An integrated risk assessment framework for proactive global surveillance of invasive pathogens and pests

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Abstract

Invasive pests pose a growing threat to global ecosystems. Current invasion risk models rarely quantify multiple species-specific drivers for the worldwide spread of transboundary pests. We propose a global invasion risk assessment framework (GIRAF) which explicitly quantifies, integrates, and maps species-specific geographic risk factors – multi-host landscapes, abiotic factors, trade networks of agricultural commodities, port accessibility, and international biosecurity policies. We applied GIRAF to assess potential scenarios for the introduction, establishment, and spread of invasive pests –*Phthorimaea absoluta*, *Ralstonia solanacearum*, tomato brown rugose fruit virus, and potato spindle tuber viroid. We found that host communities for each pest occupy ~22-37% of Earth's land surface, with Europe and Southeast Asia providing a highly suitable environment. The USA ranked among the top five countries with a high trade-mediated (re)introduction potential for each pest. GIRAF provides key starting points for proactive surveillance prioritization and geographic mitigation against the potential spread of invasive pests, supporting transnational biosecurity agencies and global food industries.

Teaser

Integrated spatial risk assessments can improve proactive surveillance for invasive species.

1. Introduction

Invasive species are an increasing challenge to ecosystems worldwide. Effective invasive species management is inherently a key component of sustainable plant ecosystems aiming to contribute to the UN Sustainable Development Goals (SDGs), particularly those oriented towards agricultural productivity, food security, human livelihoods, and ecosystem health (*1, 2*). Solely attaining agricultural sustainability on a local and global scale requires a substantial decline in the estimated 10-40% crop yield loss caused by new and re-emerging diseases and pests (*3*). Unchecked outbreaks of plant diseases and pests can inflict substantial impacts on global food baskets, international markets, plant health, and natural ecosystem functioning (*4*). Increased globalization (commodity trade, human transport, and cropland expansion) and climate change drive the unprecedented spread of invasive pathogens and pests at large scales (*5-8*). A main goal of proactive responses to this multifaceted human-driven invasion crisis is to prevent future socioeconomic, political, and ecological impacts if pathogens or pests expand farther and persist longer in a region (*2, 5, 9, 10*). An increasingly important component in invasive species management is integrated risk assessment before and shortly after the initial or repeated introduction of pathogens and pests in new areas. In the long term, this integrated assessment would anticipate invasive spread, prepare spatially explicit surveillance strategies, and formulate biosecurity geo-policies as aspired to in the One Biosecurity perspective (*2, 10, 11*).

Geographic pest risk analysis provides a general framework to identify most likely locations for pest introduction, establishment, and spread (*12-16*), regularly requiring quantification of risk factors such as host availability, climate suitability, commodity trade, and human transportation. An integrated assessment of key geographic risk factors helps appropriately prioritize often-limited resources for active surveillance of invasive species in agroecosystems, is a fundamental layer of invasion preparedness, and strengthens early warning systems for invasive pest outbreaks. Integrated risk assessments are increasingly needed owing to the unprecedented rise in current and future mass biological invasions and crop epidemics worldwide in the 21st century (*8, 17, 18*). Nevertheless, assessing these risk factors collectively and globally is challenging; consequently, anticipating the actual spread of an invasive species is highly uncertain and sometimes seems driven by random chance. High-resolution maps of plant host distribution, detailed information on international and domestic trade of high-risk commodities, and species-specific environmental requirements are important information gaps that remain open for many invasives, especially plant pathogens and pests (*1, 19-21*). Given this inherent uncertainty, a proactive data-driven approach for explicit quantification of geographic risks of invasive species is to leverage existing limited geospatial data through general principles from invasion science, disease epidemiology, pest ecology, and species distribution modeling (*22*), while assembling better data in publicly accessible platforms in the digital era (*10, 23*). Currently, expert opinion is the traditional (sometimes the only feasible) option when evaluating the national risk of an invasive pest in the immediate term (*16, 24, 25*). Hundreds of quick risk assessments are available for specific countries (*12, 16, 24*), but they represent a tiny fraction of an increasing number of pests affecting plants globally (*18*). Research over the last three decades has led to an increasingly better understanding of individual geographic drivers of pest invasions (*10, 12-15, 22, 26, 27*). Nevertheless, available frameworks are rarely applied to integrate multiple species-specific drivers of invasive pest spread across geographic scales. Here, our goal is to provide a new, integrated risk assessment framework (GIRAF 1.0) evaluating possible scenarios for spatial spread of invasive pests (Fig. 1). GIRAF harnesses advances in knowledge about invasions into a quantitative use-inspired approach and can be applied as a data-driven foundation complementary to expert assessment. GIRAF explicitly integrates common geographic risk factors underlying the most likely paths for spatial spread of invasive pest species, mapping their potential geographic distribution, and identifying candidate priority locations as a critical component of global surveillance strategies (*7, 11*).

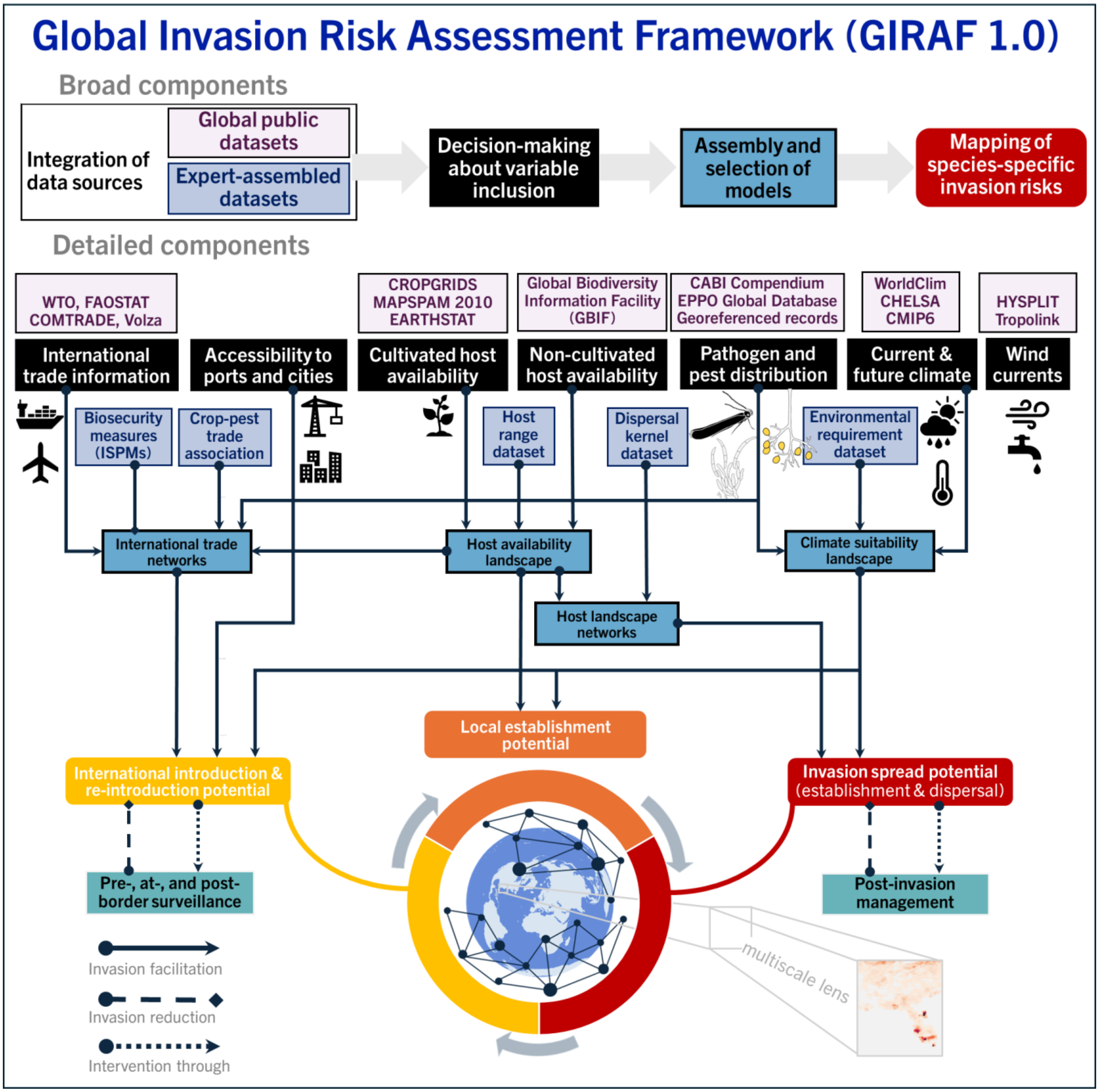

Fig. 1. The proposed global multicriteria framework of invasion risk assesses four of the five fundamental drivers of invasive species spread (environmental suitability, host availability, international trade including seed exchange, local transportation such as access to cities, but no wind patterns yet). GIRAF comprises four major components: integration of data sources (public datasets and expert-assembled datasets), decision-making on variable inclusion, assembly and selection of models, and spatial predictions of invasion risk (boxes in yellow, orange and red). Of course, GIRAF is subject to the GIGO axiom (garbage in, garbage out), where the quality of outputs is only as good as the quality of the input data. No single database used here is bias-free (see Methods for full name of datasets). In GIRAF, expert evaluation is needed in each component, from data input to model selection, parameter choices, and risk factor importance. Pest and disease prioritization is an expert-driven process external to this framework (*15*)[Note S1]. This framework's primary goal is to provide species-specific invasion risk maps for (pro)active surveillance and risk mitigation over a contemporary time horizon. The multiscale lens indicates that GIRAF is applied across geographic scales, from global to local.

As a pilot application of GIRAF, our first objective is to assess the global risk posed by four economically important invasive pests: the South American tomato leafminer (*Phthorimaea absoluta*), *Ralstonia solanacearum* phylotype IIB sequevar 1 (RSIIB-1 hereafter; former assignation "*Ralstonia solanacearum* race 3 biovar 2"), tomato brown rugose fruit virus (*Tobamovirus fructirugosum*; ToBRFV hereafter), and potato spindle tuber viroid (*Pospiviroid fusituberis*; PSTVd hereafter). Specifically, we assessed four geographic risk factors expected to promote the potential spread of these and many other invasive species and their establishment risk in new suitable habitat regions: (i) international trade of high-risk agricultural commodities, (ii) cropland accessibility to ports and cities as potential introduction points, (iii) host landscape connectivity, and (iv) spatial projections based on the species' environmental suitability (Fig. 1). Mapping international trade of agricultural commodities – along with cropland accessibility to ports and cities – points out which locations may serve as critical entry points for initial or repeated introductions if a targeted pest or infected vectors inadvertently trespass international borders and successfully overcome biosecurity boundaries (*28-31*). Once a pest is introduced into a new area, host landscape connectivity indicates local spread potential of pests based on host availability and dispersal opportunities between host areas (*32-34*). Likewise, measures based on prevailing climate or edaphic variables indicate which locations in a host landscape are more environmentally suitable for establishment and local spread of an invasive pest (*35, 36*). Together with wind patterns and human transportation networks (not implemented directly in GIRAF1.0) (*25, 27, 36*), these are the main geographic habitat factors facilitating pest invasion and epidemic risk in global plant ecosystems (*12, 37, 38*).

These four transboundary pests have wreaked havoc on solanaceous crops and ornamental industries, with devastating impacts on plant health globally, and possibly affecting natural plant ecosystems. The global value of solanaceous crops (peppers, potatoes, and tomatoes) jointly accounted for US$296 billion in production and US$38 billion in international trade in 2022 (*39*), making them key for food security, income generation, and livelihoods. Over the past century, transcontinental and transoceanic range expansion of these targeted pests on multi-species host landscapes exemplifies both large-scale and local invasions of global ecosystems dominated by large, cultivated plant populations (Fig. S1-4). Reconstructing biogeographic dynamics of these pests belonging to four taxonomically distant groups enabled us to identify which ecological scenarios are frequently plausible in pest invasions. Applying GIRAF on these globally concerned pests allowed us to keep a balance between general invasion dynamics by considering common drivers of species spread (*5, 31*) and idiosyncratic ecological niche differences among invasive species, such as host diversity, and dispersal pathways (*10*)[Note S1-2]. Although this article focuses on these invasives as real-world case studies, GIRAF has practical and cross-disciplinary relevance beyond these studied systems, provided minimal data input is available to reproduce the geographic risk analysis for the invasion of a target plant, animal, or microbial taxa. GIRAF also has multiscale lens (Fig. 1) supporting invasion risk assessments at smaller geographic extents and finer spatial resolutions. Our second objective is to apply GIRAF to understand local invasion risk of the same target pests in Florida and surrounding areas, including Alabama, Georgia, and South Carolina.

Materials and methods

GIRAF relies on four fundamental components, which are not mutually exclusive: (i) defining ecologically or epidemiologically important risk factors, (ii) collecting or compiling fine- or broad-scale data related to these risk factors, like dispersal pathways, species geographic occurrence, and host range, (iii) selecting and (re)training the model(s) based on digitally accessible information, and (iv) generating evidence-based maps of potential priorities for surveillance and mitigation. Risk analysts, policymakers, and biosecurity practitioners can provide periodic feedback on each component's input and iteratively fine-tune the resulting spatial projections of pest invasion risk, particularly if relevant information like informal trade of agricultural commodities is privately or unofficially documented.

Data assembly for ecologically important species traits. We built (i) a geographic distribution spreadsheet including the reported countrywide extent of each pest species, the earliest year of the pest collection or detection in the country, the first year of the country report publication, and georeferenced presence records wherever available; and (ii) a host-parasite association list including plant species naturally or experimentally infected by the pathogen or infested by the pest, and the reported countries of these associations (Data S1). These spreadsheets represent a comprehensive data compilation based on publicly available reports until 2023 including journal articles and official reports by National Plant Protection Organizations (NPPOs). Despite this extensive data compilation effort, global systematic sampling or highly standardized reporting exists is rare for these pest species. While the spread of pests at large spatiotemporal scales cannot always be systematically represented or studied well by small-scale field and laboratory experiments (*40*), 'national- or continental-scale controlled trials' are certainly not pragmatic or realistic at this time (*41*). Alternatively, notwithstanding being systematically incomplete, geographically biased, and often sampled based on convenience, observational distribution data serves as a primary source of empirical information for mapping potential spread of invasive pests across broad-scale crop-growing regions.

For each natural host species listed in the host-parasite association spreadsheet, but unavailable in the CROPGRIDS dataset (*42*), we created maps of relative host density. We manually downloaded species-specific georeferenced occurrence records from the Global Biodiversity Information Facility (GBIF) database on July 5th, 2024 (*43-45*). In a global map with grid cells of about 2.3 km at the equator (or 1.25-minute spatial resolution), we assigned each grid cell the square root of the number of presence records of host species, or 0 if there were no georeferenced records. These global maps represent the geographic distribution of individual plant species at a relatively high spatial resolution and are expected to be highly biased in places where sampling effort is smaller. We thus aggregated each map at a ~55 km resolution (i.e., 0.5° per grid cell), calculating the mean grid cell values at coarse resolution, and expecting to partially reduce sampling bias (*44*). These maps represent a first approximation of relative host density; future approaches could train species distribution models to provide better maps of each host. For cultivated natural host species of each pest, we obtained global maps of crop-specific harvested areas available in the CROPGRIDS dataset, which are more accurate than maps built from GBIF records of crop species.

Spatial coverage. Below, each analysis targeted two geographic extents. Global analyses are presented at 0.5° spatial resolution. Each trained model also produced risk maps for each pest focusing on Florida, Alabama, Georgia, and South Carolina resampled at 3' spatial resolution.

Mapping invasion risk based on species bioclimatic modelling. We obtained global gridded maps of the 19 bioclimatic variables from CHELSA Bioclim, representing climates for 1989-2013 (*46*), and of 12 soil properties from SoilGrids 2.0, representing edaphic conditions at 15-30 cm standard depth (*47*). We also gathered 13 available maps of physical accessibility of the mainland and islands, representing travel time to ports and cities (*48, 49*). Four maps represent accessibility to airports and maritime ports, each aggregated at one of four port sizes. We assigned individual weights to each port size map because each may have a different degree of importance to the entry of commodities and associated pests (Table S1). We then built an overall accessibility index to ports (A_p) as a weighted average of accessibility to individual port sizes. The remaining nine maps represent accessibility to urban and rural locations, each aggregated at one of nine settlement classes. We assigned a different weight to each settlement class to calculate a weighted average of overall access to cities (A_c) across the nine settlement classes (Table S2).

We trained four probabilistic machine learning algorithms – MaxEnt, random forest, XGboost, and logistic regression – which are commonly used for presence-only data (*35, 50*). Each algorithm represented a correlative species distribution model (SDM), in which the response variable was 1 for reported georeferenced presence records and 0 for pseudo-absences (i.e., background points randomly selected from a world land map). Each SDM was initially trained and evaluated on the following selected predictor variables: annual mean temperature, mean diurnal range in temperature, isothermality, annual precipitation, precipitation seasonality, chemical soil properties (pH, and soil organic carbon content), physical soil properties (clay, sand and silt content), port accessibility (A_p) and city accessibility (A_c). These predictors are a subset of all variables available in each dataset considered, allowing us to avoid multi-collinearity, while still maintaining a substantial variation of ecologically relevant covariates. These initially trained SDMs indicated A_p as the most important variable explaining the reported distribution of each invasive species (54%, 27%, 72%, 53% contribution in presence predictions for PSTVd, RSIIB-1, ToBRFV, and *P. absoluta* based on MaxEnt, respectively; Data S1). However, we excluded the contribution of port accessibility in the final predictions by each SDM. Instead, we adopted a mechanistic approach for analyzing both A_p and A_c along with international trade, and host distribution to consider explicitly the individual ecologies of each invasive pest (see below).

This multi-model approach was used to generate a global map of ensemble predictions, which equally weighted the spatial projections of these four SDMs, as a quantitative consensus approximation of abiotic environmental suitability for each invasive species. These species-presence predictions based on occurrence-environment associations are an initial and provisional approximation for a species' environmental suitability since true mechanistic ecological interactions between abiotic environmental conditions and invasive pest occurrence have generally not been characterized quantitatively (ecological niche modelling). Importantly, some locations are likely to have a higher climate suitability than predicted by the ensemble approximation, which will be discovered as each pest continues invading new environments and geographical spaces. We lack a quantitative understanding of how edaphic or climate conditions directly restrict or facilitate geographic occurrence and each stage in the life cycle of these invasive species, which is a prevalent situation for non-vector-transmitted plant viruses causing infectious diseases (a knowledge gap in plant virus ecology). However, once this ecological information becomes available, process-based, component-based, or mechanistic models for these pest species can be preferentially used to explicitly incorporate direct climate effects on pathogen distribution or a species' physiological response to environmental conditions.

We adjusted our probabilistic bioclimatic ensemble with known environmental parameters for each species (model calibration). We used Shelford's law of tolerance to adjust the maps of ensemble predictions of environmental suitability for *Phthorimaea absoluta* and RSIIB-1. The law of tolerance states that an organism's success is determined by a set of certain minimum, optimum, and maximum environmental conditions (*51*). Using this ecological principle, we applied a generalized beta distribution model to project the potential invasion risk as a response function dependent on temperature (*52, 53*). In this thermal niche model, invasion risk ($r(T)$) depends on three cardinal temperatures for a species' population development (Data S10): the minimum temperature (T_{min}), optimum temperature (T_{opt}), and maximum temperature (T_{max}). We used the monthly mean temperature of each location ($T_{x,y}$, where x and y refer to geographic coordinates) in the world to estimate pest invasion risk locally:

$$r(T) = \max\left\{0, \left(\frac{T_{max}-T_{x,y}}{T_{max}-T_{opt}}\right)\left(\frac{T_{x,y}-T_{min}}{T_{opt}-T_{min}}\right)^{\frac{T_{opt}-T_{min}}{T_{max}-T_{opt}}}\right\}.$$

Invasion risk is highest at locations with T_{opt}, decreases at temperatures higher or lower than T_{opt}, and reaches zero beyond critical thermal limits tolerated by a species (below T_{min} or above T_{max}). This temperature-driven physiological response is common in arthropods, plants, nematodes, fungi, and bacteria, and applies to *P. absoluta* as well as the cold-tolerant RSIIB-1 strains (*54-56*). Here, cumulative pest invasion risk in a location over a year is proportional to the sum of $r(T)$ of each month. We regarded climatically unfavorable locations as those with $T_i < T_{min}$ or $T_i > T_{max}$, defining geographically possible thermal range frontiers of a species.

Surface water such as rivers may serve as an aquatic habitat for the dissemination, survival, inoculum source, and evolution of plant pathogens in almost every major taxonomic group (*57-59*). We incorporated river networks in GIRAF as a possible plant health risk and a dispersal pathway for RSIIB1. Using the HydroATLAS database (*60*), we calculated the mean river water discharge as a relative proxy for the likelihood that RSIIB-1 would disperse to any climatically suitable location globally. No information was available about the direct effect of environmental variables on disease risk caused by ToBRFV and PSTVd.

We cross-validated each SDM individually using ten folds and 1000 iterations. The model's average accuracy ranged between 0.9 and 0.96, 0.85 and 0.92, 0.83 and 0.98, and 0.61 and 0.73 for MaxEnt, random forest, XGBoost, and logistic regression. Each algorithm effectively identified an environmental signal for each pest species that is different from random variation (i.e., accuracy > 50%). Among SDMs, MaxEnt had the highest accuracy for predicting the occurrence of each pest species. Georeferenced occurrences capture only a fraction of the reported geographic distribution of each invasive species. We used the country-level distribution without georeferenced occurrences of an invasive pest as a geographically and statistically separate dataset (test data). We calculated the number of pixels with > 50% presence likelihood in each country of the test dataset averaged across SDMs as a performance metric for the ensemble predictions.

Mapping (re)introduction risk based on international trade of crop commodities

As a candidate precursor to developing safe trade strategies, we characterized the structure of trade networks to identify likely geographic paths of pest spread and the relative risks of locations to each pest species' potential initial or repeated introduction(s) (*10, 12, 18*). Hereafter, we define invasion risk as the relative likelihood that a pest or pathogen (i.e., hazard) potentially reaches or occurs in a host location (*13, 14, 32*). In all our analyses, we used relative indices to estimate the likelihood of spread of an invasive species as approximations for invasion risk. In the global trade networks, specifically, we quantify the relative likelihood of potential spread of an invasive species through the international trade of agricultural commodities.

We gathered information on the trade volume of crop-specific commodities between each pair of countries, based on bilateral import reports in the World Trade Organization (WTO, https://stats.wto.org/) dataset for 2005-2019 and Volza (https://www.volza.com/) dataset for 2023. Our proxy for host availability within a country was the harvested area of crop species reported to be natural major hosts of each pest (Data S1), for crop species available in the FAOSTAT (https://www.fao.org/faostat/en/#data) dataset. To account for the potential effect of pest-associated trade policy landscapes, we also obtained information on international biosecurity measures targeting specific pest species, whenever available. We compiled information on the geographic extent of each pest within a country (Data S1), based on available reports in CABI Compendium, EPPO Global Database, and extensive literature scanning. In these international trade networks, nodes represent countries and link weights indicate the relative potential of pest spread between countries.

We propose the trade index for potential accidental pest movement from an exporting country i to an importing country j (or $\tau_{i\rightarrow j}$) as a quantitative proxy characterizing pest invasion risk in trade networks. For any pair of trading countries, $\tau_{i\rightarrow j}$ combines explicitly and quantitatively the geographic extent of a pest species within trading countries, the host availability in trading countries, the trade volume of crop-specific commodities between countries and, whenever available, pest-specific biosecurity measures implemented by trading countries. Note S1 provides details of the methodological approach, mathematical formulations, theoretical assumptions, and available datasets used to quantify invasion risk (or $\tau_{i\rightarrow j}$) through international trade networks. We assumed that the joint relative chances that none of the exporting countries are likely to introduce the pest species into a target importing country j is $\prod_{k=1}^{z}(1 - P(\tau_{i_k\rightarrow j}))$, where z is the number of countries exporting a crop-specific commodity to country j. Finally, we assumed that the joint risk (I_j) that the target pest is introduced into a country from any exporting countries is directly proportional to $1 - \prod_{i=1}^{z}(1 - P(\tau_{i_k\rightarrow j}))$. Alternatively, we calculated four network metrics to characterize the potential introduction risk of a pest species to a country (i.e., I_j): node in-strength, betweenness centrality, and eigenvector centrality. These network metrics were important for pest or pathogen transmission in epidemic network (*61-63*).

Our geographic risk analysis on the potential (re)introduction of the four invasive species focused on individual networks of the reported international trade of specific agricultural commodities. For PSTVd, we analyzed networks of international trade of potato seeds (i.e., potato tubers for 2005-2019) and planting material of *Brugmansia* (2023). For RSIIB-1, we evaluated the international trade of potato seeds, tomato fruits, pepper fruits (2005-2019), and geranium planting materials (2023). For ToBRFV, we built individual networks of international trade of tomato fruits (2005-2019), tomato seeds, and pepper seeds (2023). For *Phthorimaea absoluta*, we assessed the international trade network of tomato fruits (2005-2019). These target commodities are important for the international dispersal of the pests of interest, given their reported specific association with the interception of these pest species (Data S1). We also focused the (re)introduction risk analysis on the international trade of these fresh crop commodities because of their potential higher likelihood in the geographic diffusion of these invasive pests, excluding processed agricultural products which may have a negligibly reduced risk. Future risk analyses could include explicit information on other primary dispersal pathways of these invasives in the longer term, like the international trade of crop-specific seed and ornamental material. Information on the international trade of crop-specific seeds or planting material over multiple years is publicly unavailable. We assumed a reduction in the introduction risk by 10% from countries with market access to the United States and imposed import biosecurity requirements. The list of countries with pest-specific biosecurity regulations is available in the 2024 Federal Order for U.S. imports of tomato and pepper seeds for ToBRFV, and the 2023 Federal Order for U.S. imports of tomato fruit for *P. absoluta*. We also focused on the introduction potential of each pest species associated with commodity imports to the USA and countries in the Caribbean Region, providing a regional assessment as a pilot experiment (a global analysis for each pest is available in Fig. S1-2).

We used country-level interception data for each pest species as an “independent” dataset to validate the (re)introduction risk analysis (Data S9). In the (re)introduction risk analyses, we used this data to determine which agricultural commodities are likely important for the international spread of each pest (Table S5), but we excluded a large part of the information about pest interceptions in specific countries (unless they were the only report available for the presence of a pest in a country). We assessed the precision of the (re)introduction risk analysis, that is, the ratio between the number of countries where the pest has been intercepted on imported agricultural commodities and introduction risk was non-zero (true positives) and the number of countries where the pest has been intercepted on imported agricultural commodities. Our analysis had a precision of 1, including all countries where the pest has been intercepted (Table S7). Using the Kolmogorov-Smirnov test, we also evaluated whether countries where the pest has been intercepted have a higher (re)introduction risk than any other countries. The KS test indicates that there is no statistically higher or lower introduction risk in countries where the pest has been intercepted (Table S7). As expected, the null hypothesis is supported because we included all the information available for the geographic distribution of each pest in our analysis. Our interpretation is that pest re-introduction is possible in most countries importing high-risk commodities, given that pest interceptions occurred in countries having a range of risk values.

Mapping invasion risk based on accessibility to ports and cities

Ports likely play a pivotal role in the (re)introduction of plant pests to a region as they may serve as primary entry points of pest-associated agricultural commodities (*5, 12*). Geographic proximity to ports generally increases the risk of introducing invasive plants, arthropods, and pathogens (*5, 28, 64-66*) and our SDMs indicated a potential major role of access to ports in the geographic distribution of each target pest. We thus assume that accessibility of croplands to ports or urban areas in a region increases (re)introduction risk of plant pests. While accessibility of croplands to ports may indicate invasion risk associated with the initial destination of imported commodities in a country, accessibility of croplands to cities may indicate invasion risk associated with urban agricultural landscapes and the final destination of commodities (*67, 68*). Specifically, we hypothesized that invasion risk associated with accessibility to ports and cities occurs in a pattern analogous to species richness resulting from species-accumulation models, where the cumulative number of species scales in an exponential pattern with sample size, area, or intensity (*69*). In our view, invasion risk of cropland locations in a region increases nonlinearly with accessibility to ports (A_p) following $I_p \propto 1 - \exp\left(-1/log\left(A_p\right)\right)$ or with accessibility to cities (A_p) following $I_c \propto 1 - \exp\left(-1/log(A_c)\right)$, where I_p and I_c range from 0 to 1.

For each invasive species, we generated a map combining the joint risk of countries to a pest’s potential introduction through international trade and the invasion risk given the access of croplands to ports in a country ($I_j \times I_p$). This resulting map aims to disaggregate the accidental introduction risk of pest species via international trade (I_p) into likely domestic distribution of imported agricultural commodities and their associated pests across initial entry locations. These maps of invasion risk can be fine-tuned in future geographically explicit evaluations, as domestic distribution of commodity trade and local spread of associated pests may vary geographically among commodity types (*28*). Information about origin location, ports of entry, and final city destination of imported agricultural commodities specifically associated with a target pest species is usually publicly unavailable.

Mapping invasion risk based on multi-host landscape connectivity

Our target invasive pests have a multi-species host range, likely constraining their potential distribution in regions where a host plant is unavailable [biotic filtering] (*70*), but increasing pest spread risk if susceptible host populations are homogeneously and densely distributed in the landscape [facilitation effect] (*71-73*). Geographic host distribution is a critical risk factor to account more realistically for biotic interactions in ecological niche modelling of plant disease (*14, 19, 70*). We categorized each plant species reported to be naturally infested by a pest as major or primary host(s) and minor or secondary hosts (Data S2). We assumed that natural secondary host species play at least a minor role in pest persistence or survival (*10, 74*). To map the geographic distribution of multiple natural host species, we used a stacked host distribution modeling approach (*14*), summing the relative density of major host(s) and secondary hosts to produce a global map of cumulative host density for each invasive pest. In these stacked host maps, we considered the potential minor role of secondary host species in pest invasion risk and potential spread by multiplying their host densities by a tenth (*12*). For crop species being natural host of a pest species, our analysis included only locations represented by 3-minute cells having ≥ 4 hectares of cropland (i.e., a host density threshold of ~0.1%), because we assumed a rare-species advantage against density-dependent diseases in excluded host locations (*71*). We then aggregated these resulting maps to a coarser spatial resolution so that each grid cell represented approximately 55.5 km × 55.5 km at the equator.

Using these global maps of cumulative host density as inputs in the geohabnet R package (*75*), we evaluated the host landscape connectivity for each pest species as proposed (*32*). Geohabnet is a component of the R2M toolbox for rapid risk assessment to support mitigation of pathogens (www.garrettlab.com/r2m). Geohabnet estimated the relative likelihood of pest movement (σ) between host locations i and j using two generic gravity models for species dispersal (*76-78*): $\sigma_{ipl} \propto c_i^k c_j^k \left(\frac{d_{ij}}{111{,}319.5}\right)^{-\beta}$ for the inverse power-law model and $\sigma_{ne} \propto c_i^k c_j^k e^{-\gamma\left(\frac{d_{ij}}{111{,}319.5}\right)}$ for the negative exponential model. In these global dispersal models, potential pest movement (σ_{ipl} or σ_{ne}) depends not only on the product of relative abundances of susceptible host species in both locations ($c_i^k c_j^k$), but also on the probability of a pest moving between host populations given their physical distance (d_{ij}). We set $k = \frac{1}{2}$ to account for potential nonlinear associations between host density and pest invasion risk (*79*). We compiled β and γ dispersal parameter values that were empirically estimated for a diverse set of plant pathogens and arthropod pests (Data S2). We used this dataset to calculate each dispersal parameter's first quartile, mean, median, and third quartile across pest species, representing a parameter space of highly likely pest spread scenarios. We evaluated these typical parameter values (0.9, 1.5, 1.7, 2.1 for β and 0.02, 0.08, 0.36, 0.24 for γ) in a sensitivity analysis to account for uncertainty in pest movement. Species-specific dispersal parameter values are unavailable for each target pest. We then built pest invasion networks, where a node represented a host location, and link weights indicated potential pest movement between host locations (σ_{ipl} or σ_{ne}). We calculated host landscape connectivity based on six standard network metrics in epidemiology and invasion ecology (*22, 38, 61, 80-82*): betweenness centrality, closeness centrality, eigenvector centrality, node strength, PageRank centrality, and sum of nearest neighbors' node degrees. Here, global maps of invasion risk represent the multi-host landscape connectivity for a target invasive pest, averaged across two gravity models, eight typical dispersal parameter values, and six standard network metrics with equal weighting (Code Vignette S1). Host landscape connectivity indicates the average relative likelihood of an invasive pest potentially spreading from a target host location to all its functional neighbors in a landscape if the invasive pest reaches the target location**.**

We assumed separately that pest survival is more likely in areas where the host species richness of a pest is higher than where only one host species is reported (*14*). We used georeferenced occurrence data for each pest species as an independent dataset to validate the multi-host connectivity estimates. We used two metrics to assess model performance based on presence-only data. First, precision is the ratio between the number of grid cells where the target pest has been reported present and the multi-host connectivity is nonzero (true positives), and the number of grid cells where the target has been reported present (true positives + false negatives). Second, we assessed whether multi-host connectivity is higher in locations where the pest is reported present than elsewhere. To assess this hypothesis, we conducted an asymptotic two-sample Kolmogorov-Smirnov test. The multi-host connectivity analyses had good precision (from 0.68 to 0.87; Table S6). The KS test revealed that multi-host connectivity tends to be higher in locations where the pest is present than elsewhere ($p < 0.001$, Table S6), supporting a likely major role of multi-host connectivity in driving the spatial occurrence of each pest.

Computational requirements. Global host landscape connectivity analyses require high-performance computing resources. For example, each analysis of host landscape connectivity based solely on betweenness centrality in the Eastern Hemisphere required using 40 CPUs and 80 GB of memory for 110 hours in the University of Florida HiPerGator.

Code availability. A template for processing R-scripts (source code) of each analysis in this study is publicly available in GitHub repositories: https://github.com/AaronPlex/pestradenet for international trade networks, https://github.com/AaronPlex/pest-env-sdm for environment-based SDMs, and https://github.com/AaronPlex/multi-host-nets for the host connectivity analysis.

Data availability. All unpublished datasets supporting results and reproducibility of this study are publicly available as supplementary material. All published datasets used in this study are correspondingly cited.

2. Results

Pest introduction risk based on trade networks of agricultural commodities

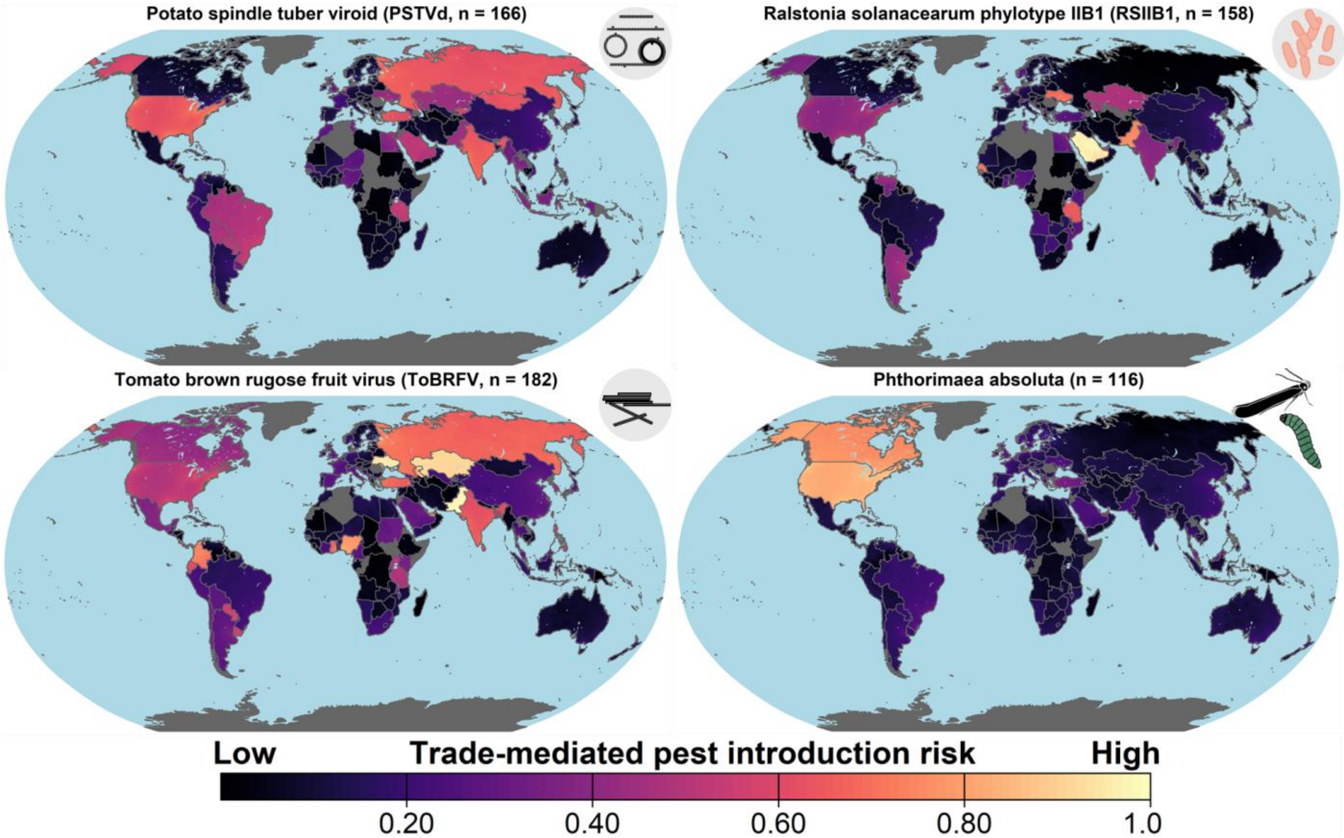

Fig. 2. Cumulative potential of (re)introduction for four invasive plant pests. This risk analysis considers international pest-specific commodity pathways, pest distribution at the country level, major crop host availability at the country level, and accessibility to ports. n is the number of importing countries with a possible introduction risk through international trade of agricultural commodities. Countries in grey have no reports of international trade of these commodities. Pest silhouettes are not drawn to scale.

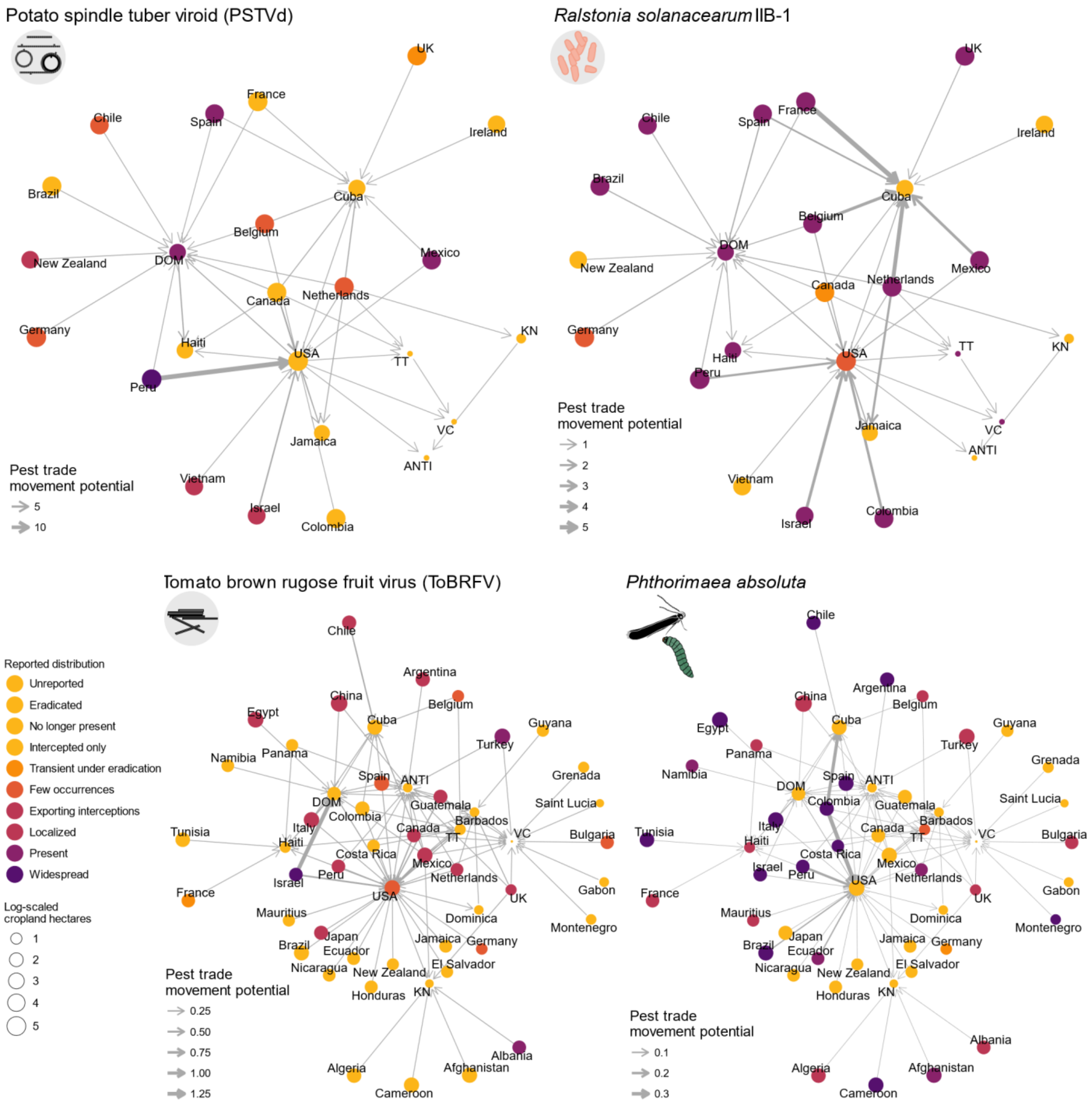

Fig. 3. Potential geographic spread routes of pathogens and pests through international trade networks in the Caribbean region and United States. Countries closer to the center of the trade networks have higher risk of pathogen or pest introduction via trade of high-risk crop commodities. Node size indicates the availability of crop species that are hosts of a pest. Pathogen or pest invasion potential and trade movement potential are relative rankings useful to compare invasion risks within (not between) trade networks. Abbreviations: ANTI – Antigua and Barbuda, DOM – Dominican Republic, KN – Saint Kitts and Nevis, TT – Trinidad and Tobago, VC – Saint Vincent and the Grenadines. Pest silhouettes are not drawn to scale.

Given resource scarcity, long-term prevention of pest invasions into new host areas is increasingly challenging for National Plant Protection Organizations (NPPOs). While local sentinel surveillance and invasion management should continue actively and recursively in pest source regions (Fig. S-4), proactive surveillance could target potential pest movement among large-scale habitat regions unintendedly mediated by international trade (Fig. 2). There is a global concern regarding the invasive pests studied here, yet each species lacks a global risk assessment, except for *P. absoluta*, which has a global map for climate-based risk. GIRAF identified candidate hotspot areas with relatively high pest introduction potential based on historical trends in global trade of pest-associated crop commodities (Fig. 2). If this historical pattern in international trade continues, crop commodity destinations with a high relative potential of trade-mediated pest introductions globally include solanaceous crop ecosystems in the USA, Niger, Saudi Arabia and Egypt for PSTVd; Pakistan, Tanzania, Saudi Arabia, and Senegal for RSIIB-1; Ukraine, United States, Canada, and Kazakhstan for ToBRFV; USA, Canada, Bahrain, Kuwait, and UAE for *P. absoluta* (Fig. 2). GIRAF emphasized these countries because they are major large-scale crop host producers. However, preventing pest introduction via safe international trade poses a broader challenge. Specifically, international trade networks of crop commodities involve many host-growing countries potentially acting as commodity destinations (Fig. 2), each pest has a global yet scattered distribution, and many countries exporting agricultural commodities may serve as possible pest source pools (Fig. 3). Historically, international trade of specific agricultural commodities has played a major role in the rapid spread of these target pests across the world (Fig. S1-4).

GIRAF also allows assessing pest introduction potential focused on specific geographic regions. For example, if the goal is proactive surveillance prioritization in the USA and the Caribbean region, GIRAF identified key regional hubs in international trade networks where the (re)introduction of each target pest is likely. These regional hubs consist of host-growing countries that import pest-associated crop commodities from many regions where a target pest is present. The USA, the Dominican Republic, and Cuba serve as regional trade hubs in this region, presenting a potential introduction risk for each target pest (Fig. 3). Likewise, Saint Vincent and the Grenadines, Antigua and Barbuda may act as possible hubs exposed to ToBRFV or *P. absoluta* (re)introduction. Lastly, GIRAF distinguished spatially explicit potential movement pathways for each target pest (Fig. 3) among these large-scale habitat regions. For example, Cuba imported potato seed from nine countries: these international trade activities represent a high movement potential for RSIIB-1 but a low movement potential for PSTVd (Fig. 3). Similarly, the USA imported tomato commodities from 27 countries: these trade connections provide a possible movement pathway for *P. absoluta* from Peru, Colombia and Brazil, but they have a low movement potential for ToBRFV.

Pest invasion risk based on environmental suitability

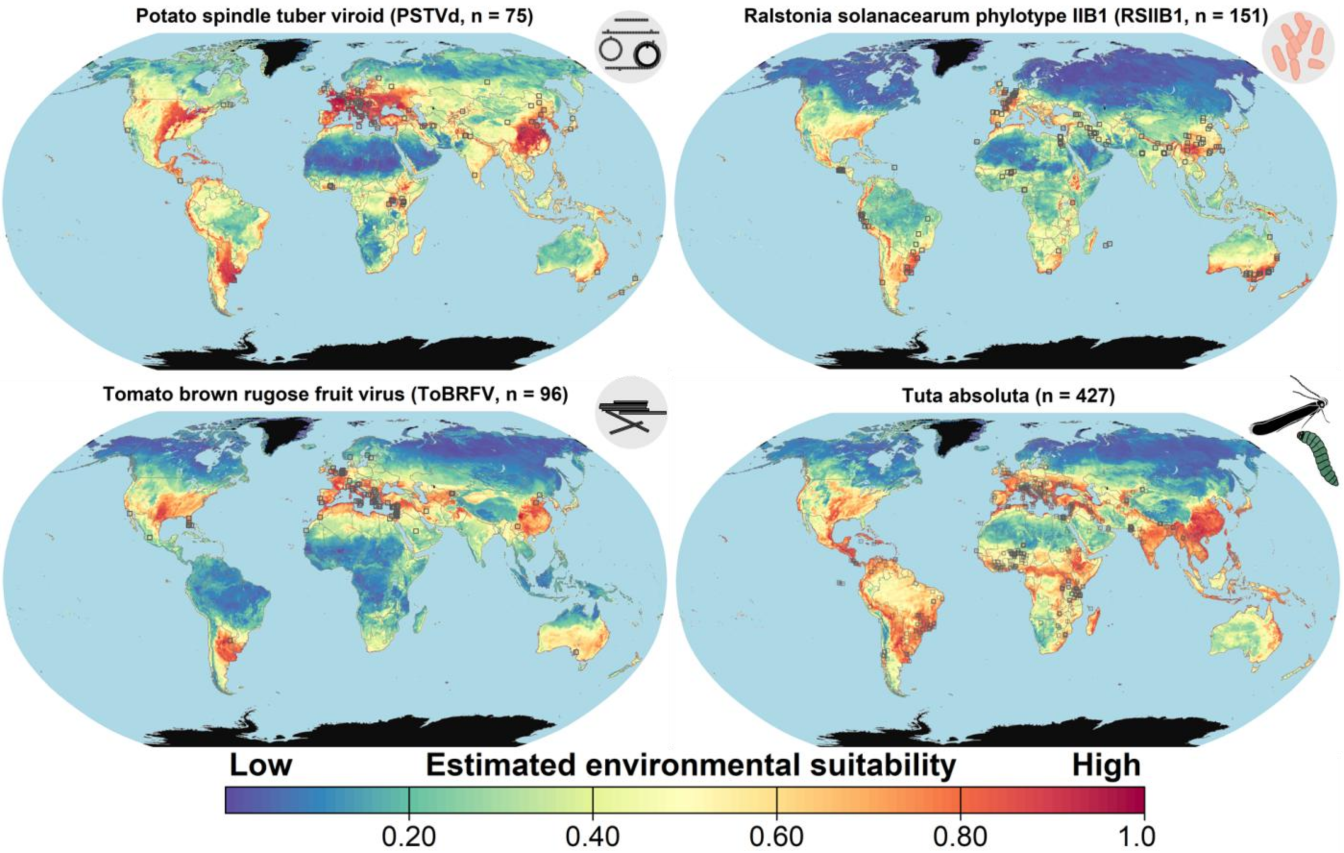

Fig. 4. Global risk hotspots for four invasive pests based on an ensemble of spatially implicit and environment-based machine-learning models. Sample size (n) is the number of historical georeferenced pest outbreak observations (black square outlines) used to train individual species distribution models. Black pixels are locations where the ensemble model predicted to be environmentally unsuitable. Pest silhouettes are not drawn to scale.

After a species' introduction, national early warning systems need to determine the degree and extent to which the local environment is suitable for establishment and spread of any invasives. In GIRAF, a suitable environment for pest invasions depends on climatic, edaphic, and hydrological conditions. Here, GIRAF inferred environmental suitability from a machine learning ensemble model trained on the most comprehensive compilation of geographically distinct outbreak observations of each target pest in the last century. This environment-based modelling approach successfully predicted the currently reported georeferenced range of each target pest (Fig. 4, average model accuracy ranging between 61% and 96% depending on the model used). The pandemic distribution of these pests calls for a globally coordinated invasion mitigation system that consistently responds to possible recurring outbreaks in already affected areas and is adapted by biosecurity agencies and plant industries to regional circumstances. Proactive response should also become routine beyond current invasion hotspots and GIRAF identified these key surveillance targets. The environmentally informed model in GIRAF provides key spatial predictions beyond reported geographical ranges of each target pest, indicating that some locations might be environmentally suitable for pest development under current conditions. For each target pest, these potential environmentally suitable locations with >50% likelihood of invasion include a large area throughout China, and an eastern region in Australia (Fig. 4). Other possibly suitable areas are specific to each target pest. For example, Southeastern USA and the US Pacific Coast are likely climatically suitable areas for RSIIB-1. If these pests are allowed to reach currently uninvaded areas through natural or human-mediated means, each target pest would have a potential broader geographic range for invasion globally. Preventing further range-expansion of these global pest risks requires (pro)active surveillance programs coordinated by international plant health communities.

Pest invasion risk based on multi-host landscape connectivity

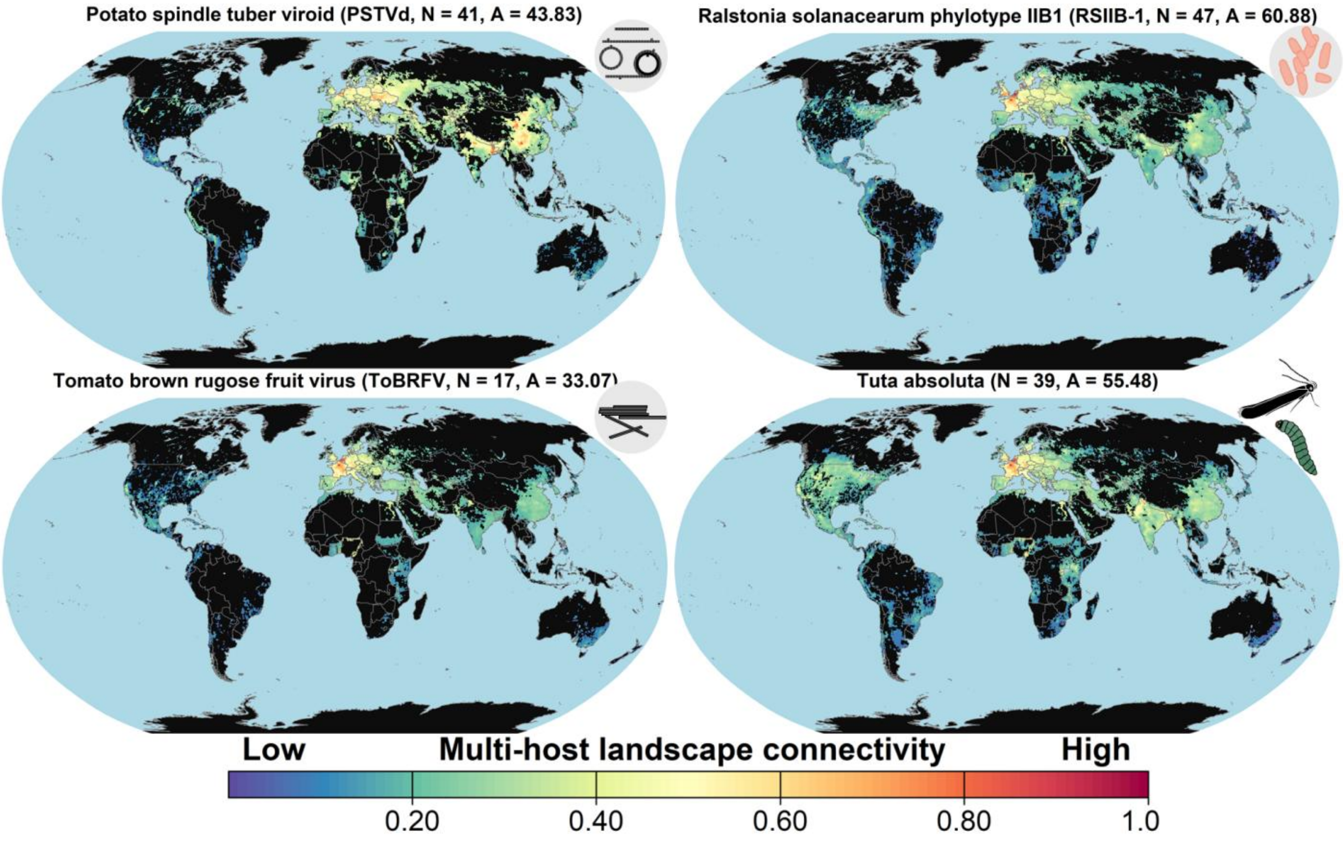

Fig. 5. Global risk hotspots for four invasive pests based on multi-host landscape connectivity. Color gradient represents the magnitude in mean host landscape connectivity of each location, calculated across a highly likely range of dispersal parameters. Global host community properties include the number of naturally infected host species used for the host connectivity assessment, including cultivated, weedy and wild species (N) and the land surface area with hosts available measured in million square kilometers (A). Grid cells in black are locations where host is not reported. Pest silhouettes are not drawn to scale.

GIRAF offers an innovative approach to mapping the global distribution of multiple hosts of a target pest using publicly accessible databases. Previous approaches provided global single-species (usually crop) assessments and occasionally national multi-species assessments. GIRAF provides a global or local multi-species connectivity assessment of crops and non-cultivated hosts associated with a target pest. Here, host connectivity refers to the relative likelihood of spread of a pest between host locations if the pest reaches a target location in the host landscape, all else being equal. GIRAF quantifies this potential functional host connectivity based on host availability (structural connectivity) and a highly likely range of pest dispersal parameters (see Methods). Mapping multi-species connectivity helped us understand possible local spread of each target pest in a realistic heterogeneous host landscape. This comprehensive approach identified candidate surveillance priorities, from possible structural geographic barriers where a host is unreported to spatially contiguous host areas and spatially fragmented host habitats.

Host availability strongly correlates with mean host connectivity (Spearsman's $\boldsymbol{r_s}$ = 0.62 for PSTVd, 0.81 for RSIIB-1, 0.65 for ToBRFV and 0.80 for *P. absoluta*, $\boldsymbol{p}$ < 2.2e-16), so highly dense host communities commonly have high functional connectivity. This pattern is also supported by small differences in ranks for locations with high host connectivity and high host density (Fig. S10). For example, Europe, Southern Asia, and China have a homogeneously dense host landscape that is likely to facilitate the local spread of each pest (Fig. 5). A homogeneously dense host landscape for *P. absoluta* is available throughout Central and North America (Fig. 5). However, within-continent host communities in the Americas and Africa are spatially fragmented for PSTVd, RSIIB-1 and ToBRFV. Despite this structurally spatial habitat fragmentation, chances of pest movement due to functional host connectivity in the Americas and Africa are proportionally greater than if we consider only host availability. For example, California, Burundi, Rwanda and a western region in Kenya have particularly high functional host connectivity for PSTVd, RSIIB-1 and *P. absoluta*. These highly connected host communities are potentially effective spread paths if the pest reaches these locations.

In the Americas, there is a conterminous host belt throughout the Andes for the potential natural dissemination of each target pest. Panama is possibly a non-host disconnection for the natural spread of PSTVd, ToBRFV, and *P. absoluta*. Nonetheless, a contiguous host landscape in Central America is expected to act as a structural and functional bridge zone for the potential gradual spread of RSIIB-1 between North America and South America. Reported host availability is scattered throughout Africa, especially for PSTVd and ToBRFV. However, a landscape along the northern and eastern border of Nigeria has a high host connectivity for each target pest (Fig. 5). This host landscape fragmentation in Africa requires a future assessment of unreported host distribution influencing potential spread of these pests. Considering only croplands substantially underestimated invasion risk compared to a multi-species host assessment for each target pest. Host species richness was weakly negatively or positively correlated with functional host connectivity (Spearsman's $\boldsymbol{r_s} = -0.04$, $\boldsymbol{p}$ = 1.486e-13 for PSTVd; $\boldsymbol{r_s}$ = 0.31, $\boldsymbol{p}$ < 2.2e-16 for RSIIB-1; $\boldsymbol{r_s}$ = 0.19, $\boldsymbol{p}$ < 2.2e-16 for ToBRFV; and $\boldsymbol{r_s}$ = 0.49, $\boldsymbol{p}$ < 2.2e-16 for

P. absoluta). We thus expect that cross-species transmission of these pests is more likely in highly connected host locations, especially if crop ranges spatially overlap with non-cultivated host species.

Pest invasion risk based on a biogeographical multi-dimensional assessment

Each component of GIRAF provides an individualistic invasion risk perspective, and decision-makers can use each risk factor map individually as a first approximation for a pest's invasion risk when geographic information of other ecological factors is lacking. Each component represents a static snapshot of a pest's potential geospatial distribution and a dimension of its spatially referenced ecological niche. Trade and transportation networks are proxies for (re)introduction pressure (long-distance dispersal niche), environmental suitability may capture environmental requirements of a target invasive (environmental niche), and host landscape connectivity highlights spatial patterns of a pest's spread through a landscape of susceptible hosts (trophic niche). GIRAF reconciles these different geospatial perspectives on a multidimensional analysis of invasion risk, representing a second ecological approximation of the relative likelihood of a pest's spread success or the potential invasion risk posed by a pest (Fig. 6). We applied the biotic, abiotic, and migration (BAM) framework (*7, 14*) to generate combined estimates of potential geographic distribution and the likely spread of an invasive species. Specifically, we considered that geographic locations where high levels of host landscape connectivity, predicted environmental suitability, and international trade along with accessibility to ports intersect are highly likely suitable geographic areas for a species' invasion (Fig. 6). This multicriteria biogeographical approach also aligns with the three widely recognized components necessary for plant disease development (i.e., environmental conduciveness, host susceptibility, and pathogen aggressiveness) in a geographical space [landscape epidemiology] (*41*). To our knowledge, GIRAF is the first pest-specific, use-inspired, and spatially explicit meta-model integrating real-world data on major drivers of pest invasions on global natural and agri-food ecosystems.

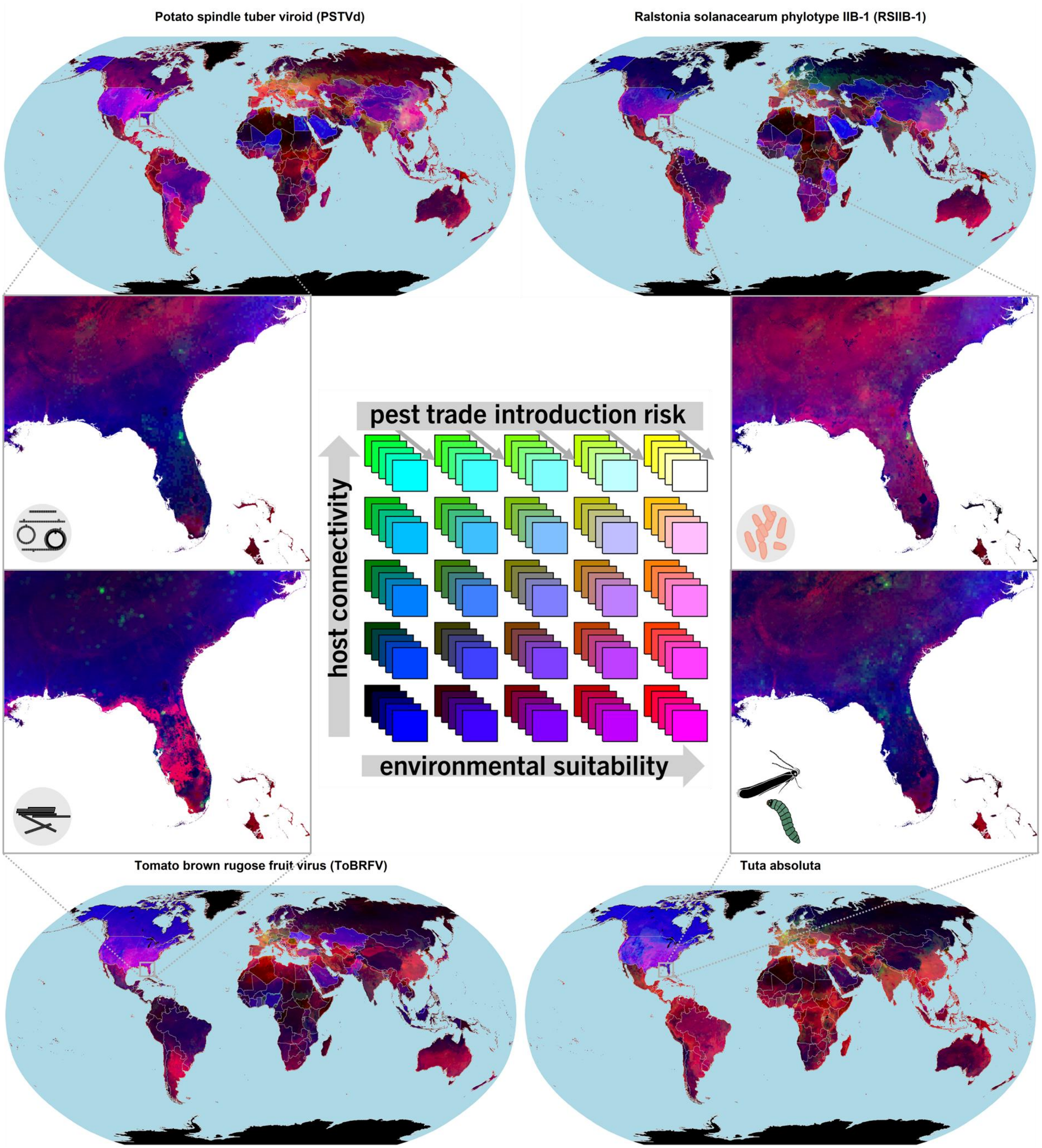

Fig. 6. Worldwide pest invasion risk based on a multi-dimensional assessment. In these multivariate choropleth maps, the intensity of each primary color represents the invasion risk level of a target pest based on environmental suitability (or environmental niche, red spectrum with low values in the left columns to high values in the right columns of the legend), host landscape connectivity (or trophic niche, green spectrum with low values in the bottom rows and high values at the top of the legend) and international trade of crop commodities (or dispersal niche, blue spectrum with low values across the base layer and increasing with layers at the front of the legend). Grid cells in black indicate areas with no invasion risk (e.g., Antarctica) and pale-yellow grid cells indicate highest-risk areas for a pest invasion where high levels of the three risk factors overlap. For example, grid cells in orange have a high environmental suitability and relatively low levels of host connectivity and trade-mediated introduction risk.

By mapping at-risk locations for potential pest spread based on three major ecological risk factors, GIRAF provides a starting point for global invasion preparedness and spatially explicit surveillance prioritization. The highest levels of these three major risk factors rarely coincided. Globally, Central Europe, India, and northern China, where the pests are present, have relatively high levels of each risk factor (Fig. 6). GIRAF allows us to identify areas where high levels of pairs of risk factors coincided. For example, large areas in the USA have high (re)introduction risk and high environmental suitability but reported host distribution may be a limiting factor. Lastly, GIRAF provides a multi-scale lens to account for likely scale-dependent processes in invasion risk. At a finer spatial resolution, GIRAF revealed better-informed patterns of invasion risk for Florida and surrounding areas (Fig. 6). For example, northern Florida had moderate levels of each risk factor for each target pest. Identifying these fine-scale patterns might be difficult in global analyses.

3. Discussion

Protecting plant health from invasive pests is key to holistically safeguarding agroecosystems' provision and natural ecosystems' functioning, especially in co-response to 21st-century global challenges like resource depletion, plant pandemics, and climate change. GIRAF 1.0 provides critical points for constructing geographic surveillance and mitigation strategies of species-specific invasive pests. GIRAF 1.0 provides a key advance for improving pest invasion risk assessments, by integrating four ecologically meaningful drivers of invasive species spread globally. Specifically, we focused on which, how, and where risk factors may be important for pest invasions (geographic risk quantification).

Here, GIRAF quantified potential risk hotspots for four pests of global concern, using species-specific biogeographic models of trade-mediated (re)introduction potential, environmental suitability, and host landscape connectivity for a contemporary timespan. Our results provide the first quantitative assessment of invasion risk for plant pests across these geographic factors globally. We provide new evidence that host communities for each target pest occupy $\sim 33.1\text{-}60.8\times10^6$ km^2 or ~22-37% of Earth's land surface. Europe and Southeast Asia have a highly suitable environment and high multi-host connectivity for each pest. The global trade networks of high-risk commodities associated with each target pest include over 100 countries. The USA ranks among the top five countries with trade-mediated (re)introduction potential, and some regions of this country are environmentally suitable for pest invasion.

These findings may have high uncertainty for invasion risk of these pests in some regions, where host availability is not reported, informal trade of planting materials occurs, implemented phytosanitary measures are not openly accessible, and along international terrestrial borders. Despite these unquantified uncertainties, our findings call for planning (pro)active responses to and effective plant protection strategies against future pest outbreaks (Fig. 1). These responses include: (1) proactive surveillance should target regions where each pest is unreported, but which have high invasion risk (Fig.2-4); (2) making international trade networks safe needs enhanced pest-specific biosecurity in over 100 countries (Fig. 2 and 3); and (3) breaking high host connectivity for these pests requires regional management efforts, particularly where solanaceous crops geographically overlap with non-cultivated host species (Fig. 5-6).

Together our findings of widespread invasion risk of each target pest underscore an urgent need for enhanced invasion and pandemic prevention, preparedness, and response globally. To prevent further introduction, establishment, and local spread of these pests of global concern, long-term transnational strategies for (pro)active surveillance and risk mitigation are the primary candidate components for reinforcing the currently nationally coordinated plant health systems (*10, 25*). Effective management of these invasive pests also needs intersectoral support from private sectors (food security crops and ornamental industries), natural ecosystem conservation, and NPPOs.

Widespread implementation of GIRAF 1.0 depends on readily available, interoperable pest information systems and timely financial support (*10*), motivating countries to build and share local databases (e.g., spatial estimates of informal domestic trade, crop yield losses, or measured area invaded by a pest). GIRAF 1.0 is yet simplistic, compared with the complex reality of biological invasions (*70*), lacking pest species interactions with natural enemies, genetic population evidence, inherent stochasticity, and fine-scale spatiotemporal dynamics. Invasion risk frameworks like GIRAF generally lack explicit quantitative impact assessments on multifaceted outcomes globally, such as crop yield losses (*74*), agriculture profit reduction, plant biodiversity losses, or environmental impacts. These research frontiers in pest information systems hinder any invasion risk framework from providing timely interventions for real-time geographic monitoring prioritization, in the context of allocating scarce operating resources for plant health protection. GIRAF 2.0 should tackle these grand challenges in invasion science as biogeographic pest information systems keep improving periodically. We hope GIRAF 1.0 serves the scientific communities as a starting reference model to design future global risk assessments for thousands of potential invasive species devastating Earth’s plant ecosystems.

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