

1 FRONT MATTER

3 Title

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

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33 Abstract

34 Invasive pests pose a growing threat to global ecosystems. Current invasion risk
35 frameworks rarely quantify multiple species-specific drivers for the spread of
36 transboundary pests worldwide. We propose a global invasion risk assessment framework
37 (GIRAF) that quantifies, maps, and integrates species-specific geographic information –
38 multi-host landscapes, abiotic factors, trade networks of agricultural commodities, port
39 accessibility, and international biosecurity policies. We applied GIRAF to evaluate

40 scenarios for the introduction, establishment, and spread of invasive pests – *Phthorimaea*
41 *absoluta*, *Ralstonia solanacearum*, tomato brown rugose fruit virus, and potato spindle
42 tuber viroid. We found that host communities for each pest occupy 22–37% of Earth's land
43 surface, with Europe and Southeast Asia providing highly suitable environments. The
44 USA ranked among the top five countries vulnerable to experiencing trade-mediated
45 (re)introduction for each pest. GIRAF provides strategic points for proactive surveillance
46 prioritization and geographic mitigation of biological invasions, in support of transnational
47 biosecurity agencies and global food industries.

48 **Teaser**

49 Integrated spatial risk assessments support proactive surveillance for invasive species.

50 **MAIN TEXT**

51 **Introduction**

52 Invasive species are an increasing challenge to ecosystems worldwide. Effective invasive
53 species management is key to supporting sustainable plant ecosystems that contribute to
54 the UN Sustainable Development Goals (SDGs), particularly agricultural productivity,
55 food security, human livelihoods, and ecosystem health (1, 2). Attaining agricultural
56 sustainability on a local and global scale requires a substantial decline in the estimated 10–
57 40% crop yield loss caused by new and re-emerging diseases and pests (3). Unchecked
58 outbreaks of plant diseases and transboundary pests can inflict substantial impacts on
59 global food baskets, international markets, plant health, and natural ecosystem functioning
60 (4). Increased commodity trade, human transport, cropland expansion, and climate change
61 drive the unprecedented large-scale translocation of pathogens and pests (5–8). A main
62 goal of proactive responses to this multifaceted human-driven invasion crisis is to prevent
63 future socioeconomic, political, and ecological impacts if pathogens or pests expand
64 farther and persist longer in a region (2, 5, 9, 10). An increasingly important component in
65 invasive species management is integrated risk assessment before and shortly after the
66 initial or repeated introduction of pathogens and pests in new areas.

67 In the long term, integrated assessments would anticipate invasive spread, providing
68 spatially explicit surveillance strategies and formulating biosecurity geo-policies as
69 aspired to in the One Biosecurity perspective (2, 10, 11). Geographic pest risk analysis
70 provides a general framework to identify the most likely locations for introduction,
71 establishment, and spread (12–16), requiring quantification of risk factors such as host
72 availability, climate suitability, commodity trade, and human transportation. An integrated
73 assessment of key geographic risk factors helps appropriately prioritize limited resources
74 for active surveillance of invasive species in agroecosystems, is a fundamental layer of
75 invasion preparedness, and strengthens early warning systems for invasive pest outbreaks.
76 Integrated risk assessments are increasingly needed owing to the unprecedented rise in
77 current and future mass biological invasions and crop epidemics worldwide in the 21st
78 century (8, 17, 18).

79 Nevertheless, assessing multiple risk factors globally is challenging. Anticipating the
80 actual spread of an invasive species is highly uncertain and sometimes seems
81 unpredictable. High-resolution maps of plant host distribution, detailed information about
82 international and domestic trade of high-risk commodities, and species-specific
83 environmental requirements are important information gaps for many invasives, especially
84 plant pathogens and pests (1, 19–21). Given this inherent uncertainty, a proactive data-

90 driven approach for explicit quantification of geographic risks of invasive species is to
91 leverage existing limited geospatial data using general principles from invasion science,
92 disease epidemiology, pest ecology, and species distribution modeling (22), while
93 assembling better data in publicly accessible platforms (10, 23). Currently, expert opinion
94 is the traditional (and for some species the only feasible) option for evaluating the national
95 risk of an invasive pest in the immediate term (16, 24, 25). Hundreds of quick risk
96 assessments are available for specific countries (12, 16, 24), but they represent only a tiny
97 fraction of a growing number of pests affecting plants globally (18). Research over the last
98 three decades has led to a better understanding of individual geographic drivers of pest
99 invasions (10, 12-15, 22, 26, 27). However, to our knowledge, available frameworks have
100 not been applied to integrate multiple species-specific drivers of invasive plant pest spread
101 across global and local scales.

102 Here, our goal is to provide a new, integrated risk assessment framework (Global Invasion
103 Risk Assessment Framework (GIRAF) 1.0) for evaluating potential scenarios for the
104 geographic spread of invasive pests (Fig. 1). GIRAF harnesses advances in knowledge
105 about invasions into a quantitative, use-inspired approach and can be applied as a data-
106 driven foundation complementary to expert assessments. GIRAF explicitly integrates
107 common geographic factors underlying the most likely paths for spatial spread of invasive
108 pest species, mapping their potential geographic distribution and identifying candidate
109 priority locations as a critical component of global surveillance planning (7, 11).

111

Global Invasion Risk Assessment Framework (GIRAF 1.0)

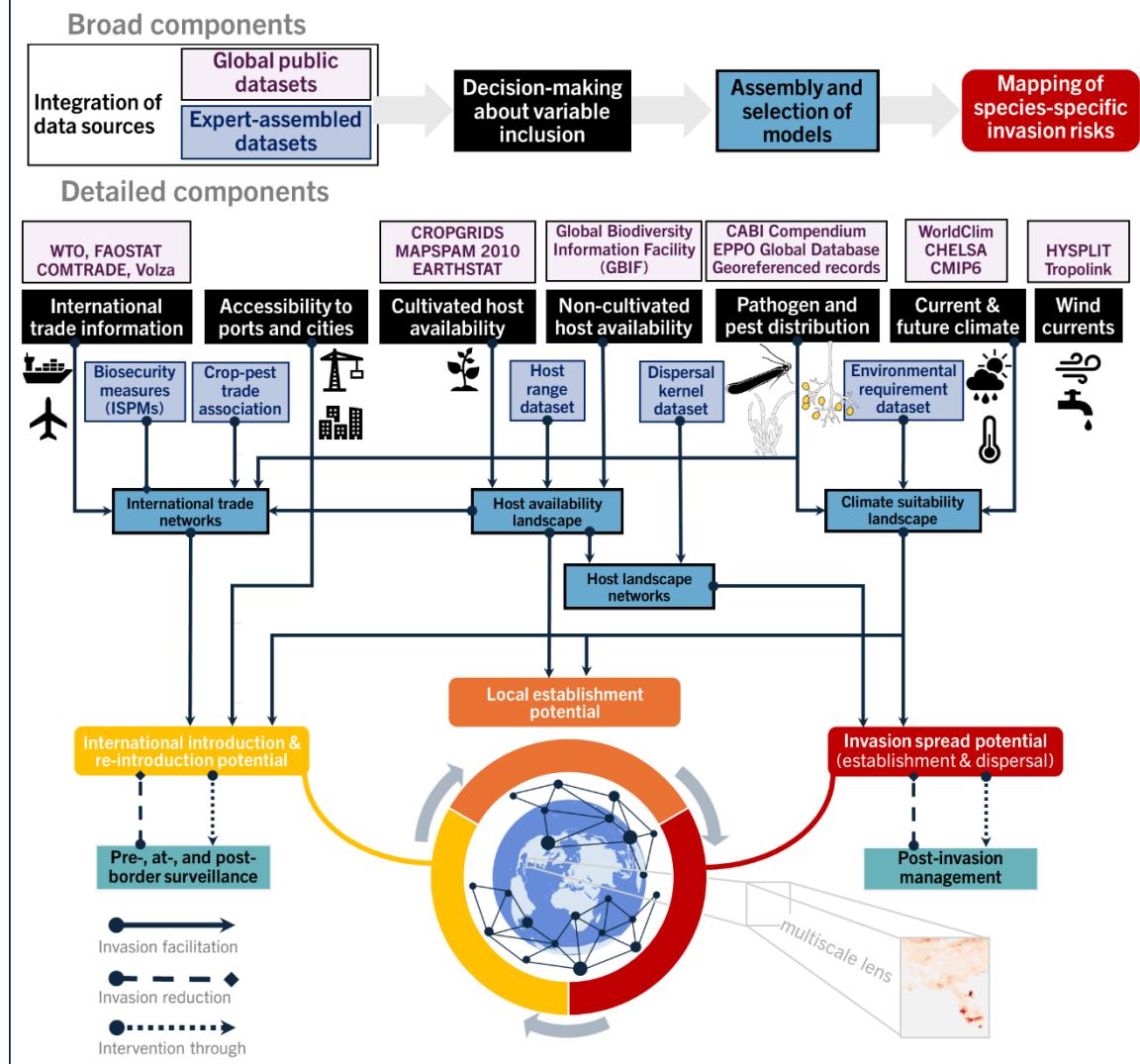


Fig. 1. GIRAF 1.0, a new global multicriteria framework for assessing invasion potential, integrates four of the five fundamental drivers of invasive species spread: environmental suitability, host availability, international trade (e.g., seed exchange), local transportation (e.g., access to cities), and wind patterns. GIRAF comprises four major components: integration of data sources (public datasets and expert-assembled datasets), decision-making on variable inclusion, model assembly and selection, and geographic predictions of invasion risk. In GIRAF, expert evaluation is needed in each component, from data input to model selection, parameter choices, and factor importance. GIRAF'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 real-world case studies showing the value of GIRAF, our first objective is to assess the global risk posed by economically important invasive pests belonging to four taxonomically distant groups. We assessed four geographic factors expected to promote the potential spread of these and many other invasive species, and their establishment potential in new locations with suitable habitat: (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 – indicates which locations may serve as critical entry points for species introduction if the targeted pest or infected vectors inadvertently cross international borders and biosecurity boundaries (28–31). Once a pest is introduced into a new area, host landscape connectivity indicates the potential for local spread 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 the establishment and local spread of an invasive pest (35, 36). These are the main geographic habitat factors facilitating pest invasion and epidemic potential in global plant ecosystems (12, 37–39).

We applied GIRAF for evaluating the global vulnerability to the South American tomato leafminer (*Phthorimaea soluta*), *Ralstonia solanacearum* phylotype IIB sequevar 1 (RSIIB-1; formerly designated as race 3 biovar 2), tomato brown rugose fruit virus (*Tobamovirus fructirugosum*; ToBRFV), and potato spindle tuber viroid (*Pospiviroid fusituberis*; PSTVd). These four transboundary pests have wreaked havoc on solanaceous crops and ornamental industries, with devastating impacts on plant health globally, and likely with substantial understudied effects on natural plant ecosystems. The global value of solanaceous crops (peppers, potatoes, and tomatoes) totaled US\$296 billion in production and US\$38 billion in international trade in 2022 (40), making them key to 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. S1-2). Reconstructing the biogeographic dynamics of these pests enabled us to identify which scenarios are likely in pest invasions. Applying GIRAF to these globally concerning pests allowed us to identify a strategic balance between evaluation of general invasion dynamics, considering common drivers of spread across species (5, 31), and ecological niche differences specific to particular 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 analysis for the invasion of a target plant, animal, or microbial taxon. GIRAF also has a multiscale lens (Fig. 1), supporting invasion assessments at smaller geographic extents and finer spatial resolutions. Our second objective is to apply GIRAF to quantify local invasion potential posed by the same target pests in Florida and the surrounding region, including Alabama, Georgia, and South Carolina.

Results

Pest introduction vulnerabilities in trade networks of agricultural commodities

Given scarce resources, long-term prevention of pest invasions into new host areas is increasingly challenging for National Plant Protection Organizations (NPPOs). While local sentinel surveillance and ongoing management need to continue actively in regions where pests are already present (Fig. S1-2), proactive surveillance can target potential accidental pest movement among countries through international trade (Fig. 2). There is global concern about the invasive pests studied here, yet three of the species lack a global

risk assessment; there is only a global map of climate-based risk for *P. absoluta* (41). 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, and phytosanitary activities are not strengthened, solanaceous crop ecosystems in many countries will continue to have high estimated vulnerability to trade-mediated introduction. Particularly highly vulnerable countries include USA, Canada, Bahrain, Kuwait, and UAE for *P. absoluta*; the USA, Niger, Saudi Arabia and Egypt for PSTVd; Pakistan, Tanzania, Saudi Arabia, and Senegal for RSIIB-1; and Ukraine, United States, Canada, and Kazakhstan for ToBRFV (Fig. 2). GIRAF results emphasize 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 (Fig. S1-2), and many countries exporting agricultural commodities may serve as possible pest source pools (Fig. 3). Historically, international trade of specific agricultural commodities (seed, planting materials, and food products) has played a major role in the rapid spread of these target pests globally (Data S10).

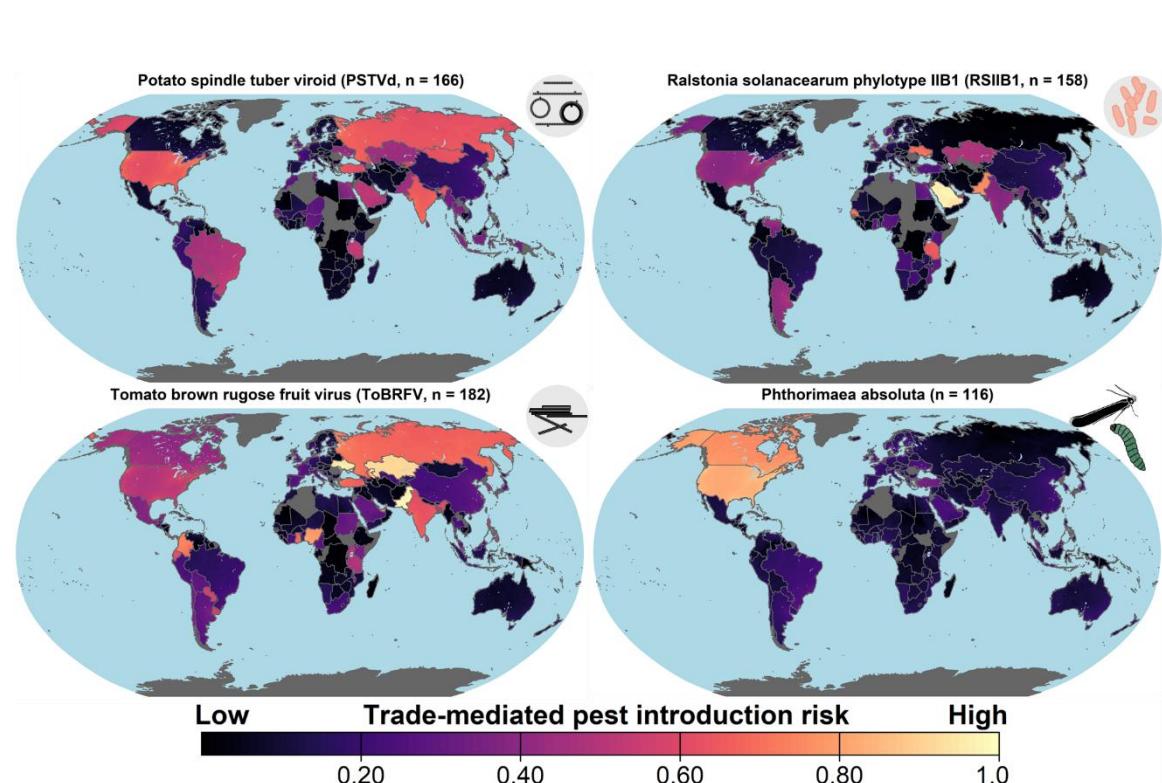
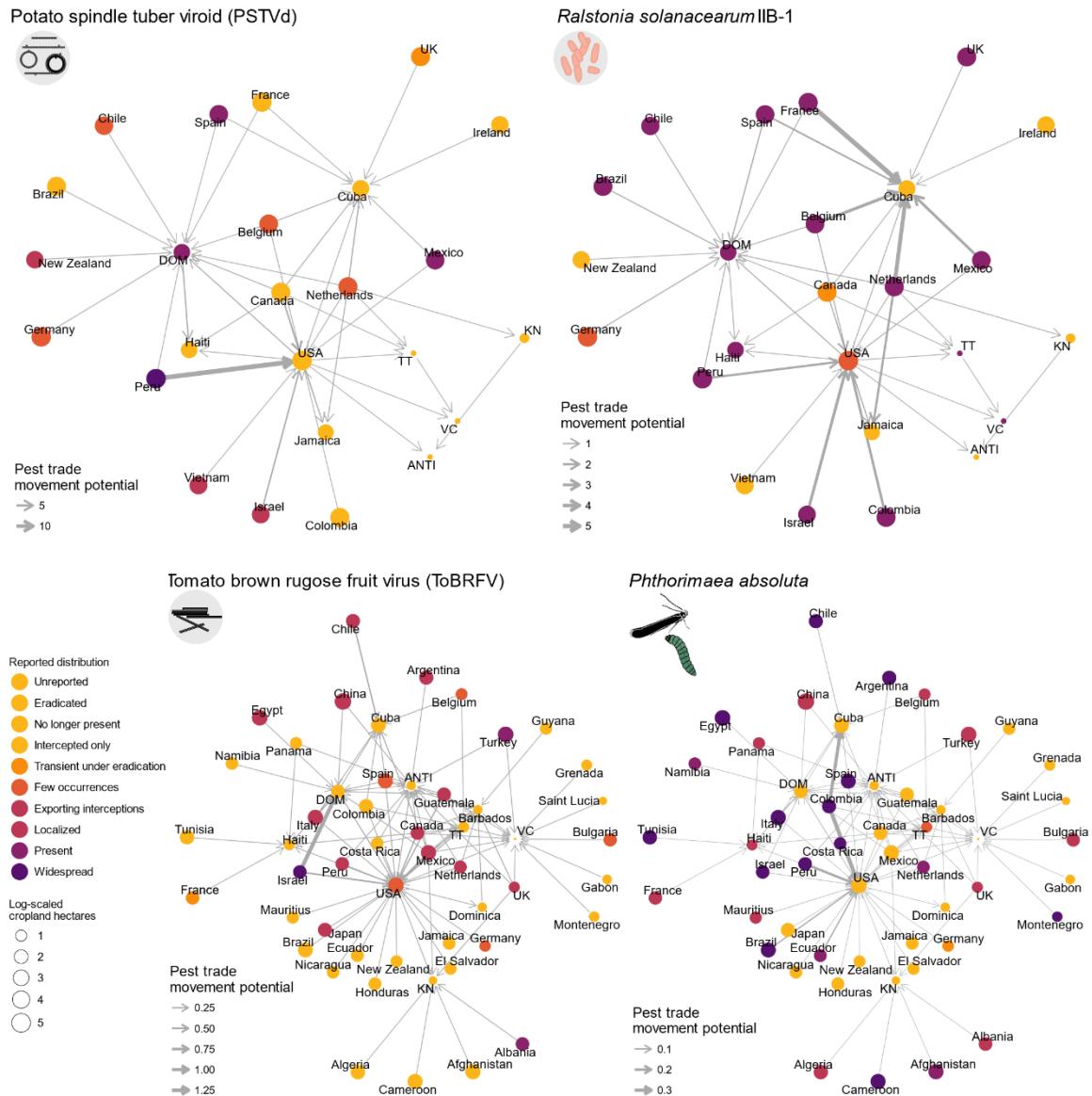


Fig. 2. Cumulative vulnerability to (re)introduction of four invasive plant pests. This vulnerability analysis considers international pest-specific commodity pathways, pest distribution at the country level, major crop host availability at the country level, and accessibility to ports. n is the number of importing countries with a possible introduction vulnerability 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.)



206
207 **Fig. 3. Potential geographic spread routes of pathogens and pests through
208 international trade networks linked to the Caribbean region and United States.**

209 Countries closer to the center of the trade networks have higher vulnerability to pathogen
210 or pest introduction via trade of high-risk crop commodities. Node size indicates the
211 availability of crop species that are hosts of the pest. Pathogen or pest invasion potential
212 and trade movement potential are relative rankings to compare invasion potential in a
213 species-specific trade network (not for comparison between species networks).

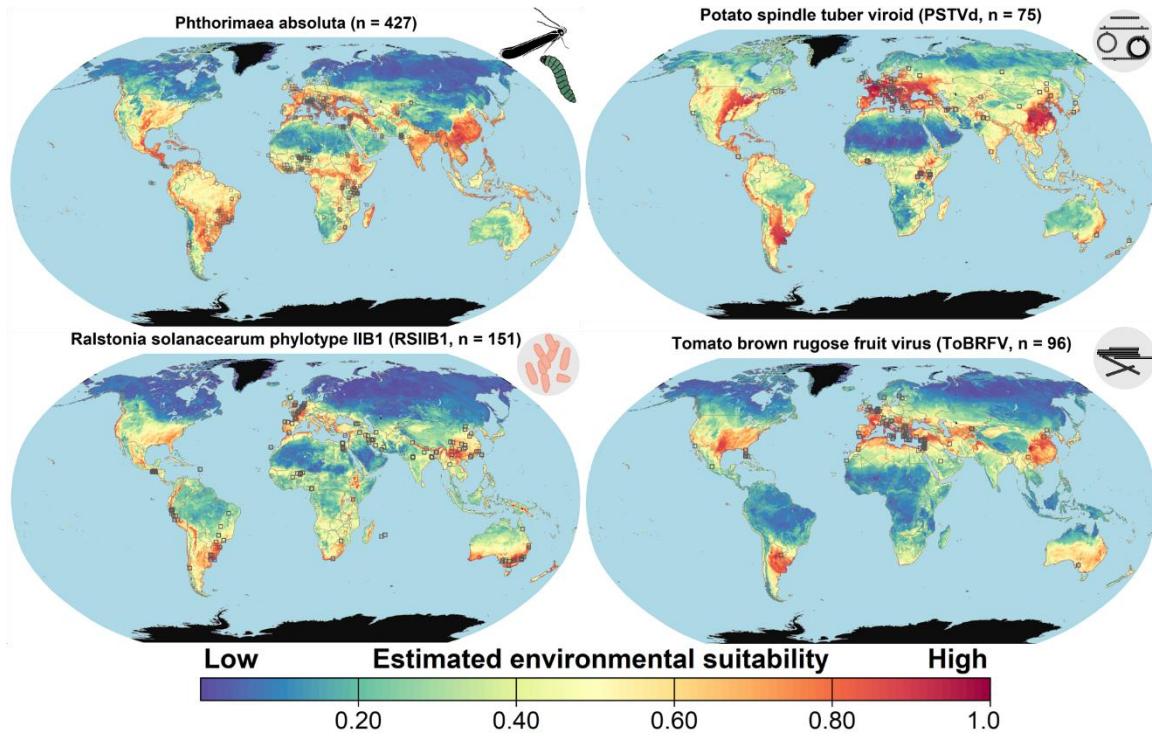
214 Abbreviations: ANTI – Antigua and Barbuda, DOM – Dominican Republic, KN – Saint
215 Kitts and Nevis, TT – Trinidad and Tobago, VC – Saint Vincent and the Grenadines.

216
217 GIRAf also supports assessment of the potential for pest introduction in specific
218 geographic regions. For example, for proactive surveillance prioritization in the USA and
219 the Caribbean region, GIRAf identified key regional hubs in international trade networks
220 that are more vulnerable to (re)introduction of each target pest. These regional hubs
221 consist of host-growing countries that import pest-associated crop commodities from

many regions where the target pest is present. The USA, the Dominican Republic, and Cuba serve as trade hubs in these regional networks and experience a potential introduction vulnerability for each target pest (Fig. 3). Likewise, Saint Vincent, the Grenadines, Antigua, and Barbuda may act as possible hubs vulnerable to *P. absoluta* or ToBRFV (re)introduction. Lastly, GIRAF distinguished spatially explicit potential movement pathways for each target pest (Fig. 3) between these habitat regions. For example, Cuba imported potato seed from nine countries: these international trade activities represent a high vulnerability for RSIIB-1 introduction but a low vulnerability for PSTVd introduction (Fig. 3). Similarly, the USA imported tomato commodities from 27 countries: these trade connections provide a possible movement pathway for *P. absoluta* from South America, but low movement potential for ToBRFV.

Pest invasion vulnerabilities based on environmental suitability

After introduction of a pest species, national early warning systems need to determine the degree and extent to which the local environment is suitable for establishment and spread. GIRAF defines a suitable environment for pest invasions based on climatic, edaphic, and hydrological conditions. For the four pests in this study, 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 modeling approach predicted the currently reported georeferenced range of each target pest (Fig. 4 and Fig. S3, where the average model accuracy ranged from 61% to 96% across all models evaluated). Proactive response should become routine beyond current invasion hotspots, and GIRAF identified these key surveillance targets. The model of environmental suitability 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. Across these four pests, potential environmentally suitable locations with >50% likelihood of invasion include a large area in China, and an eastern region in Australia (Fig. 4). Other possibly suitable areas are specific to each target pest. For example, the Southeastern USA and the US Pacific Coast are likely climatically suitable areas for RSIIB-1. Preventing range-expansion of these global pest risks into new areas requires (pro)active surveillance programs coordinated by the international plant health community.



254
255 **Fig. 4. Global vulnerability hotspots for four invasive pests based on an ensemble of**
256 **environment-based machine-learning models.** Sample size (n) is the number of
257 historical georeferenced pest outbreak observations (black square outlines) used to train
258 individual species distribution models. Black pixels are locations the ensemble model
259 predicted to be environmentally unsuitable. (Pest silhouettes are not drawn to scale.)

260 **Pest invasion vulnerabilities based on multi-host landscape connectivity**

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

274 Host availability strongly correlates with mean host connectivity (Spearsman's $r_s = 0.62$
275 for PSTVd, 0.81 for RSIIB-1, 0.65 for ToBRFV, and 0.80 for *P. absoluta*, $p < 2.2e-16$),
276 so highly dense host communities commonly have high functional connectivity (Fig. S4-
277 9). This pattern is also supported by small differences in ranks for locations with high host
278 connectivity and high host density (Fig. S5). For example, Europe, Southern Asia, and
279 China have a homogeneously dense host landscape that is likely to facilitate the local
280 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.

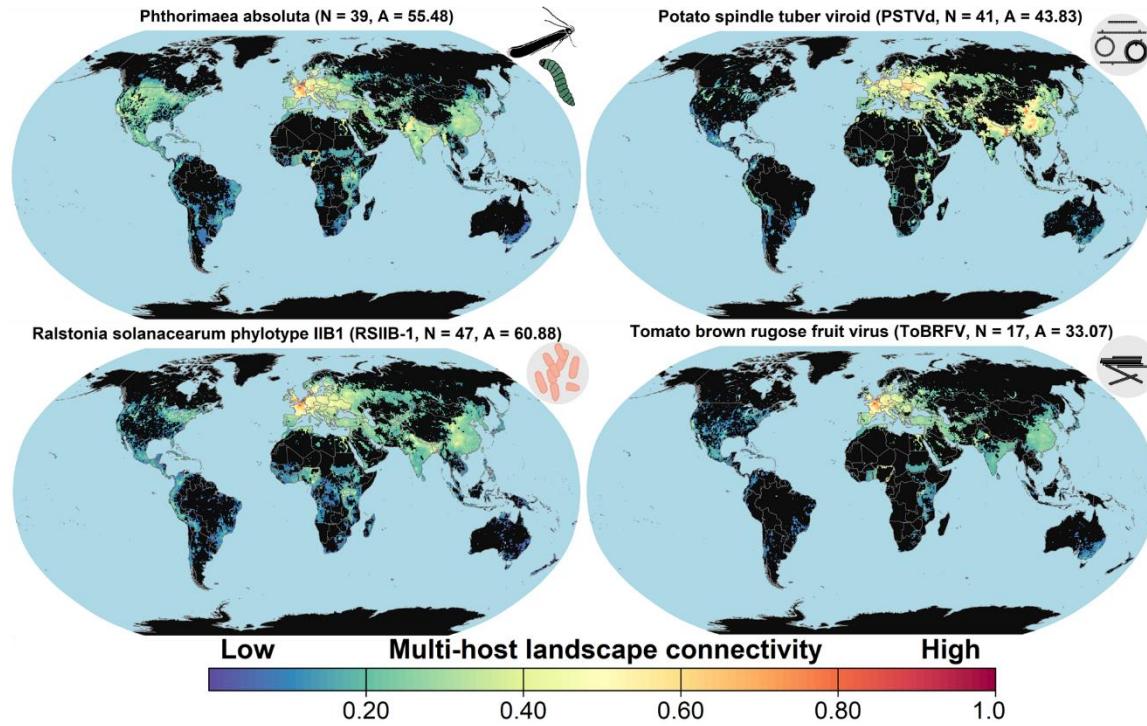


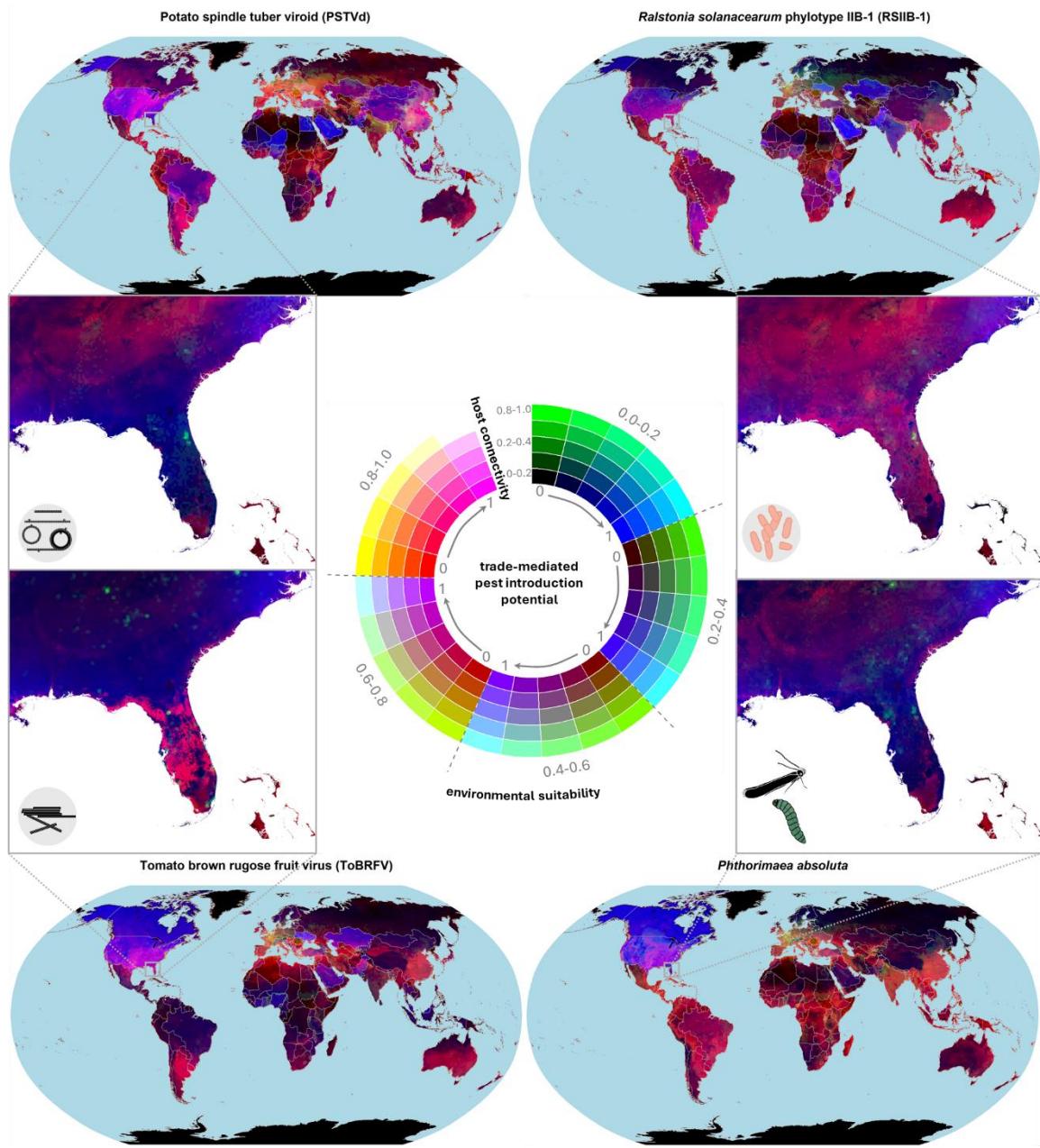
Fig. 5. Global vulnerability hotspots for four invasive pests based on multi-host landscape connectivity. Color gradient represents the magnitude in mean host landscape connectivity of each location, calculated across a range of likely dispersal parameters. Global host community traits include the number 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 (A, in million square kilometers). Grid cells in black are locations where the host is not reported. (Pest silhouettes are not drawn to scale.)

In the Americas, there is a conterminous host belt through 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). The reported host landscape fragmentation in Africa (42, 43) suggests the need for a future assessment of unreported host distribution that could influence the spread of these pests. Considering only cropland substantially reduced the estimated invasion vulnerability compared to a multi-species host assessment for each target pest. The number of host species was weakly negatively or

310 positively correlated with functional host connectivity (Spearsman's $r_s = -0.04$, $p =$
311 $1.486\text{e-}13$ for PSTVd; $r_s = 0.31$, $p < 2.2\text{e-}16$ for RSIIB-1; $r_s = 0.19$, $p < 2.2\text{e-}16$ for
312 ToBRFV; and $r_s = 0.49$, $p < 2.2\text{e-}16$ for *P. absoluta*). Cross-species transmission of these
313 pests is probably more likely in highly connected host locations, especially where crop
314 ranges spatially overlap with non-cultivated host species.

315 **Pest invasion vulnerabilities based on a multi-dimensional biogeographic assessment**

316 Each component of GIRAF provides a different perspective on invasion risk, and
317 decision-makers can use one risk factor map as a first approximation for a pest's invasion
318 risk when geographic information for other ecological factors is lacking. Each component
319 represents a snapshot of a pest's potential geospatial distribution and a dimension of its
320 spatially referenced ecological niche. Trade and transportation networks are proxies for
321 (re)introduction pressure (long-distance dispersal niche), environmental suitability may
322 capture environmental requirements of an invasive (environmental niche), and host
323 landscape connectivity highlights spatial patterns of a pest's spread through a landscape of
324 susceptible hosts (trophic niche). GIRAF integrates these different geospatial perspectives
325 in a multidimensional analysis of invasion risk, representing a second ecological
326 approximation to the relative likelihood of a pest's success in spreading or the potential
327 invasion risk posed by a pest (Fig. 6). We applied the biotic, abiotic, and migration (BAM)
328 framework (7, 14) to generate combined estimates of potential geographic distribution and
329 the likely spread of an invasive species. Specifically, we considered that geographic
330 locations with the combination of high levels of host landscape connectivity, predicted
331 environmental suitability, and international trade along with accessibility to ports, are
332 highly likely suitable geographic areas for species invasion (Fig. 6). This multicriterion
333 biogeographical approach also aligns with the three widely recognized components
334 necessary for plant disease development (environmental conduciveness, host
335 susceptibility, and pathogen aggressiveness) in a geographical space (44). To our
336 knowledge, GIRAF is the first global meta-model for pest invasions that combines (a)
337 pest-specific traits and parameters, (b) spatially explicit treatment of real-world data for
338 major drivers, and (c) integration of natural and agricultural ecosystems.



339

340 **Fig. 6. Worldwide pest invasion vulnerabilities based on a multi-dimensional**
 341 **assessment.** In these multivariate choropleth maps, the intensity of each primary color
 342 represents the potential invasion level of a target pest based on environmental niche (red
 343 spectrum), host landscape connectivity (or trophic niche, green spectrum) and introduction
 344 potential via international trade of crop commodities (blue spectrum). Grid cells in black
 345 indicate areas with no invasion vulnerability (e.g., Antarctica), and pale-yellow grid cells
 346 indicate the highest vulnerable areas for a pest invasion where high levels of the three
 347 factors coincide. As an example, grid cells in orange have high environmental suitability
 348 but relatively low levels of host connectivity and trade-mediated introduction potential.

349 By mapping at-risk locations for potential pest spread, based on three major ecological
 350 risk factors, GIRAF provides a starting point for global invasion preparedness and
 351 spatially explicit surveillance prioritization. The highest levels of these three major risk
 352 factors rarely coincided. Globally, Central Europe, India, and northern China, where the
 353 pests are present, have relatively high levels of each risk factor (Fig. 6). GIRAF allows us

354 to identify areas where high levels of pairs of risk factors coincide. For example, large
355 areas in the USA have high (re)introduction potential and high environmental suitability,
356 but reported host distribution may be a limiting factor. GIRAF provides a multi-scale lens
357 to account for likely scale-dependent processes in invasion vulnerabilities. At a finer
358 spatial resolution, GIRAF revealed more detailed patterns of invasion vulnerabilities for
359 Florida and surrounding areas (Fig. 6). For example, northern Florida had moderate levels
360 of each risk factor for each target pest. These fine-scale patterns indicate actionable
361 priorities for local biosecurity.

362 Discussion

363
364 Protecting plant health from invasive pests is key to safeguarding agroecosystem
365 provisioning and natural ecosystem functions, especially in response to 21st-century
366 global challenges like resource depletion, plant pandemics, and extreme weather events.
367 GIRAF 1.0 identifies critical points for constructing spatial surveillance and mitigation
368 strategies for invasive pest species. GIRAF 1.0 provides a key advance for improving
369 invasion risk assessments by integrating four ecologically meaningful drivers of invasive
370 species spread globally. Specifically, we focused on which, how, and where risk factors
371 are important for pest invasions.

372
373 Here, GIRAF identified potential vulnerability hotspots for four pests of global concern,
374 using new species-specific biogeographic models of trade-mediated introduction potential,
375 environmental suitability, and host landscape connectivity for a contemporary timespan.
376 Our results provide the first quantitative assessment of invasion vulnerabilities for plant
377 pests across these geographic factors globally. We provide new data-driven evidence that
378 host communities occupy areas ranging from $\sim 33.1 \times 10^6 \text{ km}^2$ for ToBRFV to 60.8×10^6
379 km^2 for RSIIB-1, or ~ 22 to 37% of Earth's land surface. Europe and Southeast Asia have a
380 highly favorable environment and high multi-host connectivity for each pest. The global
381 trade networks for high-risk commodities associated with each target pest encompass
382 more than 100 countries. The USA ranks among the top five countries with trade-
383 mediated (re)introduction vulnerability, and some regions of the country are
384 environmentally suitable for pest invasions.

385
386 These findings will tend to have higher uncertainty about the invasion risk of these pests
387 in regions where host availability is not reported, where climate variability, wind patterns,
388 or human mobility are important, where informal trade in planting materials occurs, and
389 where international borders are present (25, 27, 36). Despite these sources of uncertainty,
390 our findings support planning (pro)active responses to and effective plant protection
391 strategies against ongoing and new pest outbreaks (Fig. 1). These responses should
392 include: (1) proactive surveillance targeting regions where each pest is unreported, but
393 which have high invasion vulnerability (Figs. 2-4); (2) making international trade
394 networks safe through enhanced pest-specific biosecurity in over 100 countries (Fig. 2 and
395 3); and (3) regional management efforts to break high host connectivity, particularly
396 where solanaceous crops geographically overlap with non-cultivated host species (Fig. 5-
397 6).

398
399 Together, our findings of widespread invasion risk for each target pest underscore the
400 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 current nationally coordinated plant health systems (10, 25). Effective management of these invasive pests also needs collective support from the private sector (industries of ornamental plants and crops supporting food security), natural ecosystem conservation, and NPPOs. This globally coordinated system for invasion mitigation needs to be adapted by biosecurity agencies and plant industries to regional circumstances.

Widespread implementation of GIRAFF 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 due to pests, or the mapped area invaded by a pest). GIRAFF 1.0 integrates across multiple risk factors, but is still simplistic, compared to the complex reality of biological invasions (45), lacking pest species interactions with natural enemies, genetic population evidence, inherent stochasticity, and fine-scale spatiotemporal dynamics. Invasion risk frameworks like GIRAFF generally lack explicit quantitative impact assessments for multifaceted outcomes globally, such as crop yield losses (46), agriculture profit reduction, plant biodiversity losses, or environmental impacts. These research frontiers for pest information systems challenge any invasion risk framework designed to provide timely interventions for real-time geographic monitoring prioritization while allocating scarce operating resources for plant health protection. GIRAFF 2.0 should tackle these grand challenges in invasion science as biogeographic pest information systems improve. We hope GIRAFF 1.0 serves the scientific community as a starting reference model to design future global risk assessments for the thousands of potential invasive species currently threatening Earth's plant ecosystems.

Materials and Methods

GIRAFF incorporates four main steps for evaluating invasion risk: (i) defining ecologically or epidemiologically important risk factors, (ii) collecting or compiling fine- or broad-scale data related to these risk factors, such as 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 candidate priorities for surveillance and mitigation. GIRAFF is a metamodel in the sense that it integrates three classes of modeling approaches (species introduction modeling, environmental niche modeling, and habitat landscape connectivity). In implementations of GIRAFF, risk analysts, policymakers, and biosecurity practitioners can provide periodic feedback on each component and iteratively fine-tune the resulting spatial projections of pest invasion vulnerability, particularly if relevant information like informal trade of agricultural commodities is only privately or unofficially documented. Like all models, GIRAFF is subject to the GIGO axiom (garbage in, garbage out), where the quality of outputs is only as good as the quality of the data input. No single database used here is bias-free. We focus on the four plant pests as case studies because they are invasive species priorities for the US and globally; selection of pest and disease priorities is an expert-driven process external to GIRAFF (15)[Supplementary Text 1].

Data assembly for ecologically important species traits

We built (i) a geographic distribution dataset 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 (Data S2-7); 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 S8). These datasets present a comprehensive compilation of data from publicly available reports through 2023, including journal articles and official reports from NPPOs. Despite this extensive data compilation effort, global systematic sampling or highly standardized reporting for these pest species are rare. While the spread of pests at large spatiotemporal scales cannot always be systematically represented by small-scale field and laboratory experiments (47), ‘national- or continental-scale controlled trials’ are generally not realistic at this time (44). Despite their systematic incompleteness, geographic bias, and often convenience-based sampling, observational distribution data serve as a primary source of empirical information for mapping the 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 (43), 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 (42, 48, 49). On a global map with grid cells of approximately 2.3 km at the equator (1.25-minute spatial resolution), we assigned each grid cell the square root of the number of presence records for host species, or 0 if there were no georeferenced records. These global maps represent the geographic distribution of individual plant species at relatively high spatial resolution and are expected to be highly biased in areas with lower sampling effort. We thus aggregated each map at a ~55 km resolution (0.5° per grid cell), calculating the mean grid cell values at coarse resolution, to partially reduce sampling bias (48). These maps represent a first approximation of relative host density; future approaches could train species distribution models to produce more accurate maps for each host. For cultivated host species, we obtained global maps of crop-specific harvested areas from the CROPGRIDS dataset, which incorporate production statistics that are not included in GBIF records of crop species.

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

Mapping invasion vulnerability based on species bioclimatic modeling. We obtained global maps of the 19 bioclimatic variables from CHELSA Bioclim, representing climate conditions for 1989-2013 (50), and of 12 soil properties from SoilGrids 2.0, representing edaphic conditions at 15-30 cm standard depth (51). We also gathered 13 available maps of physical accessibility of land areas worldwide (52, 53). Four accessibility maps indicate travel time 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 for the entry of commodities and associated pests (Table S2). 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 characterize travel time to urban and rural locations, each aggregated at one of nine settlement classes (population size classes).

499 We assigned a different weight to each settlement class to calculate a weighted average of
500 overall access to cities (A_c) across the nine settlement classes (Table S3).
501

502 We trained four probabilistic machine learning algorithms – MaxEnt, random forest,
503 XGboost, and logistic regression –commonly used for presence-only data (54, 55). Each
504 algorithm represented a correlative species distribution model (SDM), in which the
505 response variable was 1 for reported georeferenced presence records and 0 for pseudo-
506 absences (i.e., background points randomly selected from the world land area). Each SDM
507 was initially trained and evaluated on the following selected predictor variables: annual
508 mean temperature, mean diurnal range in temperature, isothermality, annual precipitation,
509 precipitation seasonality, chemical soil properties (pH, and soil organic carbon content),
510 physical soil properties (clay, sand and silt content), port accessibility (A_p) and city
511 accessibility (A_c). These predictors are a subset of all variables available in each dataset,
512 allowing us to avoid multi-collinearity, while still maintaining substantial variation in
513 ecologically relevant covariates of invasive species distribution. These initially trained
514 SDMs indicated A_p as the most important variable explaining the reported distribution of
515 each invasive species (54%, 27%, 72%, 53% contribution in presence predictions for
516 PSTVd, RSIIB-1, ToBRFV, and *P. absoluta* based on MaxEnt, respectively; Data S1).
517 However, we excluded the contribution of accessibility in the final predictions by each
518 SDM to provide a more explainable, deterministic approach. In this approach, we
519 analyzed both A_p and A_c along with introduction vulnerability due to international trade to
520 explicitly consider the individual ecologies of each invasive pest (see below).
521

522 This multi-model approach was used to generate a global map of ensemble predictions,
523 equally weighting the spatial projections of these four SDMs, as a quantitative consensus
524 approximation of abiotic environmental suitability for each invasive species. These
525 species-presence predictions based on occurrence-environment associations are an initial
526 and provisional approximation for a species' environmental suitability. True mechanistic
527 ecological interactions between abiotic environmental conditions and occurrence data of
528 these invasive pests have generally not been characterized quantitatively. Importantly,
529 some locations are likely to have a higher climate suitability than predicted by the
530 ensemble approximation, as will likely be discovered as each pest continues invading new
531 environments and geographical spaces. We lack a quantitative understanding of how
532 edaphic or climate conditions directly restrict or facilitate geographic occurrence. Climate
533 effects on each stage in the life cycle of these invasive species are not currently available,
534 particularly for plant viruses that are not transmitted by vectors. However, once this
535 ecological information becomes available, process-based, component-based, or
536 mechanistic models for these pest species can be preferentially used. These models would
537 explicitly incorporate direct climate effects on pathogen distribution or a species'
538 physiological response to environmental conditions.
539

540 We adjusted our probabilistic bioclimatic ensemble with known environmental parameters
541 for each species. We used Shelford's law of tolerance to adjust ensemble predictions of
542 environmental suitability for *Phthorimaea absoluta* and RSIIB-1. The law of tolerance
543 states that an organism's success is determined by a set of minimum, optimum, and
544 maximum environmental conditions (56). Using this ecological principle, we applied a
545 generalized beta distribution model to project the potential invasion risk as a response
546 function dependent on temperature (57, 58). In this thermal niche model, invasion risk
547 ($r(T)$) depends on three cardinal temperatures for a species' population development
548 (Data S12): the minimum temperature (T_{min}), optimum temperature (T_{opt}), and maximum

549 temperature (T_{max}). We used the monthly mean temperature of each location ($T_{x,y,m}$,
550 where x and y are the geographic coordinates and m is the month considered) to estimate
551 pest invasion risk locally:

552

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

553 Invasion risk is highest at locations where $T_{x,y,m} = T_{opt}$, decreases at temperatures higher
554 or lower than T_{opt} , and reaches zero beyond critical thermal limits tolerated by a species
555 (below T_{min} or above T_{max}). This temperature-driven physiological response is common
556 in arthropods, plants, nematodes, fungi, and bacteria, and applies to *P. absoluta* as well as
557 the cold-tolerant RSIIB-1 strains (59-61). Here, cumulative pest invasion risk in a location
558 over a year $r(T_{x,y})$ is proportional to the sum of $r(T_{x,y,m})$ for each month. We regarded
559 climatically unfavorable locations as those with $T_{x,y,m} < T_{min}$ or $T_{x,y,m} > T_{max}$, defining
560 geographically possible thermal range frontiers of a species.

561 Surface water such as rivers may serve as an aquatic habitat for survival, evolution, and
562 dissemination of plant pathogens (62-64). We incorporated river networks in GIRAF as a
563 possible plant health risk and a dispersal pathway for RSIIB1 (Supplementary Text 1).
564 Using the HydroATLAS database (65), we calculated the mean river water discharge as a
565 relative proxy for the likelihood that RSIIB-1 would disperse to any climatically suitable
566 location globally.

567 No information was available about the direct effect of environmental variables on disease
568 caused by ToBRFV and PSTVd. Here, environmental risk modeling for these species is
569 based solely on the machine-learning ensemble.

570

571 **Mapping (re)introduction vulnerability based on international trade of crop 572 commodities**

573 As a key component for developing safe trade strategies, we characterized the structure of
574 trade networks to identify potential geographic paths of pest spread and the relative
575 vulnerabilities of locations to potential (re)introduction(s) for each pest species (10, 12,
576 18). Hereafter, we define invasion risk as the likelihood that a pest or pathogen (i.e.,
577 hazard) potentially reaches or occurs in a host location (13, 14, 32). We use the term
578 invasion vulnerability to make clear that our analysis focuses on the risk of pest or
579 pathogen entry into a country, rather than the risk that a country might pose as a source of
580 inoculum through trade. In all our analyses, we used relative indices to estimate the
581 likelihood of spread of an invasive species as approximations for invasion risk. In the
582 global trade networks, specifically, we quantify the relative likelihood of potential spread
583 of an invasive species through the international trade of agricultural commodities.

584 We gathered information on the trade volume of crop-specific commodities between each
585 pair of countries, based on bilateral import reports in the World Trade Organization
586 (WTO, <https://stats.wto.org/>) dataset for 2005-2019 and Volza (<https://www.volza.com/>)
587 dataset for 2023. Our proxy for host availability within a country was the harvested area of
588 crop species reported to be natural major hosts of each pest (Data S8), for crop species
589 available in the FAOSTAT dataset (40). To account for the potential effect of pest-
590 associated trade policy landscapes, we also obtained information on international
591 biosecurity measures targeting specific pest species, whenever available. We compiled
592 information on the geographic extent of each pest within a country (Data S2-7), based on
593

available reports in CABI Compendium (<https://www.cabidigitallibrary.org/journal/cabicompendium>), EPPO Global Database (<https://gd.eppo.int/>), and extensive literature review. In these international trade networks, nodes represent countries, and link weights indicate the relative potential of pest spread between countries.

We propose a trade index (or $P(\tau_{i \rightarrow j})$) for potential accidental pest movement from an exporting country i to an importing country 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 in each of the trading countries, the host availability in each of the trading countries, the trade volume of crop-specific commodities between the countries, and, when available, pest-specific biosecurity measures implemented by trading countries. Supplementary Text 2 provides details of the methodological approach, mathematical formulations, theoretical assumptions, and available datasets used to quantify invasion risk (or $P(\tau_{i \rightarrow j})$) through international trade networks. We modeled the joint relative likelihood that none of the exporting countries would introduce the pest species into a target importing country j as $\prod_{k=1}^z (1 - P(\tau_{i_k \rightarrow j}))$, 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 $1 - \prod_{i=1}^z (1 - P(\tau_{i_k \rightarrow j}))$. As an alternative measure, we also calculated three 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 have been important in predicting pest or pathogen transmission in epidemic networks (66-68).

Our geographic risk analysis of 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 seed potato (i.e., potato tubers for 2005-2019) and planting material of *Brugmansia* (2023). For RSIIB-1, we evaluated the international trade of seed potato, tomato fruit, pepper fruit (2005-2019), and geranium planting material (2023). For ToBRFV, we built individual networks of international trade of tomato fruit (2005-2019), tomato seed, and pepper seed (2023). For *Phthorimaea absoluta*, we assessed the international trade network of tomato fruit (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 S10). 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. Information about the international trade of crop-specific seed or planting material over multiple years is not available publicly. To include the potential effects of implemented policies in our assessment, we modeled a reduction in the introduction risk of 10% from countries with market access to the United States that 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 included an analysis focused on the vulnerability of the USA and countries in the Caribbean region to

644 introduction of each pest species associated with commodity imports, providing a regional
645 assessment.

646
647 We used country-level interception data for each pest species as a test dataset to validate
648 the (re)introduction vulnerability analysis (Data S10). To build the introduction model
649 above, we used this data to determine which agricultural commodities are likely important
650 for the international spread of each pest (Table S5). Below, we used a large part of the
651 information about pest interceptions in specific countries that was not used in the model
652 construction. We assessed the precision of the (re)introduction vulnerability analysis, that
653 is, the ratio between (a) the number of countries where the pest has been intercepted on
654 imported agricultural commodities and introduction vulnerability was non-zero (true
655 positives) and (b) the number of countries where the pest has been intercepted on imported
656 agricultural commodities. Our analysis had a precision of 1, including all countries where
657 the pest has been intercepted (Table S7). Using a Kolmogorov-Smirnov test, we also
658 evaluated whether countries where the pest has been intercepted have a higher
659 (re)introduction vulnerability than any other countries. The KS test did not detect evidence
660 for higher or lower introduction vulnerability in countries where the pest has been
661 intercepted (Table S7). There was not evidence to reject the null hypothesis ($p > 0.27$ for
662 all pests), so a lack of evidence that higher vulnerability values were associated with pest
663 (re)introduction.

664
665 **Mapping invasion risk based on accessibility to ports and cities**

666 Ports likely play a pivotal role in the (re)introduction of plant pests to a region, as they
667 may serve as primary entry points of pest-associated agricultural commodities (5, 12).
668 Geographic proximity to ports generally increases the risk of introducing invasive plants,
669 arthropods, and pathogens (5, 28, 69-71) and our SDMs indicated a potential major role of
670 access to ports in the geographic distribution of each target pest. Thus, our models
671 incorporate accessibility of croplands to ports or urban areas in a region as increasing
672 (re)introduction vulnerability to plant pests. Likewise, accessibility of croplands to cities,
673 in general, may increase invasion risk associated with urban agricultural landscapes and
674 the final destination of commodities (72). Specifically, we treated invasion risk associated
675 with accessibility to ports and cities as occurring in a pattern analogous to species richness
676 resulting from species-accumulation models, where the cumulative number of species
677 scales in an exponential pattern with sample size, area, or intensity (73). We modeled
678 invasion risk of cropland locations in a region as increasing nonlinearly with accessibility
679 to ports (A_p) as $I_p \propto 1 - \exp(-1/\log(A_p))$ or with accessibility to cities (A_c) as $I_c \propto$
680 $1 - \exp(-1/\log(A_c))$, where $I_p \in [0,1]$ and $I_c \in [0,1]$.

681
682 For each invasive species, we generated a map integrating the vulnerability of each
683 country to a pest's introduction through international trade and based on the accessibility
684 of croplands to ports ($I_j \times I_p$). This resulting map aims to disaggregate the accidental
685 introduction potential of pest species at the national level (I_p) into likely domestic
686 distribution of imported agricultural commodities and their associated pests across initial
687 entry locations. These maps of invasion risk can be fine-tuned in future geographically
688 explicit evaluations, as domestic distribution of commodity trade and local spread of
689 associated pests may vary geographically among commodity types (28). Information about
690 origin location, ports of entry, and final city destination of imported agricultural
691 commodities specifically associated with a target pest species is not publicly available, to
692 our knowledge.

693
694 **Mapping invasion risk based on multi-host landscape connectivity**
695

696 Our target invasive pests have multi-species host ranges. Their potential distribution in
697 regions where a host plant is unavailable is constrained (45), but the risk of pest spread is
698 higher where susceptible host populations are homogeneously and densely distributed
699 across the landscape (74-76). Geographic host distribution is a critical risk factor when
700 accounting for biotic interactions more realistically in ecological niche modeling of plant
701 disease (14, 19, 45). We categorized each plant species reported to be naturally infested by
702 a pest as a primary or secondary host (Data S8; Table S4). Natural secondary host species
703 were included as playing at least a minor role in pest persistence or survival (10, 46). To
704 map the geographic distribution of multiple natural host species, we used a stacked host
705 distribution modeling approach (14), summing the relative density of major and secondary
706 host(s) to produce a global map of cumulative host density for each invasive pest. In these
707 stacked host maps, we considered the potential minor role of secondary host species in
708 pest invasion risk and potential spread by multiplying their host densities by a tenth (12).
709 For crop species being host of a pest species, our analysis included only locations
710 represented by 3-minute cells having ≥ 4 hectares of cropland (a host density threshold of
711 $\sim 0.1\%$), incorporating a rare-species advantage against density-dependent diseases in
712 excluded host locations (74). We then aggregated these resulting maps to a coarser spatial
713 resolution so that each grid cell represented $\sim 55.5 \text{ km} \times 55.5 \text{ km}$ at the equator.

714 Using these global maps of cumulative host density as inputs in the geohabnet R package
715 version 2.2 (77), we evaluated the host landscape connectivity for each pest species (32).
716 geohabnet is a component of the R2M Plant Health Toolbox for rapid risk assessment to
717 support mitigation of pathogens and pests (www.garrettlab.com/r2m). geohabnet
718 estimated the relative likelihood of pest movement (σ) between host locations i and j

719 using two generic gravity models for species dispersal (78-80): $\sigma_{ipl} \propto c_i^k c_j^k \left(\frac{d_{ij}}{111,319.5}\right)^{-\beta}$

720 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
721 model. In these global dispersal models, potential pest movement (σ_{ipl} or σ_{ne}) depends
722 not only on the product of relative abundances of susceptible host species in both locations
723 ($c_i^k c_j^k$), but also on the probability of a pest moving between host populations given their
724 physical distance (d_{ij}). We set $k = \frac{1}{2}$ to account for potential nonlinear associations
725 between host density and pest invasion risk (81). We compiled β and γ dispersal
726 parameter values that were empirically estimated for a diverse set of plant pathogens and
727 arthropod pests (Data S11). We used this dataset to calculate the first quartile, mean,
728 median, and third quartile of each dispersal parameter across pest species, representing a
729 parameter space of likely pest spread scenarios. We evaluated these typical parameter
730 values $\beta = (0.9, 1.5, 1.7, 2.1)$ and $\gamma = (0.02, 0.08, 0.36, 0.24)$ in a sensitivity analysis to
731 account for uncertainty in pest movement. Species-specific dispersal parameter values are
732 unavailable for these target pests (as well as for most pest species). We then built pest
733 invasion networks, where a node represented a host location, and link weights indicated
734 potential pest movement between host locations (σ_{ipl} or σ_{ne}).

735
736 We calculated host landscape connectivity using six standard network metrics in
737 epidemiology and invasion ecology (22, 38, 66, 82-84): betweenness centrality, closeness
738 centrality, eigenvector centrality, node strength, PageRank centrality, and the sum of
739 nearest neighbors' node degrees. Here, global maps of invasion risk represent the multi-
740 host landscape connectivity for a target invasive pest, averaged across two gravity models,

741 eight typical dispersal parameter values, and six standard network metrics, each weighted
742 equally. Host landscape connectivity quantifies the relative likelihood that an invasive
743 pest, if it reaches the target host location, will spread to all its direct and indirect neighbors
744 in the network.

745
746 In a separate analysis, we treated pest survival as higher in areas with higher host species
747 richness than in areas with only one host species (14). We used georeferenced occurrence
748 data for each pest species as an independent dataset to validate the multi-host connectivity
749 estimates. We used two metrics to assess model performance based on presence-only data.
750 First, precision is the ratio of the number of grid cells in which the target pest is reported
751 present and multi-host connectivity is nonzero (true positives) to the total number of grid
752 cells in which the target is reported present (true positives + false negatives). Second, we
753 assessed whether multi-host connectivity is higher in locations where the pest is reported
754 to be present than elsewhere. To assess this hypothesis, we conducted an asymptotic two-
755 sample Kolmogorov-Smirnov test. The multi-host connectivity analyses had good
756 precision (from 0.68 to 0.87; Table S6). The KS test indicated that multi-host connectivity
757 tends to be higher in locations where the pest is present than elsewhere ($p < 0.001$, Table
758 S6), supporting a likely major role of multi-host connectivity in driving the spatial
759 occurrence of each pest.

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1226
1227 **Competing interests:** Authors declare that they have no competing interests.

1228
1229 **Data and materials availability:** A template for processing R scripts for each analysis in
1230 this study is publicly available on GitHub: <https://github.com/AaronPlex/pestradenet> for
1231 international trade networks, <https://github.com/AaronPlex/pest-env-sdm> for environment-
1232 based species distribution models (SDMs), and [https://github.com/AaronPlex/multi-host-](https://github.com/AaronPlex/multi-host-nets)
1233 [nets](https://github.com/AaronPlex/multi-host-nets) for host connectivity analysis. All data are available in the main text or the
1234 supplementary materials. All unpublished datasets supporting the results and
1235 reproducibility of this study are publicly available as supplementary material at
1236 http://datadryad.org/share/LINK_NOT_FOR_PUBLICATION/6mtexakLduHFj6hfkiIIRSFiBt_5InuVEty4rmlZidEE. All published datasets used in this study are correspondingly
1237 cited.
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1241 **Supplementary Materials**
1242

1243 This manuscript includes the following Supplementary Materials: Supplementary Text 1
1244 to 2, Figs. S1 to S5, Table S1 to S2, and Data S1 to S10.
1245

Science Advances



Supplementary Materials for

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

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This PDF file includes:

Supplementary Text

Figs. S1 to S5

Tables S1 to S2

Data S1 to S10 –

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Supplementary Text 1

i) The national and regional context of pest surveillance and mitigation systems

Pest invasion preparedness and risk mitigation involve a series of plant biosecurity activities (2, 9, 10). Pre-invasion biosecurity activities require periodic inspection, interception, and surveillance of potential pest entry points and likely source regions. However, complete exclusion of invasive pests in new geographic areas is often as challenging as “finding a needle in a haystack” (27). Implementing pre- and on-border biosecurity activities is economically and logically feasible in only a small fraction of imported commodities and potential pest arrival locations in a host landscape (11, 85, 86). Designing post-border surveillance is also critical for early and rapid response to plant pest invasions regionally. For example, strengthening biosecurity links between Florida and the Caribbean region is particularly important because of their relatively similar climate, high production capacity, high intraregional trade, and geographic proximity.

In the conterminous United States, USDA’s Animal and Plant Health Inspection Service’s Plant Protection and Quarantine (APHIS PPQ) and the Department of Homeland Security’s Customs and Border Protections (DHS CBP) are federal agencies in charge of conducting, developing and implementing plant biosecurity activities, from offshore detection to local management of exotic pest invasions (9). Likewise, the Cooperative Agricultural Pest Survey (CAPS) program conducts non-native plant pest surveys to protect American agriculture and natural resources (<https://www.aphis.usda.gov/plant-pests-diseases/caps>). CAPS is a national network of state and federal cooperators and stakeholders that focuses on early detection to prevent establishment of exotic plant pests (87). There are also statewide agencies that safeguard agriculture and natural resources against local plant pest invasion and initial epidemics, such as the Florida Department of Agriculture and Consumer Services (FDACS). With an annual budget of ~US\$55 million, FDACS Division of Plant Industry maintains phytosanitary programs both independently and in collaboration with the USDA, CBP and other entities, including the Cooperative Agricultural Pest Survey (CAPS) and plant inspections at agricultural interdiction stations along interstate corridors. APHIS invested approximately US\$400 million in prevention of and preparedness for plant pest invasions annually (88). Beginning with pest prioritization, a cross-sectoral committee organized by the National Plant Disease Recovery System (NPDRS) annually determined a high-priority list of invasive pests in the United States that need nationwide attention and investment (89). Similarly, during a forum in collaboration with APHIS PPQ through the Greater Caribbean Safeguarding Initiative (GCSI), the Caribbean Plant Health Directors determined that *P. absoluta* and *RSIIB* are pests of concern to safeguard the greater Caribbean (<https://www.cphdforum.org/>). We focus on the four plant pests as real-world case studies because they are invasive species priorities in the US (<https://approvedmethods.ceris.purdue.edu/>), they have the potential to be introduced or have already been introduced to the United States and the Caribbean region, and they seriously threaten major solanaceous crops globally and locally.

ii) Understanding ecological or epidemiological traits of the targeted invasive pests

Phthorimaea absoluta can infest at least 42 plant species naturally (Data S1), with tomato being the major host species (90, 91), and occasionally feeds on other cultivated solanaceous plants like potato, tobacco, pepper, and eggplant (Garzia 2009). *P. absoluta* is native to South America with an earliest known record in Peru in 1917, first reported in Spain in 2006 representing the earliest invasion of this species in Europe (90), and detected in Haiti in 2018, reaching the Caribbean Basin (92). By 2022, *P. absoluta* had a global distribution with reported occurrence in 108 countries (Fig. S1; Data S1). The long-distance rapid spread of *P. absoluta* is unintentionally mediated by international trade of infested agricultural commodities, such as tomato fruit, in packaging materials, and in sorting facilities. Active dispersal is by short-distance flying, facilitated by wind currents (90).

Ralstonia solanacearum is a species complex clustered into four phylotypes, causing infectious disease in a wide range of economically important crops and non-cultivated plant species (93, 94). RSIIB strains are known to naturally infect 54 plant species and are the most frequently reported strains in this species complex causing bacterial wilt in potato, tomato, and pepper (95, 96). Non-cultivated plant species can serve as secondary or occasional hosts of RSIIB strains (Data S1). The RSIIB phylotype has a pandemic distribution (95), with occurrence reports in 62 countries (Fig. S1; Data S1), and a possible region of diversity in South America (97). RSIIB was first detected in Florida in 2001 (98). The dissemination of RSIIB strains over long distances occurs primarily and unintentionally through the international trade of infected ornamental plants like asymptomatic geranium cuttings, potato tubers, and tomato propagative material (96, 98-100). Surface water, such as contaminated rivers, ponds, and agricultural drainage, plays a key role in the survival of RSIIB strains when used for irrigation (100-103).

Tomato brown rugose fruit virus (ToBRFV) is an emerging transboundary pathogen in tomatoes, which was first discovered in Israel in 2014 (104) and Jordan in 2015 (105). By 2024, there were reported outbreaks of ToBRFV in 50 countries (Data S1), posing a pandemic threat to the global tomato and pepper industries (106). ToBRFV was detected in a tomato greenhouse in California in 2018 with eradication efforts implemented (107) and, more recently, was reported on imported tomatoes in grocery stores and community gardens in Florida (108-110). Tomato and pepper are the main hosts of ToBRFV (106, 111). Yet, this virus can infect at least 17 solanaceous species naturally and 41 additional plant species in experimental inoculations (Data S1). Globally, ToBRFV has been intercepted at least 109 times in tomato and pepper seeds, tomato and pepper transplants, and tomato fruit (Fig. S1). These commodities are the main pathways of rapid international spread of this virus (111-113). Locally, ToBRFV is mechanically transmitted via plant-to-plant contact, contaminated farming tools, workers' hands, bumblebees carrying the primary virus inoculum passively, and possibly irrigation water and contaminated soil from previous growing cycle (106, 111, 114).

Potato spindle tuber viroid (PSTVd) has a widespread but scattered global distribution with reported incursions in 50 countries and multiple interceptions of the pathogen in new regions over the past two decades (Fig. S1-2; Data S1). PSTVd is declared eradicated only in Canada and the United States, where the pathogen was first discovered in the 1920s (115). PSTVd causes seed degeneration in potato tubers and occasionally rasta disease in tomatoes (116). It naturally

infests at least 51 cultivated and non-cultivated, mostly symptomless, plant species (Data S1). PSTVd has additionally 132 host species in inoculation experiments. PSTVd has been accidentally introduced into at least nine countries because of the international exchange of infected potato tubers, pepper or tomato seeds, and planting material of asymptotically infected solanaceous ornamentals (Fig. S2).

Supplementary Text 2

i) Estimating pest invasion potential through global trade networks

We developed a mathematical model to characterize the potential movement of pathogen or pest species between countries, which explicitly accounts for six geographic risk factors: country-level host availability, within-country pest extent, international trade of agricultural commodities, proximity to ports and cities, national biosecurity capacities and pest-specific climate suitability. This analysis can be reproduced using the R code available at the following GitHub repository <https://github.com/AaronPlex/pestradenet>

Before describing how we integrated each risk factor in a quantitative way, it is important to mention the phenomenon of directionality in trade networks. Because agricultural trade activities are a directional process, pest movement through trade networks depends on the mode of trade activity, whether a country is exporting, re-exporting, importing, or exporting and importing agricultural commodities. Distinguishing which countries are sources, intermediaries ('re-exporters'), and destinations of agricultural commodities in a trade network is thus important to understand the potential direction of unintentional pest spread mediated by trade activities [e.g., (29-31)]. While importation of agricultural commodities is associated with the possible risk of pest introduction or re-introduction to a country, patterns in exportation of commodities help us understand the possible risk of pest release from a country. We also define **invasion potential** simply as the potential movement of a species from one location to another (a country represents a location in the case of international trade networks). For simplicity, this definition of invasion risk does not explicitly distinguish whether a pathogen/pest species is native or invasive in a country. Determining invasiveness of a pathogen/pest species is challenging and often unavailable for many plant pests and pathogens (117). We also used the definition of **pest** from the International Standards for Phytosanitary Measure5 (ISPM 5) from the International Plant Protection Convention (IPPC). In accordance with this definition, we include arthropods and pathogens with a known negative impact on crops in our definition of plant pests.

ii) Invasion potential as a function of pest extent

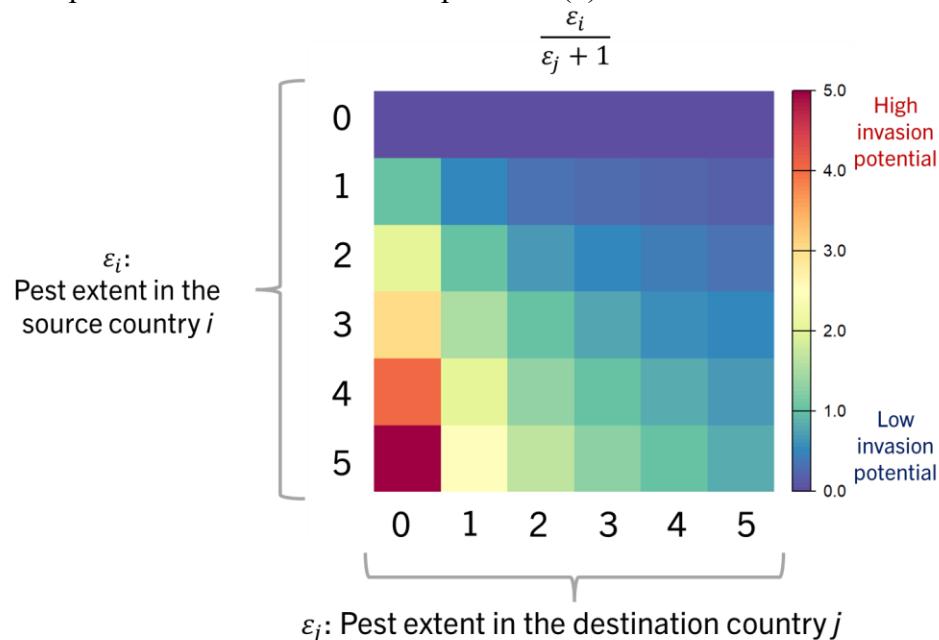
The status of pest species within a country is usually expressed as nominal categories, such as those reported by the Centre for Agriculture and Bioscience International (CABI), European and Mediterranean Plant Protection Organization (EPPO), PlantwisePlus Knowledge Bank, and scientific journal articles. These categories are based on the reported presence or geographic range of a pest species, as well as the frequency of its occurrence within a country. A standardized metric that measures the full area occupied by a pest species within a country (47) is often not available in the literature, making it difficult to estimate how widespread a pest is within a country. We proposed an ordinal and relative ranking as a first approximation for quantifying the pest status or extent within a country (Table S1). This quantitative ranking results from the interpretation of each nominal category.

Table S1. Proposed ranking for the geographic extent/status of pest species in a country.

Reported pest presence	Reported pest range or extent	Assigned score (ϵ)
Present	Widespread (CABI, EPPO)	5

Present	Native	5
Present	Without details	4
Present	Localized (CABI)	3
	Restricted distribution (EPPO)	
Present	Sporadic or episodic	3
Present	Exporting interceptions	
Present	Few occurrences	2
Present	Transient under eradication	1
Present	Transient under surveillance	1
Present	Transient nonactionable	1
Absent	Eradicated	0
Absent	Intercepted only	0
Absent	Formerly present	0
Absent	Never occurred	0
Absent	Simply not reported	0
Absent	Confirmed by survey, invalid record, intercepted only, pest eradicated, unreliable record (EPPO)	0
Not reported	Simply no reports are available	0

We formulated an invasion potential index that depends on an expected relationship between the pest extent in the exporting or source country (ε_i) and the pest extent in the importing or destination country (ε_j). This expected relationship is given by $\frac{\varepsilon_i}{\varepsilon_j + 1}$, so that the risk of a pest moving between any pair of countries based on their pest extents ranges between 0 and 5 (see the heatmap below). In this heatmap, dark red cells represent a maximum invasion potential (5), and dark blue cells represent a minimum invasion potential (0).



In general, this country-country formulation accounting only for pest extents allows us to consider the potential importance of introduction and re-introduction of a pest in a country i relative to the pest extent in the country j .

- *Scenario 1.* One can expect that the larger the pest extent in the exporting country j , the greater the risk of pest introduction in the importing country i if the pest is not yet present in country i . This hypothetical scenario is illustrated below. In this scenario, one can expect higher chances of unintentionally picking up or sampling propagule from the exporting country if the pest is widespread in the source country rather than geographically localized. The idea of ‘picking up or sampling’ here is an analogy to the quantity of possibly infected or contaminated crop commodities in the source country that is traded internationally.



- *Scenario 2.* Likewise, the potential for pest re-introduction (or repeated introduction) in the importing country increases monotonically with larger pest extents in the exporting or source country. In this scenario, the pest is already present in both countries (scenario 2), and exporting crop commodities from a source country where the pest is widespread would allow a pest to be re-introduced more likely, more frequently or in greater quantities than from a source country where the pest is localized. Considering potential re-introductions is important because these events increase the likelihood that new genetic material of a pest species is potentially introduced and mixed with local populations in the destination country. For example, re-introduction is a particularly important concern for *Rastonia solanacearum* as this species comprises multiple sequevars, races, and biovars. Likewise, the strain of *Phthorimaea absoluta* introduced in Europe is likely clonal, but other strains from South America might pose a re-introduction risk worldwide.
- *Scenario 3.* This formulation ensures that there are always higher chances of moving pest propagule from source countries where the pest extent is greater (scenario 1 and 2), if pest movement is mediated by the international trade of crop commodities. If the pest is widespread in both countries (scenario 3), the potential movement of the pest from one

country to another would be highly likely but is comparably not as important as if the pest was initially introduced in a pest-free country.

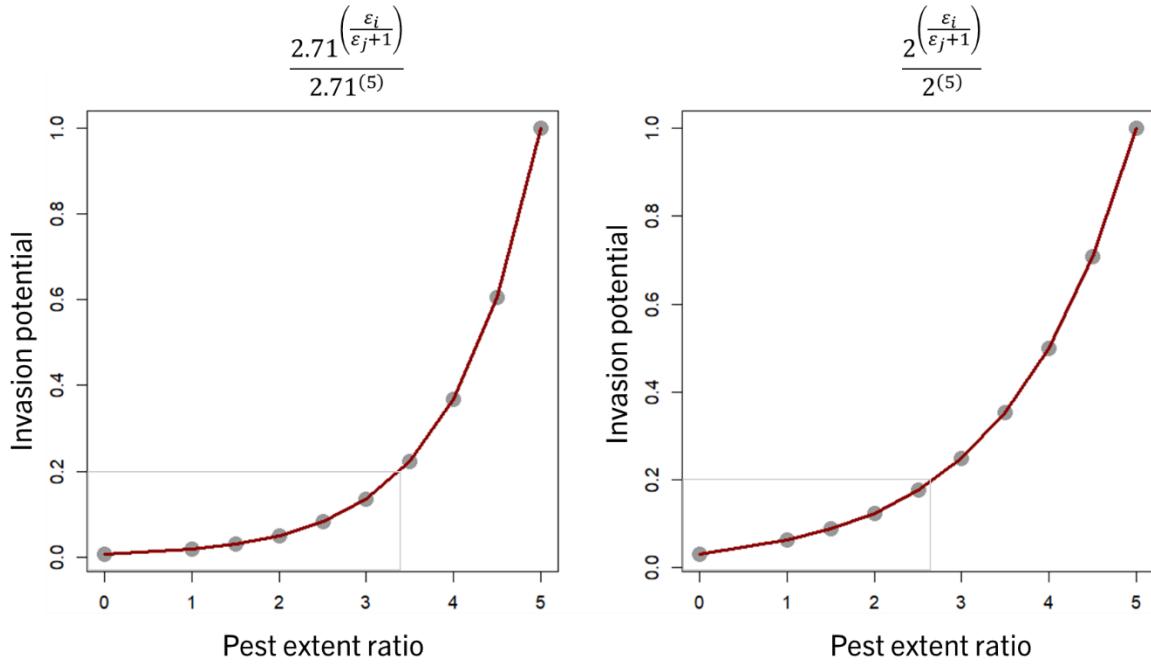
- *Scenario 4.* We finally assume that if the pest extent in the exporting country is zero (i.e., the pest is absent), the potential for pest introduction or re-introduction in the importing country is minimal but still potentially nonzero because of the possibility that some countries are re-exporting commodities from countries where the pest is present. We need to account for this idea of minimum baseline risk of pest introduction or re-introduction (118), even in the absence of the target pest in exporting countries.

To account for the above assumptions in our invasion potential analysis, we used a modified version of the above formulation in pest extents between countries as follows:

$$\tau_{i \rightarrow j} \propto \frac{A^{\left(\frac{\varepsilon_i}{\varepsilon_j + 1}\right)}}{A^5} \quad (1)$$

There are multiple beneficial features of this formulation of how invasion potential ($\tau_{i \rightarrow j}$) is proportional to a function of a positive scaling parameter (A) and pest extent in country i (ε_i).

- The maximum invasion potential index is always 1 when the pest is widespread in the source country and is absent in the destination country (the worst-case scenario). The denominator in the function (i.e., A^5) helps to keep invasion potential at a maximum value of 1.
- If there is international trade of commodities, the minimum invasion potential is not zero but a small value that depends on the base value of η . For example, the minimum invasion potential is 0.03125 if $A = 2$, $\varepsilon_i = 0$, and $\varepsilon_j = 0$; and this small value indicates that pest introduction in the destination country is 32 times less likely than the maximum invasion potential. This formulation provides a risk-averse perspective, which is a key point considering the possibility of re-exported commodities transporting pests inadvertently.
- More importantly, this formulation allows us to conceptualize invasion potential as a non-linear function of pest extent, accounting for the typical exponential growth of a pest population in a host landscape. In this formulation, the base n determines the steepness of the relationship between invasion potential and pest extent. This formulation of invasion potential based on pest extents is flexible in adjusting the base n to any value, but we set it arbitrarily to 2 in our analysis. The plot below compares two values for the steepness of this formulation in pest extents ($A = e$ or 2.71 in the left panel versus $A = 2$ in the right panel). Note that different values in pest extents (x-axis) are needed to obtain the same levels of invasion potential (y-axis = 0.2).



Notes on data sources: Currently available databases providing information on the countrywide extent of pests include the downloadable distribution lists in CABI Compendium (for example, <https://doi.org/10.1079/cabicompendium.45009> for *Ralstonia solanacearum*), PlantwisePlus Knowledge Bank (<https://plantwisenplusknowledgebank.org/>; for example, <https://doi.org/10.1079/pwkb.species.45009> for *Ralstonia solanacearum*), and EPPO Global Database (<https://gd.eppo.int/>; for example, <https://gd.eppo.int/taxon/RALSSL/distribution> for *Ralstonia solanacearum*). Many distribution lists require updates or to be created *de novo* based on published literature or unpublished expert knowledge. It is also important to note that non-reported pests do not always mean pest absence.

iii) Invasion potential as a function of international trade of commodities

The assumptions about invasion potential based on pest extent as suggested above are valid for comparison if trade between any pair of countries is constant. To incorporate the potential role of international trade on invasion potential, we assumed that the potential for pest introduction or re-introduction in a country is nonlinearly proportional to the amount of trade from the country i to the country j . We propose three mathematical formulas that satisfy this expected nonlinear proportionality between trade and invasion potential, where we explain the context for these formulas below.

$$\tau_{i \rightarrow j} \propto \left(\frac{t_{M,i \rightarrow j}}{\max(t_{M,i \rightarrow j})} \right)^{\frac{1}{m}} + \left(\frac{t_{\mu,i \rightarrow j}}{\max(t_{\mu,i \rightarrow j})} \right)^{\frac{1}{m}}, \quad (2)$$

$$\tau_{i \rightarrow j} \propto \tanh \left(m * \frac{t_{M,i \rightarrow j}}{\text{mean}(t_{M,i \rightarrow j})} \right) + \tanh \left(m * \frac{t_{\mu,i \rightarrow j}}{\text{mean}(t_{\mu,i \rightarrow j})} \right), \text{ or} \quad (3)$$

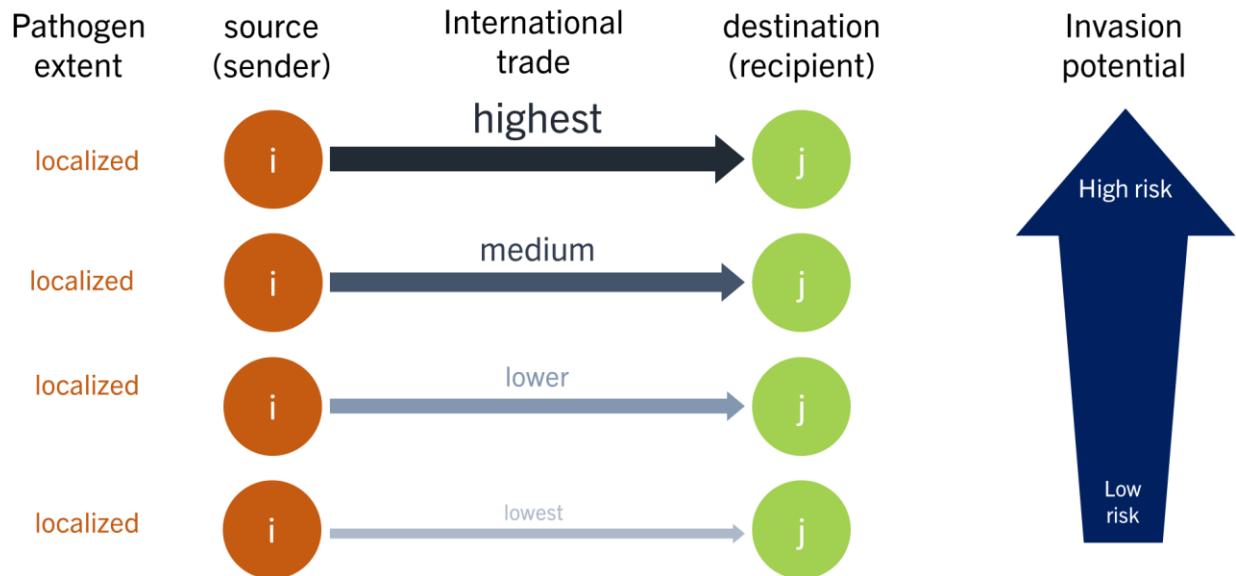
$$\tau_{i \rightarrow j} \propto \frac{t_{M,i \rightarrow j}}{t_{M,i \rightarrow j} + \text{mean}(t_{M,i \rightarrow j})} + \frac{t_{\mu,i \rightarrow j}}{t_{\mu,i \rightarrow j} + \text{mean}(t_{\mu,i \rightarrow j})} \quad (4)$$

where $t_{M,i \rightarrow j}$ is the international trade volume of 'high-risk' commodities (that is, commodities playing a major role in the dispersal of a pest species), $t_{\mu,i \rightarrow j}$ is the international trade volume of 'low-risk' commodities (that is, commodities playing a minor role in the dispersal of a pest species), m is a positive constant value, and $\max()$ (or $\text{mean}()$) are functions to calculate the

maximum (or mean) international trade volume across all international trade activities of a crop commodity.

In general, these three trade-invasion functions have the following features in common:

- They allow us to assume a high invasion potential with high volumes of international trade of a crop commodity. This is exemplified in a simple illustration below, where the pest extent in different exporting countries is the same, the pest is absent in the importing country, but there are different levels of export from exporting countries to the importing country.

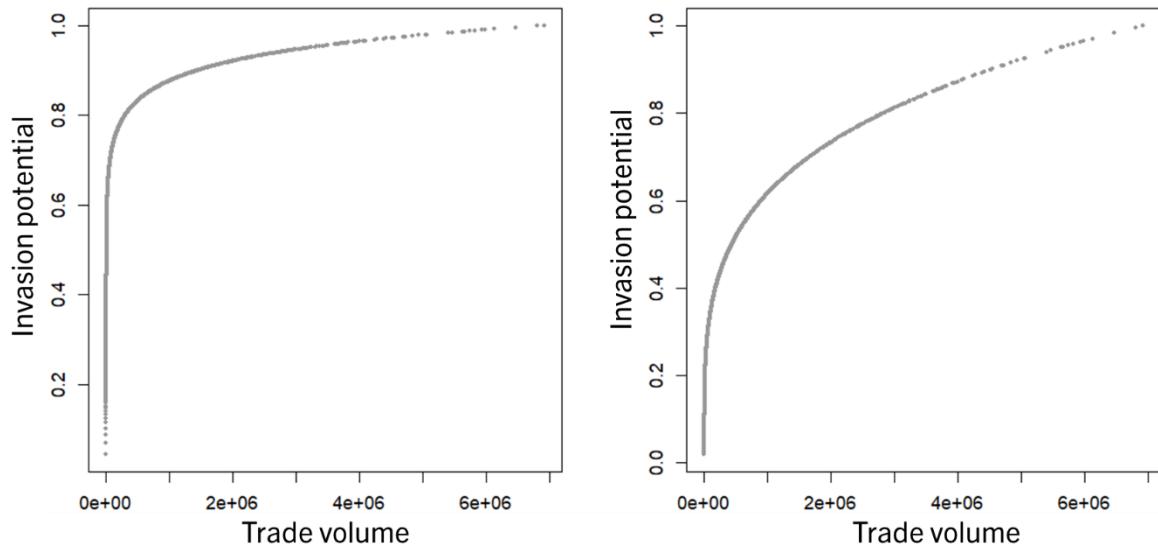


- These functions allow a non-linear association between trade volume and invasion potential (see figure below). This shape of invasion potential as a function of international trade has been suggested by some previous studies for pathogen and arthropod invasions (39, 73, 119). This shape is expected because, historically, there has been a linear increase in the number of pathogen or insect invasions, while there has been an exponential growth in international trade (39, 119). We can think of trade volume as the effort size when sampling, where with larger sample sizes (or higher trade volumes) the chances for invasion accumulates until it reaches a saturation point (73). In other words, we can think of trade volume as proportional to the number of repeated trials for the event of spread to occur.
- In other words, these nonlinear relationships between trade and potential pest movement capture canonical saturation expectations. The first function is a modified formulation of the log-log species-area model (73, 120) and specifically captures a relationship based on power law models. The second function has been used to express saturation processes (121). The third function is a modified formulation of the Michaelis-Menten model for

the species-area model (73).

$$I_j = \log_{10} t_{i \rightarrow j}$$

$$I_j = \left(\frac{t_{i \rightarrow j}}{\max(t_{i \rightarrow j})} \right)^{\frac{1}{4}}$$



- They allow scaling invasion potential between 0 and 1. The shape of these functions can be adjusted by changing the values of the constant m . In our analysis, we used the first function with m set at 4.

Trade data sources: (1) The FAOSTAT database provides a detailed trade matrix (<https://www.fao.org/faostat/en/#data/TM>) for the annual international trade of many commodity categories, reported by either the importing country (import quantity) or the exporting country (export quantity). We prefer reports on trade quantity (tons) rather than trade value (US\$) to avoid price inflation issues. Since some countries lack trade statistics on import or export reports, we calculated the mean of international trade quantity across these two report types to include all possible trade activities between any pair of countries available in this database. Importantly, the designation of countries into ‘reporting’ and ‘partner’ categories in the FAO database should be switched in one report type to correctly keep the directionality of international trade when calculating the mean international trade. (2) The World Trade Organization (<https://stats.wto.org/>) provides a comparable database for annual bilateral imports value (US\$) for many commodity categories. (3) The United Nations Comtrade Database (<https://comtradeplus.un.org/>) provides annual and monthly trade statistics, based on imports, exports, re-imports, or re-exports. Similarly as above, we prefer reports on trade quantity (kg) rather than trade value (US\$) to avoid price inflation issues. An edgelist of international trade for specific commodities can be constructed with the csv files downloaded from any of above trade databases or a consensus across all databases. (4) Volza (<https://www.volza.com/>) provides historical trade statistics with more detailed commodity descriptions, including planting material and seed trade. However, this data source is publicly available for the most recent year’s report only.

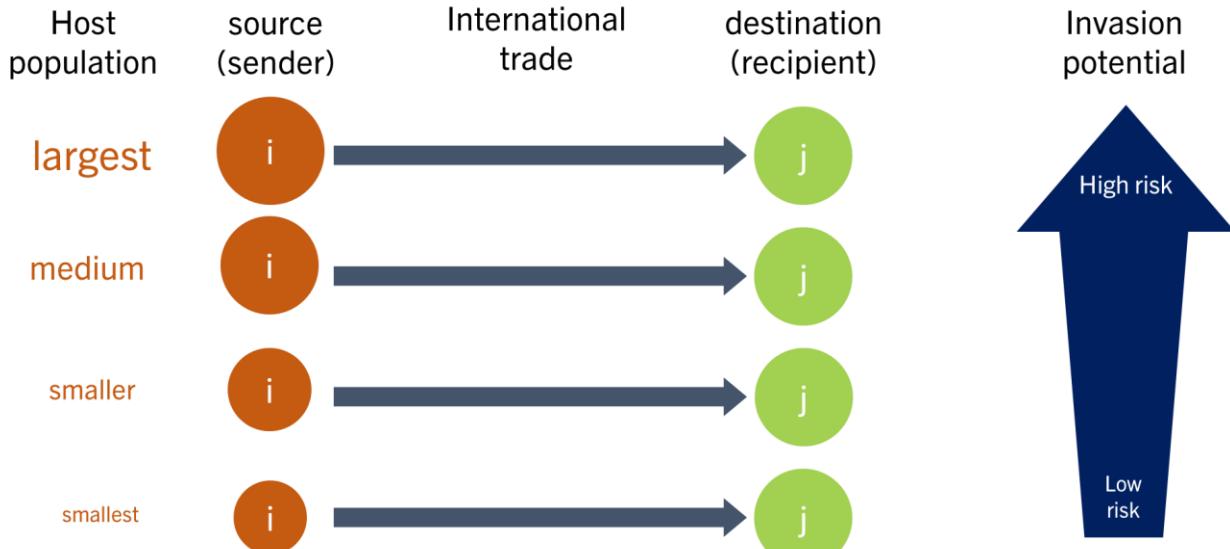
Notes on trade data caveats: (1) Not all databases provide specific information on the international trade of crop-specific planting material or seed, which is often the main pathway of spread for many plant pathogens and pests (39). (2) Informal international trade of agricultural

commodities (including planting materials) may not be reported in any of these databases, but these trade activities may pose a high risk for the spread of pathogens and pests. (3) The likelihood of commodity categories carrying or transporting a species is pathogen or pest-specific and depends on multiple factors. For example, frozen or heat-treated products may be less likely to transport pathogen inoculum or pest propagule than fresh products. Fenn-Moltu, Ollier, Caton, Liebhold, Nahrun, Pureswaran, Turner, Yamanaka and Bertelsmeier (21) provided an extensive dataset based on border interceptions to identify commodities associated with insect movement through international trade. There is not a comparable dataset and systematic analysis for pathogen-commodity associations published in a scientific journal. EUROPHYT (https://food.ec.europa.eu/plants/plant-health-and-biosecurity/europhyt/interceptions_en; https://food.ec.europa.eu/plants/plant-health-and-biosecurity/europhyt_en) provides monthly reports on interceptions of harmful (including pathogens) organisms in imported plants and other commodities. The EPPO Global Database also provides non-compliance reports for European countries (e.g., <https://gd.eppo.int/reporting/article-7329>), which include pest name (including pathogens), name of plant species consigned, type of commodity, country of origin, and country of destination based on interceptions. Expert knowledge can also be a source of unpublished or undocumented information regarding the associations between trade commodities and pest species. (4) Some commodity categories differ in resolution of classification or availability among trade databases. (5) Seasonality in the international trade of commodities is also important to understand the potential temporal dynamics in pest spread through the movement of commodities (e.g., roses are important on February 14) (1). The UN Comtrade is the only database with monthly reports on commodity trade and Volza provides specific dates of trade activities but this information is not publicly available. (6) Including trade reports covering multiple years in the analysis is important due to time lags in pest establishment, spread and discovery (39, 122). A pest introduced through international commodity trade today may be discovered some years in the future. However, determining an effective time frame or the number of years to include in a trade analysis is challenging for most invasive species. (7) While total volume of international commodity trade provides a general picture of the possible introduction of a pest species (a component of propagule pressure), the frequency of trade may also indicate potential multiple (re)introductions (frequency of propagule pressure). Considering the number of trade activities is an alternative or complementary approach to trade volume. In the future, we should build databases and modelling approaches that help us understand quantitatively the probability, magnitude and duration of pest movement through international trade of commodities.

iv) Invasion potential as a function of host availability

A third aspect, the host population present in each pair of trading countries, is key for understanding pest invasion success for two reasons.

- The idea behind inclusion of this risk factor is that the size of the host population in the exporting country i is a strong determinant of the invasion potential, which is needed to sustain a pest population. Thus, exporting countries having the same level of pest extent and the same level of export but different levels of host population (ω_i) would increase the chances of ‘sampling and exporting’ a pest in countries with larger host populations than in smaller ones. Another motivation is that when we refer to a pest as widespread, it is likely that larger host populations can sustain larger pest populations compared to smaller host populations.



- Likewise, we hypothesize that the introduction or re-introduction of a pest in an importing country increases with larger host populations in the importing country (h_j).

Since previous studies indicate that the relationship between invasion potential and host population is logarithmic at small spatial scales (74, 123), we incorporated a logarithmic function of host for quantifying invasion risk at large scales.

$$\tau_{i \rightarrow j} \propto \left(\frac{\log(\Omega_i)}{\max(\log(\Omega_i))} + \lambda_i \right) * \left(\frac{\log(\Omega_j)}{\max(\log(\Omega_j))} + \lambda_j \right), \text{ or} \quad (5)$$

$$\tau_{i \rightarrow j} \propto [1 \left(\frac{\Omega_i}{\max(\Omega_i)} \right)^k + \lambda_i] * [1 \left(\frac{\Omega_j}{\max(\Omega_j)} \right)^k + \lambda_j] \quad (6)$$

We add a parameter λ (where our analyses use $\lambda_i = \lambda_j = \frac{1}{10}$) in this formulation to make all values of invasion potential greater than zero, and $\max()$ is the maximum host population available in any country in the world. One reason why invasion potential based on the host population might not be zero is the re-export of commodities. During an exploratory analysis of international trade, we noticed that some countries re-export crop commodities even if these countries do not produce these commodities (that is, these non-producing countries may not have available hosts within their territory). This re-exporting issue motivated us to include a minimum invasion potential in countries where hosts are unavailable (λ), because of the possibility that re-exporting countries are indirectly relocating crop commodities from pest sources. Again, we scaled invasion potential, so that the maximum value is one. We used equation (5) in our analysis.

Equation (6) is a central transmission-density function proposed by Hopkins, Fleming-Davies, Belden and Wojdak (81). Equation (6) is a modified formulation of $g = c(N/A)^k$, where $\frac{N}{A}$ is the host density, $c = 1$, and $k \in (0,1)$. In the theory of island biogeography, a similar formulation is proposed for the species-area curve $S = CA^z$, where S is the number of species of a given taxon found on a region and A is the area of the region, k ranges between 0.12 and 0.17.

- Notes on host data sources: FAOSTAT (<https://www.fao.org/faostat/en/#data/QCL>) provides information about the harvested area of crop species at the national level. We used the harvested area of the crop species affected by the target pathogen as proxy for

host availability within a country. Other data sources such as CROPGRIDs (43), MAPSPAM (<https://mapspam.info/>), and EARTHSTAT (124) are available for the geographic distribution of crop species and the Global Biodiversity Information Facility (GBIF; <https://www.gbif.org/>) for wild plant species. Information about plant species' distribution from these data sources needs to be aggregated at the country level for use in the pest introduction analysis, except for FAOSTAT.

- Notes on host data caveats. For pests with multiple plant host species, the role of host species during epidemics or pest invasion may be different, requiring consideration of the availability of primary (H) and secondary (h) hosts in the country. We can incorporate this potential role differences by assuming $\omega_i \propto \ln(AH_i + ah_i)$, where H_i is the total abundance of all primary, major, or main hosts species of the targeted pest in country i and h_i is the total abundance of all secondary, minor, or alternative hosts species of the targeted pest in country i . The weights in our analyses allowed us to emphasize the importance of major hosts, where pests are more likely to survive and be transported in commodities. We arbitrarily set $A = 2$ and $a = 1$ in our analyses. Another important consideration for invasion potential is the seasonality in susceptible host availability. Pest invasion potential also depends on the geographic distribution of tolerant and resistant hosts at the intraspecies level. These two later factors are not considered in our analysis.

v) Invasion potential as a function of available biosecurity measures

Finally, we included the idea that the reported biosecurity level of the exporting country (β_i) and the biosecurity level of importing country (β_j) are inversely related to invasion potential in our analysis.

$$\tau_{i \rightarrow j} \propto \frac{1}{\beta_i * \beta_j} \quad (7)$$

We assumed that greater, more diverse, and more intense biosecurity efforts reduce invasion potential through international trade of agricultural commodities. For example, in 2023, the United States through a federal order imposed import requirements for tomato leafminer (*Phthorimaea absoluta*) hosts from infested countries. In this case, we classify countries as whether they are required to meet import requirements or not when exporting commodities (such as tomato fruits) to the United States. For the introduction potential analysis in the main paper, we set $\beta_i = 10$ if there was any type of pest-specific biosecurity measure imposed on traded commodities, and $\beta_i = 1$ otherwise. Risk analysts can modify these biosecurity parameter values (β_i or β_j) as needed.

More generally, our analysis incorporates whether countries implement biosecurity measures when trading commodities internationally, which preferentially would be specific to the target pest species or specific to an agricultural commodity. This type of biosecurity information can be the implementation or adoption of International Standards for Phytosanitary Measures (ISPMs; <https://www.ippc.int/en/core-activities/standards-setting/ispm/>), which is reported by the International Plant Protection Convention (IPPC). For example, ISPM15 is crucial to prevent the movement of pests associated with wood packing material in international trade, and IPPC provides a list of countries implementing ISPM15 (<https://www.ippc.int/en/countries/all/ispm15/>). In the absence of a biosecurity measure specific

to a pest species or agricultural commodity, an alternative approach is to consider general measures of countries' efforts in managing invasive species [e.g., Montgomery, Walden-Schreiner, Saffer, Jones, Seliger, Worm, Tateosian, Shukunobe, Kumar and Meentemeyer (30)]. A candidate measure for this alternative approach is the proactive and active response capacities of countries provided by Early, Bradley, Dukes, Lawler, Olden, Blumenthal, Gonzalez, Grosholz, Ibanez, Miller, Sorte and Tatem (5), which account for multiple aspects of national responses to invasive species.

vi) Proportional relationships of invasion potential

Chapman, Purse, Roy and Bullock (31) provided a multi-species pest invasion analysis for international trade of four broad categories of agricultural commodities (live plants, forest products, fruit and vegetables, and seeds) in Europe and the Mediterranean region. Gottwald, Luo, Posny, Riley and Louws (27) provided an introduction risk analysis for Asiatic citrus canker, citrus black spot, and citrus Huanglongbing (HLB) in the United States, where possible pest introduction is mediated by the international movement of people. Montgomery, Walden-Schreiner, Saffer, Jones, Seliger, Worm, Tateosian, Shukunobe, Kumar and Meentemeyer (30) also provided an example for the potential spread of the planthopper spotted lanternfly through the global trade network of stone commodities. To our knowledge, a detailed approach to estimating potential pest introduction through international trade networks of crop-specific commodities globally is lacking and needed. Available approaches though have not been applied to understand the possible introduction of plant pathogens.

Here our objective was to provide and apply such a detailed network-based modelling approach. In this modeling approach, we explicitly considered five major ecological, epidemiological, or biological factors for the potential introduction of pest species in a country (equation 8): crop-specific international trade (t), pest extent (ε), pest discovery duration (δ), host availability (h), and biosecurity regulations (β). In a global trade network, the relative likelihood of accidentally introducing a pest species through commodity trade in an importing country (τ_j) is proportional to the invasion potential posed by importing from a certain number (z) of exporting countries.

$$\tau_{i \rightarrow j} \propto \frac{A^{\left(\frac{\varepsilon_i}{\varepsilon_j + 1}\right)}}{A^{(5)}} * \frac{1}{\beta_i * \beta_j} * \left(\frac{t_{i \rightarrow j}}{\max(t_{i \rightarrow j})} \right)^{\frac{1}{m}} * \left(\lambda_i + \frac{\log(\Omega_i)}{\max(\log(\Omega_i))} \right) * \left(\lambda_j + \frac{\log(\Omega_j)}{\max(\log(\Omega_j))} \right) \quad (8)$$

We assume that $P(\tau_{i \rightarrow j})$ represents the relative likelihood of pest movement from country i to j . If a destination or importing country is trading only with one source or exporting country, $1 - P(\tau_{i \rightarrow j_1})$ is the relative likelihood that trading agricultural commodities from country i to j does not transport or carry pest propagule. If the importing country is trading with two exporting countries, $(1 - P(\tau_{i \rightarrow j_1}))(1 - P(\tau_{i \rightarrow j_2}))$ is the joint relative likelihood that neither of two exporting countries i introduce the target pest species into country j by the trade of agricultural commodities. We assume that the events of introduction from these two countries are independent of each other. More broadly, under the same assumption of independence, the joint relative likelihood that none exporting countries introduce the pest species into a target importing country is $\prod_{k=1}^z (1 - P(\tau_{i \rightarrow j_k}))$, where z is the number of countries exporting agricultural commodities to country j . Finally, the joint relative likelihood that the pest is introduced into a country from any exporting country is I_j , where

$$I_j \propto 1 - \prod_{k=1}^z (1 - P(\tau_{i \rightarrow j_k})) \quad (9)$$

Note that our formulation of $\tau_{i \rightarrow j}$ explicitly incorporates the three major components of species dispersal as envisioned in movement ecology or dispersal biology: source processes (departure or emigration), relocation processes (transience or transfer), and destination processes (settlement or immigration) (78, 79, 125, 126). Among the risk factors included in equation (8), international trade of commodities is most likely associated with relocation processes, while the other factors are more likely to influence source or destination processes in a global landscape.

vii) Combining ports, cities and trade connectivity

Because international trade is only available at country resolution, we allocated each grid in the global accessibility to cities and ports as belonging to its corresponding country. For each country, we used I_j . We then disaggregated I_j using accessibility to ports (I_p) and cities (I_c) to approximate initial entry points or final destinations into countries. Our final index of pest introduction potential due to trade (or Δ_t) is proportional to port accessibility within a country (I_p) and the country-level introduction risk when importing commodities (I_j):

$$\Delta_t \propto I_p \times I_j \quad (10)$$

The assumptions of combining port or city accessibility with I_j are provided in the main text of this paper.

viii) Future considerations on the introduction potential based on international trade

Our analytical framework for assessing pest introduction potential, as detailed above, originated from a growing interest in applying network analysis to enhance the understanding of biological invasions (22). Below, we briefly mention potential future avenues to improve this analytical framework if the required geographic data becomes available.

- In equation (8), each geographic risk factor is equally weighted and is equally likely to influence invasion potential. In some cases, geographic risk factors might exhibit different levels of importance in invasion potential. Thus, a generalized formulation of equation (8) is equation (11):

$$\tau_{i \rightarrow j} \propto x_1 \ln \left[\frac{\left(\frac{e_i}{e_j+1} \right)}{A^{(5)}} \right] + x_2 \ln \left[\left(\frac{t_{i \rightarrow j}}{\max(t_{i \rightarrow j})} \right)^{\frac{1}{m}} \right] + x_3 \ln \left[\left(\frac{\log(h_i)}{\max(\log(h_i))} + \lambda_i \right) * \left(\frac{\log(h_j)}{\max(\log(h_j))} + \lambda_j \right) \right] + x_4 \ln \left[\frac{1}{\beta_i * \beta_j} \right] \quad (11)$$

Where x_1, \dots, x_4 are specific weights assigned to each geographic risk factor. However, determining the specific importance of geographic risk factors for the introduction potential of a pest species is challenging.

- In their risk-based introduction analysis, Gottwald, Luo, Posny, Riley and Louws (27) considered infection duration as an important factor for estimating the relative plant pathogen strength in a source country. We expand this assumption about pest duration in a source country (δ_i), where earlier pest detections may indicate that a pest could have had greater opportunities for spread within a country. We defined pest duration (δ_i) as the difference between the current year and the year of earliest detection of the pest species in the source country. Including this assumption about pest duration is particularly important for pest species with a restricted geographic distribution but that continues expanding over other host areas.

- Our index of pest introduction potential (equation 10) does not incorporate the role of environmental factors (31), which are usually pest-specific conditions; stochasticity (30); and time lags in species discovery (39).
- Our pest introduction potential model ignores the principle of competitive exclusion between pest species, other interspecific interactions such as the populations of natural enemies of pest (127), and the Allee effect that some pests may experience (128).

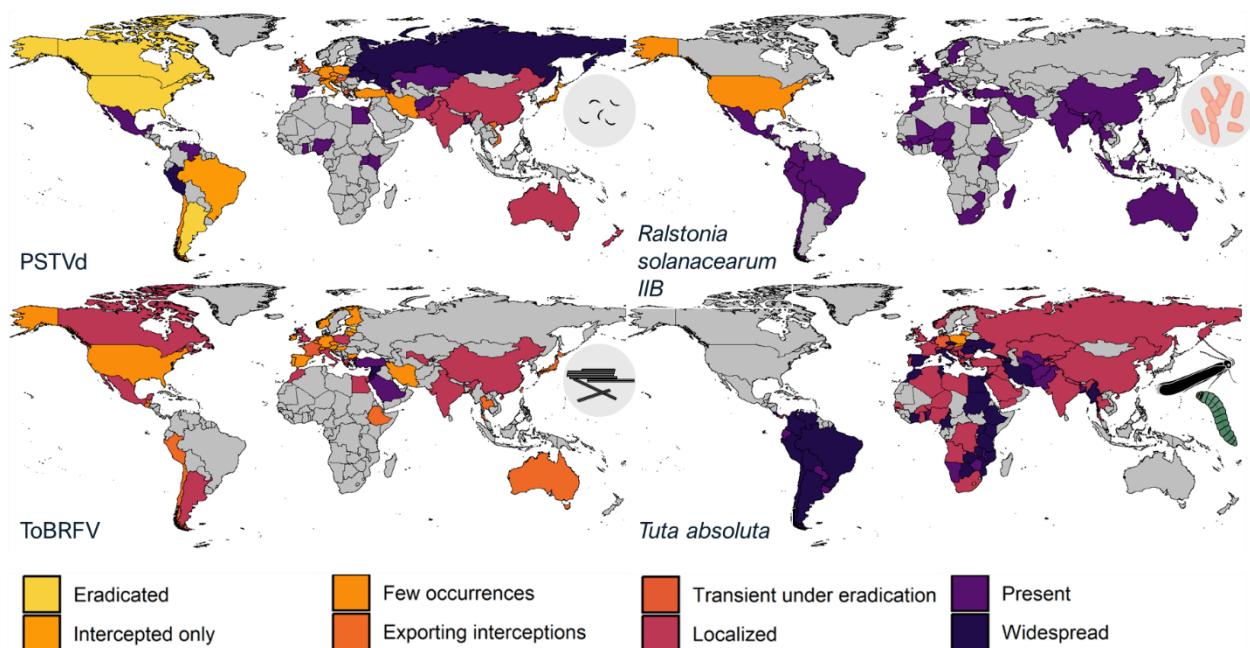


Fig. S1.

Potential pest sources for sentinel surveillance based on reported within-country distribution.

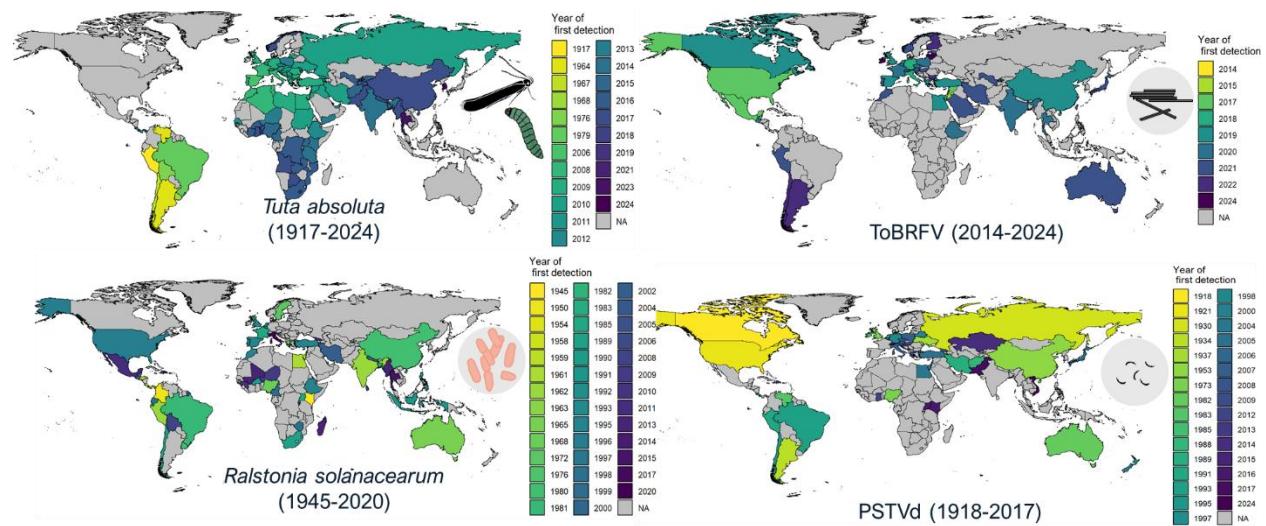


Fig. S2.

Geographic pest discovery reconstructed from earliest national observations.

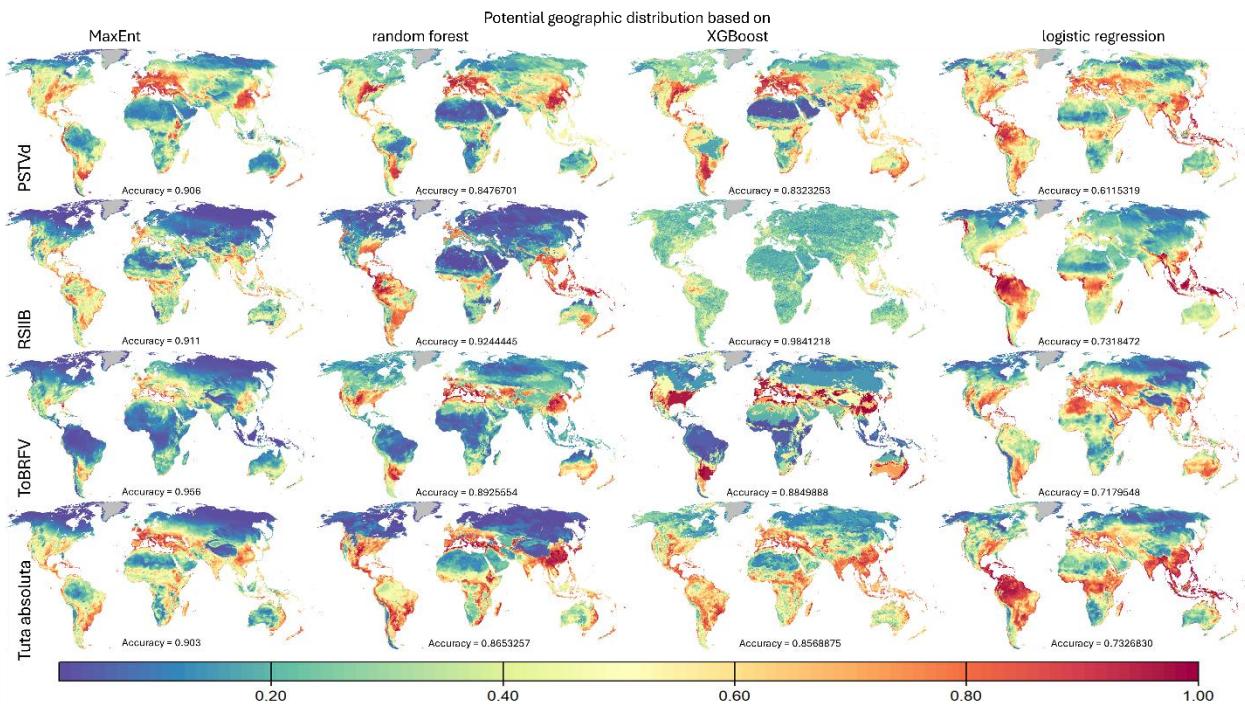


Fig. S3.

Predictions for pest presence based on four machine-learning algorithms.

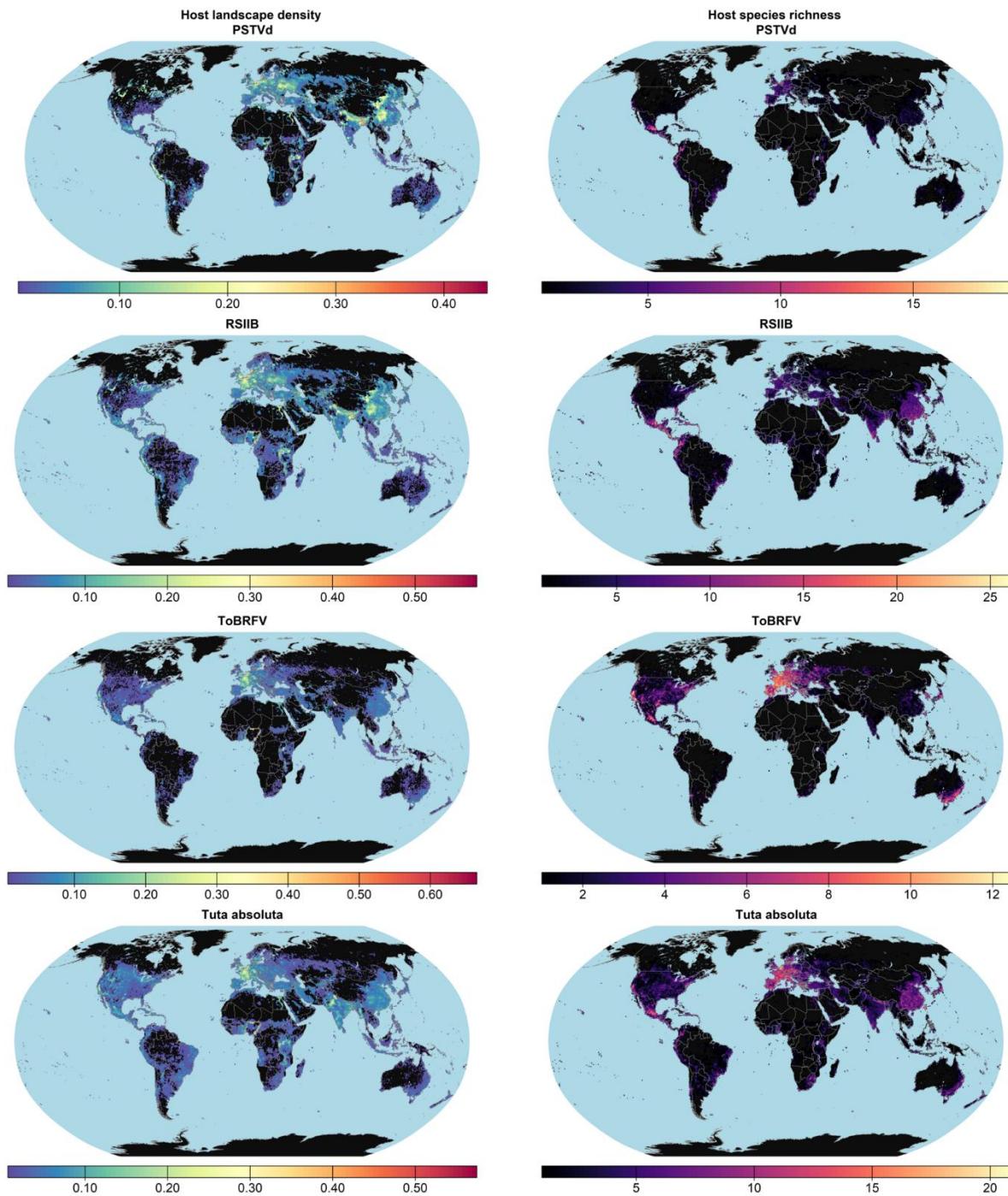


Fig. S4.

Geographic patterns in cumulative host density and host species richness for each target pest.

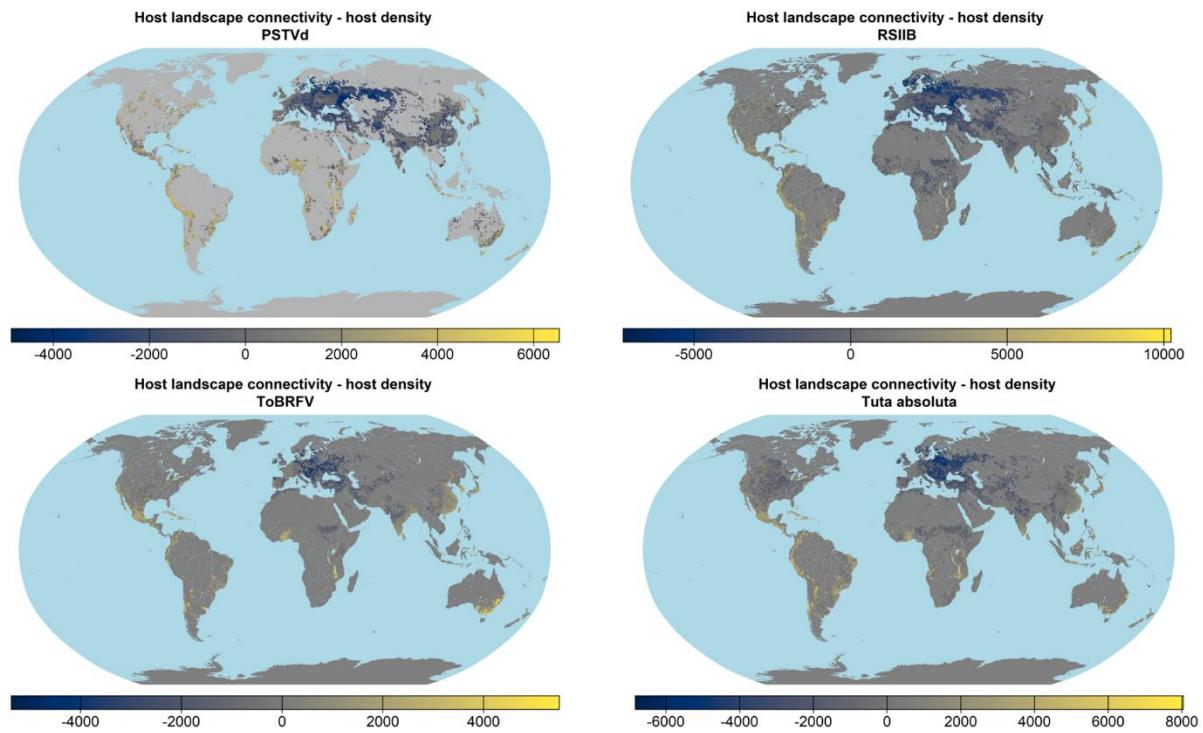


Fig. S5.

Maps of difference in ranks between mean host landscape connectivity and total host density.

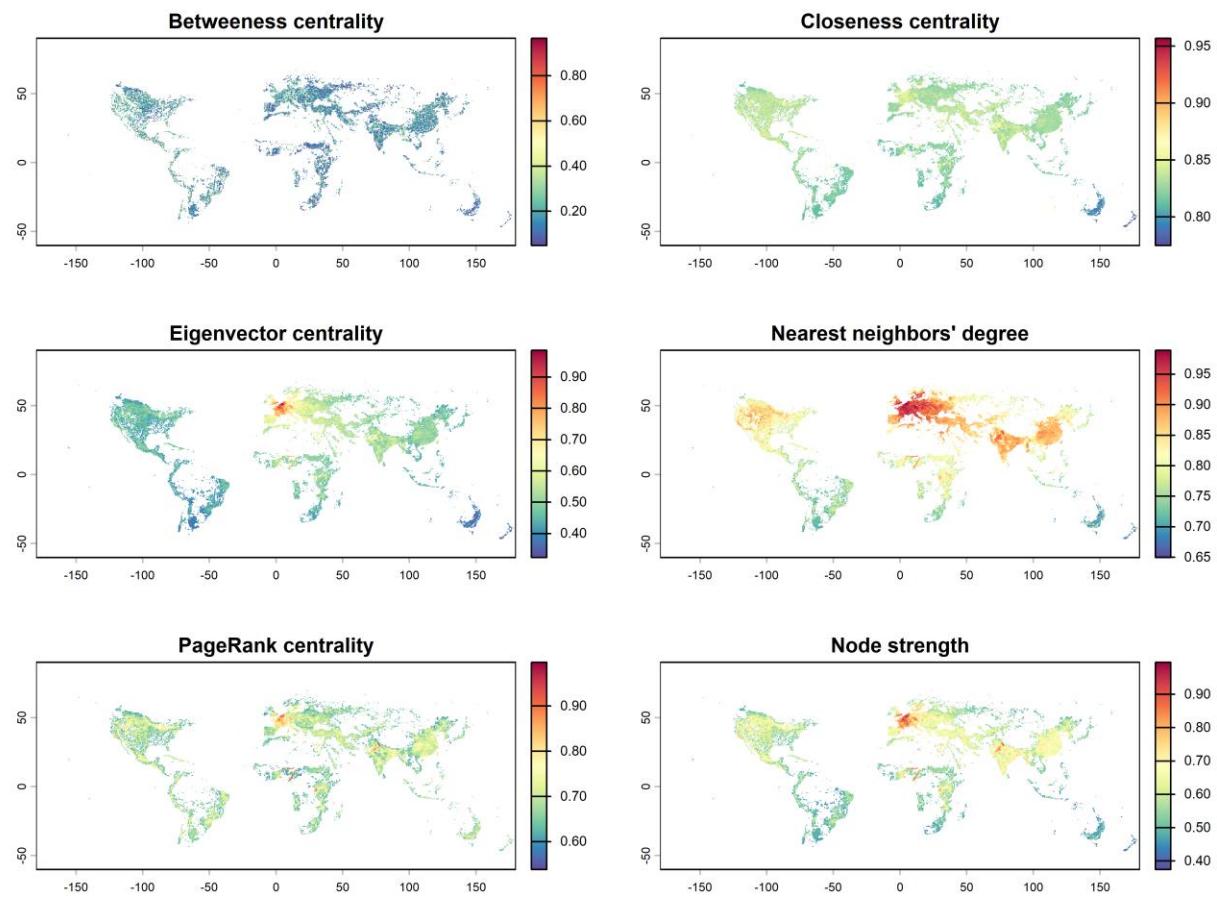


Fig. S6.

Maps of host landscape connectivity for *Phthorimaea absoluta* based on six network metrics.

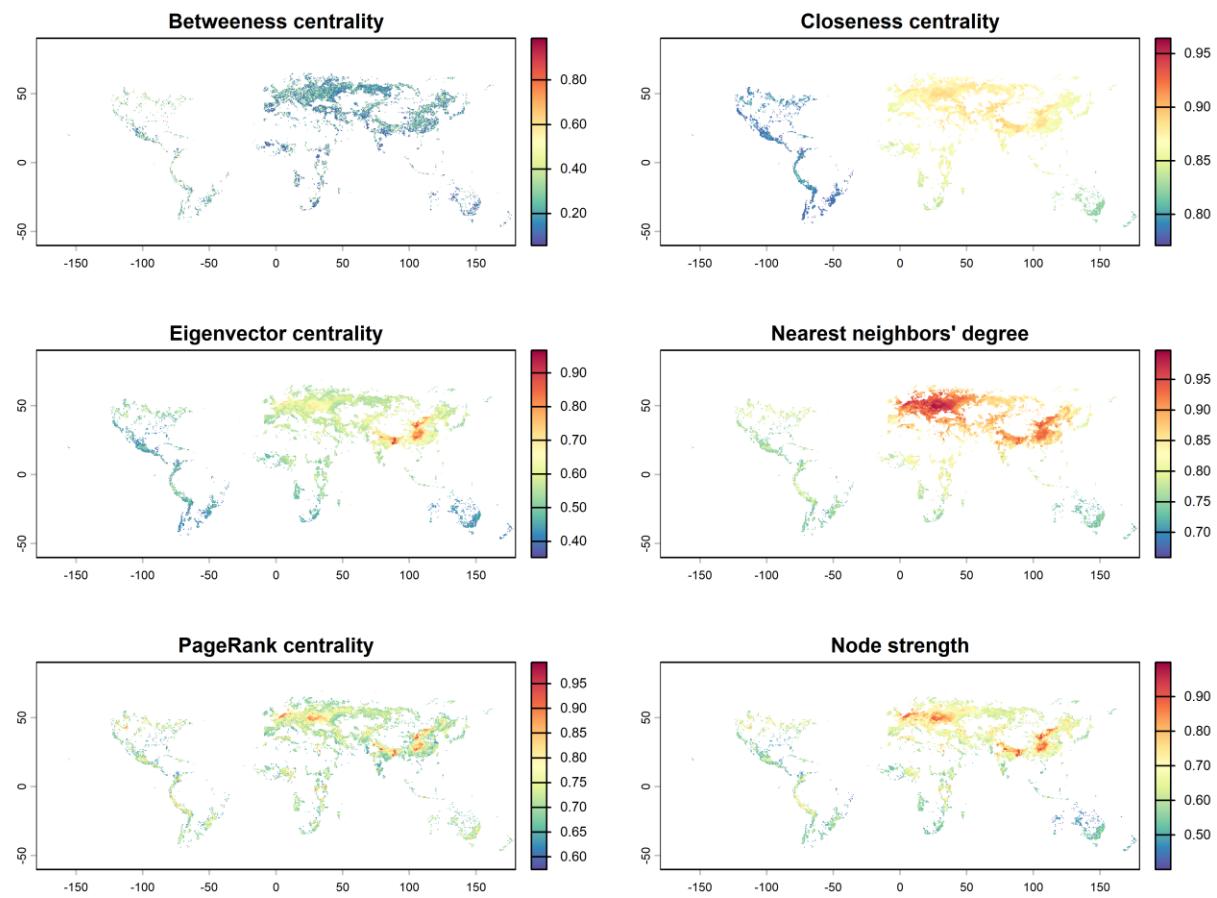


Fig. S7.

Maps of host landscape connectivity for potato spindle tuber viroid based on six network metrics.

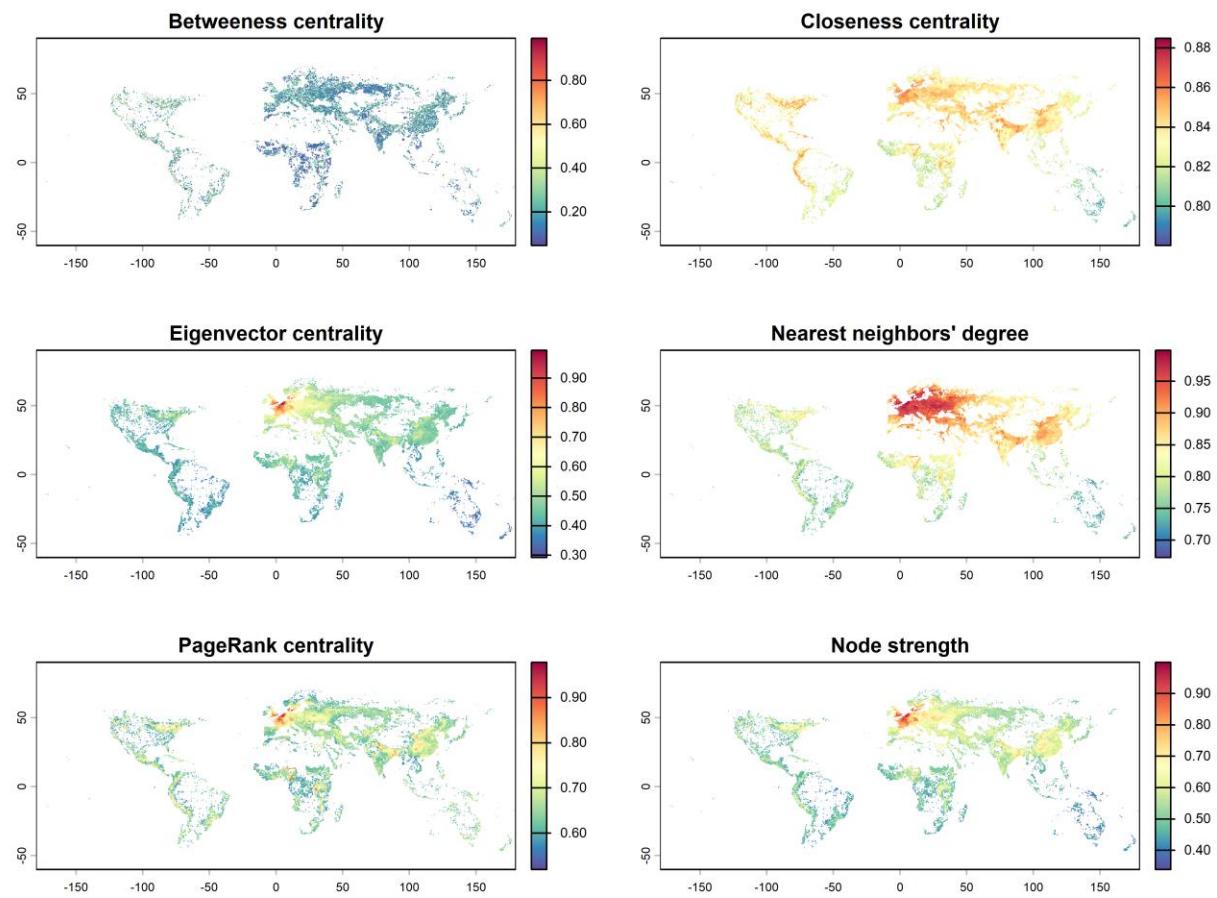


Fig. S8.

Maps of host landscape connectivity for *Ralstonia solanacearum* phylotype II-B based on six network metrics.

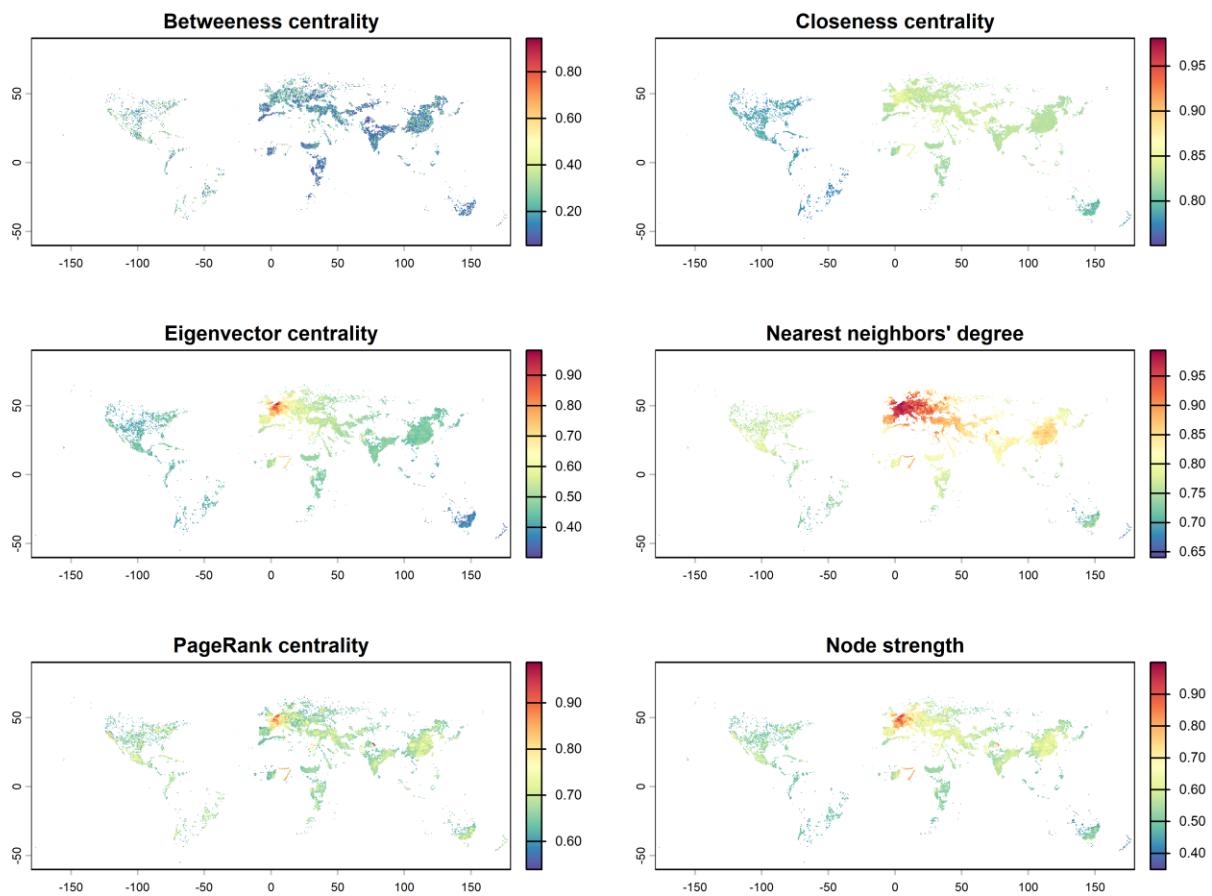


Fig. S9.

Maps of host landscape connectivity for tomato brown rugose fruit virus based on six network metrics.

Table S2.

Categories and weights assigned to global maps of accessibility to ports.

Port ID	Port size	Number of ports	Model weight	Likelihood rank
A	Large	160	0.35	Highly likely
B	Medium	361	0.3	Mild likely
C	Small	990	0.2	Low likely
D	Very small	2153	0.15	Very low likely
Total map	All sizes	3664	1	Any likely
	Average accessibility = $\frac{0.35A+0.3B+0.2C+0.15D}{4}$			

Table S3.

Categories and weights assigned to global maps of accessibility to cities.

Settlement class	Minimum population threshold	Maximum population threshold	Number of settlements	Population in settlements	Weight
1	5,000,000	50,000,000	79	941,207,809	½
2	1,000,000	5,000,000	421	851,153,118	1/3
3	500,000	1,000,000	581	400,180,511	¼
4	200,000	500,000	2,096	630,823,940	1/5
5	100,000	200,000	3,694	515,557,120	1/6
6	50,000	100,000	6,973	484,166,417	1/7
7	20,000	50,000	20,457	628,095,955	1/8
8	10,000	20,000	29,286	410,631,333	1/9
9	5,000	10,000	45,795	322,797,326	1/10

Table S4.

Major host species of the target pest used in the multi-host connectivity analysis. Note that minor host species used in the analysis are not mentioned here.

Target pest name	Abbreviation	Main host species
<i>Phthorimaea absoluta</i>		Tomato (<i>Solanum lycopersicum</i>)
<i>Tomato brown rugose fruit virus</i>	ToBRFV	Tomato (<i>Solanum lycopersicum</i>) Peppers (<i>Capsicum annuum</i>)
<i>Ralstonia solancearum</i> phylotype IIB1	RSIIB1	Bittersweet (<i>Solanum dulcamara</i>) Potato (<i>Solanum tuberosum</i>) Tomato (<i>Solanum lycopersicum</i>)
<i>Potato spindle tuber viroid</i>	PSTVd	Potato (<i>Solanum tuberosum</i>)

Table S5.

List of agricultural commodities associated with each target pest and used as a dispersal pathway in the trade-mediated (re)introduction risk analysis.

Target pest name	Commodity	Importance	Units	Data source
<i>Phthorimaea absoluta</i>	HS 0702.00 Tomatoes, fresh or chilled	Major (100%)	Tons	World Trade Organization (WTO)
<i>Tomato brown rugose fruit virus</i>	Tomato seeds	Major (100%)	Standard Qty	Volza
	HS 0702.00 Tomatoes, fresh or chilled	Minor (50%)	Tons	World Trade Organization (WTO)
<i>Ralstonia solanacearum</i> phylotype IIB1	HS0701.10 Potatoes, seed	Major (100%)	Tons	World Trade Organization (WTO)
	Pelargonium, geranium plants, geranium seeds, or geranium for sowing	Major (100%)	Standard Qty	Volza
<i>Potato spindle tuber viroid</i>	HS0701.10 Potatoes, seed	Major (100%)	Tons	World Trade Organization (WTO)
	Petunia flower, plants, seeds, and for sowing	Major (100%)	Standard Qty	Volza
	Capsicum seeds, chilli seeds, sweet, hot, green pepper seeds, red pepper seeds, charlston pepper seeds, sweet or bell pepper seeds, capsicum plants	Major (100%)	Standard Qty	Volza

Table S6.

Model performance metrics for the multi-host connectivity analysis.

Pest name	Precision	A	B	Test statistic D ⁺	p
Potato spindle tuber viroid	0.827	0.201	0.173	0.26621	0.0001586
<i>Ralstonia solanacearum</i> phylotype IIB	0.867	0.192	0.138	0.32822	8.241e-13
Tomato brown rugose fruit virus	0.677	0.225	0.126	0.45953	1.412e-12
<i>Phthorimaea absoluta</i>	0.810	0.155	0.131	0.25709	< 2.2e-16
Average	0.792	0.192	0.141		

Precision: 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 pest has been reported present (true positives + false negatives). Note that our validation is based on presence-only data, so false positives and true negatives are not calculated.

A: The mean value in multi-host connectivity of grid cells where there are georeferenced observations of the reported presence of a pest species.

B: The mean value in multi-host connectivity across all grid cells, which were relevant for the multi-host connectivity analysis of each pest species.

Table S7.

Model performance metrics for the (re)introduction vulnerability analysis.

Pest name	Precision	A	B	Test statistic D ⁺	p
Potato spindle tuber viroid	1	0.171	0.107	0.24615	0.2746
<i>Ralstonia solanacearum</i> phylotype IIB	1	0.078	0.100	0.08772	0.8037
Tomato brown rugose fruit virus	1	0.047	0.118	0.01449	0.9293
<i>Phthorimaea absoluta</i>	1	0.134	0.028	0.15607	0.5406
Average	1	0.094	0.087	0.06123	0.7296

Precision: 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 (true positives + false negatives). Note that our validation is based on presence-only data, so false positives and true negatives are not calculated.

A: Mean value in (re)introduction risk in countries where the pest has been intercepted on imported agricultural commodities.

B: Mean value in (re)introduction risk in countries where the pest has not been intercepted on agricultural commodities.

Data S1-10. (separate file)

These datasets were used to construct models in GIRAf and are available for review at

http://datadryad.org/share/LINK_NOT_FOR_PUBLICATION/6mtexakLduHFj6hfkiIIRSFiBt_5InuVEty4rmIZidEE