discussed above may aid in anticipating new diseases. The broader phytobiome is also key to disease emergence, especially for vectored pathogens. Inference about the structure of networks of host, pathogen, and vector often benefits from existing information about functional relationships, and association-based microbiome analyses may help fill in other species with functional roles that were previously more difficult to detect. Bipartite networks of two functional groups, such as plants and pollinators (41), represent an interesting analog for plant-vector networks (Figure 3). Bipartite networks can also be evaluated in terms of the indirect links between nodes within each level, in this case through shared vectors or shared hosts. The development of inference for tripartite networks would be useful for summarizing current knowledge about host-vector-pathogen interactions and their potential effects on the risk of disease emergence.

Several aspects of vector biology inform how tripartite networks function in terms of the nature of links between species. Many plant pathogens require a vector for transmissibility, including most viruses (162) and some vector-borne bacterial pathogens, e.g., *Xylella fastidiosa* and *Liberibacter* spp. (121). It could be useful to distinguish between network links based on persistent, semipersistent, and nonpersistent transmissibility (71), where the length of the time period during which the pathogen is transmissible is a key limiting factor. Hosts may have a degree of tolerance to a vector

Bipartite networks: networks with direct links only between members belonging to different functional groups, where the two functional groups might be hosts and vectors

(126) and be susceptible or resistant to the pathogen. Most viruses have few vector species but many host species (127). Vectors may be generalists or specialists (126) and sometimes are manipulated by changes in the attractiveness of plants when they are infected (70, 92). Aphid species, for example, can be polyphagous or specialist (107, 126). Probing may be sufficient for an aphid to acquire and transmit potyviruses. In contrast, the same aphid can transmit rhabdoviruses in a circulative propagative manner, where the aphid needs to feed on the infected plant to become viruliferous, but then this aphid serves as a bioreactor to produce viruses its entire life and for generations in the parthenogenic progeny (107). These biological features help determine the type of links between species, indicating the relative risk of transmission, and knowledge of them may help in understanding the mechanisms behind associations in ecological networks (41).

Ultimately, tripartite networks of host, vector, and pathogen species will need to be integrated with other types of information, such as the phylogenetic distance between taxa and similarities among genes important to pathogenesis, for effective prediction of disease emergence. Networks of host association in landscapes represent another type of risk (4, 31), where jumps across host species are more likely to occur for hosts that are frequently near each other. Climate change is another factor that may drive disease emergence by modifying species interactions (57). Ecological networks may shift across climate gradients (155), with potential changes in the invasibility of the networks (73), and altered dispersal patterns may also reorganize networks (152). In this context, as for many applications of network analysis, a key challenge is to learn to anticipate changes in network structure on the basis of observations from limited time points and locations.

Genetic Networks Across Scales

Network analysis is becoming a standard tool for evaluating genomic and proteomic processes within organisms, including pathogen effects on host individuals (e.g., 13, 160). Genetic association mapping can be used to identify genes associated with positive or negative effects on host fitness in the context of various stresses, including plant diseases, herbivores, and abiotic stressors. For example, there may be broad-spectrum defenses in response to combined stresses and trade-offs between jasmonic acid and salicylic acid pathways, where one provides increased resistance to, for example, aphids but decreased resistance to a necrotrophic fungus (149). The limits of varietal selection for resistance can be explored on the basis of such trade-offs. Genetic association mapping can also be used to explore candidate gene functions. For example, network analysis can reveal a clustering of genes by ontology and identify conserved functional groups with high node degree (hubs) (29). Genes with unknown ontology can potentially be assigned to known functional groups based on their associations in network analyses (100, 171), as for taxa in microbiome network analyses.

Phylogenetic networks are, likewise, a standard tool for understanding population genetic structure (101). Some can capture recombination and hybridization events and thus provide a nuanced view of pathogen evolutionary histories and adaptation in agricultural systems (28). For pathogens with only asexual reproduction, at least regionally (165), clonal populations can be difficult to distinguish without assessing multiple loci, making it challenging to infer a transmission network. Recent advances in both software (77) and high-throughput sequencing of single-nucleotide polymorphisms may help delineate these populations, allowing characterization of high-resolution transmission networks for previously intractable populations (97). Host phylogenies can also be used to draw inference about the probability that hosts share a pathogen, where the probability often decreases with phylogenetic distance (59). The genetic landscapes of agricultural plant species and the landscapes of their coevolved pathogens are determined by networks of crop breeders and seed systems (56, 82), as discussed below.

Node degree: the number of links a node has; may be divided into in-degree (the number of links to a node) and out-degree (the number of links from a node)

Network motifs:

patterns, such as stars and circles, that may be part of a larger network and may tend to have particular properties in the context of designing management strategies or anticipating network effects

THE RACE BETWEEN DISPERSING PATHOGENS AND INNOVATIONS

Modeling of epidemics in humans naturally suggests social network structures, whereas plant disease epidemics have a longer history of other forms of modeling dispersal across landscapes. More recent models of plant disease epidemic networks may offer a more straightforward link with human networks (5, 20). There are opportunities to link networks of ecological interactions between species with networks of geographic movement (152). There are also challenges for translating knowledge gained about epidemic networks to support decision-making through human communication networks in the development context.

Epidemic Networks: The One Health Perspective

The One Health concept is that disease requires similar approaches in many host systems, so synergies can develop from greater integration of disciplines. Future disease risk for plants, animals, and humans may be driven by common factors, such as pesticide resistance, climate change, and increased globalization (163). Thinking across systems provides not only an enhanced toolbox of analytic techniques but also a more global perspective, taking into account links between epidemics and social networks, communities, economies, and policy development. Research in zoonotic disease also offers interesting case studies to inspire further study of tripartite networks influencing crop disease.

The human health and public health sciences were pioneers in integrating the study of epidemic networks, dating back to the 1920s when the sociogram was introduced as a method for representing relationships between individuals (87). Network models are used to predict disease spread, formulate strategies for vaccines, establish quarantines, assess information diffusion, evaluate health care institution networks, and quantify the effect of disease control efforts. A key example of the utility of studying public health epidemics as actor-based networks was the original model of the HIV epidemic, starting with patient 0 as the central actor (88). A recent practical example of network models, applied to guide strategic intervention and policy, is the 2014 Ebola virus disease (EVD) outbreak in West Africa. Key EVD parameters, including network density, time to death, and time to recovery for each time window, were incorporated in an agent-based model (140) of the impact of potential policy for control through isolation.

When plant diseases emerge, organizations tasked with ensuring food security could benefit if it becomes standard practice to conduct an analysis of the effects of potential interventions, such as those deployed for EVD. Network topology can be used to infer the functions, structure, or dynamics of epidemic networks. For example, the size and structure of network motifs can be used to target management of invasive pathogens (21), and node degree centrality or betweenness centrality can guide sampling (68). However, data quality and availability are key limiting factors for fitting and evaluating models for most plant disease epidemics (34). The increasing availability and use of satellite and drone data may make possible regular mapping of disease in agricultural landscapes. A foundational task for this type of work is the generation and curation of effective data repositories.

Epidemic Networks in Plant Landscapes

The study of plant disease epidemics in networks has been addressed recently in stimulating reviews by Shaw & Pautasso (138) and across epidemic scales by Moslonka-Lefebvre et al. (102). Network concepts fit naturally in epidemiological frameworks such as identification of epidemic thresholds (76, 111, 115), modeling of metapopulations (138), and extensions to metacommunities across multiple scales (14). There is potential for characterizing cropland connectivity to create a

standard data layer for evaluating disease risk (91, 169) and developing sampling and mitigation strategies (109, 147) when data are available at the relevant scales (44, 153).

Transmission networks have often been evaluated on the basis of historical reports of diseases in new administrative regions, such as counties, states, or countries (46) (**Figure 2c** illustrates a possible transmission route for the causal agent of laurel wilt, *Raffaelea lauricola*, at multiple scales). However, sampling biases in monitoring and reporting frequently lead to uncertainty about the source of long-distance spread, as multiple modes of long-distance transport of pathogens are possible (17). Controlling emerging pathogens on the basis of administrative regions is almost always inefficient and can lead to increased economic costs (44, 153). Phylogenetic analyses have been used to infer the introduction pathway of invasive species across a landscape (46), with the potential for actively tracking pathogen populations as they emerge in new locations (75, 95). Coalescent models provide algorithms for detecting gene flow to reconstruct migration patterns (61). Phylogenetic migration network analysis can help distinguish among dynamic population scenarios, such as complete isolation, stepping-stones, full migration, and panmixia. Vector behavior adds complexity and uncertainty to landscape transmission models (130). Understanding the migration network of both pathogens and vectors is critical to inform models of disease emergence and can be instrumental in developing new control strategies.

Temporal and spatial heterogeneity in landscapes are often important input for network models. A key difference between the epidemiology of crop plants versus other types of hosts is the active global network to distribute resistance genes (56). System analysis must address the introduction of resistance genes and pesticides on a global scale, along with the adaptation of pathogen populations to both. Modeling the spatial heterogeneity of hosts as a network of nodes with different attributes can be useful for risk prediction and control (65), including the development of strategies for effective deployment of resistant cultivars across a landscape (96, 141). At smaller temporal scales, plant hosts are generally immobile, unless moved by humans, and often have windows of susceptibility to a pathogen that are temporally variable over the course of host plant phenology (34). Local spatial processes can be key when, for example, the number of links at a starting node is predictive of the future epidemic size (117). The starting points for epidemics such as soybean rust in North America may have a strong influence on epidemic progress (103) and evolution (133).

Trade Networks

Pathogens often spread through trade (10), whether in food, planting materials, wood, or packaging materials. Network models can be applied to understand these freeways that spread pathogens worldwide (34). Network analysis has been used to evaluate the structure, resilience, and function of the Worldwide Airport Network (WAN) (16, 25) and the Global Cargo Ship Network (GCSN) (42). Current limitations to understanding the role of ports and other key nodes in these systems represent an opportunity to improve global risk assessments (42). Railroads, roads, and rivers are regional risk factors for the spread of invasive species (10, 22, 128), and when data about trade structures are available, they have the potential to inform management priorities for invasive species (68). Understanding the plant disease risk from undocumented trade through dark networks is another frontier (35).

The nursery trade is both critical to production and a source of risk for pathogen introductions, motivating the development of strategies to balance maintaining movement while managing disease efficiently (37, 105, 118). The spread of *Phytophthora ramorum* and *Phytophthora kernoviae* across the United Kingdom is driven in part by trade networks (65, 170). Plant trade data are sensitive and difficult to obtain, making the study of such trade networks more challenging (116).

Pathogen spillover: spread of pathogens abundant on one host species (or differentiated population) to another

Threats of pathogen movement through trade extend to natural systems as well, when pathogen spillover creates outbreaks in native plant stands (65).

In networks of food distribution, human pathogens and mycotoxins are also important risks. The ability to trace pathogens to the initial source and the rapid identification of the locations most likely to be infected next are key components of any surveillance-eradication program (7). Traceability clearly benefits from an understanding of distribution network structures (19, 110), including larger systems, such as national grain transportation (68) and the global maize trade network (166, 167). The best-quality maize in some countries cannot meet the mycotoxin standards required for other importer countries, so trade links are broken and public health is at risk when the low-quality maize is consumed in the country of origin.

Seed Systems

Seed system networks are key to the conservation of agricultural diversity (113, 114), the distribution of improved, disease-resistant varieties, and the availability of seed that is disease-free or has an acceptably low level of disease (23). Yet seed systems also represent an important risk factor for pathogen spread, and the establishment of formal seed systems as part of an integrated seed health strategy is an ongoing challenge in low-income countries (150). In an informal seed system, farmers exchange seeds, leading to uncertain levels of seed quality and pathogen presence. Formal systems often provide higher-quality seed, although this seed may be cost prohibitive for smallholder farmers (27, 148, 150, 151). Current unknowns and misconceptions about informal seed networks (27), and how best to maintain the valuable components of informal networks when introducing formal systems, represent open questions that will require an integrated analysis of system options and likely outcomes. A general theory of management for disease in seed system networks is needed, integrating factors such as (*a*) how farmers' sources of information about integrated pest management (IPM) influence epidemic risk and management strategies (20) and (*b*) how specific strategies for identifying key nodes for sampling and mitigation affect epidemic outcomes (5).

Social Networks and Agricultural Development and Innovation

Subsistence farmers in many regions will likely experience increasing weather variability and resulting changes in disease and pest pressure while having limited access to institutional support for adaptation (24, 39, 89). Plant pathologists can address disease and pest risk in these systems with various technologies, including improved varieties, establishment of seed systems, infrastructure for storage and mycotoxin testing, improved IPM, and monitoring and diagnostic networks (6, 49, 98, 145). The likelihood that promising technologies will be adopted by stakeholders will increase if the process of innovation, adoption, and diffusion is understood and incorporated in development projects (50, 66).

Because of the inherent social learning network properties of innovation diffusion (**Figure 4**), social network analysis can be a powerful tool for understanding how, or if, technologies diffuse into societies or organizations (26). Agricultural innovation diffusion is the process of innovation spread through a population of potential adopters, where multiple factors can affect whether a technology is utilized (132). The diffusion and adoption of imported or indigenous innovations are social processes that occur within a network and involve transfers of information between potential adopters and those who inform and influence farmer opinions, beliefs, and resulting actions (78, 90, 104). An individual's adoption threshold is based on exposure to other network partners who have adopted (158); through this exposure, the potential adopter experiences a reduced sense of risk and improved capacity to adopt through seeing examples of how the innovation can be incorporated (146).

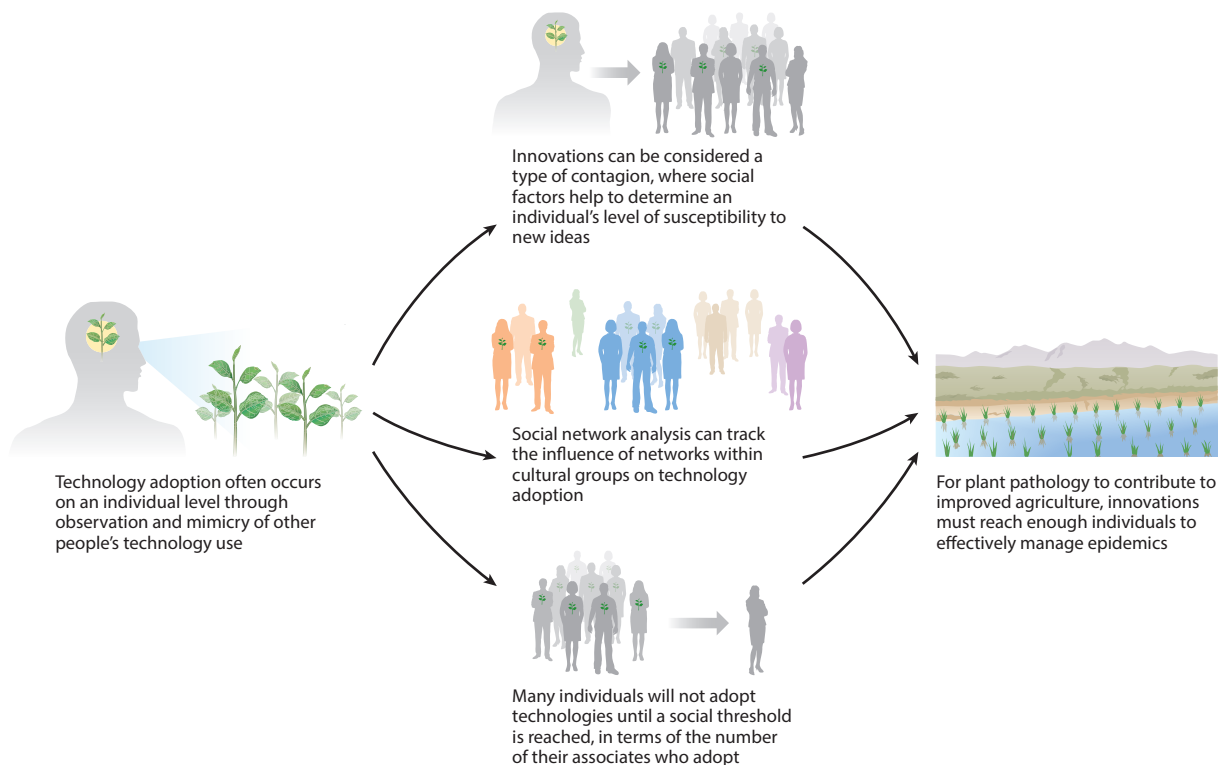


Figure 4

The diffusion of innovations for plant disease management depends on communication and influence among decision makers.

Specific network properties may predict the success of diffusion. Diffusion of an innovation to a large majority of the network is unlikely if the network is highly cliquish with few links bridging distinct portions of the network (30). For example, for rice-farming communities in Northern Vietnam, extension projects found only local leaders or prominent stakeholders were consistently engaged, to the exclusion of other more marginal members of the network (69). Individuals who connect distant portions of networks and thereby introduce variation and novelty to subcomponents are clearly important for adoption rates (144). Opinion leaders with a large number of network links may fill this role (168); however, it has been argued that a robust network of linked early adopters is more important for achieving a critical mass of support that makes widespread adoption likely (161). Scaling up and out is the ultimate goal for most development projects, and project managers can increase the chances of success by strengthening networks of adopters and supporters sharing their experiences and beliefs with potential adopters (67).

TOOLS FOR SYNTHESIS AND DESIGN

It is exciting that a wide range of disciplines, from social science to engineering to physics, are developing tools and concepts for network analysis that plant pathology can add to its toolkit. Statistical methods, such as Bayesian networks, for evaluating the relationship among variables and statistical models, such as exponential random graph models (ERGMs), for evaluating which

Decision theaters:

physical settings for evaluating the potential outcomes of policy decisions in scenario analyses, as at Arizona State University

types of nodes are more likely to be linked in a network, are available. Scenario analysis using agent-based modeling has potential for informing decision-making, including contexts such as decision theaters. These tools can be used to synthesize knowledge about networks and to design and evaluate the potential for improved network structures across a range, from microbiomes to global crop breeding and seed systems.

Bayesian Networks for Inferring Relationships

Neural networks have been used in applications such as modeling disease responses to environmental variables (38). Bayesian networks are machine learning algorithms that offer a structure for understanding the relationship between variables that can be more intuitive and visually interpretable. Visual representations of Bayesian networks show probabilistic relationships among a potentially large number of variables that are candidates for predicting responses of interest (2). The strengths of Bayesian networks relate to the explicit expression of uncertainty (via probabilities and error estimates) and the ability to address complex systems. In addition, the evidence supporting a particular hypothesis can be evaluated interactively in some software [e.g., Netica (<https://www.norsys.com>) and Hugin (<https://www.hugin.com/>)], and expert knowledge can be integrated with new observations to determine both network structure and associated probabilities. Thus, data analysis can take advantage of expert elicitation and provide a means to address gaps in empirical data (e.g., 143).

Bayesian networks have the potential for wider application in plant pathology as well as in agriculture more generally. Typical uses in other fields relate to decision support, diagnostics (58), risk assessment (142), and landscape modeling (2). Relationships among factors used for disease diagnosis can be evaluated by machine learning algorithms, as in the example of swine disease diagnosis (58). Bayesian networks have also been applied to crop management, including disease management (81). Likewise, Bayesian networks can inform policy-makers' decisions about which geographic locations to prioritize for investment, i.e., where disease management interventions are likely to have the greatest benefits (C. Buddenhagen, J. Andrade, G. Forbes, P. Kromann, I. Navarrete, S. Thomas-Sharma, Y. Xing, K. Garrett, unpublished results). The performance of Bayesian network analysis may be similar to that of other multivariate methods [e.g., in coffee rust management, decision trees were reported as better at identifying the most important explanatory factors (119)]; however, the visualization of relationships in a Bayesian network is elegant and intuitive. Another common application is in conservation biology, to map and classify suitable habitat and evaluate scenarios under specific management regimes (143). There are rich opportunities in the combination of field data and expert knowledge to examine policy or management choices across scales, potentially in combination with the other network methods described here for plant epidemiological studies. For example, associations between microbiome taxonomic groups and positive and negative relationships from a Bayesian network were used to identify functionally similar groups of taxa (120).

Statistical Analysis of Networks

Analyses of traits such as node centrality and network modularity can help in describing and comparing networks, but models such as ERGMs offer many more opportunities (18, 131). The description of an observed network can be generalized, and hypotheses about its structure can be tested by modeling the network. For example, stakeholder attributes such as gender, ethnicity, age, and marital status are sometimes predictive of human potential for behavioral change (157). In the context of development projects, such as implementation of formal seed systems, the role

of these types of farmer traits in link formation can be explicitly evaluated (20). ERGMs make it easier to evaluate the influence of social networks on plant disease epidemics.

Node and link attributes can be selected as variables in ERGMs, and hypotheses about their roles can be tested. For example, a hypothesis might include the idea that farmer wealth or farmer gender influences the likelihood of farmer links to quality seed sources. As an illustration, ten ERGMs were fit to a hypothetical data set, representing a range from simpler models to more complicated models, in an interactive interface (<http://www.garrettlab.com/arpnetworks/>) that shows the simulated networks and corresponding statistics in detail. In this case, factors such as the region in which a farmer is located are evaluated as potential predictors of how likely a link is to exist. Over multiple seasons, observed networks can change as new links form and some existing links dissolve. Separable temporal ERGMs (STERGMs) are a tool to model dynamic networks across time steps, with great potential for understanding epidemic dynamics.

Scenario Analysis for Network Systems, and Identifying Good Networks

In all areas of intervention ecology, including epidemic management, decisions must routinely be made with limited information. Scenario analyses can be used to evaluate outcomes and their uncertainty on the basis of what is currently known. System complexity is a common issue (94), where understanding ecological complexity can support, for example, financial systems (93) and the analysis of global data related to research investments (12). The structure of networks and the ways in which connectivity is achieved may be valuable intellectual properties, or even a cultural heritage when a network structure reflects long-term cultural learning and evolution (124). Employing the optimal level of complexity in studying a system makes the results more useful for a given application (63). There is strong interest in tipping points, resilience, sustainability, transformability, and critical transitions, and expressing systems in the context of network models can help make these concepts operational (40). Systems in which interactions among components lead to autonomous processes that either replicate or enhance the system are sometimes considered complex adaptive systems. Complex adaptive systems can learn, evolve, and become more complex and diverse (85, 94). This attractive concept has informed the application of adaptive management strategies, with mixed success (15, 80). It is challenging to consider how to incorporate a large number of system variables, but leaving out variables may simply disguise system uncertainty; most important applications involve wicked problems and temporal or spatial extrapolation of some kind. Uncertainty quantification can aid in identifying key variables for further study.

Integrating social network components into analyses of disease management is both a challenge, from the standpoint of representing system complexity, and an opportunity to improve system models (20, 52, 54, 99, 129). Adding a third system component that represents the type and quality of information and other technologies being distributed in systems (112) can provide a multilayer network analysis (36) to compare and evaluate the value of technologies in a broader system. Impact network analysis (55) is a framework for scenario analysis designed to integrate across these three components to evaluate the effect of technologies on biophysical networks through the effects of information and other technologies on socioeconomic networks (**Figure 5**). It can be used in scenario analyses of the potential outcomes from research investments and development interventions.

Network analyses provide the opportunity to evaluate system properties and identify potential control points, identifying traits that make systems more likely to collapse or persist (33, 94). Resilience in complex networks is of interest in terms of how the system may adapt to maintain its functions in the face of change (53, 156). Once a network structure is understood, its performance by these standards can be evaluated, with the caveat that most network data represent a snapshot

Tipping points:
thresholds for
potentially abrupt
change in a system

Transformability:
a system's ability to be
transformed from one
state to another

Wicked problems:
problems that are
difficult to solve
because of factors such
as changing and
incompletely
understood scenarios,
with complex
interactions such that
solving one
component of the
problem may create
other problems

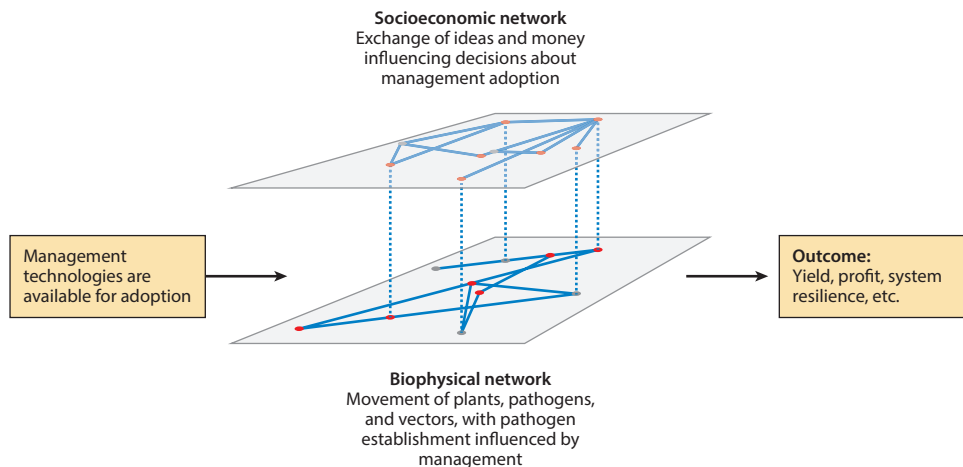


Figure 5

Impact network analysis is a framework for the analysis of how management technologies influence regional outcomes (55). Regional outcomes are a function of whether decision makers are influenced to adopt management by their socioeconomic networks, and the effects of these decisions on the management landscape and its ability to effectively manage disease spread. Nodes in the socioeconomic network are individual decision makers (such as farmers), with links in this network indicating communication and influence with regard to the management technology. Some decision makers manage land nodes in the biophysical network (such as farms), indicated by a dotted line between network layers. The management technology is or is not applied at a land node, depending on the corresponding manager's decision, and links in this network represent the potential for disease spread. The cumulative effects of the managers' decisions create a disease management landscape, and the effectiveness of this landscape determines regional outcomes.

of a system that may be in the process of changing due to influences that are not yet fully understood. Tipping points in a system may be anticipated on the basis of system architecture. When networks have a combination of modularity and heterogeneity, this may imply adaptive capacity and gradual change, while the combination of connectivity and homogeneity may imply resistance to change until reaching a threshold for critical system transitions (135). There are opportunities to explore and incorporate systems features such as modularity and connectivity, along with more integrated measures such as network controllability (86) and attack tolerance (3). When designing disease management systems, accounting for these system-level measures of risk and resilience may support better decision-making by policy makers and donors.

Controllability:

ability of a network to be changed from a given state to a desired state

Attack tolerance:

ability of a network to continue to provide desirable outcomes when key nodes are removed

RESEARCH PRIORITIES

There are many opportunities to improve the utility of network analyses for addressing complex systems in plant pathology and for translating results to inform decision-making. For many systems, there is a need to better understand what constitutes optimized sampling methods given practical constraints, for both performing adequate statistical analysis and capturing the key features of networks that support more realistic and precise scenario analysis. Many applications of network analysis would also benefit from user-friendly tools to explore the implications of network structures, as in decision-theater frameworks. The following are some current research priorities for achieving the potential of specific network analyses, where lessons learned across applications have great potential for moving plant pathology forward.

1. For microbiome networks, new approaches are needed for incorporating information about function and drawing inference about function; for integrating multiway interactions; and for incorporating concepts developed in food webs, including biocontrol effectiveness and risk to nontarget species. Other welcome methodological advances are tools for distinguishing biological interactions from shared niches and improved mathematical and statistical methods to account for compositional bias.
2. For bipartite and tripartite networks of species interactions, new approaches are needed to improve prediction of disease emergence and to draw inference about community dynamics more generally, including integration with geographic networks to link across scales.
3. For genetic, population genetic, and crop breeding networks, priorities include the development of links with other types of relevant networks, such as trade networks, to understand their effects on pathogen populations and disease risk. Disease emergence risk assessment may also be supported by integrating information about the genetic networks of potential hosts and the co-occurrence networks of potential host species.
4. For epidemic networks across individuals and landscapes, priorities include the development of better analyses of dynamic networks that evolve in response to environmental and other factors and link across scales, as well as databases to support these analyses in plant pathology.
5. For development networks, new approaches are needed for identifying key individuals and institutions for effective development projects and for integrating across data layers to identify key regions and circumstances for effectiveness. The key question of how to scale up successful development interventions requires better understanding of potential cascading and synergistic effects within networks supporting adoption, and an understanding of how disruptions from technologies affect other types of desirable network structures that support social capital for vulnerable populations.
6. For trade networks, new approaches are needed for designing efficient management, in which crop breeding networks and seed networks are key for successful deployment of disease resistance. Network-based biosecurity risk assessments for international trade would benefit from better targeting of quarantine and detection efforts at ports, estimation of rate of failure, and real-time incorporation of detection data to update risk assessments.
7. For networks of predictor and response variables, effective methods are needed for analyzing limited and unbalanced data in combined analyses of all relevant types of potential data.
8. For applications of statistical models of networks, priorities include the development of new models to capture and evaluate the key features of plant disease systems and the creation of software to facilitate the integration of these models into plant pathology.
9. For multilayer network applications, priorities include integration across disciplines to make the most of progress in the science of multilayer networks and development of databases to inform plant disease management. In times of fixed resources, understanding networks of scientific influence among scientists and in translation to nonscientists can help in prioritization and in demonstrating to the public the impact of scientific knowledge.

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Errata

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