1 Supplementary Information for

- 2 Paninvasion severity assessment of a US grape pest to disrupt the global wine market
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13 **This PDF file includes:**

- 14 Supplementary Methods
- 15 Supplementary Table 1
- 16 Supplementary References

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19	Supple	ementary Methods
20		Below, we provide additional details for terminology and methods for the analyses
21	conduc	ted in our study.
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23	Term L	Definitions
24	•	alignment correlation—multivariate relationship among invasion potentials.
25	•	establishment potential—likelihood of a region to contain suitable habitat for
26		transported individuals of a non-native species to form a spreading population.
27	•	impact potential—likelihood of a region to experience negative economic effects from
28		an established non-native species.
29	•	invasion potentials—likelihoods of a species to move through stages in an invasion
30		process across regions ¹ . We focus on the main stages: transport, establishment, impact.
31	•	MaxEnt—abbreviation for maximum entropy, a presence-only SDM methodology that
32		uses machine-learning to estimate the probability distribution of maximum entropy based
33		on environmental variables and species occurrence records ^{2,3} .
34	•	paninvasion—invasion of a species at the global scale that disturbs a global economic
35		market.
36	•	paninvasion risk—the likelihood of a regional invasive species to become a globally
37		invasive species and cause economic repercussions.
38	•	paninvasive species—globally invasive species that goes through the three main
39		invasion stages and thus can disturb global economic markets.
40	•	phylloxera—Daktulosphaira vitifoliae is grapevine root pest native to North America
41		that was responsible for the Great Wine Blight of the late 1800's, which was the largest
42		economic disturbance to the global wine market ever recorded. The disruption was
43		mitigated by widespread planting of European vines that were grafted to North American
44		grapevine root stocks. The paninvasion of phylloxera continues to this day ^{4,5} .
45	•	species distribution model (SDM)—spatial model used to predict the environmental
46		niche, habitat suitability, and establishment potential of a species.
47	•	spotted lanternfly (SLF)—Lycorma delicatula is a planthopper native to China,
48		Vietnam, and India. It invaded South Korea and Japan in the early 2000's and the

49 northeastern US ca. 2014. It is known to feed on >100 different host species, including grapes^{6,7}. 50 51 transport potential—likelihood of a region to have an introduction of a non-native • 52 species. 53 tree of heaven (TOH)—Ailanthus altissima is a paninvasive deciduous tree that is native • 54 to China, Taiwan, and northern Korea, but has been spread globally. It is a highly 55 preferred host for SLF and may determine SLF establishment potential. 56 57 Supplementary methods: Confirmation of relationship between import tonnage and SLF invasion 58 status for transport potential 59 The prevailing hypothesis on SLF transport potential is that regions that import more 60 tonnage of commodities from the invaded US region also import more total tonnage of goods and trade infrastructure (e.g., cargo containers, pallets, railcars) that inadvertently transport SLF 61 egg masses long-distances $^{6,8-12}$. To test this hypothesis, we fit two logistic regressions with our 62 63 metric of transport potential as the covariate. This metric was the \log_{10} of the average annual 64 metric total tonnage imported between 2012 and 2017 from US states invaded by SLF (main text 65 Fig. 3). We regressed the presence/absence of established populations and regulatory incidents 66 (i.e., has a state experienced and reported any observations of SLF, dead, moribund, or alive, 67 independent of the presence of established populations?). For both establishment and regulatory 68 incidents, the relationship between SLF-status and our measure of transport potential was 69 significant, thereby providing support for our estimate of SLF transport potential (Supplemental 70 Table 1). These results suggest that total tonnage of imports is a suitable proxy for transport 71 potential until new metrics are developed that include refined pathway analyses. 72 73 Supplementary methods: Modeling establishment potential and the influence of chilling periods 74 for diapause 75 We estimated establishment potential as an ensemble from three global species 76 distribution models (SDMs): a multivariate SDM of TOH (sdm_toh), a multivariate SDM of SLF 77 (sdm_slf1), and a univariate SDM of SLF that modeled SLF presence on the predicted values 78 from sdm_toh (sdm_slf2). Models were constructed with MaxEnt ver. 3.4.1 by following best practices for estimating unbiased niche models^{3,13,14}. We first queried GBIF for TOH and SLF 79

presences on October 20, 2020. For TOH, 67,100 records were obtained and for SLF 3,180 records were obtained¹⁵. Records were checked for errors, duplicate records removed, and the remaining records were rarefied (spatially filtered) by omitting records <10 km from each other to reduce bias from spatial autocorrelation^{16,17}. The result was 8,578 unique, error checked TOH presence records and 325 unique, error checked SLF presence records. Thus, *sdm_toh* was built on 8,578 TOH global presence records, and *sdm_slf1* and *sdm_slf2* were built on 325 SLF presence records (see our research compendium for the data, https://github.com/ieco-lab/slfrsk).

87 To find the best models that explained TOH and SLF presences, we started with 22 88 potential covariates hypothesized to influence SLF and TOH global distributions. The covariates 89 included 20 topographic and bioclimatic variables from WorldClim, which is a standard database 90 of covariates used in global SDMs^{18,19}. WorldClim has also been used in two previous SDMs for SLF^{20,21}. In addition to these 20 covariates, we added Global Forest Canopy Height²² because 91 SLF feeds on multiple tree species²³, and Global Access to Cities²⁴ because TOH and SLF are 92 often established along transportation networks⁹. We analyzed these covariates to identify an 93 94 uncorrelated subset to include in final best-fit SDMs with low model collinearity. To do this, we 95 calculated pairwise Pearson correlations among the 22 covariates, and fit each covariate to SLF 96 and TOH in univariate SDMs (i.e., 44 models in total). We then compared covariates that were 97 highly correlated and retained only the covariates that fit best to the TOH and SLF presences. 98 This reduction of potential covariates resulted six minimally correlated covariates (pairwise 99 absolute Pearson correlations <0.70) that we fit in our models: annual mean temperature 100 (BIO01), mean diurnal temperature range (BIO02), annual precipitation (BIO12), precipitation 101 seasonality (BIO15), elevation (ELEV), and access to cities (ATC).

102 We fit *sdm toh* and *sdm slf1* with these six covariates; *sdm slf2* was fit from the 103 *sdm_toh* predicted values. The three models were fit under default settings of the MaxEnt 104 program except for the following changes: (1) all features were enabled but still set to "Auto 105 Features", (2) response curves were created, (3) variable importance was measured via 106 jackknifing (we did not do this for *sdm slf2* because it was a univariate model), (4) the threshold 107 rule was set to "Minimum Training Presence", and (5) the number of replicates was set to five 108 for SLF and ten for TOH. This last modification sets the number of k-fold cross-validation 109 replicates and determines the test proportion from k, thus we validated the three models with k-110 fold cross-validation via evaluation of the receiver operating characteristic of the AUC (area

under the curve) and omission $\operatorname{error}^{2,25-27}$. For AUC, the fraction of true positives relative to type 111 112 I error (positive background points) is compared at all possible thresholds for each model^{2,25}. The 113 resultant AUCs were assessed relative to a random model where AUC = 0.50, such that values 114 close to 1.00 indicate strong model performance and those ≤ 0.50 suggest poor performance²⁵. 115 Given presence only data, measured AUC cannot reach 1.00, but model AUCs that approach 1.00 are considered to perform well^{2,28}. Given concerns with model evaluation with AUC²⁹⁻³¹. 116 117 we also confirmed model performance with average omission error, which is the proportion of presence point(s) predicted with suitability less than the threshold averaged across replicates^{26,27}. 118

119 All three models performed well according to AUC and omission error. Models yielded 120 test AUC values >0.75 while boasting average test omission error rates <0.01, indicating that 121 each model performed better than random and identified areas of known species presence as 122 suitable for the cross-validation partitions. sdm_toh had a slightly lower AUC (0.7779) and 123 omission error (0.0003) than sdm slf1 (AUC = 0.9828, omission = 0.0064) and sdm slf2 (AUC 124 = 0.9675, omission = 0.0032). For both multivariate SDMs, we compared the variable 125 contributions for congruence. The top four contributing variables were the same for both models 126 (ATC, BIO01, BIO12, and BIO15 in descending order). The remaining two variables (ELEV and 127 BIO02) contributed <2% in each model, with ELEV contributing more in *sdm_toh* and BIO02 128 contributing more in *sdm slf1*. For *sdm toh*, two other variables, BIO12 and BIO15 also 129 contributed <2% each but still contributed more than ELEV and BIO02 (for a more detailed 130 comparison, see our research compendium, https://ieco-lab.github.io/slfrsk/).

131 We averaged our three best-fit models to produce one ensemble image at the 30 arcsecond resolution, and intersected this image with state and country polygons¹³. We then 132 133 calculated summary statistics for the ensemble pixels within each state and country (mean, 134 median, and maximum). The R function we wrote to perform this task, extract_enm2(), is 135 available with the R companion package, slfrsk (see https://github.com/ieco-lab/slfrsk). 136 Establishment potential for the 50 US states and 223 countries was estimated as the maximum 137 pixel value for each state and country. Results and conclusions with mean and median pixel 138 values instead of max were qualitatively similar (see https://ieco-lab.github.io/slfrsk/). 139 Although our work suggests widespread establishment potential, SDM-based 140 establishment potential might overestimate suitability in warmer climates if SLF require a

141 chilling period to initiate diapause to complete development³². However, recent work suggests

that while SLF can diapause as eggs in the invaded US region, native populations across China
include sub-tropical regions that do not provide the colder temperatures necessary for completing
diapause³³, and SLF in the US do not require diapause to develop³⁴. Indeed, under lab conditions,
eggs in the US that do not undergo diapause exhibit higher survivorship than those that do
undergo diapause³⁵. This observation suggests that our global ensemble model does not
overestimate SLF establishment potential and instead may be a conservative estimate, especially
for warmer regions (main text Fig. 4).

149 In summary, our estimate of SLF global establishment potential was based on an 150 ensemble of models for SLF and TOH environmental suitabilities. Two previous estimates of 151 SLF global establishment potential have been published but did not include TOH, were not 152 ensemble estimates, and were not built on as many presence records^{20,21}. These other estimates also did not include an anthropogenic covariate like Global Access to Cities²⁴, which we found to 153 154 be important in determining TOH and SLF environmental suitability. Finally, although our 155 estimate of SLF establishment potential is broadly like these previous estimates (as observed by 156 comparing our map to theirs), it differs in three key ways: we provide our estimate in a finer 157 resolution, our estimate differs across globally important viticultural regions, and we provide the 158 data as open access. To visualize and download our estimate please see our Google Earth Engine 159 app (https://ieco.users.earthengine.app/view/ieco-slf-riskmap).

160 Supplementary Table 1 Logistic regression of spotted lanternfly (SLF) status on trade with

161 established US states as average annual metric total tonnage demonstrates a significant

- 162 relationship for all US states and Washington DC. Trade with established states predicts both
- 163 presence or absence of established SLF populations and record of SLF regulatory incidents
- 164 (identification of SLF, deceased, moribund, or alive). Logistic regression model coefficients are
- 165 shown above with standard error below in parentheses.

	Establishment Status	Regulatory Status
Log ₁₀ (average annual metric tonnage)	5.64***	3.10***
	(2.03)	(0.90)
Constant	-42.74***	-22.64***
	(15.27)	(6.49)
Observations	51	51
Log likelihood	-9.80	-18.15
Akaike information criterion	23.61	40.30
Notes:	**** <i>P</i> < .01	

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167 Supplemental References

- 168 1. Blackburn, T. M. *et al.* A proposed unified framework for biological invasions. *Trends Ecol.*
- 169 *Evol.* **26**, 333–339 (2011).
- 170 2. Phillips, S. J., Anderson, R. P. & Schapire, R. E. Maximum entropy modeling of species
- 171 geographic distributions. *Ecol. Model.* **190**, 231–259 (2006).
- 172 3. Phillips Steven J., Anderson Robert P., Dudík Miroslav, Schapire Robert E., & Blair Mary E.
- 173 Opening the black box: An open-source release of Maxent. *Ecography* **40**, 887–893 (2017).
- 174 4. Gale, G. *Dying on the vine*. (University of California Press, 2011).
- 175 5. Ordish, G. *The great wine blight*. (Charles Scribner's Sons, 1972).
- 176 6. Urban, J. M. Perspective: Shedding light on spotted lanternfly impacts in the USA. *Pest*177 *Manag. Sci.* 76, 10–17 (2019).
- 178 7. Barringer, L. & Ciafré, C. M. Worldwide feeding host plants of spotted lanternfly, with
- 179 significant additions from North America. *Environ. Entomol.* **49**, 999–1011 (2020).
- 180 8. Liu, H. Oviposition substrate selection, egg mass characteristics, host preference, and life
- 181 history of the spotted lanternfly (Hemiptera: Fulgoridae) in North America. *Environ*.
- 182 *Entomol.* **48**, 1452–1468 (2019).
- 9. Parra, G., Moylett, H. & Bulluck, R. USDA-APHIS-PPQ-CPHST Technical working group
 summary report spotted lanternfly, *Lycorma delicatula* (White, 1845). (2018).
- 185 10. Lee, D.-H., Park, Y.-L. & Leskey, T. C. A review of biology and management of Lycorma
- 186 *delicatula* (Hemiptera: Fulgoridae), an emerging global invasive species. J. Asia-Pac.
- 187 *Entomol.* **22**, 589–596 (2019).

- 188 11. Liu, H. Seasonal development, cumulative growing degree-days, and population density of
- 189 spotted lanternfly (Hemiptera: Fulgoridae) on selected hosts and substrates. *Environ*.
- 190 *Entomol.* **49**, 1171–1184 (2020).
- 191 12. Park, M., Kim, K.-S. & Lee, J.-H. Genetic structure of Lycorma delicatula (Hemiptera:
- 192 Fulgoridae) populations in Korea: Implication for invasion processes in heterogeneous
- 193 landscapes. *Bull. Entomol. Res.* **103**, 414–424 (2013).
- 13. Araújo, M. B. & New, M. Ensemble forecasting of species distributions. *Trends Ecol. Evol.*22, 42–47 (2007).
- 14. Araújo, M. B. *et al.* Standards for distribution models in biodiversity assessments. *Sci. Adv.*5, eaat4858 (2019).
- 198 15. GBIF. GBIF: The global biodiversity information facility. https://www.gbif.org/ (2019).
- 199 16. Zhu, G., Illan, J. G., Looney, C. & Crowder, D. W. Assessing the ecological niche and
- invasion potential of the Asian giant hornet. *Proc. Natl. Acad. Sci.* 117, 24646–24648
 (2020).
- 202 17. Boria, R. A., Olson, L. E., Goodman, S. M. & Anderson, R. P. Spatial filtering to reduce
- sampling bias can improve the performance of ecological niche models. *Ecol. Model.* 275,
 73–77 (2014).
- 18. Fick, S. E. & Hijmans, R. J. WorldClim 2: New 1-km spatial resolution climate surfaces for
 global land areas. *Int. J. Climatol.* 37, 4302–4315 (2017).
- 207 19. Hijmans, R. J., Cameron, S. E., Parra, J. L., Jones, P. G. & Jarvis, A. Very high resolution
- interpolated climate surfaces for global land areas. *Int. J. Climatol.* **25**, 1965–1978 (2005).

- 209 20. Jung, J.-M., Jung, S., Byeon, D. & Lee, W.-H. Model-based prediction of potential
- 210 distribution of the invasive insect pest, spotted lanternfly *Lycorma delicatula* (Hemiptera:
- 211 Fulgoridae), by using CLIMEX. J. Asia-Pac. Biodivers. 10, 532–538 (2017).
- 212 21. Wakie, T. T., Neven, L. G., Yee, W. L. & Lu, Z. The establishment risk of Lycorma
- 213 *delicatula* (Hemiptera: Fulgoridae) in the United States and globally. J. Econ. Entomol. 113,
 214 306–314 (2020).
- 215 22. Simard, M., Pinto, N., Fisher, J. B. & Baccini, A. Mapping forest canopy height globally
 216 with spaceborne lidar. *J. Geophys. Res. Biogeosciences* 116, (2011).
- 217 23. Barringer, L. E., Donovall, L. R., Spichiger, S.-E., Lynch, D. & Henry, D. The first New
- World record of *Lycorma delicatula* (Insecta: Hemiptera: Fulgoridae). *Entomol. News* 125,
 20–23 (2015).
- 24. Weiss, D. J. *et al.* A global map of travel time to cities to assess inequalities in accessibility
 in 2015. *Nature* 553, 333–336 (2018).
- 222 25. Fielding, A. H. & Bell, J. F. A review of methods for the assessment of prediction errors in
- 223 conservation presence/absence models. *Environ. Conserv.* **24**, 38–49 (1997).
- 224 26. Pearson, R. G., Raxworthy, C. J., Nakamura, M. & Peterson, A. T. Predicting species
- distributions from small numbers of occurrence records: A test case using cryptic geckos in
- 226 Madagascar. J. Biogeogr. **34**, 102–117 (2007).
- 227 27. Anderson, R. P. & Gonzalez, I. Species-specific tuning increases robustness to sampling bias
- in models of species distributions: An implementation with Maxent. *Ecol. Model.* 222, 2796–
 2811 (2011).

230	28.	Wiley, E. O., McNyset, K. M., Peterson, A. T., Robins, C. R. & Stewart, A. M. Niche
231		modeling and geographic range predictions in the marine environment using a machine-
232		learning algorithm. 16, 8 (2003).
233	29.	Peterson, A. T., Papeş, M. & Soberón, J. Rethinking receiver operating characteristic
234		analysis applications in ecological niche modeling. Ecol. Model. 213, 63–72 (2008).
235	30.	Lobo, J. M., Jiménez-Valverde, A. & Real, R. AUC: A misleading measure of the
236		performance of predictive distribution models. Glob. Ecol. Biogeogr. 17, 145–151 (2008).
237	31.	Jiménez-Valverde, A. Insights into the area under the receiver operating characteristic curve
238		(AUC) as a discrimination measure in species distribution modelling. <i>Glob. Ecol. Biogeogr.</i>
239		21 , 498–507 (2012).
240	32.	Shim, JK. & Lee, KY. Molecular characterization of heat shock protein 70 cognate cDNA
241		and its upregulation after diapause termination in Lycorma delicatula eggs. J. Asia-Pac.
242		Entomol. 18, 709–714 (2015).
243	33.	Du, Z. et al. Global phylogeography and invasion history of the spotted lanternfly revealed
244		by mitochondrial phylogenomics. Evol. Appl. (2021) doi:https://doi.org/10.1111/eva.13170.
245	34.	Xin, B. et al. Exploratory survey of spotted lanternfly (Hemiptera: Fulgoridae) and its natural
246		enemies in China. Environ. Entomol. 50, 36–45 (2020).
247	35.	Keena, M. A. & Nielsen, A. L. Comparison of the hatch of newly laid Lycorma delicatula
248		(Hemiptera: Fulgoridae) eggs from the United States after exposure to different temperatures
249		and durations of low temperature. Environ. Entomol. 1-8 (2021) doi:10.1093/ee/nvaa177.
250		