Climate and host plant availability are favorable to the establishment of Lycorma delicatula in Europe

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1 **Climate and host plant availability are favorable to the establishment of *Lycorma delicatula* in**
2 **Europe**

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10 ABSTRACT

11   1. *Lycorma delicatula*, the spotted lanternfly, is a highly successful invasive phloem-feeding
12   planthopper native to southern China. It has invaded South Korea, Japan, and the USA,
13   where it is still geographically expanding but is absent from Europe. We examined two
14   important ecological factors affecting the risk of establishment: climate suitability and the
15   availability of compatible host plants.
16   2. We developed an ensemble species distribution model based on three algorithms to assess
17   the potential geographical range of *L. delicatula* according to current and future climate
18   conditions. We reviewed the literature to assess the host repertoire of *L. delicatula* and list
19   host species present in Europe.
20   3. Current climate conditions appeared to be highly suitable for *L. delicatula* in much of Europe.
21   Climate change will marginally alter climate suitability by 2060. Numerous known host plants
22   are widely distributed in Europe.
23   4. We conclude that neither climate conditions nor the presence of compatible host plants
24   constitutes an obstacle to the establishment of *L. delicatula* in Europe. Both current and
25   future climate suitability and the list of potential hosts could be helpful to guide surveillance
26   and improve the preparedness of phytosanitary authorities.

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INTRODUCTION

Once established, eradicating invasive species is very difficult; thus, it is always best to avoid their establishment (Leung et al. 2002). Moreover, in the event of an incursion, the time between the arrival of the invasive organism and the start of the eradication campaign is crucial in determining the success of management measures (Hulme 2006). Monitoring is paramount here because it allows for the early detection of invasive species and reduces the time needed to implement management measures (Pluess et al. 2012). In this context, risk analysis is a vital element of pre-border actions as it helps direct surveillance, particularly by identifying *a priori* the most threatened geographical areas or entry routes for exotic species (Probert et al. 2020; Reaser et al. 2020). The first step in risk assessment involves distinguishing invasive from non-invasive alien species (Roy et al. 2019). Once a target species is identified, it becomes feasible to evaluate environmentally suitable areas where the potential economic or ecological impacts of invasion are significant. These regions could be the focus of regional monitoring efforts, where targeted public information campaigns can greatly enhance biological invasion management (Faulkner et al. 2020).

Climate plays a crucial role in shaping the distribution, survival, and reproduction of invasive species (Battisti et al. 2015). Environmental suitability also depends on biotic factors such as competition, predation, parasitism, and the availability of trophic resources, which are pivotal in the dynamics of biological invasions (Daly et al. 2023). For plant-feeding species, successful establishment often hinges on the presence of their preferred host plants or closely related species (Bacon et al. 2014; Bonnamour et al. 2023). While certain species may evolve rapidly to adapt to new environmental conditions or hosts (Pearman et al. 2008), the vulnerability of an ecosystem to a specific plant-feeding species largely depends on its fundamental host repertoire i.e. all compatible hosts of the species (Braga and Janz 2021). Therefore, assessing climate suitability, understanding the impact of global changes, and determining host range are central to pest risk analysis (Devorshak 2012).

Lycorma delicatula (White, 1845), the spotted lanternfly, is a phloem-feeding planthopper native to China. This species is highly polyphagous (Barringer and Ciafré 2020) and its dispersion is often passive, closely linked to human activities through human-mediated transport (Ladin et al. 2023; Montgomery et al. 2023). *L. delicatula* invaded South Korea in 2004, Japan in 2006, and finally Pennsylvania in the United States in 2014 (Barringer et al. 2015), from where it has significantly spread to adjacent states (Urban and Leach 2023). Local outbreaks of *L. delicatula* cause severe damage to a wide range of host plants, from herbaceous species (primarily as nymphs) to ornamental, woody, and fruit trees (Lee et al. 2019; Urban et al. 2021; Urban and Leach 2023). As of today, *L. delicatula* is not present in Europe. Host selection is highly dependent on available plants, but *L. delicatula* exhibits higher fitness when developing on the tree of heaven, *Ailanthus altissima* (Mill.) Swingle, 1916 (Uyi et al. 2021). *A. altissima* is present in Europe along with economically important host plant species such as grapes, fruit trees, woody trees, and ornamental trees, making *L. delicatula* a serious threat to European agriculture (Huron et al. 2022).

Several studies have assessed the potential distribution of *L. delicatula*, but they rely on different algorithms and offer contrasting results. Jung et al. (2017) reported low climate suitability in Europe using the "CLIMEX" model ("Compare Locations" option). In contrast, Wakie et al. (2020) and Huron et al. (2022) found high climate suitability in Europe using the Maxent algorithm. Namgung et al. (2020) also used the Maxent algorithm but focused their survey on South Korea. Given the conflicting results regarding Europe's climate suitability and the availability of more occurrence data since these studies were conducted, we aimed to develop a new model to assess the establishment potential of *L. delicatula* under current and future climate conditions. To achieve this, we used three different algorithms to minimize the uncertainty associated with the choice of modeling method. We also projected these models using a set of climate change scenarios, which, to our knowledge, has never

76 been done for *L. delicatula*. Although we focus here on the climate suitability of the European
77 continent, we provide worldwide assessments in the supplementary material. Our second objective
78 was to list the known host plant species of *L. delicatula* to evaluate how many host species are
79 present in Europe and in which countries. Combining climate suitability with host plant presence
80 allowed us to assess the establishment potential of *L. delicatula* in Europe.

81 METHODS

82 All statistical analyses and data management were performed using the R environment for statistical
83 computing and visualization (R Core Team 2023).

84 **Species Distribution Model**

85 *Data collection and compilation*

86 We collected occurrences of *L. delicatula* from the international database GBIF (Global Biodiversity
87 Information Facility; dataset doi: https://doi.org/10.15468/dl.tfatn5; extracted the 08/02/2023), and
88 from a literature review using the valid name *Lycorma delicatula* and its synonym *Aphaena*
89 *delicatula*. Additionally, we included records from established populations in the United States,
90 retrieved from the R package "LydemapR" (De Bona et al. 2023). "LydemapR" contains
91 spatiotemporal data and mapping functions to visualize the current spread of *L. delicatula*. We
92 compiled old publications to collect occurrences in the native range (published between 1906 and
93 2000) and recent publications tracking the progression of the invasion in the United States, Japan,
94 and South Korea (see reference list in Appendix 1 and Appendix 2). When longitude-latitude
95 coordinates were not available but the name of the observation site was provided, we assigned the
96 coordinates of the locality's centroid using Google Maps. Occurrences retrieved from the literature
97 without precise location information (only state or country mentioned) were discarded. The GBIF
98 data were examined to exclude occurrences due to questionable identification (unknown basis of
99 record) and missing geographic coordinates, as we considered these occurrences invalid.

100 *Pre-processing and data preparation*

101 At the time of the analyses (February 2023), a total of 15,211 occurrences of *L. delicatula* were
102 retrieved from GBIF, 406 from the literature, and 1,970 from the R package "LydemapR". Among the
103 GBIF occurrences, 210 were discarded due to missing coordinates. From the literature occurrences
104 (Appendix 2), 44 were excluded due to imprecise location data. Most of these imprecise occurrences
105 pertained to the historical distribution of *L. delicatula* in its native range, where locations were often
106 described only at the regional or provincial level. Finally, 17,333 occurrences were deemed valid and
107 retained for further analyses. These 17,333 records included 121 occurrences with missing dates,
108 which were excluded because it was impossible to associate them with the climate data
109 corresponding to the period of observation.

110 One record predating 2001 was removed to ensure that all remaining data could be analyzed using
111 the most recent climate data from the WorldClim database (see below). The spatial distribution of
112 the remaining 17,211 records was compared with the resolution of the climate raster data used in
113 the study (2.5 minutes, see below) to retain only one point per raster grid cell, thereby preventing
114 over-representation of certain climate conditions (Elith et al. 2006). This process resulted in a total of
115 3,416 valid occurrence records. One record from India was discarded because the presence of viable
116 populations in this country remains uncertain (Dara et al. 2015). The remaining 3,415 records are
117 distributed across four countries as follows: China 295; South Korea 407; Japan 28; and USA 2,685.

118   We applied a geographical filtering procedure to the dataset to control for sampling bias (Aiello-
119   Lammens et al. 2015). The distance threshold was arbitrarily set to 20 km, and computations were
120   conducted using the R package "spThin" (Aiello-Lammens et al. 2015). The remaining records were
121   distributed as follows: China 163; South Korea 114; Japan 8; and USA 275. Additionally, we
122   performed environmental thinning following Varela et al. (2014), utilizing the original variables rather
123   than outputs from a Principal Components Analysis (Velazco et al. 2022), as in Varela et al. (2014).
124   We employed the function "occfilt_env" from the R package "flexsdm" (Velazco et al. 2022) and a set
125   of eight bioclimatic variables available from the WorldClim database, representing average
126   temperature and precipitation across the study area from 2001 to 2018 (see below): bio8 (mean
127   temperature of the wettest quarter), bio9 (mean temperature of the driest quarter), bio10 (mean
128   temperature of the warmest quarter), bio11 (mean temperature of the coldest quarter), bio16
129   (precipitation of the wettest quarter), bio17 (precipitation of the driest quarter), bio18 (precipitation
130   of the warmest quarter), and bio19 (precipitation of the coldest quarter). This resulted in 362
131   remaining occurrence records distributed as follows: China 136; South Korea 80; Japan 8; and USA
132   138.

133   *Climate datasets*

134   The occurrence dataset used in this study is from 2001 onwards, and we utilized historical monthly
135   weather data spanning from 2001 to 2018 (https://www.WorldClim.org, Fick and Hijmans 2017) to
136   calibrate the models. Average climate descriptors for the period 2001–2018 (referred to as
137   bioclimatic variables) were computed using the function "biovars" from the R package "dismo"
138   (Hijmans et al. 2023). The resolution of the raster climate data is 2.5 minutes (≈22 km² at the
139   equator). We projected the species distribution models for the period 2041–2060 using future
140   climate data also available from WorldClim. For this purpose, we considered six Global Circulation
141   Models (GCMs): BCC-CSM2-MR (Wu et al. 2019), CNRM-CM6-1 (Voldoire et al. 2019), CNRM-ESM2-1
142   (Séférian et al. 2019), CanESM5 (Swart et al. 2019), MIROC-ES2L (Hajima et al. 2020), and MIROC6
143   (Tatebe et al. 2019). Shared Socioeconomic Pathways (SSPs) describe plausible greenhouse gas
144   emissions scenarios based on different climate policies (Riahi et al. 2017; Meinshausen et al. 2020).
145   For each period and GCM, climate suitability was modeled using simulated climate data across four
146   Shared Socioeconomic Pathways (SSPs): SSP5-8.5, SSP3-7.0, SSP2-4.5, and SSP1-2.6, representing
147   high-end, medium-to-high-end, medium, and low-end greenhouse gas forcing pathways, respectively
148   (Abram et al. 2019).

149   Our models were built using a set of 14 bioclimatic descriptors available from the WorldClim
150   database (2001-2018), which encompass both temperature and precipitation-related environmental
151   constraints: bio1 (annual mean temperature), bio5 (maximum temperature of the warmest month),
152   bio6 (minimum temperature of the coldest month), bio8 (mean temperature of the wettest quarter),
153   bio9 (mean temperature of the driest quarter), bio10 (mean temperature of the warmest quarter),
154   bio11 (mean temperature of the coldest quarter), bio12 (annual precipitation), bio13 (precipitation
155   of the wettest month), bio14 (precipitation of the driest month), bio16 (precipitation of the wettest
156   quarter), bio17 (precipitation of the driest quarter), bio18 (precipitation of the warmest quarter),
157   bio19 (precipitation of the coldest quarter) (Fick and Hijmans 2017).

158   *Pre-processing and data preparation*

159   One crucial aspect of species distribution modeling is the selection of predictors used in the model,
160   which not only affects model performance but also its transferability (Petitpierre et al. 2017),
161   particularly important when projecting processing, FOP analysis enabled us to discard variables
162   displaying noisy or bimodal curves, retaining only predictor variables that yield ecologically realistic
163   and meaningful response curves (Guevara et al. 2018; Vollering et al. 2019). FOPs were computed

164 using the R package "MIAmaxent" (Vollering et al. 2019). This process led to the exclusion of the
165 variables bio8, bio14, bio15, bio17, bio18, and bio19, while retaining bio1, bio5, bio6, bio9, bio10,
166 bio11, bio12, bio13, and bio16 for model calibration. These variables describe different aspects of
167 climate and their biological significance may vary for the species under study. Although no variables
168 were objectively ruled out *a priori*, stepwise selection procedures implemented during model
169 calibration ensured retention of those significantly contributing to the model (see below).

170 *Model algorithms*

171 We employed three distinct algorithms for species distribution modeling: 1) Random Forests (RF), 2)
172 Boosted Regression Trees (BRT), and 3) Bayesian Additive Regression Trees (BART). RF and BRT are
173 widely utilized in species distribution modeling (Guisan et al., 2017), whereas BART was introduced
174 more recently in ecology (Carlson, 2020). RF is a machine learning algorithm that combines outputs
175 from multiple decision trees through bagging (Breiman, 2001; Guisan et al., 2017). We calibrated the
176 model using the R package "randomForest" (Liaw and Wiener, 2002). Climate descriptors were
177 selected via stepwise selection based on averaged variable importance (Li et al., 2016), implemented
178 using the R package "steprf" (Li, 2022). Tuning of node size and the number of explanatory variables
179 sampled at each split was achieved using the R package "randomForestSRC" (Ishwaran and Kogalur,
180 2007). We used a large (1000) but computationally feasible number of trees (Probst and Boulesteix,
181 2018).

182 BRT follows the same principle as RF by combining different decision trees, but it diverges in its
183 sequential approach using a forward stagewise procedure. Elith et al. (2008) provided a practical
184 guide to BRT for modeling species distribution. We calibrated our BRT model using the R package
185 "dismo" (Hijmans et al., 2023). The model hyperparameters were set as follows: the tree complexity
186 parameter was fixed at 5 to allow interactions between variables, the learning rate was set to 0.005,
187 and the bag fraction (proportion of data selected at each step) was fixed at 0.5. We used the
188 "gbm.simplify" function from the R package "dismo" to identify explanatory variables that could be
189 removed for simplification. Additionally, we employed the "gbm.step" function to determine the
190 optimal number of trees.

191 Similar to the previous methods, BART estimates the probability of presence or absence using a
192 series of decision trees. It is characterized as a nonparametric Bayesian regression approach that
193 incorporates priors on tree structure, resulting in a posterior distribution of estimated classification
194 probabilities (Chipman et al., 2010). BART has recently been introduced in species distribution
195 modeling (Carlson, 2020) and has shown considerable promise (Baquero et al., 2021; Strubbe et al.,
196 2023; Rossi et al., 2024). For our analysis, we utilized the R package "embarcadero" (Carlson, 2020)
197 and employed the variable selection procedure implemented in the function "bart.step" to identify
198 the variables that significantly contributed to the model (details provided in Carlson, 2020). The
199 model was run using 1000 trees.

200 Across all algorithms, we employed a number of pseudo-absences equal to our occurrence records
201 (362) (Barbet-Massin et al., 2012), sampled from the initial 1000 points generated during the earlier
202 stages of analysis (as described above).

203 We used the 14 climate descriptors previously mentioned (bio1, bio5, bio6, bio8, bio9, bio10, bio11,
204 bio12, bio13, bio14, bio16, bio17, bio18, bio19) in our analysis. For each modeling approach—
205 random forest (RF), boosted regression trees (BRT), and Bayesian additive regression trees (BART)—
206 we utilized specific variable selection procedures to identify optimal subsets of these descriptors.
207 Specifically, we used the "steprf" function for random forest, "gbm.step" for boosted regression
208 trees, and "bart.step" for Bayesian additive regression trees. Each procedure determined a subset of

209 variables that maximized model performance, which was then used to calibrate the respective
210 model.

Pseudo-absences

212 True absence data *i.e.* localities where a species is absent because of unsuitable environmental
213 conditions are often lacking particularly in the case of invasive organisms such as *L. delicatula*.
214 Therefore, we employed pseudo-absences for model calibration (Lobo et al., 2010). Defining the
215 geographical area for generating pseudo-absences is a critical step in species distribution modeling
216 (Barbet-Massin et al., 2012). The native range of *L. delicatula* is well-known and we assumed absence
217 in the northern and southern regions beyond its current range in China. Pseudo-absences were not
218 generated to the east of its native range, as the species is currently expanding into this area,
219 including Japan and Korea. To the west, the Tibetan Plateau acts as a natural barrier, limiting the
220 species' dispersal and thereby complicating the sampling of pseudo-absences (the species may be
221 absent from areas west of the Tibetan Plateau because this geographic feature is a dispersal barrier).
222 The geographical area where pseudo-absences were sampled was thus defined as a surface
223 extending 25 decimal degrees north and south of all documented species observations within its
224 native range (see Appendix 3 for details). In North America, no pseudo-absences were generated for
225 *L. delicatula* due to its ongoing expansion on the continent.

226 We generated a total of 1000 pseudo-absences using the function "sample_pseudoabs" from the R
227 package "flexsdm" (Velazco et al., 2022). The allocation of these pseudo-absences was constrained
228 by environmental suitability as determined by the bioclim model (Booth et al., 2014), focusing on
229 four specific bioclimatic variables (bio5, bio6, bio13, and bio14) identified as climate limiting factors
230 (Velazco et al., 2022). The probability of allocating a pseudo-absence point was higher in regions
231 exhibiting lower climate suitability according to the results of the bioclim model.

Model performance

233 We evaluated the performance of our models using two metrics: the Area Under the Curve (AUC) of
234 the receiver operating characteristic (ROC) plot (Fielding and Bell 1997), and the true skill statistic
235 (TSS) (Allouche et al. 2006). These evaluations were conducted using a set of 3053 valid occurrences
236 that were withheld from the raw dataset during thinning (geographical and environmental). An equal
237 number of pseudo-absence points were generated, as described earlier, for model evaluation
238 purposes. This approach allowed us to assess the models using independent data that were not used
239 in their calibration process. The calculations of AUC and TSS were implemented using the R package
240 "dismo" (Hijmans et al., 2023.

Estimation of climate suitability

242 We assessed the climate suitability under current and future climate scenarios using the R function
243 "predict". Future climate projections were computed for the period 2041-2060 based on various
244 General Circulation Models (GCMs) and Shared Socioeconomic Pathways (SSPs), as described
245 previously.

246 To synthesize the outputs from our three models (RF, BRT, and BART), we employed a consensus
247 approach known as committee averaging (Guisan et al., 2017, Araújo and New, 2007). This method
248 involves two main steps: 1) transforming model outputs into binary (presence/absence) values using
249 a threshold and 2) averaging the binary projections from RF, BRT, and BART to compute the
250 committee averaging score. This score ranges from 0 (indicating all models predict absence) to 100
251 (indicating all models predict presence), providing an intuitive assessment of the likelihood of species

252   presence We used the threshold that optimized the TSS statistics computed with the function
253   "threshold" from the R package "dismo".

254   For future climate projections (2041-2060) under each SSP, the committee averaging process
255   described above was repeated using projections of all considered GCMs (6 in total). This resulted in
256   18 projections (3 models x 6 GCMs) per SSP.

257   *Model extrapolation*

258   To address potential issues of model extrapolation when projecting under non-analogous
259   environmental conditions, we employed the multivariate environmental similarity surface (MESS)
260   index, as introduced by Elith et al. (2010). This index quantifies how similar a point is to the training
261   dataset based on a specified set of reference explanatory variables. A negative MESS value indicates
262   that at least one of these explanatory variables falls outside the range of the reference dataset,
263   suggesting potential extrapolation. We computed the MESS index for the climate descriptors used to
264   calibrate the models (current climate conditions, 2001-2018) and for the different climate change
265   scenarios. For each SSP, the minimum value of the MESS index computed for the 6 GCM was
266   retained. Computations were done using the function "mess" from the package "dismo".

267   ***Lycorma delicatula* host plant dataset**

268   In our assessment of the risk of *L. delicatula* establishment in Europe, the presence of compatible
269   host plants plays a crucial role. We compiled a comprehensive list of host plants based on various
270   sources including reviews, research articles, theses, and pest risk analysis reports (refer to
271   Appendices 4 and 5). To differentiate host plants, we categorized them based on whether feeding
272   events were observed or if *L. delicatula* was merely observed resting or egg-laying. Our analysis
273   focused on reports where explicit feeding or damage by *L. delicatula* was documented. For
274   taxonomic classification, we updated the plant names according to the Plant of the World Online
275   (POWO) classification system (https://powo.science.kew.org). We examined the origin of each
276   feeding host plant and its distribution in native and invaded areas, as well as its status (introduced,
277   native, or cultivated) in Europe.

278   The geographical distribution (presence or absence) and status of each feeding host plant in
279   European countries were compiled from several authoritative databases: 1) Plant of the World
280   Online (POWO) and GRIN (Germplasm Resources Information Network) for native and invaded areas
281   worldwide (https://npgsweb.ars-grin.gov/gringlobal/taxon/taxonomysearch) 2) Euro+Med PlantBase
282   for European countries (https://www.emplantbase.org/home.html).

283   We defined Europe according to administrative boundaries and included the following countries:
284   Albania, Andorra, Austria, Belarus, Belgium, Bosnia and Herzegovina, Bulgaria, Croatia, Cyprus, Czech
285   Republic, Denmark, Estonia, Finland, France, Germany, Greece, Hungary, Iceland, Ireland, Italy,
286   Kosovo, Latvia, Liechtenstein, Lithuania, Luxembourg, Macedonia, Malta, Moldova, Monaco,
287   Montenegro, Netherlands, Norway, Poland, Portugal, Romania, San Marino, Serbia, Slovakia,
288   Slovenia, Spain, Sweden, Switzerland, Ukraine, and United Kingdom.

289   RESULTS

290   **Calibration and evaluation of the models**

291   The variables retained by the selection procedures in BART and BRT were similar: bio1, bio5, bio6,
292   bio9, bio11, bio12, and bio16. The selection procedure in RF yielded a slightly different set: bio1,

bio6, bio9, bio10, bio11, bio12, and bio16, where bio5 was replaced by bio10. The AUC was respectively 0.999, 0.998 and 0.999 for RF, BRT and BART. The TSS was respectively 0.994, 0.996 and 0.994 for RF, BRT and BART. These results indicated a very good performance of the 3 models. The suitability thresholds that maximized the TSS were 0.623, 0.362 and 0.540 respectively for RF, BRT and BART.

Current climate suitability (2001-2018)

Figures 1A-C depict climate suitability for the period 2001-2018 according to each model (RF, BRT, BART), showing very high suitability in western Europe with a northern boundary through England and Scandinavia (Sweden, Finland) and Russia. Southern Europe also exhibited suitability extending into northern Morocco, Algeria, and northeastern Tunisia. Figure 1D illustrates committee averaging of RF, BRT, and BART model outputs, highlighting areas of consensus and divergence, particularly around the Mediterranean basin and northern Europe. The MESS index map (Figure 1E) indicates minimal model extrapolation in western Europe (positive values), contrasting with increased extrapolation in North Africa, the Middle East, and northern Europe's Novaya Zemlya region (negative values).

Climate suitability in 2041-2060

The committee averaging of projections across the four SSPs is depicted in Figures 2A, 2C, 2E, and 2G. In the period 2041-2060, suitable areas expanded slightly northward, particularly under scenarios with high greenhouse gas emissions, notably affecting northern Scandinavia and the north-western Ural Plain in Russia (Figure 2G). Conversely, there was a decrease in suitability observed in the southern Iberian Peninsula (southern Spain and Portugal) and North Africa (Morocco). Figures 2B, 2D, 2F, and 2H display maps of the MESS index, which showed a similar spatial pattern compared to the period 2001-2018. However, the MESS index increased across all considered SSPs in central Spain, the Middle East, southern Kazakhstan, Uzbekistan, and Turkmenistan. These findings underscore the need for caution when interpreting projections in these regions, due to potential extrapolation beyond the range of environmental conditions corresponding to the dataset used for models' calibration.

Host plants

A total of 104 taxa were identified as feeding host plants of *L. delicatula*, comprising 103 species and 1 subspecies (*Betula pendula* subsp. *mandshurica*), distributed across 65 genera and 39 botanical families (see Appendix 5). Additionally, *L. delicatula* was associated with 72 plant species and 11 botanical families where feeding observations were absent. Among these, 12 species were noted with observations of both eggs and nymphs/adults, 33 species with only observations of nymphs/adults, and 17 species solely reported as egg supports. The number of host plants varied significantly by country (Appendix 7).

During the invasion of Japan, South Korea, and the USA, *L. delicatula* acquired 68 new host species, with specific host plant numbers for these countries being 1, 28, and 33, respectively. Only 22 host species were exclusively reported from China, while one feeding host species (*Ailanthus altissima*) was common across China, Japan, South Korea, and the USA (see Appendix 8).

Among the 103 feeding host taxa of *L. delicatula*, 57 species were identified in Europe (see Figure 3, Appendix 9). Some species had wide geographic distributions (Eurasiatic) and were native to both China or Europe (e.g., *Arctium lappa*, *Betula pendula*, *Rosa pendulina*, *Vitis vinifera*), or were invasive (e.g., *A. altissima*, *Celastrus orbiculatus*), cultivated (e.g., apricot: *Prunus armeniaca*, kaki persimmon:

336 *Diospyros kaki*), and/or ornamental (e.g., honeysuckle: *Lonicera maackii*, *Melia azedarach*, weeping
337 willow: *Salix babylonica*). Certain American hosts introduced to Europe as ornamental or cultivated
338 species include *Quercus rubra*, *Juglans cinerea*, and *Acer rubrum*, some of which have become
339 invasive like *Prunus serotina*. Two American hosts, *Acer platanoides* and *Acer pseudoplatanus*, are
340 native to Europe. Countries with the highest risk of *L. delicatula* establishment, based on the
341 availability of host plants, include Ukraine, France, and Germany, each hosting more than 40 host
342 species (see Figure 3).

343 **Worldwide distributions**

344 The worldwide projections for current climate conditions are detailed in Appendix 10, highlighting
345 regions of high climate suitability in both the native range and invaded areas (South Korea, Japan,
346 and extensive parts of the USA). The MESS index provided in Appendix 11 shows positive values in
347 these regions, indicating minimal issues with extrapolation. Additionally, certain regions of South
348 America (Chile, Argentina), South Africa, and Australia (specifically Victoria, New South Wales, and
349 Queensland) exhibited high climate suitability according to all three models. Appendices 12 to 19
350 present worldwide projections for the period 2041-2060 under different Shared Socioeconomic
351 Pathways (SSPs), along with corresponding MESS maps. These projections indicated an increase in
352 climate suitability towards the north and a decrease towards the south relative to the current
353 potential range.

354 DISCUSSION

355 The three algorithms employed in this study demonstrated strong performance and provided
356 consistent projections for Europe. While some discrepancies were noted in Southern Finland and
357 Western Russia, the majority of Western Europe exhibited current climate conditions that are
358 deemed suitable for *L. delicatula*. This finding aligns with the conclusions drawn by Wakie et al.
359 (2020), although our models indicated higher and more uniform climate suitability across the
360 European continent. Both Wakie et al. (2020) and our study suggest that *L. delicatula* would struggle
361 to establish in tropical zones, contrasting with the findings of Jung et al. (2017). This disparity could
362 stem from differences in the algorithm used or variations in available data during the respective
363 analyses. Beyond Europe, regions with climatically favourable conditions extend to North America
364 (Mexico, USA), South America (Argentina, Chile), Africa (South Africa), Asia (China, Korea, Japan),
365 Southeast Australia, and the North Island of New Zealand (Appendix 10).

366 Numerous known host plants are already established in Europe, with countries like Germany, France,
367 and Ukraine hosting more than 40 identified host species. In addition, European host species that *L.*
368 *delicatula* could potentially acquire upon establishment should also be considered. The insect's
369 ability to adapt to new hosts is evident from its acquisition of numerous American species during the
370 invasion of the USA (Barringer and Ciafré 2020). Our findings also reveal minimal overlap among host
371 plant species across the three Asian countries where *L. delicatula* is present. While this could partly
372 be due to gaps in literature information, it's important to note that China, Japan, and Korea naturally
373 exhibit relatively low overlap in plant species (Guowen 1997; Wang et al. 2023).

374 *L. delicatula* is a notable invasive species, particularly because its preferred host, *Ailanthus altissima*,
375 is itself a highly successful invasive plant with a global distribution (Park et al. 2009). *A. altissima* is
376 recognized as one of the most pervasive invasive plants (Sladonja et al. 2015), and despite regulatory
377 efforts within the European Union (Regulation 1143/2014), its spread continues. This situation could
378 potentially facilitate the establishment of *L. delicatula* if introduced, presenting a scenario akin to
379 invasional meltdown (Simberloff and von Holle 1999). Although *L. delicatula* reduces the annual
380 growth of *A. altissima* (Dechaine et al. 2023), its non-specific feeding behavior typically excludes it

381 from consideration as a suitable biocontrol agent (Ding et al. 2006), though Brooks et al. (2020)
382 explored its potential role in vectoring plant pathogens.

383 Climate change is anticipated to have diverse impacts on both crop species and pest organisms, such
384 as range shifts (Bebber et al. 2013; Battisti and Larsson 2015) and potentially heightened crop losses
385 (Deutsch et al. 2018). While the specific impact on crop losses due to *L. delicatula* in Europe remains
386 uncertain, our findings suggest that its potential range by 2060 is not likely to undergo significant
387 changes. There may be a slight contraction in southern Europe, particularly in regions of South
388 Portugal and Spain, but this effect is expected to be limited. Conversely, there could be a modest
389 northward expansion of suitable climate conditions, particularly in Scandinavia and Russia. It is
390 important to note that model extrapolation increases in regions where climate suitability is projected
391 to decrease, indicating that these results should be interpreted cautiously. On a global scale, there is
392 an anticipated increase in climate suitability in the southwest of Australia and New Zealand.

393 The risk associated with the spread of *L. delicatula* in Europe encompasses both environmental and
394 economic dimensions, as framed by the hazard-exposure-vulnerability model widely used in risk
395 analysis (Field et al. 2015). The hazard, characterized by the probability of introduction and
396 establishment, is deemed high due to substantial trade connections between Europe and regions
397 where the insect is native or has invaded (Huron et al. 2022). Should L. *delicatula* be introduced,
398 favourable climatic conditions and abundant host plants would likely facilitate its widespread
399 dispersal across Europe, aided either by human transport or natural means. The exposure
400 component of the risk is significant given the diverse range of plant species that could potentially be
401 impacted, many of which hold considerable agricultural (e.g., *Vitis*, *Prunus*, *Malus*, *Juglans*) or
402 forestry (e.g., *Populus*, *Acer*, *Fraxinus*) value. Previous research indicates that *L. delicatula* can
403 complete its lifecycle on multiple hosts beyond *A. altissima*, including *Acer saccharinum*, *Salix
404 babylonica*, *Humulus lupulus*, *Juglans* species, *Liriodendron tulipifera*, *Melia azedarach*, and *Quercus
405 acutissima* (Uyi et al. 2020, 2021; Murman et al. 2020). A recent study by Huron et al. (2022)
406 underscored the potential for global disruption in the wine market if *L. delicatula* were to establish in
407 viticultural regions. Finally, the vulnerability term of the risk encompasses the propensity to be
408 adversely affected and the lack of capacity to cope and adapt. Preparedness measures are crucial,
409 including rapid response capabilities, expert workforce readiness, and informed public awareness
410 aligned with current and projected climate conditions (Ricciardi et al. 2021). Strengthening pest
411 surveillance programs and enhancing international information exchange are also pivotal (Giovani et
412 al. 2020) regarding vulnerability.

413 While climate suitability maps and host analyses indicate widespread threat across Europe, they
414 provide no clues toward the spatio-temporal dynamics of a potential invasion. For that, population
415 dynamics models (Smyers et al. 2021; Lewkiewicz et al. 2022) or phenology models (Maino et al.
416 2023, Barker et al. 2023) could be developed. Early warning systems could benefit from targeted
417 monitoring of *A. altissima* and other potential sentinel plants, as recommended by the European
418 Food Safety Authority (EFSA et al. 2023). Promoting preemptive biocontrol programs, i.e. biocontrol
419 developed prior to the arrival of invasive pests, has proven effective and could mitigate European
420 vulnerability to *L. delicatula* (Avila et al. 2023; Gómez Marco et al. 2023). Implementing such
421 strategies is important to protect European biodiversity and agricultural sectors from the potential
422 impacts of this invasive insect.

423 CONCLUSION

424 Neither the climate conditions nor the presence of compatible host plants constitutes an obstacle to
425 the establishment of *L. delicatula* in Europe. Climate assessments under different scenarios suggest
426 that conditions will remain favorable for *L. delicatula* in the coming decades across much of Europe.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Host plant datasets are available from the supplementary files associated with this article. *L. delicatula* occurrence datasets are available from the gbif database, the R package "LydemapR" and the supplementary files associated with the article. Model projections, the corresponding committee averaging and the MESS index for current and future climate conditions are available from the repository: https://doi.org/10.57745/U1YKUR.

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697

Fig. 1 Potential geographical distribution of *Lycorma delicatula* in Europe under current climate
conditions (2001-2018). A. Climate suitability according to the random forest model (RF), B. Climate
suitability according to the boosted regression trees model (BRT), C. Climate suitability according to
the Bayesian additive regression trees model (BART), D. Committee averaging F. Multivariate
environmental similarity surfaces (MESS) comparing current climate conditions in Europe to
reference points used for model calibration. Analogous environments are shown in red (positive
values) and novel environments are shown in blue (negative values).
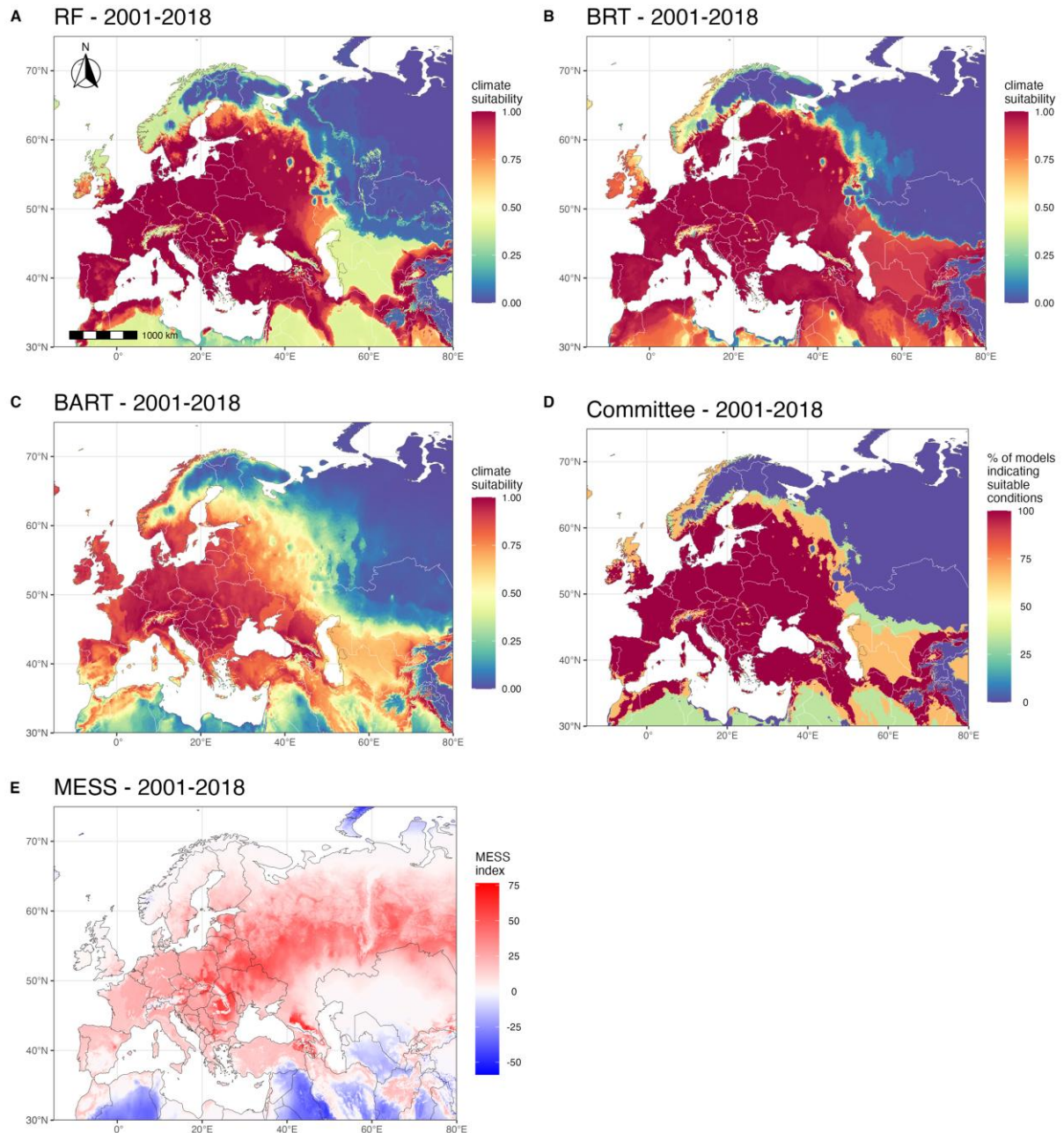

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707

708 **Fig. 2** Climate suitability and MESS index for the period 2041-2060. A. Climate suitability for SSP1-2.6,
709 B. MESS index for SSP1-2.6, C. Climate suitability for SSP2-4.5, D. MESS index for SSP2-4.5, E. Climate
710 suitability for SSP3-7.0, F. MESS index for SSP3-7.0, G. Climate suitability for SSP5-8.5, H. MESS index
711 for SSP5-8.5. For a given SSP, the climate suitability map depicts the committee averaging of values
712 obtained for 3 model algorithms and 6 global circulation models (see text for details).
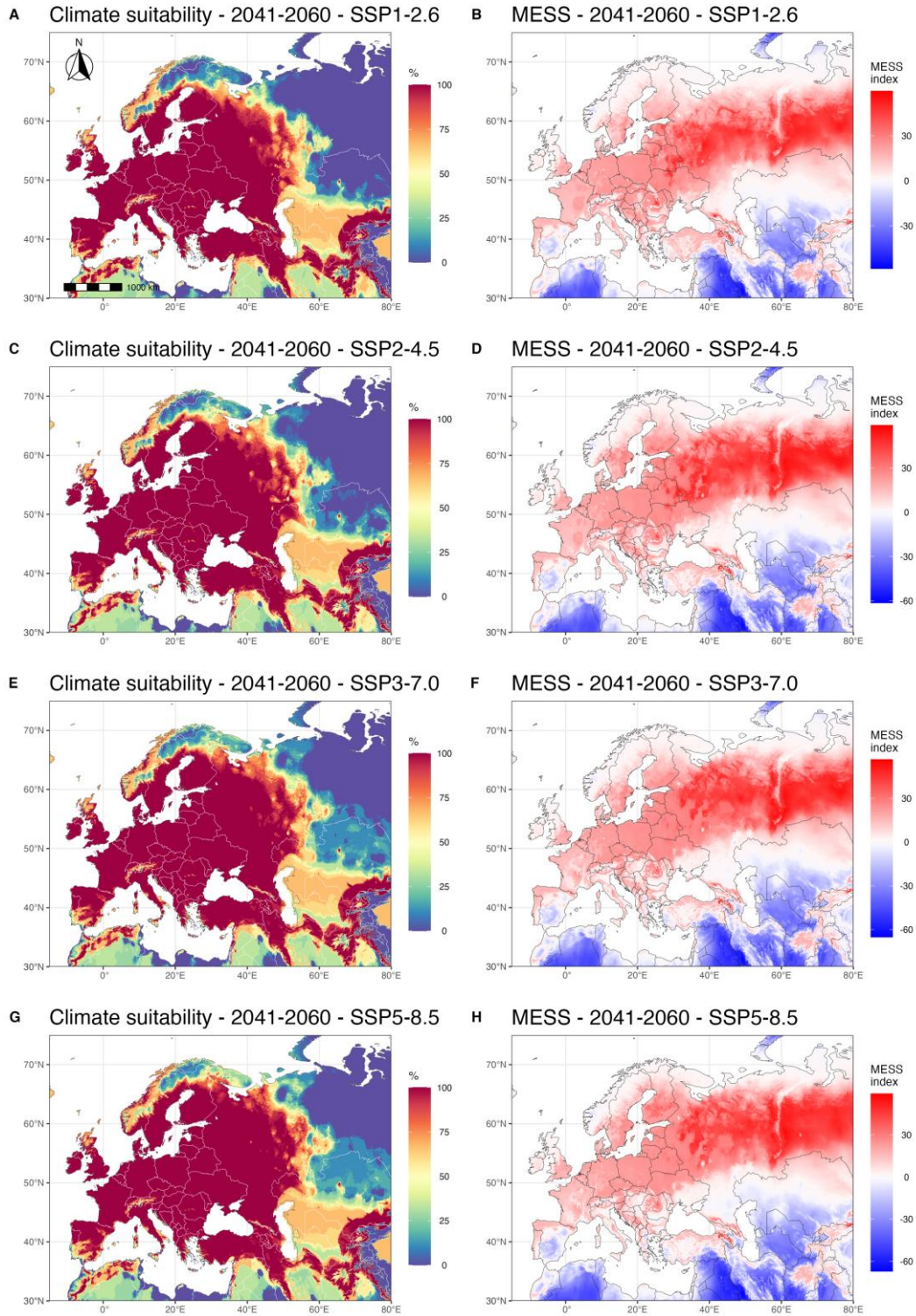
713

714 **Fig. 3** Number of host plants in European countries where climate conditions are suitable for
715 *Lycorma delicatula.*

Number of known plant host species

716

717
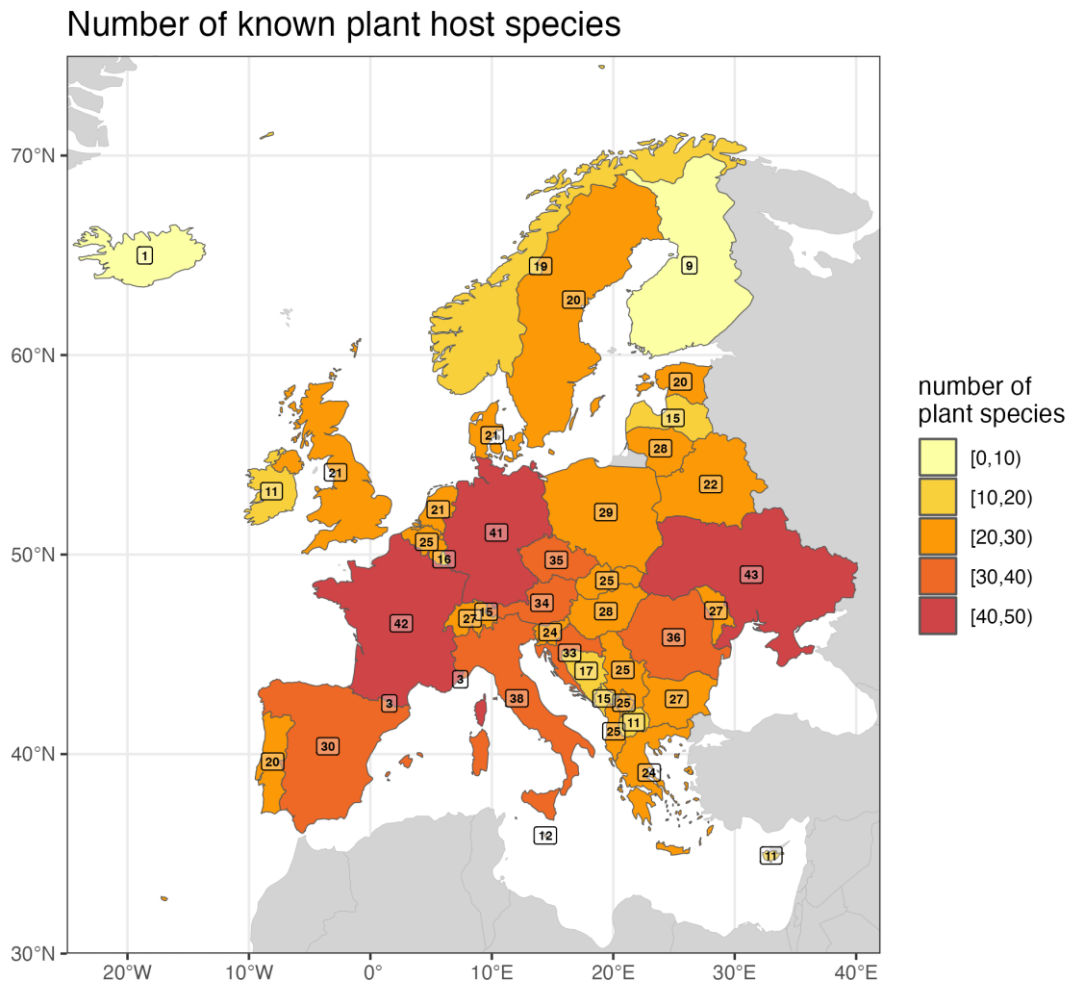
719   SUPPORTING INFORMATION

720   Additional supporting information may be found in the online version of the article at the publisher's
721   website.

722   Appendix 1: References for occurrences of *Lycorma delicatula*.

723   Appendix 2: Occurrences of *Lycorma delicatula* collected from the literature. Status indicates if the
724   occurrence is valid. References are given in Appendix 1.

725   Appendix 3: Maps of the occurrence points and areas where pseudo-absence points were randomly
726   generated for the species distribution modelling of the *Lycorma delicatula*.

727   Appendix 4: References for host plants of *Lycorma delicatula*.

728   Appendix 5: List of host plants of *Lycorma delicatula*. References are given in Appendix 4.

729   Appendix 6: Reclassified maps of the climate suitability for *Lycorma delicatula* according to 3
730   algorithms. A Random forests (RF) B. Boosted regression trees (BRT) C. Bayesian additive regression
731   trees (BART). The climate conditions represent the period 2001-2018.

732   Appendix 7. List of feeding host species and the country of observation.

733   Appendix 8. Venn diagram showing the number of feeding host plants of *Lycorma delicatula* by
734   country. Shape overlaps contain the number of species shared by countries. All countries: N=104
735   feeding species.

736   Appendix 9. Number of known feeding hosts and non-feeding plant species present in European
737   countries. Feeding host species include all plant species on which *L. delicatula* feeding events have
738   been explicitly reported in the literature. Non-feeding species include plant species on which *L.
739   delicatula* has been observed but on which no explicit feeding event was reported (e.g. resting, egg
740   laying).

741   Appendix 10. Potential geographical distribution of *Lycorma delicatula* under current climate
742   conditions (2001-2018). The map depicts the committee averaging of values obtained for three
743   algorithms (see text for details).

744   Appendix 11. Multivariate environmental similarity surfaces (MESS) comparing current climate
745   conditions (2001-2018) for the world to reference points used for model calibration. Analogous
746   environments are shown in red (positive values) and novel environments are shown in blue (negative
747   values).

748   Appendix 12. Potential geographical distribution of *Lycorma delicatula* under future climate
749   conditions (2041-2060, SSP1-2.6). The map depicts the committee averaging of values obtained by
750   projecting the data of 6 GCM using 3 species distribution models (see text for details).

751   Appendix 13. Multivariate environmental similarity surfaces (MESS) comparing future climate
752   conditions (2041-2060, SSP1-2.6) for the world to reference points used for model calibration. At
753   each pixel, the map shows the lower value of the index computed for the projections of 3 models

754 according to the climate conditions associated with 6 GCM. Analogous environments are shown in
755 red (positive values) and novel environments are shown in blue (negative values).

756 Appendix 14. Potential geographical distribution of *Lycorma delicatula* under future climate
757 conditions (2041-2060, SSP2-4.5). The map depicts the committee averaging of values obtained by
758 projecting the data of 6 GCM using 3 species distribution models (see text for details).

759 Appendix 15. Multivariate environmental similarity surfaces (MESS) comparing future climate
760 conditions (2041-2060, SSP2-4.5) for the world to reference points used for model calibration. At
761 each pixel, the map shows the lower value of the index computed for the projections of 3 models
762 according to the climate conditions associated with 6 GCM. Analogous environments are shown in
763 red (positive values) and novel environments are shown in blue (negative values).

764 Appendix 16. Potential geographical distribution of *Lycorma delicatula* under future climate
765 conditions (2041-2060, SSP3-7.0). The map depicts the committee averaging of values obtained by
766 projecting the data of 6 GCM using 3 species distribution models (see text for details).

767 Appendix 17. Multivariate environmental similarity surfaces (MESS) comparing future climate
768 conditions (2041-2060, SSP3-7.0) for the world to reference points used for model calibration. At
769 each pixel, the map shows the lower value of the index computed for the projections of 3 models
770 according to the climate conditions associated with 6 GCM. Analogous environments are shown in
771 red (positive values) and novel environments are shown in blue (negative values).

772 Appendix 18. Potential geographical distribution of *Lycorma delicatula* under future climate
773 conditions (2041-2060, SSP5-8.5). The map depicts the committee averaging of values obtained by
774 projecting the data of 6 GCM using 3 species distribution models (see text for details).

775 Appendix 19. Multivariate environmental similarity surfaces (MESS) comparing future climate
776 conditions (2041-2060, SSP5-8.5) for the world to reference points used for model calibration. At
777 each pixel, the map shows the lower value of the index computed for the projections of 3 models
778 according to the climate conditions associated with 6 GCM. Analogous environments are shown in
779 red (positive values) and novel environments are shown in blue (negative values).

780