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ARTICLE
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Forecasting global spread of invasive pests and pathogens through international trade

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Abstract

Non-native plant pests and pathogens threaten biodiversity, ecosystem function, food security, and economic livelihoods. As new invasive populations establish, often as an unintended consequence of international trade, they can become additional sources of introductions, accelerating global spread through bridgehead effects. While the study of non-native pest spread has used computational models to provide insights into drivers and dynamics of biological invasions and inform management, efforts have focused on local or regional scales and are challenged by complex transmission networks arising from bridgehead population establishment. This paper presents a flexible spatiotemporal stochastic network model called PoPS (Pest or Pathogen Spread) Global that couples international trade networks with core drivers of biological invasions—climate suitability, host availability, and propagule pressure—quantified through open, globally available databases to forecast the spread of non-native plant pests. The modular design of the framework makes it adaptable for various pests capable of dispersing via human-mediated pathways, supports proactive responses to emerging pests when limited data are available, and enables forecasts at different spatial and temporal resolutions. We demonstrate the framework using a case study of the invasive planthopper spotted lanternfly (*Lycorma delicatula*). The model was calibrated with historical, known spotted lanternfly introductions to identify potential bridgehead populations that may contribute to global spread. This global view of phytosanitary pandemics provides crucial information for anticipating biological invasions, quantifying transport pathways risk levels, and allocating resources to safeguard plant health, agriculture, and natural resources.

KEYWORDS
biological invasions, bridgehead effects, international trade, iterative forecasting, network model, plant pests and pathogens

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INTRODUCTION

Worldwide, plant pests and pathogens (hereafter "pests" for brevity) are responsible for destroying up to 40% of crop yields and disrupting species composition and structure of forest ecosystems (Fones et al., 2020; Paini et al., 2016; Pyšek & Richardson, 2010; Savary et al., 2019). Invasions by non-native pests have increased in recent decades and show no signs of slowing (Seebens et al., 2017), with corresponding damage and management costs roughly doubling every six years since 1970 (Diagne et al., 2021). This acceleration is largely driven by globalization and international trade, which facilitates long-distance movement beyond natural geographic barriers (Brasier, 2008; Chapman et al., 2017; Epanchin-Niell et al., 2021). The establishment of successful invasive populations, termed bridgehead populations, then become additional pest sources and accelerate global spread (Bertelsmeier et al., 2018; Bertelsmeier & Keller, 2018; Lombaert et al., 2010). Furthermore, propagule transport from these bridgehead populations results in complex patterns of repeated introductions and population admixture that can increase invasive population fitness and establishment success (Garnas et al., 2016; Rius & Darling, 2014). Accounting for global transport and bridgehead effects in invasive plant pest risk assessments can help inform prevention and management efforts taking place at the range of spatial scales known as the biosecurity continuum (Magarey et al., 2009) and improve global spread forecasts.

Research in biological invasions has increasingly turned to mathematical models and computational simulations to understand drivers and dynamics of invasive species spread (Douma et al., 2016; Lewis et al., 2016b; Parnell et al., 2017). Population models have been used to predict species survival and growth following an introduction, incorporating complicated interspecific interactions (Lewis et al., 2016a; Petrovskii, Malchow, et al., 2005; Petrovskii, Morozov, et al., 2005). Species distribution models, meanwhile, provide insights for invasive pest management by identifying areas where a pest could establish based on statistical relationships between current distributions and relevant environmental factors (Elith & Leathwick, 2009; Václavík & Meentemeyer, 2009; Wakie et al., 2020). Spatially explicit epidemiological simulations that capture local and long-distance dispersal mechanisms are especially useful for predicting patterns and rates of invasive plant pest spread (DeAngelis & Yurek, 2017; Jones et al., 2021; Meentemeyer et al., 2011). Network models are well suited for modeling complex human-mediated dispersal and can be coupled with grid-based diffusion models (Banks et al., 2015; Harwood et al., 2009; Strickland et al., 2015; Xing et al., 2020). Although computational models have been extensively used to study biological invasions and provide valuable insights, most models focus on local or regional scales of establishment and spread and do not attempt to model the multiscale processes of bridgehead effects. The immensely challenging task of invasive plant pest management, however, must be supported by forecasts that consider local, regional, and global dynamics to understand complex patterns of movement and invasion success (Chapman et al., 2017; Garnas et al., 2016; Meentemeyer et al., 2012).

Multiscale network modeling frameworks that couple global models of organism movement with local or regional models of population dynamics have been used to predict rates and patterns of pandemic spread among humans and, more recently, invasive species. The GLEAMvis framework for human infectious disease modeling (Balcan et al., 2010) uses global airline and regional commuter data to simulate movement of infected individuals between geographically dispersed metapopulations and compartmental models to simulate spread dynamics within each metapopulation. The flexible Spatiotemporal Epidemiological Modeler (STEM; Ford et al., 2006) also couples network models with local compartmental or agent-based disease models. For invasive marine species, Seebens et al. (2013, 2016) developed a probabilistic network model that couples ballast water transport through international shipping networks with port biogeographic conditions to identify invasion routes and predict establishment. Gottwald et al. (2019) published a general census-travel model that integrates international passenger movement, demographic data, and source strength to assess plant, human, and animal pathogen introduction risk for land parcels. These multiscale modeling approaches represent a promising paradigm for global biological invasion forecasting; however, their applicability to phytosanitary risk analysis is limited by the unique challenges posed by plant pests. Plant pests often exhibit long detection lag times (e.g., years vs. days), complex host preferences, temporal and spatial irregularity of host availability, and diverse dispersal mechanisms (Crooks, 2005; Cunniffe et al., 2015). Furthermore, traits of emerging plant pests are often not well understood, and occurrence data for model calibration and validation are limited. Phytosanitary agencies tasked with preventing and managing emerging invasive plant pests need tools that can quickly be deployed for a broad range of pest–host systems when data are limited to simulate global transport and bridgehead population establishment.

This paper introduces PoPS (Pest or Pathogen Spread) Global—a flexible, stochastic simulation and forecasting framework adapted for plant pests and pathogens from the network modeling approach developed by Seebens et al. (2013, 2016) and builds on the local-to-regional scale PoPS Forecasting Platform (Jones et al., 2021). PoPS is a modular, spatially explicit, discrete-time forecasting platform that simulates reproduction, dispersal, and establishment of pests based on weather, multiscale dispersal, and other biotic and abiotic factors. It has been used in collaboration with government and other partners to forecast the spread of *Phytophthora ramorum*, the causal agent of sudden oak death, and spotted lanternfly (Gaydos et al., 2021; Jones et al., 2021). Together with PoPS Border, a consignment inspection simulator used for designing dynamic, risk-based sampling protocols at national ports of entry (Montgomery et al., 2023), these three models form a suite of tools developed to support phytosanitary management decisions along the biosecurity continuum.

PoPS Global is broadly applicable for forecasting plant pest invasions accelerated by international trade and bridgehead populations. It can be adapted for a wide range of pest–host systems, targeting pest species associated with specific commodities. The modular design enables quick implementation to support management of poorly understood emerging pests using general, open data, while also providing options to integrate more specialized information when available. PoPS Global is multiscale, addressing calls to incorporate temporal dynamics of local spread and global transmission concurrently; multiscale dynamics (e.g., latency between invasion and population build up) are critical to understanding the timing of pandemics (Balcan et al., 2009; Chapman et al., 2017). The framework also allows for scenario testing by adjusting inputs to explore the impact of management (e.g., phytosanitary efforts and trade policy) or pest ecology (e.g., polyphagy and host availability). This paper describes the modeling framework, highlighting the modular design, core drivers, and data requirements and presents a case study of an emerging plant pest, spotted lanternfly (*Lycorma delicatula*) to demonstrate how the framework can be used to forecast global species movement. We conclude by highlighting opportunities for expansion of this open-source framework and priorities for data and future research.

METHODS

The PoPS Global forecasting framework integrates an automated open-data pipeline that supports model calibration and validation, scenario testing and analytics to inform management decisions, and iterative updating as new data become available (Figure 1; Appendix S1: Section S1). The open data pipeline acquires and formats pest observations, core driver data, and optional inputs to the model. A calibration loop incorporates a parameter grid search and leave-one-out cross-validation to compute calibrated model parameters, validate results, and enable sensitivity analyses (Figure 1b; Appendix S1: Section S5). Users can visualize forecast and scenario results (Figure 1a) to inform biosecurity management decisions, including the deployment of novel surveillance approaches like web scraping and text mining to automatically monitor online information sources (Tateosian et al., 2023). The model is then confronted with new pest occurrence data as they become available to update and improve the forecast (Figure 1c). This framework provides a practical approach for leveraging currently existing data to quickly provide quantitative forecasts of plant pest invasions and to iteratively improve the forecast over time.

Modeling framework

PoPS Global is a spatiotemporal stochastic network modeling approach wherein network nodes represent geographical areas (e.g., countries, regions, and ports) and bidirectional network edges (i.e., connections between nodes) represent human-mediated dispersal pathways, for example, the movement of goods via trade. Potential plant pest import and export is modeled along these pathways by integrating global trade data, pest occurrence, host species distribution, and climate conditions. The model incorporates changing environmental and host conditions (e.g., annual agricultural crops or perennial forest species) and the impact of biosecurity and control measures on spread (Figure 2a,b), which can be updated as new data become available (Dietze et al., 2018; Jones et al., 2021; Parnell et al., 2017). The model predicts the probability of introduction (i.e., successful entry and establishment) for every node in the network. Nodes with successful introductions in the stochastic simulation then become bridgehead populations with the potential for transmitting the pest in the subsequent time step, or after an optional latency period, described in more detail in *Drivers and data* (Figure 2c,d).

The model consists of three equations (Figure 3) calculating separate but related probabilities: (1) entry, (2) establishment, and (3) introduction. These terms align with definitions used by the United States Department of Agriculture Animal and Plant Health Inspection Service (USDA APHIS) and correspond, respectively, to transport, introduction, and establishment as defined by Blackburn et al. (2011). Probability of entry (Figure 3a) captures processes controlling human-mediated movement between globally distributed nodes. It is a function of the amount of traded goods capable of transporting the pest, the likelihood of a pest surviving the journey, and,

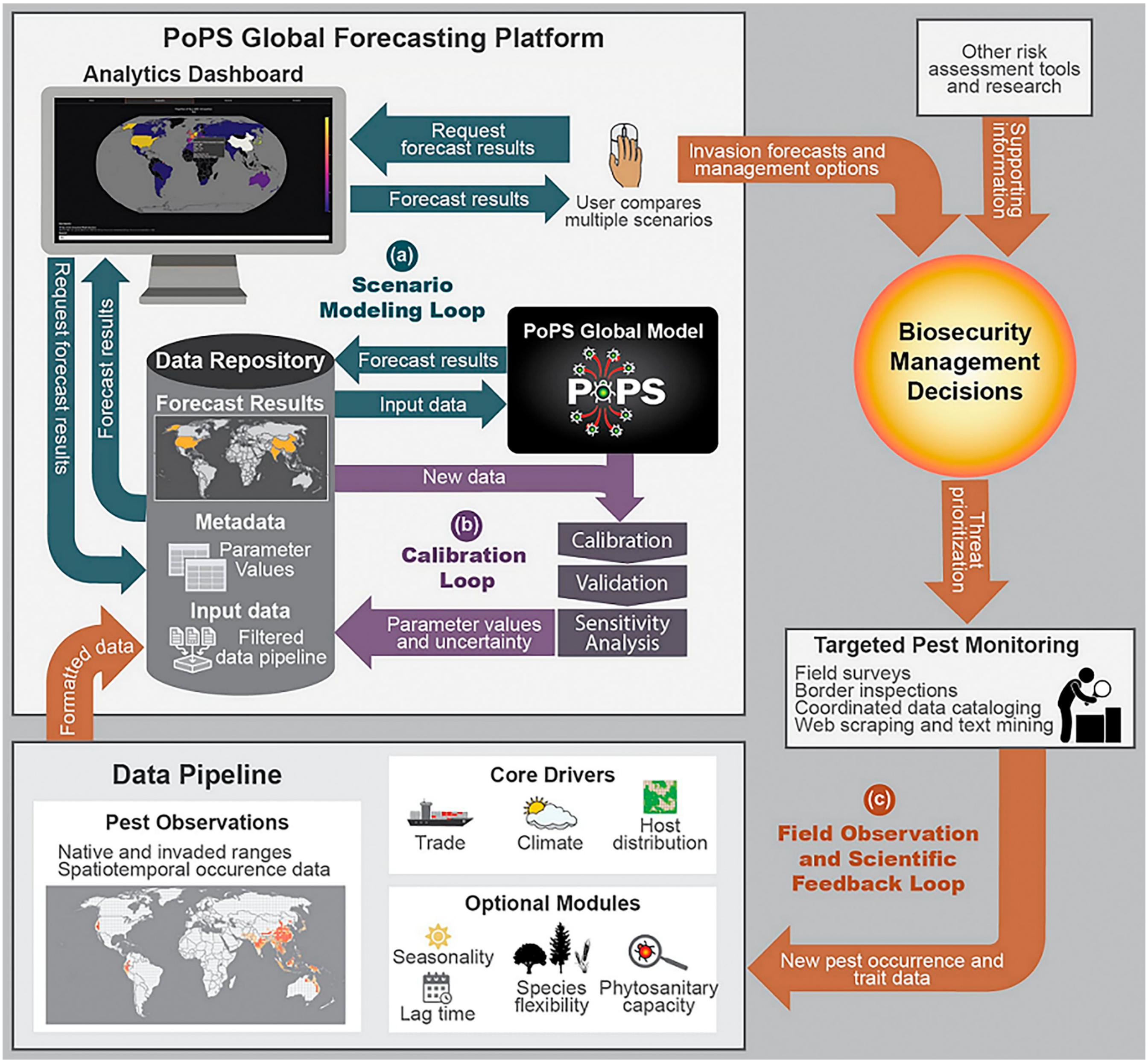


FIGURE 1 The Pest or Pathogen Spread (PoPS) Global forecasting framework includes an automated data pipeline using open data sources that acquires, aggregates, and formats model input data to support three iterative components: (a) a scenario modeling loop, (b) a calibration loop, and (c) a field observation and scientific feedback loop. Results from these loops are visualized on an analytics dashboard to support user interaction and decision-making, incorporating new data as they become available to iteratively update and improve forecast accuracy.

optionally, the phytosanitary capacity of importing and exporting countries for preventing quarantine species movement. Probability of establishment (Figure 3b) captures conditions and ecological processes within a node area. Establishment probability increases with environmental suitability, which is modeled as a Gaussian function of the climate dissimilarity between the two trading nodes and percent area without host species in the destination node. Optionally, the probability can be adjusted by the pest's ability to survive on multiple hosts (e.g., number of host taxonomic families). Probability of introduction (Figure 3b) is a function of the probability of entry (internode processes) and the probability of establishment (intra-node processes) and is used in a binomial distribution to determine whether a successful introduction occurs.

Drivers and data

PoPS Global applies broad theoretical concepts of biological invasion drivers at a global scale to provide an

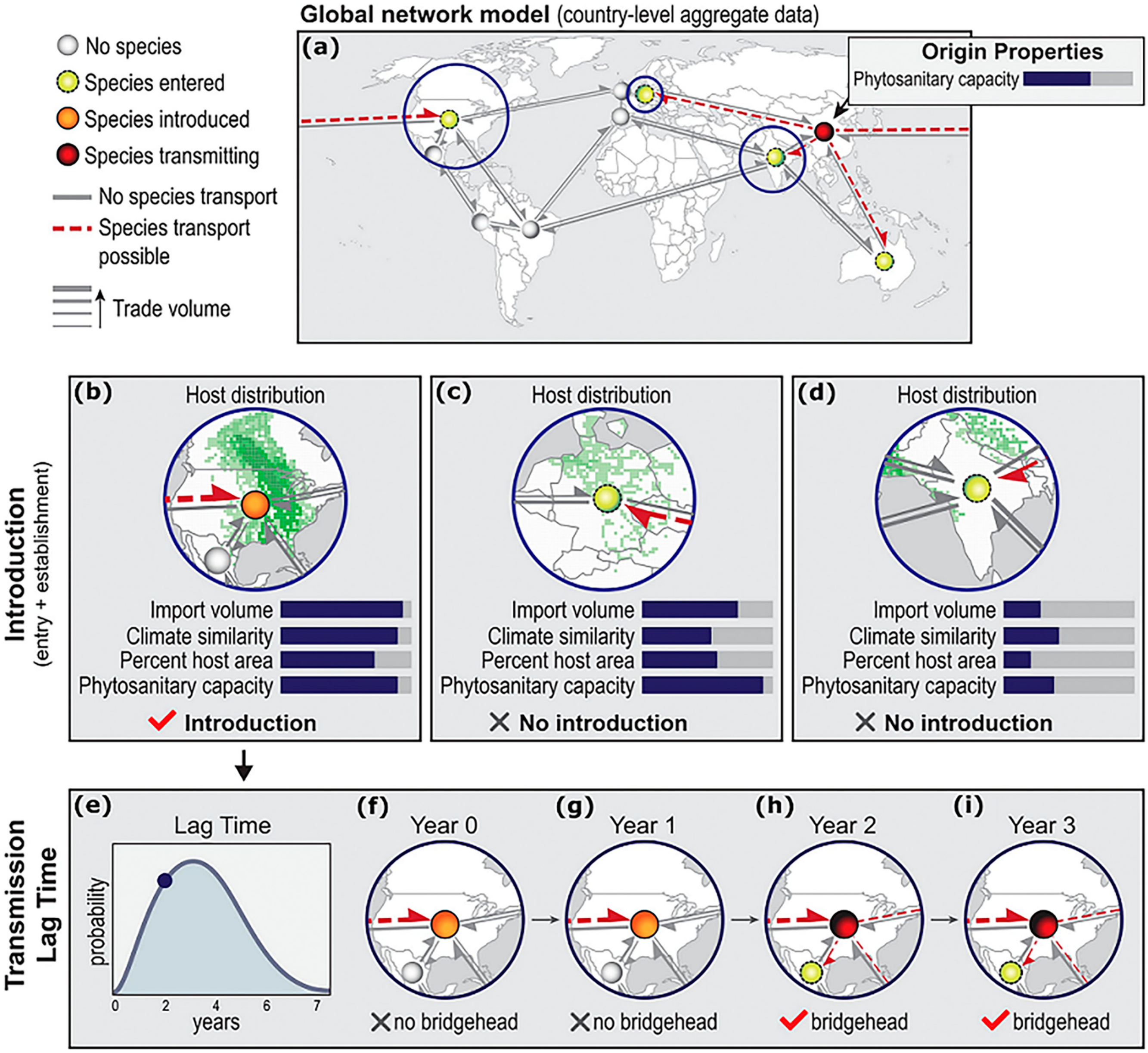
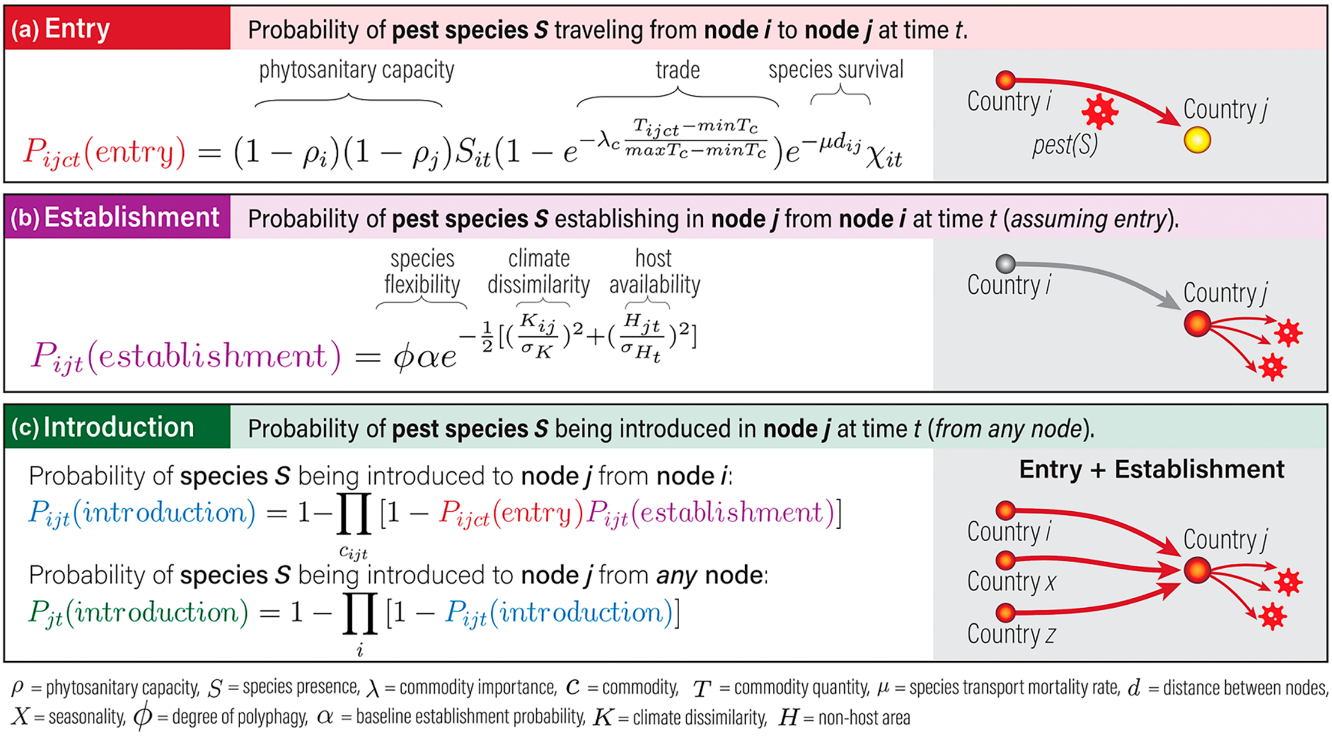


FIGURE 2 The Pest or Pathogen Spread Global spatiotemporal network model (a) simulates spread from node to node via edges weighted by trade volume. (b–d) The environmental conditions, phytosanitary capacity, and import volume (proxy for propagule pressure) in the destination nodes determine the probability of pest introduction. Following a predicted introduction, the destination can become a bridgehead population in subsequent time steps (f–i), either immediately or after a lag drawn from a distribution (e).

estimate of the likelihood and timing of pest arrival (Bellard et al., 2016; Hulme, 2009; Lenzner et al., 2019). Three core drivers are required to run the network model: quantity (i.e., value or weight) of goods traded between nodes over time, climate dissimilarity between nodes, and the area within nodes without hosts. Future versions of the model may incorporate other active and passive dispersal mechanisms, such as diffusive overland or aerial spread. The spatial scale represented by the nodes determines the degree to which these drivers are aggregated and should be chosen for each use case based on data availability and the desired network resolution. The amount of traded goods is obtained from the United Nations Comtrade database, which provides historical annual or monthly records of traded goods using the Harmonized Commodity Description and Coding System (HS) for countries since the 1960s (DESA/UNSD, n.d.). The U.S. Bureau of Labor Statistics Consumer Price Index (CPI) is used to adjust trade values for inflation (United States Bureau of Labor Statistics, n.d.). Trade values should be limited to include only goods known to transport the species being modeled to provide a better



(a) Entry Probability of **pest species *S*** traveling from **node *i*** to **node *j*** at time *t*.

$$P_{ijct}(\text{entry}) = \underbrace{(1-\rho_i)(1-\rho_j)}_{\text{phytosanitary capacity}} S_{it}\underbrace{(1-e^{-\lambda_c \frac{T_{ijct}-minT_c}{maxT_c-minT_c}})}_{\text{trade}}\underbrace{e^{-\mu d_{ij}}}_{\text{species survival}}\chi_{it}$$

(b) Establishment Probability of **pest species *S*** establishing in **node *j*** from **node *i*** at time *t* (*assuming entry*).

$$P_{ijt}(\text{establishment}) = \phi\alpha e^{-\frac{1}{2}[(\frac{K_{ij}}{\sigma_K})^2+(\frac{H_{jt}}{\sigma_{H_t}})^2]}$$

species flexibility, climate dissimilarity, host availability

(c) Introduction Probability of **pest species *S*** being introduced in **node *j*** at time *t* (*from any node*).

Probability of **species *S*** being introduced to **node *j*** from **node *i***:

$$P_{ijt}(\text{introduction}) = 1-\prod_{c_{ijt}}[1-P_{ijct}(\text{entry})P_{ijt}(\text{establishment})]$$

Probability of **species *S*** being introduced to **node *j*** from ***any*** node:

$$P_{jt}(\text{introduction}) = 1-\prod_{i}[1-P_{ijt}(\text{introduction})]$$

ρ = phytosanitary capacity, S = species presence, λ = commodity importance, C = commodity, T = commodity quantity, μ = species transport mortality rate, d = distance between nodes, X = seasonality, ϕ = degree of polyphagy, α = baseline establishment probability, K = climate dissimilarity, H = non-host area

FIGURE 3 The forecasting framework uses a graph structure with nodes (geographical areas) and edges (transport of pests) driven by three equations for calculating event probabilities within the network: (a) probability of entry represents internode processes; (b) probability of establishment represents intra-node processes; (c) probability of introduction is the combined outcome of inter- and intra-node processes.

proxy for propagule pressure (e.g., solanaceous commodities for *Phthorimaea absoluta* or rhododendron, viburnum, or other host plants for *Phytophthora ramorum*; Bacon et al., 2012; Chapman et al., 2017). An exploratory data analysis, including pairwise plots and statistical modeling, is used to identify which trade commodities are most closely related to past pest introductions (Appendix S1: Section S4).

Climate dissimilarity and nonhost area are computed only for areas that are likely to be commodity destinations and, therefore, where the pest will have the opportunity to establish. For consumer commodity destinations, we use the Global Human Influence Index to identify areas within each node with direct human influence (e.g., cities and working lands) and accessibility (e.g., highways), retaining areas above a threshold index value of 16 (Sanderson et al., 2002; WCS & CIESIN-CU, 2005). This threshold was approximated by identifying the lowest index values assigned to developed areas, and major transportation corridors to ensure those areas were retained in the analysis. For agricultural inputs (e.g., seeds for sowing), a global map of cropland like the NASA-funded Global Food-Support Analysis Data (Teluguntla, 2015) could be similarly used for identifying commodity destinations.

To determine climate dissimilarity between origin and destination nodes, we use the Köppen-Geiger Climate Classification (Beck et al., 2018) and compute the percent area of the destination node that contains the same climate subclass(es) as the origin node(s) and then subtract from 100%. The Köppen-Geiger Climate Classification consists of 30 climate subclasses derived from bioclimatic variables that describe seasonal patterns in temperature and precipitation and is widely used for mapping ecosystem conditions (Chen & Chen, 2013; Cui et al., 2021). We use climate classes as a convenient and sufficiently precise way to compute climate dissimilarity for the broad spatial extent of the areas being compared (i.e., country to country). However, a summary metric describing the difference between multiple bioclimatic variables in the origin and destination nodes could be used in place of the climate class dissimilarity metric as the intent is to produce a parameter that describes the proportion of suitable area in each node. Non-host area is computed as the percent node area that does not contain, or is not suitable for, at least one host. For agricultural hosts, harvested area per country is obtained from the Food and Agriculture Organization Statistics (FAOSTAT) database (FAO, n.d.). Maps of other hosts can be created with species distribution models, such as Maximum Entropy (Maxent; Phillips et al., 2006) or BIOMOD (Thuiller et al., 2009), using input data from the Global Biodiversity Information Facility (GBIF) species distribution database (GBIF, n.d.) or the Centre for Agriculture and Biosciences International (CABI) Crop Protection Compendium (CABI, n.d.).

Beyond the core required inputs, several additional optional components can be included: phytosanitary capacity of each node, degree of pest polyphagy, seasonality in the likelihood of a pest being transported, and transmission lag. An exploratory visualization and statistical analysis module is included in the workflow to help the modeler identify relevant data drivers to include in a given case study (Appendix S1: Section S4). Phytosanitary capacity represents measures taken by origin and destination countries to prevent or mitigate cargo contamination. We use an index developed by Early et al. (2016) based on a review of Convention on Biological Diversity national reports to determine a country's capacity to proactively address invasive species threats. The degree of pest polyphagy, specified as a count of host families, can be used to increase the likelihood of establishment for more generalist species. The seasonality component is used to constrain transmission of the pest to certain months depending on species biology. If seasonality is not incorporated, the pest can be transported between nodes during any month. The transmission lag specifies the time between when a pest is introduced to a node and when that node can become a source to other nodes in the network, representing local population growth and spread. The transmission lag can be set to a static interval (e.g., 3 years) or can be dynamic and stochastic (e.g., drawn from a gamma distribution informed by literature or available data). With a dynamic transmission lag and repeated introductions, a new lag time is drawn for each reintroduction and the lag time resulting in the earliest transmission date is chosen, simulating the effect of increasing propagule pressure. If lag time is not used in the model, a node can become a source of the pest in the time step immediately following introduction. See Supporting information for additional description of model and data assumptions (Appendix S1: Section S2).

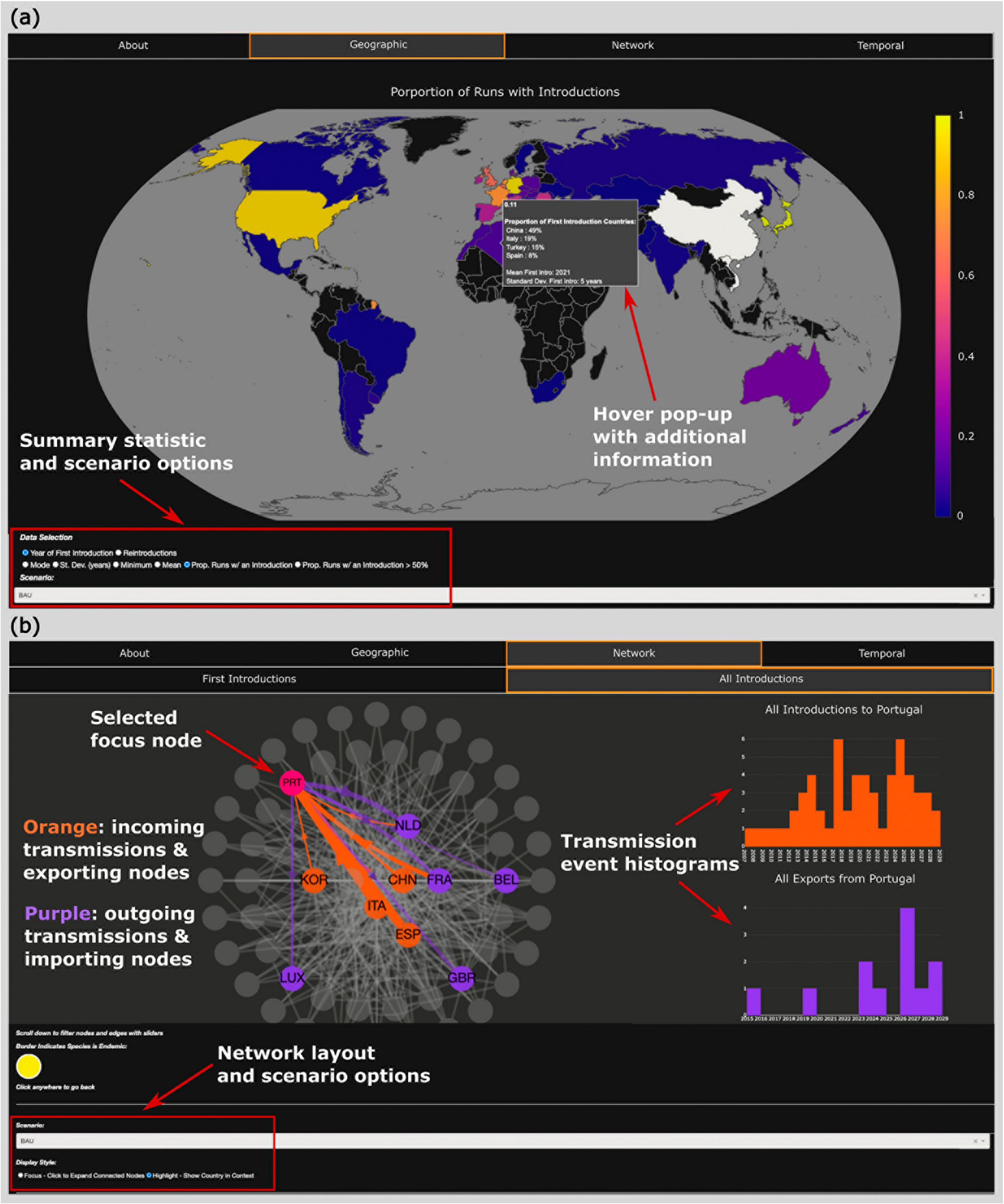
Decision analytics

The PoPS Global modeling framework was collaboratively developed with USDA APHIS practitioners tasked with rapid response to threats from emerging plant pests. Visualization of global spread over time allows users to analyze predicted locations and timing of introductions with associated levels of uncertainty and compare outcomes of different intervention strategies. We are working with analysts and managers to create a web-based decision analytics dashboard that will use the open-data pipeline to run the model, test scenarios, and provide multiple, interactive views of the model output. The first dashboard iteration (available at https://popsglobaldemo.popsmodel.org/) allows users to view the model results as a world map with country-level summary statistics of introduction probability, timing, and sources (Figure 4a). Model results can also be viewed as a network graph and filtered to nodes of interest to examine spread pathways from native and bridgehead pest populations (Figure 4b). Statistics summarizing transmission network characteristics, for example, the most susceptible and transmissive nodes, are also provided. Graphs of forecasted introductions over time show predicted rates of pandemic spread. Users can toggle between model runs to compare outcomes of management scenarios. Collectively, these visualizations and statistics provide insight into the spread network to support decision-making. See Appendix S2 for additional details about the analytics dashboard.

Applying the framework: A case study of spotted lanternfly

We demonstrate the framework by simulating the global spread of spotted lanternfly, a phytophagous planthopper and emerging pest of many commercially important fruit plants and timber. Spotted lanternfly is native to China and possibly other subtropical regions of Southeast Asia (Dara et al., 2015; Kim et al., 2011, 2013). We used China and Vietnam as origin countries (Lee et al., 2019; Wakie et al., 2020) and ran the simulation through 2030. We modeled transmission lag as a stochastic process by drawing a lag time at each simulated introduction from a gamma probability distribution ($\alpha = 4$, $\beta = 1$), with a mean lag time of 4 years. The lag time distribution was parameterized based on a review of 35 invasive insects in Japan that found the median lag time between first and second occurrences of a pest was 4 years (Kiritani & Yamamura, 2003), providing an approximation of the interval between first introduction and population buildup and spread.

Spotted lanternfly feeds on more than 70 plant species but has a strong preference for tree of heaven (*Ailanthus altissima*; Murman et al., 2020). We created a tree of heaven host map by using observations from the GBIF database to create a Maxent species suitability model (Appendix S1: Section S3). Spotted lanternfly can hitchhike long distances by depositing egg masses on surfaces like trees, vehicles, or stone. Experts suspect that egg masses arrived in the United States on imported stone, although plant material and wood packing material are also suspected carriers (Dara et al., 2015; USDA-APHIS-PPQ-CPHST, 2018). In our simulation, we used monthly imported values (2019 US$) of stone



0.11

Proportion of First Introduction Countries:
China : 49%
Italy : 19%
Turkey : 15%
Spain : 8%

Mean First Intro: 2021
Standard Dev. First Intro: 5 years

Data Selection
◉ Year of First Introduction ○ Reintroductions
○ Mode ○ St. Dev. (years) ○ Minimum ○ Mean ◉ Prop. Runs w/ an Introduction ○ Prop. Runs w/ an Introduction > 50%
Scenario:
BAU

Scroll down to filter nodes and edges with sliders
Border Indicates Species is Endemic:
Click anywhere to go back

Scenario:
BAU
Display Style:
○ Focus - Click to Expand Connected Nodes ◉ Highlight - Show Country in Context

FIGURE 4 The first iteration of the Pest or Pathogen Spread Global analytics dashboard (https://popsglobaldemo.popsmodel.org/) displays (a) a geographic view of forecast results with country-level summary statistics of pest introduction probability, timing, and sources and (b) an interactive pest transmission network, which allows users to filter the network and explore the timing and magnitude of predicted spread pathways. See Appendix S2 for additional screenshots and description of the analytics dashboard.

commodities (HS 6801, 6802, 6803, and 6804) obtained from the UN Comtrade database and included only stone commodities that provide a solid substrate for carrying eggs, given that adults are very unlikely to survive long-distance transport. Through visual and statistical data exploration, we removed commodities HS 6801, 6803, and 6804, which did not show positive correlation with known spotted lanternfly introductions (Appendix S1: Section S4), and ran the model only with HS 6802.

We created a simple trade forecast to 2030 by randomly drawing a value for each month per country from their respective 2016–2020 values. We did not forecast a change in trade patterns for this case study; however, trade increase or decrease scenarios can easily be included in PoPS Global by applying a percent change to the drawn forecast data or through the inclusion of trade forecasts from other sources. We incorporated seasonality by constraining the potential for transporting the pest to only those months suitable for egg-laying in each origin country. In the Northern Hemisphere, the model allowed transmission from September through April. This is based on several reports stating that eggs are laid from September to December and will begin hatching in May (Dara et al., 2015; USDA-APHIS-PPQ-CPHST, 2018; Wakie et al., 2020). The model allowed transmission from May through October in the Southern Hemisphere.

Literature reports for spotted lanternfly include the years of first observation for three established populations outside the native range: the Republic of Korea in 2004, Japan in 2009, and the United States in 2014 (Dara et al., 2015; Han et al., 2008; Nakashita et al., 2022). These three observations were used to calibrate the network model with leave-one-out cross-validation (Appendix S1: Section S5). We conducted a grid search for the unknown parameters, alpha (i.e., baseline establishment probability), lambda (i.e., commodity importance weight), and simulation start year, resulting in 1984 parameter sample sets. The parameter sets were ranked using F_β scores averaged across 80 stochastic runs. To implement leave-one-out cross-validation, three separate F_β scores were calculated for each parameter set that used just two of the three known introductions, leaving one out for each (i.e., $F_{\beta\_\text{USA-KOR}}$, $F_{\beta\_\text{JPN-KOR}}$, and $F_{\beta\_\text{USA-JPN}}$). The top performing calibration parameter sets (90th percentile) were used to fit a multivariate normal distribution for each start year considered (2000 through 2003). For the final output, the model was run 1000 times using parameters drawn from each distribution in proportion to that start year's representation in the top calibration set.

RESULTS

We used PoPS Global to simulate the international spread of spotted lanternfly through trade, starting between 2000 and 2003 and forecasting spread through 2030, to identify potential global patterns of invasion pressure over space and time (Figure 5). Introductions in the three countries with known invasive populations were predicted in most of the stochastic realizations (Republic of Korea 99.6%, Japan 99.9%, and the United States 84.3%). Introductions were also predicted for several European countries, particularly Germany, which had the most consistent introductions out of the countries where the pest has not been observed (81.8% of runs). The overall F_β score averaged over the 1000 runs was 0.6 (0.005 ± SE). The first introduction year was relatively consistent for the Republic of Korea and Japan with median first introduction years of 2004 and 2002 and interquartile ranges of 4 and 3 years, respectively. The first introduction years for the United States and Germany, however, were more variable, with the median first introduction year for both being 2010 and interquartile ranges of 11.5 and 9 years, respectively (Figure 5).

The framework's network approach illuminates likely indirect pathways of pest movement via bridgehead populations over time. While China was the primary exporter of spotted lanternfly in the simulation, Italy, Spain, and Turkey emerged as potentially important bridgehead populations (Figure 6). The frequency of spotted lanternfly introductions in these countries was relatively low (Italy 36.6%, Spain 30.0%, Turkey 28.4%), but when they did occur, these populations became important sources for spreading the pest to other countries with environmental conditions suitable for pest establishment. These bridgehead countries became additional sources of pest introductions to France, the Netherlands, Germany, Romania, the United Kingdom, Ireland, and the United States (Figure 7). The main exporter of the pest to the United States was China (2.02 introductions per run on average), followed by Turkey and Italy (0.20 and 0.15 introductions per run on average, respectively). The known introduced populations in Japan, the Republic of Korea, and the United States did not act as significant bridgehead populations in the simulation with only 100 introductions coming from these countries combined over 1000 runs.

DISCUSSION

Our case study of spotted lanternfly demonstrates the utility of the PoPS Global framework to forecast the

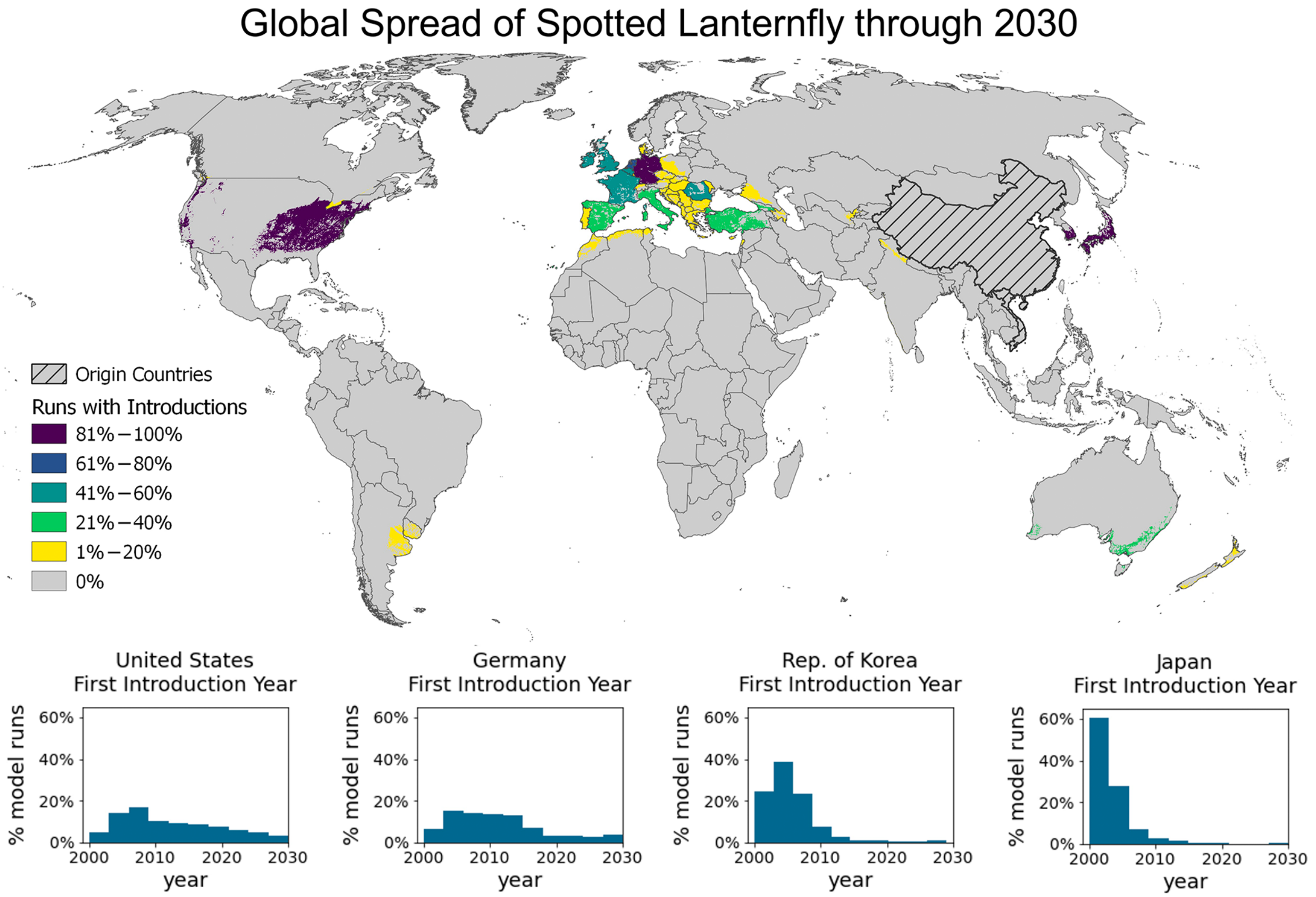


FIGURE 5 Predicted global distribution of spotted lanternfly by 2030. Colors indicate the proportion of the 1000 stochastic model realizations that predicted introductions for each country. Histograms of predicted first introduction years are shown for the countries most consistently predicted to be invaded.

international spread of emerging pests and identify potential bridgehead populations. Identifying these bridgeheads is important for directing pre-border biosecurity efforts in infested areas and for prioritizing inspection of goods from bridgehead countries at ports of entry (Epanchin-Niell et al., 2021). PoPS Global successfully simulated spotted lanternfly spread to the three countries in the known invaded range to date (Japan, the Republic of Korea, and the United States) as well as identified potential bridgehead populations in Europe and quantified pathway risk. There is phylogenomic evidence that suggests the U.S. spotted lanternfly population originated from the Republic of Korea (Du et al., 2021); however, PoPS Global only simulated seven introductions to the United States from the Republic of Korea over 1000 runs, due to the low volume of stone trade between the two countries. While the exact invasion pathway cannot be known, this discrepancy highlights the possible scenario of a pest being transported regionally between countries with frequent transport interactions and then subsequently being exported to more geographically dispersed areas through trade. This seems especially likely with hitchhiking pests that attach to or lay eggs on nonhost material, like vessels or containers, that frequently move between ports. This scenario implies the need for a model mechanism to create more direct connections between a "super-spreader's" outgoing edges and other adjacent nodes.

The PoPS Global framework addresses critical needs for forecasting plant pest invasion pathways when very little is known about historical pest movement. It leverages globally available open data to implicitly model the effect of propagule pressure from international trade, and each simulated introduction encompasses the entire establishment process, from overcoming movement barriers to developing a self-sustaining population (Blackburn et al., 2011). The transmission lag time provides a simplified, stochastic conceptualization of the time required for a newly introduced population to successfully expand and be subsequently exported. This is a necessary simplification as population spread is highly variable and difficult to generalize at a global scale

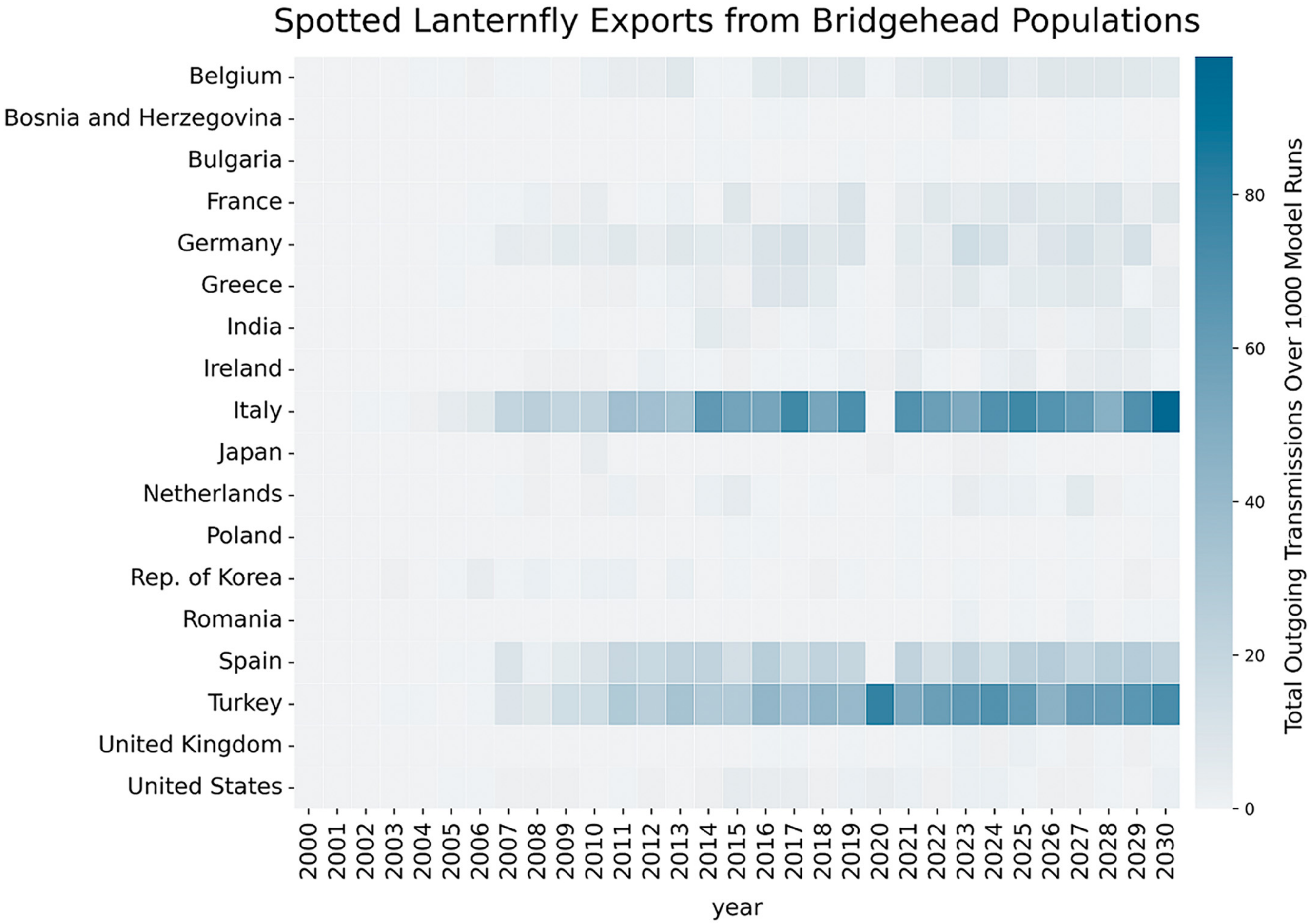


FIGURE 6 Frequency of exports predicted from bridgehead populations with at least five pest exports, summed over 1000 stochastic model realizations. The pest was not consistently introduced in Italy, Spain, and Turkey in the simulation; however, when it was introduced, populations in these countries acted as important bridgeheads.

(Garnas et al., 2016; Vose, 2008). Lag time will depend on myriad factors such as intra- and interspecific interactions (e.g., competition, predation, and Allee effect), dispersal mechanisms, detection rates, and other complex processes (Crooks, 2005; Morimoto et al., 2019). However, if subsequent introductions are simulated, the impact of increasing propagule pressure is incorporated by drawing another transmission lag from a probability distribution and using the shortest time drawn. While the effect of reintroductions and population growth are not explicitly modeled, the likelihood of short transmission lag times is higher for countries with simulated repeat introductions.

Fine resolution temporal data on the timing of species introductions are often not readily available and will be very challenging to obtain with high accuracy due to inherent lags in detection (Crooks, 2005). Temporal imprecision is likely to persist in this type of forecast. Initial model conditions, including species distribution and simulation start year, are a source of forecast uncertainty for PoPS Global. Species distributions, in both native and invaded ranges, are often poorly documented, limiting the ability to estimate the potential for propagule transport between countries (Bebber et al., 2019; McGeoch et al., 2010; Rouget et al., 2016). The simulation is also sensitive to the start year used. We conceptualized “start year” as the year that an unobserved event results in species range expansion and propagule transport. The optimal simulation start year was calibrated alongside the other unknown model parameters, alpha and lambda, and used to estimate parameter distributions. Future application of the framework could streamline model calibration through approximate Bayesian computation (Minter & Retkute, 2019). Furthermore, as with all efforts to model ecological systems, the complex, nonlinear nature of invasion biology makes the prediction of introductions very challenging, with events often occurring due to idiosyncratic, unknowable factors and random chance. PoPS Global focuses on the major components known to be important drivers of introductions

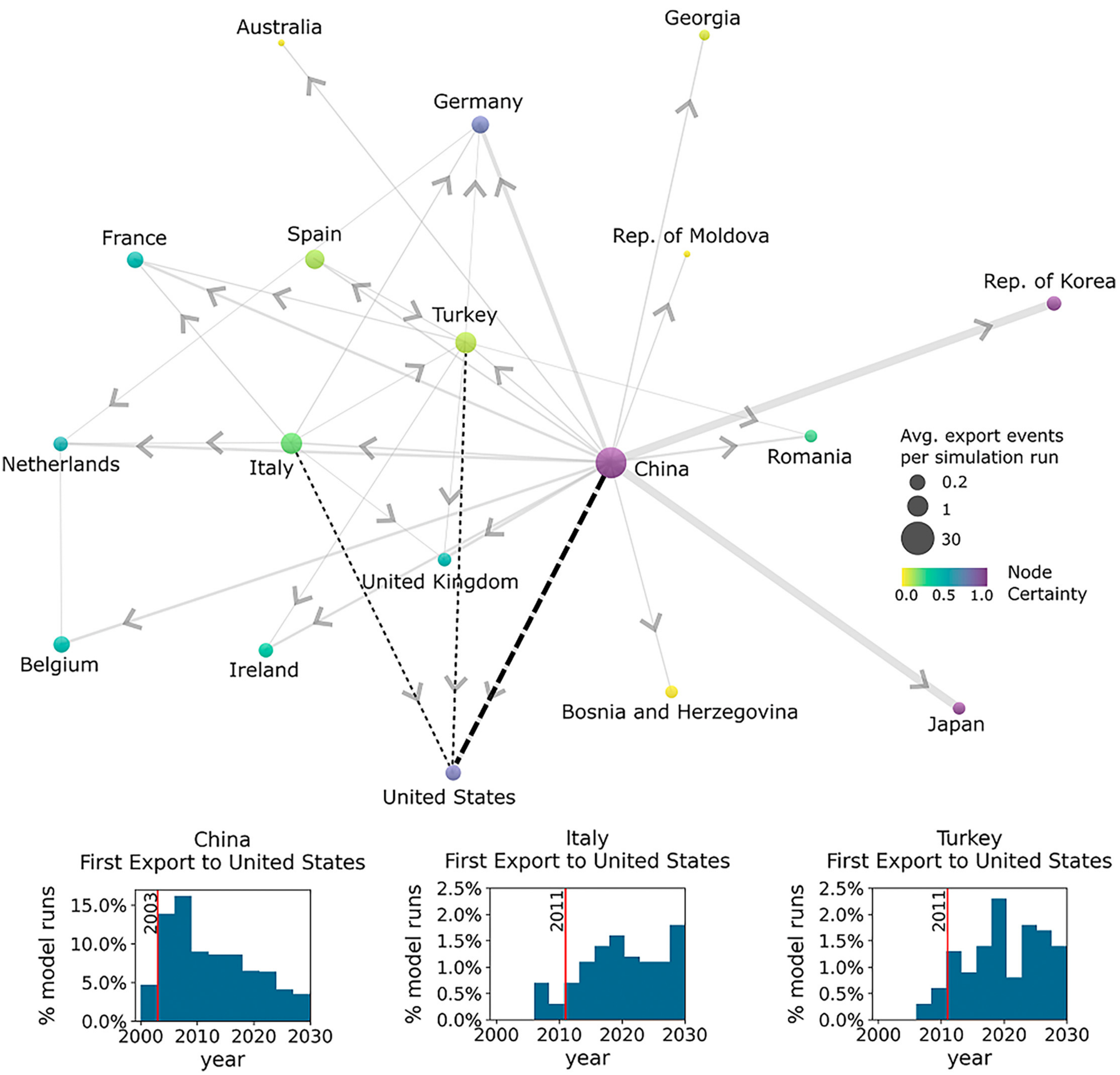


FIGURE 7 Simulated spotted lanternfly transmission network. Node size indicates the number of times the country exported the pest between 2000 and 2030. Node color represents certainty, that is, the proportion of 1000 stochastic realizations predicting transmission to or from the node. Edge weight represents the number of transmissions between countries. Edges directly connected to the United States are dashed black lines. The network is filtered to include nodes with at least 200 incoming or outgoing transport events and edges with at least 50 transport events over 1000 stochastic model realizations. Histograms of the simulated first export event are shown for each node that acted as a bridgehead to the United States; the vertical red line marks the 10th percentile year.

and presents a range of possible outcomes based on how these drivers interact. The model also uses a modular design so that additional drivers can be included on a case-by-case basis.

Despite these limitations, the PoPS Global simulation provides insights into broad patterns of introduction timing and sequence (e.g., native country A transmits to bridgehead country B, which then transmits to country C after a latency period). There are opportunities to increase the spatial resolution by reducing the area represented by nodes to regions around ports of entry, similar to subpopulation areas surrounding airports used by Balcan et al. (2010). Modeling transport between smaller, subnational regions could be especially useful for large countries with concentrated areas of susceptible hosts, such as fruit-producing regions of the West Coast of the United States. Higher spatial resolution also provides opportunities for explicitly modeling natural dispersal mechanisms and regional transmission between adjacent nodes. Modeling multiple dispersal mechanisms could be achieved by overlaying additional network edges with probability of entry functions that capture different spread processes. For example, local spread may be incorporated by including a set of edges quantified by Euclidean distance and the length of shared border between nodes (Brooks et al., 2008). When adequate global data are available, PoPS Global can also be coupled with spatially explicit models of overland (Jones et al., 2021; Meentemeyer et al., 2011) or aerial (Stein et al., 2015) landscape-scale dispersal. Further research is needed to understand how the large uncertainties in temporal and spatial data used for model calibration may limit the usefulness of modeling species movement at higher resolutions.

While statistical approaches provide important insights, the network approach of PoPS Global can uncover relationships between origin and destination nodes and provides a mechanism for users to test spatially and temporally dynamic intervention strategies. Each input module used in the framework can be manipulated to simulate scenarios and understand the impact of changes. For example, available host area could be decreased to simulate efforts to eradicate invasive tree of heaven. From a national phytosanitary perspective, an agency might also want to explore how to disrupt the transmission network, such as by increasing resources for phytosanitary activities or revoking market access for goods known to carry pests from areas with established populations.

Creating actionable insights when very little information is available for model calibration and validation is challenging. However, the threats posed by emerging plant pests and pathogens necessitate quick, data-driven decisions. A near-term forecasting approach creates opportunities for frequent, iterative updating with new observations to improve understanding of global biological invasions, build predictive capacity, and reduce uncertainty (Dietze et al., 2018). The PoPS Global framework can be used to identify when and where data are needed to create dynamic, adaptive monitoring efforts in response to forecast uncertainties (Figure 1c). Novel techniques, such as web scraping and text mining, represent an opportunity to leverage free, publicly available information from online news articles, social media, technical forums, and research journals to collect up-to-date information about where pest species are being discovered globally, reducing latency between data collection and availability (Jarić et al., 2021; Tateosian et al., 2023). Critical to improving our ability to forecast invasions is coordinated global surveillance to catalog pest occurrence data from native and introduced ranges, species traits, and the potential impacts of spread (Carvajal-Yepes et al., 2019). In addition to these data, biosecurity efforts need to be framed within a global context by treating the spread of invasive plant pests as pandemics and learning from advances made in global public health (Hulme, 2021; Ristaino et al., 2021). The PoPS Global framework provides a modular approach for risk assessment that enables phytosanitary agencies to quickly evaluate and visualize globally connected invasion processes at multiple scales.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Software and tools developed through this research are open-source and freely available under GNU General Public License. The PoPS Global code (Walden-Schreiner et al., 2023), along with version history, is available from Zenodo: http://doi.org/10.5281/zenodo.7665849. An early version of the PoPS Global visualization dashboard to view the case study results can be accessed via https://popsglobaldemo.popsmodel.org/. The national phytosanitary capacity data were obtained from Dr. Regan Early (Early et al., 2016; https://doi.org/10.1038/ncomms12485). Other publicly available data sets utilized for this research are cited within the manuscript text. Code used to obtain and format these data is available in the PoPS Global repository listed above. The data sources used include UN Comtrade International Trade Statistics Database (https://comtrade.un.org/); Köppen-Geiger Climate Classification Maps (https://doi.org/10.1038/sdata.2018.214); Global Biodiversity Information Facility (https://www.gbif.org/); Center for Agriculture and Bioscience International (CABI) Invasive Species Compendium (www.cabi.org/isc); Human Influence Index (https://doi.org/10.7927/H4BP00QC);

FAOSTAT Database (http://www.fao.org/faostat); EarthStat (https://doi.org/10.1029/2007GB002947); US Bureau of Labor Statistics Consumer Price Index (https://www.bls.gov/cpi/).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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