DDRP: real-time phenology and climatic suitability modeling of invasive insects

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Short title: DDRP: a new modeling tool for invasive insects

Abstract

1 Rapidly detecting and responding to new invasive species and the spread of those that are

2 already established is essential for reducing their potential threat to food production, the

3 economy, and the environment. We describe a new multi-species spatial modeling platform that

4 integrates mapping of phenology and climatic suitability in real-time to provide timely and

5 comprehensive guidance for stakeholders needing to know both where and when invasive insect

6 species could potentially invade the conterminous United States. The Degree-Days, Risk, and

7 Phenological event mapping (DDRP) platform serves as an open-source and relatively easy-to-

8 parameterize decision support tool to help detect new invasive threats, schedule monitoring and

9 management actions, optimize biological control, and predict potential impacts on agricultural

10 production. DDRP uses a process-based modeling approach in which degree-days and

11 temperature stress are calculated daily and accumulate over time to model phenology and

12 climatic suitability, respectively. Products include predictions of the number of completed

13 generations, life stages present, dates of phenological events, and climatically suitable areas

14 based on two levels of climate stress. Species parameters can be derived from laboratory and

15 field studies, and from published and newly fitted CLIMEX models. DDRP is written entirely in

16 R, making it flexible and extensible, and capitalizes on multiple R packages to generate gridded

17 and graphical outputs. We illustrate the DDRP modeling platform and the process of model

18 parameterization using two invasive insect species as example threats to United States

19 agriculture: the light brown apple moth, *Epiphyas postvittana*, and the small tomato borer,

20 *Neoleucinodes elegantalis*. We then discuss example applications of DDRP as a decision support

21 tool, review its potential limitations and sources of model error, and outline some ideas for future

22 improvements to the platform.

Introduction

24 Invasive insects in the United States are a significant threat to the economy, environment, food

25 security, and human health [1–3]. They cause billions of dollars in damage to forests each year

26 [1,2], and their potential cost to food crop production is among the highest of any country [3].

27 Insect invasions in the United States also reduce the abundance and diversity of native species,

28 which negatively impacts ecosystem functions and services such as soil health, nutrient cycling,

29 and wildlife habitat [1,2]. Rapidly detecting and responding to new invasive insects and the

30 spread of those that are already established before they can cause significant economic and

31 environmental damage has therefore become a major priority [2,4].

32   Modeling climatic suitability (risk of establishment) and the timing of seasonal activities

33 (phenology) of invasive insect species can help stakeholders including farmers, natural resource

34 managers, and surveillance teams detect and prevent their establishment, slow their spread, and

35 manage existing populations more sustainably and economically [5]. Estimates of climatic

36 suitability identify areas to concentrate surveillance or management resources and efforts [6–8],

37 whereas real-time (i.e. current) or forecasted predictions of phenology can improve the timing of

38 surveillance and integrated pest management (IPM) efforts such as monitoring device

39 installation, pesticide applications, and biological control release [9–11]. Additionally, estimates

40 of climatic suitability, phenology, and voltinism (number of generations per year) can help

41 growers predict the impact of pests and diseases on agricultural production and associated

42 economic losses [12].

43   Degree-day models that predict insect phenology are an established tool for decision support

44 systems that assist stakeholders with scheduling surveillance, monitoring or IPM operations for

45 numerous pest species over the growing season [13–16]. Most degree-day models predict

46   phenology by measuring linear relationships between temperature and development rate, and

47   they employ daily time steps to estimate degree-days using daily minimum and maximum

48   temperature (T_{min} and T_{max}, respectively) data. In the daily time step, degree-days accumulate if

49   heat exceeds the lower developmental temperature threshold of a species (and below its upper

50   threshold for some calculation methods) during a 24-hour period [13,14,16]. Several web-based

51   platforms host degree-day models for insect pest species in the United States, offering users

52   opportunities to model phenology of multiple species at single locations (site-based model) or

53   across a certain area (spatialized model). These platforms include but are not limited to Michigan

54   State University's Enviroweather (https://www.enviroweather.msu.edu), Oregon State

55   University's USPEST.ORG (https://uspest.org/wea/), and the USA National Phenology Network

56   (https://www.usanpn.org) [17,18].

57   Despite their widespread use, currently available degree-day modelling platforms are in need

58   of improvements. None of them integrate predictions of phenology and climatic suitability,

59   which would provide guidance on the question of both where and when—e.g. is an area at high

60   risk of establishment, and if so, then when will the species emerge or begin a specific activity?

61   For most species, addressing this two-part question would require finding, potentially

62   purchasing, and learning how to use two separate platforms. Additionally, many phenology

63   modeling platforms use oversimplified models that make broad assumptions about insect

64   biology, such as assuming a single lower developmental temperature threshold for multiple

65   species, or assuming that an entire population emerges from overwintering at a single time.

66   However, developmental temperature thresholds may vary widely across insect species, and

67   development rates often vary within populations [19–21]. A biologically unrealistic model may

68   produce inaccurate predictions of phenological events (e.g. spring emergence, first adult flight,

4

69   egg-hatching) or voltinism. Moreover, most platforms are capable of forecasting phenology only

70   a week or two into the future in specific states or regions. However, stakeholders may need to

71   plan operations several weeks in advance, potentially in areas that are outside the geographic

72   bounds of predictive models.

73   In this study, we introduce a new spatial modeling platform, DDRP (short for <u>D</u>egree-<u>D</u>ays,

74   establishment <u>R</u>isk, and <u>P</u>henological event maps) that generates real-time and forecast

75   predictions of phenology and climatic suitability (risk of establishment) of invasive insect

76   species in the conterminous United States (CONUS). The objective of DDRP is to improve the

77   efficiency and effectiveness of programs that aim to detect new or spreading invasive insect

78   species in the United States, or to monitor and manage species that are already well-established.

79   The platform is written entirely in the R statistical programming language (R Development Core

80   Team 2019), making it flexible and extensible, and has a simple command-line interface that can

81   be readily implemented for online use. Gridded temperature data for DDRP may include the

82   entire CONUS or a specific region or state, and may be at any spatial resolution that can be

83   handled by the user's computing system. DDRP will generally use observed and future (forecast

84   or recent average) temperature data because it was designed to be run as a within-season decision

85   support tool that can provide guidance on where and when to expect the pest to appear each year,

86   but it will accept temperature data for any time period. Model products include gridded (raster)

87   and graphical (map) outputs of life stages present, number of generations, phenological events,

88   and climatic suitability.

89   First, we describe the modeling process and workflow of DDRP, summarize types of model

90   products (Fig 1), and review its system and software requirements. Next, we demonstrate its

91   capabilities and the process of model parameterization using two invasive insect species which

92   threaten agricultural biosecurity in the United States: the small tomato borer, *Neoleucinodes*

93   *elegantalis* [Guenée (Lepidoptera: Crambidae)], and the light brown apple moth, *Epiphyas*

94   *postvittana* [Walker, 1863 (Lepidoptera: Tortricidae)]. These species were chosen because they

95   have been well-studied in terms of their developmental requirements, and previous climatic

96   suitability studies provide a basis for parameterizing the climatic suitability model in DDRP.

97   Additionally, models for these species are intended to aid surveillance teams at the Cooperative

98   Agricultural Pest Survey (CAPS) pest detection program, which supports the USDA Animal and

99   Plant Health Inspection Service (APHIS) as it works to safeguard agricultural and environmental

100   resources in the United States. The DDRP platform will be a useful decision support tool for

101   preventing, monitoring, and managing new and emerging invasive pests in the United States.

102

Methods

1) Model inputs

Temperature data

106   DDRP requires daily T_{min} and T_{max} data in a gridded format for an area of interest in CONUS.

107   For real-time modeling, we have been using daily T_{min} and T_{max} data at a 4 km spatial resolution

108   from the PRISM (Parameter-elevation Relationships on Independent Slopes Model) database

109   (available at http://www.prism.oregonstate.edu) [22]. Daily PRISM data become available *ca.* 1

110   day after weather station observations are reported, and are typically updated and improve in

111   quality as more observations are added (see PRISM website for details). The phenology mapping

112   system of the USA National Phenology Network [18] uses Real-Time Mesoscale Analysis

113   (RTMA) weather data at a 2.5 km resolution, which are available within hours after data are

114   observed. The daily T_{min} and T_{max} RTMA data set could potentially be used in DDRP; however,

115   the RTMA methodology lacks PRISM's update and quality control regimes [22]. Another

116   alternative is Daymet v3, which offers daily climate data for North America, Hawaii, and Puerto

117   Rico at a very high spatial resolution (1 km) (https://daymet.ornl.gov) [23]. However, Daymet

118   data are released months after the end of each year, so they would be less useful for within-

119   season modeling and decision support.

120   For forecast modeling, DDRP is currently configured to use either monthly-updated, daily-

121   downscaled NMME (North American Multi-Model Ensemble) 7-month forecasts at a 4 km

122   resolution [24], or recent 10-year average PRISM daily data that are calculated on a bi-monthly

123   basis. We consider 10-year average data to be an improvement over 30-year climate normals for

124   producing forecasts because temperatures in CONUS have significantly increased over the past

125   30 years [25,26]. The match of mean forecasts of the NMME model's ensemble to the observed

126   value (i.e. skill) varies both spatially and temporally due to topography, season, and the presence

127   of an El Niño-Southern Oscillation (ENSO) signal [27,28]. It may therefore be more

128   conservative, and provide more consistent predictions, to use 10-year averages instead of NMME

129   data to avoid potential issues with skill. However, we caution that the 10-year average data do

130   not have simulated variation in daily T_{min} and T_{max}, which may result in the under-prediction of

131   degree-day accumulation in the spring or fall as daily T_{max} only slightly exceeds the lower

132   developmental threshold of a species, or for cooler sites that have temperatures that are often

133   near the threshold. We have also prepared and plan to use the National Weather Service gridded

134   National Digital Forecast Database (NDFD) 7-day forecasts

135   (https://www.weather.gov/mdl/ndfd_info) [29] for use in DDRP.

136

137   ***Phenology modeling: species data and parameters***

138   The life history and behavior of a target species must be considered for appropriateness to model

139   in DDRP. In its current form, the platform can model four separate life stages (the egg, the larva

140   or nymph, the pupa or pre-oviposition, and the adult) plus a separately parameterized

141   overwintering stage. As movement and migration are not handled by DDRP, it is currently

142   limited in its ability to model migratory species, such as those that may establish in southern

143   areas of their potential range and migrate yearly to more northern areas. Species that lack an

144   overwintering stage, which are common in tropical and subtropical areas, may be difficult to

145   model because the timing of first spring activities and stages present cannot be accurately

146   estimated. Currently DDRP is entirely temperature-driven, so species whose growth and

147   reproduction are strongly influenced by additional environmental factors such as day length or

148   moisture may not be accurately modeled.

149   DDRP requires data on the developmental temperature thresholds (in either degrees Celsius

150   or Fahrenheit) and durations for each life stage of an insect species in degree-days (Fig 1 and

151   Table 1). These data are typically collected in the laboratory by measuring how temperature

152   influences the rate of development, although data derived from season-long monitoring studies

153   are also used [15,30]. A different developmental threshold may be assigned to each stage,

154   although we typically solve for a common threshold if differences across the stages are minimal.

155   Presently, the model depends upon a fixed starting date such as January 1, specified by the user

156   for the entire region of interest. The duration of the overwintering stage represents the number of

157   degree-days that must accumulate from the start of the year for the stage to complete, and

158   indicates the start time for the model since other stages would then commence develop.

159   Users must specify the number of degree-days that are required for the overwintering stage to

160   complete development and emerge for the growing season. These data are typically gathered

161   using field monitoring studies, whereby the temporal distribution of emergence times and

162   number of individuals that emerge on a given date is documented [e.g. 32]. Assigning a single

163   value to the overwintering stage duration parameter would assume that an entire population

164   develops simultaneously, which may not be biologically realistic because several intrinsic (with

165   a genetic basis) and extrinsic (e.g. microclimate, nutrition) factors can produce variation in

166   development rates within a species [21,32]. Indeed, phenology models that incorporate

167   developmental variability in a population may have increased predictive power [19,21,33].

168   DDRP therefore allows the duration of the overwintering stage to vary across a user-defined

169   number of cohorts (groups of individuals in a population). Much of the intrinsic variability in

170   insect development during a generation often occurs in the first stadium after overwintering [34],

171   although developmental variation may occur in any life stage [19,35,36]. DDRP uses five

172   parameters to generate a frequency distribution of emergence times: the mean, variance, low

173   bound, and high bound of emergence times, and the shape of the distribution (Gaussian or

174   lognormal; Table 1). The platform uses these data to estimate the relative size of the population

175   represented by each cohort, which initializes the population distribution that is maintained during

176   subsequent stages and generations. Individuals within each cohort develop in synchrony.

177   Users may specify the timing (in degree-days) of phenological events that are important to

178   their target system to generate phenological event maps in DDRP, which depict the estimated

179   calendar dates of the event over a time frame of interest. We typically generate phenological

180   event maps based on temperature data for an entire year so that events for multiple generations of

181   each of the five life stages are modeled. For example, phenological event maps that depict when

182   the overwintering stage would emerge may be useful for identifying start dates for surveillance

183   operations for a species, whereas maps for subsequent generations could help with planning

184   operations later in the year. The timing of phenological events may be based on life stage

185   durations (e.g. the end of the egg stage signifies egg-hatching), or on occurrences within a stage

186   such as midpoint (to approximate peak) of oviposition or midpoint of adult flight. Currently, one

187   user-defined phenological event for each life stage for up to four generations may be modeled,

188   although the platform could be modified to predict multiple events for each stage (e.g. first,

189   midpoint, and end of the stage) for any numbers of generations.

190

191   *Climate suitability modeling: species data and parameters*

192   Climatic suitability modeling in DDRP is based on cold and heat stress accumulation and

193   requires data on temperature stress threshold and limits of a species (Fig 1 and Table 1). While

194   estimates of these parameters may be estimated from laboratory or field experiments, such data

195   are lacking for most species. Additionally, extrapolating laboratory data to the field to project

196   accumulation of stress is difficult due to oversimplification of the number of variables and the

197   temporal and spatial variation in natural environments [37]. We have been using the CLIMEX

198   software [38] (Hearne Scientific Software, Melbourne, Australia) to assist with climatic

199   suitability model parameterization in DDRP, which is one of the most widely used species

200   distribution modeling tools for agricultural, livestock and forestry pests and non-pests [6,7].

201   Laboratory collected data may help with parameterizing a CLIMEX model; however, model

202   parameters are fine-tuned and the model is fitted using observations from the species' known

203   geographical distribution [38,39]. CLIMEX uses a similar process-based modeling approach as

204   DDRP, wherein climatic suitability of an area to a species is influenced by climate stress

205   accumulation. Model products generated by the two programs, including maps of temperature

206   stress accumulation, are therefore directly comparable.

207   DDRP was designed to be complementary to CLIMEX is several ways to facilitate climatic

208   suitability model parameterization, but the two programs also differ in several respects (Table 2).

209   Importantly, DDRP was designed to model climatic suitability based on daily current or forecast

210   temperature data at fine spatial scales (e.g. a single state or region), which would give users

211   insight into the potential risk of establishment or spread during a particular season or year. In

212   contrast, CLIMEX is normally used to estimate a species' potential distribution using coarse-

213   scale 10′ and 30′ resolution global gridded 30-year monthly climate normals centered on 1975

214   (1961–1990) or future projections from selected global circulation models (GCMs) [40]. In

215   theory CLIMEX could be used for real-time climatic suitability, but it has no native ability to

216   import and process common gridded formats and is incapable of using daily resolution climate

217   data. Thus, DDRP's climate suitability models are intended to improve the efficiency of

218   surveillance and trap deployment at a relatively small focal area for a current or near-future time

219   period, whereas CLIMEX models provide a more general and coarse-scale assessment of

220   suitability based on averaged climate data.

221   Relying on real-time climatic suitability models for decision support on where to employ pest

222   management and eradication operations for a given year or season is preferable to using models

223   based on 30-year climate normals. A model that uses current climate data is more biologically

224   relevant because the risk of establishment in an area would be affected by the conditions that a

225   species physically experiences, not by averages of historical climate. Additionally, climate in

226   CONUS is changing rapidly, so models based on climate normals may produce unrealistic

227   predictions of present-day climatic suitability. Over the past *ca*. 30 years, the average annual

228   temperature in CONUS has increased by 1.2°F (0.7°C), the number of freezing days has

229   declined, and extreme temperature events have increased in frequency and intensity [25,26].

230   Nonetheless, DDRP is not currently capable of including moisture factors in the modeling

231   process like CLIMEX, so model predictions for moisture-sensitive species in very arid or wet

232   areas should be interpreted with caution. We present a more detailed comparison of the features

233   of each platform in Table 2, and discuss the potential implications of generating a climate

234   suitability model based solely on temperature in the 'Discussion.'

235   We compare CLIMEX's predictions of temperature stress accumulation and overall climate

236   suitability to similar products in DDRP to help parameterize a DDRP climate suitability model.

237   Temperature stress thresholds may be calibrated so that predictions of cold and heat stress

238   accumulation at the end of the year are spatially concordant with CLIMEX's predictions.

239   Climatic suitability in CLIMEX is estimated with the Ecoclimatic Index (EI), which is scaled

240   from 0 to 100, and integrates the annual growth index and climate stress indices to give an

241   overall measure of favorableness of a location or year for long-term occupation by the target

242   species [38,39]. Typically an EI approaching 0 indicates an unfavorable climate for long-term

243   survival, while an EI exceeding 20 or 30 (depending on the species) indicates a highly suitable

244   climate [38,39]. As discussed in more detail in 'Case Studies', temperature stress limits in DDRP

245   can be adjusted so that areas predicted to have highly suitability according to CLIMEX are also

246   included in DDRP's prediction of the potential distribution.

247   Comparing DDRP climatic suitability model products to those of CLIMEX for model fitting

248   purposes is naturally more appropriate when temperature data are derived from the same time

249   period. We have therefore been using a PRISM T_{min} and T_{max} 30-year average dataset centered on

250   1975 (1961−1990) to match the time-schedule of the CliMond CM10 (also 1961−1990) world

251   climate dataset currently supplied with CLIMEX [40]. We temporally downscaled monthly

252   PRISM estimates for 1961−1990 because DDRP requires daily data and PRISM daily

253   temperature data for years prior to 1980 are not available. For each month of a given year, a

254   bilinear interpolation method was used to assign each day an average temperature value that was

255   iteratively smoothed and then adjusted so that the monthly averages were correct.

256

2) Daily time step

258   DDRP models insect phenology and climatic suitability by stepping through each day of a

259   specified time period and calculating degree-day and temperature stress accumulation at each

260   grid cell of a focal area (Fig 1). The time period may span the entire year of interest, or include

261   only a subset of days such as those during the growing season. Users may sample and save daily

262   modeling results every 30 days, 14 days, 10 days, seven days, two days, or one day. Results are

263   saved in multi-layer rasters that are processed and analyzed after the daily time step to produce

264   final model products. We describe the phenology and climatic suitability modeling process and

265   products in more detail in the following sections.

266

Phenology model

268   DDRP calculates daily degree-days over the specified time period using developmental

269   temperature threshold information and gridded temperature data that have been cropped to the

270   extent of the focal area (Fig 1). Currently DDRP has three methods to calculate degree-days: a

271   simple average, the simple average using an upper threshold with a horizontal cutoff, and the

272   single triangle method with upper threshold [41–43]. All three methods calculate degree-days

273   from the daily T_{min} and T_{max} data and a specified base (lower developmental threshold)

274   temperature, but the latter two methods also include the upper developmental threshold in

275   calculations. The single triangle method is also used as a close approximation to the more

276   complex sine-curve calculation method [43].

277   With the exception of phenological event maps, which are computed only for the last day of

278   the daily time step, DDRP saves the following phenology model results for each sampled day:

279   1. *Accumulated degree-days.* While daily degree days are calculated for each life stage, the

280   cumulative degree-days are summed only for the first cohort of the larval stage, as these

281   degree-day maps are representative for all cohorts and life stages. Accumulated degree-days

282   calculated for larva will be the same for other life stages if common developmental

283   thresholds are used.

284   2. *Life stages*. The life stage present (overwintering stage, eggs, larvae, pupae, and adults) for

285   each cohort.

286   *3. Number of generations*. The current generation count for each cohort. If the model is run for

287   an entire year, then the output for the last day of the year would represent the potential

288   voltinism of the species. The generation count increases when adults progress to the egg

289   stage (i.e. oviposition occurs).

290   4. *Phenological event maps (optional).* The timing of phenological events is estimated by

291   computing daily degree-day totals from the gridded temperature data, and storing the day of

292   year when an event threshold is reached. Event results are generated only on the last day of

293   the daily time step (typically, the last day of the year) because the entire time period must be

294   analyzed for all potential event days to be considered.

295

296   ***Climatic suitability model***

297   Independently from the phenology model simulations, DDRP steps through each day and

298   calculates cold and heat stress accumulation to predict the potential distribution of the species

299   (Fig 1). To simplify model parameterization and increase processing efficiency, it assumes that

300   all life stages have the same climatic tolerances. Cold stress units are calculated as the difference

301   between daily T_{min} and the cold stress temperature threshold, whereas heat stress units are

302   calculated as the difference between daily T_{max} and the heat stress temperature threshold. Stress

303   units accumulate across the entire time period of interest (i.e. across all life stages and

304   generations) and are presumed to kill individuals either directly or indirectly when they exceed

305   the moderate or severe stress unit limits. Stress could indirectly kill individuals by restricting

306   their activity, or directly cause mortality through extreme cold or heat events such as a hard

307   freeze. For CONUS, the northern range limit is typically delineated by cold stress and the

308   southern range limit, if any, is delineated by heat stress.

309   We opted to use moderate and severe stress limits to reflect two distinct themes. First, they

310   may provide a way to depict the potential for short term vs. longer term establishment. For most

311   species, the potential distribution could be represented by areas where cold and heat stress have

312   not exceeded the severe or moderate stress limits, as these should allow for long-term population

313   persistence. DDRP depicts these areas with maps of cold stress exclusion, heat stress exclusion,

314   and all stress exclusion (cold plus heat stress exclusions; Fig 1). Areas under moderate stress

315   exclusion may represent temporary zones of establishment in which a species establishes only

316   during a favorable season, such as after an annual migration event. Conversely, areas under

317   severe stress exclusion do not allow for even short-term establishment. Typically we visualize

318   exclusion maps calculated for the last day of the year (day 365) under investigation to provide

319   insight into the potential distribution for an entire growing season.

320   Second, using two levels of stress may provide a way to represent uncertainty for estimating

321   the potential distribution. As discussed in more detail in the 'Discussion,' several sources of

322   uncertainty and error in the modeling process may bias model predictions, such as applying

323   inappropriate parameter values, using climate data with low skill or poor spatial resolution,

324   ignoring biotic factors such as species interactions, or ignoring non-temperature abiotic factors

325   such as microclimate effects, moisture, and photoperiod [32,44]. Defining the potential

326   distribution as areas under severe stress only would typically provide a broader estimate than a

327   definition based on both stress levels. While this approach may over-predict the risk of

328   establishment, conducting surveys over too broad an area is probably better than surveying too

329   small of an area, which may allow a new invasive species to establish and spread.

330

331   **3. Post time step processing**

332   After the daily time step has completed, DDRP combines and analyzes results across cohorts and

333   generates final multi-layer rasters and summary maps (".png" image files) for each sampled day.

334   If multiple cohorts were modeled, then DDRP uses estimates of the relative size of the

335   population represented by each cohort to calculate the relative size of the population (totaling

336   100%) in any given life stage and generation. For phenological event maps, the earliest and

337   average day of year that an event occurs across cohorts is calculated.

338   DDRP integrates mapping of phenology and climate suitability so that users can use a single

339   model product to obtain guidance on their "where" and "when" questions (Fig 1). For example, a

340   user involved with planning surveys may want to know where a target species may establish, and

341   within those areas, when populations may emerge from over-wintering. Each output of the

342   phenology model with the exception of accumulated degree-days will be associated with two

343   additional products for each sampled day (or the last day for a phenological event map): 1) one

344   that includes severe stress exclusion only, and 2) one that includes both severe and moderate

345   stress exclusions. For example, a phenological event map with severe and moderate stress

346   exclusions for 2018 (all 365 days) would present predicted dates of the selected event only in

347   areas where long-term establishment is predicted (Fig 2).

348

349   ***System and software requirements***

350   DDRP requires the R statistical software platform and can be run from the command line or

351   within RStudio [45]. It takes advantage of functions from several R packages for data

352   manipulation, analysis, and post-model processing. The 'raster' package [46] is used to crop

353   daily temperature rasters to the focal area, store and manipulate daily loop raster results, and

354   process and further analyze results for each cohort. Many non-spatial data manipulations are

355   conducted with functions in the 'dplyr,' 'tidyr,' and 'stringr' packages [47–49]. The 'ggplot2'

356   package [50] is used to generate and save summary maps of raster outputs, and options from the

357   command line argument are parsed using the 'optparse' package [51].

358   DDRP capitalizes on the multi-processing capabilities of modern servers to run multiple

359   operations in parallel, which is made possible with the 'parallel' and 'doParallel' packages in R

360   [52]. This significantly reduces computation times, particularly in cases where modeling is

361   conducted with multiple cohorts and across large areas. For example, parallel processing is used

362   to crop rasters for multiple dates, run multiple cohorts in the daily time step, and to analyze time

363   step outputs for multiple days or files simultaneously. For very large areas (currently defined as

364   the Eastern United States and CONUS), temperature rasters are split into four tiles and both the

365   tiles and cohorts are run in parallel in the daily time step.

366   We recommend running DDRP on a Linux OS because its multicore functionality supports

367   the fork system calls of the 'parallel' package in R. The script can easily be modified to be run

368   on a Windows OS; however, certain processes are very memory intensive and may execute

369   slowly or stall without parallel processing. Additionally, DDRP was designed to run on a Linux

370   server, and has not been sufficiently tested on Windows servers to know how well it would

371   perform.

372

Case studies

Climatic suitability, voltinism, and phenological events in Epiphyas postvittana

375   The light brown apple moth (LBAM), *E. postvittana* (Walker 1863) (Lepidoptera: Tortricidae),

376   is a leafroller pest native to southeastern Australia, including Tasmania [53]. The species invaded

377   Western Australia, New Zealand, New Caledonia, England, and Hawaii more than 100 years ago

378   [54–56], and has been established in coastal California since 2006 [57,58]. It poses a significant

379   threat to agricultural production in the United States because it feeds on more than 360 host

380   plants, including economically important fruits such as apple, pear, citrus and grapes [53,59,60].

381   For example, an economic risk analysis of *E. postvittana* to four major fruit crops (apple, grape,

382   orange, and pear) in CONUS estimated an annual mean cost of US$105 million associated with

383   damage to crops and control, quarantine, and research [59]. The CAPS program at APHIS

384   conducts annual surveys for *E. postvittana* at various counties across CONUS.

385   A summary of phenology and climatic suitability model parameters used for *E. postvittana* in

386   DDRP is reported in Table 2. We assigned all life stages a lower developmental threshold of

387   7.1°C (45°F) and an upper developmental threshold of 31.1°C (88°F). Although DDRP allows

388   for different temperature thresholds for each stage, the site-based phenology modeling tool that

389   we use at USPEST.ORG requires common thresholds, and these are presented as whole numbers

390   in Fahrenheit scale for easy interpretation by end-users. Building the model for both platforms

391   keeps models simpler and facilitates cross-comparison. Additionally, laboratory studies revealed

392   small differences in the lower developmental threshold ($< 1°C$) across different life stages

393   [53,60]. The upper developmental threshold value is based on studies showing that all life stages

394   cease development between 31–32°C [53,60,61]. We derived life stage durations (in degree-days

395   °C; hereafter DDC) for *E. postvittana* based on our analysis of published research [53,60,62],

396   which resulted in 127, 408, 128, and 71 DDC for eggs, larvae (females on young apple foliage),

397   pupae, and adults to 50% egg-laying, respectively. This analysis is presented in S1 Appendix.

398   We set the overwintering stage to larva because the predominant overwintering stage of *E.*

399   *postvittana* in the United States are the late larval instars [31,63]. We applied seven cohorts to

400   approximate a normal distribution of emergence times that spanned 100 to 320 DDC (average =

401   210 DDC) based on a report that overwintering larvae at four sites in California required

402   between 102 and 318 degree-days to finish development [31]. This would correspond to the time

403   required for mid-stage (3rd-5th instars, average 4th instar) female larval feeding on old foliage

404   (0.45×494 DDC = 210 DDC), after a January 1 start date.

405   We generated a CLIMEX model for *E. postvittana* using CLIMEX version 4.0 [38] to help

406   parameterize the climatic suitability model in DDRP. The model applied a combination of

407   parameter values (Table 3) derived from two previous CLIMEX studies of this species [64,65].

408   However, we used a cold stress threshold (TTCS) of 3°C, which is lower than He et al.'s (2012)

409   value (5°C)[64], and higher than Lozier and Mill's (2011) value (1.5°C) [65]. We applied a top-

410   up irrigation (additional simulated rainfall) rate of 2.5 mm day^{-1} for the winter and summer

411   season because irrigation mitigates the hot-dry climate that limits distribution of *E. postvittana*

412   within CLIMEX. We assessed the fit of the CLIMEX model to observation-based data from 530

413   locality records for the species from Australia (N = 317), New Zealand (N = 76), and California

414   (N = 137), which were obtained from GBIF.org (18th July 2019; GBIF Occurrence Download

415   https://doi.org/10.15468/dl.a4ucei) and Nick Mills (pers. comm.). The model correctly predicted

416   suitable conditions (EI > 20) at all 530 localities where the species is known to occur (S1 Fig).

417   In DDRP, we generated a climatic suitability model for *E. postvittana* using the daily

418   downscaled PRISM T_{max} and T_{min} estimates for 1961–1990 and calibrated model parameters in

419   accordance with the CLIMEX model (Fig 3). We compared maps of temperature stress

420   accumulation, and adjusted temperature stress limits so that most areas predicted to be under

421   moderate and severe climate stress by DDRP had low (20 > EI > 0) or zero (EI = 0) suitability

422   according to CLIMEX, respectively. Finally, we modeled phenology and climatic suitability for

423   *E. postvittana* in 2018 to provide insight into its potential voltinism, seasonal activities, and risk

424   of invasion in particularly warm temperatures. The summer of 2018 in the United States was the

425   warmest since 2012 and tied for the fourth-warmest on record (NOAA website

426   https://www.noaa.gov/news/summer-2018-ranked-4th-hottest-on-record-for-us last accessed

427   11/21/19). We generated a phenological event map that depicted the date of first egg laying by

428   first generation females, because this activity is relevant to monitoring both eggs and the

429   emergence of adults, which typically occurs two to three days prior to egg laying.

430

431   ***Climatic suitability, voltinism, and phenological events in* Neoleucinodes elegantalis**

432   The small tomato borer (STB), *N. elegantalis* (Guenée) (Lepidoptera: Crambidae), is native to

433   South America and is distributed throughout the Neotropics including in Mexico, Central

434   America, and the Caribbean [66,67]. A major insect pest of tomato (*Solanum lycopersicum*), it

20

435   also attacks fruits of other plants belonging to the family Solanaceae including eggplant, paprika,

436   naranjilla, and green and red pepper [67]. There are at least 1175 recorded interceptions of the

437   species from the United States, where it is considered a serious threat to agricultural biosecurity

438   because it lowers tomato production in South America [68]. The CAPS program has conducted

439   surveillance for *N. elegantalis* since at least 2011.

440   A summary of phenology and climatic suitability model parameters used for *N. elegantalis* in

441   DDRP is reported in Table 2. We re-analyzed data from a laboratory study on the development

442   of *N. elegantalis* on hybrid tomato (Paronset) at five temperatures [69] to estimate a common

443   lower temperature threshold for all life stages, which involved adding a point to force the x-

444   intercept to an integer value in degrees Fahrenheit. We weighted the analysis to select a common

445   lower threshold for immature stages, which are the longest in duration, because this should

446   produce the lowest error for the overall life cycle. The lower threshold values for immature

447   stages were very similar to the overall egg-to-adult value of 8.89°C (48°F), so we chose 8.89°C

448   as the common threshold instead of a higher one solved for the adult pre-oviposition stage

449   (11.5°C). We estimated the duration for eggs, larvae, pupae, and adults to peak oviposition as 86,

450   283, 203, and 96 DDC, respectively. This analysis is presented in S2 Appendix.

451   We compared the results of our method to estimate a common threshold to the alternative,

452   whereby separate thresholds for each life stage are derived and used in the DDRP model (S2

453   Appendix). The error resulting from a slight forcing of the linear regression model was nominal.

454   For example, the values for the x-intercept and 1/slope for the egg-to-adult interval of *N.*

455   *elegantalis* without forcing the regression were 8.64°C (47.6°F) and 1048.3, respectively. After

456   constructing the model with forcing, these values were 8.89°C (48.0°F) and 1030.8, respectively.

457   Further, models that used egg-to-adult development times calculated by the forced versus

458   unforced method were run with various start dates including January 1 and April 1, and

459   predictions differed by only 1 day.

460   *Neoleucinodes elegantalis* has no apparent photoperiodic response, diapause, or specific

461   overwintering stage. In subtropical climates in Brazil, the insect remains active throughout the

462   year if host plants are available [69]. We used January 1 as the model start date for CONUS

463   because few host plants would be available for immature stages at this time, leaving adults as the

464   overwintering stage. We assumed that adult feeding and host search activities could begin

465   immediately if temperatures are suitable, and that first egg-laying would subsequently occur after

466   the estimated pre-oviposition period of *ca*. 55 DDC. The durations of later events (1st to peak

467   oviposition, immature development, etc.) were estimated from previously published data [69,70].

468   We applied seven cohorts to approximate a normal distribution of emergence times that spanned

469   0 to 111 DDC (average = 50 DDC) because over-wintered adults begin finding hosts over this

470   time frame.

471   We parameterized the DDRP climatic suitability model by working with previously

472   published CLIMEX models for *N. elegantalis*, which were constructed using data on its

473   development at different temperatures, its known distribution in the Neotropics, and a sensitivity

474   analysis of CLIMEX parameters [71–73]. We produced a CLIMEX model for *N. elegantalis* in

475   CONUS that applied the "best-fit" parameter values proposed by da Silva et al. 2018 [71](Table

476   3) and a top-up irrigation rate of 2.5 mm day^{-1} for the winter and summer season. However, we

477   applied a cold stress threshold of 2°C because the species may experience this temperature at

478   high-elevation areas where it occurs in Colombia (Bogota, elevation = *ca.* 2600 m) [74] and in

479   Ecuador (El Chaco, elevation = 1600 m), as documented in records of the lowest monthly

480   temperatures for these areas (available for 2017 to the present-day at https://rp5.ru/ and

481   https://www.worldweatheronline.com, respectively) [75].

482   We calibrated climatic suitability parameters for *N. elegantalis* in DDRP in accordance with

483   CLIMEX results (Fig 4) using the same approach taken for *E. postvittana.* Next, we modeled

484   phenology and climatic suitability in DDRP using temperature data from 2018. We generated a

485   phenological event map for the average date of the beginning of egg hatch of the overwintered

486   generation. Predictions of egg hatch could enhance population control of *N. elegantalis* because

487   this species is most vulnerable to pesticides before larvae enter the fruit of host plants [76].

488

Results

490   Cold stress was the major determinant of the potential distribution of *E. postvittana* and *N.*

491   *elegantalis* according to the DDRP analyses based on 30-year climate normals (1961–1990).

492   Both species were excluded from the northern half of CONUS by cold stress, with the exception

493   of (mostly) western parts of Oregon and Washington (Figs 3D and 4D). Heat stress excluded *E.*

494   *postvittana* from most of the Southwest and from southern parts of Gulf Coast states (Fig 3E),

495   whereas *N. elegantalis* was excluded only from the hottest parts of the Southwest in southern

496   California, Arizona, and Texas (Fig 4E). When considering both cold and heat stress exclusions,

497   the potential distribution of both species included western parts of the Pacific states (California,

498   Oregon, and Washington), most of the Southeast, and southern parts of the Northeast (in

499   Delaware, Maryland, New Jersey, and Rhode Island) and the Midwest (in Kansas, Missouri,

500   Illinois, and Indiana). The potential distribution for *N. elegantalis* included a greater area of

501   Oklahoma and Texas than the distribution for *E. postvittana.*

502   DDRP may be over-predicting the potential distribution of *E. postvittana* and *N. elegantalis*

503   in particularly arid regions of the Southwest. According to CLIMEX, high levels of dry stress

504   (S2 Fig) were associated with low climatic suitability (EI < 10) throughout most of western

505   Texas, southern New Mexico, and Arizona (Figs 3C and 4C). Conversely, DDRP did not exclude

506   the species from some of these same areas (Figs 3F and 4F), which is most likely due to the

507   platform's current inability to consider moisture factors in the modeling process.

508   DDRP predicted a smaller potential distribution for *E. postvittana* and *N. elegantalis* in 2018

509   compared to 1961–1990 (Figs 2 and 5). High levels of heat stress in 2018 (S3 and S4 Figs)

510   excluded both species from warm areas of CONUS that were included in the potential

511   distribution under historical conditions, including parts of Arizona, New Mexico, Texas, and the

512   Central Valley of California. Additionally, *E. postvittana* was excluded from several areas in the

513   Southeast that were historically suitable (e.g. in South Carolina, Louisiana, Alabama, and

514   Arkansas). In the East, moderate stress exclusion resulting from cold stress (S3 and S4 Figs)

515   pushed the northern range limit for each species slightly farther south, although this shift was

516   more pronounced for *N. elegantalis.*

517   Predictions of potential dates for phenological events and voltinism for *E. postvittana* and *N.*

518   *elegantalis* in 2018 varied substantially by latitude (Figs 2 and 5). The earliest date of egglaying

519   for the first generation of *E. postvittana* was predicted to be as early as February in Florida to as

520   late as December in the Pacific Northwest (Fig 2A). The average date of first generation

521   beginning of egg hatch for *N. elegantalis* was predicted to begin in the first week of January in

522   Florida but not until late June in the Pacific Northwest (Fig 2B). Thus, the timing of monitoring

523   trap installation to detect ovipositing adults and eggs of *E. postvittana*, or larvae of *N.*

524   *elegantalis*, could vary widely across CONUS. For both species, DDRP predicted as many as

525   seven to nine generations in coastal areas of the Southeast, compared to only one or two

526   generations in parts of the Pacific Northwest (Fig 5). Three to six generations were predicted for

527   most other regions of CONUS. These findings may indicate that the Southeast would experience

528   the longest duration of pest pressure.

529

530   ## Discussion

531   ### DDRP as a decision support tool

532   DDRP is a new spatial modeling platform that generates real-time and forecast predictions of

533   phenology and climatic suitability (risk of establishment) of invasive insect pests in CONUS.

534   These predictions may help with detecting the presence of invasive species in the shortest time

535   possible after they arrive and reproduce, which increases the chance of eradication success and

536   makes other rapid response measures (e.g. deployment of biological control) possible and less

537   costly [4]. In particular, DDRP's unique ability to produce integrated climatic suitability and

538   phenology model products can provide biosurveillance personnel with insights into both where

539   and when to focus detection efforts for a given year or growing season. For example,

540   phenological event maps for *E. postvittana* and *N. elegantalis* (Fig 2) identify high-risk areas

541   where surveillance activities could be concentrated, in addition to providing estimated dates of

542   activities that can ensure timely trap placement. Thus, users can use a single program to address

543   decision support needs for early pest detection.

544   DDRP was designed to be a multi-species platform, which makes it broadly applicable to

545   monitoring and managing populations of IPM pests and classical biological control agents. For

546   example, growers have used predictions of the timing of first egg hatch for codling moth [*Cydia*

547   *pomonella* (Linnaeus)], first emergence of western cherry fruit fly [*Rhagoletis indifferens*

548   (Curran)], and first spring oviposition of spotted wing drosophila [*Drosophila suzukii*

549   (Matsumura)] to help monitor and reduce populations of these major crop pests [77–80].

550   Phenology models for biological control insects can help managers schedule sampling trips to

551   coincide with insect presence on the target organism, and to estimate the synchrony of insect and

552   host phenology at a given location [81,82]. DDRP's estimates of voltinism may provide insights

553   into expected pressure on target organisms, as higher voltinism should translate to greater agent

554   population growth and biocontrol success.

555   Our models for *E. postvittana* and *N. elegantalis* indicated that heat stress excluded

556   populations from a greater area of the Southwest compared to 1961–1990, which is consistent

557   with studies showing that global warming may reduce species' distributions in warmer parts of

558   their range [83]. However, determining whether these putative range shifts are persistent or

559   temporary would require combining model runs for multiple recent years or seasons. For

560   example, trends in the geographic distribution of stress exclusions over several years or seasons

561   could be visualized with a probability surface map. Estimating the direction of range shifts may

562   also provide insights into the response of the species to future climate change. Nonetheless, the

563   differences that we documented in predictions of climatic suitability based on climate data for

564   1961–1990 compared to 2018 suggests that an area's contemporary risk of establishment is

565   different than it was *ca.* 30 years ago. DDRP's ability to produce climatic suitability models in

566   real-time may provide more meaningful insights into areas that are presently suitable for an

567   invasive species, and therefore allow for more effective placement of surveillance operations.

568   DDRP considers several aspects of insect development in the modeling process, which

569   should increase the realism of model predictions compared to simpler platforms that are based

570   solely on generation time degree-days. For example, DDRP's estimates of voltinism and spring

571 activity will likely be more accurate if knowledge of the biology of a given species is sufficient,

572 because different temperature thresholds for multiple life stages may be used, and the

573 overwintering stage is parameterized separately from the post-winter stage (e.g. overwintering

574 adult vs. adult). Additionally, it accounts for developmental variation within populations by

575 generating and combining results across multiple cohorts that complete the overwintering stage

576 at different times, which is more realistic than assuming a single population cohort and single

577 model start time.

578   From a historical perspective, DDRP could be considered a partial descendant and spatialized

579 version of the PETE (Predictive Extension Timing Estimator) phenological modeling platform

580 that was established as a standard in the mid-1970s [84]. Features in common include a cohort

581 approach to population phenological modeling using daily degree-days as the main input,

582 provision for major insect life stages and a separately parameterized overwintering distribution,

583 an open-source non-proprietary standard for sharing, and a focus on agricultural extension

584 (applied decision support). Unlike PETE, DDRP is spatialized and therefore able to produce a

585 variety of mapping products including phenological event maps, and it also includes options to

586 use separate thresholds for different life stages and to generate climatic suitability models. DDRP

587 could be improved by adding certain features of the PETE platform including the use of a

588 diapause trigger, and a distributed delay function that would allow the generation time to

589 lengthen with each subsequent generation.

590   DDRP is one of the first open-source platforms that can model both phenology and climatic

591 suitability of insect pests. The Insect Life Cycle Modelling (ILCYM) software [85,86] is another

592 open-source R program that can model temperature-based phenology and establishment risk for

593 insects in a spatial context. However, ILCYM is a full population dynamics modeling platform

594 that requires life table data at constant and variable temperatures, which are seldom available for

595 anticipated but not yet present invasive insect species. ILCYM has primarily been used to

596 simulate models with climate normals or GCMs at global or regional scales [85,87], whereas

597 DDRP was designed to use real-time and forecast climate data for within-season decision

598 support. PhenModel is another R program that can model insect phenology, but it is unclear how

599 adaptable the program would be to other insect species besides leaf-feeding beetles, and it is not

600 spatialized or capable of modeling climatic suitability [88].

601 There are numerous opportunities for improving and extending the applications of DDRP,

602 especially given that it is written in R, an open source programming language. For example, the

603 program could be modified to use climate data for a region outside of CONUS, or to model other

604 types of organisms such as non-insect invertebrates, plants, plant-pathogenic bacteria and fungi,

605 and insect plant and animal virus vectors. The platform has been tested for and could be used

606 through an on-line web interface, although there is the potential for overload issues on a server

607 host. This issue, as yet untested, could be addressed by using a cloud computing platform. We

608 describe some additional features that could be added to potentially improve model accuracy and

609 expand the list of products in more detail below. The most recent code for DDRP is available at

610 GitHub (https://github.com/bbarker505/ddrp_v2.git), where we invite scientists and practitioners

611 to jointly develop the platform and database of species models.

612

Uncertainties, limitations, and other considerations

613

Linear (degree-day) modeling

614

615 DDRP uses a relatively simple degree-day modeling approach, whereas some platforms

616 including ILCYM, phenModel, and devRate [89] offer complex functions to model nonlinear

617 responses of insects to temperature. Degree-day models are ideal for multi-species platforms like

618 DDRP because there are sufficient data to parameterize a degree-day model for most insect pest

619 species of economic importance in the United States [20,90]. Linear degree-day models are also

620 readily calibrated and sometimes constructed entirely using field data, making them more

621 practical for extension and decision support use [15]. Additionally, degree-day models require

622 only daily T_{min} and T_{max} data (as opposed to hourly data for most nonlinear models), which are

623 available at a high spatial resolution for CONUS from multiple sources including PRISM and

624 RTMA. Nonetheless, it is important for users to recognize potential sources of error and lack of

625 precision in degree-day models, such as their limited ability to accurately model development at

626 supra-optimal temperatures [15,91].

627

628 *Environmental inputs*

629 DDRP is intentionally parameterized in a simple, conservative manner, which will hopefully

630 achieve the goal of a parsimonious balance of both model simplicity and accuracy [15,92].

631 Nonetheless, DDRP is driven entirely by temperature, and therefore ignores other factors that

632 may affect the development and distribution of insects such as photoperiod, moisture, dispersal,

633 resources, disturbance, and biotic interactions [7,93]. The potential consequences of this

634 limitation will depend on the biology of the organism under study. For example, dry stress is the

635 major factor restricting the current distribution of *N. elegantalis* in its native range [72,74,94],

636 and it limits the distribution of *E. postvittana* both in its native range [53,95] and in Southern

637 California and Arizona [62]. The absence of moisture factors in DDRP most likely explains why

638 it predicted higher climatic suitability for these species in arid regions of CONUS compared to

639 CLIMEX, which considers wet and dry stress in the modeling process. However, this

640   conservative-leaning error may in fact better reflect human manipulation of the landscape (e.g.

641   greenhouse and irrigation usage) that may allow the species to exist in such regions. Future

642   versions of DDRP that can process gridded moisture data and incorporate moisture stress factors

643   into climatic suitability models may help overcome our current limitations in matching CLIMEX

644   models, and they may improve predictions for moisture-sensitive species such as *E. postvittana*

645   and *N. elegantalis.* Additionally, we are developing a version of DDRP that incorporates

646   photoperiodically induced life history events such as winter diapause and summer aestivation,

647   which builds on earlier phenology modeling work that estimated voltinism of photoperiod-

648   sensitive insects [96].

649

650   ***Presumptive models***

651   Uncertainties regarding the accuracy of temporal or spatial predictions of invasive species that

652   are not yet established is inevitable, in part because no validation data are yet available, and

653   species interceptions do not imply establishment [7,97]. DDRP models for species for which

654   only presumptive models exist should therefore be used conservatively. For example,

655   surveillance or management actions could be implemented in advance of predicted phenological

656   events as a precautionary measure (e.g. installing traps even earlier than estimates for the earliest

657   date of overwintering adult emergence). To potentially avoid under-predicting the risk of

658   establishment, the potential distribution could be defined as areas not under severe climate stress

659   as opposed to defining it using both stress levels. Additionally, climatic suitability models

660   generated by DDRP could be combined with those produced using different modeling methods

661   (e.g. correlative, semi-mechanistic, mechanistic) to create a "hybrid" model, which may increase

662   the reliability of predictions [7,93].

663   Web platforms that support sharing of pest observations and related expert commentary will

664   be valuable resources for validating and increasing the predictive performance of DDRP models.

665   For example, the iPiPE and its sister platforms (http://www.ipipe.org, https://ipmpipe.org) have

666   created a national information technology infrastructure for sharing pest observations in near

667   real-time and contributing them to a national depository [98]. Similarly, the USA National

668   Phenology Network provides a depository of plant and insect phenology observations

669   contributed by citizen scientists [9]. The National Agricultural Pest Information System (NAPIS;

670   https://napis.ceris.purdue.edu/home) currently has over 5.17 million records from pest detection

671   surveys, and is another potential source of validation data. Unfortunately, there were insufficient

672   data from these sources to validate our DDRP model for *E. postvittana*, which we hope will

673   change in the near future.

674

675   *Geographic variation*

676   A major challenge for insect phenology modeling in general is how to account for geographic

677   variation in insect responses to temperature [32,44]. Populations of an invading species may

678   diverge in thermal physiology traits when genetically divergent individuals are introduced to

679   different areas, or when evolutionary changes including rapid adaptation to new environments or

680   hybridization occurs [99,100]. If sufficient data on the amount and geographic distribution of

681   variation in relevant traits exists, then model accuracy may be improved by building separate

682   models for each genotype. For example, an egg hatch phenology model for a subspecies of the

683   Asian gypsy moth, *Lymantria dispar asiatica* (Vnukovskij), had reduced error compared to a

684   similar model constructed for the European subspecies that has invaded North America,

685   *Lymantria dispar dispar* (Linnaeus), which has a markedly different predominant phenotype

686   [101]. An alternative approach may be to run several models, each with a different value for the

687   parameter of interest, and present a range of model predictions. Conversely, DDRP could be

688   modified to accept a grid of parameter values so that geographic variation would be accounted

689   for in a single model run.

690   A lack of knowledge on how early-season environmental conditions or events that initiate the

691   first spring activity of a species (biofix) vary geographically may be a source of error because the

692   model start date affects all downstream predictions. For example, how does first spring activity

693   vary across the wide range of warming conditions possibly encountered for a large region such

694   as CONUS? As a case in point, our phenology model for *N. elegantalis* assumes that moths have

695   only 55 DDC before egg-laying behaviors may occur. This assumption may not be valid for sub-

696   tropical zones of the United States, where flight and reproduction could occur even earlier.

697   Conversely, a much longer spring warm-up may be needed in temperate zones because

698   commercial tomatoes are transplanted much later in the year. Studying how first spring activity

699   (adult flight) in *N. elegantalis* potentially varies geographically in Central or South America

700   would help to refine a range of model start times. The phenology model for DDRP could then be

701   parameterized using a necessarily conservative selection of start dates or by inputting a grid of

702   start dates. Using a broad distribution of emergence times to initiate the cohorts could be another

703   approach to accommodate uncertainty in first spring activity.

704

705   ***Distributed delay***

706   There is currently no distributed delay function in DDRP, meaning that the overlap in

707   generations and life stages of cohorts does not increase over multiple generations. Modeling

708   distributed delay can be important because the timing of surveillance activities or IPM events

709   like spraying or trapping need to be adjusted for later generations [35,36,84]. Not accounting for

710   distributed delay may be a greater issue for species that continue to develop throughout winter

711   months or lack a temperature or photoperiodic event that synchronize populations, such as *E.*

712   *postvittana* [31,56,60]. For many multivoltine species, DDRP may accurately predict peak events

713   in each generation, but inaccurately predict the first appearance of one or more life stages after

714   the first or second generations because of increasing overlap in generation cohorts. Thus,

715   phenological event maps produced for species that have significant overlap in generations should

716   be most reliable for the first few generations. This will be among the high priority issues in

717   development of future versions of the platform.

718

Conclusion

720   DDRP is a new modeling tool that can integrate mapping of phenology and climatic suitability in

721   real-time to provide timely and comprehensive guidance for stakeholders needing to known

722   where and when invasive species may establish. When used for surveillance, the platform will

723   hopefully increase chances for early detection of new or spreading invasive threats in the United

724   States, and therefore help pest management programs mitigate their potential damage to

725   agricultural and environmental resources. Additionally, DDRP may help plan monitoring and

726   management efforts for IPM pests and biological control insects, and to predict pest pressure on

727   host plants.

728   The case studies we presented provided examples of how models for DDRP may be

729   parameterized and then run to produce various products including gridded and graphical

730   predictions of the number of generations, life stages present, dates of phenological events, and

731   areas of climatic suitability based on two levels of climate stress. We encourage users of DDRP

732   to consider the limitations of the platform, to report the conditions that their model was designed

733   to work under (e.g. a particular region, life stage event, or generation), and to document and any

734   known sources of model error that could not be accounted for when providing validation and

735   other feedback reports. The flexible and open-source nature of DDRP will facilitate making

736   modifications and improvements, such as adding new environmental factors, using it for other

737   regions besides CONUS, modeling non-insect organisms, expanding the types of model

738   products, and adding features to improve model accuracy.

739

740   **Supporting information**

741   **S1 Appendix Estimating phenology model parameters for *Epiphyas postvittana*.**

742   (DOC)

743

744   **S2 Appendix Estimating a common lower temperature threshold and other phenology**

745   **model parameters for *Neoleucinodes elegantalis*.**

746   (DOC)

747

748   **S1 Fig Predictions of climatic suitability for *Epiphyas postvittana* in Australia, New**

749   **Zealand, and California according to CLIMEX (a, b) and DDRP (c) models based on**

750   **1961–1990 climate normals.** Climatic suitability of an area in CLIMEX is represented by the

751   Ecoclimatic Index (EI), where EI = 0 indicates unsuitable conditions. In DDRP, long-term

752   establishment is indicated by areas not under moderate or severe climate stress. Blue circles

753   depict known localities for the species (Australia $N = 317$; New Zealand $N = 76$; California $N =$

754   137).

755   (DOC)

756

757   **S2 Fig CLIMEX predictions of dry stress in CONUS for *Epiphyas postvittana* and**

758   ***Neoleucinodes elegantalis* based on 1961–1990 climate normals.**

759   (DOC)

760

761   **S3 Fig DDRP predictions of cold and heat stress for *Epiphyas postvittana* for 2018.**

762   (DOC)

763

764   **S4 Fig DDRP predictions of cold and heat stress for *Neoleucinodes elegantalis* for 2018.**

765   (DOC)

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Acknowledgements

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778

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792 Gericke Cook

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Data availability

795 The most current R code for DDRP is available at github.com/bbarker505/ddrp_v2. The version

796 of DDRP used for this study has been archived at Zenodo

797 (https://doi.org/10.5281/zenodo.3832731). Perl and Octave scripts used for temporal

798 downscaling of monthly climate averages to daily averages are at GitHub

799 (github.com/bbarker505/dailynorms) and Zenodo (https://doi.org/10.5281/zenodo.3601671).

800   Output data produced by this analysis are at GitHub (github.com/bbarker505/1990_daily_30yr)

801   and Zenodo (https://doi.org/10.5281/zenodo.3833053).

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1114

1115 **Tables and Figures**

1116

1117 **Table 1**. **Species-specific parameters used in DDRP with corresponding values for *Epiphyas postvittana* (light brown apple**

1118 **moth) and *Neoleucinodes elegantalis* (small tomato borer)**. For both species, the phenological events for egg, larvae, and adults are

1119 beginning of egg hatch, mid-larval development, and first egg-laying, respectively. The phenological event for pupae is first adult

1120 emergence for *E. postvittana* and mid-pupal development for *N. elegantalis*. The duration and timing of the phenological event for the

1121 overwintering stage will vary according to the number of cohorts applied in model runs (see text for details).

1122

Parameter	Code	*E. postvittana*	*N. elegantalis*
Lower developmental thresholds (°C)			
Egg	eggLDT	7.2	8.89
Larvae	larvaeLDT	7.2	8.89
Pupae	pupaeLDT	7.2	8.89
Adult	adultLDT	7.2	8.89
Upper developmental thresholds (°C)			
Egg	eggUDT	31.1	30

Table 1 cont.

Larvae	larvaeUDT	31.1	30
Pupae	pupaeUDT	31.1	30
Adult	adultUDT	31.1	30
Stage durations (°C degree-days)			
Egg	eggDD	127	86
Larvae	larvaeDD	408	283
Pupae	pupDD	128	203
Adult	adultDD	71	96
Overwintering larvae	OWlarvaeDD	varies	–
Overwintering adult	OWadultDD	–	varies
Phenological events (°C degree-days)			
Overwintering stage event	OWEventDD	varies	varies
Egg event	eggEventDD	126	80
Larvae event	larvaeEventDD	203	140
Pupae event	pupaeEventDD	128	100

Table 1 cont.

Adult event	adultEventDD	22	55
Cold stress			
Cold stress temperature threshold (°C)	coldstress_threshold	3	−1
Cold degree-day (°C) limit when most individuals die	coldstress_units_max1	875	300
Cold degree-day (°C) limit when all individuals die	coldstress_units_max2	1125	700
Heat stress			
Heat stress temperature threshold (°C)	heatstress_threshold	31	32
Heat stress degree-day (°C) limit when most individuals die	heatstress_units_max1	160	180
Heat stress degree-day (°C) limit when all individuals die	heatstress_units_max2	220	340
Cohorts			
Degree-days (°C) to emergence (average)	distro_mean	210	50
Degree-days (°C) to emergence (variation)	distro_var	2500	1500
Minimum degree-days (°C) to emergence	xdist1	100	0
Maximum degree-days (°C) to emergence	xdist2	320	111
Shape of the distribution	distro_shape	normal	normal

1123 **Table 2. Comparison of the characteristics, parameters, and products of climatic suitability models in CLIMEX and DDRP.**

1124 For simplicity, we do not show CLIMEX parameters related to interaction stress indices (hot-wet stress, hot-dry stress, cold-wet stress,

1125 and cold-dry stress) or to radiation, substrate, light and diapause indices.

1126

Attributes	DDRP	CLIMEX
Temporal range (time frame)	Any – historical, real-time, near forecast, and climate change forecasts	Historical (1961–1990), and future climate change forecasts for 2030, 2050, 2070, 2080, 2090, and 2100
Temporal scale (time step)	1-day (daily) for PRISM data – others potentially accommodated	Typically weekly values interpolated from monthly data
Spatial scale	Any – default is 2′ (~4 km) for PRISM data	CliMond data at a 30′ (~55 km at equator) or 10′ (~20 km) resolution; others potentially accommodated
Factors influencing climatic suitability	Cold and heat stress only	Cold, heat, dry, and wet stress plus population growth

Table 2 cont.

Modeling process overview	Estimates daily cold and heat stress accumulation and determines whether total accumulations exceed the moderate (max1) or severe (max2) cold and heat stress limits	Estimates weekly population growth and the accumulation of stress (cold, heat, dry, and wet); population growth is reduced when daily accumulations are too low or too high to maintain metabolism
Climate stress parameters		
Temperature thresholds	Upper and lower cold and heat stress temperature thresholds, beyond which stress accumulates as cold and heat stress units	Upper and lower cold and heat stress thresholds in Celsius or degree-day units
Temperature stress rates	Cold and heat stress accumulation limits (max1 and max2); stress units accumulate linearly over time (consecutive days not weighted higher than non-consecutive weeks)	Type 1 – weekly cold and heat stress accumulation rate (similar to DDRP)
		Type 2 – stress accumulates exponentially in cases of consecutive weeks of stress

Table 2 cont.

|		
Moisture stress thresholds	None	Upper and lower dry and wet stress thresholds
Moisture stress rates	None	Weekly dry and wet stress accumulation rate for species
Total no. of parameters possible	6	38
Total no. of parameters typically used	6	21
Depiction of climatic suitability	Areas not under moderate or severe cold and heat stress exclusions	Typically areas with a high ecoclimatic index (> 20 or 30), which is calculated using annual growth and stress indices
Products	Gridded and summary map outputs of 1) cold and heat stress unit accumulation, and 2) cold, heat, and all (cold plus heat) stress exclusions	Tabular and summary map outputs of 1) cold, heat, dry, and wet stress unit accumulation, and 2) the temperature, moisture, growth, and ecoclimatic index

1127   **Table 3. Parameter values used to produce a CLIMEX model for *Epiphyas postvittana* (light brown apple moth) and**

1128   ***Neoleucinodes elegantalis* (small tomato borer)**.

1129

CLIMEX parameter	Code	*E. postvittana*			*N. elegantalis*	
		Lozier & Mills (2011)	He et al. (2012)	This study	da Silva et al. (2018)	This study
Temperature						
Lower temperature threshold (°C)	DV0	7.5	7	7	8.8	8.8
Lower optimal temperature (°C)	DV1	15	13	13	15	15
Upper optimal temperature (°C)	DV2	25	23	23	27	27
Upper temperature threshold (°C)	DV3	31	30	31	30	30
Degree-days per generation (°C days)	PDD	673.6	673.6	673.6	588.2	588.2
Moisture						
Lower soil moisture threshold	SM0	0.15	0.25	0.15	0.35	0.35
Lower optimal soil moisture	SM1	0.5	0.8	0.5	0.7	0.7
Upper optimal soil moisture	SM2	0.8	1.5	0.8	1.5	1.5

Table 3 cont.

Upper soil moisture threshold	SM3	1.4	2.5	1.4	2.5	2.5
Cold stress						
Cold stress temperature threshold (°C)	TTCS	1.5	5	3	–	2
Cold stress temperature rate (week^{-1})	THCS	0.005	0.0005	0.0005	–	0.001
Cold stress degree-day threshold (°C days)	DTCS	–	–	–	15	–
Cold stress degree-day rate (week^{-1})	DHCS	–	–	–	0.001	–
Heat stress						
Heat stress temperature threshold (°C)	TTHS	31	31	31	30	30
Heat stress temperature rate (week^{-1})	THHS	0.0045	0.01	0.0045	0.0007	0.0007
Dry stress						
Dry stress threshold	SMDS	0.15	0.2	0.15	0.35	0.35
Dry stress rate (week^{-1})	HDS	0.005	0.01	0.005	0.001	0.001
Wet stress						
Wet stress threshold	SMWS	1.4	2.5	1.4	2.5	2.5
Wet stress rate (week^{-1})	HWS	0.001	0.002	0.001	0.002	0.002

1130   **Fig 1. Schematic of the DDRP model framework.** 1) Input datasets (blue shaded boxes)

1131   include a) data on the developmental requirements, climatic tolerances (optional), and emergence

1132   time(s) of population cohort(s) of a species (Table 1), and b) daily minimum and maximum

1133   temperature data (T_{min} and T_{max}, respectively). 2) Hollow blue boxes indicate calculations

1134   conducted on each daily time step, where a dashed outline represents calculations for climatic

1135   suitability. Phenological event map (PEM) calculations for each life stage (E = egg, L = larva, P

1136   = pupa, A = adult) are shown in green font. A full generation is counted when adults lay eggs (in

1137   red), and the number of generations subsequently increases. 3) After the daily time step

1138   completes, DDRP combines the results across all cohorts and exports the model outputs as multi-

1139   layer raster and summary map (".png") files (orange shaded boxes). Orange shaded boxes with a

1140   dashed line represent model outputs for PEMs and climatic suitability.

1141
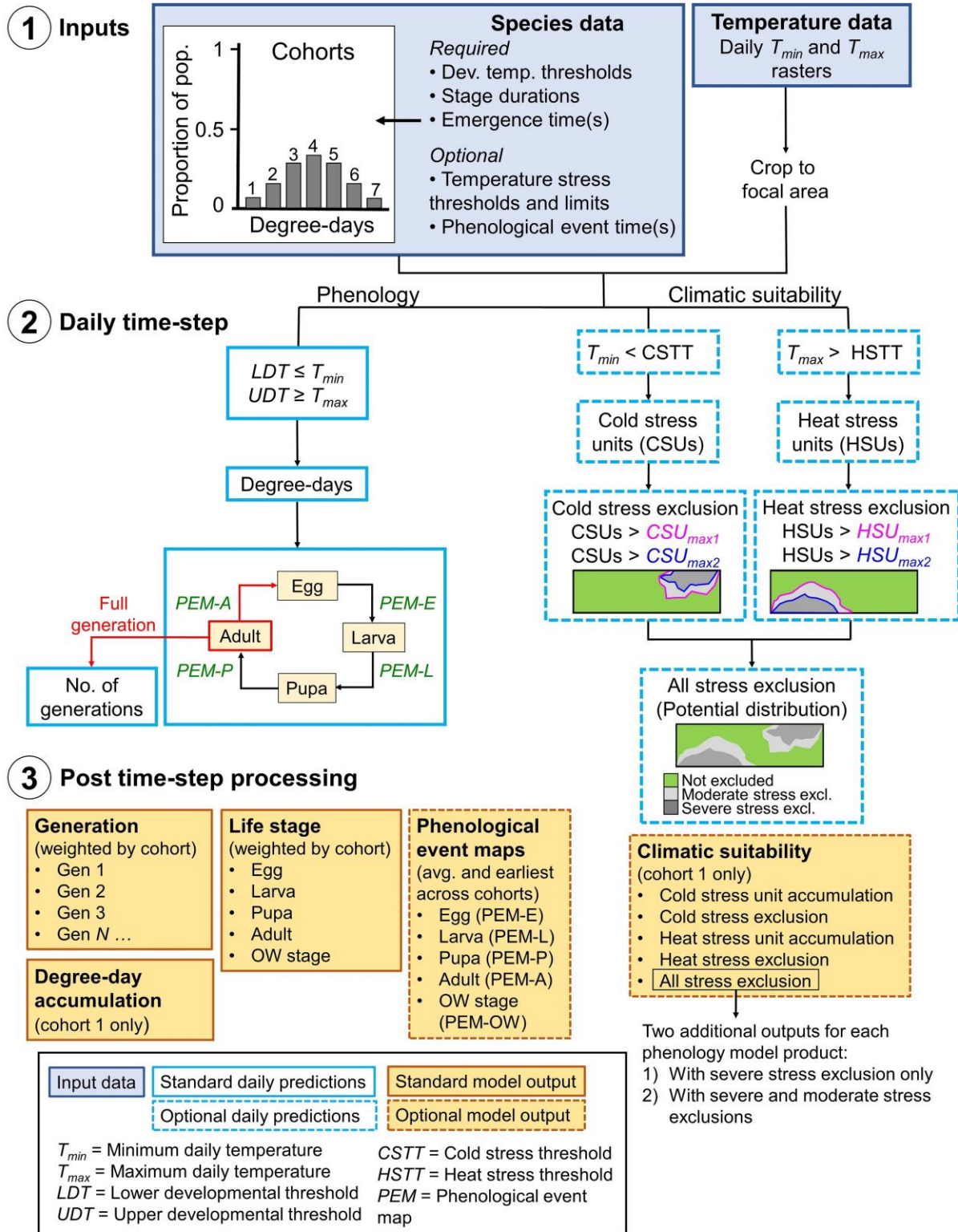
1142   **Fig 2. Phenological event maps generated by DDRP for (A)** *Epiphyas postvittana* **(light**

1143   **brown apple moth) and (B)** *Neoleucinodes elegantalis* **(small tomato borer) in CONUS in**

1144   **2018.** The map for *E. postvittana* shows the average date of egg-laying by first generation

1145   females, whereas the map for *N. elegantalis* shows the average date of first generation beginning

1146   of egg hatch. Both maps include estimates of climatic suitability, where long-term establishment

1147   is indicated by areas not under moderate (excl.-moderate) or severe (excl.-severe) climate stress

1148   exclusion.
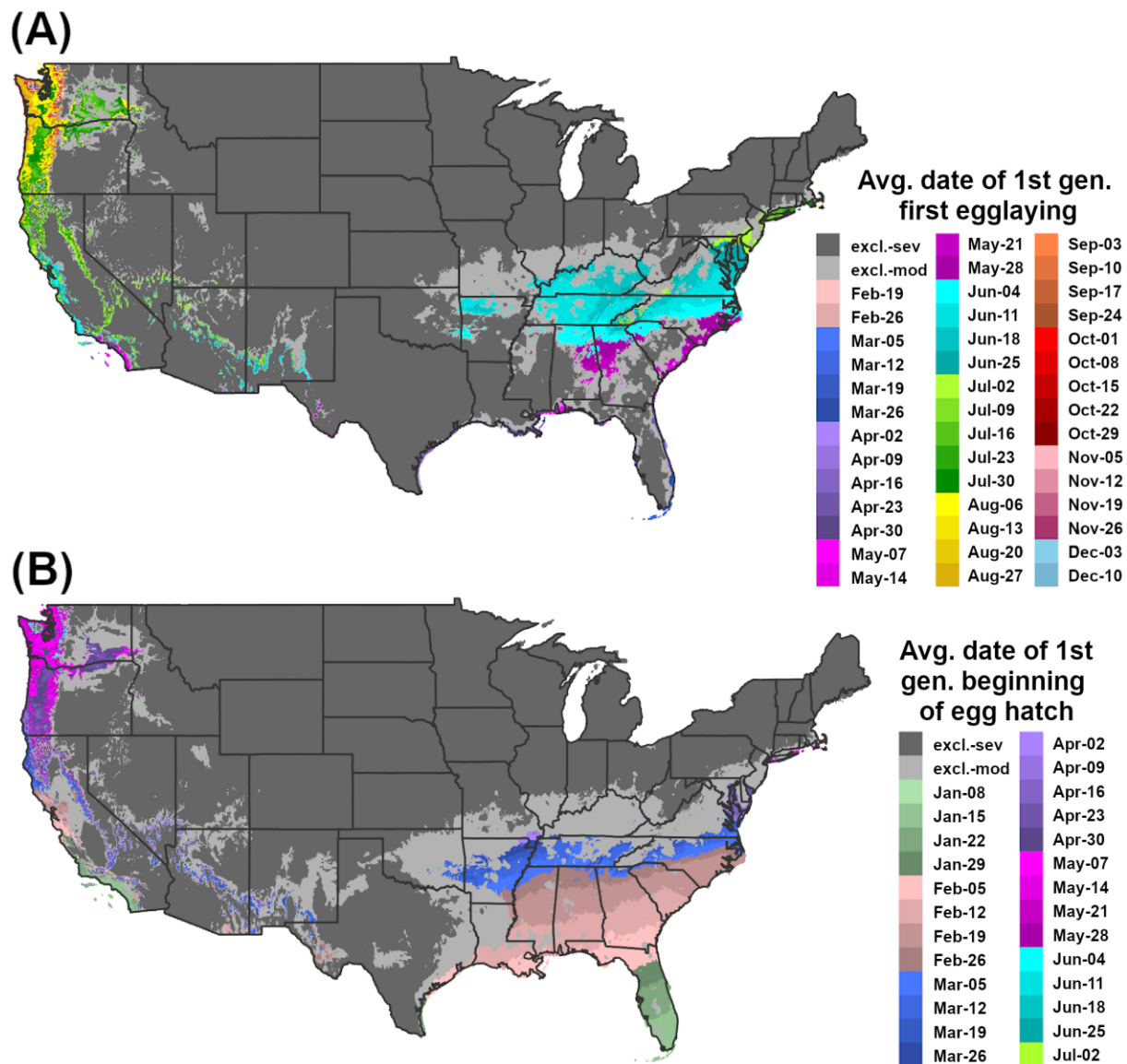
1149

1150 **Fig 3. Predictions of cold stress, heat stress, and climatic suitability for *Epiphyas postvittana***

1151 **(light brown apple moth) in CONUS produced by CLIMEX (A–C) and DDRP (D–F) based**

1152 **on 1961–1990 climate normals.** Climatic suitability is estimated by the Ecoclimatic Index (EI)

1153 in CLIMEX, and by combining cold and heat stress exclusions in DDRP. In DDRP, long-term

1154 establishment is indicated by areas not under moderate (excl.-moderate) or severe (excl.-severe)

1155 climate stress exclusion. Cold and heat stress units in DDRP were scaled from 0 to 100 to match
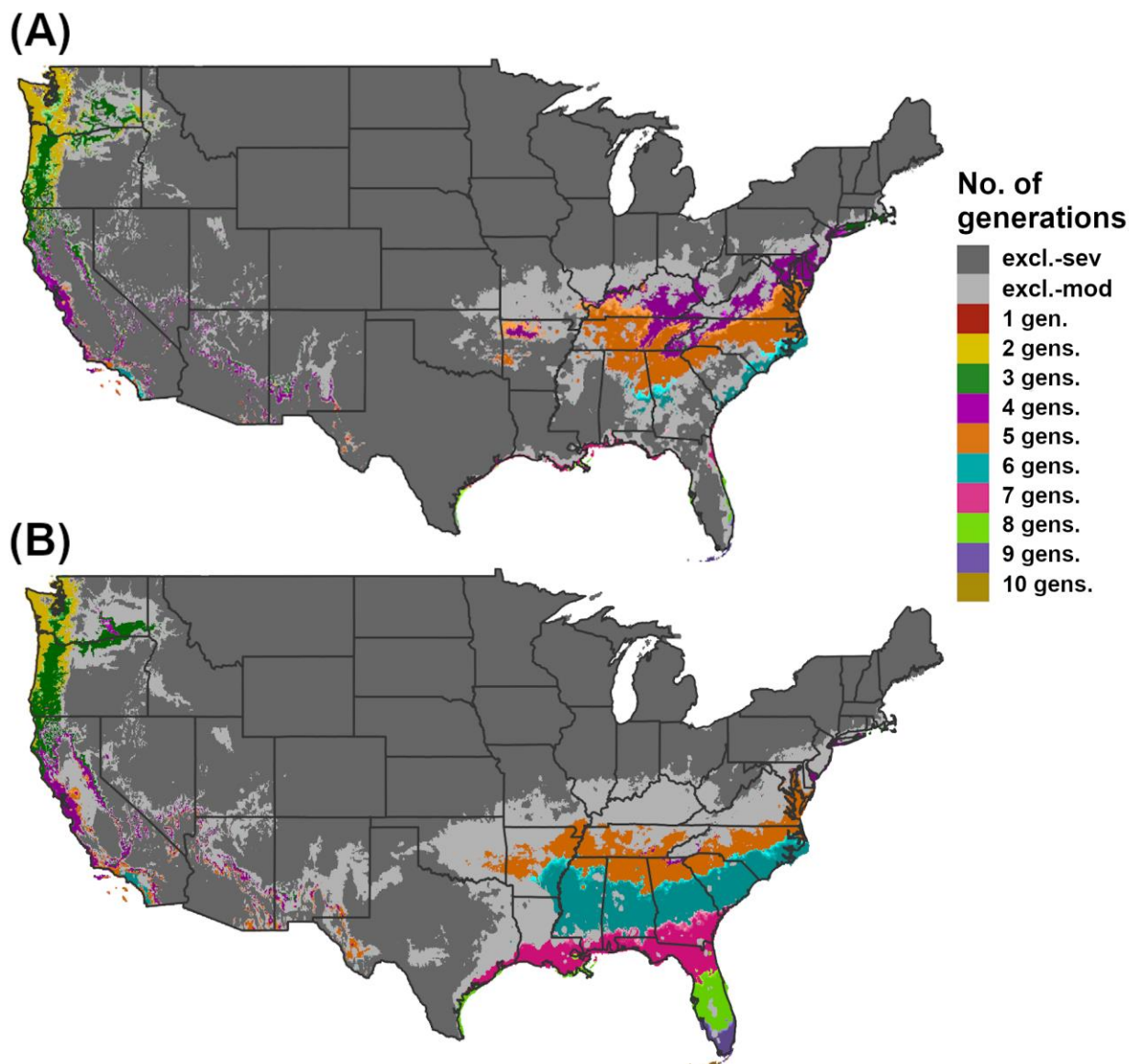
1156 the scale in CLIMEX.
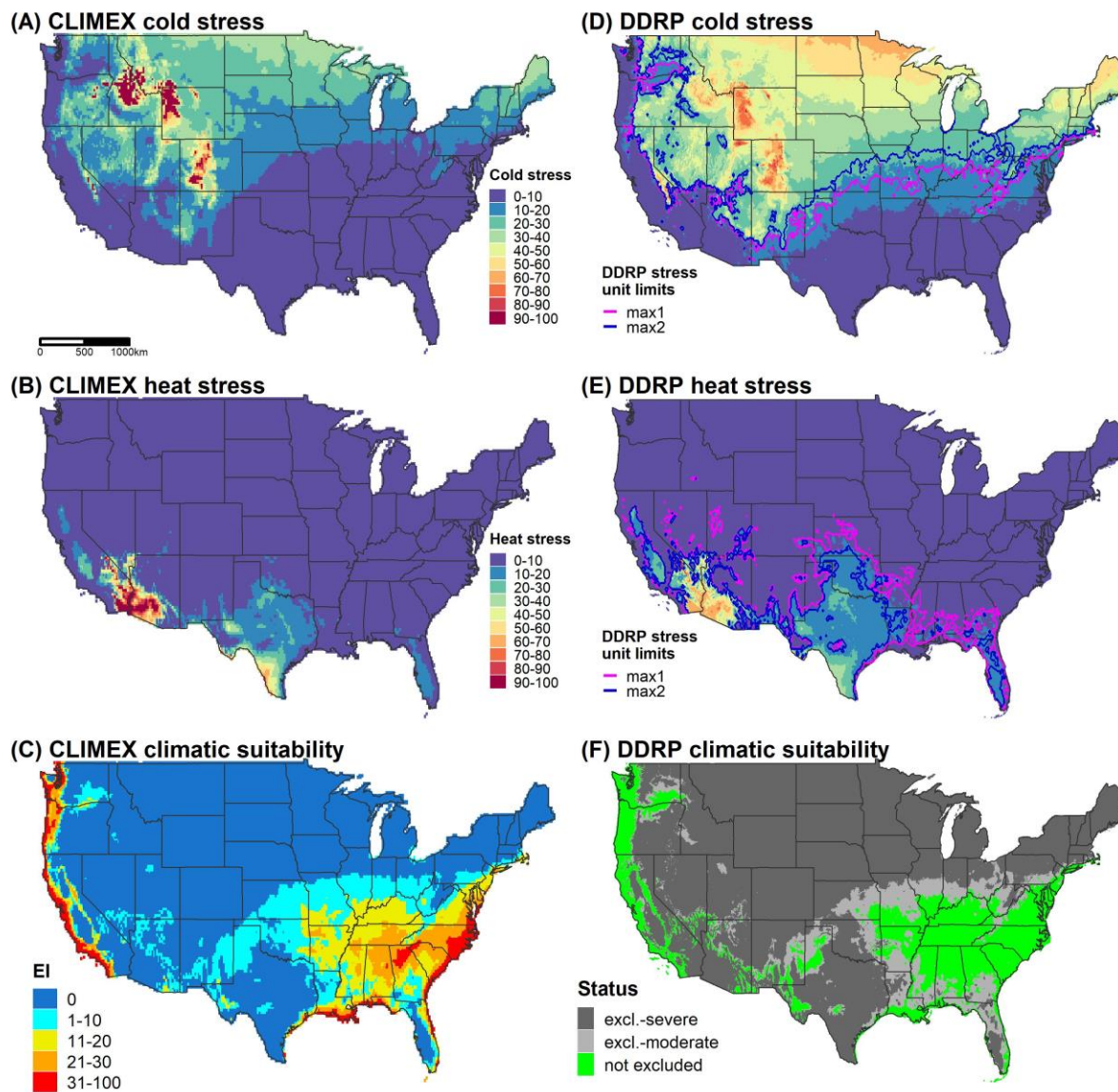
1157

1158 **Fig 4. Predictions of cold stress, heat stress, and climatic suitability for *Neoleucinodes***

1159 ***elegantalis* (small tomato borer) in CONUS produced by CLIMEX (A–C) and DDRP (D–F)**

1160 **based on 1961–1990 climate normals.** Climatic suitability is estimated by the Ecoclimatic

1161 Index (EI) in CLIMEX, and by combining cold and heat stress exclusions in DDRP. In DDRP,

1162 long-term establishment is indicated by areas not under moderate (excl.-moderate) or severe

1163 (excl.-severe) climate stress exclusion. Cold and heat stress units in DDRP were scaled from 0 to

1164 100 to match the scale in CLIMEX.
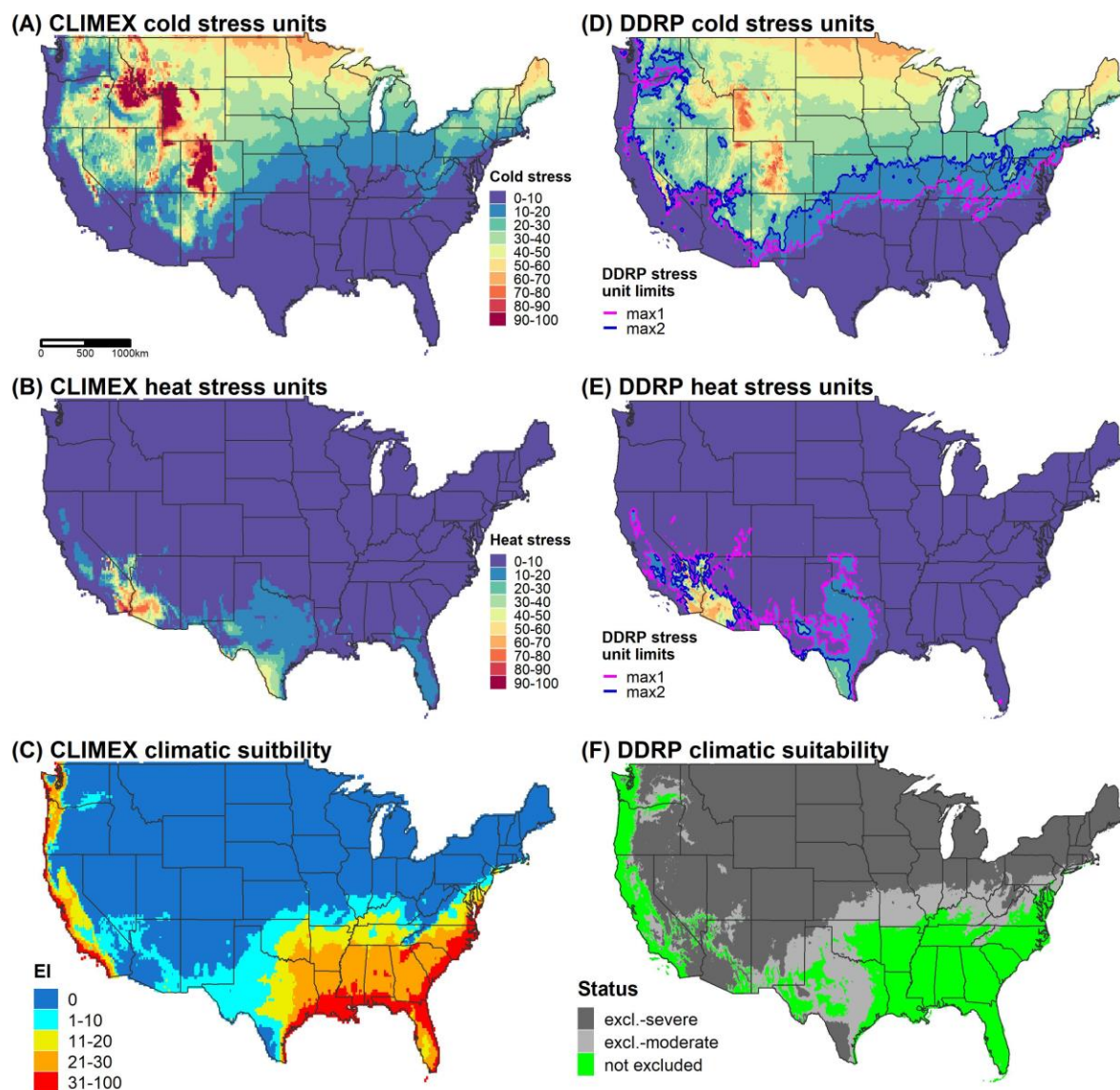
1165

1166 **Fig 5. DDRP model predictions of voltinism (number of generations per year) in (A)**

1167 *Epiphyas postvittana* **(light brown apple moth) and (B)** *Neoleucinodes elegantalis* **(small**

1168 **tomato borer) in CONUS for 2018.** Maps include estimates of climatic suitability, where long-

1169 term establishment is indicated by areas not under moderate (excl.-moderate) or severe (excl.-

1170 severe) climate stress exclusion.

1171