

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

2

3 **Nicholas A. Huron\***

4 **Jocelyn E. Behm**

5 **Matthew R. Helmus**

6

7 Integrative Ecology Lab, Center for Biodiversity, Department of Biology, Temple University,

8 Philadelphia, PA 19122 USA.

9

10 \* corresponding author, [nahuron@temple.edu](mailto:nahuron@temple.edu)

11

12 **Abstract**

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

26

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

39 Despite the importance of identifying emerging paninvasives, existing approaches lack a  
40 cohesive and universal framework for rapidly assessing and effectively communicating such risk  
41 to stakeholders<sup>7</sup>. To address this gap, we developed the paninvasion severity assessment  
42 framework by adapting the US CDC pandemic severity assessment framework to invasion  
43 process theory, which describes translocations of species in terms of transport, establishment,  
44 and impact potentials (Fig. 1, 2)<sup>2,8-10</sup>. Although invasive species frameworks are increasingly  
45 adapted to understand infectious diseases like COVID-19<sup>11-16</sup>, adapting public-health  
46 frameworks to invasion science is novel and leverages an increasingly universal risk vocabulary  
47 (Fig. 2)<sup>17</sup>. Under this framework, we assessed the paninvasion risk of the spotted lanternfly  
48 planthopper (Hemiptera: *Lycorma delicatula*; SLF, Fig. 1). SLF was introduced to South Korea  
49 and Japan in the early 2000s and then to the U.S. (ca. 2014) on goods imported from its native  
50 China<sup>18</sup>. SLF has rapidly spread from Pennsylvania to several other states, presenting increased  
51 opportunities for stepping-stone invasions to additional regions<sup>19-21</sup>. SLF greatly impacts grape  
52 production<sup>22-26</sup> and has been presented to the public as one of the worst invasive species to  
53 establish in the US in a century<sup>27-29</sup>, but its paninvasion risk has not been assessed<sup>19</sup>.

54 SLF likely has high global transport potential because it lays inconspicuous egg masses  
55 on plants, stone, and trade infrastructure (e.g., containers, railcars, pallets), which facilitates  
56 long-distance transport when eggs are laid on exported items (Fig. 1a-c). Landscaping stone  
57 imported from China was the likely vector of the US invasion<sup>18</sup>. Following successful transport,

58 SLF global establishment potential is likely enhanced by the cosmopolitan distribution of its  
59 preferred host plant, the tree-of-heaven (*Ailanthus altissima*, TOH, Fig. 1d–f)<sup>21</sup>. The native  
60 ranges of SLF and TOH overlap in China, but for >250 years TOH has escaped cultivation into  
61 disturbed habitats and agricultural margins in temperate, subtropical, and Mediterranean regions  
62 globally (Fig. 1 map). Once established, SLF likely has high global impact potential to wine  
63 markets because grape is an equally suitable host. SLF develops at similar rates when fed grape  
64 or TOH, and fecundity increases when fed a mixed diet of these two preferred hosts<sup>25,30–33</sup>. Asian  
65 vineyard production is impacted by SLF infestations<sup>34,35</sup>; and SLF-invaded US vineyards have  
66 reported vine deaths, >90% yield losses, and closure (Fig. 1g–i)<sup>21,23,36</sup>.

67 To assess paninvasion risk, we calculated invasion potentials from estimates of SLF  
68 transport, establishment, and impact potentials from the US invaded region to uninvaded US  
69 states and countries using trade, species distribution models, and grape and wine production data.  
70 We then mapped invasion potentials, calculated alignment correlations, and estimated risk to the  
71 \$300B global wine market<sup>37</sup>.

72

## 73 **Results**

### 74 *Spotted lanternfly invaded range*

75 To assess SLF paninvasion risk, we first estimated the current US invaded range (ca.  
76 2020). We aggregated distributional data from multiple sources, including announcements made  
77 by state departments of agriculture on cargo interceptions that did not lead to established  
78 populations (i.e., regulatory incidents). By 2020, SLF had established in nine US states, with  
79 clear incidents of long-distance transport and establishment in Virginia, New York, and  
80 Pennsylvania. In eight additional states, individuals were intercepted in cargo and on transported  
81 goods originating from states with established SLF. California had intercepted the most with >40  
82 individual SLF on 35 flights found during cargo inspections, but all were dead or moribund and  
83 not egg masses<sup>38</sup>. No international reports of regulatory incidents from the US have been  
84 published. These regulatory incidents suggest that cargo with SLF were frequently transported  
85 from the invaded range in the US northeast to at least as far as to the US west coast (Fig. 3).

86

### 87 *Alignment of invasion potentials*

88 We estimated the three invasion potentials—transport, establishment, impact—for 50 US  
89 states and 223 countries. For transport potential, we used the total metric tonnage of goods  
90 imported from invaded states<sup>39,40</sup>. The current SLF spread in the US (Fig. 3) was explained by  
91 this transport potential metric (SI, Supplementary Table 1). States with the highest transport  
92 potential were mostly in the eastern US, but Illinois, Texas, and California also heavily traded  
93 with the invaded states, indicating that SLF had high potential to be transported both regionally  
94 and transcontinentally (Fig. 4a, 5a). Globally, transport potentials were highest in several  
95 European countries, Canada, and Brazil (Fig. 4b, 5b).

96 We based establishment potential on an ensemble estimate of species distribution models  
97 (SDMs) built on SLF and TOH geolocations (see SI for SDM methods, Fig. 4)<sup>41</sup>. Our ensemble  
98 estimate of SLF establishment potential was spatially similar to other SDMs<sup>42,43</sup> and  
99 physiologically based demographic models of SLF<sup>44,45</sup>. However, our estimate indicated urban  
100 landscapes as likely establishment locations and showed fine spatial-scale variation in  
101 establishment potential (see our interactive map [https://ieco.users.earthengine.app/view/ieco-slf-](https://ieco.users.earthengine.app/view/ieco-slf-riskmap)  
102 [riskmap](https://ieco.users.earthengine.app/view/ieco-slf-riskmap)). For each state and country, we extracted the mean, median and max predicted  
103 suitability to estimate establishment potential (see SI). Most US states had high establishment  
104 potential (Fig. 4a, 5a), and all the countries with highest transport potential also had the highest  
105 establishment potential (Fig. 4b, 5b).

106 We estimated SLF impact potential as the annual average tonnage of grapes and wine  
107 produced for each US state and country<sup>46–48</sup>. States and countries with many important  
108 viticultural regions were geographically clustered (Fig. 4), suggesting that should one become  
109 invaded, neighboring high impact potential states or countries are likely to also become invaded  
110 like the spread observed in the US (Fig. 3). States with high impact potential included California,  
111 Washington, New York, Pennsylvania, and Oregon (Fig. 4a, 5a), and countries with high impact  
112 potential include Italy, France, and Spain (Fig. 4b, 5b).

113 SLF invasion potentials across states and countries were aligned. Alignment correlations  
114 calculated as Spearman's rank correlations ( $\rho$  statistic) among transport, establishment, and  
115 impact potentials were positive for impact potential measured as state grape production ( $\rho =$   
116  $0.41, P < 0.005$ ), state wine production ( $\rho = 0.52, P < 0.001$ ), country grape production ( $\rho = 0.67,$   
117  $P < 0.001$ ), and country wine production ( $\rho = 0.63, P < 0.001$ ). This alignment of potentials is clear  
118 in the invasion-potential alignment plots (Fig. 5). Major grape producing regions fall in the

119 upper-right quadrant of the plots where regions have both high transport and high establishment  
120 potentials.

121

### 122 ***Paninvasion risk***

123 We estimated the risk of SLF to disrupt the global wine market to be an 8 out of 10 (Fig.  
124 6). To derive this value, we regressed country grape production on country transport and  
125 establishment potentials. Each predicted value from this multivariate regression can be  
126 considered an estimate of the risk of SLF to invade and impact a country's grape production. We  
127 then rescaled these predicted values from 1–10 and correlated them to wine export market size ( $\rho$   
128 = 0.66,  $P < 0.001$ ). To place SLF on a scale of paninvasion severity, we rescaled the correlation  
129 coefficient,  $\rho$ , from 1–10, so that 1 is a complete negative correlation and 10 is a complete  
130 positive correlation between predicted impact and market size. Low values on this scale indicate  
131 that the global market is buffered against a paninvasion, while high values indicate that a  
132 paninvasion is likely unless mitigation actions are taken to reduce invasion potentials.

133

### 134 **Discussion**

135 The risk of a SLF paninvasion is high and coordinated effort should be made to reduce its  
136 invasion potentials globally. In the US, efforts to reduce SLF transport potential are primarily  
137 through quarantine and inspection of goods, and the USDA is working towards implementing  
138 consistent, science-based, and nation-wide transport protocols<sup>21,49,50</sup>. We recommend that  
139 estimates of SLF transport potential should be updated regularly: as more states become invaded,  
140 by matching seasonal trade dynamics to SLF phenology, and by including new information on  
141 high transport potential pathways such as rail, landscaping stone, and live tree shipments<sup>18,21,34</sup>.  
142 Reduction of establishment potential focuses on removing TOH, but US agricultural agencies  
143 lack resources to remove TOH, and businesses and private citizens are increasingly burdened  
144 with TOH removal costs<sup>21</sup>. We suggest eliminating the horticultural sale of TOH; increasing  
145 funding for TOH removal; research on cost-effective TOH biocontrol methods<sup>e.g., 51</sup>; and because  
146 SLF are generalists, more research to identify other suitable hosts found in the landscapes  
147 surrounding high transport and impact potential locations like railyards and vineyards<sup>21,30,52</sup>.  
148 Finally, reduction to impact potential currently relies on reducing SLF populations with tree-  
149 band trapping and broad-spectrum insecticides (e.g., carbamates, organophosphates, pyrethroids,

150 neonicotinoids) that have high nontarget mortality, do not prevent vineyard reinfestations, and  
151 often overlap with grape harvest when adults move into vineyards<sup>18,36,53,54</sup>. Damaged vines can  
152 be pruned, but grape yield is reduced<sup>54</sup>, and therefore we suggest more research on long-term  
153 control methods, such as trapping technologies that reduce bycatch, host-specific biocontrol  
154 agents, and SLF-specific RNAi insecticides to control outbreaks in vineyards and beyond<sup>21,55-59</sup>.

155 To date, SLF has yet to invade a major viticultural area, so its impact on such regions  
156 with larger, wealthier, and interconnected wine economies is unknown. It is also unclear whether  
157 market elasticity might weaken or strengthen the disruption of a SLF paninvasion to the global  
158 wine market. When a pest like SLF with high paninvasion risk emerges, coordinated efforts can  
159 mitigate such global market disruptions. For example, the Great Wine Blight of the late 19<sup>th</sup>  
160 century caused by grapevine phylloxera (Hemiptera: *Daktulosphaira vitifoliae*) was the largest  
161 shock to the global wine market ever recorded<sup>60</sup>. Phylloxera fundamentally changed viticultural  
162 pest management, and solutions to manage it were developed through US-European  
163 collaborations coordinated by the French federal government<sup>60</sup>. However, US federal  
164 coordination is hampered for SLF. In 2019, the National Invasive Species Council was defunded,  
165 and the US Invasive Species Advisory Committee, which coordinated federal invasive species  
166 control efforts since 2000, was terminated. These cuts decrease US capacity to respond to SLF  
167 and other emerging paninvasive pests and pathogens<sup>61</sup>. We suggest the committee be reinstated  
168 and council refunded so they may collaborate with the USDA and state agricultural agencies who  
169 are working to reduce SLF invasion potentials. Going forward, invasion potentials for other  
170 species are likely to increasingly align and coordinated governmental efforts will be needed to  
171 reduce invasion potentials in the US and internationally. The paninvasion severity assessment  
172 framework is a simple tool to assess such invasion potentials for any emerging invasive species  
173 and then communicate its risk to stakeholders whose involvement is necessary to mitigate any  
174 market, environmental, and human-health disruptions.

175

## 176 **Methods**

177 Here, we provide a methodological discussion of the paninvasion severity assessment  
178 framework (Fig. 2) and SLF paninvasion risk assessment (Fig. 1). To make the SLF assessment  
179 easy to refine once new data and insights are available, we provide both an open-source R  
180 package that includes all data to reproduce all results (<https://ieco-lab.github.io/slfrsk/>) and a

181 Google Earth Engine application to map SLF paninvasion severity from global to local scales  
182 (<https://ieco.users.earthengine.app/view/ieco-slf-riskmap>). These open-science tools also are  
183 adaptable to other emerging regional invasives at risk of paninvasion<sup>e.g., 62</sup>. Here, we focused on  
184 agricultural and economic data most relevant to assess pest risk, but for non-pest invasives, data  
185 on environmental and human health may be a higher priority.

186

### 187 ***Paninvasion Severity Assessment Framework***

188 Although the invasion process can be divided into many stages, the paninvasion severity  
189 assessment framework focuses on the three main stages most often estimated in invasion risk  
190 assessments<sup>2</sup> and that are analogous to the disease potentials that public-health scientists quantify  
191 for pathogens (Fig. 2)<sup>8</sup>. When a pathogen with pandemic risk emerges, public health scientists  
192 place it within scaled measures of transmissibility and infectivity (often combined and termed  
193 transmissibility), and virulence (clinical severity) to assess its risk<sup>8,9</sup>. For example, when SARS-  
194 CoV-2 emerged during the COVID-19 pandemic, the initial understanding was that different age  
195 groups had similar potentials to transmit and become infected (Fig. 2a, y-axis), but different age  
196 groups varied in their clinical severity once infected (Fig. 2a, x-axis)<sup>8,63,64</sup>. To adapt this public-  
197 health framework to invasion process theory<sup>2,65-68</sup>, we equated transmission, infectivity, and  
198 virulence potentials of a pathogen across different human populations to the transport,  
199 establishment, and impact potentials of an invasive species across different regions (see colored  
200 arrows between Fig. 2a and b). For example, in Fig. 2b we placed several hypothetical regions  
201 that together indicate strong alignment (i.e., multivariate correlation) among invasion potentials  
202 across the regions. In this example, predicted invasion risk (Fig. 2c, x-axis) for these three  
203 hypothetical regions is strongly correlated to a measure of their contributions to a global market  
204 (Fig. 2c, y-axis), indicating an overall high paninvasion risk.

205 Paninvasion assessments comprise four steps (Fig. 2d): 1) estimate invasion potentials, 2)  
206 calculate alignment of invasion potentials, 3) quantify paninvasion risk, and 4) articulate caveats,  
207 which we describe in detail for SLF below and in the SI methods.

208

### 209 ***Step 1: Estimate Invasion Potentials***

210 *Transport Potential*



211 Transport potential is a measure of propagule pressure<sup>69</sup>. The prevailing hypothesis on  
212 SLF transport potential is that regions that import more tonnage of commodities from the  
213 invaded US region also import more total tonnage of goods and trade infrastructure (e.g., cargo  
214 containers, pallets, and railcars) that inadvertently transport SLF propagules, such as egg masses,  
215 long-distances<sup>18,21,26,34,70,71</sup>. To estimate which states were invaded and identify SLF  
216 transportation events, we obtained a database of SLF records from the USDA and aggregated  
217 first-find and regulatory incident reports<sup>e.g., 38</sup>. As of December 2020, the invaded states were  
218 Connecticut, Delaware, Maryland, New Jersey, New York, Ohio, Pennsylvania, Virginia, and  
219 West Virginia (Fig. 3). We estimated transport potentials from the US invaded region as the log<sub>10</sub>  
220 of the average annual metric total tonnage of all goods imported between 2012–2017 by states  
221 and countries from the invaded US states. This date range encapsulates both pre- and post-  
222 introduction of SLF to the US and maximized temporal overlap across different data sources.  
223 Tonnage data from these invaded states were from the US Freight Analysis Framework for  
224 interstate imports<sup>39</sup> and from the US Trade Online database for international imports<sup>40</sup>, both  
225 accessed on June 14, 2019. Current SLF spread in the US was explained by our transport  
226 potential metric suggesting that using total tonnage is a valid metric of transport potential for  
227 SLF (SI, Supplementary Table 1).

228

### 229 *Establishment Potential*

230 Establishment potential is the set of species-specific and environmental characteristics of  
231 a region that determine if a transported species can generate a self-sustaining population<sup>2</sup>. We  
232 determined SLF establishment potential from an ensemble estimate from three global species  
233 distribution models (SDMs): a multivariate SDM of TOH (*sdm\_toh*), a multivariate SDM of SLF  
234 (*sdm\_slf1*), and a univariate SDM of SLF that modeled SLF presence on the predicted values  
235 from *sdm\_toh* (*sdm\_slf2*). Models were constructed using MaxEnt ver. 3.4.1 according to  
236 unbiased niche modeling best practices (see SI for detailed SDM methods)<sup>72–74</sup>. Specifically, our  
237 SDMs were built from unique, error checked, and spatially rarefied presence records: *sdm\_toh*  
238 on 8,578 TOH presence records, and *sdm\_slf1* and *sdm\_slf2* on 325 SLF presence records  
239 obtained from GBIF on October 20, 2020. To find the best-fit models that explained TOH and  
240 SLF presences, we identified a subset of six covariates, from 22 candidate covariates<sup>75–78</sup>, that  
241 minimized model collinearity: annual mean temperature, mean diurnal temperature range, annual

242 precipitation, precipitation seasonality, elevation, and access to cities. We fit *sdm\_toh* and  
243 *sdm\_slf1* with these six covariates. *sdm\_toh* represents our best estimate of the global distribution  
244 of TOH, thus we fit *sdm\_slf2* that modeled SLF suitability from the predicted values of *sdm\_toh*.  
245 As such, *sdm\_slf2* represents suitability that considers a primary plant host (TOH)<sup>25</sup> that is also  
246 invasive but likely not at equilibrium<sup>79</sup> and the same abiotic covariates as *sdm\_slf1* (*sdm\_toh*  
247 uses the same covariates). We evaluated model performance with *k*-fold cross-validation,  
248 specifically the receiver operating characteristic of the AUC (area under the curve) and omission  
249 error<sup>80–82</sup>.

250 Each model estimated suitability at a 30-arc-second (at the equator approximately 1 km<sup>2</sup>)  
251 global resolution with pixel values scaled 0–1, which we averaged across models per pixel to  
252 produce one ensemble image and intersected this image with state and country polygons<sup>74</sup>.  
253 Establishment potential for the 50 US states and 223 countries was estimated as the maximum  
254 pixel value for each state and country. Results and conclusions with mean and median pixel  
255 values instead of max were similar (see <https://ieco-lab.github.io/slfrsk/>).

256

### 257 *Impact Potential*

258 We used log<sub>10</sub>-transformed average annual production tonnages of grapes and wine as  
259 two separate estimates of impact potential. For consistency, we used grape and wine production  
260 during the same span of time as transport potential estimates, 2012–2017. Grape production for  
261 countries was from the Food and Agriculture Organization of the United Nations crop database<sup>46</sup>  
262 and for states from the USDA National Agricultural and Statistics Service commodity  
263 database<sup>47</sup>, both accessed on January 24, 2020. Wine production in metric tons was from  
264 FAOSTAT for countries<sup>46</sup>, accessed on June 21, 2019, and from the Alcohol and Tobacco Tax  
265 and Trade Bureau (TTB) for states<sup>48</sup>, accessed on June 22, 2019, which was in gallons but we  
266 converted it to metric tons assuming 3.776e-3 t/gallon<sup>83</sup>. Major viticultural regions (Fig. 4) were  
267 aggregated and georeferenced from a TTB US state data set<sup>84</sup> and the global viticultural regions  
268 Wikipedia list<sup>85</sup> to better visualize impact within states and countries, both accessed on April 22,  
269 2020.

270

### 271 *Step 2: Calculate Alignment Correlations*

272 To consider how all three invasion potentials may coincide for regions, we calculated  
273 alignment correlations for states and countries separately. Alignment was calculated for each of  
274 the two measures of impact potential as Spearman rank correlations between impact potential  
275 and the predicted values from linear regressions models of each impact potential regressed on  
276 transport and establishment potentials together<sup>86</sup>. We then visualized these multiple multivariate  
277 correlations as quadrant plots following a stakeholder-friendly and approachable format adapted  
278 from the pandemic severity assessment framework<sup>8,9</sup>.

279

### 280 ***Step 3: Quantify Paninvasion Risk***

281 To determine if invasion risk for countries corresponds with economic impact to the  
282 global wine industry, we investigated the relationship between wine market size and predicted  
283 risk of invasion for individual countries. We estimated wine market size for 223 countries  
284 (including some that export but do not produce wine) as the value of wine exports corresponding  
285 with the years for our trade data (2012–2017, log<sub>10</sub> USD) downloaded from the FAOSTAT  
286 detailed trade matrix<sup>46</sup>, accessed August 31, 2020. Then, we regressed country grape production  
287 on transport and establishment potentials with multiple linear regression. Each predicted value  
288 from this regression can be considered an estimate of the risk of SLF to invade and impact a  
289 country's grape production. We rescaled these estimates from 1–10 to create an easily interpreted  
290 estimate of risk and then correlated these predicted values to wine export market size. To place  
291 overall SLF paninvasion severity on a clear scale for both researchers and stakeholders, we  
292 simply rescaled the Pearson correlation from 1–10, so that 1 is a complete negative correlation  
293 and 10 is a complete positive correlation between country risk and wine export market size.

294

### 295 ***Step 4: Articulate Caveats***

296 Paninvasion risk assessments should be performed iteratively as the invasion process  
297 continues across regions and responses are mobilized. Early assessments of emergent pests have  
298 great utility to support early responses but often come with caveats. The fourth step of the  
299 framework is to articulate the caveats of a current assessment to guide future research. These  
300 caveats should explicitly consider the assumptions made when estimating invasion potentials and  
301 how those potentials and risk could change as the invasion process continues. Below we

302 articulate caveats of our SLF assessment to provide a basis for future refined assessments of SLF  
303 to disrupt the global wine market.

304 We calculate paninvasion risk of SLF via stepping-stone transport from the eastern US.  
305 However, major wine producing nations also heavily trade with China, Japan, and South Korea,  
306 where SLF is also established. Total SLF transport potential is thus greater than our estimates,  
307 meaning paninvasion risk is higher than what we report here. Future work should account for  
308 global trade network dynamics to other nations with established SLF populations. However,  
309 comprehensive surveys are first needed on the distribution of SLF in these other countries and  
310 the trade emanating from regions with established populations. Further research should focus on  
311 the identification of which industries and commodities are most likely to increase long-distance  
312 spread. This requires linking trade dynamic models to phenological models to indicate if high  
313 risk trade is occurring at the same time as egg laying, because eggs are the life-stage most likely  
314 to be transported long-distances<sup>21</sup>. Additionally, refinement of SLF propagule pressure  
315 dynamics<sup>69</sup>, specifically propagule number and ratio of successful to failed transportation events,  
316 can improve estimates of transport potential.

317 Establishment potential should be improved as additional data and models become  
318 available. Because we use MaxEnt, a presence only, correlative SDM method to estimate  
319 establishment, we measure suitability for SLF in a way that does not account for how SLF  
320 population density and possible plastic and adaptive responses to novel environmental conditions  
321 in invaded regions may affect establishment success. Omission of population density and other  
322 demographic variables can hinder accurate prediction, especially for SDMs<sup>87</sup>, and whenever  
323 possible, priority should be placed on using them alongside models that rely on pest physiology  
324 to predict establishment potential<sup>88</sup>. For SLF, two physiologically based models<sup>44,45</sup> largely  
325 correspond with our SDM-based establishment potentials and thus support the global  
326 establishment potential for SLF we report here. Early assessments of paninvasion severity are  
327 unlikely to account for plasticity and adaptation that is common for invasive pests, especially  
328 when combined with variation in local weather patterns and climate change. Indeed, a recent  
329 analysis suggests that SLF will experience increased suitable habitat and a greater impact in  
330 China in the future due to climate change<sup>89</sup>. The expected effect of climate change is likely more  
331 complicated for SLF, which has a flexible life cycle that can include but does not require,  
332 temperature-linked diapause for overwintering in cooler regions<sup>24,90,91</sup>. Survivorship appears

333 greater without such diapause<sup>90</sup>, and thus establishment potential may be even higher than  
334 expected in warmer climes.

335         Variation in weather, climate change, host preference, and pest density can influence pest  
336 impacts. Such factors often act at different scales and in a spatially heterogenous manner. For  
337 example, SLF prefers grapes, but the degree to which it does over alternative hosts near  
338 vineyards remains poorly known, which is important, since SLF appear to have their highest  
339 densities at vineyard edge habitats<sup>92</sup>. The vulnerability of viticultural regions may be affected by  
340 the prevalence of particular grape cultivars or alternative hosts, but additional research is  
341 necessary to elucidate SLF feeding presence. Similarly, the relationship of SLF density within a  
342 vineyard and density in the surrounding landscape remains poorly known, which is in turn likely  
343 to be influenced by weather patterns and plant phenology<sup>36</sup>. As SLF host preference and its  
344 relationship to landscape variables become better understood, they should be incorporated into  
345 considerations of impact potential.

346         Lastly, to refine the SLF paninvasion risk assessment, future work should calculate  
347 invasion potentials for other grape pests like phylloxera to place SLF on an absolute scale of risk  
348 severity<sup>93</sup>. Our assessment of SLF relativizes invasion potentials with the assumption that  
349 regions with high potentials relative to other regions also have high absolute potentials. SLF has  
350 broad environmental suitability, a flexible life cycle, ability to lay many discrete egg masses on  
351 numerous substrates (Fig. 1b), observed rapid spread (Fig. 3) and realized impacts to grape and  
352 wine production<sup>21–26,36</sup>, so its absolute potentials are likely very high. However, absolute  
353 potentials can only be assessed by comparing multiple paninvasive species, like what is done for  
354 pathogens. When a pathogen with pandemic potential emerges, the pandemic severity  
355 assessment framework compares the severity of the potentials of the current outbreak pathogen  
356 to past pandemic producing pathogens<sup>8,9,63</sup>. The next step towards a mature paninvasion  
357 framework is to estimate invasion potentials for current paninvasive species, so that the  
358 likelihood of a paninvasion for any emerging regional pest can be placed on an absolute scale of  
359 severity.

360

361 **References**

- 362 1. Ristaino, J. B. *et al.* The persistent threat of emerging plant disease pandemics to global food  
363 security. *Proc. Natl. Acad. Sci.* **118**, (2021).
- 364 2. Blackburn, T. M. *et al.* A proposed unified framework for biological invasions. *Trends Ecol.*  
365 *Evol.* **26**, 333–339 (2011).
- 366 3. Chapman, D., Purse, B. V., Roy, H. E. & Bullock, J. M. Global trade networks determine the  
367 distribution of invasive non-native species. *Glob. Ecol. Biogeogr.* **26**, 907–917 (2017).
- 368 4. Liebhold, A. M. *et al.* Plant diversity drives global patterns of insect invasions. *Sci. Rep.* **8**,  
369 1–5 (2018).
- 370 5. Bradshaw, C. J. A. *et al.* Massive yet grossly underestimated global costs of invasive insects.  
371 *Nat. Commun.* **7**, 1–8 (2016).
- 372 6. Wyckhuys, K. A. G. *et al.* Biological control of an invasive pest eases pressures on global  
373 commodity markets. *Environ. Res. Lett.* **13**, 094005 (2018).
- 374 7. Leung, B., Finnoff, D., Shogren, J. F. & Lodge, D. Managing invasive species: Rules of  
375 thumb for rapid assessment. *Ecol. Econ.* **55**, 24–36 (2005).
- 376 8. Reed, C. *et al.* Novel framework for assessing epidemiologic effects of influenza epidemics  
377 and pandemics. *Emerg. Infect. Dis.* **19**, 85 (2013).
- 378 9. Qualls, N. *et al.* Community mitigation guidelines to prevent pandemic influenza—United  
379 States, 2017. *MMWR Recomm. Rep.* **66**, 1 (2017).
- 380 10. Grarock, K., Lindenmayer, D. B., Wood, J. T. & Tidemann, C. R. Using invasion process  
381 theory to enhance the understanding and management of introduced species: A case study  
382 reconstructing the invasion sequence of the common myna (*Acridotheres tristis*). *J. Environ.*  
383 *Manage.* **129**, 398–409 (2013).

- 384 11. Nuñez, M. A., Pauchard, A. & Ricciardi, A. Invasion science and the global spread of SARS-  
385 CoV-2. *Trends Ecol. Evol.* **35**, 642–645 (2020).
- 386 12. Ogden, N. H. *et al.* Emerging infectious diseases and biological invasions: A call for a one  
387 health collaboration in science and management. *R. Soc. Open Sci.* **6**, 181577 (2019).
- 388 13. Hatcher, M. J., Dick, J. T. A. & Dunn, A. M. Disease emergence and invasions. *J. Ecol.* **26**,  
389 1275–1287 (2016).
- 390 14. Bright, C. Invasive species: Pathogens of globalization. *Foreign Policy* **1**, 50–64 (1999).
- 391 15. Simberloff, D., Meyerson, L. & Fefferman, N. Invasive species policy and COVID-19.  
392 (2020).
- 393 16. Comizzoli, P., Pagenkopp Lohan, K. M., Muletz-Wolz, C., Hassell, J. & Coyle, B. The  
394 interconnected health initiative: A Smithsonian framework to extend one health research and  
395 education. *Front. Vet. Sci.* **8**, (2021).
- 396 17. Katella, K. Our new COVID-19 vocabulary—what does it all mean? > Stories at Yale  
397 Medicine. *Yale Medicine* <https://www.yalemedicine.org/stories/covid-19-glossary/> (2020).
- 398 18. Parra, G., Moylett, H. & Bulluck, R. USDA-APHIS-PPQ-CPHST Technical working group  
399 summary report spotted lanternfly, *Lycorma delicatula* (White, 1845). (2018).
- 400 19. Floerl, O., Inglis, G. J., Dey, K. & Smith, A. The importance of transport hubs in stepping-  
401 stone invasions. *J. Appl. Ecol.* **46**, 37–45 (2009).
- 402 20. Barringer, L. E., Donovall, L. R., Spichiger, S.-E., Lynch, D. & Henry, D. The first New  
403 World record of *Lycorma delicatula* (Insecta: Hemiptera: Fulgoridae). *Entomol. News* **125**,  
404 20–23 (2015).
- 405 21. Urban, J. M. Perspective: Shedding light on spotted lanternfly impacts in the USA. *Pest*  
406 *Manag. Sci.* **76**, 10–17 (2020).



- 407 22. Nixon, L. J. *et al.* Survivorship and development of the invasive *Lycorma delicatula*  
408 (Hemiptera: Fulgoridae) on wild and cultivated temperate host plants. *Environ. Entomol.*  
409 *nvab137* (2021) doi:10.1093/ee/nvab137.
- 410 23. Urban, J. M., Calvin, D. & Hills-Stevenson, J. Early response (2018–2020) to the threat of  
411 spotted lanternfly, *Lycorma delicatula* (Hemiptera: Fulgoridae) in Pennsylvania. *Ann.*  
412 *Entomol. Soc. Am.* **114**, 709–718 (2021).
- 413 24. Du, Z. *et al.* Global phylogeography and invasion history of the spotted lanternfly revealed  
414 by mitochondrial phylogenomics. *Evol. Appl.* (2021) doi:<https://doi.org/10.1111/eva.13170>.
- 415 25. Lee, J.-E. *et al.* Feeding behavior of *Lycorma delicatula* (Hemiptera: Fulgoridae) and  
416 response on feeding stimulants of some plants. *Korean J. Appl. Entomol.* **48**, 467–477  
417 (2009).
- 418 26. Lee, D.-H., Park, Y.-L. & Leskey, T. C. A review of biology and management of *Lycorma*  
419 *delicatula* (Hemiptera: Fulgoridae), an emerging global invasive species. *J. Asia-Pac.*  
420 *Entomol.* **22**, 589–596 (2019).
- 421 27. Roush, R. How we can contain the spotted lanternfly — maybe the worst invasive pest in  
422 generations | Opinion. <https://www.inquirer.com> (2018).
- 423 28. Imbler, S. The dreaded lanternfly, scourge of agriculture, spreads in New Jersey. *The New*  
424 *York Times* (2020).
- 425 29. Morrison, R. Invasive insects: The top 4 ‘most wanted’ list. *Entomology Today*  
426 <https://entomologytoday.org/2018/06/21/invasive-insects-the-top-4-most-wanted-list/> (2018).
- 427 30. Murman, K. *et al.* Distribution, survival, and development of spotted lanternfly on host  
428 plants found in North America. *Environ. Entomol.* **49**, 1270–1281 (2020).



- 429 31. Derstine, N. T. *et al.* Plant volatiles help mediate host plant selection and attraction of the  
430 spotted lanternfly (Hemiptera: Fulgoridae): A generalist with a preferred host. *Environ.*  
431 *Entomol.* **49**, 1049–1062 (2020).
- 432 32. Dechaine, A. C. *et al.* Phenology of *Lycorma delicatula* (Hemiptera: Fulgoridae) in Virginia,  
433 USA. *Environ. Entomol.* nvab107 (2021) doi:10.1093/ee/nvab107.
- 434 33. Uyi, O. *et al.* Spotted lanternfly (Hemiptera: Fulgoridae) can complete development and  
435 reproduce without access to the Ppreferred host, *Ailanthus altissima*. *Environ. Entomol.*  
436 (2020) doi:10.1093/ee/nvaa083.
- 437 34. Park, M., Kim, K.-S. & Lee, J.-H. Genetic structure of *Lycorma delicatula* (Hemiptera:  
438 Fulgoridae) populations in Korea: Implication for invasion processes in heterogeneous  
439 landscapes. *Bull. Entomol. Res.* **103**, 414–424 (2013).
- 440 35. Dara, S. K., Barringer, L. & Arthurs, S. P. *Lycorma delicatula* (Hemiptera: Fulgoridae): A  
441 new invasive pest in the United States. *J. Integr. Pest Manag.* **6**, 1–6 (2015).
- 442 36. Leach, H. & Leach, A. Seasonal phenology and activity of spotted lanternfly (*Lycorma*  
443 *delicatula*) in Eastern U.S. vineyards. *J. Pest Sci.* **93**, 1215–1224 (2020).
- 444 37. International Organisation of Vine and Wine. *2019 Statistical Report on World*  
445 *Vitiviniculture*. 23 (2019).
- 446 38. California Department of Food and Agriculture. *Pest detection advisory no. PD17-2020*  
447 *spotted lanternfly PD/EP activity summary 2020*. 1–7 (2020).
- 448 39. Oak Ridge National Lab. Freight analysis framework version 4. <http://faf.ornl.gov/fafweb/>  
449 (2017).
- 450 40. U.S. Census Bureau. U.S.A. Trade Online. <https://usatrade.census.gov/index.php?do=login>  
451 (2019).

- 452 41. Derived dataset GBIF.org. Filtered export of GBIF occurrence data. (2021)  
453 doi:10.15468/DD.KS6ACS.
- 454 42. Jung, J.-M., Jung, S., Byeon, D. & Lee, W.-H. Model-based prediction of potential  
455 distribution of the invasive insect pest, spotted lanternfly *Lycorma delicatula* (Hemiptera:  
456 Fulgoridae), by using CLIMEX. *J. Asia-Pac. Biodivers.* **10**, 532–538 (2017).
- 457 43. Wakie, T. T., Neven, L. G., Yee, W. L. & Lu, Z. The establishment risk of *Lycorma*  
458 *delicatula* (Hemiptera: Fulgoridae) in the United States and globally. *J. Econ. Entomol.* **113**,  
459 306–314 (2020).
- 460 44. Lewkiewicz, S. M., De Bona, S., Helmus, M. R. & Seibold, B. Temperature sensitivity of  
461 pest reproductive numbers in age-structured PDE models, with a focus on the invasive  
462 spotted lanternfly. *ArXiv211211448 Q-Bio* (2021).
- 463 45. Maino, J. L., Schouten, R., Lye, J. C., Umina, P. A. & Reynolds, O. L. Mapping the life-  
464 history, development, and survival of spotted lantern fly in occupied and uninvaded ranges.  
465 *InReview* 1–18 (2021) doi:10.21203/rs.3.rs-400798/v1.
- 466 46. FAOSTAT. FAOSTAT statistical database. <http://www.fao.org/faostat/en/#data/QC> (2019).
- 467 47. USDA National Agricultural Statistics Service. National agricultural statistics service - quick  
468 stats. <https://quickstats.nass.usda.gov/> (2019).
- 469 48. U.S. Alcohol and Tobacco Tax and Trade Bureau. Wine statistics.  
470 <https://www.ttb.gov/wine/wine-stats.shtml> (2019).
- 471 49. Crowe, J. Spotted lanternfly control program in the Mid-Atlantic region environmental  
472 assessment. *USDA APHIS Rep.* 46 (2018).
- 473 50. US Animal and Plant Health Inspection Service. USDA provides \$7.1 million to  
474 Pennsylvania to support projects that protect agriculture and natural resources.

- 475 [https://www.aphis.usda.gov/wcm/connect/APHIS\\_Content\\_Library/SA\\_Newsroom/SA\\_News/SA\\_By\\_Date/SA-2019/pennsylvania-](https://www.aphis.usda.gov/wcm/connect/APHIS_Content_Library/SA_Newsroom/SA_News/SA_By_Date/SA-2019/pennsylvania-funding?presentationtemplate=APHIS_Design_Library%2FPT_Print_Friendly_News_release)  
476 [funding?presentationtemplate=APHIS\\_Design\\_Library%2FPT\\_Print\\_Friendly\\_News\\_releas](https://www.aphis.usda.gov/wcm/connect/APHIS_Content_Library/SA_Newsroom/SA_News/SA_By_Date/SA-2019/pennsylvania-funding?presentationtemplate=APHIS_Design_Library%2FPT_Print_Friendly_News_release)  
477 [e](https://www.aphis.usda.gov/wcm/connect/APHIS_Content_Library/SA_Newsroom/SA_News/SA_By_Date/SA-2019/pennsylvania-funding?presentationtemplate=APHIS_Design_Library%2FPT_Print_Friendly_News_release) (2019).
- 479 51. Brooks, R. K., Wickert, K. L., Baudoin, A., Kasson, M. T. & Salom, S. Field-inoculated  
480 *Ailanthus altissima* stands reveal the biological control potential of *Verticillium nonalfalfae*  
481 in the Mid-Atlantic region of the United States. *Biol. Control* **148**, 104298 (2020).
- 482 52. Barringer, L. & Ciafré, C. M. Worldwide feeding host plants of spotted lanternfly, with  
483 significant additions from North America. *Environ. Entomol.* **49**, 999–1011 (2020).
- 484 53. Leach, H., Biddinger, D. J., Krawczyk, G., Smyers, E. & Urban, J. M. Evaluation of  
485 insecticides for control of the spotted lanternfly, *Lycorma delicatula*, (Hemiptera:  
486 Fulgoridae), a new pest of fruit in the Northeastern U.S. *Crop Prot.* **124**, 104833 (2019).
- 487 54. Penn State Extension. Spotted lanternfly management in vineyards.  
488 <https://extension.psu.edu/spotted-lanternfly-management-in-vineyards> (2021).
- 489 55. Whyard, S., Singh, A. D. & Wong, S. Ingested double-stranded RNAs can act as species-  
490 specific insecticides. *Insect Biochem. Mol. Biol.* **39**, 824–832 (2009).
- 491 56. Liu, H. & Mottern, J. An old remedy for a new problem? Identification of *Ooencyrtus*  
492 *kuvanae* (Hymenoptera: Encyrtidae), an egg parasitoid of *Lycorma delicatula* (Hemiptera:  
493 Fulgoridae) in North America. *J. Insect Sci.* **17**, 1–6 (2017).
- 494 57. Yang, Z.-Q., Choi, W.-Y., Cao, L.-M., Wang, X.-Y. & Hou, Z.-R. A new species of  
495 *Anastatus* (Hymenoptera: Eulpelmidae) from China, parasitizing eggs of *Lycorma delicatula*  
496 (Homoptera: Fulgoridae). *Zool. Syst.* **40**, 290–302 (2015).

- 497 58. Clifton, E. H. *et al.* Applications of *Beauveria bassiana* (Hypocreales: Cordycipitaceae) to  
498 control populations of spotted lanternfly (Hemiptera: Fulgoridae), in semi-natural landscapes  
499 and on grapevines. *Environ. Entomol.* **49**, 854–864 (2020).
- 500 59. Francese, J. A. *et al.* Developing traps for the spotted lanternfly, *Lycorma delicatula*  
501 (Hemiptera: Fulgoridae). *Environ. Entomol.* **49**, 269–276 (2020).
- 502 60. Ordish, G. *The great wine blight*. (Charles Scribner’s Sons, 1972).
- 503 61. Simberloff, D. *et al.* U.S. action lowers barriers to invasive species. *Science* **367**, 636–636  
504 (2020).
- 505 62. Zhu, G., Illan, J. G., Looney, C. & Crowder, D. W. Assessing the ecological niche and  
506 invasion potential of the Asian giant hornet. *Proc. Natl. Acad. Sci.* **117**, 24646–24648  
507 (2020).
- 508 63. Freitas, A. R. R. *et al.* Assessing the severity of COVID-19. *Epidemiol. E Serviços Saúde* **29**,  
509 1–5 (2020).
- 510 64. Prevent Epidemics. *COVID-19 Key COVID-19 metrics based on the latest available science*.  
511 <https://preventepidemics.org/covid19/science/weekly-science-review/> (2020).
- 512 65. Lockwood, J. L., Hoopes, M. F. & Marchetti, M. P. *Invasion ecology*. (Wiley-Blackwell,  
513 2013).
- 514 66. Ehler, L. E. Invasion biology and biological control. *Biol. Control* **13**, 127–133 (1998).
- 515 67. Ludsin, S. A. & Wolfe, A. D. Biological invasion theory: Darwin’s contributions from *The*  
516 *Origin of Species*. *BioScience* **51**, 780 (2001).
- 517 68. Schulz, A. N., Lucardi, R. D. & Marsico, T. D. Strengthening the ties that bind: An  
518 evaluation of cross-disciplinary communication between invasion ecologists and biological  
519 control researchers in entomology. *Ann. Entomol. Soc. Am.* **114**, 163–174 (2021).

- 520 69. Lockwood, J. L., Cassey, P. & Blackburn, T. The role of propagule pressure in explaining  
521 species invasions. *Trends Ecol. Evol.* **20**, 223–228 (2005).
- 522 70. Liu, H. Oviposition substrate selection, egg mass characteristics, host preference, and life  
523 history of the spotted lanternfly (Hemiptera: Fulgoridae) in North America. *Environ.*  
524 *Entomol.* **48**, 1452–1468 (2019).
- 525 71. Liu, H. Seasonal development, cumulative growing degree-days, and population density of  
526 spotted lanternfly (Hemiptera: Fulgoridae) on selected hosts and substrates. *Environ.*  
527 *Entomol.* **49**, 1171–1184 (2020).
- 528 72. Phillips, S. J., Anderson, R. P., Dudík, M., Schapire, R. E. & Blair, M. E. Opening the black  
529 box: An open-source release of Maxent. *Ecography* **40**, 887–893 (2017).
- 530 73. Araújo, M. B. & New, M. Ensemble forecasting of species distributions. *Trends Ecol. Evol.*  
531 **22**, 42–47 (2007).
- 532 74. Araújo, M. B. *et al.* Standards for distribution models in biodiversity assessments. *Sci. Adv.*  
533 **5**, eaat4858 (2019).
- 534 75. Fick, S. E. & Hijmans, R. J. WorldClim 2: New 1-km spatial resolution climate surfaces for  
535 global land areas. *Int. J. Climatol.* **37**, 4302–4315 (2017).
- 536 76. Hijmans, R. J., Cameron, S. E., Parra, J. L., Jones, P. G. & Jarvis, A. Very high resolution  
537 interpolated climate surfaces for global land areas. *Int. J. Climatol.* **25**, 1965–1978 (2005).
- 538 77. Weiss, D. J. *et al.* A global map of travel time to cities to assess inequalities in accessibility  
539 in 2015. *Nature* **553**, 333–336 (2018).
- 540 78. Simard, M., Pinto, N., Fisher, J. B. & Baccini, A. Mapping forest canopy height globally  
541 with spaceborne lidar. *J. Geophys. Res. Biogeosciences* **116**, (2011).

- 542 79. Sladonja, B., Sušek, M. & Guillermic, J. Review on Invasive Tree of Heaven (*Ailanthus*  
543 *altissima* (Mill.) Swingle) Conflicting Values: Assessment of Its Ecosystem Services and  
544 Potential Biological Threat. *Environ. Manage.* **56**, 1009–1034 (2015).
- 545 80. Fielding, A. H. & Bell, J. F. A review of methods for the assessment of prediction errors in  
546 conservation presence/absence models. *Environ. Conserv.* **24**, 38–49 (1997).
- 547 81. Pearson, R. G., Raxworthy, C. J., Nakamura, M. & Peterson, A. T. Predicting species  
548 distributions from small numbers of occurrence records: A test case using cryptic geckos in  
549 Madagascar. *J. Biogeogr.* **34**, 102–117 (2007).
- 550 82. Anderson, R. P. & Gonzalez, I. Species-specific tuning increases robustness to sampling bias  
551 in models of species distributions: An implementation with Maxent. *Ecol. Model.* **222**, 2796–  
552 2811 (2011).
- 553 83. AVCALC. Density of alcoholic beverage, wine, table, all (food). [https://www.aqua-](https://www.aqua-calc.com/page/density-table/substance/alcoholic-blank-beverage-coma-and-blank-wine-coma-and-blank-table-coma-and-blank-all)  
554 [calc.com/page/density-table/substance/alcoholic-blank-beverage-coma-and-blank-wine-](https://www.aqua-calc.com/page/density-table/substance/alcoholic-blank-beverage-coma-and-blank-wine-coma-and-blank-table-coma-and-blank-all)  
555 [coma-and-blank-table-coma-and-blank-all](https://www.aqua-calc.com/page/density-table/substance/alcoholic-blank-beverage-coma-and-blank-wine-coma-and-blank-table-coma-and-blank-all) (2019).
- 556 84. U.S. Alcohol and Tobacco Tax and Trade Bureau. Established AVAs.  
557 <https://www.ttb.gov/wine/established-avas> (2019).
- 558 85. Wikipedia. [https://en.wikipedia.org/wiki/List\\_of\\_wine-producing\\_regions](https://en.wikipedia.org/wiki/List_of_wine-producing_regions). (2020).
- 559 86. Allison, P. D. *Multiple regression: A primer*. (Pine Forge Press, 1999).
- 560 87. Ponti, L. *et al.* Biological invasion risk assessment of *Tuta absoluta*: Mechanistic versus  
561 correlative methods. *Biol. Invasions* **23**, 3809–3829 (2021).
- 562 88. Briscoe, N. J. *et al.* Forecasting species range dynamics with process-explicit models:  
563 Matching methods to applications. *Ecol. Lett.* **22**, 1940–1956 (2019).

- 564 89. Wang, C.-J. *et al.* Risk assessment of insect pest expansion in alpine ecosystems under  
565 climate change. *Pest Manag. Sci.* **77**, 3165–3178 (2021).
- 566 90. Keena, M. A. & Nielsen, A. L. Comparison of the hatch of newly laid *Lycorma delicatula*  
567 (Hemiptera: Fulgoridae) eggs from the United States after exposure to different temperatures  
568 and durations of low temperature. *Environ. Entomol.* 1–8 (2021) doi:10.1093/ee/nvaa177.
- 569 91. Xin, B. *et al.* Exploratory survey of spotted lanternfly (Hemiptera: Fulgoridae) and its natural  
570 enemies in China. *Environ. Entomol.* **50**, 36–45 (2020).
- 571 92. Leach, A. & Leach, H. Characterizing the spatial distributions of spotted lanternfly  
572 (Hemiptera: Fulgoridae) in Pennsylvania vineyards. *Sci. Rep.* **10**, 1–9 (2020).
- 573 93. Granett, J., Walker, M. A., Kocsis, L. & Omer, A. D. Biology and management of grape  
574 phylloxera. *Annu. Rev. Entomol.* **46**, 387–412 (2001).

575

## 576 **Acknowledgments**

577 We thank Julie Urban, Heather Leach, Nadège Bélouard, Stefani Cannon, Seba De Bona, Jason  
578 Gleditsch, Stephanie Lewkiewicz, Victoria Ramirez, Payton Phillips, Timothy Swartz and the  
579 Integrative Ecology Lab at Temple University for comments and feedback on earlier drafts of  
580 this manuscript. This work was funded by the United States Department of Agriculture Animal  
581 and Plant Health Inspection Service Plant Protection and Quarantine under Cooperative  
582 Agreements AP19PPQS&T00C251 and AP20PPQS&T00C136; the United States Department of  
583 Agriculture National Institute of Food and Agriculture Specialty Crop Research Initiative  
584 Coordinated Agricultural Project Award 2019-51181-30014; and the Pennsylvania Department  
585 of Agriculture under agreements 44176768, 44187342, and C9400000036.

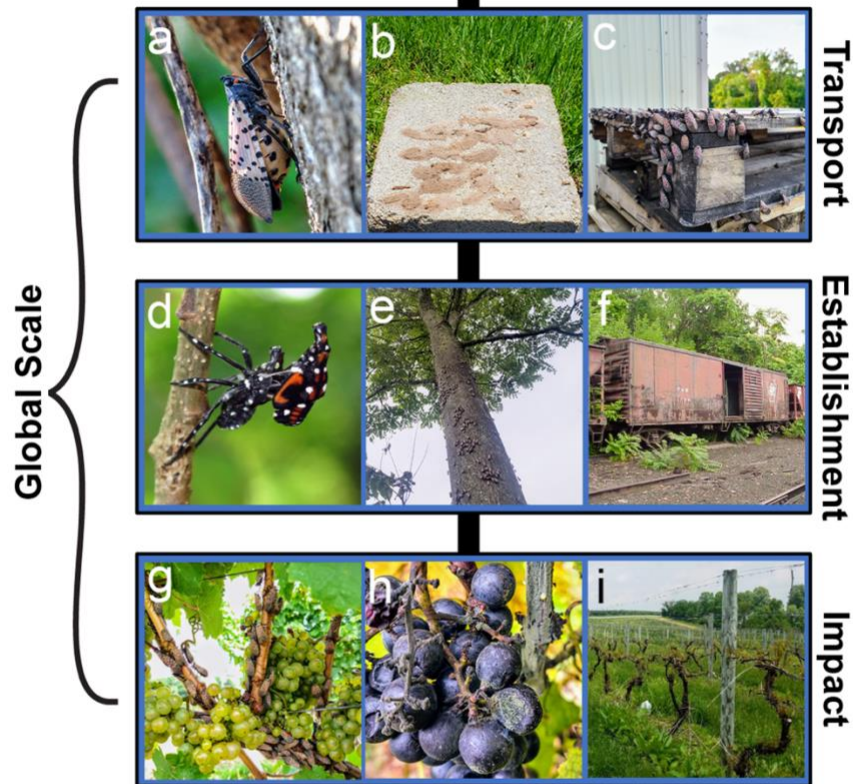
586



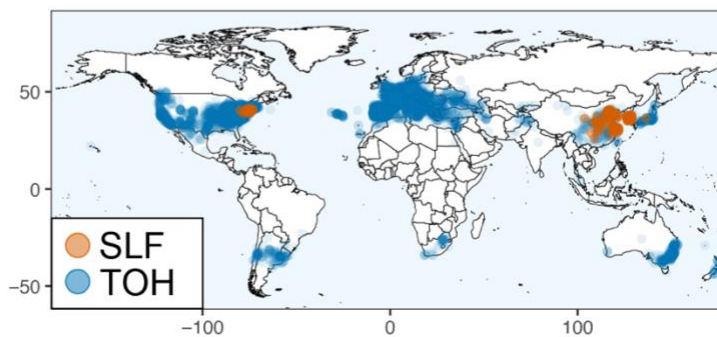
587 **Figures and Tables**

## Emerging Paninvasive Species Spotted Lanternfly

*Lycorma delicatula*



## Paninvasion



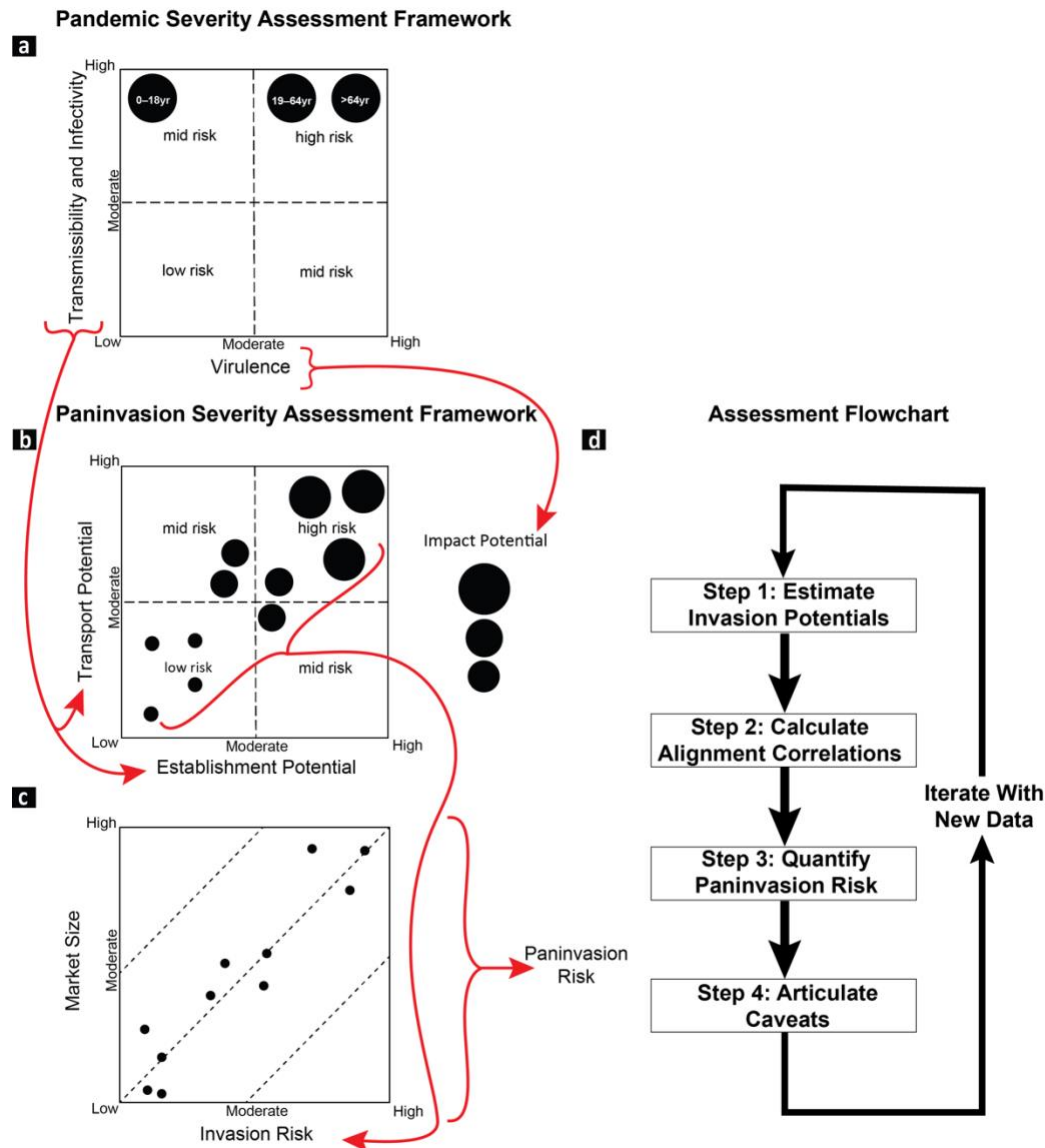
588

589 **Fig. 1** Our concept of paninvasive species is based on invasion process theory, whereby any

590 species has potentials to complete three sequential stages (depicted by the arrow) to become



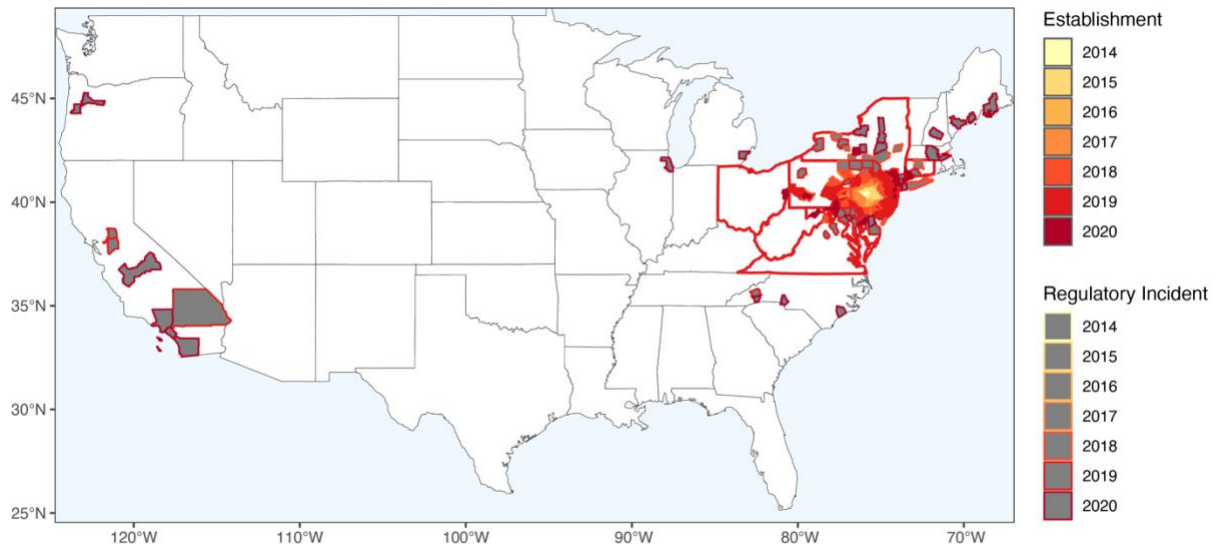
591 invasive in a region (i.e., transport to the region, establishment in the region, impact to the  
592 region's economy)<sup>2</sup>. For a pest paninvasion to occur, a pest must be transported and establish in  
593 suitable regions globally where it impacts susceptible agriculture disrupting markets at a global  
594 scale (depicted by the bracket). Here, we focus on estimating invasion stage potentials for the  
595 spotted lanternfly planthopper (*Lycorma delicatula*, SLF), an emerging US pest at risk of  
596 disrupting the global wine market. Photos introduce SLF biology. Gravid females (**a**) lay eggs on  
597 many surfaces like stone (**b**) and transport infrastructure (**c**). Once eggs hatch, SLF develop by  
598 molting through three black and one red nymphal instars (**d**) before molting into winged adults  
599 (top, **a**). SLF feed on phloem of many plants but develop quickly on tree-of-heaven (*Ailanthus*  
600 *altissima*, TOH, **e, f**), a paninvasive tree commonly found in habitat fragments around railroads  
601 (**f**) and warehouses (**c**). SLF also heavily feed on grape (**g**), reducing yield (**h**) and contributing to  
602 vine death (**i**). Photo credits: S. Cannon (**e**), M. Helmus (top, **a, d**), H. Leach (**c, g-i**), J. Losiewicz  
603 (**b**), G. Parra (**f**). The map is of SLF (orange) and TOH (blue) presences (ca. 2020) we used to  
604 estimate paninvasion risk (see Methods).  
605



606

607 **Fig. 2.** The paninvasion severity assessment framework is adapted from the US CDC pandemic  
608 severity assessment framework used to estimate the risk of emerging human pathogens. For  
609 pandemics (a), quadrant plots of pathogen transmissibility and infectivity (combined on one  
610 axis) vs. pathogen virulence (clinical severity) are used to compare the risk of a pathogen across  
611 different populations or age groups<sup>8,9,11</sup>. For paninvasions (b), invasion potentials for an  
612 emerging regional invasive species are estimated (d Step 1) by equating pathogen transmission  
613 with transport potential, infectivity with establishment potential, and virulence with impact  
614 potential (follow the arrows) across regions (black circles) to construct quadrant plots that depict  
615 their alignment based on multivariate correlations (d Step 2; see Methods). Next, paninvasion  
616 risk (c) is estimated from the correlation between regional invasion risk estimated from the

617 multivariate regression of invasion potentials (**d** Step 3; see Methods) and the size of regional  
618 markets that could be disrupted. The steps of the paninvasive severity assessment framework (**d**),  
619 culminating by articulating caveats in the current assessment that direct future research (**d** Step  
620 4) that provide data to inform the next assessment iteration.  
621



622

623 **Fig. 3** Spotted lanternfly (*Lycorma delicatula*, SLF) had invaded nine states in the US by 2020.

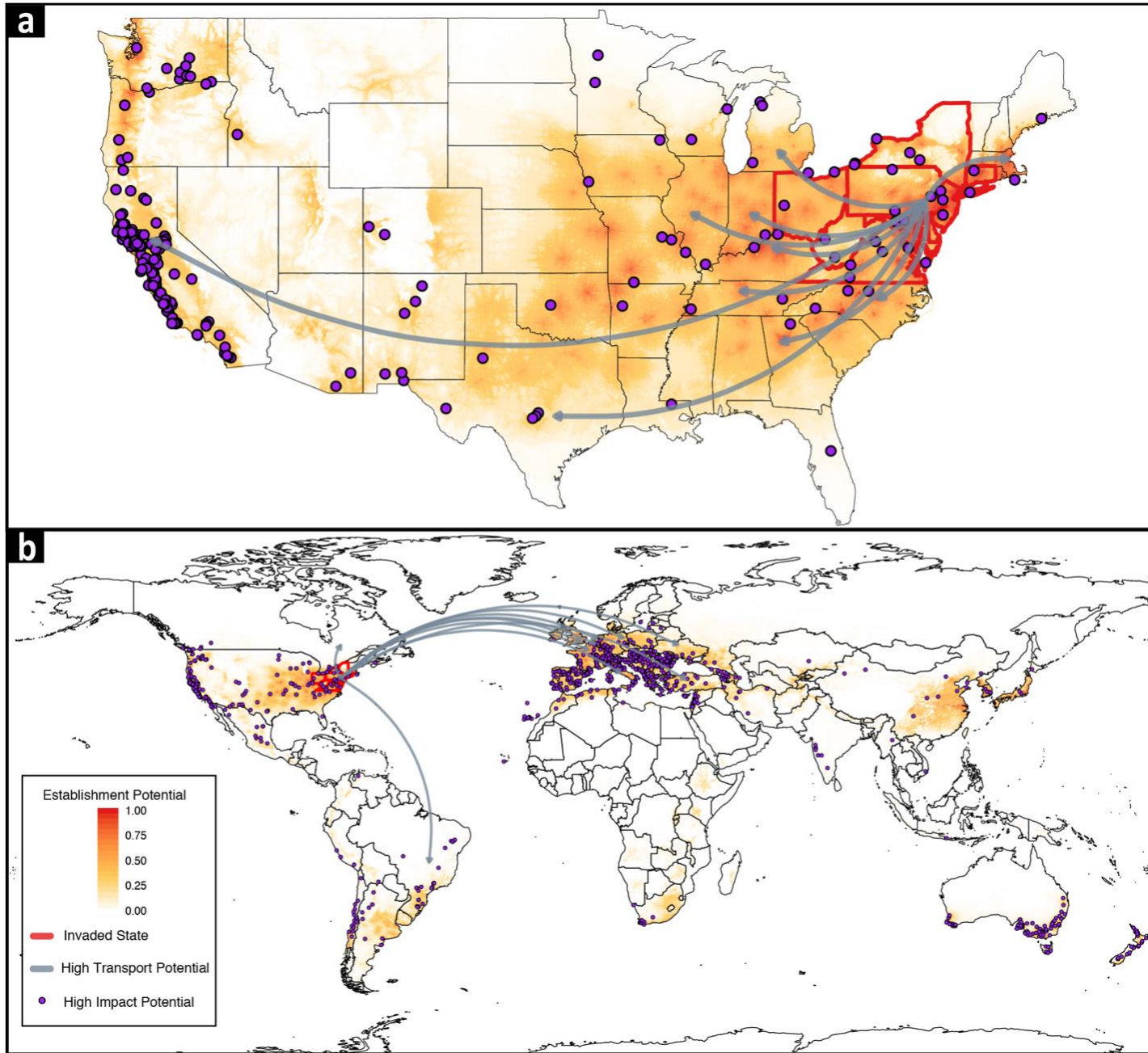
624 Colored polygons are counties with established SLF populations. Grey-filled polygons are

625 counties where SLF have been transported but have not established. These regulatory incidents

626 include any egg cases, living, moribund, and dead individuals found in cargo. Red outlined states

627 have established SLF populations.

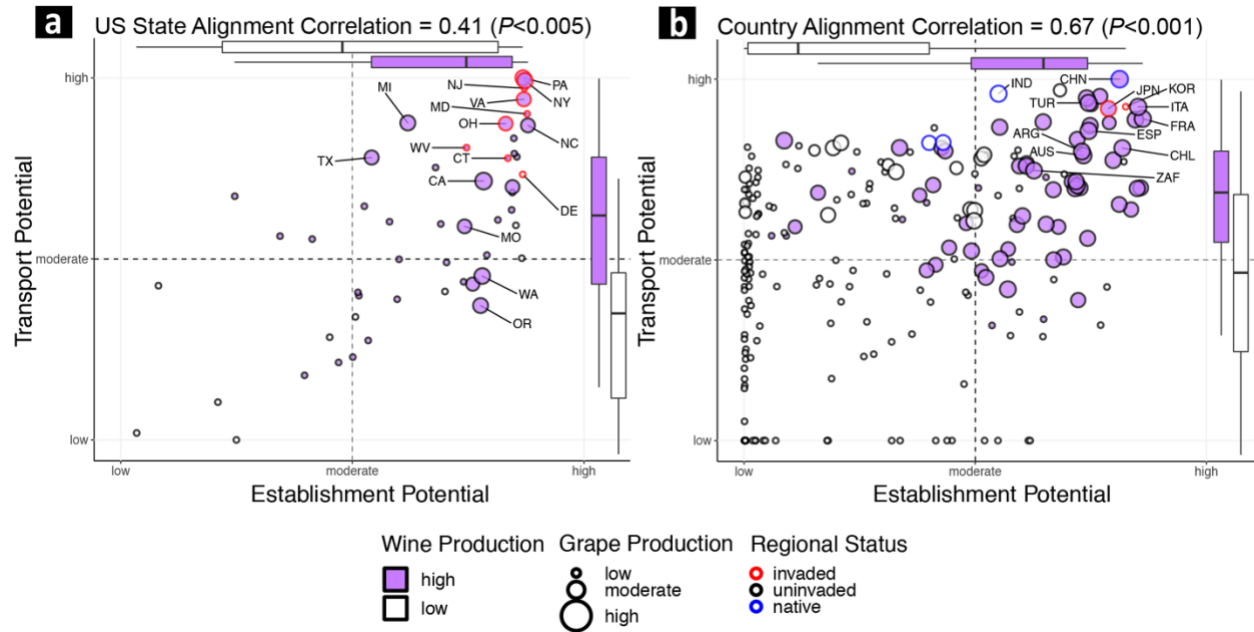
628



629

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

634



635

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

646



