Connectivity of the American Agricultural Landscape: Assessing the National Risk of Crop Pest and Disease Spread

MARGARET L. MARGOSIAN, KAREN A. GARRETT, J. M. SHAWN HUTCHINSON, AND KIMBERLY A. WITH

More than two-thirds of cropland in the United States is devoted to the production of just four crop species—maize, wheat, soybeans, and cotton—raising concerns that homogenization of the American agricultural landscape could facilitate widespread disease and pest outbreaks, compromising the national food supply. As a new component in national agricultural risk assessment, we employed a graph-theoretic approach to examine the connectivity of these crops across the United States. We used county crop acreage to evaluate the landscape resistance to transmission—the degree to which host availability limits spread in any given region—for pests or pathogens dependent on each crop. For organisms that can disperse under conditions of lower host availability, maize and soybean are highly connected at a national scale, compared with the more discrete regions of wheat and cotton production. Determining the scales at which connectivity becomes disrupted for organisms with different dispersal abilities may help target rapid-response regions and the development of strategic policies to enhance agricultural landscape heterogeneity.

Keywords: geographic information systems, graph theory, invasive species, landscape connectivity, networks

The United States contains one of the most important crop production areas in the world. According to the most recent national agricultural census, 1.8 billion bushels of wheat, 10.5 billion bushels of maize, and a wide range of other crops were produced in 2006 from 126 million hectares (315 million acres) in the conterminous United States (USDA NASS 2007). However, owing to the concentrated nature of the agricultural landscape and limited genetic diversity of many crops (Parker 2002, Harrington 2003), crop production is vulnerable to disease and damage by insect pests. Farm legislation that provides subsidies to growers for only a small number of crop species may inadvertently contribute to this homogeneity (e.g., Biermacher et al. 2006). Meanwhile, an average of 10 new crop pests are estimated to enter the United States accidentally each year, usually through shipments of plant materials, produce, or packing materials from other continents through US ports (Work et al. 2005). The economic damage caused by the spread of exotic crop pests is significant. The US Department of Agriculture (USDA) and other US government agencies spend more than $1 billion annually (Parker 2002) in research, risk assessment, and emergency response to outbreaks, and in public education, outreach, and extension.

Government agencies in the United States have begun to assess food security issues (Parker 2002), and organizations concerned with agricultural emergency response, such as the USDA Animal and Plant Health Inspection Service (APHIS), have procedures in place that target prevention, response, and recovery from a crop biosecurity breach (USDA and USDOI 2005). Geospatial analytical tools, such as the North Carolina State University/APHIS Plant Pest Forecasting System (NAPPFAST; Magarey et al. 2007) and CLIMEX (Sutherst et al. 1999), have been applied to forecast the risk that pathogens and pests pose to agriculture as a result of climatic conditions. Additional geospatial tools that incorporate models of pathogen and pest dispersal are still needed, both to anticipate and react to new outbreaks and to evaluate risk and form priorities for management of ongoing problems. However, tool and model development are hampered by the complexity of interactions among host, pest or pathogen, and

environment, as well as by the inaccessibility of field-level crop data and a paucity of data describing disease and pest damage and movement across broad scales. Even when information is available for commonly studied pests and diseases, the data and models developed for these species may not be relevant to a newly introduced or understudied pathogen or pest.

In lieu of data-intensive process-based models, an assessment of the overall connectivity of the agricultural landscape provides a useful proxy for evaluating the risk of spread of introduced crop diseases or insect pests. Landscape connectivity refers to the functional linkage among habitat patches (e.g., fields) through the dispersal capabilities of the organism in question (e.g., pathogen or insect pest) (With et al. 1997). Landscape connectivity is thus influenced both by the abundance and configuration of habitat or land-use types on the landscape (structural connectivity) and by the ability of organisms to access them (functional connectivity). For example, landscapes that are dominated by a single habitat or crop type (monoculture) are obviously connected, but even heterogeneous or seemingly fragmented landscapes can be connected if a pathogen, vector, or pest has sufficient dispersal capability to colonize otherwise isolated patches or fields. Although agricultural landscapes often are considered well connected, given that agricultural practices dominate land use in many regions of the country, considerable heterogeneity exists at scales of both the landscape (mix of crop types or management practices) and the field (mix of cultivars that differ in susceptibility to disease or pests). Because the spread of exotic pest or pathogen species may be facilitated in connected landscapes (With 2002), an analysis of landscape connectivity and the spatial scale or scales at which it emerges provides the first step in a risk assessment, and can assist with disease or pest mitigation and containment by identifying and targeting locations where landscape connectivity can be disrupted to halt or slow the rate of spread (With 2004). Locations that are more strongly connected will also tend to be at greater risk for recurrent problems with established pathogens or pests, as new immigrants can more readily compensate for any reductions in local pest or pathogen populations.

Graph-theoretic approaches have become an established tool in the study of networks and landscape connectivity (Calabrese and Fagan 2004, Urban 2005, May 2006, Jeger et al. 2007, Minor and Urban 2007), especially where landscape information is available only at a coarse resolution. Many biological systems can be modeled as networks, from gene flow (McRae and Beier 2007) to plants linked by mycorrhizae (Southworth et al. 2005). A common approach to identifying connected regions within graph systems and the locations that are key to maintaining connectivity is a "dropped-edge" analysis, which is done by systematically removing edges on the basis of relevant threshold values (e.g., Bunn et al. 2000, Van Langevelde 2000, Lamour et al. 2007). A similar approach is adopted here to summarize and quantify the connectivity of the US agricultural landscape for four major crop species (maize, wheat, soybeans, and cotton) to help inform a national risk assessment of their pathogens and pests.

Graph theory and representation of the agricultural landscape

In the context of graph theory, a graph includes "nodes" that represent discrete areas or objects and "edges," or lines, that establish a relationship between or among the nodes in a landscape matrix (Urban and Keitt 2001). Graphs may be used to model relationships between mobile individuals or groups of organisms, such as those involved in a human epidemic (Keeling and Eames 2005), or movement among actual ground features in geographic space. In ecological applications, graph theory has been used to quantify connectivity of habitat patches or populations within landscapes, where the matrix is assumed to be of little use to the organism traversing it (figure 1). However, the definition of a habitat patch node and the landscape matrix may be adapted, depending on the nature of the environment and the data available for describing the landscape. Such a modification is used here, where we apply graph theory by placing a node inside each county administrative unit, as in Steinwendner's (2002) example of applying a graph to pixels in remotely sensed imagery. Variables associated with the landscape matrix, such as its resistance to movement by organisms, can then be assigned to edges. This "county-as-node" graph structure can readily incorporate a landscape resistance variable for a particular crop species, where lower crop production indicates a higher resistance to movement for a pathogen or pest that is dependent on that crop species.

Developing a geospatial graph in geographic information systems

Commonly available geographic information system (GIS) software products, such as ArcGIS 9.x (Environmental Systems Research Institute, Redlands, CA), offer the capability to create, manage, analyze, and map geographic data in the
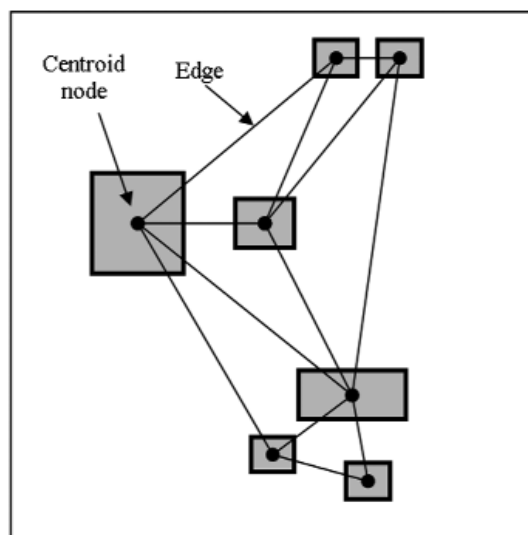

Figure 1. An example of a graph representing patchy habitat in a hypothetical landscape matrix. Centroid nodes represent the patch, regardless of size, and edges represent the connections among them.

form of a "network." A network is a vector-based, topologically connected system of linear features with attributes that describe the flow of objects or entities between connected places. GIS networks use graph algorithm tools to model actual movement.

A common network application in GIS is the analysis of movement within transportation systems, wherein nodes represent intersections between streets, and streets (edges) are assigned descriptive attributes that affect costs to movement, such as length or maximum speed. For ecological applications, the resistance of the intervening landscape to movement is often a weighted function of Euclidean distance (Chardon et al. 2003). In our analysis, we evaluate the movement or transmission through the network as a function of the density of the host crop species. Where the host species is more common, the landscape resistance to transmission (LRT) is lower, reflecting the higher probability of successful reproduction, dispersal, and establishment for pathogens or pests that rely on that host species. Because different species of pathogens and pests will be able to tolerate different levels of LRT, and the degree of tolerance for any given species will depend on how conducive weather conditions are to reproduction, dispersal, and establishment, we evaluate a range of different LRT thresholds to represent the range of possibilities.

To adapt a typical GIS network to a graph for the study of connectivity, nodes that ordinarily represent street intersections in a transportation study were instead used to represent habitat patches (counties), while street edges were used to represent connections between patches. Nodes were positioned at the geographic centroid of each county in the conterminous United States. These nodes, in turn, were linked by edges to the centroid of each adjacent county (figure 2). To best represent pathogen or pest movement among counties, adjacency was defined as counties sharing a common border or having
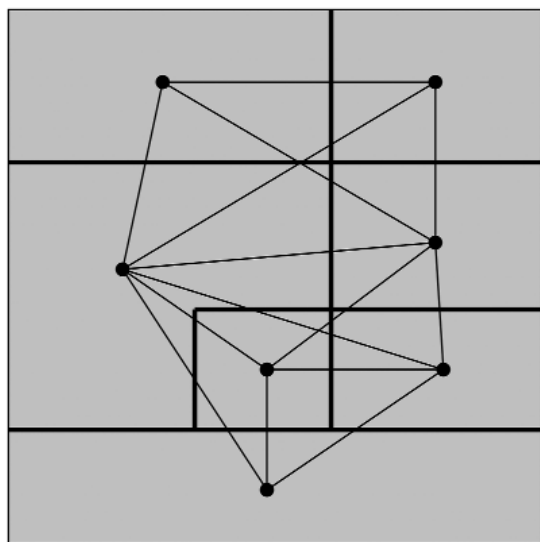
common corners. Given the irregular shapes of US counties, the resulting network included some edges that crossed. However, no additional nodes at these points of intersection were included in the final network.

After edge development, an edge list database table (ELDT) was created. The records in the ELDT store the unique identification number for each edge and the Federal Information Processing Standards (FIPS) codes for the two counties it connects. This table is similar to the connectivity table generated by ArcGIS 9.x when a network is built, but the ArcGIS-generated table is held by the software in the background during geospatial operations and is inaccessible to the GIS user. In contrast, the ELDT is separate from geospatial operations in the GIS and can be manipulated, allowing the user to freely transfer attribute data from the nodes to the edges and back through tabular joins and field calculations in the GIS. County-level information assigned to nodes, such as agricultural census data, can then be used in calculations related to movement along the edges, such as the LRT discussed above. Additional information entered in the ELDT for use in calculating the LRT included attributes for the length of each edge and the percentage of each edge contained in the two counties traversed.

Assigning LRT estimates to edges on the basis of host availability

We assume that the spread of pathogens or pests is facilitated by greater host species density. Recent crop acreage data for soybeans, maize, wheat, and cotton were acquired from the US National Agricultural Statistics Service (USDA NASS 2006) and used to calculate the LRT between adjacent counties. Crop data were added to the ELDT through a tabular join, using county FIPS codes as the key field. The LRT between two counties connected by an edge was defined as:

$$LRT = \frac{1}{\left(Z_a * \frac{L_a}{L_{ab}}\right) + \left(Z_b * \frac{L_b}{L_{ab}}\right)}, \qquad (1)$$

where L_{ab} = length of the edge connecting centroids of counties a and b, L_a = length of that edge within county a, L_b = length of that edge within county b, Z_a = density (harvested crop acres/total acres in county) of crop species in county a, and Z_b = density of crop species in county b.

The weighted mean proportion of crop acreage along the length of an edge provides a measure of host availability across two counties. The inverse value provides a unitless measure of the relative LRT between counties, which increases as host availability decreases. For example, if two neighboring counties each have 1%, 5%, or 20% of their acreage in maize, the LRT would be 100, 20, or 5, respectively. Calculated LRTs are lower (e.g., 5) between adjacent counties in which host crops are relatively more abundant (e.g., 20%). The LRT operationalizes the expectation that the spread of diseases or pests should occur more readily between areas of higher host densities. High LRTs imply a lower risk of spread because the host species is not locally abundant (i.e., the landscape is more heterogeneous), and a low host density may

Figure 2. A graph adapted to a situation where the landscape matrix is divided by geopolitical boundaries (e.g., counties).

be insufficient to permit the movement of pathogens or pests across the landscape.

Analysis of connectivity, patch structure, and risk of spread

In many examples from landscape ecology (e.g., Bunn et al. 2000, Van Langevelde 2000), the connectivity of graphs has been evaluated through dropped-edge analysis, in which edges are removed from the graph if it is unlikely that an organism will traverse them because the landscape resistance, often a function of distance, is above a threshold tolerated by the organism (figure 3). In this study, connectivity was evaluated using a dropped-edge analysis in which a range of representative LRT thresholds was evaluated. For each threshold, those edges with LRTs exceeding the threshold were "dropped" from the graph, leaving disconnected subgraphs (e.g., figure 4). The threshold value represents the highest LRT that can be successfully overcome by a particular hypothetical combination of pathogen or pest species and weather conditions. The dropped-edge analysis for a high threshold value (e.g., LRT = 100) indicates which counties are connected when disease or pest spread is likely even for the higher resistance resulting from lower host crop densities, while the analysis for a low threshold value (e.g., LRT = 3) indicates which counties are connected when spread can occur only for the lower resistance resulting from higher crop densities.

The appropriate threshold corresponding to any particular combination of host, pathogen, and environment would not be known without study, but we can generalize about the types of scenarios for which relatively higher or lower thresholds are relevant. A higher threshold is relevant to scenarios where pathogen or pest reproduction, dispersal, and establishment can occur across lower host densities. This might be the case because some of these processes are relatively more independent of the host for particular pests or pathogens, such as wind-dispersed organisms. Higher thresholds might also be relevant because weather conditions are highly conducive to these processes. For example, leaf-surface wetness is well known to favor infection by many pathogens (Huber and Gillespie 1992), so even if few pathogen propagules successfully disperse to a new region, they may have a high probability of successful establishment if leaf-surface wetness is available to support new infections and establishment. Conversely, if weather conditions are not conducive, even large numbers of propagules may not result in establishment. Lower thresholds are relevant to scenarios where a pathogen or pest species requires high host abundance for reproduction, dispersal, and establishment, or weather conditions are not conducive, or both.

The result of the dropped-edge analysis is presented as one map for each combination of host crop species and particular LRT threshold values. This identifies landscape regions that are internally well connected and where spread is possible, given the assumed constraints to movement caused by host density for each threshold. The same result, visualized as a
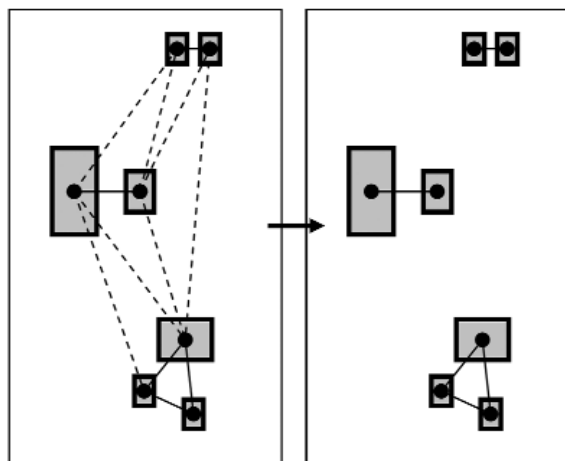

Figure 3. Example of dropped-edge analysis in a patch habitat graph. Edges that are too long for an organism to use as a dispersal route are removed, creating disconnected groups of subgraphs.

series of maps for a specific host crop (figure 4 and supplemental figures at *http://hdl.handle.net/2097/1049*), and constructed across the range of LRT thresholds, is effectively an assay of the functional connectivity of the landscape for any combination of pathogen or pest type (defined by the degree of ability to reproduce, disperse, and establish at lower crop densities) and conduciveness of weather (conduciveness for reproduction, dispersal, and establishment). Three separate landscape metrics were also used to assess the patch structure and overall connectivity of the US agricultural landscape for each LRT threshold evaluated.

First, the connectivity of the graph configuration at each threshold level was quantified using the gamma (γ) index (Forman and Godron 1986, Turner et al. 2001):

$$\gamma = \frac{L}{3(V-2)}, \tag{2}$$

where L = number of edges in network and V = number of nodes in network.

Possible values for γ range from a low of 0 to a high of 1, with low values indicating lower connectivity and high values, higher connectivity.

Second, the proportional abundance of a crop species was measured using the percentage of landscape (*PLAND*) (McGarigal et al. 2002):

$$PLAND = \frac{\sum_{j=i}^{n} a_{ij}}{A} * 100, \tag{3}$$

where a_{ij} = area of counties containing crop species i in patch j, for patches included in the graph for a given LRT threshold value (square meters [m^2]), and A = total landscape area (m^2).

For this study, A was the total geographic area of the lower 48 conterminous United States. Values for *PLAND* have a maximum of 100 (where the entire landscape consists of one crop patch) and approach a low of 0 (the presence of a given crop patch becomes more uncommon).
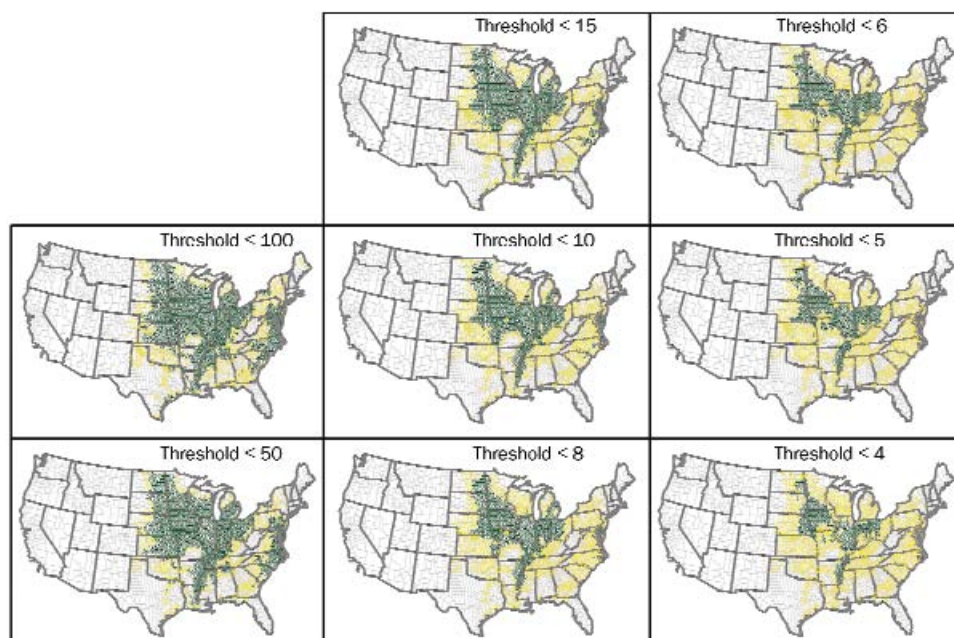
Figure 4. Dropped-edge analysis of the soybean network. A threshold indicates the highest landscape resistance to transmission (LRT; defined in terms of host availability) that still allows dispersal by a particular pest or pathogen. Green edges between counties meet the threshold criterion and yellow edges between counties have been dropped because the LRT is above the threshold being evaluated.

Graphs for soybeans had the second highest mean gamma index among the four crop species, only slightly less than that for maize graphs, and the highest maximum gamma index (for LRT = 50) (table 1, figures 4, 5, 6). The percentage of the landscape made up by connected soybean counties was also comparable to the percentage for maize for the range of threshold values from 3 to 15. However, the rate of increase in the percentage of the landscape for soybean from LRT = 25 to LRT = 100 was minimal. Soybean graphs had the second highest average percentage (18.3%), slightly more than wheat counties (18.2%), though with a higher minimum and lower maximum value. Soybean graphs were similar to those for maize in minimum percentage (4.7%), representing disconnected subgraphs for those crops present at the lowest LRT threshold (LRT = 3). Soybeans graphs also had consistently high landscape subdivision values, second only to cotton.

Third, the magnitude of the patch fragmentation, or the degree to which one or more large patches breaks down into several smaller patches as LRT thresholds decrease, was measured with the landscape subdivision (*DIVISION*) (McGarigal et al. 2002):

$$DIVISION = \left[1 - \sum_{j=i}^{n} \left(\frac{a_{ij}}{A} \right) \right], \qquad (4)$$

where a_{ij} = area of counties containing crop species *i* in patch *j*, for patches included in the graph for a given LRT threshold value (m²), and *A* = total landscape area (m²).

DIVISION is interpreted as the probability that two locations within the study area, chosen at random, will not be contained within the same patch. Possible values range between 0 and less than 1. As with *PLAND*, the total landscape area used was that of the lower 48 conterminous United States.

Soybean network

Although soybeans are commonly grown across the country, the majority of the US soybean harvest occurs in the Corn Belt states of Illinois, Iowa, and Nebraska, and in southern Minnesota (USDA NASS 2006). Fields of soybeans are also common landscape features along rivers from eastern North Dakota south to Louisiana, and along the eastern seaboard. At the continental scale, landscape connectivity was high for cases where low host availability could be tolerated (LRT thresholds ≥ 6; figure 5). For lower thresholds, however, the landscape appears more fragmented, corresponding to several key soybean production regions.

Soybean production can be characterized in the context of pathogen and pest dispersal as a large, interconnected core of counties that expands with increasing LRT thresholds, and in the process incorporates neighboring patches. However, given the consistent number of soybean patches that form across the range of threshold values examined, for each formerly distant patch that becomes integrated into the growing core, a comparable number of spatially distinct replacement patches form.

For example, the midcontinental landscape consists of a very large complex in the Upper Midwest and two regional disconnected subgraphs (e.g., Mississippi Valley and coastal North Carolina) at LRT ≤ 4. For 6 ≤ LRT ≤ 15, the Upper Midwest and Mississippi Valley complexes consolidate, while distant disconnected subgraphs begin forming along the eastern seaboard. For 15 ≤ LRT ≤ 100, these two distinct regions continue a gradual peripheral expansion, but remain distinct because of a topographic barrier in the form of the Appalachian range. Given the low threshold value at which the Upper Midwest and Mississippi Valley regions merge into one (LRT ≥ 6), those regions are especially susceptible to extensive and rapid pest or disease outbreaks. However, regional connectivity along the eastern seaboard remains low even at intermediate threshold values (e.g., LRT ≤ 10), requiring pests or pathogens to overcome nonoptimal conditions in order to spread throughout the eastern portion of the country.

Maize network

The US maize crop is similar to soybean in terms of its national distribution, although the National Agricultural Statistics Service provides data for more maize counties than it does for soybean counties. Gamma indexes for maize were among the highest of all crop species, indicating a consistently high degree of connectivity across LRT thresholds (table 1, figures 5, 6, and supplemental figure at *http://hdl.handle.*

net/2097/1049). Only at the lowest LRT threshold (LRT = 3) did the gamma index differ substantially from the mean of 0.793. Connected maize counties also had the highest minimum, maximum, and mean percentage of the landscape compared with other crop species across the range of threshold values examined. Conversely, landscape subdivision for maize was the lowest of the four crop species studied. The number of disconnected maize subgraphs that formed at each LRT threshold increased from 2 to 25 patches until LRT = 25, at which point the number dropped sharply to 7 and then to 6 at LRT = 50 and LRT = 100, respectively.

These numbers are indicative of the spatial dominance of maize production in the United States, which consists of a large and highly connected core area of counties that expands slowly as higher LRT thresholds are considered. At the same time, significant numbers of new and distant disconnected subgraphs form until the highest LRTs (LRT ≥ 50) are reached and patch consolidation begins. As with soybeans, the large, well-connected maize landscape in the Midwest persists across a wide range of LRT thresholds, meaning that the potential for pest outbreaks or disease spread is enhanced for species that can tolerate or overcome even modest LRTs. As before, there is a spatially distinct eastern seaboard region that initially appears at LRT = 6, but does not consolidate to form a single region until LRT ≥ 25, reflecting lower connectivity for maize compared with connectivity in the Midwest.

Table 1. Summary statistics for the gamma index, percentage of landscape covered by each crop, landscape subdivision, and the number of patches or disconnected subgraphs for four crop species.

Statistic		Maize	Wheat	Soy	Cotton
Gamma index	Min	**0.737**	0.385	0.586	0.417
	Max	0.813	0.718	**0.836**	0.665
	Mean	**0.793**	0.595	0.790	0.551
	SD	0.027	**0.109**	0.081	0.081
Percentage of landscape	Min	**4.8**	1.3	4.70	0.8
	Max	**45.7**	44.6	33.6	17.7
	Mean	**20.7**	18.2	18.3	6.7
	SD	14.7	**15.8**	9.9	6.3
Landscape subdivision	Min	0.791	0.801	0.887	**0.969**
	Max	0.998	**1.00**	0.998	**1.00**
	Mean	0.940	0.947	0.959	**0.992**
	SD	**0.077**	0.076	0.039	0.012
Number of patches	Min	2	**5**	3	4
	Max	15	**17**	7	10
	Mean	8	**11**	5	7
	SD	**4.702**	3.640	1.269	2.279
Patch size (millions of hectares)	Min	**37.6**	10.0	36.3	6.2
	Max	**356.1**	347.7	261.4	137.5
	Mean	**161.2**	141.9	142.4	52.2
	SD	107.3	**115.8**	70.8	46.0

Max, maximum; min, minimum; SD, standard deviation.
Note: The gamma index is a measure of connectivity; the landscape subdivision is a measure of fragmentation. Bold font indicates the highest value among the four crops for the minimum, maximum, mean, and standard deviation.
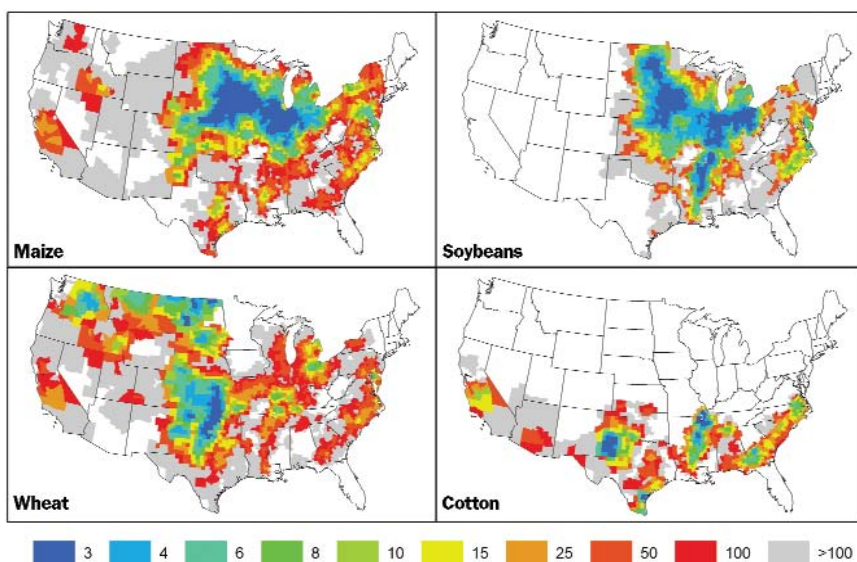

Figure 5. Connectivity of four US crop species measured by the landscape resistance to transmission, across a range of thresholds for host availability requirements by a pathogen or pest.

Wheat network

Unlike soybean and maize, wheat production is concentrated within three distinct geographic regions: the central Great Plains, the northern Great Plains, and the Columbia Plateau region of Washington, Oregon, and Idaho. Wheat graphs had the second lowest gamma index, but the highest standard deviation (table 1, figures 5, 6, and supplemental figure at *http://hdl.handle.net/2097/1049).* The percentage of the landscape made up of wheat counties was low—second lowest to cotton—across a wide range of LRT thresholds. However, for LRT ≥ 15, the percentage of the United States with connected wheat production increased dramatically. Landscape subdivision for wheat was very similar to that of maize across all LRT values, reflecting the relatively large number of disconnected subgraphs formed by each of these crops at LRT ≤ 25. Wheat also had the highest number of disconnected subgraphs (minimum,
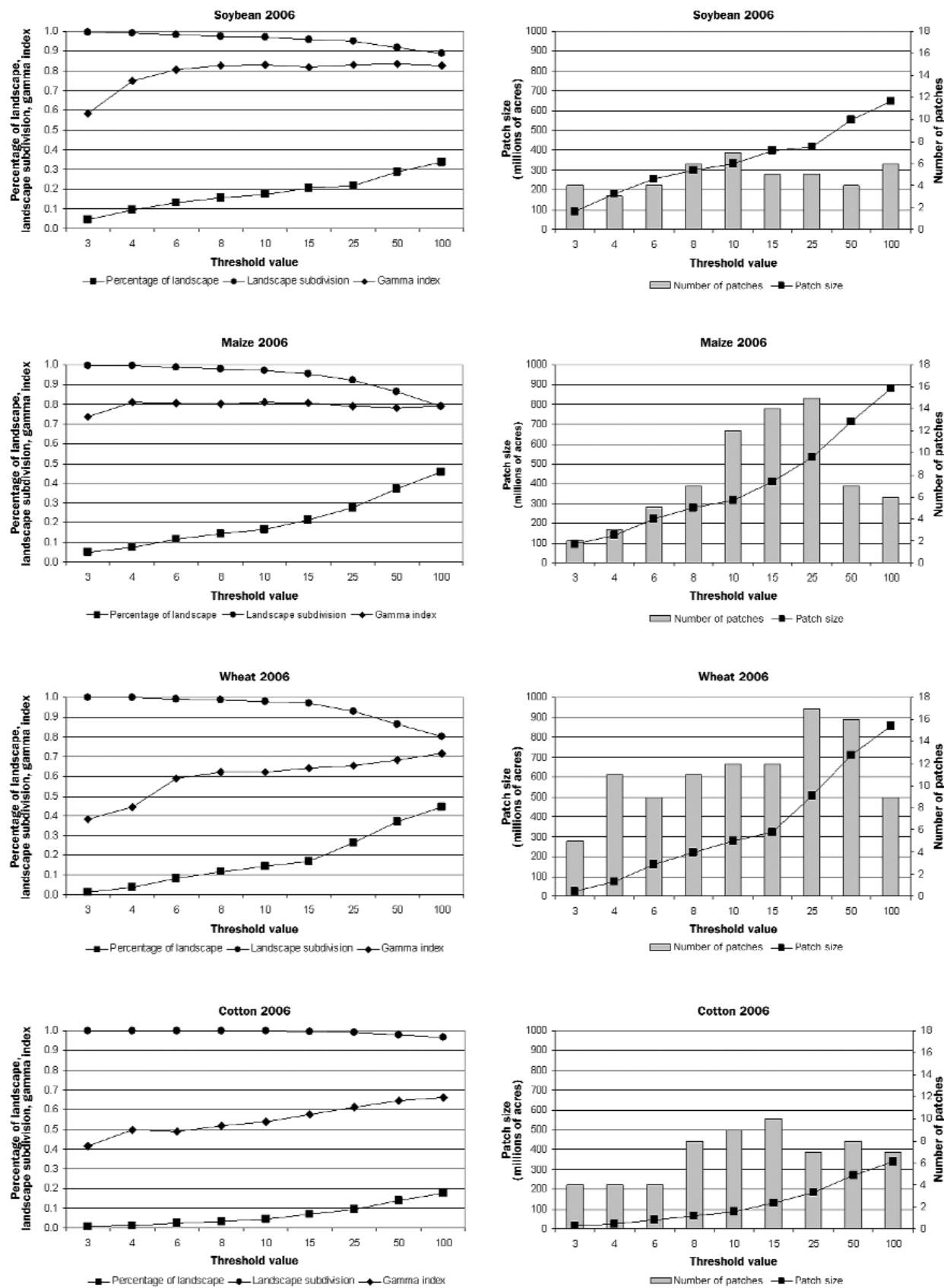
Figure 6. Graphs for each crop studied, with summary statistics for the gamma index (a measure of connectivity), percentage of landscape covered by each crop, landscape subdivision (a measure of fragmentation), and number of patches.

maximum, and mean) of the four crops described here. The number of disconnected subgraphs increased substantially at LRT = 4 and again at LRT = 25, after which subgraph consolidation began.

The three core wheat production regions form at low LRT thresholds (LRT ≤ 4) and continue expanding as higher thresholds are assessed. Smaller and more-isolated disconnected subgraphs first begin to appear in northeastern Ohio and southeastern Missouri (LRT = 6), Maryland and Delaware (LRT = 8), Michigan (LRT = 10), the Carolinas (LRT = 15), and California (LRT = 25). However, it is only for LRT ≥ 25 that these isolated areas begin to merge into larger connected units. Because of the persistence of this regionalized production pattern, many pathogenic or pest species introduced into one such patch would most likely be contained within that region for at least some period of time, and unable to overcome significantly higher LRTs to successfully spread between regions.

Cotton network

Despite recent increases in planted acreage, cotton remains a specialized regional crop, with centers of production in the southeastern United States, lower Mississippi River Valley, Texas high plains and Gulf Coast, south central Arizona, and the Central Valley of California. Gamma indexes indicated that cotton graphs were the least connected (table 1, figures 5, 6, and supplemental figure at *http://hdl.handle.net/2097/1049*). Though the minimum gamma index for cotton was larger than that for wheat, cotton had the lowest mean and lowest maximum value. Cotton connectivity began to drop substantially at LRT = 8. The percentage of landscape in cotton counties was the lowest of the four crops studied. In addition, cotton landscape subdivision was the highest and least variable across all LRT thresholds, indicating the isolated nature of cotton production within a few spatially distinct US subregions (figure 5). The area initially occupied by four very small centers of production increased gradually as higher threshold values were evaluated until LRT = 8, when the total number of disconnected subgraphs doubled (4 to 8), with most new disconnected subgraphs forming in the southern and southeastern United States. Beginning at LRT ≥ 25, these remote disconnected subgraphs were consolidated into approximately seven subgraphs.

Putting analyses of connectivity in context

Although much of the United States is devoted to the agricultural production of just a few economically important crops (especially in the midwestern United States), our analysis has demonstrated the scales across which connectivity is maintained, and most importantly, where regional connectivity becomes disrupted. The rapid spread of a plant pathogen or crop pest through such a highly connected landscape could be economically devastating, especially given the difficulty inherent in mounting a rapid response and attempting to manage or quarantine outbreaks at broad regional or national scales. For widespread crop species such as maize and soybean, the agricultural landscape is expected to maintain high connectivity across much of the United States for all but the pathogens or pests that are most host-dependent or for the least conducive weather conditions. In contrast, the overall landscape connectivity for wheat and cotton, as assayed by the gamma index, was 11% to 21% and 18% to 34%, respectively, less than that for maize. Production of both of these species was in discrete regions, as illustrated in the threshold analysis. Selecting areas for quarantine and disease management would be more easily accomplished for wheat and cotton than for maize or soybeans because of these spatial patterns.

The graph-theoretic approach developed here can be used to characterize areas of the country that form discrete regions, even for those crops in which connectivity is widespread. With and Crist (1995) demonstrated how a critical level of connectivity influences the dispersal of a species; if that critical threshold can be determined from farm field-scale studies, it can be applied using this connectivity method to seek out the discrete regions into which the agricultural landscape resolves. To accomplish this, new modeling theory and methodologies are needed to translate the farm field-scale transmission estimates into a critical threshold for larger-scale processes and to appropriately modify the form of the LRT in equation 1 to fit particular systems (Urban 2005, May 2006, Jeger et al. 2007, Plantegenest et al. 2007). Once identified, natural breaking points for dispersal among host populations can be monitored and potentially taken advantage of to disrupt connectivity before or during an outbreak, as with the efforts being made to isolate North American ash species infested with emerald ash borer (BenDor et al. 2006). These discrete areas may also serve as useful management units for disease quarantine, in which many of the finer-scale strategies discussed below may be employed.

When applying the connectivity analysis to a particular pest or pathogen species, it is necessary to consider the full range of factors that influence successful reproduction, dispersal, and establishment, as well as how these will determine what LRT threshold is most relevant. In plant disease epidemiology, the "disease triangle" is often used to indicate that disease can occur when a susceptible host, conducive environment, and competent pathogen (and vector, as needed) are all present (Agrios 2004). These same three factors are important for the successful spread of pathogens or pests. Our analysis of connectivity has emphasized host availability, treating the host species as homogeneous. In fact, crop species planted in the United States often have little intraspecific variation, which has resulted in problems such as the epidemics of southern corn leaf blight that were particularly widespread because the same form of male sterility was common throughout the US maize plantings (Ullstrup 1972). The environment is not likely to be equally conducive across all relevant spatial and temporal scales, however, so specific connectivity analyses will benefit from adjustment for weather variation (Truscott and Gilligan 2003), as well as for changes in climate that may shift both functional and structural connectivity in the future

(Garrett et al. 2006). The life-history characteristics of pathogens and pests will also determine how rapidly they may spread; the long-term connectivity for a slow-dispersing pathogen may be comparable to the short-term connectivity for a fast-dispersing pathogen. For our connectivity analysis, one of the most important characteristics is the relative ability of a pest or pathogen to reproduce, disperse, and establish under conditions of lower host availability, helping to determine what LRT threshold is relevant. As an extreme example of the ability to disperse across areas of low host availability, pathogens or pests capable of long-distance aerial dispersal may move across even those counties devoid of hosts (Brown and Hovmøller 2002, Aylor 2003, Shaw et al. 2006), though host availability along the route of movement will still tend to increase the probability of successful stages of reproduction, dispersal, and establishment. Human transportation networks also may inadvertently move pathogens or pests through regions without hosts. Analyses of connectivity can be adapted to incorporate the potential for long-distance aerial dispersal and for human transportation. Reproduction and establishment at low crop host densities may also occur because a pest or pathogen can use other plant species in addition to the crop species evaluated here. For example, other legume species such as kudzu (*Pueraria lobata*) have the potential to play important roles in soybean rust epidemics (Bonde et al. 2008). In such cases, connectivity analyses can be improved by including the mapped density of the other host species.

Disruption of connectivity within subgraph areas can be achieved through various measures, and that strategy is already in use in many cropping systems at a finer spatial scale (Skelsey et al. 2005). Mixing susceptible and resistant crop genotypes within a field is a fairly common disease management tool internationally (Garrett and Mundt 1999, Mundt 2002) that has proven extremely successful in some cases (Zhu et al. 2000). Higher plant diversity also tends to reduce insect herbivory (Andow 1991). Over fine spatial scales, such as within experimental plots or within fields, mechanisms for reduced disease in plant mixtures include dilution of inoculum, barriers to dispersal provided by nonhosts, changes in microclimate, and the potential for disease resistance induced by exposure to microbes associated with other plant types (Mundt 2002, Cowger et al. 2005). The importance of these mechanisms and the magnitude of their effects can vary as a function of the life-history characteristics of particular host-pathogen systems (Garrett and Mundt 1999). Over broader spatial scales, the relative importance of these and other potential mechanisms is not well understood, though broader-scale ecosystem services for disease and pest regulation (Cheatham et al. forthcoming) are probably being provided by whatever degree of plant diversity is present. If pathogen or pest populations are subject to an Allee effect, or lower per-capita reproductive success in small populations, the effects of reduced host availability may be even greater than would otherwise be predicted, as for Karnal bunt of wheat and gypsy moths (Garrett and Bowden 2002, Liebhold and Bascompte 2003). Greater crop hetero-geneity may also have benefits beyond lower immediate losses to disease, such as a lowered risk of the breakdown of disease resistance (Mundt et al. 2002). The potential effects of a proposed cultivar mixture can be evaluated before implementation through the use of graphs like those used in this study and other connectivity analyses (Skelsey et al. 2005).

By characterizing the scales at which regional connectivity becomes disrupted, our analysis may serve in the formulation of better strategies for dealing with invasive pathogens and pests, and potentially for developing strategies for changing cropping patterns. Although policies to direct which crop species are to be grown in particular areas are likely to be highly controversial, at the least, policies that promote greater crop homogeneity should be avoided. One strategy to better protect the national production of maize, soybean, and other widely planted crop species from pathogens and pests would be to encourage planting patterns that disrupt connectivity at critical spatial scales, as suggested by the regional production areas of wheat and cotton crops. When farm policies that change crop diversity are evaluated, their effects on host densities and the resulting connectivity of crop species should be taken into account. Policies that encourage widespread monocultures, such as subsidy programs for a small number of crops (e.g., Biermacher et al. 2006), may result in higher connectivity and therefore greater risk to the security of the overall crop. At whichever scale action is ultimately taken, measures to reduce connectivity in at-risk crops should be in place before pests or pathogens arrive on the landscape, which will reduce the severity of an incident and the cost of the response. Since the critical scale of connectivity for future invasive pest or pathogen species is not known, evaluations might focus on regions where disconnections can be produced across a wide range of LRT thresholds

When a new pest or pathogen species is introduced, connectivity analysis can contribute a unique perspective for decisionmaking, such as the decision tree we provide here (figure 7). Many of the first stages of risk assessment may be based on characteristics of the abiotic environment, pathogen or pest environmental requirements, and "age" of the introduction. After these risk components are evaluated using programs such as NAPPFAST (Magarey et al. 2007) or CLIMEX (Sutherst et al. 1999), connectivity analysis can contribute additional information about adjacent susceptible areas and the extent to which the national crop might be threatened. Such decision trees are generalizations that exclude details useful for the evaluation of a specific pathogen or pest, such as the potential use of multiple host species by the introduced pest or pathogen and the availability of crop species at different times of the year. However, the general concepts can be applied in most introduction scenarios, with additional information included as available for specific cases.

This analysis of the connectivity of the American agricultural landscape represents a broadscale assessment of the potential for pest or disease spread, as a first step in a national risk assessment and rapid response framework that incorporates crop plant connectivity. Information about connec-

tivity is also important input for evaluations of pest or disease risk at any given location, since more highly connected locations will tend to experience higher risk. Changes in agricultural connectivity over time in response to economic shifts, changes in farm policy, and climate change will need to be monitored to evaluate new risks. Agricultural connectivity analysis provides important input for the initial development and implementation of policies related to the management of pests and diseases of these four economically important crops, and the approach can readily be extended to other crop species or wild plant species for which maps of abundance are available (Holdenrieder et al. 2004). The development of risk assessments that integrate host, pathogen, and environmental factors at national scales is a grand challenge for the future.

Figure 7. Decision tree for a response to an introduced pathogen or pest.

Acknowledgments

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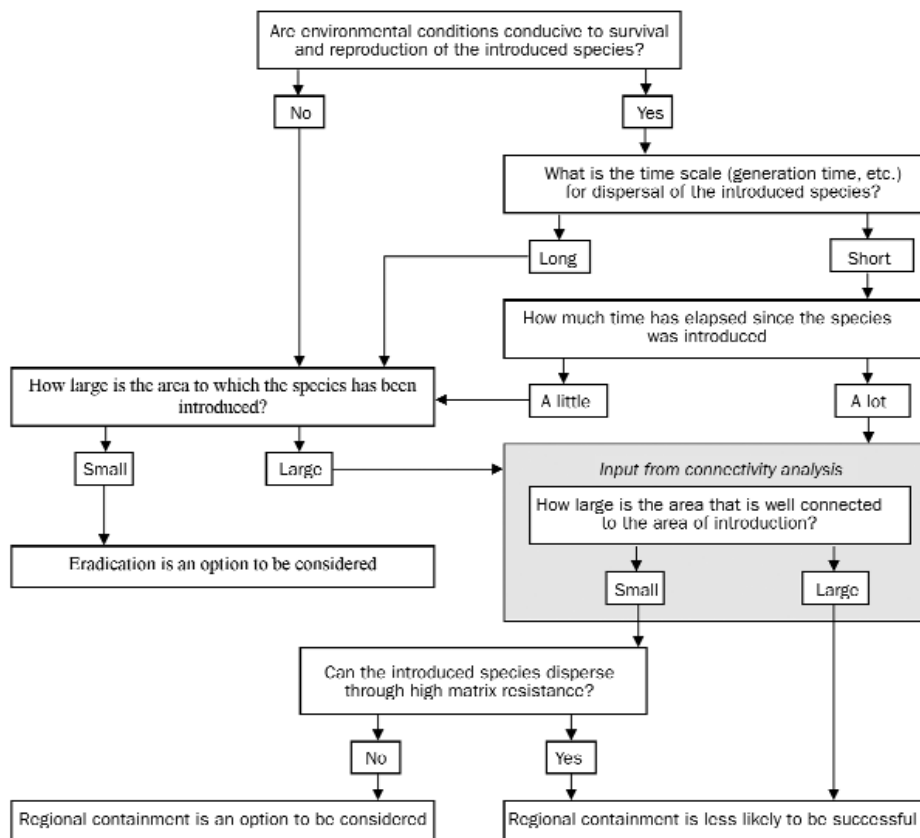
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Margaret L. Margosian is a USDA APHIS geographer, Karen A. Garrett (e-mail: kgarrett@ksu.edu) is an associate professor in the Department of Plant Pathology, J. M. Shawn Hutchinson is an associate professor in the Department of Geography, and Kimberly A. With is an associate professor in the Division of Biology, all at Kansas State University in Manhattan.