Japanese beetle
Popillia japonica (Coleoptera: Scarabaeidae)
Phenology/Degree-Day and Climate Suitability Model Analysis for USPEST.ORG
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Summary

A phenology model and temperature-based climate suitability model for the Japanese beetle (JPB), *Popillia japonica* (Coleoptera: Scarabaeidae), was developed for the DDRP (Degree-Days, Risk, and Pest event mapping; under development for uspest.org) platform using data from available literature and from occurrence records in online biodiversity databases.

1. Introduction

Popillia japonica is a highly polyphagous pest that feeds on >300 different types of important crops, including various fruits, vegetables, flowers, trees, field crops, and turf (USDA-APHIS 2015, EPPO 2020). The pest also feeds on many native plant species, some of which are endangered or culturally important to tribes. Both the larval and adult stages cause damage to hosts. Native to Japan, *P. japonica* was first discovered in North America in 1916 in New Jersey and has since spread throughout the eastern U.S. and southeastern Canada (Allsopp 1996, Althoff and Rice 2022). Eradication efforts for local infestations in the western U.S. states are ongoing. The pest is also established in parts of the Azores, India, and southern Europe (EPPO 2020). Efforts to control the pest in the U.S. are estimated to cost more than $460M annually in damage to trees, crops and grasses (USDA-APHIS 2015).

2. Methods

This is a summary of the spreadsheet analysis that is available online (https://uspest.org/wea/Popillia_japonica_model.pdf). Final parameters used in the DDRP model are presented in Table 1.

2.1. Phenology model

2.1.1. Life cycle and overwintering stage

The model uses a start date of 1 January and assumes a one-year (univoltine) life cycle in which 3rd instar larvae are the overwintering stage. The model stops after a full life cycle completes (*obligate_diapause* = 1) because of evidence that larvae remain in diapause until soil temperatures increase in the spring (Ludwig 1928, Fleming 1972). *Popillia japonica* is known to have a two-year (semivoltine) life cycle in cooler climates, in which insects spend the first winter as a second instar (Fleming 1972, Vittum 1986). However, a semivoltine life cycle could not be modeled because of DDRP's single-year modeling structure. Thus, DDRP is only used to model the portion of a population which emerges from diapause in a given season or year.

2.1.2. Temperature thresholds for development

We re-interpreted temperature vs. development rate data from several laboratory studies (Ludwig 1928) and monitoring studies (Vittum 1986, Wawrzynski and Ascerno 1998). For lab studies conducted at multiple temperatures, we used linear regression (x-intercept method) with forcing through the x-intercept to estimate a common lower developmental threshold and degree-day (DD) requirements for major stages of the species. From these works, we solved for a lower temperature threshold of 10°C common to eggs, larvae, pupae and egg-to-adult. The results all had high R-squared values, ranging from a low of 0.94 for 2nd instars to a high of 0.99 for eggs. An upper developmental temperature threshold of 33.3°C was applied based on results of Ludwig (1928) and Gilioli et al. (2022), which showed maximum developmental rates near 33°C with a slight decline above this temperature. It is likely that these ground-dwelling beetles are protected from higher temperatures by soil insulation or shelter seeking behaviors by adults.

2.1.3. Development in degree days

DDRP models include four separate life stages (egg, larva, pupa, and adult) plus a separately parameterized overwintering stage. Results including stage durations, first and peak event DD requirements for major stages of *P. japonica* are reported in Table 1. At a lower threshold of 10°C, overwintering larval, egg, larval (assuming in the future a multi-voltine model is implemented), pupal, egg-to-adult and mating plus pre-oviposition, DD requirements were 361, 172, 1148, 150, 1470, and 132 DDs, respectively. This species is known to be univoltine, but the presumption of possible multivoltinism can be estimated by summing all stage developmental requirements as a potential generation time. The estimated generation time is 1602 DDs, for the interval from first egg to first egg.

An extensive monitoring data set consisting of 400,000 beetles trapped over two years (1983−1984) in Massachusetts was used for model validation (Vittum 1986). Average days difference between observed and predicted adult emergence was 1 day for 2% emergence, 4 days for 10% emergence, 0.5 days for 50% emergence, and 3 days for 90% emergence.

2.1.4. Cohort parameters

Cohort parameters in DDRP allow for variation in the development in overwintered eggs of *P. japonica*. The low, average, and high bound values (*xdist1, distro_mean,* and *xdist2*) for pupation were set to 335, 535, and 735 DDC10, respectively. These values were estimated using monitoring data collected in Massachusetts in 1983 (Vittum 1986). Specifically, we calculated the cohort spread (time between *xdist1* and *xdist2*) from the extensive egg and pupal monitoring data from this study as

$$(\text{last date sampled} - \text{first date sampled}) - \text{average stage duration}$$

where dates sampled were in degree-day units and average stage duration was 400 DDC10 (rounded up from 399 and 397 DDC10 for eggs and pupae, respectively). The rounded value of 400 DDC10 was then used for the spread between the *xdist1* and *xdist2* values. As partial validation, the less accurate but still extensive data for adult and first instar stages from the same 1983 data set were used to calculate similar spread values of 370 and 394 DDC10, respectively (see spreadsheet analysis for details). The model applied seven time-distributed cohorts to approximate a normal distribution of pupation times based on evidence for an overall normal distribution in counts of adults during a season (Vittum 1986, Ebbenga et al. 2022).

2.2. Climate suitability model

A climatic suitability model for *P. japonica* for DDRP was developed using eco-physiological information and presence records from North America. Gridded daily climate data for Japan are not publicly available, which prevented us from using native range records for model development. Presence records were derived from peer-reviewed literature, theses, reports, the iNaturalist database, and the Global Biodiversity Information Facility (GBIF.org 2024) (http://gbif.org, accessed 29 Jul 2024). Duplicate records, GBIF records with a geographic uncertainty of >10 km, and records that occurred outside of climate grid cells were excluded. Finally, three GBIF records that occurred much farther (300−1100 km) north of other records were removed because they may represent species misidentifications or observations of transient populations. The resulting dataset of 39,993 records was randomly divided into separate sets comprised of 75% and 25% of for use in model calibration and validation, respectively.

Climatic suitability modeling used daily estimates of T_{min} and T_{max} for North America [the contiguous United States (CONUS) and southern Canada] for 2004 to 2023 (https://daymet.ornl.gov/getdata, accessed 1 Sep 2024) (Thornton et al. 2021). Over this 20-year period, *P. japonica* invaded some of the coldest and hottest parts of its distribution in North America. Climate data were aggregated from a spatial resolution of 1 km^2 to 4 km^2 to decrease model run times. Modeling used climate data for individual years as well as averages for all years, as described below. When analyzing predictions for *P. japonica* records for model fitting and validation, we only considered years that occurred after the record collection date. For example, a record from 6/1/2021 would include predictions for 2022 and 2023.

2.2.1. Cold stress parameters

To help identify an appropriate cold stress threshold, we extracted estimates of T_{min} of the coldest week (based on 20-year averages) for each presence record in the calibration set. Most records (82%) occurred in areas with average weekly T_{min} values < –15 °C (Fig. 1A), which is the cold stress threshold used in a CLIMEX "Compare Locations" model for *P. japonica* (Kistner-Thomas 2019). For >99% of the records, the daily average T_{min} fell below −15°C for < 5 consecutive days during winter months (December, January, and February), which suggests that survival-limiting cold stress accumulates under these conditions. We therefore set the moderate cold stress limit in DDRP to correspond roughly to areas that experienced > 5 consecutive days below −15 °C based on 20-year averages (Fig. 1A). The cold stress limits were calibrated by minimizing the number of records that were excluded due to cold stress accumulations. After this process, no records were excluded by cold stress for years after the collection date. Fig. 1 depicts averages of annual cold stress accumulations between 2004 and 2023 (Fig. 1B) and accumulations for an extreme year in terms of the total area excluded by cold stress (Fig. 1C).

2.2.2. Heat stress parameters

The CLIMEX model for *P. japonica* applied a heat stress threshold of 34 °C but the rationale for this value was unclear (Kistner-Thomas 2019). We used a heat stress threshold of 36 °C because 1504 (5%) of the calibration records occurred in areas with an average weekly $T_{max} \geq 34$ °C, which suggests that the CLIMEX threshold was too low. Conversely, all records except for 12 occurred in areas that experienced an average weekly $T_{max} \leq 36$ °C, and only one experienced > 5 days under these conditions (Fig. 1B). This finding is consistent with a laboratory study that found poor survival rates of *P. japonica* pupae at temperatures ≥ 37 °C (Ludwig 1928), and with records of the pest in warm parts of southern India, where it was likely introduced (Dubey and Venkataraman 1980). For example, recent records from Karnataka, India (India Biodiversity Portal 2016, GBIF.org 2024) are from locations that experienced average T_{max} of 35 °C (95 °F) between 2012−2021 (CustomWeather 2024).

The heat stress limits for *P. japonica* were calibrated by minimizing the number of records that were excluded due to heat stress accumulations. After calibrations, none of the records were excluded by severe heat stress for years after they were collected; however, 45 were excluded by moderate heat stress. In particular, moderate heat stress for 2022 excluded several records in western Oklahoma and surrounding areas. Fig. 2 depicts averages of annual heat stress accumulations between 2004 and 202i3 (Fig. 2B) and accumulations for an extreme year in terms of the total area excluded by heat stress (Fig. 2C).

2.2.1. Estimating the potential distribution and model validation

As an estimate of the potential distribution of *P. japonica* in North America, we combined predictions of all stress exclusions for each year between 2004 and 2023 (Fig. 3). In DDRP, areas that are not excluded by moderate or severe stress exclusion across all modeled years would likely be at high risk of establishment. The climatic suitability model was validated by estimating the number of years in which presence was correctly predicted for records in the validation set. Only years that occurred after the record collection date were considered. According to this analysis, the model predicted presence of *P. japonica* for 99.9% (9961/9967) of presence records for the 20 modeled years (2004−2023), which provides evidence for high model sensitivity. Most of CONUS was climatically suitable for establishment for all years except for the coldest parts of the Midwest and hot parts of California and the Southwest.

3. Demonstration

To provide an example of DDRP model output for *P. japonica*, we produced phenological event maps for the average date of adult emergence and egg hatch for CONUS for 2024, which was the warmest year on record in the United States. The model applied seven cohorts and used data from the PRISM database at a spatial resolution of 4 km^2 (https://prism.oregonstate.edu) (Daly et al. 2006). For most of northern CONUS, the average date of adult emergence for 2024 occurred between June and July (Fig. 4) and the average date of egg hatch occurred between late June and August (Fig. 5). Dates for these events were earliest in the Southeast and latest in the upper Midwest and Intermountain West. Severe heat stress was predicted for the hottest areas of California (e.g., parts of the Central Valley) and for the Southwest, including parts of southwestern Arizona and Texas. Degree-day accumulation was insufficient for egg hatch to occur in high elevation areas of the Intermountain West and Pacific Northwest. This finding may suggest that *P. japonica* would be unable to complete its life cycle in those areas.

4. Discussion

The CLIMEX "Compare Locations" model for *P. japonica* predicted a similar potential distribution as DDRP except that it excluded certain parts of the arid West owing to its inclusion of dry stress parameters (Kistner-Thomas 2019). Similarly, a CLIMEX "Match Climates" model developed for this pest revealed reduced suitability in western areas due to dry summers (Allsopp 1996). However, neither CLIMEX model accounted for supplemental irrigation, which may allow *P. japonica* to survive during periods of drought because eggs and young larvae can avoid desiccation (Fleming 1972, Allsopp et al. 1992). Ongoing work to include soil moisture factors in DDRP could potentially be useful in predicting this pest's potential distribution in non-irrigated arid regions as well as very wet and cold areas. Excessive soil moisture may hinder egg development, and moisture during freezing events has been associated with mortality events of overwintering larvae (Hawley and Dobbins 1941).

Modeling cold and heat stress experienced by *P. japonica* using air temperature data is challenging because larvae and pupae protect themselves from ambient air temperature fluctuations by burrowing up to 12 inches into the soil (Fox 1935). Overwintering larvae can survive under natural conditions (in the soil) to temperatures as low *ca.* −9.4 °C (Fox 1935). However, the insulating effects of snow cover can keep soil temperatures close to 0 °C even when air temperatures are well below freezing (Fox 1935, Hawley and Dobbins 1941, Fleming 1972). Thus, microclimatic conditions experienced by *P. japonica* will likely be a source of model error.

5. Suggested applications

The DDRP model may be run to test where *P. japonica* may become established and reproduce under past, current and future climate conditions, and to estimate the dates when specific pest events will occur. Near real-time forecasts for CONUS are possible using PRISM data. Forecasts of adult emergence and egg hatch may be particularly useful for improving the timing of surveillance and management. Adults are targeted for surveillance using pheromone traps and are controlled using physical methods (e.g., hand removal and barriers), insecticides, and the parasitoid *Istocheta aldrichi* (Mesnil) (Althoff and Rice, 2022). Forecasts of egg hatch may be useful for applying treatments that target grubs and for optimizing control with larval parasitoids, such as *Tiphia vernalis* (Rohwer), and with *Bacillus thurigiensis*.

6. Conclusions

The DDRP model for *P. japonica* requires further validation, which could use observations of phenology and presence for this pest in North America. Understanding whether presence records were collected from transient vs. established populations in climatically extreme areas would help with calibrating the climatic suitability model. Future work could assess whether the use of moisture stress in the climatic suitability model may increase predictive accuracy. Forecasting life cycle completion of the pest across the coldest parts of CONUS over multiple years could provide additional insights into establishment risk.

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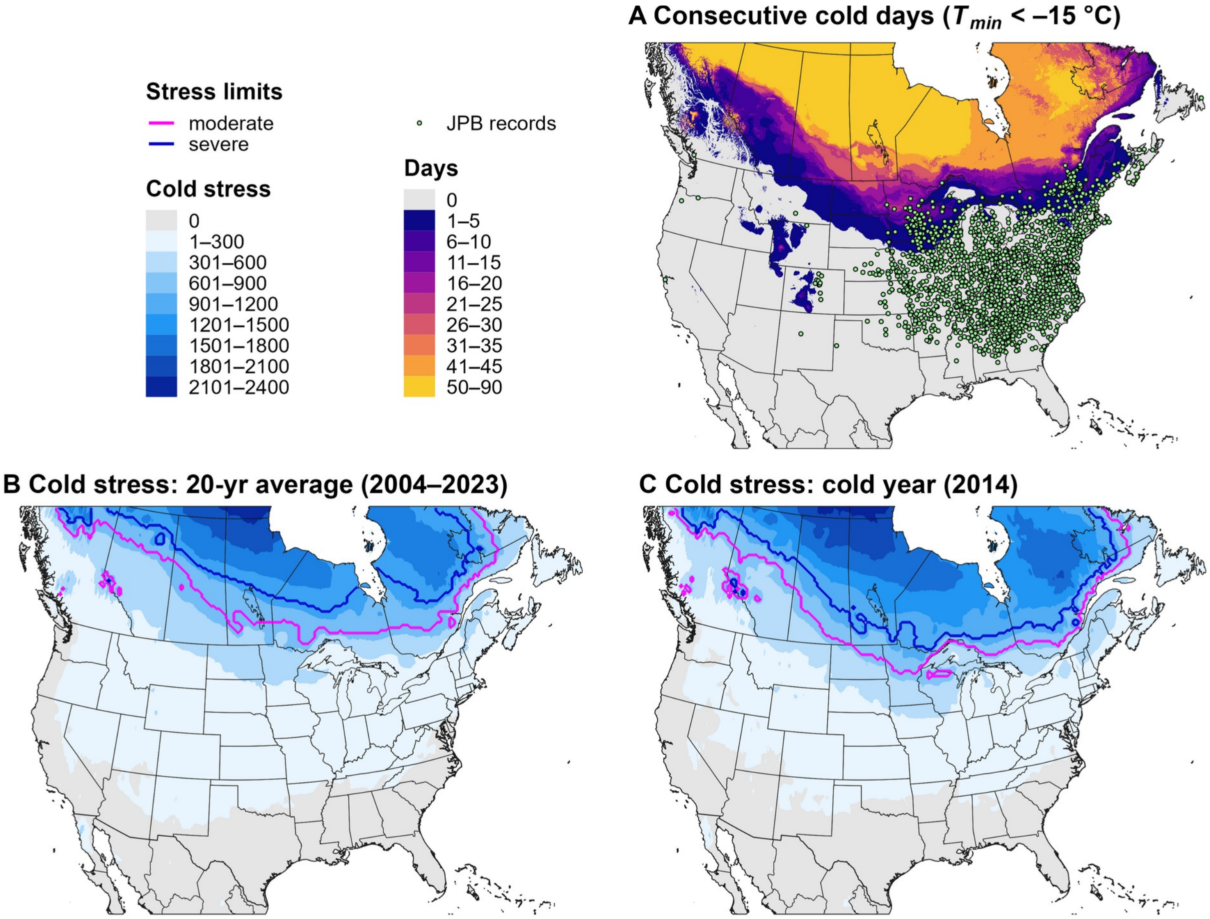
Tables and Figures

Table 1. DDRP parameter values for *Popillia japonica* (JPB).

Parameter	Code	Value
Lower developmental threshold (°C)		
Egg	eggLDT	10
First and second instar nymph	larvaeLDT	10
Third and fourth instar nymph	pupaeLDT	10
Adult	adultLDT	10
Upper developmental threshold (°C)		
Egg	eggUDT	33.3
Larvae	larvaeUDT	33.3
Pupae	pupaeUDT	33.3
Adult	adultUDT	33.3
Stage durations (°C degree-days)		
OWLarvae	OWlarvaeDD	361
Egg	eggDD	172
Larvae (not actually used for this univoltine model)	larvaeDD	1148
Pupae	pupDD	150
Adult (mating plus pre-oviposition time only)	adultDD	132
Pest events (°C degree-days)		
Egg event – suggested label “egg hatch”	eggEventDD	172
Larva event – suggested label “pupation in spring”	larvaeEventDD	361
Pupa event – suggested label “adult emergence”	pupaeEventDD	150
Adult event – suggested label “egg laying”	adultEventDD	132
Cold stress		
Cold stress temperature threshold (°C)	coldstress_threshold	–15
Cold degree-day (°C) limit when most individuals die	coldstress_units_max1	700
Cold degree-day (°C) limit when all individuals die	coldstress_units_max2	1000
Heat stress		
Heat stress temperature threshold (°C)	heatstress_threshold	36
Heat stress degree-day (°C) limit when most individuals die	heatstress_units_max1	75
Heat stress degree-day (°C) limit when all individuals die	heatstress_units_max2	150
Cohorts		
Degree-days (°C) to complete egg development (average)	distro_mean	535
Degree-days (°C) to complete egg development (variation)	distro_var	1600
Minimum degree-days (°C) to complete egg development	xdist1	335
Maximum degree-days (°C) to complete egg development	xdist2	735
Shape of the distribution	distro_shape	normal
Other		
Order of stages	stgorder	OL, P, A, E, L
Obligate diapause (1 = TRUE)	obligate_diapause	1
Degree day calculation method	calctype	triangle

Figure 1. Maps depicting cold days, presence records, and model-predicted cold stress accumulation for *P. japonica* (JPB) in North America (CONUS, southern Canada, and northern Mexico). Maps depict (A) consecutive days of minimum temperatures (T_{min}) below –15 °C based on 20-year climate averages centered on 2013 (2004−2023 (B) averages of annual cold stress accumulation between 2004 and 2023, and (C) annual cold stress accumulation for a particularly cold year (2014). Presence records in map A were thinned to one per county for visualization purposes.

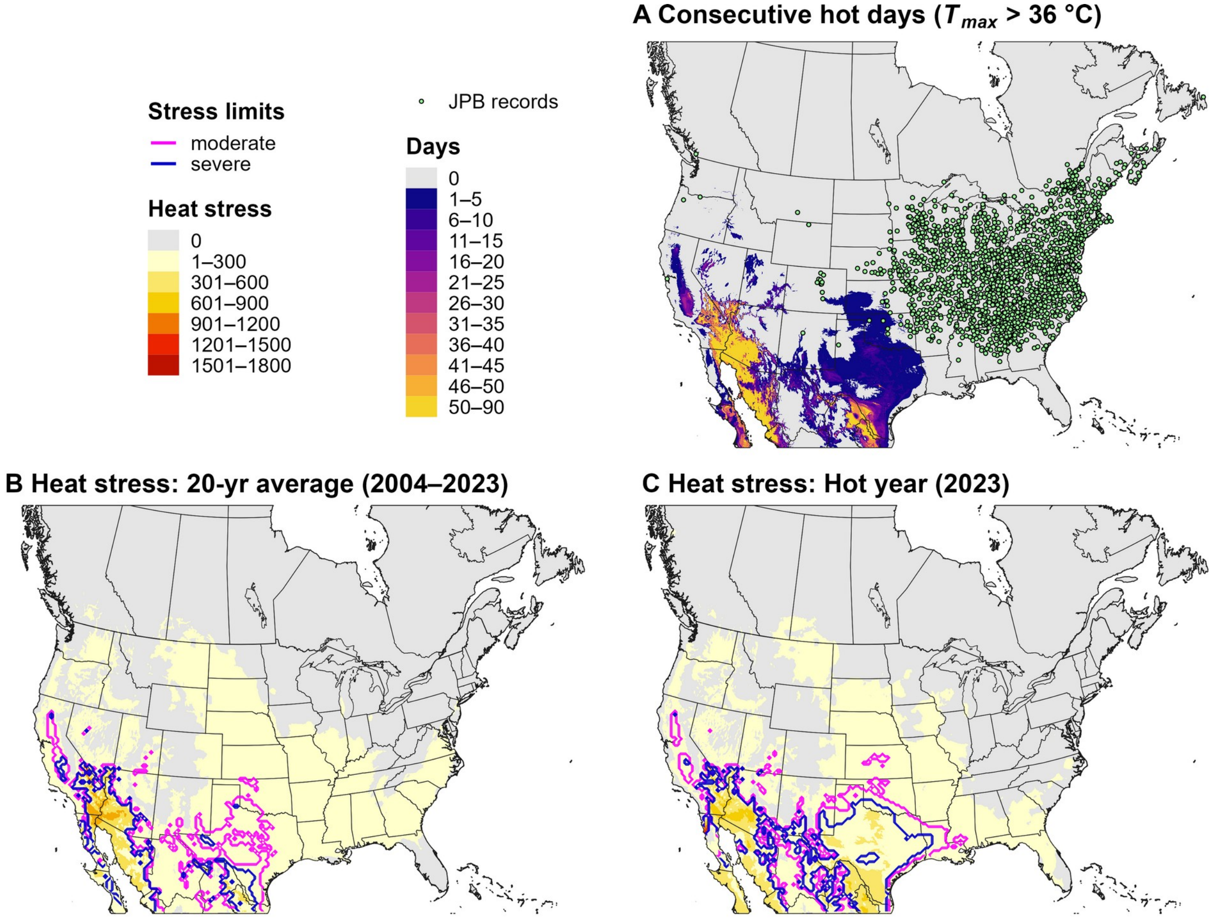


A Consecutive cold days (T_{min} < –15 °C)

B Cold stress: 20-yr average (2004–2023)

C Cold stress: cold year (2014)

Figure 2. Maps depicting hot days, presence records, and model-predicted heat stress accumulation for *P. japonica* (JPB) in North America (CONUS, southern Canada, and northern Mexico). Maps depict (A) consecutive days of maximum temperatures (T_{max}) above 36 °C based on 20-year climate averages centered on 2013 (2004−2023), (B) averages of annual heat stress accumulation between 2004 and 2023, and (C) annual heat stress accumulation for a particularly hot year (2023). Presence records in map A were thinned to one per county for visualization purposes.



A Consecutive hot days (T_{max} > 36 °C)

B Heat stress: 20-yr average (2004–2023)

C Heat stress: Hot year (2023)

Figure 3. The modeled potential distribution for *P. japonica* (JPB) in North America (CONUS, southern Canada, and northern Mexico) according to DDRP runs for 20 recent years (2004−2023). Yellow areas were included in the potential distribution for all 20 years, whereas areas with cooler colors were excluded by moderate or severe climate stresses for ≥1 years.

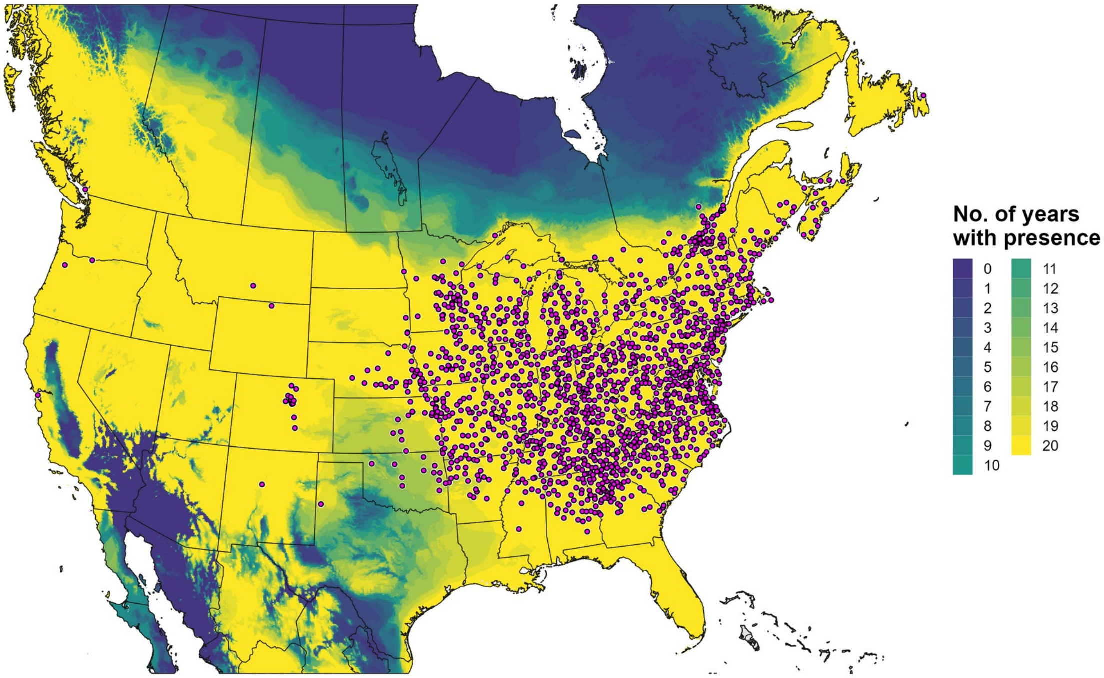


Figure 4. Map depicting the average date of first adult emergence of *P. japonica* (JPB) with severe climate stress exclusion (based on cold and heat stress units) for CONUS for 2024 produced by DDRP.

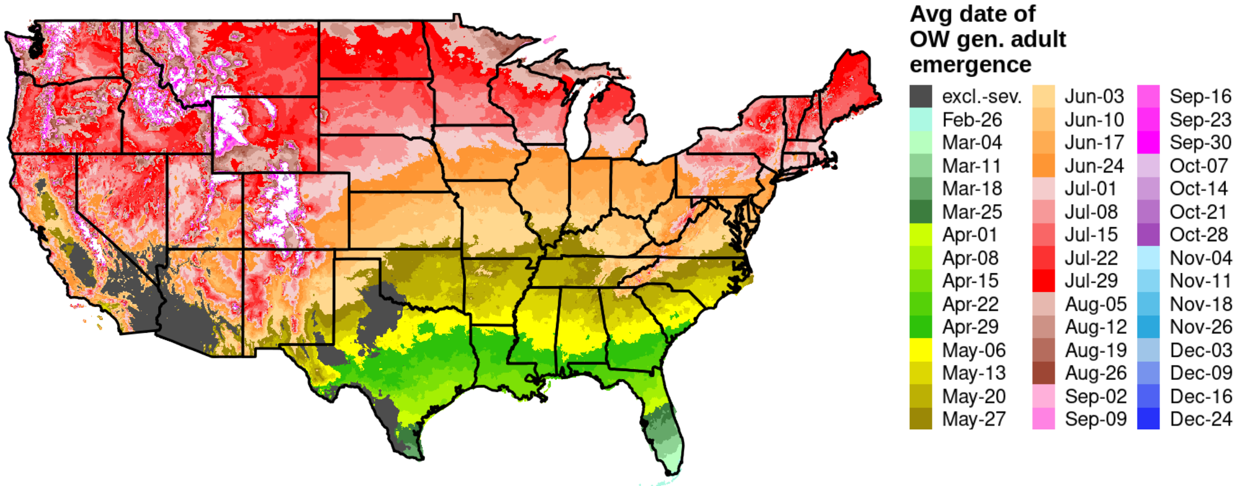


Figure 5. Map depicting the average date of first egg hatch of *P. japonica* (JPB) with severe climate stress exclusion (based on cold and heat stress units) for CONUS for 2024 produced by DDRP.