Proactive global biosecurity priorities for pest invasions on crop landscapes and trade networks

Aaron Isaí Plex Sulá*[1,2,3], Ricardo Iván Alcalá Briseño[4], Yanru Xing[1,2,3], Berea A. Etherton[1,2,3], Kelsey Andersen Onofre[5], Jorge L. Andrade-Piedra[6,7], Jacques Avelino[8,9], Monica Carvajal-Yepes[10], Wilmer Cuellar[10], Miguel Angel Dita Rodriguez[10], Romina Gazis[1,11], David Hodson[12], Andrew Jarvis[10], Lawrence Kenyon[13], Jan F. Kreuze[6, 7], James Legg[14], Gloria M. Mosquera Cifuentes[15], Kai Sonder[15], Suresh L. Mahabaleswara[16], Gary Vallad[1,17], and Karen A. Garrett*[1,2,3]

[1]Plant Pathology Department, University of Florida, Gainesville, FL, 32611, USA. [2]Global Food Systems Institute, University of Florida, Gainesville, FL, 32611. [3]Emerging Pathogens Institute, University of Florida, Gainesville, FL, 32611. [4]Department of Botany and Plant Pathology, Oregon State University, Corvallis, OR, 97330, USA. [5]Department of Plant Pathology, Kansas State University, Manhattan, KS, 66502, USA. [6]International Potato Center (CIP), Lima, Peru. [7]CGIAR Research Program on Roots, Tubers and Banana, Peru. [8]CIRAD, UMR PHIM, F-34398 Montpellier, France, [9]PHIM, Université de Montpellier, CIRAD, INRAE, Institut Agro, IRD, Montpellier, France. [10]The Alliance of Biodiversity International and International Center for Tropical Agriculture (CIAT), Colombia. [11]Tropical Research and Education Center, University of Florida, Homestead, FL, 33031, USA. [12]International Maize and Wheat Improvement Center (CIMMYT), Ethiopia. [13]World Vegetable Center, Taiwan. [14]International Institute of Tropical Agriculture (IITA), Tanzania. [15]International Maize and Wheat Improvement Center (CIMMYT), Mexico. [16]International Maize and Wheat Improvement Center (CIMMYT), Kenya. [17]Gulf Coast Research and Education Center, University of Florida, Wimauma, FL, 33598, USA.

Abstract

An unresolved issue faced by the plant health community is where to prioritize proactive biosecurity responses globally. Here, we address this problem by identifying candidate priority locations for the potential spread of emerging pathogens and pests through global crop-species networks crucial to pursuing sustainability. Candidate global priorities posing high epidemic risks include locations usually having or connecting to croplands with large host populations, and countries with high imports or acting as trade intermediaries. Our simulations indicate that epidemics may expand more rapidly in countries with larger cropland networks. Trade networks exhibit different priority locations compared to those in cropland networks, underscoring the need for a multi-purpose strategy to mitigate these crop epidemic challenges worldwide. These network-based priorities are starting points for strengthening surveillance efforts in global and national preparedness strategies, especially when integrating additional geographic factors, such as climate suitability, genetic host vulnerability, and socioeconomic affordability.

Main

Our life depends on healthy plants. The increasing vulnerability of agroecosystems to the unprecedented emergence and spread of plant diseases and pests (hereafter pests) persistently affects the likelihood of achieving the UN Sustainable Development Goals (SDGs), such as zero hunger (SDG2), national economic capacities (SDG8), human livelihoods (SDG3), biodiversity loss reduction (SDG15), and cultural values. Timely reducing pest invasion risks help sustain current and future food systems, particularly in an era of global human population growth and rapid changes in ecological conditions. Notably, preventing food losses caused by pests contributes to satisfying the basic needs of millions in countries with limited resources, which is an integral aspect to ensuring sustainable agriculture. Nevertheless, a primary challenge faced by the global plant health community, such as national and regional plant protection organizations (NPPOs & RPPOs), global biosecurity agencies, agricultural research and development organizations, disease diagnostic networks, and global agri-food industries, is where to allocate always-limited resources for (pro)active pest surveillance efforts[1].

Pest risk mapping has helped much in solving this geographic resource allocation problem, accounting for spatial risk factors facilitating the long-distance spread of (re)introduced or (re)emerging pests[2,3]. Integrated geographic risk assessments of pest invasions need to incorporate explicitly species-specific climatic suitability[4], wind patterns[5], local and international trade[6] and human movement[7], and host landscapes[8]. These integrated assessments are essential to design evidence-based strategies that effectively mitigate conditions making agroecosystems vulnerable to the emergence and geographic spread of pests, that is, the dynamic interplay among species invasiveness, host susceptibility, conducive environment, and dispersal opportunities.

Additionally, network analysis has offered innovative opportunities to quantitatively assess the risks associated with increasing ecological connectivity and the rapid spread of emerging pests globally[9,10]. Evaluating landscape and trade patterns of crops as network structures could help anticipate the potential spread of invasive pests[6,11], and enhance effective identification of geographic risk priorities. Explicitly incorporating network characteristics such as neighborhood[12], or more broadly the connectivity between locations, has shown that structures such as topological hubs and bridges are crucial to inform which locations might play key roles during early stages of pest invasions[5,9,13-15]. Assessment of the global network structures in cropland and trade of crop-specific industries is a key first step to building spatially explicit risk-reduction management programs. Despite their potential to strengthen current national capacities in early warning systems for pest outbreaks, we often lack global data-driven assessments of cropland and trade networks, especially for low- and middle-income countries coping with new crop epidemic threats[16]. We fill this research gap by assessing the potential roles of contemporary cropland and trade networks of agricultural commodities in the spread of invasive pests. Understanding cropland connectivity provides a general idea of the potential gradual expansion of pests within major host landscapes. Quantifying international trade connectivity offers insights into the potential human-mediated routes for pest translocation, especially for long-distance dispersal between geographically isolated host regions.

Because many aspects of pest outbreaks are inherently uncertain when pests have recently (re)emerged or invaded, risk assessments are crucial to early identify high-risk locations before a pest species spreads farther and to inform anticipatory responses for invasion mitigation. Many existing studies often focused on crop-specific national risk assessments and previous global analyses often lack crop-specific structures (e.g., [6,16]). However, these crop-insensitive or country-specific approaches may lack important geographic patterns that are useful for enhancing large-scale pest management. Here, we show how characterization of global cropland and trade networks of individual crop species identifies geographic crop-specific patterns that are likely important for pest invasions, allowing enhanced applications such as targeted invasion surveillance. NPPOs and global crop industries are fundamental lines of (pro)active invasion response, especially if biosecurity infrastructures are installed nationally and long-term coordinated governance for improved plant health is maximized locally.

All else being equal, pest invasion risk is likely higher with larger host populations and increasing opportunities for long-distance dispersal between croplands, forming cropland network structures such as cropland hubs and bridges that might facilitate pest spread[8,17,18]. The potential key role of highly connected croplands is expected to result in more opportunities for pests to spread, especially given current scenarios of cropland expansion within continents[19,20], increasing cropland area that may be vulnerable to pest invasions[21,22]. Likewise, spatial patterns in international trade are key factors for pests to spread globally[23,24] and locally[9] while overcoming biogeographic barriers. Greater understanding of potential pest translocation through global trade networks can inform (pro)active strategies of NPPOs. An unprecedented exponential increase in international commodity trade likely increases risk of pest invasions nonlinearly[16,24-27]. International trade has the potential to spread pests through diverse species-specific pathways[25,28,29], as exemplified in several pest invasions through trade of agricultural commodities[30-32](Table S1). The invasion risk of plant pests through global trade networks depends on which crop products are transported, postharvest processing[33], dispersal opportunities, and the success of current biosecurity efforts[26].

Proactive responses are aimed at preventing potential future costs that otherwise would be incurred at advanced stages when pest invasions expand across larger geographic areas and persist longer within or across nations[34]. Anticipatory responses against pest invasions need integration of early global surveillance systems across scales[1], so informing simultaneously about local, regional and global risks. In this paper, our first objective is to provide a global first approximation to geographic priorities for pest surveillance based on cropland connectivity, motivating countries and other regions to iteratively improve risk assessments for specific pests. Our second objective is to provide a comparable first approximation for the global risk of pest spread through formal trade networks and identify candidate countries for targeting (pro)active surveillance for the potential (re)introduction of a set of key emerging pests. Our third objective is to identify countries in the Americas with particularly high risk of pest spread based on landscape structure effects across simulated invasions, which are candidates for extra attention in international programs for mitigating pest spread risks.

Proactive responses are commonly needed at the level of individual crop industries and for use by their dependent stakeholders. We evaluated the global pest invasion risk for twelve major crops important for food security and livelihood of millions – avocado, bananas, beans, cacao, cassava, coffee, maize, pepper, potato, tomato, sweetpotato, and wheat. We additionally provide detailed assessments of both cropland and trade connectivity to support sustainable agriculture in Central America and Mexico. Central America offers complexities for responses to pests – in some cases it is a source of pest-specific resistance genes as a center of diversity, domestication, or origin of major crops, it structurally bridges the Americas and connects inter-maritime trade, it has a varying range of biosecurity capacity for pests[4,16], and regional climatic and socioeconomic uncertainties often collide with pest threats[16].

RESULTS

In this section, we first respond to a long-standing practical question: which locations in the global networks of crop-specific industries are candidate priorities for pest surveillance?

Geographic risk priorities based on cropland connectivity

We first evaluated the risk of global cropland connectivity considering the network topology for the twelve major crops (Figure 1). We conducted a sensitivity analysis across 192 parameter combinations within relevant ranges of dispersal parameters (details provided in *Methods*), so the mean cropland connectivity for each cropland grid cell is the mean across the most likely risk scenarios for each location. We focused on high-risk locations and summarized these global results across the twelve crops with examples of subnational locations having a high mean cropland connectivity (global hubs in Table 1).

The difference between mean cropland connectivity and cropland density helped us to distinguish which locations are identified as more important based on network topology rather than simply accounting for local large host populations (Figure S1 provides global maps of this difference). Our global results are summarized with examples of subnational locations having mean cropland connectivity that is substantially higher ranked compared to their ranking for cropland density (potential global bridges in Table 1). Our results are also supported by the variance in cropland connectivity across dispersal parameters, which indicates the consistency of projected risk across all parameter combinations (Figure S2).

We also focused on cropland connectivity at a regional scale and finer spatial resolution for Central America and Mexico for these twelve crops. Our regional analysis provided more detailed information about the role of cropland structures based on the mean cropland connectivity and the difference in ranks between mean cropland connectivity and cropland density (Figure 2). We highlight some examples of these regional structures for the twelve crops from a sensitivity analysis (potential regional hubs and bridges in Table 1). Our regional analysis indicates that invasion risk relies on spatial resolution and extent of focus, thus providing a better understanding of which landscape structures need prioritization in regional and national surveillance strategies.

Overall, where a crop had consistent higher density across many contiguous cells, the topology of cropland networks at both global and regional scales did not provide additional information for prioritization. For instance, the importance of network topology was globally high for common beans, maize and tomato in Africa, Europe, and Asia, but showed only slight influence in wheat croplands (Figure S1). More detailed maps of cropland connectivity in the Americas are also available in Figure S3-5. The most notable advantage of cropland connectivity was thus the identification of underlying high-risk structures considerably not captured by cropland density alone, especially in areas where continuous croplands are not highly dense. Our cropland connectivity assessment suggests that global and regional surveillance and phytosanitary efforts are first required to target cropland hubs and bridges. While cropland hubs might regularly drive invasions to spread (including dispersal and establishment potential), cropland bridges account for a unique role in geographic patterns of invasion corresponding to a more net dispersal potential and so depending on invasive-species dispersal abilities and opportunities.

Geographic risk priorities based on global trade networks

The role of countries in networks of reported formal international trade of targeted commodities, and thus in the potential spread of CPPs, was evaluated globally for each crop (Figure 3). We summarized the trade connectivity of each country, highlighting locations likely more important in these real-world networks. First, our analysis shows two types of trade connectivity because of the bidirectional movement and asymmetric nature of trade: export neighborhood and import neighborhood. An export neighborhood considers only exports of a country, and an import neighborhood provides only information about imports, where each is evaluated as a mean index based on a set of network metrics (details provided in *Methods*). Examples of countries with the highest export or import neighborhood are illustrated in Table 1. (Table S7 provides a complete list of the top ten countries with the highest export or import neighborhood). We illustrated the connectivity of countries in trade networks in terms of unprocessed commodities and the status of key CPPs for each crop (Table S4 provides trade importance ranks for spread of individual target pathogens). However, users can accommodate changes in the analysis for the distribution of any specific CPPs of interest and crop commodity depending on information availability.

Second, our analysis also shows the occurrence of two distinct types of countries in these trade networks (Figure 3). As opposed to producer countries, intermediaries trade crop commodities but no harvested area is reported for intermediaries (detailed country typologies provided in Figure S6).

The number of countries not producing a particular crop commodity in our trade networks varies from ~14% in maize to ~70% in cacao with a mean of 18.97±19.7% across the twelve crops (details for each crop provided in Table S9). Failing to recognize the role of intermediaries in these networks may lead to biases about the risks of pathogen dispersal via trade among countries, especially when intermediaries are likely to re-export commodities. This country classification certainly helps us better understand how the spread potential of some CPPs might pass undetected but explained by previously unconsidered re-export and how highly connected intermediaries and producers potentially trigger bridge effects[15,35] – a vulnerability situation frequently jeopardizing international phytosanitary efforts and so calling for (pro)active compensatory surveillance.

Next, we examined the risk from target countries based on the international trade of individual countries in Central America or Mexico, the global map of cropland connectivity, and the geographic distribution of a set of important CPPs (details provided in *Methods*). Third, our analysis of international trade of target countries showed how invasion risk varies among country types (whether producer or trade intermediary), crops, and target CPPs (Figure S7).

The geometry of epidemics through national cropland networks

We also simulated CPP invasions using the impact network analysis framework[21], basing biophysical networks for invasion on the underlying topological structures of croplands at the national level in an analysis of the Americas (detailed scenarios provided in *Methods*). We identified which countries are likely to have a high proportion of CPP establishment (hereafter average invasion rate), high variation in invasion rate under a set of scenarios (hereafter variance invasion rate), and high network link density (Figure 4a, b, c). We assessed these three aspects of invasion rate as a function of the size (number of nodes) of cropland networks. We found four geospatial patterns consistent across crops (Figure 4d-g). First, the average invasion rate increased with the size of national cropland networks, across 384 parameter combinations representing different CPP establishment, management, and technology adoption scenarios ($y = 0.19 \log x + 0.21,\ R^2 = 0.68,\ p < 2 \times 10^{-16}$) (Figure 4d). Second, network size was negatively related with the variance invasion rate ($y = -0.05 \log x + 0.17,\ R^2 = 0.62,\ p < 2 \times 10^{-16}$), suggesting that small cropland networks are expected to have variable invasion rates and that variance invasion rate is reduced as cropland networks become larger (Figure 4e).

Interestingly, there are scaling anomalies to these patterns, i.e., some smaller national networks have higher invasion rates after considering results adjusted for their cropland network size (deviated dots above trendline in Figure 4f). We provide some examples of these exceptional locations having higher invasion rates than would be typical for their cropland size for countries in The Americas (scenario analysis in Table 1; details for individual crops are provided in Figure S8). For example, Ecuador and Paraguay have common bean cropland networks of ~100 nodes, but invasion rates are as nearly high as Brazil, with >1000 nodes (Figure S8). Identifying large croplands or scaling anomalies is crucial to quantify the epidemic management challenge needed to face by countries.

The relationship between network size and link density reveals two groups of cropland networks in the Americas (Figure 4f). Most small national cropland networks with less than 50 nodes had a high link density. Network density, however, dropped precipitously for large cropland networks with more than 50 nodes, extending to size of cropland networks of about 2000 nodes ($y = -0.54 \log x + 0.07\ \ for\ x > 50\ ,\ R^2 = 0.75,\ p = 2.2 \times 10^{-16}$). We also found a concave shape in the relationship curve between the average invasion rate and its variance (Figure 4g). National cropland networks with a high invasion rate tended to have a low variance in invasion rate. The variance invasion rate is highest for national cropland networks with an intermediate invasion rate. The national croplands with a particularly low invasion rate had a low level of variation. There was higher uncertainty in scenario outcomes for national cropland networks with intermediate invasion rates. In summary, these relationships suggest that larger national cropland networks are often important for the risk of the spread of CPPs, but trade-offs occur for some smaller networks, thus greatly challenging epidemic management if obviating these geospatial patterns in international prioritization strategies of crop industries.

Generic patterns of risks across crop-species networks

We have hitherto shown that geographic priorities for phytosanitary efforts are diverse, depending on network type, country type, crop species and geographic extent of the analysis, requiring implementation of multi-location surveillance programs. But are underlying generalities established across these complex crop-species networks? We now turn our attention to basic identifiable signs that render crop-species networks with particular risk roles in the spread of CPPs.

The distribution of global cropland connectivity of crops is not continuous along the potential values of cropland connectivity. For all crops, most cropland grid cells peak at intermediate levels of connectivity (right peak in Figure 4h) and some crops also showed a second peak at low levels of connectivity. Geographic locations with high host density tended to maintain high cropland connectivity, and it is known that dense croplands are generally important locations for disease transmission[18]. Locations that are highly connected but have relatively low host density pose the potential of acting as cropland bridges for disease spread. Cropland bridges occurred in most of the crops, either gradually scaling regions from high to low cropland connectivity or interconnecting cropland hubs. The spatial structure of cropland hubs varied across a continuum from large cropland hubs surrounded by moderately homogeneous croplands to small cropland hubs surrounded by more or less “fragmented” croplands.

We found that crop trade networks are scale-free networks (for other general network attributes see Table S9), a key indication that invasion networks through international trade have few locations that are highly connected (left tail of distributions in Figure 4i) while most locations have few international trade links, also indicative that links formed in a process other than expected by chance (compare distribution of trade connectivity of crops with that of randomly generated networks in Figure 4i). The negative assortativity of trade networks (Table S10) was also common across crops, a key indication that trading countries with similar connectivity level are poorly interconnected. Highly connected locations tend to be trade intermediaries having a high potential for invasion spread but a low risk of introduction (see countries not producing commodities in trade networks in Figure 3). Countries having both high export and import neighborhoods include the United States, the Netherlands, United Kingdom, France, Spain, Italy, United Arab Emirates, and Germany (Table S7-8). These ten-top countries have the highest export and import neighborhood in at least eight of twelve trade networks evaluated here.

DISCUSSION

Invasion risk assessments based on cropland and trade connectivity are candidates for decision-support on proactive intervention strategies, especially when information about ever-evolving CPPs is limiting. These geographic risk assessments illustrate how understanding which locations have a high risk of CPP (re)invasion[8] can help in designing surveillance plans and prioritizing phytosanitary efforts. We provide advances in invasion risk assessment for the spread of CPPs, linking the “classical” emphasis on host landscape structure[18] and patterns in trade[27] to the proposed deterministic network-based approach for CPP invasions. We used trade and cropland networks to identify which locations potentially acting as hubs and bridges may be key for evaluating the spread of CPPs, and for intervening with strategies that could slow this spread.

Highly connected locations represent potentially effective starting points to prioritize surveillance for these complex networks of cropland and trade. Predicting the presence or probability of prevalence of CPPs is out of the scope of this study. In the risk assessments of cropland and trade networks, we projected and deterministically approximated more likely risks through relative rankings across a comprehensive range of scenarios in the face of uncertainty. We built our risk assessments on lessons from previous empirical studies and theoretical concepts (see *Methods*), so operationalizing them for the pursuit of an effective biosecurity strategy and providing candidate guidance for spatially allocating limited resources such as surveillance.

Our results in cropland connectivity are consistent with previous findings[8] (for crops also included here), but we provide and update these with finer resolution maps and their resulting risk areas. We also used network analysis of formal international trade of commodities as a proxy for the global spread of CPPS[6], to understand potential roles of countries on invasion risk and to highlight that invasion risk often differs among CPPs. Other relatively comparable studies on trade[16] often differ in the way connectivity is measured, especially lacking network analysis or crop specificity. Our maps of cropland connectivity and trade networks can be used either individually for prioritizing plant protection at global, regional, national, and sub-national levels or in combination to evaluate the risk of CPP release or introduction of any focus countries for their national strategy (**Figure Sn**). These maps together with our scenario analysis of epidemic spread are three key criteria when prioritizing phytosanitary efforts globally in a stepwise approach.

Our geographic analyses pinpoint key components of CPP invasion risk, focusing on the global need to strengthen prevention strategies through safe trade and cultivation. However, understanding the full extent of CPP invasion risk will require incorporating geographic dynamics of planting material exchange[36-38], landscape interfaces with urban agriculture and non-cultivated hosts, wood packaging networks[28], CPP-specific climate suitability[39], genetic host vulnerability[40,41], multi-host landscapes[42,43], current implementation of local and international invasion management[16], globalization trends[44] such as online trading markets, and transport systems such as entry ports[45]. These global change factors often shape the (re)emergence and spread of CPP invasion, but data unavailability largely hinders our ability to design holistic global proactive strategies. Undocumented informal trade and incomplete geographic distribution of CPPs and host contribute to these challenges. Shifts in temporal connectivity due to seasonality and long-term dynamics of trade and cropland networks are also necessary for future quantification of invasion risk (Figures S5-6).

A next big step is to iteratively tune these criteria with more detailed assessments as more information becomes available. Because the spatial patterns for individual criteria vary considerably, the role of joint optimizations in capturing synergies merit evaluation. An effective surveillance strategy should systematically account for aspects such as metapopulations of CPPs, and imperfect detection. A global optimal solution strategy for surveillance and mitigation should be built on a multicriteria approach and urgently needs to coordinate the most cost-effective alternatives and current operating and investing capacities due to socioeconomic contexts, the current regional diversity of CPPs for each crop, and the governance (including intergovernmental support in policies and regulations, designating collateral or mutual responsibilities and benefits, and engaging public awareness) in large-scale biosecurity efforts applied globally to locally.

METHODS

Risk assessment based on cropland connectivity

We evaluated cropland connectivity as a risk factor for twelve crop species in global and regional analyses, calculating the cropland connectivity risk index (CCRI) defined by Xing et al.[8] and using the geohabnet package[46]. We used Monfreda et al.[47], IFPRI and IIASA[48] and IFPRI[49] as data sources for the harvested area fraction of each of the twelve crops with original spatial resolution 5 × 5 minutes. We aggregated grid cells into maps of spatial resolution approximately 111 by 111 km at the equator (that is, land units or grid cells of 1-degree or equivalent to 12 × 12 grids of the original spatial resolution) for global analysis and 55 by 55 km (grid cells of 0.5-degree) for regional analysis.

For the network analysis, we considered each aggregated land grid cell as a node, and the relative risk of pest dispersal between nodes as weighted links[50]. The relative risk of pest movement based on proximity between each pair of nodes was calculated for each of two commonly used dispersal kernels: an inverse power-law function $\left(\frac{d_{ij}}{111{,}319.5}\right)^{-\beta}$, and a negative exponential function $e^{-\gamma\left(\frac{d_{ij}}{111{,}319.5}\right)}$. The Vincenty ellipsoid distance d_{ij} between the centroids of each pair of cropland nodes *i* and *j* was calculated using the geographic coordinates in the maps of mean crop harvested area proportion. The distance between nodes was transformed to Vincenty ellipsoid distances in meters and then scaled by dividing by the reference distance for one degree of Vincenty ellipsoid distance at the equator (111,320 m).

An uncertainty quantification, or sensitivity analysis, evaluated how model outcomes change when one or more parameters varied across a relevant range. Sensitivity analysis allows us to report results for a range of types of pests with different dispersal kernels. Species-specific dispersal kernel estimates are often unavailable, so including a range of dispersal kernels allows us to explore the parameter space likely to be relevant for most pest species. An uncertainty quantification was performed for dispersal parameters by selecting three levels of parameter β (**0.5, 1.0, and 1.5**) for the inverse power-law function and five levels of parameter γ (**0.05, 0.1, 0.2, 0.3, and 1.0**) for the negative exponential function. This range of parameter values is based on empirical estimates for several pests[40,41,51,52]. Lower values of parameters β and γ indicate higher likelihood of long-distance dispersal[53]. When using dispersal kernels of the inverse power-law and time-steps of 1-degree at the equator, relative chances of pests moving between two cropland nodes are ~35, 19 and 12% for $\beta = 1.5$ while ~50, 33 and 25% for $\beta = 1$ for nodes separated by ~111, 222 and 334 km, respectively.

The relative risk due to larger host populations (or greater cropland area)[54] for any two nodes was accounted for by multiplying together the mean cropland density (c) associated with each node i and j ($c_i c_j$) in two gravity models for dispersal risk[55]. These models consider the risk due to the proportion of cropland area within cropland grid cells (our proxy for host availability) and the probability of dispersal between each pair of cropland grid cells: $\sigma_{ipl} \propto c_i c_j \left(\frac{d_{ij}}{111{,}319.5}\right)^{-\beta}$ for the inverse power-law model and $\sigma_{ne} \propto c_i c_j e^{-\gamma\left(\frac{d_{ij}}{111{,}319.5}\right)}$ for the negative exponential model. We used both gravity model outcomes to represent the risk of pest movement as link weights between each pair of nodes in adjacency matrices.

Four standard network metrics for evaluating the importance of nodes in network processes[56] were calculated and combined in a weighted sum in the CCRI. The likely importance of nodes as bridges was evaluated by emphasizing ½ of the mean index weight with betweenness centrality, highlighting roles of locations that are often not obvious when the cropland density is considered in only one cell. When calculating betweenness centrality, link weights are generally treated as distances or costs to estimate shortest paths between nodes, so only for betweenness centrality we transformed the link weights in the adjacency matrix as $1 - e^{-\sigma_{ipl}}$ for the inverse power law model and $1 - e^{-\sigma_{ne}}$ for the negative exponential model. The other half of the index weight included three metrics that measure the connectivity of a node (node strength weighted by 1/6), its neighbors (1/6 sum of a node's nearest neighbors' node degree), and its neighbors'

neighbors (1/6 eigenvector centrality; see Table S2). Before summing, each metric was scaled by dividing by the maximum value observed for that metric for a given crop species.

Threshold minimum values of cropland density and link weight were also evaluated in the uncertainty quantification. It is unclear, and probably system-specific, the extent to which very low levels of cropland density facilitate pest dispersal. Use of a threshold focuses the analysis on the more important production areas. The range of values of cropland density varies by crop. Although cropland density values generally range between 0 and 1, there are also croplands with locations where proportion of harvested area is recorded as greater than 1 due to multiple production cycles a year[47]. We employed two methods for selecting values of cropland density thresholds. The first "crop-general" method consists of selecting three constant values as thresholds across all the crop species, to make crop species comparisons more straightforward (three density values representing locations with at least **0.01%, 0.2%, and 0.25**% cropland coverage). The second "crop-specific" method includes analyzing the data distribution of cropland proportion values for each crop species separately, and identifying the 15, 20, or 25th percentile of the cropland density data for use as thresholds for that crop species. Because the data distributions of cropland density are positively skewed, we selected small percentile thresholds while keeping a large portion of the croplands (85, 80 and 75%, respectively; Table S3). Usually the crop-general method retains smaller portions of the cropland dataset (Table S3).

Cropland connectivity for twelve global crop landscapes – avocado, banana and plantain, beans, cacao, cassava, coffee, maize, pepper, potato, sweetpotato, tomato, and wheat – was evaluated both globally and in a targeted regional analysis of Central America and Mexico. In some cases, multiple categories of the same crop species (e.g., dry beans and green beans) were combined because pests affect the categories similarly (Table S3). We explore the landscape and trade of these crops for a wide variety of reasons: their importance in sustaining global food security, the relevance for many smallholder farmers in the tropics who strongly depend on them, some have their center of origin, diversity or domestication in the Americas, the many pest invasions affecting them, and each crop combines different landscape and trade structures, allowing our analyses to illustrate and inform across various circumstances.

Interpretation of cropland connectivity maps

Three maps based on the CCRI summarize many features of cropland connectivity. A map of the mean CCRI, across the results of the uncertainty quantification, shows which regions or locations in a landscape are likely to be particularly important for many CPP species. A map of the variance in CCRI across the uncertainty quantification indicates the consistency of the importance of a location. A map of the difference between CCRI and cropland density points out locations where the CCRI reveals likely roles for a location that are not simply based on cropland density at the location. Locations with high cropland connectivity can act as cropland hubs (locations through which CPPs may effectively spread). Locations with a high, positive difference between rankings for CCRI and cropland density (locations with high CCRI and relatively low crop density) often have a potential role as cropland bridges. Because our analysis focuses on the general risk of disease spread, we consider cropland hubs and bridges in the broad sense as defined above. In the regional analysis, we refer to these structures as regional cropland hubs or bridges. However, network analysis usually considers hubs as locations with high node strength, and bridges are locations with high betweenness centrality. Cropland connectivity risk maps help to identify which counties, states, or countries potentially have the highest connectivity based on crop hosts.

Risk assessment based on international trade of agricultural commodities

We analyzed information about pairwise trade transactions from the FAOSTAT database[57], using the annual export and import quantity in tonnes for commodities of each crop during the most recent fifteen-year period reports for 2005 to 2019. We selected crop commodities more likely to be risk pathways for CPP spread by excluding those categories processed by fermentation, roasting, or sterilization (Table S4). In the FAOSTAT dataset, each transaction takes place between a pair of reporting countries. In an export activity, the reporter is a country that reports exporting the commodity. Because some smaller transactions may not be reported individually by both importer and exporter countries, we took the mean of export and import volumes for each pair of countries to generate a dataset of the trade amount. We excluded 'unspecified areas' transactions from the dataset, for both reporter and partner countries.

For global structures of international trade, we built network visualizations in which nodes represent countries and directed links represent the potential pathogen or pest movement between countries due to international trade[13]. Link weights represent the log-transformed mean annual trade volume over fifteen years between each pair of countries combined with the level of epidemic invasion of countries. Because available evidence suggests that volume of trade has often increased exponentially and the associated invasion rate of CPPs has a linear increase over time[26,27,58], we considered the invasion rate as following a cumulative power-law relationship with trade volume (Figure Sn). For a trading activity from i to j, $\tau_{i\to j}$, the invasion rate $I_{i\to j} \propto \left(\frac{\tau_{i\to j}}{max(\tau_{i\to j})}\right)^{\frac{1}{n}}$. The exponent n (set at 2) quantifies the intensity at which invasion rate changes with trade, and the maximum value of $\tau_{i\to j}$ for a crop is a constant to adjust the invasion rate so that it ranges between 0 and 1.

We construct a ranking for the potential of geographic CPP invasion inspired by concepts previously developed in a theoretical framework that employs three main factors for invasion success[4]. In a global trade network, the relative likelihood of introducing a pest species through commodity trade in an importing country (I_j) is proportional to the sum of the level of invasion risk posed by importing from a certain number (z) of exporting countries. We calculated I_j for each country involved in the global trade network of specific commodities using the following proportional relationship.

$$I_j \propto \sum_{i=1}^{z} \frac{n^{\left(\frac{\varepsilon_i}{\varepsilon_j+1}\right)}}{n^{(5)}} * \left(\frac{t_{i\to j}}{\max\left(t_{i\to j}\right)}\right)^{\frac{1}{m}} * \frac{log_{10}(h_i+\frac{11}{10})}{\max\left(log_{10}(h_i+\frac{11}{10})\right)} * \frac{log_{10}(h_j+\frac{11}{10})}{\max\left(log_{10}(h_j+\frac{11}{10})\right)} * \frac{1}{\beta_i * \beta_j}$$

M is a scaling exponent set at 2. We categorized the levels of each risk factor as in Table S5-6 and Vignette S1. We approximate local population size (ε) of a pathogen/pest as the national status and extent of a pathogen/pest. Importation results in the risk of CPP introduction to a country, and exportation results in the risk of CPP release from a country. Disease risk due to CPP status and extent varies from introduction to release (Figure S8-9). We refer to habitat specificity (host specificity as a proxy) (ω) as the crop host range of a CPP, a function of the number of major hosts (H) and alternative hosts (h): $\omega \propto \ln(2H + h)$. Because there can be a great difference between a wide host range and a narrow host range, we log-transformed the weighted sum of the number of crop species affected by a CPP[59,60]. We refer to geographic range as the number of countries where a CPP is present (n) divided by the number of countries that produce the crop (N). We also adjusted the geographic range by the extent of the overall crop-specific producing area of the country[57] (CPA) and ranked the results between 1 and 5: $\delta_i = \frac{n}{N} * \ln(CPA) \quad \rightarrow \quad \delta = 1 + \frac{\delta_i}{\delta_{max}} * 4$.

The overall invasion potential of a country i to a specific pathogen/pest is, therefore, a function of the likely local extent of the focal pathogen/pest (ε_r or ε_d for release or introduction, respectively), its plant host specificity (φ), and its geographic range (δ_i): $\varphi_{r,i} \propto (\varepsilon_{\boldsymbol{r,i}}) \times (\omega_i) \times (\delta)$. We propose this general conceptual framework as a proxy for the potential CPP invasion in a country ($\varphi_{r,i}$). We combined the level of potential CPP invasion with the level of trade in a gravity model. We first consider the level of potential invasion from two perspectives, based on whether the country evaluated is the source or destination location of trade. If a pest or pathogen is widespread in a country, the country may act as a source of invasion when exporting commodities. A country where a pest or pathogen is absent may be a destination of invasion when importing commodities. The likelihood of being a source or destination location might vary along a continuum depending on local pathogen/pest population sizes, host specificity of the pathogen, and geographic host distribution (Table S5). The potential of CPP invasion is a function of the potential initial population size in the exporting country and the final risk in a disease-free importing country. We used a gravity model to represent dispersal processes of CPP, in which a relocation function ($\mathrm{I}_{i\rightarrow j}$ and $\mathrm{I}_{i\leftarrow j}$ for export and import trade activity, respectively) indicates the potential of the movement of a pathogen/pest due to the amount of international trade between countries and whether the CPP invasion potential is higher in the source country ($\varphi_{r,i}$) than in the destination country ($\varphi_{r,j}$): $\sigma_r \propto \frac{\varphi_{r,i} I_{i\rightarrow j}}{\varphi_{r,j}}$. In our analysis, the structure of trade networks of crop commodities represents a relocation function as suggested by Jongejans et al[55] and Chapman et al[6]. Outcome values of σ_r represent entries in an adjacency matrix and link weights in our trade networks, a proxy for the relative likelihood of very long distance, accidental invasion dispersal events occurring annually due to formal trade between countries (henceforth pathogen or pest trade movement potential).

The analysis of trade networks as directed networks allows us to determine the potential influence of each node in terms of its outgoing or incoming links[9]. To evaluate the role of a country in the risk of disease dispersal in a trade network, we used four basic measures of network centrality for each node: node strength, betweenness centrality, PageRank centrality, and eigenvector centrality (see the rationale for the inclusion of each centrality in Table S2). We scaled each country centrality value x_i by subtracting the minimum and then dividing by the variance of the initial unscaled centrality values, $x_n = \frac{x_i - \min(x)}{var(x)} \rightarrow x_s = \frac{x_n}{\max(x_n)}$, so that the resulting country centrality values x_s ranged between 0 and 1. Because combining different network metrics tends to be more predictive in epidemic networks[56] and because we were most interested in the overall patterns of trade connectivity (separate analyses of each centrality are available in Figure S10-15), we present an analysis of focal disease dispersal risk due to trade activity based on a weighted centrality, summing the contribution from each scaled centrality: 1/3 node strength, 1/3 betweenness centrality, 1/6 PageRank and 1/6 eigenvector. To represent the importance of each country in the trade network, we scaled the resulting weighted centrality between 0 and 1, here named as a trade connectivity risk index (TCRI).

We distinguish three modes of country node strength in trade networks (out-strength for exports, in-strength for import, and total-strength for both export and import; details in Table S2). When calculating TCRI with only outgoing links across the four network metrics (export neighborhood risk), countries with high TCRI may be more likely to release invasive CPPs. When calculating TCRI only with incoming links across the four network metrics (import neighborhood risk), countries with high TCRI are at higher risk of introducing invasive CPPs. When calculating TCRI with both incoming and outgoing links across the four network metrics, trading countries with high TCRI may be at risk of release, introduction, or bridge functionality (often not mutually exclusive and depending on whether a country produces the crop commodity or not), which implies an easier path for a CPP to spread throughout a trade network. We used node out-strength in our results as this has been found to be more predictive for epidemic processes of CPPs in directed networks[5,6,44] such as trade (Table S2). To illustrate the risk among trading countries, we provide an analysis of CPP invasion risk for each crop system for important example species (next section giving details about specific CPPs).

Regional analysis of crop-commodity trade

We also integrated international trade networks with cropland connectivity maps. In these networks, each node represents a country centroid (the central location in latitude and longitude of a country). Although we used country centroids to illustrate the CPP introduction locations in a country, they only represented entry points at coarse resolution as actual introduction locations more likely correspond to ports and surrounding areas. Each link represents the existence of at least one trade event between two countries, where the arrow point represents the importing country. Because visualizing multi-link networks (networks with many links between each pair of countries) on a CCRI map can be impractical, we focused on a set of exporting countries. We focused on the intercountry trade for countries trading with Central America and Mexico, and on emerging/reemerging crop CPPs.

Each crop has many CPPs so, for practicality we focused on the major CPPs with a restricted geographic distribution, focusing on three groups: emerging, reemerging, and endemic CPPs. We defined diseases as emerging if the disease is becoming of greater importance, with increases in the incidence, geographic or host range, and virulence[61]. There can be a lag phase between introduction and emergence that has a length specific to a given CPP[4,16]. We focused mainly on geographic distribution at the country level, CPP category (e.g., oomycete), center of emergence (the location where the CPP was first reported affecting the crop or where symptoms were first reported), major and alternative hosts, and main carriers for transmission (this information is provided in Table S4). The CABI[59] and EPPO[60] databases provide the geographic distribution of CPPs at the country scale, we complemented this information with individual literature about these CPPs. Reports on the geographic distribution tend to be biased toward lack of reports where there are fewer efforts to characterize systems or incentives to avoid formally reporting presence. We used formal reports and, in the absence of public, explicit information, we conducted an expert knowledge assessment of the relative importance of trade for the spread of these CPPs. From the list of CPPs for each crop, several of the present authors evaluated the geographic distribution of CPPs based on own expert experience, and to rank the relative importance of CPPs in terms of the risk for spread through trade using a rating scaled between 1 to 5 (see details in vignette S3).

Our analysis of global cropland connectivity corresponds to a greater range in latitude [-58°, 60 °] and longitude [-140°, 180°], while the regional analyses focused on a smaller range in latitude [5°, 32 °] and longitude [-115°, -75°]. Our regional analyses of cropland focused on eight countries: Mexico, Guatemala, Belize, El Salvador, Honduras, Nicaragua, Costa Rica, and Panama. Analyses and visual representations were generated using multiple packages in the R programming environment version 4.1.2.

Scenario analysis for invasion in cropland networks

We aggregated original maps of cropland density into maps of 0.5-degree spatial resolution. We apportioned each aggregated cropland location in the map of the Americas into their respective country. Because decisions and strategies are commonly formulated at the national level, we generated crop-specific adjacency matrices of cropland networks by country. Nodes in each national cropland network represent cropland locations with land unit size ≅ 55.7 × 55.7 km^2. Evaluating national networks allows comparison of countries, although it does not specifically include the risk of invasions across borders. Link weight (ω) indicates the likelihood of the spread of epidemic invasions between cropland locations calculated with a gravity model of the inverse power-law: $\omega = c_i c_j d_{ij}^{-\beta}$. Parameters were the same as in the cropland connectivity analysis. Cropland thresholds were the crop-specific threshold values used for cropland connectivity analyses. After applying the crop-specific thresholds, cropland density was scaled so that the maximum value was 1. We evaluated a single value of the parameter β (1.5) and a single threshold for the value of link weights that considers the formation of links only when the distance between croplands was 500 km or shorter (known as maximum search radius).

We used the INAscene function of the INA package[21] to evaluate scenario analyses of CPP establishment, spread, and management on the cropland network of each country in the Americas as follows (see Vignette S2 and the INA user guide[62] for complete descriptions and definitions of parameters). We evaluated scenarios for cropland locations initially having information about management (initinfo.p = 0.01,0.05, 0.1, or 0.2), and CPPs established (a proxy for outbreak size, initbio.p = 0.01, 0.05, or 0.1). Socioeconomic and biophysical cropland networks by country were generated using gravity models as described above in this section. We also evaluated scenarios based on different probabilities of the adoption of management (probadoptmean = 0.1, 0.5 and probadoptsd = 0.1, 0.3), probabilities of establishment of CPPs (probestabmean = 0.5, 0.7 and probestbsd = 0.1, 0.25), and different effect sizes for management (maneffmean = 0.3, 0.5 and maneffsd = 0.1). We conducted 10 realizations for each scenario to evaluate, for each country, the mean invasion rate (proportion of croplands in the national network with the invasive species established) after five-time steps from randomly assigned initial invasion locations (nreals = 100 and ntimesteps = 5). We conducted a sensitivity analysis for the 384 scenarios to determine the mean and variance of the national invasion rates, comparing the risk of spread of CPPs for each combination of country and crop. We considered only countries having at least five cropland cells for a given crop.

We also evaluated the network density of each national cropland network. Network density is the proportion of links formed over the total number of potential links of an epidemic network and is a measure of the likely epidemic connectivity of a cropland network. We examined the relationship between these variables by fitting the log-transformed size of national cropland networks (number of cropland nodes) as a potential explanatory variable for the average proportion of establishment, the variation of the establishment, and density of cropland network. We selected linear regression models based on R^2 and statistical significance ($P<0.001$).

Risk commonalities in cropland and trade networks

We explore common characteristics among crop connected landscapes through comparison of distribution of CCRI values. We assessed the consistency of available cropland density maps with our knowledge of actual distributions of cropland. We identified three general patterns in cropland connectivity across crops. Whether locations with high cropland density remain with a high CCRI (1), whether the position of cropland bridges in reference to cropland hubs is common across crops (2) and whether the size and location of cropland hubs in relation to the remaining landscape vary across crops (3).

Network science provides a unified perspective on the characteristics of international crop trade systems. Trade networks of crop commodities are complex, and their general attributes can influence the risk of the spread of CPPs. We evaluated whether national connectivity in agricultural trade networks follows a scale-free power-law distribution – a general network feature likely to influence CPP spread[9]– using a Kolmogorov-Smirnov (KS) test. A KS test evaluates whether a network fits the power-law distribution and if so, finds the exponent that fits the model based on maximum likelihood. To evaluate whether countries with similar levels of centrality are connected (i.e., whether there is preferential connectivity among two countries with high node strength), we calculated the assortativity among countries based on five centralities (node strength, node degree, betweenness, PageRank and eigenvector centrality). We also built a matrix to identify which countries with the highest TCRI are the same in multiple trade networks (Table S7-8).

Data availability

Data sources are provided with this paper. Maps of cropland connectivity are available at https://figshare.com/account/home#/projects/147823, markdown reports.

Code availability

The latest versions of code templates for reproducing the analyses presented in this article is available at: https://github.com/GarrettLab/CroplandConnectivity for cropland connectivity, https://github.com/AaronPlex/InternationalTradeNetworks for trade networks and https://github.com/GarrettLab/INA for scenario analysis.

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Author contributions

AIPS and KAG conceived of and designed the study; AIPS performed the analyses; AIPS and KAG wrote the manuscript with substantial contributions from all other co-authors; all authors interpreted the results.

Competing interests

The authors declare no competing interests.

Supplementary information

Supplementary information is available at .