

The Potential Global Distribution and Voltinism of the Japanese Beetle (Coleoptera: Scarabaeidae) Under Current and Future Climates

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Abstract

Japanese beetle, *Popillia japonica* (Newman), is a severe invasive insect pest of turf, landscapes, and horticultural crops. It has successfully colonized much of the United States and has recently established in mainland Europe. The distribution and voltinism of *P. japonica* will undoubtedly change as a consequence of climate change, posing additional challenges to the management of this species. To assess these challenges, a process-oriented bioclimatic niche model for *P. japonica* was developed to examine its potential global distribution under current (1981–2010) and projected climatic conditions (2040–2059) using one emission scenario (representative concentration pathway [RCP] 8.5) and two global climate models, ACCESS1-0 and CNRM-CM5. Under current climatic conditions, the bioclimatic niche model agreed well with all credible distribution data. Model projections indicate a strong possibility of further range expansion throughout mainland Europe under both current and future climates. In North America, projected increases in temperature would enable northward range expansion across Canada while simultaneously shifting southern range limits in the United States. In Europe, the suitable range for *P. japonica* would increase by 23% by midcentury, especially across portions of the United Kingdom, Ireland, and Scandinavia. Under the RCP 8.5 scenario, cumulative growing degree-days increased, thereby reducing the probability of biannual life cycles in northern latitudes where they can occur, including Hokkaido, Japan, northeastern portions of the United States, and southern Ontario, Canada. The results of this study highlight several regions of increasing and emerging risk from *P. japonica* that should be considered routinely in ongoing biosecurity and pest management surveys.

Key words: CLIMEX, climate change, *Popillia japonica*, voltinism, pest risk

The Japanese beetle, *Popillia japonica* (Newman 1841) (Coleoptera: Scarabaeidae), is a highly polyphagous invasive scarab, which has over 300 reported host plants (Fleming 1972). Originally from Japan, this insect has invaded vast areas of North America over the last hundred years and has recently established in mainland Europe (EPPO 2016). Today, *P. japonica* is the most widespread and destructive insect pest of turfgrass, as well as of landscape and nursery crops in the United States (Potter and Held 2002). Whereas severe outbreaks of *P. japonica* can occur sporadically, little to no beetle activity can be observed in other years. Adults damage the foliage and fruit surfaces of many valuable plant species. The larvae damage the roots of various plants and grasses, which often leads to the destruction of turfgrass. Over U.S. \$460 million is spent annually for direct control costs and renovating or replacing damaged turf and ornamental plants (USDA 2015).

Popillia japonica is univoltine throughout most of its native and invaded range (Fleming 1972, Potter and Held 2002). In North America, a portion of some populations may take 2-yr to

complete a generation including populations in southern Ontario, as well as New Hampshire, New York, Massachusetts, New Jersey, and Pennsylvania (Vittum 1986, Vittum et al. 1999). In Hokkaido Japan, most beetles exhibit a 2-yr life cycle (Clausen et al. 1927). Both larvae and adult *P. japonica* are considered as destructive plant pests. Adult beetles emerge from the soil between May and July depending on their geographic location (Fleming 1972), and they feed on the fruit, flowers, and foliage of the host plants, particularly damaging ornamental and garden plants. Adults can also damage fruits, corn, soybean, and additional crops with notable yield reductions occurring in some instances (Gould 1963, Szendrei and Isaacs 2006, USDA 2015). Within a 4- to 6-wk life span, female adults mate, feed, and lay their eggs in moist grasslands (Potter and Held 2002). Eggs hatch after 10–14 d, and the larvae feed on grass roots for the rest of the summer (Fleming 1972). Larvae undergo three instar stages and move deeper into the soil (>15 cm) to overwinter at the beginning of late autumn. Root-feeding larvae cause substantial damage to turf in lawns, parks, golf courses, and pastures (Potter

and Braman 1991). In its native Japan, *P. japonica* is regarded as a minor agricultural pest, which is probably because much of Japan's terrain is not suitable for larval development in conjunction with an abundance of natural enemies keeping its populations under control (Clausen et al. 1927, Fleming 1968). Despite concerted state and federal effort to limit the spread of this pest, *P. japonica* has progressively extended its U.S. range since its initial 1916 detection in a nursery near Riverton, NJ. By 1998, *P. japonica* had established in all states east of the Mississippi River except Florida. Moderate infestations also occur in states west of the Mississippi River including Arkansas, Iowa, Kansas, Minnesota, Missouri, Nebraska, North Dakota, Oklahoma, Colorado, and South Dakota (USDA 2015). The beetle also extended its range northward into Canada where it has successfully established in portions of southern Quebec, New Brunswick, Nova Scotia, and Ontario provinces as well as Prince Edward Island (EPPO 2003, CFIA 2015). A combination of factors enabled *P. japonica* to be a successful invader in North America, including favorable climatic conditions (Allsopp 1996, Zhu et al. 2017), vast expanses of turf and pasture grasses for root-feeding larvae, hundreds of suitable often non-native adult food plants, and no effective natural enemies at the time of introduction (Fleming 1976, Potter and Held 2002). Over time, beetle populations rose and then spread naturally as well as accidentally by human commerce across the North American continent. Successful establishment of *P. japonica* populations across the western United States and Canada was further aided by the increased conversion of the North American landscape into grassy areas.

To reduce further spread of this pest, U.S. and Canadian governments maintain *P. japonica* quarantines and regulations that restrict air and land shipments of nursery stock from the Eastern United States to nine other western states and eight Canadian provinces (NPB 2017). Area-wide *P. japonica* monitoring and eradication programs have proven to be effective control methods when entry prevention fails. In California, multiple *P. japonica* infestations in Sacramento and San Diego counties have been chemically eradicated (Clair and Kramer 1989) with *P. japonica* detection trapping occurring annually throughout the state (CDFA 2018). Isolated infestations in Las Vegas, NV, have also been successfully eradicated (Potter and David 2004). Despite the quarantine measures, westward spread of the beetle has escalated over the last decade with partial infestations now occurring in Idaho, Utah, Oregon, and Montana (NPB 2017, ODA 2017). Isolated detections have also been reported in Hawaii, Arizona, Washington, and New Mexico, but breeding populations have not yet been discovered (CERIS 2018).

Elsewhere in the world, *P. japonica* is established on Terceira Island, part of Portugal's Azores Islands, due to an accidental introduction originating from a U.S. air base in the early 1970s (Simões et al. 1993). It has since spread to multiple other Azores Islands. In Russia, *P. japonica* has been observed on the Kuril Islands, where its occurrence is sporadic and restricted to the South Kirile region of Sakhalin, on the island of Kunashir (Chebanov 1977, EPPO 2018). Although a single adult beetle was recovered from an airstrip in Darién, Panama (Krell 2012), there are no other creditable *P. japonica* reports from Central and South America. In 2014, *P. japonica* was detected for the first time in mainland Europe within the Ticino Valley of Italy (Pavesi 2014). Rising beetle populations in this region resulted in substantial fruit tree damage (peach and sweet cherry) within the Ticino Valley in 2015 (EPPO 2016). In 2017, *P. japonica* was detected in Ticino, Switzerland (EPPO 2017) and Paderborn, Germany (Urban 2018), but the pest has not established permanent breeding populations in these countries. Given that much of mainland Europe has favorable climate and landscapes for *P. japonica* establishment (Bourke 1961,

Allsopp 1996, Zhu et al. 2017), further range expansion and potential crop, pasture, turfgrass damage can be expected throughout much of mainland Europe if vulnerable countries do not develop contingency plans for outbreaks of this pest (EPPO 2016).

To date, a few studies have examined the climatic niche and the potential geographic distribution of *P. japonica* under current climatic conditions (Bourke 1961, Allsopp 1996, Zhang et al. 2002, Zhu et al. 2017). Temperature, soil moisture, and human activities are probably important factors limiting the beetle's ability to establish in novel environments. However, none of these studies address possible changes in the geographic distribution and voltinism of *P. japonica* that may occur under future climate change. Previous research suggests that potential climate change impacts on *P. japonica* will vary across its vast geographic range. Rising temperatures may exacerbate the negative impacts of *P. japonica* on certain host plants, with potentially large economic costs associated with reduced crop yields. Empirical model projections indicate that the projected 3.5°C increase in temperature across the central United States for 2050 would increase the optimal feeding window for adult beetles by 290% (Niziolek et al. 2013). In contrast, Petty et al. (2015) found that recent *P. japonica* population declines in Arkansas were likely due to increasingly hot and dry conditions. Therefore, the increasingly long warm and dry periods projected under future climate scenarios for the southwestern United States (Carter et al. 2014) may reduce the plant health threats posed by *P. japonica*. To address these issues, a bioclimatic niche model for *P. japonica* was developed to assess the sensitivity of this pest's potential global distribution and life cycle to the future climate change scenario RCP 8.5 in the middle 21st century.

Materials and Methods

Species Occurrence Data

The known distribution of *P. japonica* was assembled from the Global Biodiversity Information Facility (GBIF.org 2018), the European and Mediterranean Plant Protection Organization global database (EPPO 2018), the Center for Environmental and Research Information Systems (CERIS 2018), and the literature (Clausen et al. 1927, Fleming 1976, Chebanov 1977, Simões et al. 1993, Krell 2012, Pavesi 2014, EPPO 2017, Urban 2018; Fig. 1). Occurrences were verified where possible through either validated photos or specimen records. Records with incomplete locality information were omitted. Reports of this species in portions of China and North Korea are unreliable, and the species has yet to be confirmed on the mainland of Asia (Fleming 1976, Reed et al. 1991, Allsopp 1996, Potter and Held 2002). In total, 1,028 occurrence localities were found with 40 in Asia (e.g., Japan and Russia), 6 in Europe, and 981 in North America and 1 in Central America.

CLIMEX Software

To model *P. japonica* distribution under recent and future climates, we used CLIMEX, a process-oriented climate-based niche modeling package (Sutherst and Maywald 1985, Kriticos et al. 2015). It utilizes an ecophysiological growth model that enables users to explore the effects of climate on the distribution and phenology of poikilothermic organisms. CLIMEX is a model of moderate complexity that combines the strengths of correlative modeling methods (fitting stress parameters based on geographical occurrence data) and deductive modeling methods (utilizing laboratory studies and phenological observations for growth function fitting; Kriticos et al. 2015). This software has been used widely to model the potential distribution

of many invasive arthropod pests under both current climatic conditions and possible future climates (Sutherst and Maywald 2005, Stephens et al. 2007, Jaramillo et al. 2011, Kocmánková et al. 2011, Khormi and Kumar 2014, Ge et al. 2017, Kistner 2017).

The key assumption behind CLIMEX is that climate is the primary determinant of the geographical distribution of a species. It uses weekly growth and stress-related indices to evaluate the potential for species to persist and grow at a given location for which relevant climatic data are available. The final output of CLIMEX is an overall annual index climatic suitability, the Ecoclimatic Index (EI), which describes the climatic suitability of a given location for the persistence of the species under investigation. The EI is scaled from 0 (unsuitable) to 100 (climatically perfect all year round), and theoretically, species can establish if $EI > 0$. In practice, EI values of 100 are rarely achieved and only then in locations with high climatic

stability, such as equatorial environments. In CLIMEX, the annual growth index (GI_A) describes the potential for population growth during favorable climatic conditions and is determined from a given species' specific temperature (TI) and moisture (MI) growth preferences. The four primary stress indices (Cold, Heat, Dry, Wet) describe the probability of a given population surviving under unfavorable conditions and often limit the potential growth of a population in a given location. These stress indices are useful for determining a target species' geographic range limits. Sutherst and Maywald (1985) and Kriticos et al. (2015) provide a full description of the theory behind the CLIMEX modeling software.

Climate Data

The *P. japonica* model was fitted using a 1981–2010 global climatological data set (D. J. Kriticos, personal communication). This

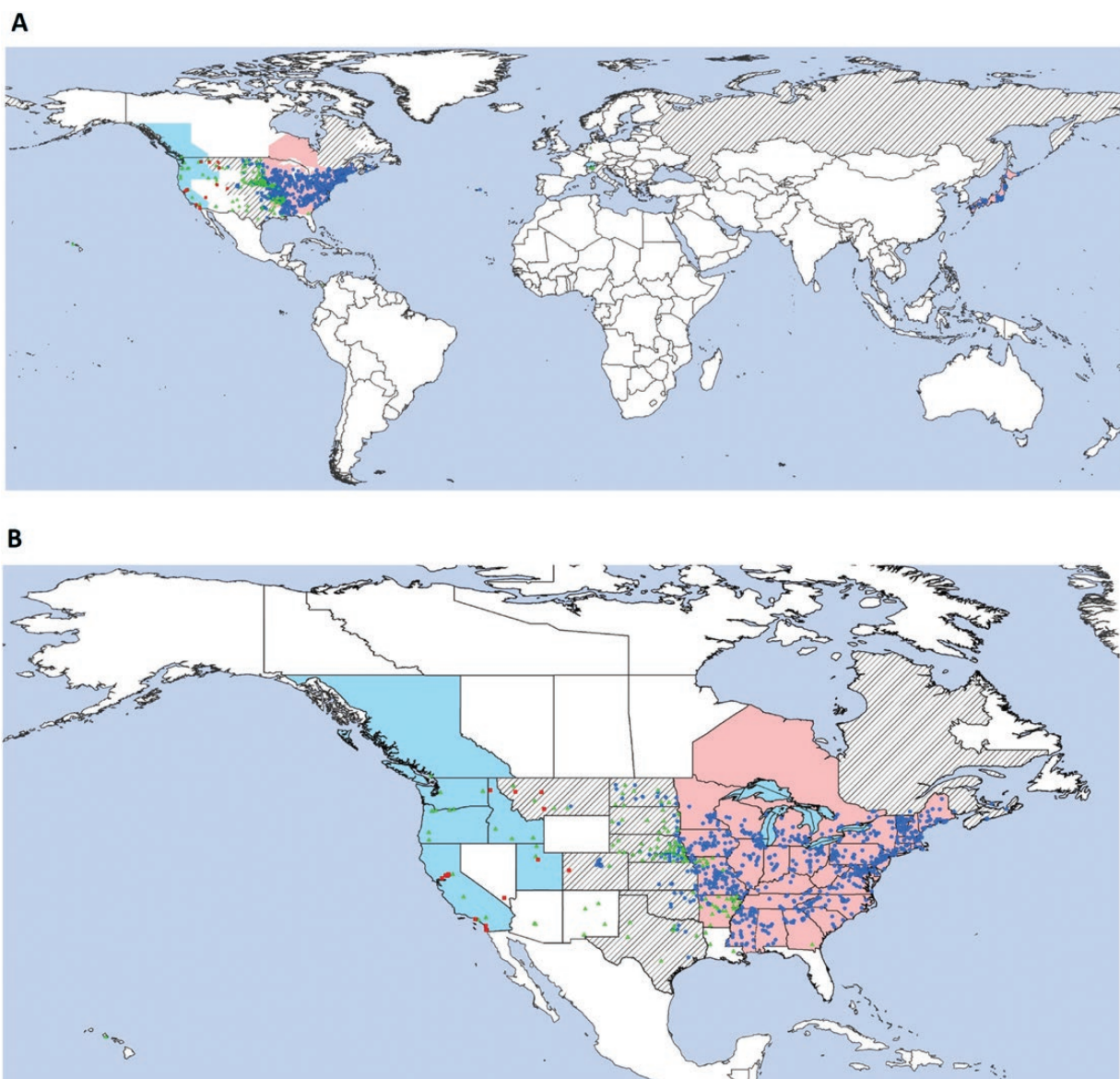


Fig. 1. Known global (A) and North American (B) distribution of *Popillia japonica*. Blue circles represent established populations, green triangles indicate locations where *P. japonica* has been detected, and red triangles represent locations where *P. japonica* has been eradicated. Pink areas represent national or subnational administrative units where the species has been recorded as established, dashed areas indicate national or subnational administrative units that are partially infested, and blue areas represent national or subnational administrative units currently under annual surveillance and chemical control programs.

data set represents the baseline climate and consists of monthly long-term averages for daily minimum and maximum temperature (°C), relative humidity (%), and rainfall totals (mm; Kriticos et al. 2012). The averages are centered on the year 1995. Two global climate models (GCMs), ACCESS1-0 (CAWCR-CSIRO, Australia) and CNRM-CM5 (CNRM-CERFACS, France) with the representative concentration pathway (RCP) 8.5 emission scenario for the year 2050 were used in this study to represent possible future climates (Moss et al. 2010). The two GCMs represent different climate sensitivities, defined as the amount of global warming for a doubling CO₂ concentration by midcentury compared with 1990s levels. Predictions of long-term climate change are highly variable, so only midcentury climate projections (2040–2059 centered on 2050) were assessed in the content of this study. Currently, global greenhouse emissions are tracking the highest representative concentration pathway (RCP 8.5) used by the IPCC to assess projected climate change (Sanford et al. 2014). The RCP 8.5 represents the ‘worst case’ scenario in which current trends in greenhouse gas emissions continue unabated and predicts the greatest increases in global mean temperatures ranging from 1.3 to 2.0°C by 2050. Harris et al. (2014) provide detailed explanations of GCM and emission scenario selection in terms of ecological niche modeling. All gridded global climate data sets used in the CLIMEX modeling had a spatial resolution of 30 arc minutes (0.5° × 0.5°; D. J. Kriticos, personal communication).

Fitting CLIMEX Parameters

The CLIMEX Compare Location model was fitted to the known distribution of *P. japonica* in Asia. Model parameters were iteratively adjusted to fit its known distribution in Japan and its occurrence on the far eastern Russian island of Kunashir, part of the Kurile Islands. The final model was then verified using the North American records and validated against the European presence records. All model parameters were checked to ensure that they were biologically reasonable. The parameters used in the CLIMEX model for *P. japonica* are summarized in Table 1. The role and meaning of

these parameters are fully described in Kriticos et al. (2015), and their values are discussed below.

Growth Indices

Laboratory studies indicate that threshold growth temperatures and development rates vary across the beetle’s different life stages (Ludwig 1928, 1930, Régnière et al. 1981a). Ludwig (1928, 1930) observed that eggs did not hatch at temperatures below 13°C. Adult beetles lay their eggs in July and August. These eggs hatch within ~2 wk, and most larvae will reach the cold tolerant third-instar life stage before the onset of winter (Fleming 1972). Consequently, cold intolerant eggs and early instar grubs are probably not exposed to winter temperatures below their developmental threshold. As such, a value of 10°C was set as the minimum temperature for development (DV0), which is consistent with the lower developmental threshold for *P. japonica* third-instar grubs and pupae (Régnière et al. 1981a). The optimal development temperature is 30°C for eggs, 27.5°C for larvae (first to third instars), and between 30 and 32°C for pupae (Ludwig 1928). Therefore, the lower (DV1) and upper (DV2) optimal temperatures were set at 27.5 and 31°C, respectively. The maximum temperature threshold is 35°C for pupae, 34°C for eggs and third instars, and 31°C for first and second instars (Ludwig 1928, Régnière et al. 1981a). Adult beetles will stop feeding and seek shelter at a temperature above 35°C. (Fleming 1972). Given that larvae should be able to escape extreme soil temperatures by vertical soil movement while eggs cannot (Fleming 1972, Kaya 1990), the upper temperature threshold (DV3) was set as 34°C. Taken together, these values provided a good fit to the observed global distribution and enable persistence in southern limits of *P. japonica*’s North American range where summer soil temperatures up to 10 cm below the turf often reach above 31°C (Régnière et al. 1981b).

Suitable soil moisture conditions are crucial for the development and oviposition of *P. japonica*. Adult females preferentially oviposit in moist areas as long as the soil is not waterlogged since egg survival declines in oversaturated soils (Régnière et al. 1981b, Allsopp et al. 1992). Experimental results showed that adult beetle oviposition

Table 1. CLIMEX parameter values for *Popillia japonica*

Index	Parameter	Values
Temperature	DV0 = limiting low average weekly temperature	10°C
	DV1 = lower optimal average weekly minimum temperature	27.5°C
	DV2 = upper optimal average weekly maximum temperature	31°C
	DV3 = limiting high average weekly temperature	34°C
Threshold Annual Heat Sum	PDD = minimum heat sum required each year in order to complete its life cycle	525°C degree-days
Moisture ^a	SM0 = lower soil moisture threshold	0.2
	SM1 = lower optimal soil moisture	0.5
	SM2 = upper optimal soil moisture	1
	SM3 = upper soil moisture threshold	1.5
Cold Stress	TTCS = cold stress threshold (average minimum weekly temperature)	-15°C
	THCS = rate of cold stress accumulation	-0.007 wk ⁻¹
Heat Stress	TTHS = heat stress threshold (average maximum weekly temperature)	34°C
	THHS = rate of heat stress accumulation	0.01 wk ⁻¹
Dry Stress	SMDS = dry stress threshold (average weekly minimum soil moisture)	0.2
	HDS = rate of dry stress accumulation	-0.008 wk ⁻¹
Wet Stress	SMWS = wet stress threshold (average weekly maximum soil moisture)	1.5
	HWS = rate of wet stress accumulation	0.007 wk ⁻¹
Hot–Wet Stress	TTHW = hot–wet temperature threshold (average maximum weekly temperature)	27°C
	MTHW = hot–wet moisture threshold (average weekly maximum soil moisture)	1.4
	PHW = rate of hot–wet stress accumulation	0.01 wk ⁻¹

^aValues without units are dimensionless indices of available soil moisture, scaled from 0 (oven dry), with 1 representing field capacity.

preference decreased significantly when soil moisture was below 20% (Allsopp et al. 1992). The immature stages are well adapted to moderate to high soil moisture levels and are vulnerable to desiccation (Fleming 1972, Régnière et al. 1981b). Therefore, the CLIMEX parameters for Moisture Index were set as SM0 = 0.2, SM1 = 0.5, SM2 = 1, and SM3 = 1.5 (Table 1). In the absence of turf or pastoral grasslands, it is reasonable to assume that *P. japonica* would be unable to establish in arid environments.

Stress Indices

Larval winter kill can be substantial, particularly when unusually cold weather occurs without an insulating layer of snow (Fox 1935, 1939; Fleming 1972). In Japan, overwintering larvae exhibit a supercooling point of -7°C (Hoshikawa et al. 1988), while Fox (1939) observed near 100% larval mortality at soil temperatures below -9.4°C in New Jersey. In the northern limits of its North American range, soil temperature rarely falls below 0°C because snow acts an insulating blanket over the winter months (Fleming 1972). For instance, snow cover keeps soil temperatures in New Jersey near 0°C , even when air temperature falls around -15°C (Fox 1935, Hawley and Dobbins 1941). A threshold temperature cold stress of -15°C (TTCS) and a stress accumulation of -0.007 wk^{-1} (THCS) allowed the northern most records to barely persist.

Hot-wet stress is probably limiting the potential for *P. japonica* to establish in wet tropical regions (Table 1). A combination of a threshold temperature (TTHW) of 27°C and a threshold soil moisture index of (MTHW) of 1.4, and a stress accumulation (PHW) of 0.01 wk^{-1} , reduced the potential range of *P. japonica* in tropical and subtropical portions of the Southern Hemisphere where the species has not established, but includes the maritime subtropical Azores Islands where the species is widespread.

Annual Heat Sum Threshold

The annual heat sum threshold (PDD) is the number of degree-days of thermal accumulation above DV0 required by a given species to complete one generation (Kriticos et al. 2015). In its northernmost range limits, some portions of a given population may take up to 2-yr to complete a single generation (Clausen et al. 1927, Vittum 1986, Vittum et al. 1999). Therefore, the PDD represents the minimum heat sum required each year to complete the *P. japonica* life cycle (egg to egg). With a base and upper developmental threshold of 10 and 34°C , *P. japonica* requires 524°C degree-days from January first before adult beetles begin to emerge (Ludwig 1928, Régnière et al. 1981a, Magarey et al. 2015). A threshold PDD of 525°C degree-days above DV0 (10°C) just allowed the persistence of the species at the limits of its distribution on the Kuril region's Kunashir island.

Régnière et al. (1981a) estimated that degree-day requirements for *P. japonica* $1,422^{\circ}\text{C}$ degree-days above 10°C for complete development (egg to egg). Therefore, areas that accumulated a minimum of $1,422^{\circ}\text{C}$ degree-days were defined as areas where annual life cycles occur. Areas that accumulated less than the $1,422^{\circ}\text{C}$ degree-day developmental threshold were defined as areas where biannual life cycles may occur. It is important to note that the degree-day accumulations calculated by CLIMEX are based on the mean annual accumulated degree-days calculated over multiyear climatological data sets. For instance, in its invaded range in the Northeastern United States, 2-yr life cycles occur sporadically in New Jersey and Pennsylvania (Fleming 1972, Vittum 1986, Vittum et al. 1999). Likewise, the northernmost section of *P. japonica*'s native range,

Hokkaido, Japan, larvae normally exhibit a 2-yr life cycle, but a 1-yr life cycle may occur in years with above average temperatures (Clausen et al. 1927).

Results

Potential Distribution under Current and Future Climates

Overall, modeled potential distribution of *P. japonica* under current climate agrees well with the known distribution of this species in both its native and invaded ranges (Fig. 2A). In general, areas of the world that are climatically suitable for *P. japonica* invasion (i.e., locations where the model gives $\text{EI} \geq 1$) include eastern Asia, central Europe, large portions of southern and eastern South America, sub-Saharan Africa, the North Island of Zealand, and along the eastern coast of Australia (Fig. 2A, Table 2). In the equatorial tropics, consistent excessive hot-wet stress prevents population growth. In its non-native North American range, areas of highest modeled climatic suitability accord strongly with the highest densities of occurrence records in the eastern and Midwestern United States (Fig. 3A). There is also potential for further spread along the western coastline and infill in the north central states. Discordant records in New Mexico, Colorado, Idaho, Texas, Arizona, and Nevada were found to be either isolated infestations associated with anthropogenic landscapes (e.g., parks, golf courses, lawns), or single detections around airports (Figs. 1 and 3A). Over half of Europe is climatically suitable for *P. japonica* (Table 2), indicating a strong possibility of further spread and establishment across the continent (Fig. 4A).

On a global scale, the percentage of climatically suitable ranges for *P. japonica* does not vary much between current climatic conditions and possible future climates for midcentury (Table 2), but rather the positioning of suitable range tends to shift northward (Fig. 2). Under the RCP 8.5 emission scenario, notable range contractions occur in portions of eastern Asia and North America below the 40th Parallel North due to increased heat stress (HS) over the summer months (i.e., extended exposure to weekly maximum temperatures above an upper temperature threshold of 34°C ; Fig. 2B and C). In the southern United States, these range contractions are much more extensive under the ACCESS1-0 model with a 29.09% reduction in climatically suitable U.S. range ($\text{EI} \geq 1$) compared with the 3.13% reduction observed in the CNRM-CM5 model (Fig. 3). Likewise, range expansions in Canada are more pronounced under the ACCESS1-0 model (Table 2). In Canada, large portions of British Columbia, Saskatoon, and Manitoba became climatically suitable as growing degree-day requirements could now be met (Fig. 3B and C). Suitable range also expanded northward from previously restricted southern portions of Ontario and Quebec as cold stress limits were overcome (Fig. 3B and C). In Europe, suitable *P. japonica* range expanded northward across portions of Norway, Sweden, Finland, Ireland, and the United Kingdom under both GCMs (Fig. 4B and C). Under the CNRM-CM5 model, highly climatically suitable range in Europe increased by over threefold compared with current climatic conditions (Fig. 4B, Table 2).

In the Southern Hemisphere, projected suitable *P. japonica* range contracts compared with current climatic conditions with greatest reductions occurring in South America and Africa by midcentury (Table 2). Projected rising temperatures reduced previously suitable areas in these continents due to increased summer heat stress. Only minor range reductions occur in Australia, whereas suitable range

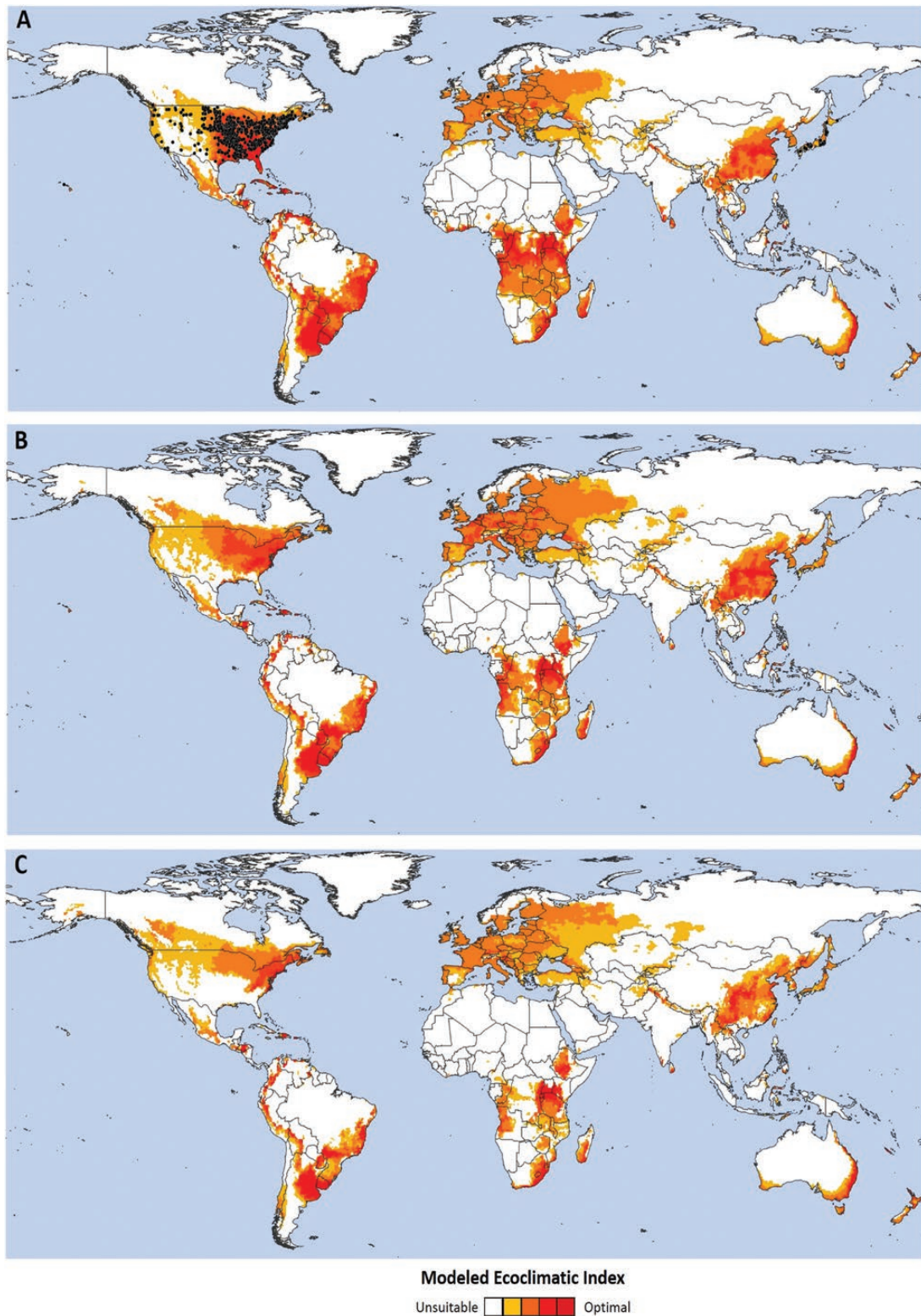


Fig. 2. The modeled global climatic suitability (CLIMEX Ecoclimatic Index) for *Popilla japonica* based on current (A) and future climate projections under CNRM-CM5 (B) and ACCESS1-0 (C) global climate models running the RCP 8.5 emission scenario for 2050. Black circles designate reported occurrences.

occurs in New Zealand expands (Fig. 2). Although these range contractions were similar between the two GCMS (Fig. 2B and C), range reductions are more pronounced under the ACCESS1-0 model (Fig. 2C, Table 2).

Volitinism

The model's degree-day requirements for *P. japonica* (1,422°C degree-days above 10°C for a 1-yr life cycle) under current climate (1995) are fairly consistent with observed annual and biannual life

Table 2. Climatically suitable area (EI > 0) for *Popillia japonica* expressed as an area (km²) and the percentage of total land area per country or region under current climate and future climates for the year 2050 based on two general circulation models (CNRM-CM5 and ACCESS1-0) under the RCP 8.5 emission scenario

Areas	Current climate (1995)		CNRM-CM5 RCP 8.5 (2050)		ACCESS1-0 RCP 8.5 (2050)	
	Total suitable areas km ² (EI > 0)	% suitable areas (EI > 0)	Total suitable areas km ² (EI > 0)	% suitable areas (EI > 0)	Total suitable areas km ² (EI > 0)	% suitable areas (EI > 0)
North America	6,387,714	26.10	7,095,013	28.99	6,583,506	26.90
United States	5,527,479	56.25	5,354,531	54.49	3,919,843	39.89
Canada	592,090	5.93	1,578,576	15.81	2,144,707	21.48
Europe	5,996,589	60.34	7,374,990	74.21	7,202,069	72.47
Italy	281.61	93.49	284.41	94.42	286.91	95.35
Asia	6,516,034	14.87	7,541,422	17.21	7,247,828	16.54
Japan	353,199	93.46	353,199	93.46	311,062	82.31
South America	8,120,768	45.52	6,286,816	35.69	5,435,848	30.47
Africa	10,650,068	35.24	8,323,010	27.54	5,745,113	19.91
Australia	1,837,926	23.91	1,460,502	19.12	1,411,306	18.36
New Zealand	200,351	74.27	219,288	81.29	226,140	83.83
World	40,049,966	26.89	39,126,538	26.27	34,017,896	22.84

EI (Ecoclimatic Index).

cycles across its known global geographic range (Figs. 5A and 6A). Model outputs show annual life cycles across the recently invaded Piedmont and Lombardy regions of northern Italy, which is consistent with observed *P. japonica* phenology in Italy (EPPO 2016). However, model outputs also indicate that much of central and northern Europe will exhibit biannual year life cycles under current climatic conditions (Fig. 5A).

Under the climate change scenario explored, changes in projected *P. japonica* voltinism varied across regions, within regions, and between GCMs (Fig. 5). In Canada, new suitable range mostly fell in cold regions where minimum growing degree-day requirements for consistent annual life cycles could not be met. However, suitable range in southern Ontario under current climatic conditions shifted from biannual to annual life cycles under both GCMs (Fig. 5). In its northern U.S. range limits, many areas exhibiting biannual life cycles under current climatic conditions switched to annual life cycles by 2050 with few differences between GCMs (Fig. 5). In Europe, the simulated number of cumulative growing degree-days increase and the proportion of areas exhibiting annual life cycles subsequently rise under both GCMs, but more so under the ACCESS1-0 (Fig. 5B and C). In Japan, projected gains in cumulative growing degree-days increase the portion of the areas capable of supporting an annual life cycle by 10.6% under the CNRM-CM5 (Fig. 6B) and 19.4% under the ACCESS1-0 models (Fig. 6C), respectively. Current climatic conditions and the CNRM-CM5 model projections for 2050 on Honshu Island indicate the co-occurrence of both annual and biannual life cycles (Fig. 6A and B), whereas the ACCESS1-0 model suggests that all of Honshu Island would exhibit an annual life cycle by 2050 (Fig. 6C). Likewise, the western coastline of the island of Hokkaido would switch from a biannual to an annual life cycle by 2050 under the ACCESS1-0 model (Fig. 6C).

Discussion

In terms of this model's projections for the potential global *P. japonica* distribution under current climatic conditions, the results are mostly consistent with previous climate niche modeling work done on this widespread pest (Allsopp 1996, Zhang et al. 2002, Zhu et al. 2017). Extreme cold winter temperatures limit *P. japonica* distribution in northern latitudes, whereas prevailing warm

and wet conditions restrict its potential range in the humid tropical southern latitudes. These findings are not surprising given *P. japonica*'s specific temperature and soil moisture requirements for development and oviposition (Ludwig 1928, Fleming 1972, Allsopp et al. 1992). Under the RCP 8.5 scenario, rising winter temperatures reduce cold stress in the Northern Hemisphere, converting previously unsuitable areas into new climatically suitable ranges. Therefore, it is plausible that *P. japonica* will expand its current Canadian range further northward and invade additional countries across northern Europe in the coming decades. In addition, warmer midcentury temperatures enhance *P. japonica* population growth potential across its current northern North America range, which in turn could increase the frequency and severity of *P. japonica* outbreaks particularly in Southern Ontario, New England, and the Midwest (Niziolek et al. 2013). In contrast, increasingly hot and dry conditions projected under the RCP 8.5 reduce previously suitable range in the southeastern United States, southeastern Asia, and all continents in the Southern Hemisphere by midcentury. Given that the southeastern United States is expected to become increasingly warm and dry under climate change (Carter et al. 2014) and that recent *P. japonica* declines in Arkansas have been linked to rising temperatures (Petty et al. 2015), it is plausible that this beetle will soon become a minor pest within its current southeastern U.S. range.

The CLIMEX model for *P. japonica* indicates the possibility of substantial range expansion and infill across Europe under both current climatic conditions and midcentury projections under the RCP 8.5. Spain, France, Romania, Ireland, and the United Kingdom are especially at risk for *P. japonica* invasion due to a combination of favorable climate and large expanses of pasture lands (EPPO 2016). To date, *P. japonica*'s presence in mainland Europe is still limited to the Ticino Valley of Italy (EPPO 2018). Recent detections of *P. japonica* in Switzerland (EPPO 2017) and Germany (Urban 2018) suggest that this pest will probably spread and eventually establish elsewhere in Europe. Regardless, European biosecurity managers still have time to prevent or, at the very least, slow the spread of this pest across mainland Europe. Coordinated early detection and eradication efforts will help prevent further spread of this invasive pest throughout Europe. Traps with a combined pheromone and floral attractant lure have proven very effective in detecting isolated

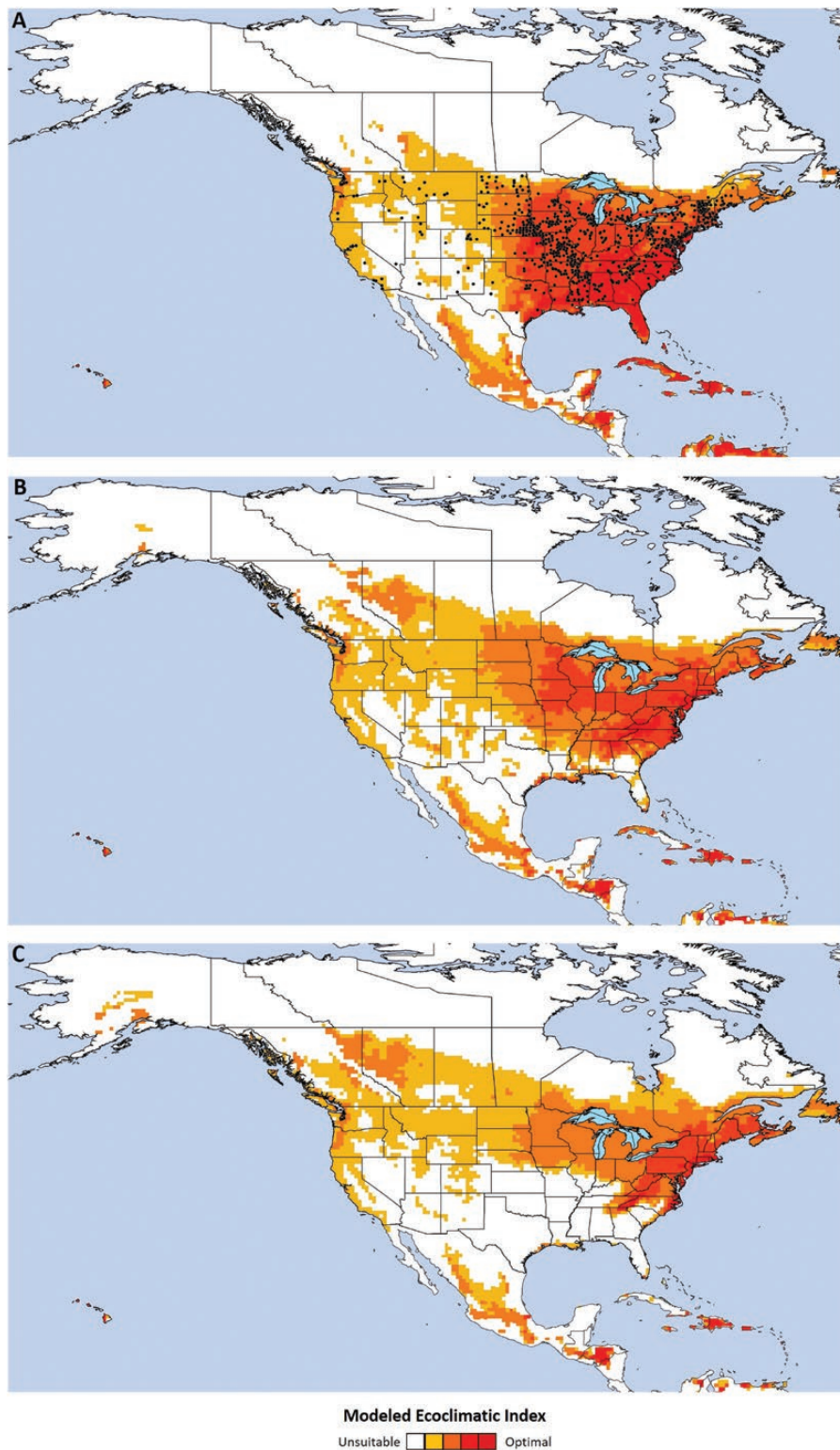


Fig. 3. The modeled climatic suitability (CLIMEX Ecoclimatic Index) for *Popilla japonica* in North America based on current (A) and future climate projections under CNRM-CM5 (B) and ACCESS1-0 (C) global climate models running the RCP 8.5 emission scenario for 2050. Black circles designate reported distribution locations.

infestations in the western United States (ODA 2017, CDFA 2018) and are strongly recommended in high-risk sites throughout central Europe (EPP0 2016). Increasing public awareness among the horticultural industry as well as agencies and stakeholders working in

high-risk areas (e.g., parks, nurseries, golf courses, and entry and exit points) is warranted.

In the Southern Hemisphere, New Zealand is especially vulnerable to *P. japonica* invasion given that the already large portion of

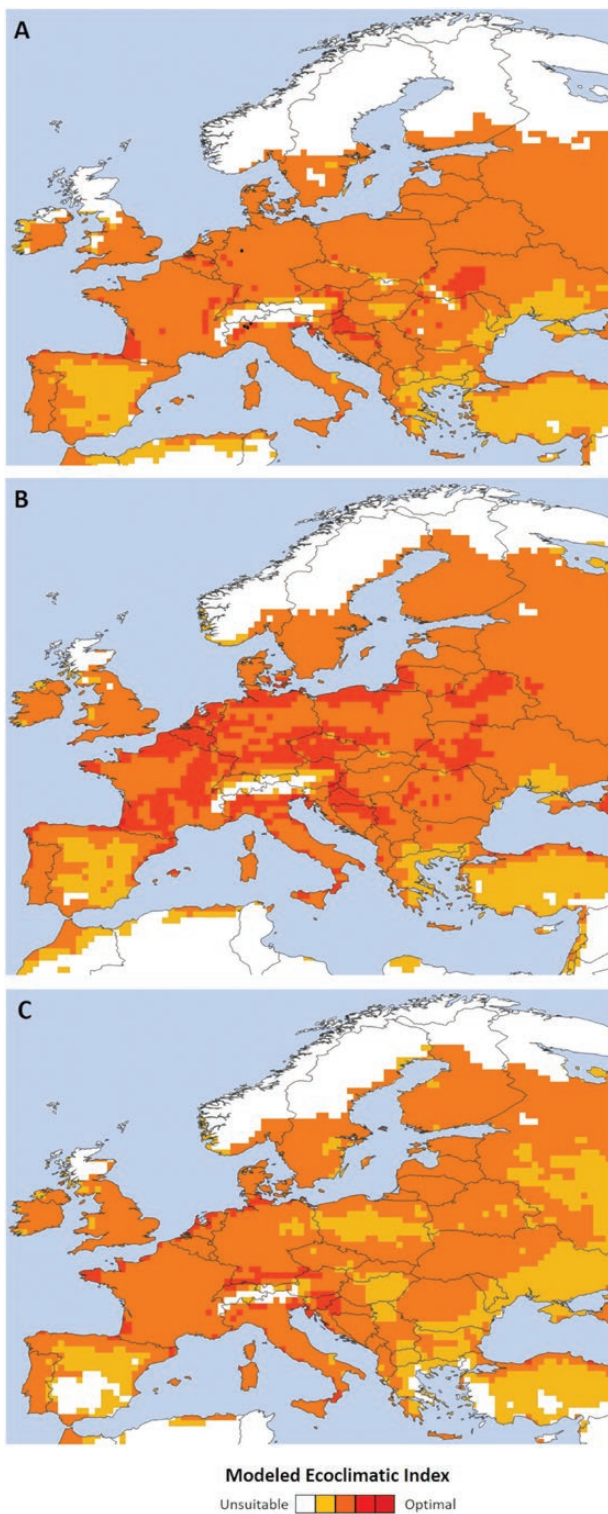


Fig. 4. The modeled climatic suitability (CLIMEX Ecoclimatic Index) for *Popilla japonica* in Europe based on current (A) and future climate projections under CNRM-CM5 (B) and ACCESS1-0 (C) global climate models running the RCP 8.5 emission scenario for 2050. Black circles designate reported distribution locations.

climatically suitable range under current conditions expands under both GCMs by 2050. In addition, New Zealand's vast expanses of pastureland would provide ideal habitat for oviposition and subsequent larval development (Stats NZ 2018). Large portions of

southern and eastern South America, sub-Saharan Africa, and the eastern coast of Australia are also at risk for *P. japonica* establishment now and under possible midcentury future climates in spite of some notable range contractions. Biosecurity authorities in high-risk Southern Hemisphere jurisdictions may want to consider enhancing quarantine and monitoring efforts at national or subnational administrative entry and exit points (e.g., airports, ferry docks, railway stations).

Nonclimatic factors, which are not included in CLIMEX, also affect insect pest distribution and abundance such as natural enemies, topography, human activity, and host plant distribution. In the case of *P. japonica*, the presence of appropriately moist landscapes needed for successful larval development can be augmented by human-made pasture lands and urban turfgrass, thereby enabling this insect to establish in areas often deemed too dry by CLIMEX. Zhu et al. (2017) found that the inclusion of anthropogenic landscape factors improved their Maxent model performance in areas of high human activity. Therefore, the CLIMEX model's projections should be approached with some caution, especially in normally dry landscapes altered by human activity as *P. japonica* readily invades irrigated parks, golf courses, and pasture lands (USDA 2015).

As with previous climate-based modeling approaches (Allsopp 1996, Zhang et al. 2002, Zhu et al. 2017), these results indicate large portions of unfilled climatically suitable space in eastern Asia, particularly in eastern central China and the Korean peninsula. To date, no *P. japonica* specimens have ever been recovered from mainland Asia (Fleming 1976, Reed et al. 1991) where abundant natural enemies probably hinder *P. japonica* establishment (Clausen et al. 1927, Fleming 1968, Chen et al. 2006). Under the RCP 8.5 scenario, large portions of northeastern Asia will become climatically suitable for *P. japonica* by 2050 as projected increases in winter temperatures break down previous cold barriers to *P. japonica* survival in these regions. It is plausible that *P. japonica* may be able to successfully establish in mainland Asia if the pest is inadvertently transported to these newly climatically favorable habitats outside the distribution of their natural enemies (Furlong and Zalucki 2017). Furthermore, the biological control efficacy of natural enemies against *P. japonica* in its native and invaded ranges may decrease if climate change leads to a phenological mismatch between this pest and its enemies. There is compelling evidence that an increasingly variable and warmer climate will disrupt the phenological synchrony between parasitoids and their insect hosts (Stireman et al. 2005, Grabenweger et al. 2007, Evans et al. 2013). *Tiphia vernlals* (Rohwer 1924) (Hymenoptera: Tiphidae) and *Tiphia popillivora* (Rohwer 1924) (Hymenoptera: Tiphidae) are parasitoids that attack *P. japonica* larvae and can provide moderate levels of control in both *P. japonica*'s native range as well as areas in the United States where they were deliberately released (Fleming 1968, Chen et al. 2006, Ramoutar and Legrand 2007). Future studies examining *P. japonica*'s associated parasitoids' responses to changing climatic conditions are warranted to better predict possible effects of climate change on the biological control of this pest.

The simulated occurrence of biannual life cycles is concordant with those reported in the literature and similar *P. japonica* degree-day model projections conducted by Korycinska and Baker (2017). Field surveys conducted in these regions found that biannual life cycles occur sporadically in the northeastern United States and southern Ontario, Canada (Fleming 1972, Vittum 1986, Vittum et al. 1999), whereas in the northern most portion of its native range, Hokkaido, Japan, beetles regularly undergo biannual life cycles (Clausen et al. 1927). Under the RCP 8.5 scenario, these lower outbreak risk regions are projected to switch from a 2-yr life cycle to a 1-yr life cycle by

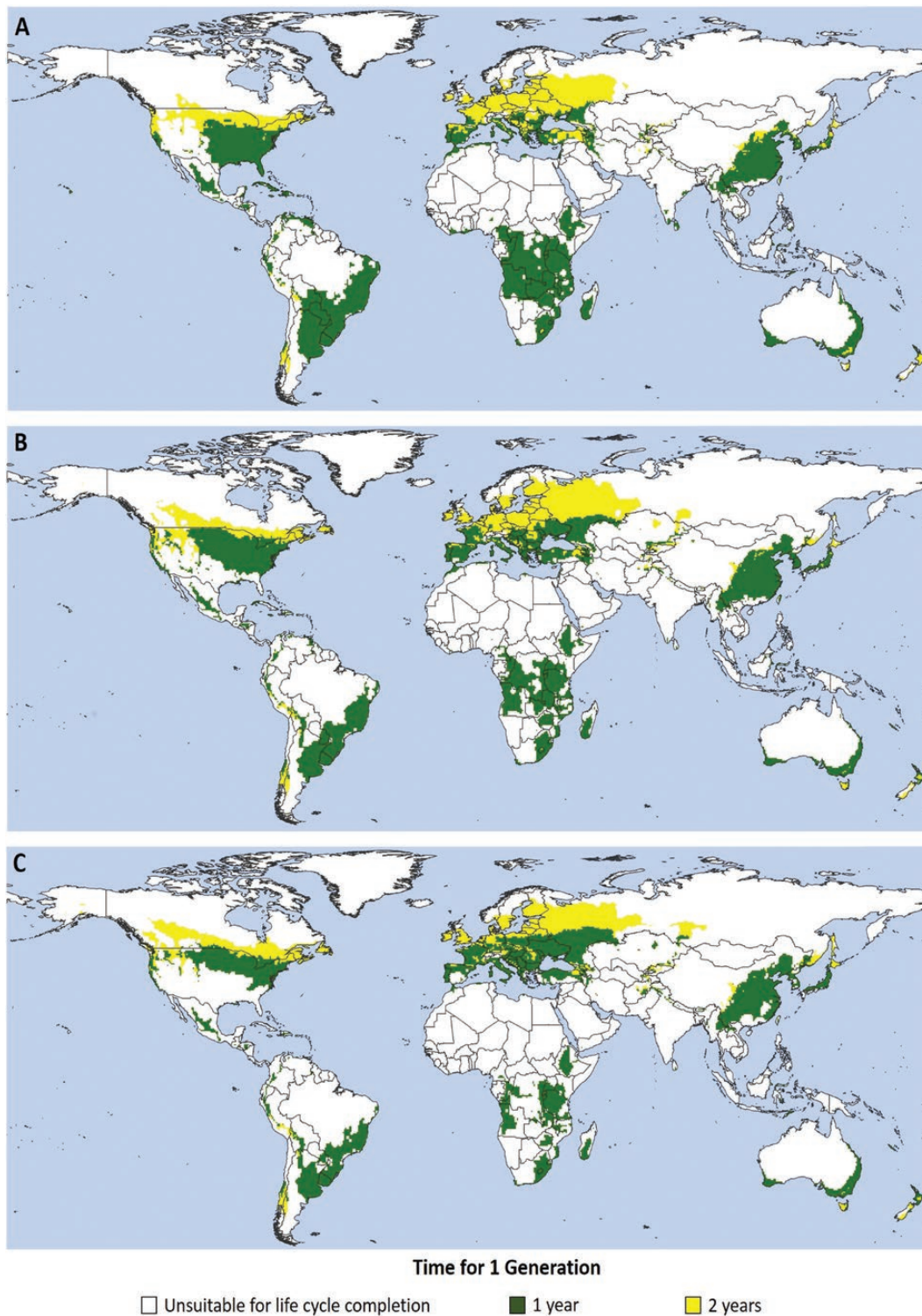


Fig. 5. The simulated global number of years for one generation of *Popillia japonica* to complete development (threshold 10°C and 1,422 egg-to-egg degree-days) under current climatic conditions (A) and future climate projections under CNRM-CM5 (B) and ACCESS1-0 (C) global climate models running the representative concentration pathway (RCP) 8.5 emission scenario for 2050.

2050, indicating *P. japonica* outbreaks may occur more frequently on a year-to-year basis. In the context of this study, projected changes in *P. japonica* voltinism were consistent with previous work examining the effects of climate change on biannual insect life cycles. For instance, longer and warmer growing seasons are expected to enable several species, including North American spruce beetles, to complete

their life cycle in a single year in areas where previously a generation took at least two (Bentz et al. 2010, Everall et al. 2015).

This study highlights some areas under threat of invasion by *P. japonica* under current and possible future climates. It also reveals that ongoing plant health risks posed by *P. japonica* in certain northern portions of its current known range may become more severe

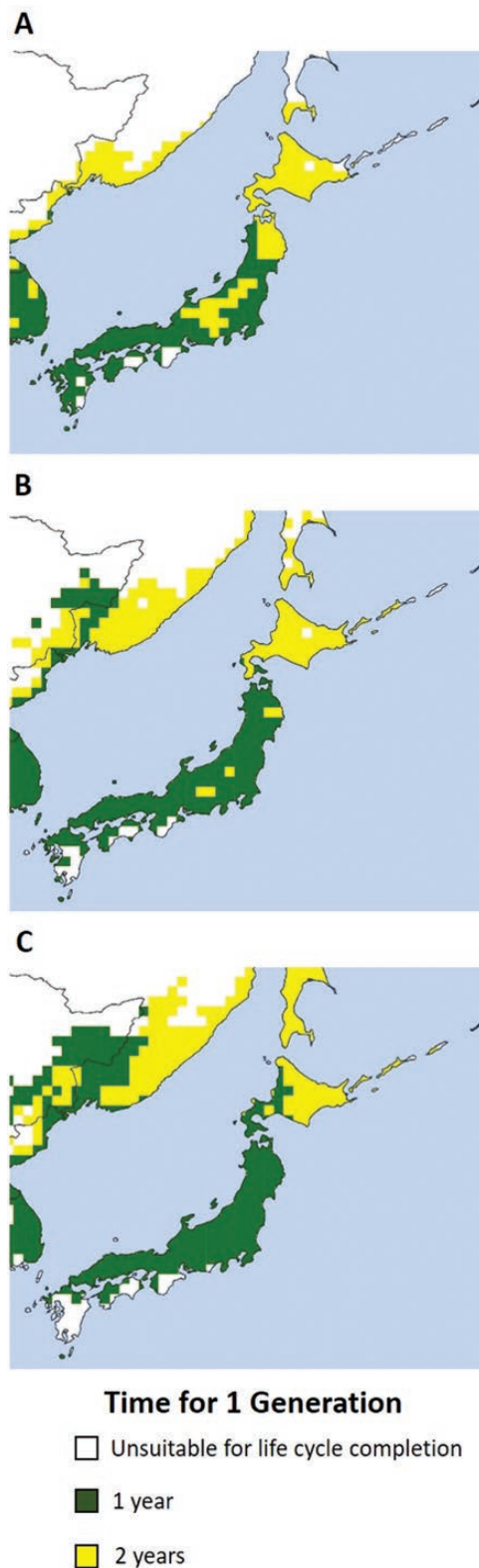


Fig. 6. The simulated number of years for one generation of *Popillia japonica* to complete development in Japan (threshold 10°C and 1,422 egg-to-egg degree-days) under current climatic conditions (A) and future climate projections under CNRM-CM5 (B) and ACCESS1-0 (C) general circulation models running the representative concentration pathway (RCP) 8.5 emission scenario for 2050.

in light of climate change. The differences in the outcomes between the two GCMs emphasize the uncertainties associated with current climate change modeling (Harris et al. 2014). Therefore, the possible future climates presented here should be considered indications of the potential changes in suitable geographical range and voltinism of *P. japonica* in response to climate change. To prevent the introduction and spread of *P. japonica*, enhanced public awareness about the threat it poses along with adequate quarantine and monitoring efforts should be implemented in areas under high invasion risk from this pest under both current and possible future climates.

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