Mapping the global distribution of invasive pest *Drosophila suzukii* and parasitoid *Leptopilina japonica*: implications for biological control

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Insect pest invasions cause significant damage to crop yields, and the resultant economic losses are truly alarming. Climate change and trade liberalization have opened new ways of pest invasions. Given the consumer preference towards organic agricultural products and environment-friendly nature of natural pest control strategies, biological control is considered to be one of the potential options for managing invasive insect pests. *Drosophila suzukii* (Drosophilidae) is an extremely damaging fruit pest, demanding development of effective and sustainable biological control strategies. In this study, we assessed the potential of the parasitoid *Leptopilina japonica* (Figitidae) as a biocontrol agent for *D. suzukii* using ecological niche modeling approaches. We developed global-scale models for both pest and parasitoid to identify four components necessary to derive a niche based, target oriented prioritization approach to plan biological control programs for *D. suzukii*: (i) potential distribution of pest *D. suzukii*, (ii) potential distribution of parasitoid *L. japonica*, (iii) the degree of overlap in potential distributions of pest and parasitoid, and (iv) biocontrol potential of this system for each country. Overlapping suitable areas of pest and parasitoid were identified at two different thresholds and at the most desirable threshold ($E = 5\%$), potential for *L. japonica* mediated biocontrol management existed in 125 countries covering 1.87×10^7 km^2, and at the maximum permitted threshold ($E = 10\%$), land coverage was reduced to 1.44×10^7 km^2 in 121 countries. Fly pest distributional information as a predictor variable was not found to be improving parasitoid model performance, and globally, only in half of the countries, >50% biocontrol coverage was estimated. We therefore suggest that niche specificities of both pest and parasitoid must be included in site-specific release planning of *L. japonica* for effective biocontrol management aimed at *D. suzukii*. This study can be extended to design cost-effective pre-assessment strategies for implementing any biological control management program.

1 **Mapping the global distribution of invasive pest *Drosophila suzukii* and parasitoid *Leptopilina***

2 ***japonica*: implications for biological control**

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10 **ABSTRACT**

11 Insect pest invasions cause significant damage to crop yields, and the resultant economic losses

12 are truly alarming. Climate change and trade liberalization have opened new ways of pest

13 invasions. Given the consumer preference towards organic agricultural products and

14 environment-friendly nature of natural pest control strategies, biological control is considered

15 to be one of the potential options for managing invasive insect pests. *Drosophila suzukii*

16 (Drosophilidae) is an extremely damaging fruit pest, demanding development of effective and

17 sustainable biological control strategies. In this study, we assessed the potential of the

18 parasitoid *Leptopilina japonica* (Figitidae) as a biocontrol agent for *D. suzukii* using ecological

19 niche modeling approaches. We developed global-scale models for both pest and parasitoid to

20 identify four components necessary to derive a niche based, target oriented prioritization

21 approach to plan biological control programs for *D. suzukii*: (i) potential distribution of pest *D.*

22 *suzukii*, (ii) potential distribution of parasitoid *L. japonica*, (iii) the degree of overlap in potential

23 distributions of pest and parasitoid, and (iv) biocontrol potential of this system for each

24 country. Overlapping suitable areas of pest and parasitoid were identified at two different

25 thresholds and at the most desirable threshold (E = 5%), potential for *L. japonica* mediated

26 biocontrol management existed in 125 countries covering 1.87 x 10^7 km^2, and at the maximum

27 permitted threshold (E = 10%), land coverage was reduced to 1.44 x 10^7 km^2 in 121 countries.

28 Fly pest distributional information as a predictor variable was not found to be improving

29 parasitoid model performance, and globally, only in half of the countries, >50% biocontrol

30 coverage was estimated. We therefore suggest that niche specificities of both pest and

31 parasitoid must be included in site-specific release planning of *L. japonica* for effective

32 biocontrol management aimed at *D. suzukii*. This study can be extended to design cost-effective

33 pre-assessment strategies for implementing any biological control management program.

34 **Keywords** *Drosophila suzukii*, *Leptopilina japonica*, Pest, Parasitoid, Invasion, Biological control,

35 Ecological niche modeling

42   **INTRODUCTION**

43   Over recent decades, the world has witnessed significant increases in agricultural

44   production, but increases in crop yields have often been reduced by diverse insect pests

45   (Vreysen et al., 2007; Savary et al., 2019). Assessment of all of the components of agricultural

46   productivity and food security must include consideration of insect pests, as they are an

47   integral part of anthropogenic crop ecosystems (Food and Agriculture Organization, 2013;

48   Savary et al., 2019). Global warming and economic globalization accelerate development of

49   new routes of pest invasion (Girod et al., 2018), presenting new challenges. As pests pose

50   serious threats in the functioning of global food systems (Savary et al., 2017), various strategies

51   have been developed for insect pest management, each with its own advantages and

52   disadvantages (Dara, 2021). Improvement in the management of invasive pest populations

53   includes consideration of sustainable and eco-friendly approaches, with the goal of achieving

54   long-term benefits (Bernaola & Holt, 2021).

55   A broad (fruit) host range (Lee et al., 2011; Bellamy, Sisterson & Walse, 2013), combined

56   with an ability to infest ripening soft fruits (Gabarra et al., 2015), has made *Drosophila suzukii*

57   (Matsumura) (Diptera: Drosophilidae) an economically damaging, globally invasive fruit pest of

58   serious concern (Walsh et al., 2011). Preference for not-quite-ripe or just-ripe fruits over

59   damaged or decaying fruits (Mitsui, Takahashi & Kimura, 2006), and the presence of a

60   sclerotized ovipositor of females (Kienzle & Rohlfs, 2021) with serrations to pierce undamaged

61   fruit epicarps for laying eggs, are two notable traits (Walsh et al., 2011) that contribute

62   significantly to economic threats imposed by *D. suzukii*. Bacterial and fungal pathogens can

63   cause secondary infections in fruits after infestation by *D. suzukii,* augmenting economic losses

64   (Molina et al., 1974; Louis et al., 1996; Walsh et al., 2011).

65   *Drosophila suzukii* is native to eastern and southeastern Asia (Bolda et al., 2010); it was

66   initially detected in Japan in 1916 (Kanzawa, 1935) and described as a distinct species in 1931

67   (Hauser, 2011). In 2008, *D. suzukii* was identified as an invasive species for the first time with

68   populations in both North America (Hauser, 2011) and Europe (Calabria et al., 2012). Its host

69   range covers 13 angiosperm families (Cloonan et al., 2018), and its invaded geographic range

70   has now extended to South America (Deprá et al., 2014; Andreazza et al., 2017) and Africa

71   (Kwadha et al., 2021). As *D. suzukii* larvae feed inside of fruits (Fanning, Grieshop & Isaacs,

72   2018), and the fruit export trade strictly follows zero-tolerance towards infestations (Tait et al.,

73   2021), much high-value fruit is rendered unsellable every year. Economic impact assessments

74   in the United States (Bolda, Goodhue & Zalom, 2010; Walsh et al., 2011; Goodhue et al., 2011;

75   Farnsworth et al., 2017; DiGiacomo et al., 2019; Yeh et al., 2020), Europe (Knapp et al., 2021),

76   and South America (Benito, Lopes-da-Silva & Santos, 2016), have indicated losses on the order

77   of US$550M per year.

78   Various preventive and post-infestation control measures (Lee et al., 2011; Landolt,

79   Adams & Rogg, 2012; Haye et al., 2016; Schetelig et al., 2018; Shawer et al., 2018; Tait et al.,

80   2021) have been developed so far, but none with complete efficacy (Kehrli et al., 2017; Knapp,

81   Mazzi & Finger, 2019). Management strategies for *D. suzukii* can be classified broadly into four

82   categories: (1) chemical control (Beers et al., 2011; Van Timmeren & Isaacs, 2013; Shawer et al.,

83   2018; Shawer, 2020), (2) microclimate manipulation (Lee et al., 2016; Rendon et al., 2020), (3)

84   RNA interference biopesticides (Murphy et al., 2016), and (4) biological control (Chabert et al.,

85 2012; Daane et al., 2016; Mazzetto et al., 2016; Knoll et al., 2017; Daane et al., 2021). Extensive

86 use of chemical methods to control *D. suzukii* infestations can lead to increased pest resistance,

87 and concerns regarding food and environmental safety (Santoiemma et al., 2019). Microclimate

88 manipulation approaches to control *D. suzukii* are more likely to perform well in hot and dry

89 regions (Schöneberg et al., 2022), as *D. suzukii* is sensitive to high temperatures and low

90 humidity (Rendon et al., 2020). RNA interference methods involve higher development costs

91 and involve much labor (Bramlett, Plaetinck & Maienfisch, 2020). Finally, biological control

92 involves release of enemies of *D. suzukii* from the region of its origin (Asia) in invaded areas, as

93 a means to reduce its population growth (Girod et al., 2018). This method is recommended

94 (Cock et al., 2010; van Lenteren, 2012) in view of improved food safety, environment-friendly

95 characteristics, economic feasibility, and long-term control solutions that are established

96 (Kruitwagen, Beukeboom & Wertheim, 2018).

97   Parasitoid wasps of the genera *Asobara* (Braconidae), *Ganaspis* (Figitidae), and

98 *Leptopilina* (Figitidae) have been studied extensively as biological control agents with potential

99 to suppress growth of *D. suzukii* populations (Kacsoh & Schlenke, 2012; Rossi Stacconi et al.,

100 2015; Daane et al., 2016; Giorgini et al., 2019; Wang et al., 2019; Biondi, Wang & Daane, 2021).

101 In particular, the species *A. japonica*, *G. brasiliensis*, and *L. japonica* are potential biocontrol

102 agents (Wang et al., 2019). However, some researchers do not recommend *A. japonica* for

103 biological control programs aimed at *D. suzukii* (Daane et al., 2016; Girod et al., 2018; Abram et

104 al., 2020), owing to its broad host range (Ideo et al., 2008; Furihata et al., 2016). Indeed, given

105 its host specificity, *G. brasiliensis* has been proposed as a candidate for biological control of *D.*

106 *suzukii* (Wang et al., 2020), yet, in a scenario when these three wasps coexist, *L. japonica* is

107   unique in being able to outcompete the other two species thanks to its relatively faster egg-

108   hatching potential (Wang et al., 2019). Relatively high host specificity (Wang et al., 2020),

109   demonstrated competence in multi-parasite systems (Wang et al., 2019), and recent range

110   expansions into areas invaded by *D. suzukii* in Europe (Puppato et al., 2020) and North America

111   (Abram et al., 2020, 2022), make *L. japonica* a particularly promising biocontrol agent of *D.*

112   *suzukii*.

113   Ecological niche modeling (ENM) has been used extensively to identify potential

114   distributions of species for a variety of purposes (Raxworthy et al., 2007; Escobar, 2020;

115   Kolanowska & Jakubska-Busse, 2020; Wan et al., 2020; Valencia-Rodríguez et al., 2021; Agboka

116   et al., 2022; Demján et al., 2022; Outammassine, Zouhair & Loqman, 2022). In pest-parasitoid

117   systems, identifying and comparing relative habitat suitability of pest and parasitoid can help to

118   guide effective biological control programs (Pérez-de la O et al., 2020; Tepa-Yotto et al.,

119   2021a,b). The utility of ENM in applications to biological control of pests can be attributed to

120   two factors: alien parasitoid species must survive and reproduce in the geographic regions

121   where they are released (Mills, 2018; Schulz, Lucardi & Marsico, 2019), and unfavorable abiotic

122   factors can reduce the long-term efficacy of biological control measures (Olfert et al., 2016).

123   Modeling climatic preferences of deliberately introduced parasitoid species can also provide

124   insights into possible range expansions, an important aspect to be tested in improving

125   effectiveness of classical biological control programs (Pérez-de la O et al., 2020).

126   In this study, we used ENM approaches to explore, discuss, and highlight five aspects of

127   a biological control strategy for *D. suzukii* that can directly benefit producers, extension agents,

128   and policy makers. (1) We estimated the potential distribution of the invasive pest *D. suzukii*,

129   and (2) that of the parasitoid *L. japonica*. (3) We assessed the degree of overlap in the potential

130   distributions of *D. suzukii* and *L. japonica*, and (4) estimated the biocontrol potential of this

131   system for each country. Finally, (5) we assessed parasitoid model performance to see if

132   incorporating distributional information for the pest improves model performance for the

133   parasitoid.

134

135   **METHODS**

136   **Occurrence data**

137   Occurrence records of *D. suzukii* were downloaded from five online biodiversity data

138   portals: Global Biodiversity Information Facility (GBIF; www.gbif.org, accessed on 2 August,

139   2022), Biodiversity Information Serving Our Nation (BISON; www.gbif.us, accessed on 2 August,

140   2022), Berkeley Ecoinformatics Engine (Ecoengine; ecoengine.berkeley.edu, accessed on 2

141   August, 2022), iNaturalist (www.inaturalist.org, accessed on 2 August, 2022), and Integrated

142   Digitized Biocollections (iDigBio; www.idigbio.org, accessed on 2 August, 2022) using Spocc

143   version 1.2.0 R package (Chamberlain, Ram & Hart, 2021); occurrence data were also drawn

144   from the Centre for Agriculture and Bioscience International (CABI; www.cabi.org, accessed on

145   3 August, 2022). This initial harvest of occurrence data yielded an initial total of 2369 records.

146   A five-step data cleaning process was adopted: (1) removal of records with no date of

147   observation, (2) removal of incomplete coordinates (*i.e.*, lacking valid latitude and longitude),

148   (3) removal of unlikely coordinates (e.g., 0.00ºN, 0.00ºE), (4) removal of duplicated coordinates,

149 and (5) removal of coordinates with fewer than two decimal places. Data cleaning was

150 performed using scrubr version 0.1.1 R package (Chamberlain, 2016). The cleaned dataset

151 (1385 records) was overlaid on climatic raster layers (5' or ~10 km spatial resolution, see below)

152 to remove points falling outside the raster boundaries. The resulting occurrence dataset (1377

153 records) was subjected to visual inspection to detect clusters of points (often related to points

154 of access or concentrations of people), and eliminate disproportionate data density at random,

155 maintaining a minimum distance of ≥ 30km among points, to avoid model overfitting (Raghavan

156 et al., 2019). The final dataset of 314 points (Figure 1; Supplementary file 1) showed no

157 excessive clustering of occurrences across the known distribution of *D. suzukii.* Spatial filtering

158 was performed using spThin R package (Aiello-Lammens et al., 2015).

159 Occurrence records of *L. japonica* were sourced from published literature (Beers et al.,

160 2022; Abram et al., 2020; Puppato et al., 2020; Giorgini et al., 2019; Girod, 2018; Novković et

161 al., 2011), as online data portals held few or no records. A distance filter of 12 km was applied

162 to the occurrences extracted, and the final dataset comprised 31 points (Figure 1;

163 Supplementary file 2). *Leptopilina japonica* has two subspecies: *L. japonica japonica* and *L.*

164 *japonica formosana*, occurring in Japan and Taiwan respectively (Novković et al., 2011); both

165 have the ability to parasitize *D. suzukii* (Kimura & Novković, 2015). Our final dataset included

166 mostly the nominate subspecies, and only a single occurrence record of *L. j. formosana*

167 (Novković et al., 2011).

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171 **Environmental data**

172   Bioclimatic raster layers at 5' spatial resolution (~10 km at the Equator) were

173 downloaded from WorldClim 2.1 for present conditions (1975-2000; Fick and Hijmans, 2017).

174 Variables combining temperature and precipitation measurements (*i.e.*, mean temperature of

175 wettest quarter, mean temperature of driest quarter, precipitation of warmest quarter, and

176 precipitation of coldest quarter) were excluded (Escobar et al., 2014) owing to discontinuous

177 patterns of those variables in many areas (Booth, 2022).

178   To define the set of limits and conditions for ENM, identification of areas accessible to

179 species over relevant time periods (Soberón & Peterson, 2005; Peterson & Soberón, 2012) is

180 essential to development of robust models (Barve et al., 2011) . The development of a

181 hypothesis of accessible area **M** is crucial for rigorous characterization of niche characteristics

182 of species (Barve et al., 2011; Machado-Stredel, Cobos & Peterson, 2021). Considering the near-

183 global distribution of *D. suzukii* and *L. japonica,* the entire world (excluding Antarctica) was

184 defined as the accessible area for the two species. The 15 climatic data layers were clipped to

185 the extent of this area. Multi-collinearity and dimensionality among the clipped bioclimatic

186 layers were minimized using principal components analysis, in effect transforming correlated

187 climatic variables into fewer, uncorrelated principal components (PCs), and these multivariate

188 environmental variables were used as the independent variables in ENM. Principal components

189 analysis of raster variables was done using the kuenm_rpca function of the kuenm R package

190 (Cobos et al., 2019).

191

192 **Ecological niche modeling**

193   In separate ENM analyses, occurrences of each species (pest and parasitoid) were

194 partitioned randomly into training and testing data in two different proportions: 70:30 for *D.*

195 *suzukii*, and 50:50 for *L. japonica*. Considering the small number of records, data-splitting ratio

196 was reduced to 0.5 for *L. japonica* to maintain a balance between predictive accuracy and

197 performance estimation of models as very low sample size for testing can cause errors in

198 estimating predictive accuracy (Peterson, Ball & Cohoon, 2002). Modeling experiments were

199 performed using six combinations of three feature classes (l-linear, q-quadratic, p-product; l, q,

200 lq, qp, lp, and lqp; product response types were not used in isolation owing to occasional

201 problems that result), 10 regularization multipliers (0.1, 0.3, 0.6, 0.9, 1, 2, 3, 4, 5, 6), and nine

202 sets of principal components summarizing climate data. The first 10 PCs accounted for >99% of

203 the total variation: set 1 (PCs 1 and 2), set 2 (PCs 1-3), etc., up to set 9 (PCs 1-10). Best models

204 were selected by applying three criteria sequentially (Cobos et al., 2019): (1) choosing

205 statistically significant models using partial ROC tests, (2) filtering statistically significant models

206 to those with < 5% omission error (*E*), and (3) ranking all remaining models based on Akaike

207 information criterion (AICc) values; the subset of significant, low-omission models within 2 AICc

208 units of the minimum were selected as the best models (Warren & Seifert, 2011). Top models

209 were replicated 10 times using the bootstrap method to produce final models, and the median

210 of the median outputs across all replicates was used to interpret results for each species.

211   To assess the potential role of fly distributional information in improving the

212   performance of the parasitoid model, the final *D. suzukii* model output was added to each

213   multivariate environmental variable set. We then re-calibrated the *L. japonica* model using the

214   same set of feature class types and regularization multiplier values to develop a two-species

215   model for the wasp (see Ashraf et al., 2021). We compared models with and without the fly

216   distributional information using the same 3 criteria described above. Occurrence data

217   partitioning exercises were done using caTools R package (Tuszynski, 2021). All modeling

218   experiments were performed using maximum entropy approaches (Maxent) (Phillips, Anderson

219   & Schapire, 2006), as implemented in the kuenm R package (Cobos et al., 2019).

220   To represent suitable and unsuitable regions for the pest and the parasitoid, Maxent

221   models in the form of continuous logistic outputs were transformed into binary presence-

222   absence models by applying two different least-training presence thresholds (*i.e.*, allowable

223   omission $E = 5\%$ and $E = 10\%$). These two thresholds were chosen as indices of most desirable

224   ($E=5\%$) and maximum permitted ($E = 10\%$) omission rates to represent relative habitat

225   suitability, and also to avoid overinterpretation of predictions (Ashraf, Chaudhry & Peterson,

226   2021). These thresholds were applied using QGIS Tisler desktop version 3.24.3 (QGIS

227   Geographic Information System, 2022).

228   For both thresholds, overlapping potential habitats of *D. suzukii* and *L. japonica* were

229   identified. The ratio between the land areas of predicted potential distribution of parasitoid

230   and pest in each country was estimated to determine the country-wise biocontrol coverage

231   potential percentage, for both thresholds. Identification of overlapped area and estimation of

232   land area in terms of biocontrol coverage were done in QGIS Tisler desktop version 3.24.3 (QGIS

233   Geographic Information System, 2022). All models were represented in an Eckert IV equal-area

234   map projection (Qiao et al., 2019).

235   **RESULTS**

236   For each of the two species, we developed 540 candidate models, of which 510 models

237   for *D. suzukii* and 533 models for *L. japonica* were statistically significantly better than random

238   expectations according to the partial ROC tests ($P < 0.05$). Of the statistically significant models,

239   53 models for *D. suzukii* and 11 models for *L. japonica* were also acceptable in having low (<5%)

240   omission. Finally, based on low model complexity (*i.e.*, low AICc value), our top model for *D.*

241   *suzukii* included linear and quadratic feature classes, a relatively low regularization multiplier

242   value (0.6), and four multivariate environmental variables (PC 1–PC 4) (Table 1). Our best model

243   for *L. japonica* had a higher regularization multiplier value (2.0), and included more multivariate

244   environmental variables (PC 1–PC 7), also with linear and quadratic feature types (Table 1). In

245   the two-species modeling experiment, we developed 540 models, and all models were

246   statistically significantly better than random expectations ($P < 0.05$). However, none of the

247   models met the omission rate threshold ($E = 5\%$). We found that, even relaxing the threshold (E

248    $= 7\%$) did not result in the selection of any of the two-species models as best model for

249   parasitoid. We therefore confirmed that inclusion of pest model as a predictor variable did not

250   improve model performance for the parasitoid.

251   Our model for *D. suzukii* predicted potential distributional areas in southern and eastern

252   China, with some extensions towards central Asian regions (Figure 2). Farther north in Asia,

253   Japan and the Korean Peninsula were predicted to hold broad suitable areas for *D. suzukii*.

254   Predicted suitable areas covered seven nations [Afghanistan, Pakistan, India, Nepal, China

255   (Tibetan Autonomous Region), Bhutan, and Myanmar] across the entire northwest-southeast

256   spread of the Himalayas. In Oceania, southeastern Australia and much of New Zealand were

257   predicted to hold suitable conditions for *D. suzukii* invasion.

258   Already-invaded parts of western Europe and the southeastern United States were

259   identified as highly suitable for *D. suzukii* populations, which is logical given that occurrences

260   there were part of the model training data. In South America, the entire geographic extent of

261   Uruguay, known to hold invasive populations, was identified as suitable for *D. suzukii*; parts of

262   other known-invaded countries (Chile, Argentina, Brazil) were also identified as suitable:

263   eastern and northeastern Argentina, southern Brazil, and western and southern Chile. Peru is

264   the only country in South America predicted to hold suitable areas for *D. suzukii* invasion for

265   which no invasive populations are known; predicted potential distributional areas spanned the

266   Andean Cordillera.

267   The modeled potential geographic distribution for *L. japonica* was broad and continuous

268   in Asia, covering southern and northeastern Asian countries (India, China (Tibetan autonomous

269   region), Nepal, Bhutan, North Korea, South Korea, and Japan). Other potential distributional

270   areas were more sparse, in northwestern Europe, western North America, and in western and

271   southern Chile in South America.

272   **Binary models and biocontrol coverage estimation**

273   Binary model outputs were developed for *D. suzukii* and *L. japonica* (Figure 3) to identify

274   presence or absence of the two species in the area of interest. At the 5% threshold, potential

275   presence of *D. suzukii* was predicted in 162 countries (Supplementary file 3), covering a total

276   area of ~4.82 x 10^7 km^2. Potential presence of *L. japonica* was predicted in 148 countries

277   (Supplementary file 3), covering a total area of 2.71 x 10^7 km^2. At the 10% threshold, total

278   coverage of predicted area was reduced to 3.44 x 10^7 km^2 in 152 countries for *D. suzukii*, and

279   2.46 x 10^7 km^2 in 146 countries for *L. japonica* (Supplementary file 3)*.

280   Overlapping suitable areas of *D. suzukii* and *L. japonica* to identify possible biocontrol

281   regions for both thresholds (Figure 4) showed that potential for *L. japonica*-mediated biocontrol

282   management of *D. suzukii* existed in 125 nations at *E* = 5%, and 121 nations at *E* = 10% (Table

283   2). At a global level, the total possible biocontrol area was estimated to range 1.44 x 10^7 km^2-

284   1.87 x 10^7 km^2 based on the different thresholds. Country-wise biocontrol coverage estimation

285   revealed that about half of the countries (65) had more than 50% biocontrol potential (*i.e.*, area

286   suitable for both fly and wasp; Table 2), with broadest areas in China (~4.4 x 10^6 km^2), India

287   (~1.1 x 10^6 km^2), Zambia (4.5 x 10^5 km^2), and Angola (~4.2 x 10^5 km^2).

288

289   **DISCUSSION**

290   Extremely fast range expansion as a consequence of globalization (Iacovone et al.,

291   2015), with severe economic damage to the fruit trade industry (Bolda, Goodhue & Zalom,

292   2010; Gabarra et al., 2015), has led to efforts to model ecological niches and predict potential

293   distributions for *D. suzukii* both locally (Castro-Sosa et al., 2017; de la Vega & Corley, 2019) and

294   globally (Santos et al., 2017; Ørsted & Ørsted, 2019; Reyes & Lira-Noriega, 2020). Comparing

295   with previous global-scale models, our models predicted highly suitable areas for *D. suzukii*

296   most similar to the model developed by Ørsted and Ørsted (2019), and less similar to those of

297   Santos et al (2017) and Reyes and Lira-Noriega (2020). Relatively broad geographic areas in the

298   southern part of central and eastern Africa were predicted to be suitable in the models

299   developed by Santos et al (2017) and Reyes and Lira-Noriega (2020) compared to our model

300   and that of Ørsted and Ørsted (2019). Unlike the predictions of Santos et al (2017) and Reyes

301   and Lira-Noriega (2020), Patagonian region of Argentina was not included as suitable habitat for

302   *D. suzukii* in our model and that of Ørsted and Ørsted (2019). Another major difference

303   between our model and those of Santos et al (2017) and Reyes and Lira-Noriega (2020) is that

304   their models predicted a large extent of eastern India as suitable habitats for *D. suzukii*.

305   However, according to our model, the suitability was more prominent in far north, and also in

306   some parts of Western Ghats in southern India. Although similar in many aspects of predicted

307   distributions, our model differed notably from that of Ørsted and Ørsted (2019) in predicting

308   the east-west continuity of potential distribution of *D. suzukii* in United States as our model

309   showed a discontinuous distribution of potential habitats.

310   For obvious reasons, choosing biological control agents for *D. suzukii* that have niche

311   preferences similar to those of the fly will be helpful (Robertson, Kriticos & Zachariades, 2008;

312   Olfert et al., 2016; Tepa-Yotto et al., 2021a,b) in the global-scale biological control challenge.

313   Matching the climatic niche requirements of pest and parasitoid will increase chances of long-

314   term establishment of the parasitoid across key regions (Robertson, Kriticos & Zachariades,

315   2008), resulting in more successful management via biological control. Despite various previous

316   studies modeling the climatic niche of *D. suzukii*, to the best our knowledge, no effort has been

317   made so far to study the potential distribution of climatic niches of any parasitoid of *D. suzukii*

318   in combination with analyses of the climatic niche of the fly pest.

319   Range expansion of *D. suzukii* in Europe and North America occurred after initial

320   outbreaks in California, Spain, and Italy, all in 2008 (Rota-Stabelli, Blaxter & Anfora, 2013;

321   Asplen et al., 2015). Niche filling related to absence of competitors or natural enemies, high

322   adaptability to temperate climates, high dispersal ability, and high reproductive output, are

323   major factors contributing to the unprecedented invasion of *D. suzukii* (Rota-Stabelli, Blaxter &

324   Anfora, 2013). As niche filling is an important factor, assessing the geographic distribution of

325   climatic niches of *D. suzukii* becomes an indispensable step in biological control programs, as it

326   can provide an initial estimate of the geographic limits for successful parasitoid release

327   (Puppato et al., 2020). Development of niche models for parasitoids, and identification of

328   geographic regions exhibiting overlapping climatic niches between pest and parasitoid, further

329   delimits regions for parasitoid release, making field trials involving elaborate and time-

330   consuming experiments more economical (Sun et al., 2017).

331   In its native distributional areas, *Leptopilina japonica* is one of most abundant potential

332   parasitoids of *D. suzukii* (Kimura & Novković, 2015; Puppato et al., 2020); its occurrence in

333   Europe (Puppato et al., 2020) and North America (Abram et al., 2020, 2022; Beers et al., 2022)

334   was identified only recently. Previous laboratory experiments in the United States indicated

335   that South Korean *L. japonica* strains attacked the North American strains of *D. suzukii* readily

336   (Daane et al., 2016), supporting at least in part the suitability of *L. japonica* as a biocontrol

337   agent for *D. suzukii*. Although occurrence records of *L. japonica* were scarce, our modeled

338   climatic niche for *L. japonica* overlapped broadly with that of *D. suzukii* in known-invaded

339   regions (Figure 2-4), meeting one of the major ecological requirements for a 'natural enemy

340   species' to be a candidate biological control agent (Robertson, Kriticos & Zachariades, 2008;

341   Olfert et al., 2016). The two-species model developed for gaining insight into the biotic

342   interactions shaping the potential geographic distribution of *L. japonica* underperformed

343   compared to the climate-only model. These results thus contrasted with previous findings

344   highlighting the importance of including biotic predictors in ecological niche modeling

345   procedures to improve model performance (Araújo & Luoto, 2007; Giannini et al., 2013;

346   Dormann et al., 2018; Simões & Peterson, 2018; Bebber & Gurr, 2019; Ashraf, Chaudhry &

347   Peterson, 2021).

348   We recommend a niche-based, target-oriented prioritization approach in designing

349   biological control programs aimed at *D. suzukii.* In Europe, three interlinked factors, (1) recently

350   recorded occurrences (Puppato et al., 2020), (2) predicted suitability in 17 European countries

351   (~39% of European countries) with biocontrol coverage of >80% at both thresholds (E = 5% and

352   E = 10%) (Table 2), and (3) increasing consumer preference towards organic fruits (Murphy et

353   al., 2022), make *L. japonica* a promising parasitoid for control of *D. suzukii*. In the remaining

354   European countries, in particular those exhibiting biocontrol coverage <50%, we suggest extra

355   care in defining appropriate geographic boundaries for *L. japonica* release plans (Table 2). In the

356   United States and Canada, the potential distribution of *L. japonica* overlapped only one-third of

357   *D. suzukii's* potential distributional area, demanding strict site-specific release planning. Site-

358   specific pest management utilizing pest distributional information is preferred over uniform

359   pest management (Park, Krell & Carroll, 2007). However, for effective site-specific biological

360   control of pests, not only the pest distributional information but also the niche overlap

361   between pest and parasitoids must be taken into account. Irrespective of the biocontrol

362   coverage in *D. suzukii* invaded regions, any *L. japonica* release strategy has to rely strictly on

363   specific details of both site and niche considerations.

364   In conclusion, this study illustrates a cost-effective pre-assessment strategy that can be

365   applied to any biological control management program before beginning the labor-intensive,

366   time-consuming, and expensive field experiments. Availability of a greater number of

367   occurrence records of *L. japonica* would further enhance the understanding of the

368   distributional potential of this potential biocontrol agent worldwide.

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Figure 1

Distributional information

Representation of the known distribution of the pest *Drosophila suzukii*, and parasitoid *Leptopilina japonica* based on occurrence databases and published literature.

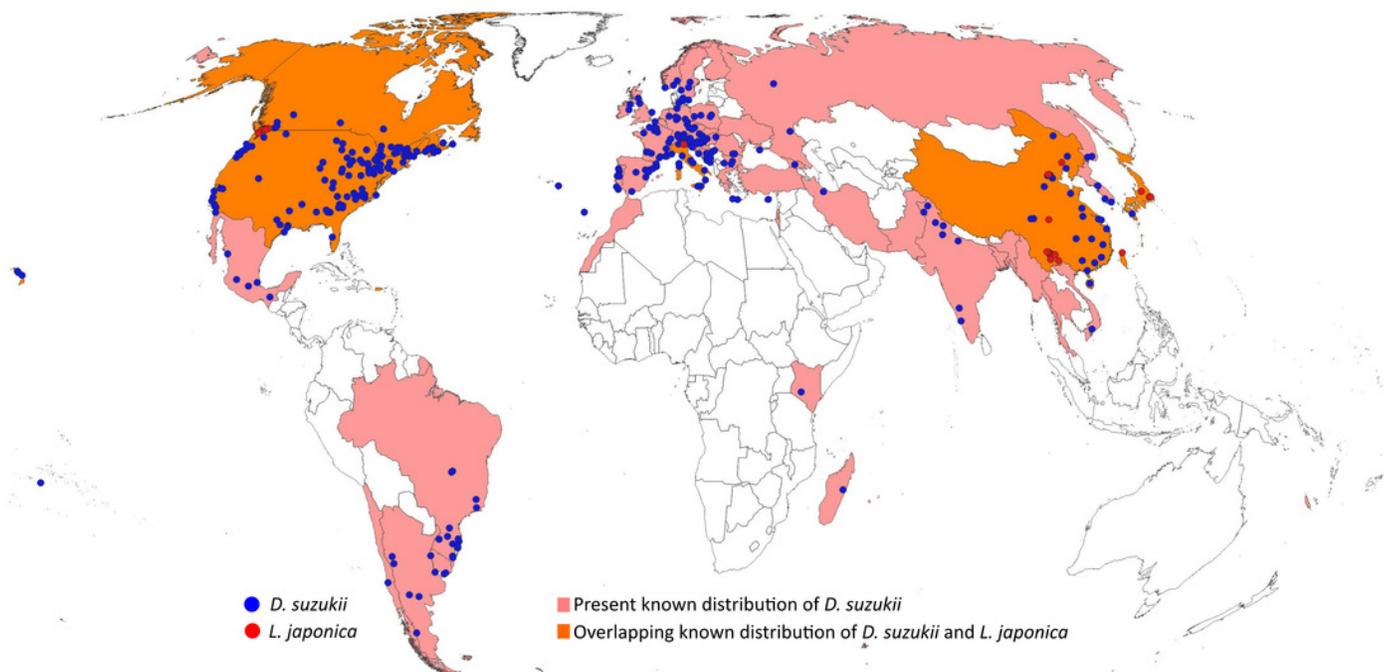
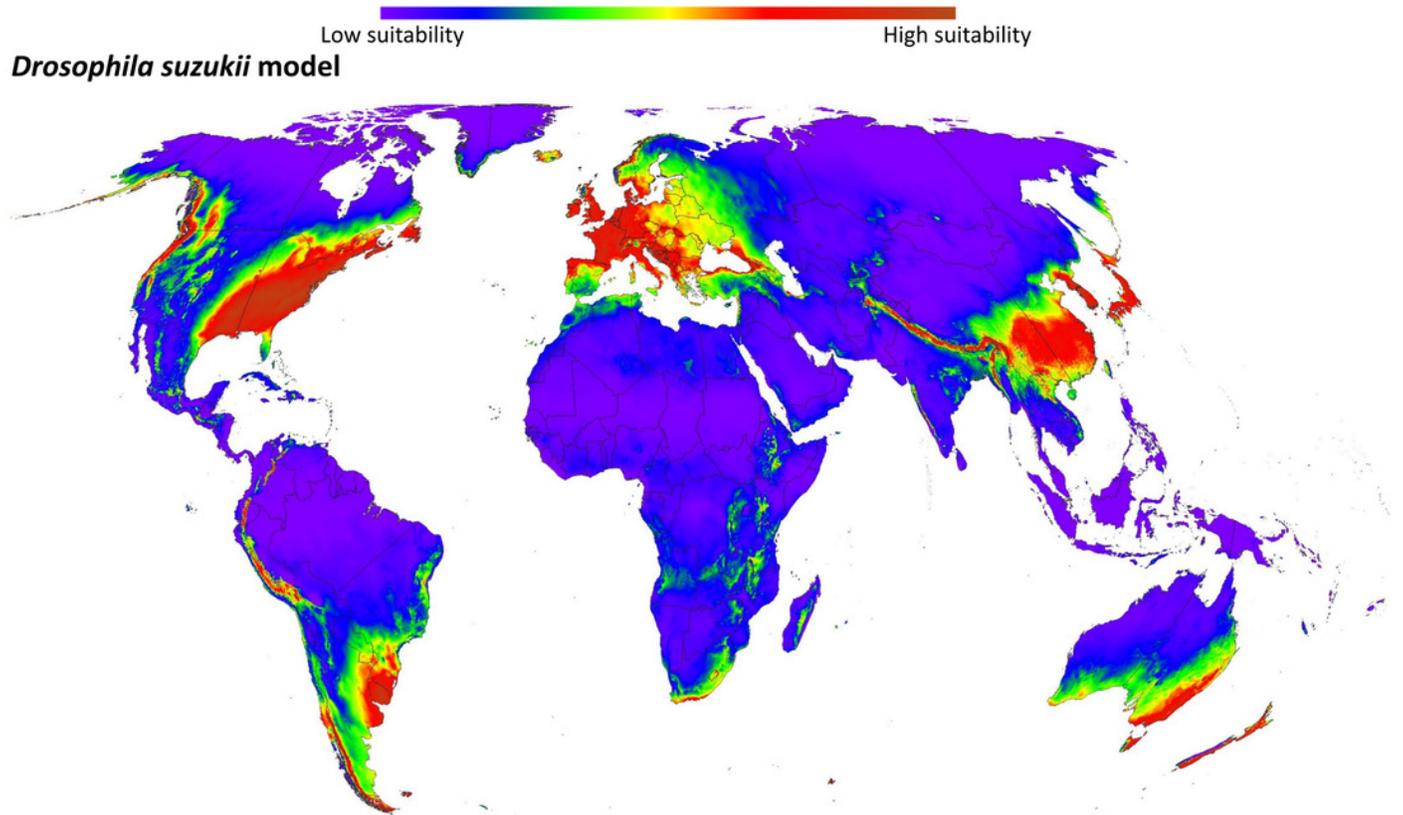



Figure 2

Ecological niche models

Predicted distribution of potential distributional areas of *Drosophila suzukii* and *Leptopilina japonica* across the world

Low suitability ██████████████████████ High suitability

Drosophila suzukii model

Leptopilina japonica model

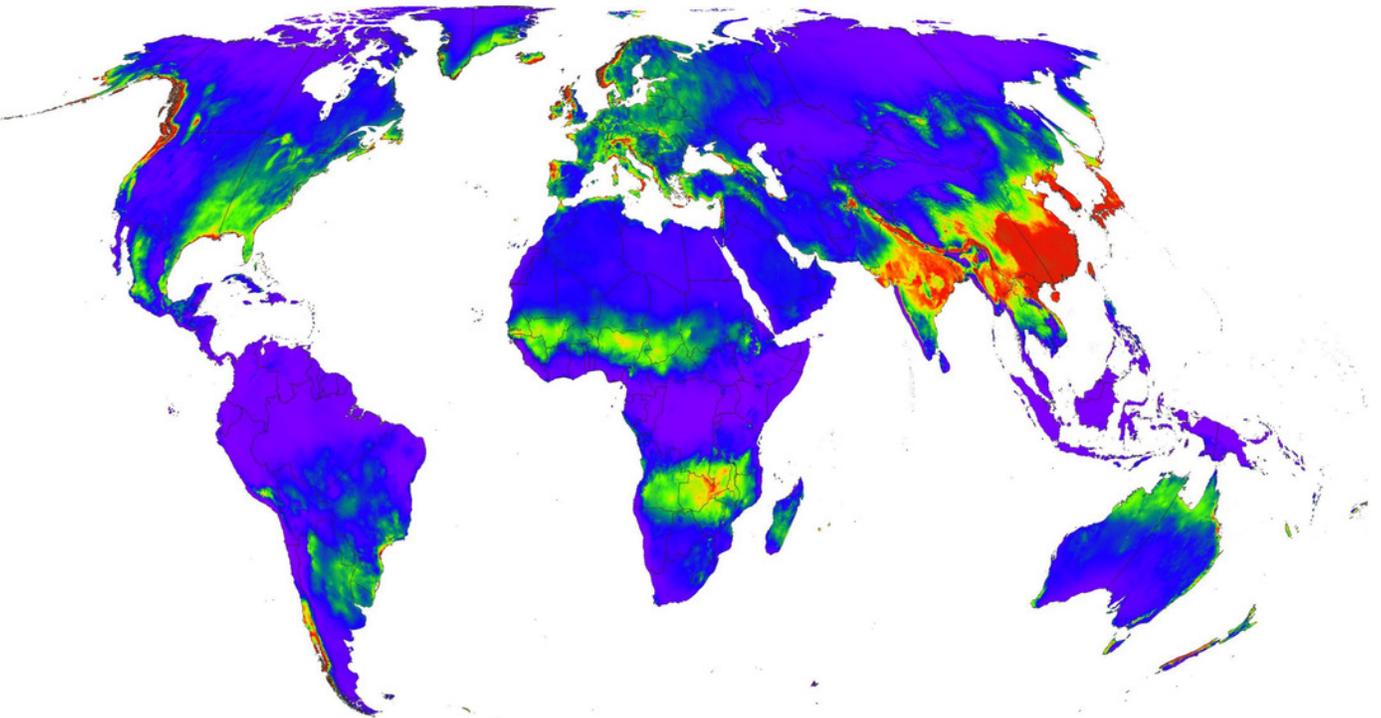
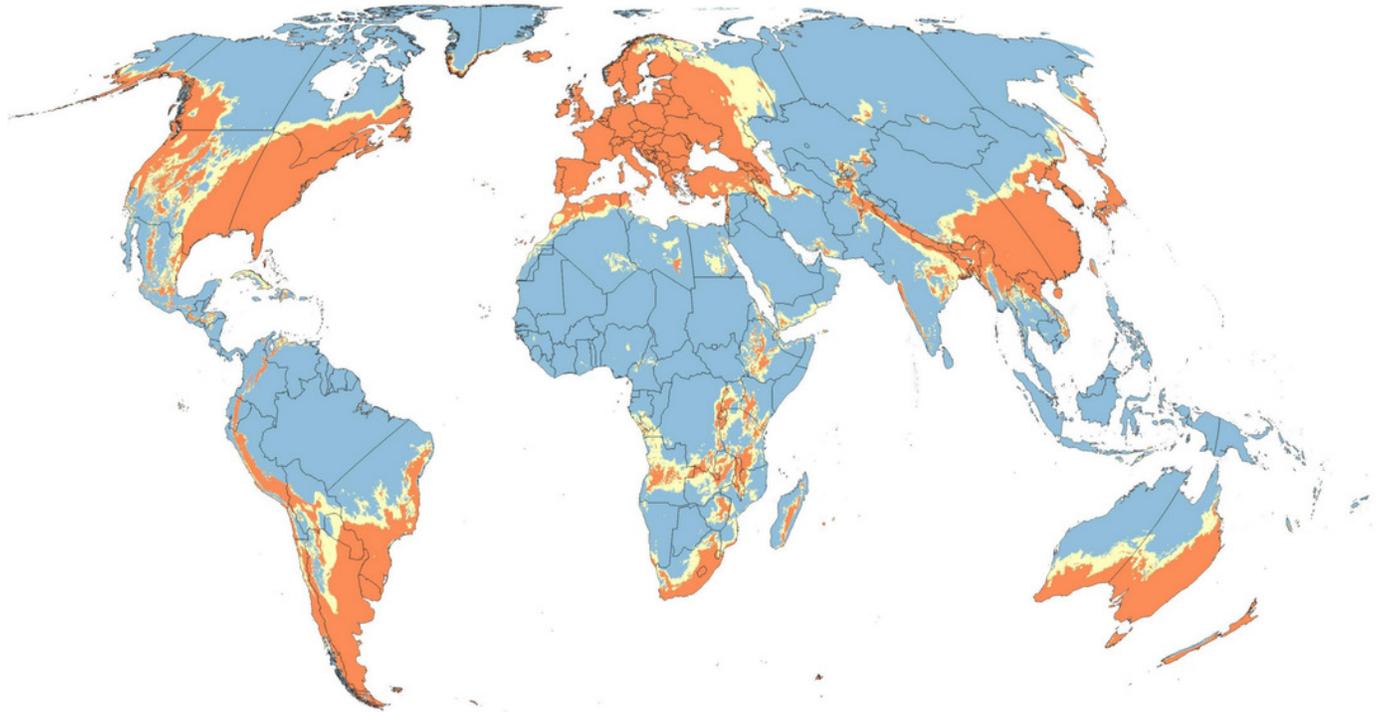



Figure 3

Binary models

Modeled suitable areas for *Drosophila suzukii* and *Leptopilina japonica* based on thresholding at E = 5% and E = 10%

Drosophila suzukii binary model

Leptopilina japonica binary model

■ Absence
■ Extension of suitability at $E = 5\%$
■ Suitability at $E = 10\%$

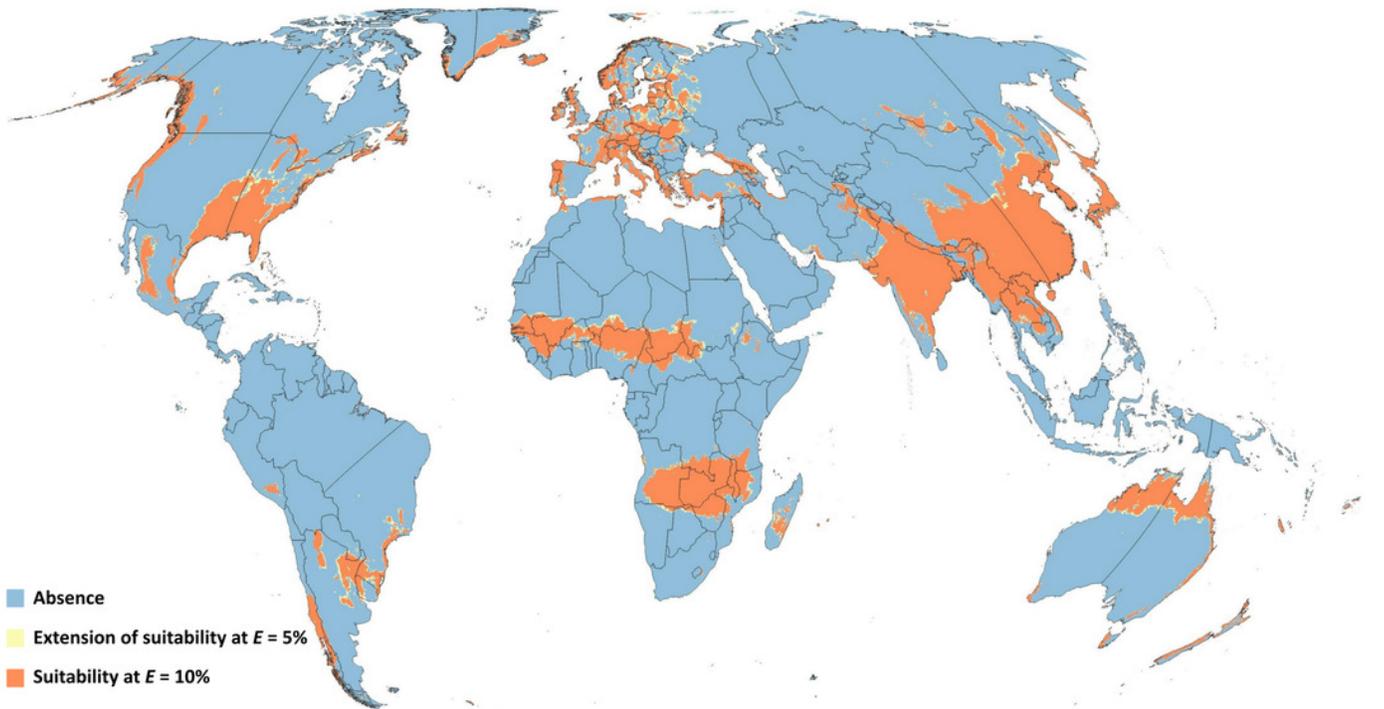
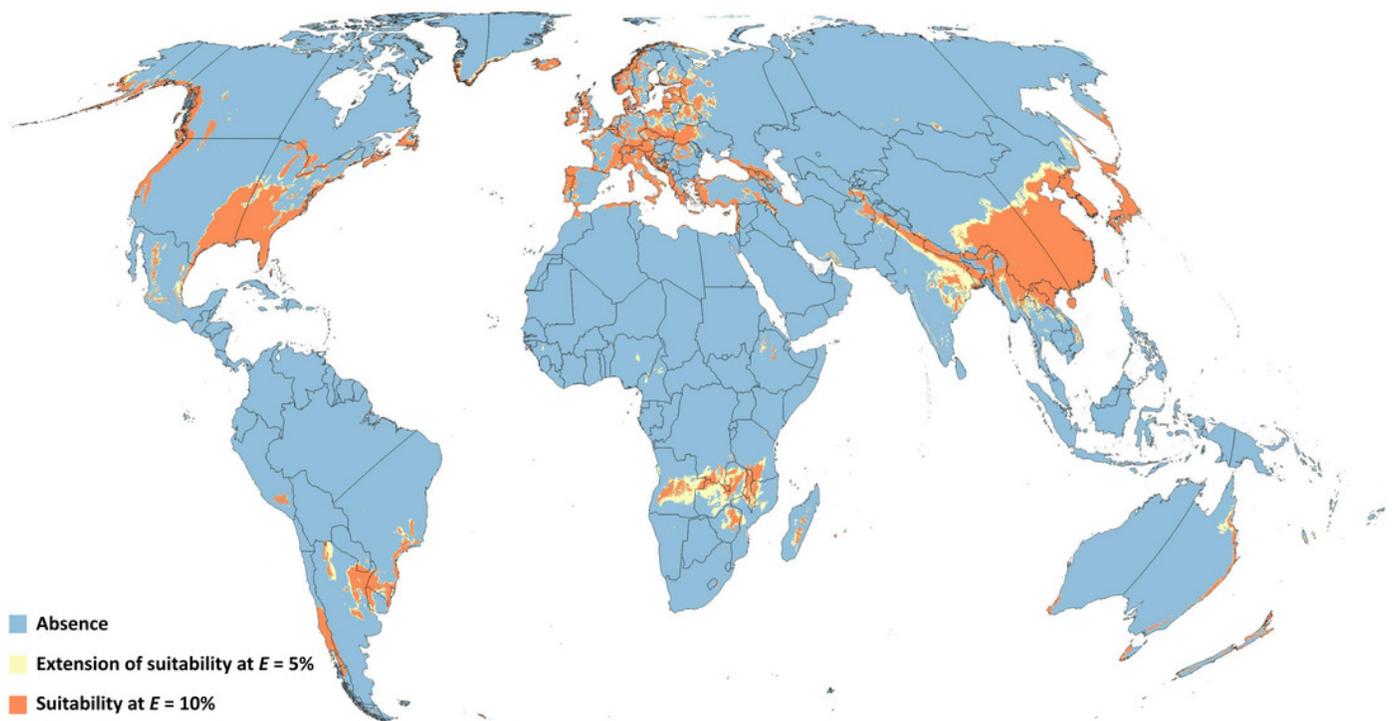



Figure 4

Overlapped niches

Representation of modeled suitable biocontrol areas in terms of overlapping climatic niches of *Drosophila suzukii* and *Leptopilina japonica*

Model evaluation

Performance summary of pest, parasitoid, and two-species parasitoid models

Species	Models	Mean AUC ratio	OR	AICc
Leptopilina japonica	M_2.0_F_lp_Set_7	1.76	0.00	839.55
Drosophila suzukii	M_0.6_F_lq_Set_4	1.47	0.04	8365.78
Two-species	M_1.0_F_l_Set_6	1.79	0.07	798.08

OR-Omission rate. Name of models indicates the details of regularization multiplier value, feature class and environmental dataset.

Biocontrol coverage

Modeled potential for biocontrol coverage corresponding to the potential distribution of pest (*Drosophila suzukii*) and parasitoid (*Leptopilina japonica*). E indicates thresholding level

Country	Pest distribution (km²)		Overlapping wasp distribution (km²)		Biocontrol coverage (%)	
	$E = 5\%$	$E = 10\%$	$E = 5\%$	$E = 10\%$	$E = 5\%$	$E = 10\%$
Afghanistan	120756.19	77038.50	87583.33	69587.73	72.53	90.33
Albania	28019.74	28019.74	27942.43	27810.06	99.72	99.25
Algeria	444458.49	222597.11	46214.07	43026.86	10.40	19.33
Andorra	452.25	452.25	407.86	344.49	90.19	76.17
Angola	725060.74	209636.29	422423.06	152662.75	58.26	72.82
Argentina	2610531.21	2136682.12	487246.09	326141.97	18.66	15.26
Armenia	29588.31	27565.71	9573.41	7333.56	32.36	26.60
Australia	4132533.88	2994970.31	284270.56	200146.28	6.88	6.68
Austria	83993.20	83993.20	77002.77	73155.41	91.68	87.10
Azerbaijan	85470.21	82660.14	29145.06	24386.68	34.10	29.50
Bahamas	9429.07	9429.07	7814.62	7766.95	82.88	82.37
Bangladesh	128942.02	101548.17	88769.51	75811.84	68.84	74.66
Belarus	207499.14	207499.14	131398.08	72083.15	63.32	34.74
Belgium	30597.07	30597.07	27115.20	24893.18	88.62	81.36
Bhutan	38954.11	37112.34	33859.02	32179.91	86.92	86.71
Bolivia	475959.05	203932.55	3394.30	1816.23	0.71	0.89
Bosnia and Herzegovina	51824.53	51824.53	32450.62	28581.47	62.62	55.15
Brazil	2088214.01	1385571.53	365390.65	278811.34	17.50	20.12
Brazilian Island	2.82	2.82	2.82	2.82	100.00	100.00
Bulgaria	112513.51	112513.51	1544.03	971.72	1.37	0.86
Cabo Verde	1750.55	630.75	479.08	269.84	27.37	42.78
Cambodia	6253.09	790.65	2055.16	133.61	32.87	16.90
Cameroon	26383.63	1809.00	14635.67	169.68	55.47	9.38
Canada	2793734.16	2155273.21	565894.51	487960.16	20.26	22.64
Chile	582097.31	475909.40	205933.41	193145.19	35.38	40.58
China	4488161.45	3862635.87	4374430.56	3827973.12	97.47	99.10
Colombia	91947.38	68214.15	340.13	340.13	0.37	0.50
Croatia	52932.84	52932.84	40105.39	36135.71	75.77	68.27
Cuba	81360.79	7022.89	510.20	26.30	0.63	0.37
Cyprus	5122.47	3433.88	4427.71	3433.88	86.44	100.00
Cyprus No Mans	296.73	33.20	72.49	33.19	24.43	99.98
Czechia	78758.87	78758.87	68665.32	58491.87	87.18	74.27
Democratic Republic of the Congo	420374.68	150483.68	161159.34	75871.68	38.34	50.42
Denmark	202079.28	130500.31	166506.11	111597.35	82.40	85.52
Djibouti	13137.52	--	467.25	--	3.56	--
Egypt	180965.62	--	120.06	--	0.07	--
Equatorial Guinea	14.17	14.17	14.17	14.17	100.00	100.00
Estonia	44389.34	44389.34	43945.97	37804.22	99.00	85.17
Ethiopia	413796.88	155614.76	39007.25	21656.50	9.43	13.92
Finland	300806.37	238124.40	93531.28	50354.32	31.09	21.15
France	562246.74	556671.13	274309.40	231951.91	48.79	41.67
Gabon	45201.71	2552.27	1222.11	267.10	2.70	10.47
Georgia	69301.13	69301.13	61604.07	58319.71	88.89	84.15
Germany	355684.24	355684.24	192739.07	159474.97	54.19	44.84
Greece	123576.16	123576.16	84346.67	79969.84	68.25	64.71
Guatemala	22913.49	16722.41	2064.41	1734.17	9.01	10.37

Guinea	4192.93	83.65	3857.20	83.65	91.99	100.00
Hungary	93200.95	93200.95	7046.93	3609.03	7.56	3.87
Iceland	98272.76	94978.48	88865.07	83482.50	90.43	87.90
India	1274811.80	685789.21	1102039.55	543419.47	86.45	79.24
Iran	336850.53	116130.87	63329.32	37732.16	18.80	32.49
Iraq	34709.55	21099.93	29371.04	19865.20	84.62	94.15
Ireland	66629.91	66332.38	55507.01	52328.26	83.31	78.89
Israel	13449.48	8745.65	11881.97	8745.68	88.35	100.00
Italy	295635.80	295613.28	264427.13	250415.73	89.44	84.71
Japan	357893.96	356945.12	357893.91	356945.07	100.00	100.00
Jordan	4921.88	507.56	1872.74	507.56	38.05	100.00
Kazakhstan	201132.14	41577.90	706.08	190.06	0.35	0.46
Kosovo	10913.08	10913.08	1765.30	1373.59	16.18	12.59
Kyrgyzstan	90256.07	43305.48	1333.13	63.53	1.48	0.15
Laos	186149.10	124451.87	149422.53	103577.26	80.27	83.23
Latvia	64162.08	64162.08	60919.43	54215.14	94.95	84.50
Lebanon	9800.04	8682.25	9001.50	8503.74	91.85	97.94
Lesotho	30106.52	30106.52	318.96	28.00	1.06	0.09
Libya	184279.76	37328.30	5699.73	4033.72	3.09	10.81
Liechtenstein	137.25	137.25	137.25	137.25	100.00	100.00
Lithuania	64816.37	64816.37	40725.99	27301.77	62.83	42.12
Luxembourg	2608.47	2608.47	2608.47	2328.89	100.00	89.28
Madagascar	187519.17	104765.96	79329.34	39438.11	42.30	37.64
Malawi	111209.70	74340.02	108138.07	72489.54	97.24	97.51
Malta	270.90	270.90	270.90	270.90	100.00	100.00
Mauritius	1802.79	94.64	1752.24	44.08	97.20	46.58
Mexico	691072.40	296644.27	251952.23	125678.99	36.46	42.37
Moldova	33206.48	33206.48	4811.96	1963.38	14.49	5.91
Monaco	3.96	3.96	3.97	3.97	100.04	100.04
Montenegro	13631.45	13631.45	11836.29	11080.44	86.83	81.29
Morocco	354222.81	165793.77	27266.40	23178.86	7.70	13.98
Mozambique	278561.34	73923.95	154695.03	54111.84	55.53	73.20
Myanmar	445821.06	375179.90	361982.68	301972.44	81.19	80.49
Namibia	66288.68	--	483.94	--	0.73	--
Nepal	145624.62	141915.07	121958.80	119500.60	83.75	84.21
Netherlands	36761.20	36260.59	17922.53	15136.66	48.75	41.74
New Zealand	217910.77	212122.44	96771.30	83214.96	44.41	39.23
Nigeria	15934.24	566.67	12716.29	337.88	79.80	59.63
North Korea	120894.87	118933.68	120894.94	118933.71	100.00	100.00
North Macedonia	25385.27	25385.27	3664.82	3358.17	14.44	13.23
Northern Cyprus	2290.99	429.38	1414.83	429.39	61.76	100.00
Norway	285817.32	263207.96	225627.24	206147.09	78.94	78.32
Oman	28552.55	1859.00	3159.53	1543.99	11.07	83.06
Pakistan	153944.54	83124.10	85069.07	49372.57	55.26	59.40
Paraguay	341582.31	230965.19	37691.58	29169.69	11.03	12.63
Peru	495995.98	431000.71	49307.80	45336.48	9.94	10.52
Poland	312841.88	312841.88	214155.94	156484.69	68.46	50.02
Portugal	89463.23	89463.23	73702.57	68237.60	82.38	76.27
Republic of Serbia	77628.71	77628.71	8713.93	5548.68	11.23	7.15

Republic of the Congo	72181.30	6283.59	446.79	26.96	0.62	0.43
Romania	235895.13	235895.13	79961.95	62526.40	33.90	26.51
Russia	3710679.26	2033909.21	662712.71	395046.93	17.86	19.42
San Marino	60.32	60.32	60.32	60.32	100.00	100.00
Slovakia	48457.79	48457.79	25232.78	22596.49	52.07	46.63
Slovenia	20295.63	20295.63	19931.57	19671.10	98.21	96.92
South Africa	902797.42	591473.81	7170.51	5131.33	0.79	0.87
South Korea	94652.90	94652.90	94652.97	94652.97	100.00	100.00
Spain	502618.58	495648.00	136222.35	112053.05	27.10	22.61
Sudan	2656.20	--	83.33	--	3.14	--
Sweden	436539.07	378204.51	158054.75	115334.67	36.21	30.50
Switzerland	41344.82	40890.87	37361.01	36701.13	90.36	89.75
Syria	22207.60	12452.65	14768.48	12044.15	66.50	96.72
Taiwan	24849.72	20605.88	21861.78	18151.55	87.98	88.09
Tajikistan	73944.07	45547.87	38519.69	25750.20	52.09	56.53
Thailand	117459.90	22050.79	103622.02	22024.89	88.22	99.88
Tunisia	78947.05	53298.18	10701.95	8871.64	13.56	16.65
Turkey	761388.06	678724.38	257025.95	224311.08	33.76	33.05
Turkmenistan	59106.76	4758.25	160.83	160.83	0.27	3.38
Ukraine	570440.95	570440.95	182074.04	152631.46	31.92	26.76
United Arab Emirates	428.91	15.84	155.89	15.84	36.35	100.00
United Kingdom	247439.54	243271.25	134076.15	124951.47	54.19	51.36
Tanzania	540638.96	197481.86	110629.43	79486.65	20.46	40.25
United States of America	7267495.86	5752263.93	2879003.63	2546609.52	39.61	44.27
Uruguay	176465.55	176465.55	75249.12	56325.26	42.64	31.92
Uzbekistan	64090.46	22578.88	12752.88	9003.24	19.90	39.87
Vatican	0.01	0.01	0.01	0.01	100.00	100.00
Vietnam	208079.26	173719.30	179340.06	158519.90	86.19	91.25
Zambia	471456.61	148179.91	452563.86	146359.35	95.99	98.77
Zimbabwe	186694.49	78523.17	135058.40	69964.04	72.34	89.10