Paninvasion severity assessment of a US grape pest to disrupt the global wine market

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Abstract

Economic impacts from plant pests are often felt at the regional scale, yet some impacts expand to the global scale through the alignment of a pest's invasion potentials. Such globally invasive species (i.e., paninvasives) are like the human pathogens that cause pandemics; and like pandemics, assessing paninvasion risk for an emerging regional pest is key for stakeholders to take early actions that avoid market disruption. Here, we develop the paninvasion severity assessment framework and use it to assess a rapidly spreading regional US grape pest, the spotted lanternfly planthopper (*Lycorma delicatula;* SLF), to spread and disrupt the global wine market. We found that SLF invasion potentials are aligned globally because important viticultural regions with suitable environments for SLF establishment also heavily trade with invaded US states. If the US acts as an invasive bridgehead, Italy, France, Spain, and other important wine exporters are likely to experience the next SLF introductions. Risk to the global wine market is high unless stakeholders work to reduce SLF invasion potentials in the US and globally.

Invasive plant pests cause substantial economic impacts[1], but most pests and their impacts are confined to specific regions. For a regional pest to become a globally invasive species (i.e., paninvasive) that disrupts global markets, ecological and economic factors that determine the pest's transport, establishment, and impact potentials must be aligned at the global scale (Fig. 1, SI)[2]. First, paninvasive pests have high transport potential because they can be easily transported among regions, often through global trade[3]. Second, paninvasive pests have high establishment potential, because their environmental needs for population growth are met in many regions[4]. Third, paninvasive pests have high impact potential, because invaded regions have sizeable agricultural production and industries vulnerable to the pest[5]. If these invasion potentials are correlated across multiple regions globally for an emerging regional pest, there is a high risk of the pest spreading to cause supply crashes in regional markets that cascade to disrupt global markets[6].

Despite the importance of identifying emerging paninvasives, there is no framework for rapidly assessing and effectively communicating such risk to stakeholders[7]. To address this gap, we developed the paninvasion severity assessment framework by adapting the US CDC pandemic severity assessment framework to invasion process theory (Fig. 1, 2)[2,8–10]. Although invasive species frameworks are increasingly adapted to understand infectious diseases like COVID-19[11–14], adapting public-health frameworks to invasion science is novel and leverages an increasingly universal risk vocabulary[15] (Fig. 2). Under this framework, we assessed the paninvasion risk of the spotted lanternfly planthopper (Hemiptera: *Lycorma delicatula*; SLF, Fig. 1). SLF was introduced to South Korea and Japan in the early 2000s and then to the U.S. (ca. 2014) on goods imported from its native China[16]. SLF has rapidly spread from Pennsylvania to several other states, presenting increased opportunities for stepping-stone invasions to additional regions[17–19]. SLF greatly impacts grape production and has been presented to the public as one of the worst invasive species to establish in the US in a century [20–22], but its paninvasion risk has not been assessed[19,23,24].

SLF likely has high global transport potential because it lays inconspicuous egg masses on plants, stone, and trade infrastructure (e.g., containers, railcars, pallets), which facilitates long-distance transport when eggs are laid on exported items (Fig. 1a–c). Landscaping stone imported from China was the likely vector of the US invasion[16]. Following successful transport, SLF global establishment potential is likely enhanced by the cosmopolitan distribution of its preferred host plant, the tree-of-heaven (*Ailanthus altissima*, TOH, Fig. 1d–f)[19]. The native ranges of SLF and TOH overlap in China, but for >250 years TOH has escaped cultivation into disturbed habitats and agricultural margins in temperate, subtropical, and Mediterranean regions globally (Fig. 1 map). Once established, SLF likely has high global impact potential to wine markets because grape is an equally suitable host[25–27]; Asian vineyard production is impacted by SLF infestations[28,29]; and SLF-invaded US vineyards have reported vine deaths, >90% yield losses, and closure[19,30] (Fig. 1g–i).

To assess paninvasion risk, we calculated invasion potentials from estimates of SLF transport, establishment, and impact potentials from the US invaded region to uninvaded US states and countries using trade, species distribution models, and grape and wine production data. We then mapped invasion potentials, calculated alignment correlations, and estimated risk to the $300B global wine market[31].

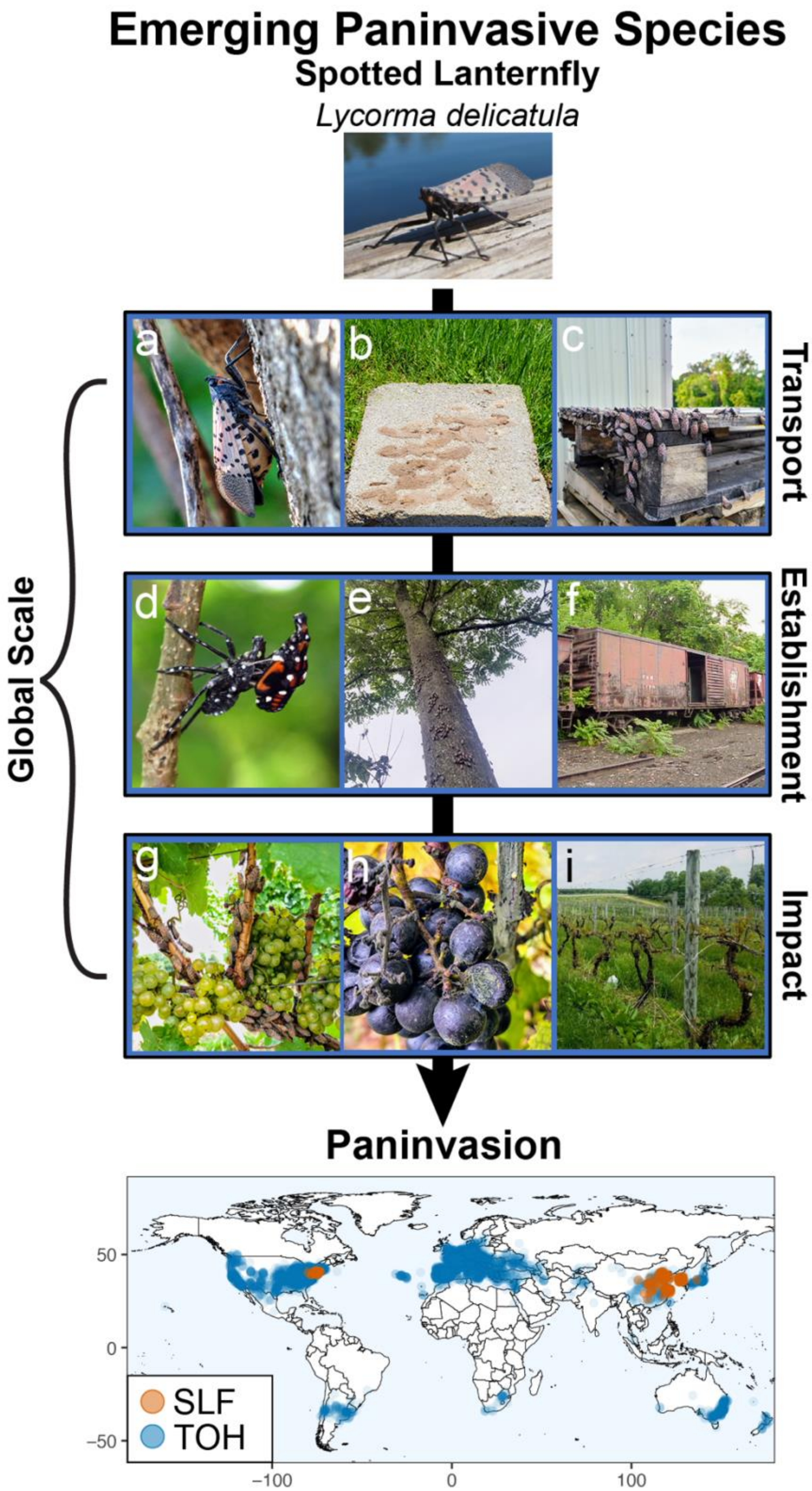

Fig. 1 Our concept of paninvasive species is based on invasion process theory, whereby any species has potentials to complete three sequential stages (depicted by the arrow) to become

invasive in a region (i.e., transport to the region, establishment in the region, impact to the region's economy)[2]. For a pest paninvasion to occur, a pest must be transported and establish in suitable regions globally where it impacts susceptible agriculture disrupting markets at a global scale (depicted by the bracket). Here, we focus on estimating invasion stage potentials for the spotted lanternfly planthopper (Hemiptera: *Lycorma delicatula*, SLF), an emerging US pest at risk of disrupting the global wine market. Photos introduce SLF biology. Gravid females (**a**) lay eggs on many surfaces like stone (**b**) and transport infrastructure (**c**). Once eggs hatch, SLF develop by molting through three black and one red nymphal instars (**d**) before molting into winged adults (top, **a**). SLF feed on phloem of many plants but develop quickly on tree-of-heaven (*Ailanthus altissima*, TOH, **e**, **f**), a paninvasive tree commonly found in habitat fragments around railroads (**f**) and warehouses (**c**). SLF also heavily feed on grape (**g**), reducing yield (**h**) and contributing to vine death (**i**). Photo credits: S. Cannon (**e**), M. Helmus (top, **a, d**), H. Leach (**c**,**g–i**), J. Losiewicz (**b**), G. Parra (**f**). The map is of SLF (orange) and TOH (blue) presences (ca. 2020) we used to estimate paninvasion risk (see Methods).

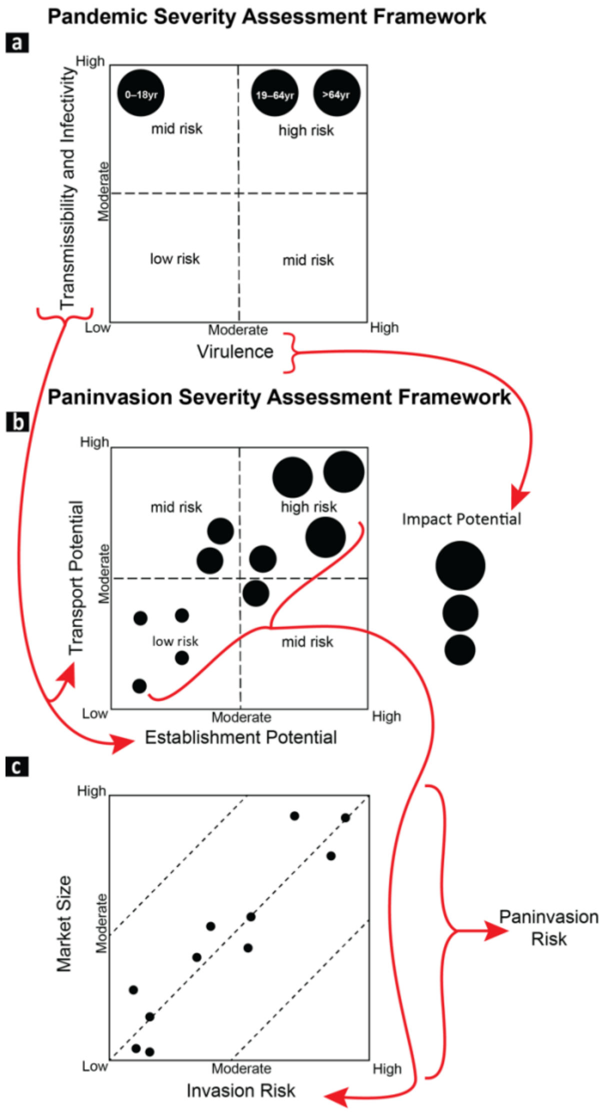

Fig. 2. The paninvasion severity assessment framework is adapted from the US CDC pandemic severity assessment framework used to estimate the risk of emerging human pathogens. For pandemics (**a**), quadrant plots of pathogen transmissibility and infectivity (combined on one axis) vs. pathogen virulence (clinical severity) are used to compare the risk of a pathogen across different populations or age groups[8,9,11]. For paninvasions (**b**), we first constructed quadrant plots that depict the alignment (i.e., multivariate correlation, see Methods) of invasion potentials for an emerging regional invasive species by equating pathogen transmission with transport potential, infectivity with establishment potential, and virulence with impact potential (follow the arrows) across regions (black circles). Next, paninvasion risk is estimated from the correlation between regional invasion risk estimated from the multivariate regression of invasion potentials (see Methods) and the size of regional markets that could be disrupted (**c**).

Results

To assess SLF paninvasion risk, we first estimated the current US invaded range (ca. 2020). We aggregated distributional data from multiple sources, including announcements made by state departments of agriculture on cargo interceptions that did not lead to established populations (i.e., regulatory incidents). By 2020, SLF had established in nine US states, with clear incidents of long-distance transport and establishment in Virginia, New York, and Pennsylvania. In eight additional states, individuals were intercepted in cargo and on transported goods originating from states with established SLF. California had intercepted the most with >40 individual SLF on 35 flights found during cargo inspections, but all were dead or moribund and not egg masses [32]. No international reports of regulatory incidents from the US have been published. These regulatory incidents suggest that cargo with SLF were frequently transported from the invaded range in the US northeast to at least as far as to the US west coast (Fig. 3).

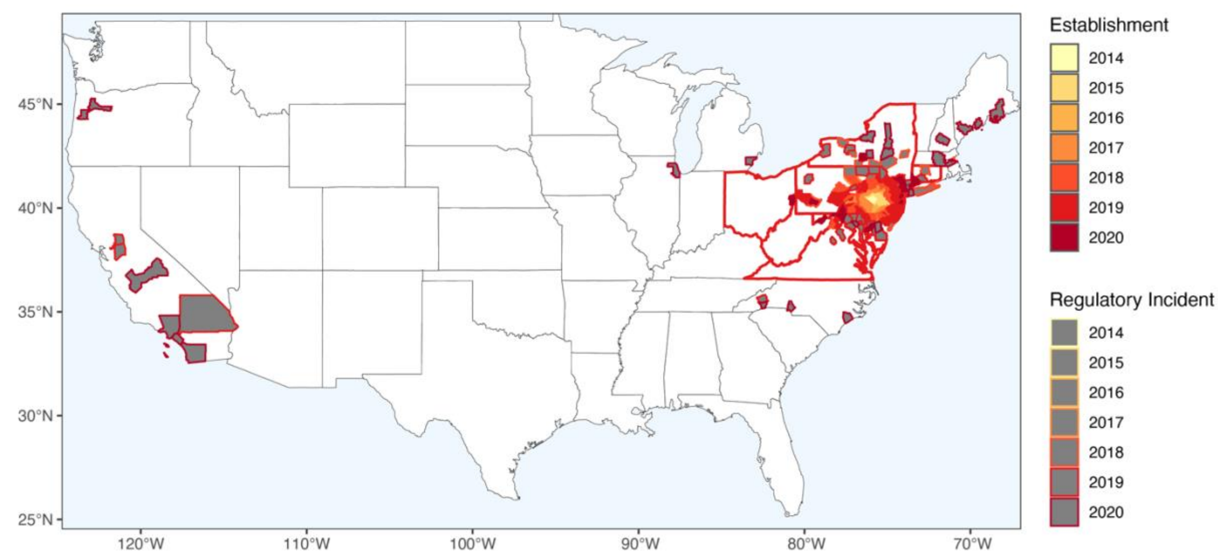

Fig. 3 Spotted lanternfly (*Lycorma delicatula*, SLF) had invaded nine states in the US by 2020. Colored polygons are counties with established SLF populations. Grey-filled polygons are counties where SLF have been transported but have not established. These regulatory incidents include any egg cases, living, moribund, and dead individuals found in cargo. Red outlined states have established SLF populations.

We estimated the three invasion potentials—transport, establishment, impact—for 50 US states and 223 countries. For transport potential, we used the total metric tonnage of goods imported from invaded states[33,34]. States with the highest transport potential were mostly in the eastern US, but Illinois, Texas, and California also heavily traded with the invaded states, indicating that SLF had high potential to be transported both regionally and transcontinentally (Fig. 4a, 5a). Globally, transport potentials were highest in several European countries, Canada, and Brazil (Fig. 4b, 5b).

We based establishment potential on an ensemble estimate of species distribution models (SDMs) built on SLF and TOH geolocations (see SI for SDM methods, Fig. 4)[35]. Our ensemble estimate was similar to other SLF SDMs, but indicated urban landscapes as likely establishment locations and showed fine spatial-scale variation in establishment potential (see our interactive map https://ieco.users.earthengine.app/view/ieco-slf-riskmap)[36,37]. For each state and country, we extracted the mean, median and max predicted suitability to estimate establishment potential (see SI). Most US states had high establishment potential (Fig. 4a, 5a), and all the countries with highest transport potential also had the highest establishment potential (Fig. 4b, 5b).

We estimated SLF impact potential as the annual average tonnage of grapes and wine produced for each US state and country[38–40]. States and countries with many important viticultural regions were geographically clustered (Fig. 4), suggesting that should one become invaded, neighboring high impact potential states or countries are likely to also become invaded like the spread observed in the US (Fig. 3). States with high impact potential included California, Washington, New York, Pennsylvania, and Oregon (Fig. 4a, 5a), and countries with high impact potential include Italy, France, and Spain (Fig. 4b, 5b).

SLF invasion potentials across states and countries were aligned. Alignment correlations among transport, establishment, and impact potentials were positive for impact potential measured as state grape production (ρ = 0.41, P<0.005), state wine production (ρ = 0.52, P<0.001), country grape production (ρ = 0.67, P<0.001), and country wine production (ρ = 0.63, P<0.001). This alignment of potentials is clear in the invasion-potential alignment plots (Fig. 5). Major grape producing regions fall in the upper-right quadrant of the plots where regions have both high transport and high establishment potentials.

We estimated the risk of SLF to impact the global wine market to be an 8 out of 10 (Fig. 6). To derive this value, we regressed country grape production on country transport and establishment potentials. Each predicted value from this multivariate regression can be considered an estimate of the risk of SLF to invade and impact a country's grape production. We then rescaled these predicted values from 1–10 and correlated them to wine export market size (ρ = 0.66, P<0.001). To place SLF on a scale of paninvasion severity, we rescaled the correlation coefficient, ρ, from 1–10, so that 1 is a complete negative correlation and 10 is a complete positive correlation between predicted impact and market size. Low values on this scale indicate that the global market is buffered against a paninvasion, while high values indicate that a paninvasion is likely unless mitigation actions are taken to reduce invasion potentials.

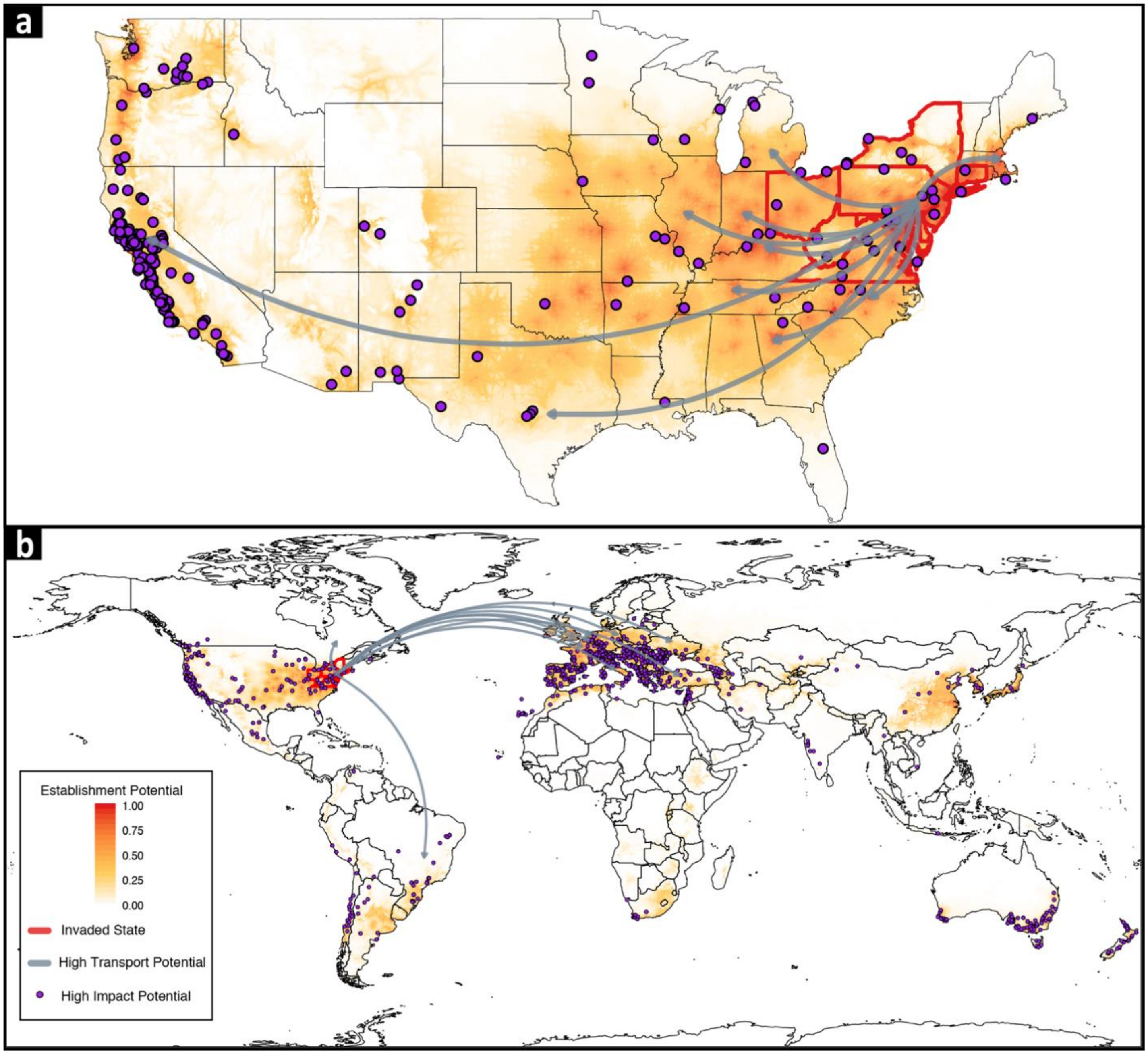

Fig. 4 There is strong spatial alignment of spotted lanternfly (*Lycorma delicatula*, SLF) transport, establishment, and impact potentials. Arrows point from the US invaded region to the top ten states (**a**) and countries (**b**) with the highest transport potentials. Purple points are locations of important viticultural areas.

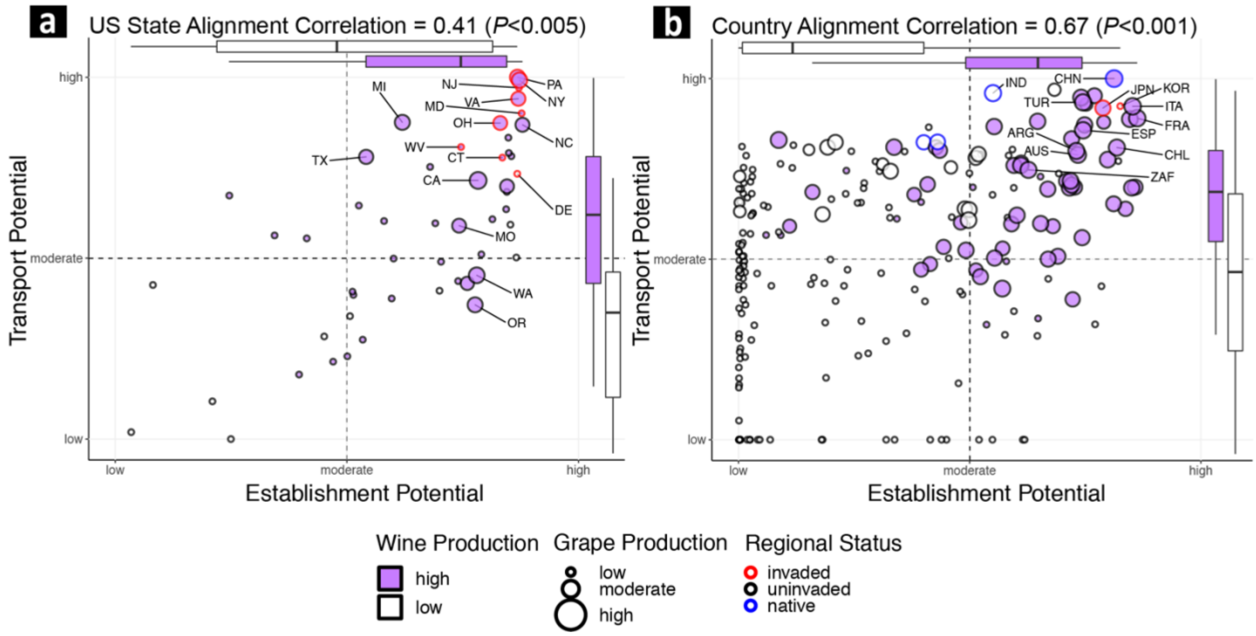

Fig. 5 Spotted lanternfly (*Lycorma delicatula*, SLF) invasion-potential alignment plots illustrate that states (**a**) and countries (**b**) that produce most of the global supply of grapes (point size) and wine (point fill color) also have high transport and establishment potentials. Invaded regions and the top-10 grape producing regions are labeled; box plots split the distributions of establishment potential and transport potential into high (purple) and low (white) wine producing regions (center line is the median, box limits are the upper and lower quartiles, and whiskers are 1.5x the interquartile range); dashed lines divide the data into high-high, high-low, and low-low potential quadrants; and axes are scaled and formatted as suggested by the pandemic severity assessment framework[8,9]. Point color indicates high and low wine producing regions. Point and label size depict wine production in metric tons.

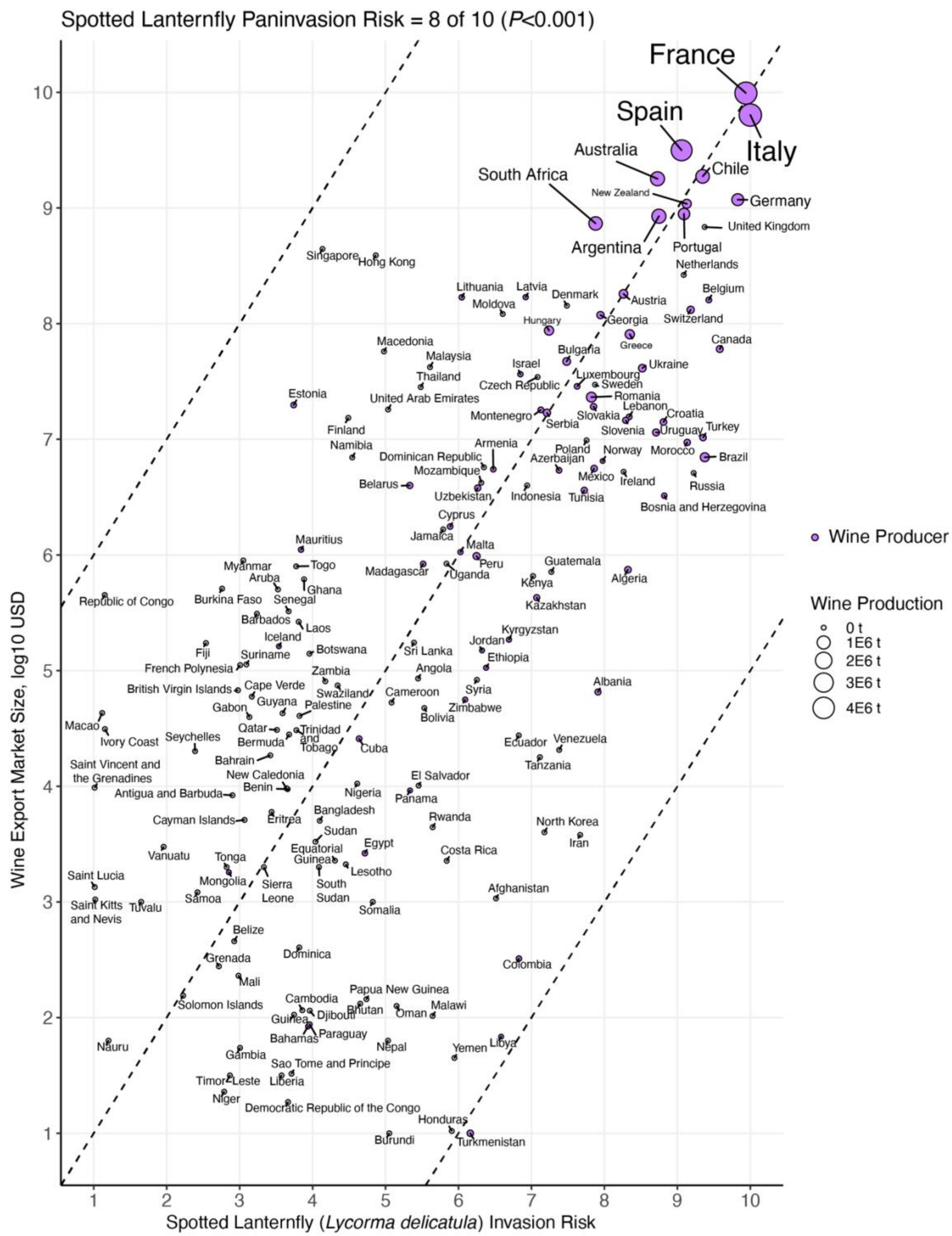

Fig. 6 Spotted lanternfly (*Lycorma delicatula*, SLF) paninvasion risk is an 8 out of 10 due to the correlation between country wine export market size and invasion risk. Dashed lines are one-to-one guidelines at -0.5, 0, 0.5 intercepts. Point color indicates high and low wine producing regions. Point and label size depict wine production in metric tons.

Discussion

The risk of a SLF paninvasion is high and coordinated effort should be made to reduce its invasion potentials globally. In the US, efforts to reduce SLF transport potential are primarily through quarantine and inspection of goods, and the USDA is working towards implementing consistent, science-based, and nation-wide transport protocols[19,41,42]. We recommend that estimates of SLF transport potential should be updated regularly: as more states become invaded, by matching seasonal trade dynamics to SLF phenology, and by including new information on high transport potential pathways such as rail, landscaping stone, and live tree shipments[16,19,28]. Reduction of establishment potential focuses on removing TOH, but US agricultural agencies lack resources to remove TOH, and businesses and private citizens are increasingly burdened with TOH removal costs[19]. We suggest eliminating the horticultural sale of TOH; increasing funding for TOH removal; research on cost-effective TOH biocontrol methods [e.g., 43]; and because SLF are generalists, more research to identify other suitable hosts found in the landscapes surrounding high transport and impact potential locations like railyards and vineyards [19,25,44]. Finally, reduction to impact potential currently relies on reducing SLF populations with tree-band trapping and broad-spectrum insecticides (e.g., carbamates, organophosphates, pyrethroids, neonicotinoids) that have high nontarget mortality, do not prevent vineyard reinfestations, and often overlap with grape harvest when adults move into vineyards[16,45,4630,46]. Damaged vines can be pruned, but grape yield is reduced[46], and therefore we suggest more research on biocontrol and SLF-specific RNAi insecticides to control outbreaks in vineyards and beyond[19,47–49].

To date, SLF has yet to invade a major viticultural area, so its impact on such regions with larger, wealthier, and interconnected wine economies is unknown. It is also unclear whether market elasticity might weaken or strengthen the disruption of a SLF paninvasion to the global wine market. When a pest like SLF with high paninvasion risk emerges, coordinated efforts can mitigate such global market disruptions. For example, the Great Wine Blight of the late 19th century caused by grapevine phylloxera (Hemiptera: *Daktulosphaira vitifoliae*) was the largest shock to the global wine market ever recorded[50]. Phylloxera fundamentally changed viticultural pest management, and solutions to manage it were developed through US-European collaborations coordinated by the French federal government[50]. However, US federal coordination is hampered for SLF. In 2019, the National Invasive Species Council was defunded, and the US Invasive Species Advisory Committee, which coordinated federal invasive species control efforts since 2000, was terminated. These cuts decrease US capacity to respond to SLF and other emerging paninvasive pests and pathogens[51]. We suggest the committee be reinstated and council refunded so they may collaborate with the USDA and state agricultural agencies who are working to reduce SLF invasion potentials. Going forward, invasion potentials for other species are likely to increasingly align and coordinated governmental efforts will be needed to reduce invasion potentials in the US and internationally. The paninvasion severity assessment framework is a simple tool to assess such invasion potentials for any emerging invasive species and then communicate its risk to stakeholders whose involvement is necessary to mitigate any market, environmental, and human-health disruptions.

Methods

Paninvasion Severity Assessment Framework

Although the invasion process can be divided into many stages, here we focused on the three main stages most often estimated by invasion risk assessments and that are analogous to the potentials that public-health scientists quantify for pathogens (Fig. 2)[e.g., 2]. When a pathogen with pandemic risk emerges, public health scientists place it within scaled measures of transmissibility and infectivity (often combined and termed transmissibility), and virulence (clinical severity) to assess its risk[8,9]. For example, when SARS-CoV-2 emerged during the COVID-19 pandemic, the initial understanding was that different age groups had similar potentials to transmit and become infected (Fig. 2a, y-axis), but different age groups varied in their clinical severity once infected (Fig. 2a, x-axis)[8,52,53]. To adapt this public-health framework to invasive species, we equated transmission, infectivity, and virulence potentials of a pathogen across different human populations to the transport, establishment, and impact potentials of an invasive species across different regions (see colored arrows between Fig. 2a and b). For example, in Fig. 2b we placed several hypothetical regions that together indicate strong alignment (i.e., multivariate correlation) among invasion potentials across the regions. In this example, predicted invasion risk (Fig. 2c, x-axis) for these three hypothetical regions is strongly correlated to a measure of their contributions to a global market (Fig. 2c, y-axis), indicating an overall high paninvasion risk.

The paninvasion assessment of SLF comprised three steps: estimate invasion potentials, calculate alignment of invasion potentials, and quantify paninvasion risk, which we describe in detail below and in the SI methods. To make our framework accessible, we provide an open-source R package that includes all data and reproduces all results (https://ieco-lab.github.io/slfrsk/) and a Google Earth Engine application to map SLF paninvasion severity from global to local scales (https://ieco.users.earthengine.app/view/ieco-slf-riskmap). These open-science tools support assessments for other emerging regional invasives at risk of paninvasion[e.g., 54]. Finally, in this study we focused on a plant pest, thus agricultural and economic metrics were most relevant to assess paninvasion risk. For other invasive species, estimates of impact and disruption that include environmental or human health metrics may be a higher priority.

Step 1: Estimate Invasion Potentials

Transport Potential

Transport potential is a measure of propagule pressure[55]. The prevailing hypothesis on SLF transport potential is that regions that import more tonnage of commodities from the invaded US region also import more total tonnage of goods and trade infrastructure (e.g., cargo containers, pallets, and railcars) that inadvertently transport SLF propagules, such as egg masses, long-distances[16,19,24,28,56,57]. To estimate which states were invaded and identify SLF transportation events, we obtained a database of SLF records from the USDA and aggregated first-find and regulatory incident reports[e.g., 32]. As of December 2020, the invaded states were Connecticut, Delaware, Maryland, New Jersey, New York, Ohio, Pennsylvania, Virginia, and West Virginia (Fig. 3). We estimated transport potentials from the US invaded region as the $\log_{10}$ of the average annual metric total tonnage of all goods imported between 2012–2017 by states and countries from the invaded US states. This date range encapsulates both pre- and post-introduction of SLF to the US and maximized temporal overlap across different data sources. Tonnage data from these invaded states were from the US Freight Analysis Framework for interstate imports[33] and from the US Trade Online database for international imports[34], both accessed on June 14, 2019. We found that SLF spread in the US is explained by our transport potential metric (SI, Supplementary Table 1).

Establishment Potential

Establishment potential is the set of species-specific and environmental characteristics of a region that determine if a transported species can generate a self-sustaining population there[2]. We determined SLF establishment potential from an ensemble estimate from three global species distribution models (SDMs): a multivariate SDM of TOH (*sdm_toh*), a multivariate SDM of SLF (*sdm_slf1*), and a univariate SDM of SLF that modeled SLF presence on the predicted values from *sdm_toh (sdm_slf2)*. Models were constructed using Maxent ver. 3.4.1 according to unbiased niche modeling best practices (see SI for detailed SDM methods)[58–60]. Specifically, our SDMs were built from unique, error checked, and spatially rarefied presence records: *sdm_toh* on 8,578 TOH presence records, and *sdm_slf1* and *sdm_slf2* on 325 SLF presence records obtained from GBIF on October 20, 2020. To find the best-fit models that explained TOH and SLF presences, we identified a subset of six covariates, from 22 candidate covariates[61–64], that minimized model collinearity: annual mean temperature, mean diurnal temperature range, annual precipitation, precipitation seasonality, elevation, and access to cities. We fit *sdm_toh* and *sdm_slf1* with these six covariates, and fit *sdm_slf2* with the *sdm_toh* predicted values. We evaluated model performance with *k*-fold cross-validation, specifically the receiver operating characteristic of the AUC (area under the curve) and omission error[65–67].

Each model estimated suitability at a 30-arc-second (at the equator approximately 1 km^2) global resolution with pixel values scaled 0–1, which we averaged across models per pixel to produce one ensemble image and intersected this image with state and country polygons[60]. Establishment potential for the 50 US states and 223 countries was estimated as the maximum pixel value for each state and country. Results and conclusions with mean and median pixel values instead of max were similar (see https://ieco-lab.github.io/slfrsk/).

Impact Potential

We used log_{10}-transformed average annual production tonnages of grapes and wine as two separate estimates of impact potential. For consistency, we used grape and wine production during the same span of time as transport potential estimates, 2012–2017. Grape production for countries was from the Food and Agriculture Organization of the United Nations crop database[38] and for states from the USDA National Agricultural and Statistics Service commodity database[39], both accessed on January 24, 2020. Wine production in metric tons was from

FAOSTAT for countries[38], accessed on June 21, 2019, and from the Alcohol and Tobacco Tax and Trade Bureau (TTB) for states[40], accessed on June 22, 2019, which was in gallons but we converted it to metric tons assuming 3.776e-3 t/gallon[68]. Major viticultural regions (Fig. 4) were aggregated and georeferenced from a TTB US state data set[69] and the global viticultural regions Wikipedia list[70] to better visualize impact within states and countries, both accessed on April 22, 2020.

Step 2: Calculate Alignment Correlations

To better consider how all three invasion potentials may coincide for particular regions, we calculated alignment correlations for states and countries separately. Alignment was calculated for each of the two measures of impact potential as Spearman rank correlations between impact potential and the predicted values from linear regressions models of each impact potential regressed on transport and establishment potentials together[71]. We then visualized these multiple multivariate, correlations as quadrant plots following a stakeholder-friendly and approachable format adapted from the pandemic severity assessment framework[8,9].

Step 3: Quantify Paninvasion Risk

To determine if invasion risk for countries corresponds with economic impact to the global wine industry, we investigated the relationship between wine market size and predicted risk of invasion for individual countries. We estimated wine market size for 223 countries as the value of wine exports corresponding with the years for our trade data (2012–2017, $\log_{10}$ USD) downloaded from the FAOSTAT detailed trade matrix[38], accessed August 31, 2020. Then, we regressed country grape production on transport and establishment potentials. Each predicted value from this regression can be considered an estimate of the risk of SLF to invade and impact a country’s grape production. We rescaled these estimates from 1–10 to create an easily interpreted estimate of risk and then correlated these predicted values to wine export market size. To place overall SLF paninvasion severity on a clear scale for both researchers and stakeholders, we simply rescaled the Pearson correlation from 1–10, so that 1 is a complete negative correlation and 10 is a complete positive correlation between country risk and wine export market size.

Caveats

We note two caveats to our approach of quantifying paninvasion severity for SLF. First, our assessment only estimates paninvasion severity of SLF via a stepping-stone introduction from the eastern US. Because major wine producing nations also heavily trade with China where SLF is native and Japan and South Korea where SLF is established, SLF transport potential is greater than our estimates, meaning that paninvasion severity is also likely higher than what we report here, and future work should account for global trade network dynamics. Second, our approach relativizes invasion potentials with the assumption that regions with high relative potentials have high absolute potentials. However, this assumption is well met for SLF based on its apparent broad environmental suitability, flexible life cycle (e.g., egg development with or without diapause-termination via chilling)[72,23,73], and ability to lay many discrete egg masses on numerous substrates (Fig. 1b), as well as rapid spread (Fig. 3) and realized impacts to grape and wine production in the invaded region of the US[19,30]. When a pathogen with pandemic potential emerges, the pandemic severity assessment framework compares the severity of the potentials of the current outbreak pathogen to past pandemic producing pathogens[8,9,52]. Thus, the next step towards a mature paninvasion framework is to estimate invasion potentials for current paninvasive species, so that the likelihood of a paninvasion for any emerging regional pest can be placed on an absolute scale of severity.

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