A winner in the Anthropocene: changing host plant

distribution explains geographic range expansion in the gulf

fritillary butterfly

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Abstract:

1.   The changing climate is altering the geographic distributions

of species around the world with consequences for population

dynamics, resulting in winners and losers in the

Anthropocene.

2.   *Agraulis vanillae*, the gulf fritillary butterfly, has expanded its

range in the past one hundred years in the western United

States. We combine time series analysis with species

distribution modeling to investigate factors limiting the

distribution of *A. vanillae* and to predict future shifts under

warming scenarios.

3.   In the western US, where we have time series and geographic

data, urban development has a positive influence (the host

plant is an ornamental in gardens), being associated with year

of colonization. Colonization was also associated to a lesser

extent with winter maximum temperatures, while a negative

impact of minimum temperatures and precipitation was

apparent on population growth rates.

4.   Across the country, the butterfly is primarily limited by host

availability and positively affected by human presence.

Perhaps counter-intuitively for a largely tropical ectotherm,

current effects of a warming climate (in the years post-

colonization) are either negative (on population growth rate)

or indirect, likely mediated through availability of areas that

can support the host.

5.   Under future climate scenarios, conditions are predicted to

become more suitable for *Passiflora* in many urban areas,

which would likely result in further expansion of *A. vanillae*

during the dispersive season. These results illustrate the value

of combining time series with spatial modeling to understand

and predict shifting geographic ranges in the Anthropocene.

Keywords: *Agraulis vanillae, Passiflora*, climate change,

expansion, distribution

Introduction

Recent climate change has had numerous consequences for

species around the world, including shifts in geographic

distribution (Chen et al., 2011). In some cases, ranges are

expanding, while for many others geographic ranges are shifting

or contracting (Parmesan, 2006). Ectotherms, including

butterflies and other insects, are particularly sensitive to changes

in the climate and have often been exemplar species for the study

of these issues (Parmesan et al., 1999; Warren et al., 2001).

Recently, attention has been paid not only to changes in

geographic ranges, but also to declines in insect populations

around the world, which are driven by a combination of habitat

loss, pesticide use, climate change, and other factors (Hallmann et

al., 2017; Lister & Garcia, 2018; Salcido et al., 2019; Sanchez-

Bayo & Wyckhuys, 2019; Wepprich et al., 2019). We can expect

these factors will have different impacts on different species, and

even that some species will be "winners" under altered conditions

(McKinney & Lockwood, 1999). Identifying successful species

and the reason for their success in the face of change is important

for understanding the potential of individual species and

ecosystems to persist and thrive in future climates. In particular,

understanding how aspects of global change negatively impact

some species, while benefiting others, will improve our ability to

predict future species assemblages. One example of a butterfly

that appears to be benefitting from anthropogenic influence is the

gulf fritillary (*Agraulis vanillae),* which has recently expanded its

range in the western United States (Shapiro, 2007). In this study

we seek to better understand the drivers underlying this expansion

using a combination of spatial data and long-term population

records.

Agraulis vanillae is a neotropical butterfly associated with

riparian and weedy/disturbed habitats (Shapiro, 2009). Over its

entire distribution, from temperate North America to temperate

South America, there are eight identified sub-species. Previous

work has demonstrated genetic divergence between North

American and South American lineages (Runquist et al., 2012).

In the United States, *A. vanillae* is multi-voltine and in some areas

flies almost all year, however diapause has been observed in both

the larval and pupal stages in Florida (Sourakov, 2008). The

butterfly is sensitive to frost, which can be lethal to all life stages

(Shapiro, 2007). Eastern populations are known to undergo

northward dispersal in the spring (Walker, 1991), with sightings

as far north as North Dakota and New York (Scott, 1986). These

life history traits raise the possibility that the range of *A. vanillae*

may be limited by low overwintering temperatures, thus milder

winters could reduce the risk of extinction along the northern

range margin and explain the success of this butterfly.

Agraulis vanillae utilizes most plants from the genus

Passiflora as hosts (May, 1992). The two most common species

in the United States are *Passiflora incarnata* and *Passiflora lutea*,

both of which are found across much of the southeastern United

States (Gremillion, 1989). *Passiflora* prefers well-drained soils

and is often found in disturbed sites. In the west, *Passiflora* is not

present in natural areas, however various species have been

introduced to urban areas as ornamentals (Graves & Shapiro,

2003). Winter low temperatures likely limit the distributions of

wild populations, however survival can be improved by active

management in cultivated populations (McGuire, 1999). In

California, the introduction of *Passiflora* and its association with

A. vanillae, are well documented. In Southern California, these

species have been associated since 1875. It was first sighted in

San Francisco as early as 1908, however it did not permanently

establish until 1955 (Powell, 2000). In the 1960's and 1970's the

butterfly was seen in Sacramento, but was extirpated and has only

recently reestablished in the region. The presence of *Passiflora*

offers another, non-mutually exclusive, explanation for the

success of *A. vanillae*. It is possible that *A. vanillae* is currently

not limited by temperature, but instead by the distribution of

Passiflora. As this plant expands due to cultivation, so does the

gulf fritillary.

In this study, we address the following questions. First, using

data from a long-term observational study, we ask if climate or

urban development better explain the establishment and success of

the butterfly in recent years in the Sacramento Valley. Second,

using citizen science observational data, we ask if the current

distribution of the butterfly in the continental United States is

better explained by host plant or climate limitation. Finally, using

species distribution modeling, we ask if the butterfly is likely to

continue to expand its distribution under different climate change

scenarios.

Materials and methods

Sacramento Valley time series data

Observational data were collected every other week by a single

observer (AMS) across five sites in the Sacramento Valley. Count

data of individual butterflies at these five sites have been collected

since 1999 and presence/absence data have been collected since

the 1970's or 1980's, depending on the site. At these five low

elevation sites, data are recorded year round. Site descriptions

and additional details have been reported elsewhere (Forister et

al., 2010). *Agraulis vanillae* did not consistently appear at any of

these five sites until 2001 and did not appear at every site until

2012. Climate data in California were derived from 270m grid

climate maps of monthly and annual values for minimum and

maximum temperature and precipitation (Flint & Flint 2012; Flint

et al. 2013; Thorne et al. 2015). We extracted the values for grid

cells that overlapped with each of the sample sites in the

Sacramento Valley and averaged the values for each monthly

variable for each year. We calculated seasonal variables by further

averaging monthly values to season and converting to water year

(the start of September through the end of August).

Sacramento Valley statistical analysis

We approached the analysis of times series data in two phases.

First, we used annual presence/absence data to examine

colonization, attempting to model the difference between years in

which the butterfly was absent across our focal sites and years in

which it was present (spanning 1984 through 2018). Specifically,

random forest regression was used with presence at a site in a

given year as the response variable and percent urban land cover

(at a county level), seasonal means of minimum temperature,

seasonal means of maximum temperature, and seasonal means of

precipitation as covariates. A total of 500,000 trees were made

with a node size of 5. Variable importance was determined by

examining the increased mean squared error of the model when

each variable was randomly permuted. The most influential

variables identified by random forest analysis were moved

forward into a Bayesian hierarchical model. While the random

forest is useful for judging the potential importance of a large

number of variables, including some that are highly correlated, the

Bayesian model allows us to estimate coefficients and associated

uncertainty in a hierarchical framework (simultaneously within

and across sites). Following a previous model used for data from

these study sites (Nice et al, 2019), presence was modeled both at

the individual site level and at a higher level across all sites using

a Bernoulli distribution. Uninformative priors were used for

means and variance, with means drawn from normal distribution

(mu = 0, tau = 0.01) and variances drawn from a gamma

distribution (r = 0.01, lambda = 0.01).   The Bayesian model was

comprised of four chains each run for 5,000,000 iterations with an

adaptive phase of 500,000 iterations.

As a second phase, we examined annual population dynamics

post-colonization at the same focal sites, using individual survey

count data summarized by year and transformed into population

growth rates. Population growth was calculated as the natural log

of the current year's total count divided by the previous year's

total count (Sibly & Hone, 2002). To determine the most

influential climate variables, population growth in a given year

was then modeled using a random forest regression. Covariates in

the model included abundance in the previous year, seasonal

means of minimum monthly temperature, seasonal means of

maximum monthly temperature, seasonal means of precipitation,

and these same variables lagged by one year to allow in particular

for effects mediated through host plants. Again, a total of 500,000

trees with a node size of 5 was used. Variable importance was

determined by examining the increased mean squared error of the

model following permutation of each variable, and this was done

both within and among sites. Like the colonization analysis, the

most influential variables identified by random forest analysis

were moved forward into a Bayesian hierarchical model in which

population growth was modeled both at the individual site level

and at a higher level across all sites using a normal distribution.

Means of covariates were drawn from an uninformed normal

distribution (mu = 0, tau = 0.01) and variances drawn from an

uninformed gamma distribution (r = 0.01, lambda = 0.01). This

model was comprised of four chains each run for 100,000

iterations with an adaptive phase of 10,000 iterations. All

analyses were conducted using the randomForest (RColorBrewer

& Liaw, 2018) and jagsUI (Kellner, 2019) packages in R Studio.

National data

For US-wide spatial analyses, geo-referenced data points for

both *A. vanillae* and *Passiflora* were acquired from "research

grade" observations on inaturalist. Additional observations of

Passiflora were obtained from Cal flora and additional

observations of *A. vanillae* from the Butterflies and Moths of

North America. Only observations with an uncertainty under 1km

were used for analysis.   Both *Passiflora* and *A. vanillae* are

distinct and identification is likely not a concern, however a

random subset of 100 observations with photos were checked and

all were found to be correct IDs. Current climate data and future

projections were obtained from WorldClim (Hijmans et al., 2005).

A human population density raster was obtained from the

Socioeconomic Data and Applications Center, which used data

from the 2010 census (Center for International Earth Science

Information Network, 2018). All raster layers were cropped to

only include the 48 contiguous states, although *A. vanillae* is also

an exotic in Hawaii. Finally, *A. vanillae* points were separated

based on being from the dispersal season or before. Points from

January to March were labeled as pre-dispersal, which is earlier

than the earliest observed spring migrant from a study of this

movement in Florida (Walker, 1991). In this paper, dispersal will

refer to the maximum distribution that the butterfly achieves

during the year.

National statistical analysis

Species distribution models were built for both *Passiflora* and

Agraulis vanillae. All host plant models were built at the genus

level, however *Passiflora* species known not to be host plants

were excluded. The western and eastern distributions were

modeled both separately and together, to allow for the possibility

of different factors affecting range limits in the different regions.

For all models, we used the maxent algorithm, which models

presence only data by comparing observations with random

background points. For every model, 10,000 random background

points were taken within the continental United States. *Passiflora*

was modeled using temperature, mean precipitation, and human

population density as covariates. Models were built and evaluated

using mean temperature in the coldest month, mean annual

temperature, and max temperature in the warmest month as the

temperature variables. The best performing host plant model was

later used as part of the butterfly spatial model. Since the host

plant, especially in the western United States, is found almost

exclusively in urban environments, human population density was

used as a proxy for urban cultivation of the plant. For *A. vanillae,*

both the overwintering distribution and dispersal distributions

were modeled. The overwintering distribution was modeled using

the *Passiflora* distribution model and temperature variables. The

dispersal distribution was similarly modeled using the *Passiflora*

distribution model and temperature as covariates. As with

Passiflora analyses, various temperature variables were used for

model building and comparison, and only the highest performing

model for both overwinter and dispersal distributions were used

for inference and projection. The models were trained on 70% of

the data and tested with the remaining 30%. For all models, data

were thinned in order to reduce overfitting due to sampling bias,

which was done by creating a grid that was overlaid onto the

study area. Individual grid cells were approximately 50 km^2 and

if more than five observations were located within a single grid,

only a random subset of five was kept for analysis. If a grid cell

had less than five observations all were kept. A sensitivity

analysis was also performed to examine the impacts of the

thinning method. All data used in models were thinned

substantially, often by over fifty percent (Table S1). Model

evaluation was performed by examining the AUC scores and

omission error rates of both the real model and 1000 permuted

null models. Methods and code for null model permutation are

described by Bohl et al. (2019), but briefly, observations from the

real model are randomly moved around the study area and

compared to the real model using the same covariates and testing

data. All analyses were performed in R Studio using the dismo

package (Hijmans et al., 2013).

Results

Time Series

For the first twenty-five years of the time series, *Agraulis vanillae*

only appeared as an occasional visitor, however beginning in 2001

it became a frequent visitor to all sites across the Sacramento

Valley. This rise in the presence of *A. vanillae* occurred during a

time of rising temperature and increasing urban development in

the area (fig. 1). The random forest model attributed high

importance to winter maximum temperatures and percent urban

land cover in predicting presence at a site (fig. 2). Both maximum

temperature and urban land cover have increasing trends over

time, especially land cover, which is highly correlated with year

(correlation coefficients for year and land cover range from 0.973

in Solano county to 0.989 in Yolo county). For the Bayesian

model, the model successfully converged (as judged by visual

inspection of posterior probability distributions) at both the

individual site level and at the higher across site level. The

Bayesian model confirms that both maximum winter temperatures

and development are positively associated with colonization at the

higher across site level. Specifically, the probability that

maximum temperature has a greater than zero effect is 0.98 and

the probability that urban development has a greater than zero

effect is 0.88. The coefficient estimate for urban development

shows high uncertainty for any particular value, however the

posterior distribution is almost entirely greater than the maximum

temperature posterior, thus there is support for a stronger effect of

urbanization.

For annual population dynamics (represented by the natural log

of the current to previous population density), the random forest

analysis attributed high importance to abundance in the previous

year, winter minimum temperature in the current year, winter

precipitation in the current year, and summer precipitation in the

current year for predicting population growth (fig. 2, fig. S1).

Urbanization, while one of the covariates in the model, was not

found to be important for population growth rates. Coefficients in

the Bayesian model for population growth converged at both the

across site and individual site level. Previous year's abundance,

winter minimum temperature, and winter precipitation all had

negative effects on population growth. The model is confident in

the negative impacts of previous year's abundance, winter

minimum temperature, and winter precipitation (fig. 3).

Specifically, the probability that previous year's abundance has a

negative effect is 0.84, the probability that winter minimum

temperature has a negative effect is 0.80, and the probability that

winter precipitation has an effect is 0.88. There does not appear

to be a strong effect of summer precipitation in the Bayesian

hierarchical regression, despite the importance attributed to it in

the random forest. All three variables have approximately equal

estimated effect sizes. At the individual site level, there is

variation in estimated effects, however negative density

dependence is observed at all sites. Winter climate is also

important at all sites, however some sites have higher estimated

impacts of winter precipitation while others more heavily weight

winter minimum temperatures (fig. S4).

Species Distribution Models

Overall, the geographic distribution of *Passiflora* is best

predicted by mean annual temperature and human population

density, with the former being the most important variable (Table

S2, Table 1). When examining regions (eastern and western US)

separately, urban density is a more important predictor in the

west, while minimum temperature is more important in the east

(Table 1). All models, both combined and regional, achieved high

AUC values and performed exceptionally well when compared to

permuted null models (Table 1, fig. S5). Under the RCP 4.5 and

8.5 scenarios, suitable habitat along *Passiflora's*, northern range

boundary is predicted to expand. The expansion is especially

strong in urban areas, with much of the urban mid-Atlantic and

Northwest predicted to become more suitable (fig. 4 a,b; fig. S6

a,b).

The current overwintering range of *A. vanillae* is primarily in

Florida and Texas, and is best explained by both *Passiflora* and

winter temperature lows, as can be seen in the best-performing

model with minimum temperature (Table S2). Like the host plant

model, all models performed well in regards to AUC scores and in

comparison to permuted null models (Table 1, fig. S5). The

importance of minimum temperature in the east is greater,

however in both regions host plant is more important, although it

is not clear if the differences in variable importance between the

east and west are meaningful given different sample sizes in the

two areas (Table 1). Future climate scenarios project a slight

increase in the suitability of some areas in the southeast for

overwintering, but not a major expansion into new urban areas

(fig. 4 c,d). The results from the models of dispersal distribution

tell a different story. Models for dispersal range using different

temperature variables all performed equally well, with little

importance being attributed to any temperature variable in any

model (Table S2). Again, models performed well using both the

AUC metric and permuted null model comparison (Table 1, fig.

S5). The dispersal range of the butterfly is almost entirely limited

by the host plant (Table 1). This is reflected in the fact that

models predict expansion in areas that closely match areas of

Passiflora expansion (fig. 4 e,f). Thus while overwintering gains

appear marginal under future warming, expansion of the range

during dispersal in the summer is potentially substantial.

Projections under RCP 8.5 show a slightly greater expansion,

however do not dramatically vary from RCP 4.5 predictions (fig.

S6 e,f).

Discussion

Species are currently encountering novel biotic and abiotic

conditions, which can positively or negatively impact population

dynamics and geographic distributions (McKinney & Lockwood,

1999). Building models that parse these various stressors furthers

our understanding of these impacts and allows for better

prediction of future assemblages. In this study, we found that

years in which the butterfly had colonized our focal sites were

characterized by warmer winter maximum monthly temperatures,

while winter minimum temperatures had a negative impact on

population growth rates in the years after colonization. In

particular, if the previous winter was cooler and drier the butterfly

was found in higher abundance the next year. It is possible that

the negative impact of winter climate on *A. vanillae* that we have

observed is mediated through interactions with host plants or other

insects. It could be the case that warmer and wetter winters

negatively impact *Passiflora*, but another and perhaps more likely

explanation is that wetter and warmer winters increases parasitoid

pressure and/or disease leading to reduced adult emergence the

following year (Harvell et al., 2002; Stireman et al., 2005).

Additionally, *A. vanillae* is known to host nucleopolyhedrovirus

(Rodriguez et al., 2011), which could be one mechanism that

generated the observed negative density dependence (fig. S1),

however this is not known to impact California populations.

Finally, at our focal sites there is a slight positive trend over time

in winter precipitation and winter minimum temperature (fig. S7),

suggesting that if anything the butterfly is persisting and

expanding in the Sacramento Valley despite of climate, not

because of it.

The local impact of climate on the population dynamics of

Agraulis vanillae in the Sacramento Valley also has implications

for explaining the limiting factors for its current distribution in the

west. The western United States species distribution model places

almost all of the variable importance on the distribution of the

host plant. One explanation for the recent colonization of the area

by the butterfly is thus the increasing urbanization of the

Sacramento Valley. Over the past twenty years the suburbs of

Sacramento have expanded at a steady rate (Forister et al., 2010),

which has likely resulted in an increase in *Passiflora* in the region.

Random forest analysis ranked urban land cover over climate

when predicting colonization and the Bayesian model found a

much greater effect of urbanization (fig. 2a; fig. 3). In the eastern

United States, the impacts of temperature, specifically minimum

temperatures, are apparent in geographic distribution models. In

the east, the distribution of *Passiflora* extends further north in the

winter compared to *A. vanillae,* while in the west the

overwintering distribution closely resembles that of *Passiflora*.

Once the weather warms in the east, the butterflies can then

expand to cover the distribution of the host plant. Thus, while

minimum temperature plays an important role in the

overwintering locations of the eastern gulf fritillary, its maximum

extent appears to be host plant limited in both the eastern and

western United States.

By understanding these current limits on *A. vanillae*, it is clear

that any major expansion in geographic distribution will be the

result of a host plant expansion. Models using the RCP 4.5 and

8.5 climate scenarios both predict geographic expansion for the

host plant, and thus an expanding dispersal distribution for the

butterfly. In particular, the host is predicted to have a greater

presence in urban areas on both the east and west coasts,

presumably through more frequent plantings into gardens that will

become more suitable to the plant over time in a warming climate.

If this occurs, the dispersal distribution of *A. vanillae* will also

expand, as the butterfly currently tracks *Passiflora* very

successfully. Dispersal ability may be an issue in the Pacific

northwest, as major metropolitan areas are further apart, however

given how far the butterfly currently disperses in the east each

summer, it is likely this area will also be included in its

distribution. Increasing temperatures may also impact the

overwintering distribution of the butterfly, but given the impact of

minimum temperature from the temporal analysis and the lack of

major shifts from the SDM projections, this is much more

uncertain. Although the full distribution of the butterfly does not

appear to be directly limited by temperature, there is an indirect

effect mediated by its host plant, which is limited by temperature.

Projected rising temperatures will still have a major impact on the

distribution of this butterfly through this indirect interaction.

Thus far, this butterfly is a notable example of a "winner" in

the Anthropocene. While insect declines are occurring on a large

scale (Hallmann et al., 2017; Lister & Garcia, 2018; Salcido et al.,

2019; Sanchez-Bayo & Wyckhuys, 2019; Wepprich et al., 2019),

altered conditions create opportunities for some insects to prevail.

The intricacies of each success story are different; but an

overarching theme of increasing temperature is playing a vital role

in facilitating the distributional expansion of many of these insect

winners. This has occurred directly by increasing the

overwintering survival along a northern range margin for some

species (Streifel et al., 2017), by increasing access to food

resources for others (Raffa et al., 2013), or by increasing diet

breadth (Pateman et al., 2012). In the case of the gulf fritillary,

expansion has thus far been driven by human-mediated host plant

propagation and future warming will allow this process to

continue further north in the United States. While not all insect

expansions will be due to temperature, ectotherms continue to be

prime candidates for temperature driven distributional change, for

better or for worse. Continuing to observe these phenomena and

developing methods by which to understand them is critical. Here

the combination of long-term time series data and large-scale

citizen science spatial data allowed for a detailed examination of

the underlying causes for such an expansion. As these types of

data continue to become more widely accessible, the common

themes behind insect distributional change in the Anthropocene

will continue to become more apparent.

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Contribution of authors

A.M.S. collected the Sacramento Valley observational data. J.H.T. and D.P.W. provided the climate data. C.A.H. conducted the statistical analyses. C.A.H. and M.L.F. wrote the manuscript with input from co-authors.

References

Bohl, C.L., Kass, J.M. & Anderson, R.P. (2019) A new null model approach to quantify performance and significance for ecological niche models of species distributions. *Journal of Biogeography*, **46**, 1101-1111.

Calflora: Information on California plants for education, research and conservation.
[web application] (2014) Berkeley, California: The Calflora Database [a non-profit organization].
Available: https://www.calflora.org/ (Accessed: May 1, 2019).

Center for International Earth Science Information Network – CIESIN – Columbia University. (2018) Gridded Population of the World, Version 4 (GPWv4): Population Density, Revision 11. Palisades, NY: NASA Socioeconomic Data and Application Center (SEDAC). https://doi.org/10.7927/H49C6VHW. (Accessed May 5, 2019),

Chen, I.C., Hill, J.K., Ohlemuller, R., Roy, D.B. & Thomas, C.D. (2011) Rapid Range Shifts of Species Associated with High Levels of Climate Warming. *Science,* **333**, 1024-1026.

Flint, L. E., & Flint, A.L. (2012) Downscaling future climate scenarios to fine scales for hydrologic and ecological modeling and analysis. *Ecological Processes* 1:1-15.

Flint, L. E., Flint A.L., Thorne J. H. & Boynton, R. (2013) Fine-scale hydrologic modeling for regional landscape applications: the California Basin Characterization Model development and performance. *Ecological Processes* 2:1-21.

Forister, M.L., McCall, A.C., Sanders, N.J., Fordyce, J.A.,
Thorne, J.H., Obrien, J., Waetjen, D.P. & Shapiro, A.M. (2010)
Compounded effects of climate change and habitat alteration shift
patterns of butterfly diversity. *Proceedings of the National*
Academy of Sciences, **107**, 2088-2092.

Graves, S.D. & Shapiro, A.M. (2003) Exotics as host plants of the
California butterfly fauna. *Biological Conservation,* **110**, 413-433.

Gremillion, K.J. The Development of a mutualistic relationship
between humans and maypops (*Passiflora incarntata L.*) in the
Southeastern United States. *Journal of Enthnobiology*, **9**, 135-155.

Hallmann, C.A., Sorg, M., Jongejans, E., Siepel, H., Hofland, N.,
Schwan, H., Stenmans, W., Muller, A., Surnser, H., Horren, T.,
Goulson, D. & de Kroon, H. (2017) More than 75 percent decline
over 27 years in total flying insect biomass in protected areas.
PLoS One, **12**, e0185809.
542
543 Harvell, C.D., Mitchell, C.E., Ward, J.R., Altizer, S., Dobson,
544 A.P., Ostfeld, R.S. & Samuel, M.D. (2002) Climate Warming and
545 Disease Risks for Terrestrial and Marine Biota. *Science,* **296**,
546 2158 – 2162.
547
548 Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G. & Jarvis, A.
549 (2005) Very high resolution interpolated climate surfaces for
550 global land areas. *International Journal of Climatology* 25: 1965-
551 1978.
552
553 Hijmans, R.J., Phillips, S., Leathwick, J. & Elith, J. (2013) dismo:
554 Species distribution modeling. *R package version 0.8-17.*
555
556 iNaturalist. Available from https://www.inaturalist.org. Accessed
557 [2019-05-01].

558 Kellner, K. (2019) jagsUI: A Wrapper Around 'rjags' to
559 Streamline 'JAGS' Analyses. *R package version 1.5.1.*
560
561 Lister, B.C. & Garcia, A. (2018) Climate-driven declines in
562 arthropod abundance restructure a rainforest food web.
563 *Proceedings of the National Academy of Sciences,* **115**, 10397-
564 10406.
565
566 Lotts, K. & Naberhaus, T coordinators. (2017) Butterflies and
567 Moths of North America. Data set accessed (or exported) 2019-
568 06-13 at http://www.butterfliesandmoths.org/.
569
May, P.G. (1992) Flower Selection and the Dynamics of Lipid
Reserve in Two Nectarivorous Butterflies. *Ecology*, **73**, 2181-
2191.

McGuire, M. (1999) Passiflora incarnata (Passifloraceae): A New
Fruit Crop. *Economic Botany,* **53**, 161-167.

McKinney M.L. & Lockwood J.L. (1999) Biotic homogenization:
a few winners replacing many losers in the next mass extinction.
Trends in Ecology and Evolution, **14**, 450-453.

Nice, C.C., Forister, M.L., Harrison, J.G., Gompert, Z., Fordyce,
J.A., Thorne, J.H., Waetjen, D.P. & Shapiro, A.M. (2019)
Extreme heterogeneity of population response to climatic
variation and the limits of prediction. *Global Change Biology*,
2019,1-10.

Parmesan, C. (2006) Ecological and Evolutionary Responses to
Recent Climate Change. *Annual Review of Ecology, Evolution,*
and Systematics, **37**, 637-669.

Parmesan, C., Ryrholm, N., Stefanescu, C., Hill, J.K., Thomas,
C.D., Descimon, H., Huntley, B., Kaila, L., Kullberg, J.,
Tammaru, T., Tennent, W.J., Thomas, J.A. & Warren, M. (1999)
Poleward shifts in geographical ranges of butterfly species
associated with regional warming. *Nature,* **339**, 579-583.

Pateman, R.M., Hill, J.K., Roy, D.B., Fox, R. & Thomas, C.D.
(2012) Temperature-Dependent Alterations in Host Use Drive
Rapid Range Expansion in a Butterfly. *Science,* **336**, 1028-1030.
594

Powell, J.A., Russell, P., Russell, S. & Sperling, F.A.H. (2000)
Northward expansion of two mint-feeding species of *Pyrausta* in
California (Lepidoptera: Pyraloidea: Crambidae). *Holarctic*
Lepidoptera, **7**, 55-58.

R Development Core Team. (2013) R: A language and
environmentfor statistical computing. R Foundation for Statistical
Computing,Vienna, Austria. [WWW document]. URL
http://www.R-project.org/ [acessed on 1 August 2019].

RColorBrewer, S., Liaw, M.A. (2018) randomForest: Breiman
and Cutler's Random Forests for Classification and Regression. *R*
package version 4.6-14.
606

Raffa, K.F., Powell, E.N. & Townsend, P.A. (2013) Temperature-
driven range expansion of an irruptive insect heightened by
weakly coevolved plant defenses. *Proceedings of the National*
Academy of Sciences, **110**, 2193-2198.

Rodriguez, V.A., Belaich, M.N., Gomez, D.L.M., Sciocco-Cap,
A. & Ghiringhelli, P.D. (2011) Identification of
nucleopolyhedrovirus that infect Nymphalid butterflies *Agraulis*
vanillae and *Dione juno*. *Journal of Invertebrate Pathology,* **106**,
255-262.

Runquist, E.B., Forister, M.L. & Shapiro, A.M. (2012)
Phylogeography at large spatial scales: incongruent patterns of
population structure and demography of Pan-American butterflies
associated with weedy habitats. *Journal of Biogeography,* **39**,
382-396.

Salcido, D. M., Forister, M., Lopez, H. G. & Dyer, L. A. (2019)
Ecosystem services at risk from declining taxonomic and
interaction diversity in a tropical forest. bioRxiv, 631028.

Sanchez-Bayo, F. & Wyckhuys, K.A.G. (2019) Worldwide
decline of the entomofauna: A review of its drivers. *Biological*
Conservation, **232**, 8-27.

Scott, J.A. **1986**. The butterflies of North America: A natural
history and field guide.

Shapiro, A.M. (2009) The Neo-Riparian butterfly fauna of
western Argentina. *Journal of Research on the Lepidoptera,* **41**,
24-30.
632
633 Shapiro, A.M. & Manolis, T.D. (2007) Field Guide to Butterflies
634 of the San Francisco Bay and Sacramento Valley Regions.

635 Sibly, R.M. & Hone, J. (2002) Population growth rate and its
636 determinants: an overview. *Philosophical Transactions of the*
637 *Royal Socity B,* **357**, 1153-1170.

638
639 Sourakav, A. (2008) Notes on the biology of the gulf fritillary
640 *Agraulis vanillae* (Lepidoptera: Nymphalidae), in North-Central
641 Florida. *Journal of the Lepidopterists' Society,* **63**, 127.
642
Stireman III, J.O., Dyer, L.A., Janzen, D.H., Singer, M.S., Lill,
J.T., Marquis, R.J., Ricklefs, R.E., Gentry, G.L., Hallwachs, W.,
Coley, P.D., Barone, J.A., Greeney, H.F., Connahs, H., Barbosa,
P., Morais, H.C. & Diniz, I.R. (2005) Climatic unpredictability
and parasitism of caterpillars: Implications of global warming.
Proceedings of the National Academy of Sciences, **102**, 17384-
17387.
650
651 Streifel, M.A., Tobin, P.C., Kees, A.M. & Aukema, B.H. (2019).
652 Range expansion of Lymantria dispar dispar (L.) (Lepidoptera:
653 Erebidae) along its north-western margin in North America
654 despite low predicted climatic suitability. *Journal of*
655 *Biogeography,* **46**, 58-69.
656
657 Thorne, J.H., Boynton, R.M., Flint, L.E. & A.L. Flint (2015)
658 Comparing historic and future climate and hydrology for
659 California's watersheds using the Basin Characterization
660 Model. *Ecosphere* 6(2). Online.
661
662 Walker, T.J. (1991) Butterfly migration from and to peninsular
663 Florida. *Ecological Entomology,* **16**, 241-252.
664
665 Warren, M.S., Hill, J.K., Thomas, J.A., Asher, J., Fox, R.,
666 Huntley, B., Roy, D.B., Telfer, M.G., Jeffcoate, S., Harding, P.,
667 Willis, S.G., Greatorex-Davies, J.N., Moss, D., Thomas, C.D.

668   (2001) Rapid responses of British butterflies to opposing forces of
669   climate and habitat change. *Nature,* **414**. 65-69.
670
671   Wepprich, T., Adrion, J.R., Ries, L., Wiedmann, J. & Haddad,
672   N.M. (2019) Butterfly abundance declines over 20 years of
673   systematic monitoring in Ohio, USA. *Plos ONE,* **14**, e0216270.
674

Figure 1. (a) Change in detection probability (the ratio of days
observed to total visits) over time across all sites. (b) Annual ratio
of urban land cover to total land cover at a county level for the
three counties containing long-term study sites: North Sacramento
and Rancho Cordova are in Sacramento County; Suisun Marsh
and Gates Canyon are in Solano County. (c) Mean monthly
maximum winter temperature over time.

Figure 2. (a) Variable importance of model covariates in
predicting the presence of *A. vanillae* at a site in the Sacramento
Valley over time. (b) Variable importance of model covariates in
predicting the annual population growth after establishment.

Figure 3. Bayesian posterior distributions for important
coefficients (as determined by random forest). Y-axis shows
scaled coefficient estimates. (a) Estimates of coefficients for
establishment. (b) Estimates of coefficients for population growth.

Figure 4. The expanding gulf fritness landscape. (a) Current
distribution of suitability for *Passiflora*. (b) 2050 distribution of
suitability for *Passiflora* under RCP 4.5. (c) Current distribution
of suitability for overwintering *A. vanillae*. (d) 2050 distribution
of suitability for overwintering *A. vanillae* under RCP 4.5. (e)
Current distribution of suitability for dispersal *A. vanillae*. (f)
2050 distribution of suitability for dispersal *A. vanillae* under RCP
4.5.

Table 1. Variable importance and model fit of all species distribution models. Rows represent different regional models and columns are the different variables in the model. AUC (area under the curve) is the performance metric of model fit.

		Temperature	Population	Precipitation	AUC	OR	*P*-value
Host plant	Combined	48.8	41.5	9.7	0.915	0.127	**0.013**
	East	53.9	39.9	6.2	0.891	0.115	**0.004**
	West	12.5	79.9	7.8	0.983	0.167	**0.020**
Overwintering	Combined	29.0	71.0	N/A	0.979	0.112	**0.024**
	East	30.5	69.5	N/A	0.978	0.067	**0.026**
	West	17.8	82.2	N/A	0.992	0.200	**0.047**
Dispersal	Combined	1.8	98.2	N/A	0.925	0.113	**0.030**
	East	7.3	92.7	N/A	0.925	0.066	**0.025**
	West	4.9	95.1	N/A	0.985	0.061	0.057

Figure 1

Figure 2

Figure 3

Figure 4