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Extreme Heterogeneity of Population Response to Climatic Variation and the Limits of Prediction

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1 Abstract

2 Certain general facets of biotic response to climate change, such as shifts in phenology and

3 geographic distribution, are well characterized, however, it is not clear whether the

4 observed similarity of responses across taxa will extend to variation in other

5 population-level processes. We examined population response to climatic variation using

6 long-term incidence data (collected over 42 years) encompassing 149 butterfly species and

7 considerable habitat diversity (10 sites along an elevational gradient from sea level to over

8 2,700 meters in California). Population responses were characterized by extreme

9 heterogeneity that was not attributable to differences in species composition among sites.

10 These results indicate that habitat heterogeneity might be a buffer against climate change,

11 and highlight important questions about mechanisms maintaining inter-population

12 differences in responses to weather. Despite overall heterogeneity of response, population

13 dynamics were accurately predicted by our model for many species at each site. The

14 overall correlation between observed and predicted incidence in a cross validation analysis

15 was relatively high ((Pearson's $r = 0.43$, SE 0.01) and 96% of observed data fell with the

16 predicted 95% credible intervals. Prediction was most successful for more abundant species

17 and those that maintain year-round breeding populations (e.g. resident species), as well as

18 for sites with lower annual turnover. However, recent years with severe drought conditions

19 were much less predictable. Population-level heterogeneity in response to climate variation

20 and the limits of our predictive power highlight challenges for a future of increasing

21 climatic variability.

Introduction

One of the chief ecological discoveries of recent decades is the finding that biotic responses to climatic variation include dramatic changes in phenology and geography. For example, the first flowering date for many temperate zone plant species has advanced by many weeks (Parmesan, 2007; Root *et al.*, 2003), and elevational and geographic range limits for many species of both plants and animals are shifting (Chen *et al.*, 2011; Parmesan & Yohe, 2003; Walther *et al.*, 2002). These biotic responses appear to be robust and generalizable across species, but some variation in responses has been observed (Mills *et al.*, 2017; Thomas & Lennon, 1999; Sagarin *et al.*, 1999). While we also know that populations can respond directly to climate variation (Andrewartha & Birch, 1954; Diamond *et al.*, 2016), understanding and predicting more nuanced responses is an ever more pressing need as climate patterns shift. For example, physiological stress associated with abiotic variation has led to morphological evolution (Parmesan, 2006; Smith *et al.*, 1995) and to population declines (Both *et al.*, 2006; Gibbons *et al.*, 2000), although considerably less is known about the generality of these phenomena compared to changes in phenology and geography. Nor do we know the extent to which responses to climate variation are consistent among populations of a species that occur in different habitats. In part, this is because many of these population responses are not as easily standardized across studies (as compared to, for example, first flowering date or upper elevational limit, but see Mills *et al.* (2017)). One way to address this gap in our knowledge is with single studies that encompass a large number of species and habitat types (Oliver *et al.*, 2010). Sufficiently large studies, of which we offer one here, should be able to ask, for example, if certain climate variables have more or less widespread effects (positive or negative) on population dynamics across species, and if these effects are specific to local environmental or habitat conditions. Such studies can also provide an assessment of our ability to predict responses to climate change.

Here we examine a large, single-observer butterfly dataset encompassing 149 species

observed along an elevational gradient that includes one of the highest mountain ranges in North America (Fig. 1, Table S1). The ten sites comprise a transect that extends from sea level to the east side of the Sierra Nevada Mountains. These sites were visited approximately every two weeks (excluding months at higher elevations when temperatures are below the level at which insects are active), and the presence or absence of individual butterfly species was noted by AMS. The duration of surveys varies across sites, with Suisun Marsh (SM) having the longest record (42 years analyzed here (1972-2013)) and the shortest records being 26 years (1988-2013) for three sites (West Sacramento (WS), North Sacramento (NS) and Washington (WA) (Fig. 1)) (mean = 34.7 years, Table S1). We considered every species by site combination to be a population. From these observations, our index of population dynamics (which we refer to as "day positives") was calculated as the number of days in a year that a given species was observed, out of the total number of visits to a site. This incidence-based approach is logistically feasible for a large fauna, and day positives encompass multiple population features including overall abundance and duration of flight window (Casner *et al.*, 2014b; Forister *et al.*, 2011) (Supporting Information). The effects of weather variables on day positives can be effectively modeled in a hierarchical Bayesian framework (Nice *et al.*, 2014; Harrison *et al.*, 2015) that estimates the effect of climatic variation at multiple levels including individual populations (population-level parameters) and among populations at individual sites (site-level parameters) (Fig. 1). Here we employ this Bayesian hierarchical modeling approach and focus specifically on site-level parameters that capture the response to climatic variation of the constituent populations of species at each site (Nice *et al.*, 2014). In this way, we can specifically quantify effects across species at a community level. We ask whether responses to climate variation are similar among sites, and explore our ability to predict these responses and the factors that limit prediction.

Materials and Methods

Data Collection, Climate Covariates and Statistical Model

Data on the presence and absence of butterflies were collected by a single observer (AMS) from biweekly visits to ten sites that comprise a transect across California (Fig. 1, Table S1). We used data from 1972 to 2013. These data were pruned to remove any species that was observed less than five years at a particular site. Further details of data collection have been described elsewhere (Forister *et al.*, 2010, 2011; Shapiro, 2011). Parts of these data have been used to address a variety of questions about butterfly responses to climate change (Forister & Shapiro, 2003; Thorne *et al.*, 2006; Espeset *et al.*, 2016; Forister *et al.*, 2010, 2011; Shapiro, 2011; Harrison *et al.*, 2015; Nice *et al.*, 2014; Pardikes *et al.*, 2015, 2017; Forister *et al.*, 2018) and other factors (Forister *et al.*, 2016). Here we present the first hierarchical analysis of these data focused on site-level variation.

We examined the response of populations (i.e. "population-level responses") and entire butterfly assemblages at sites (i.e. "site-level responses") to climatic variation using data for 12 local variables and one regional variable (Fig.s 2, 3). The population, that is, a particular species at a particular site, is the basic unit of analysis. For example, monarch butterflies (*Danaus plexippus*) at Donner Pass (DP) constitute a population that is distinct from monarchs at Suisun March (SM), or painted ladies (*Vanessa cardui*) at Donner Pass (DP). The weather variables included measures of precipitation, maximum and minimum temperatures and monthly sea-surface temperatures. Quarterly precipitation and temperature records were obtained using PRISM (Parameter-elevation Relationships on Independent Slopes Model, PRISM Climate Group, see http://prism.oregonstate.edu) and represent the year from September of the preceding year to August of the current year. Thus, these climate variables were chosen to include factors likely to influence the butterfly flight season for each year. Precipitation values used here are average daily measures calculated as monthly averages and then averaged over each season (i.e. "Fall
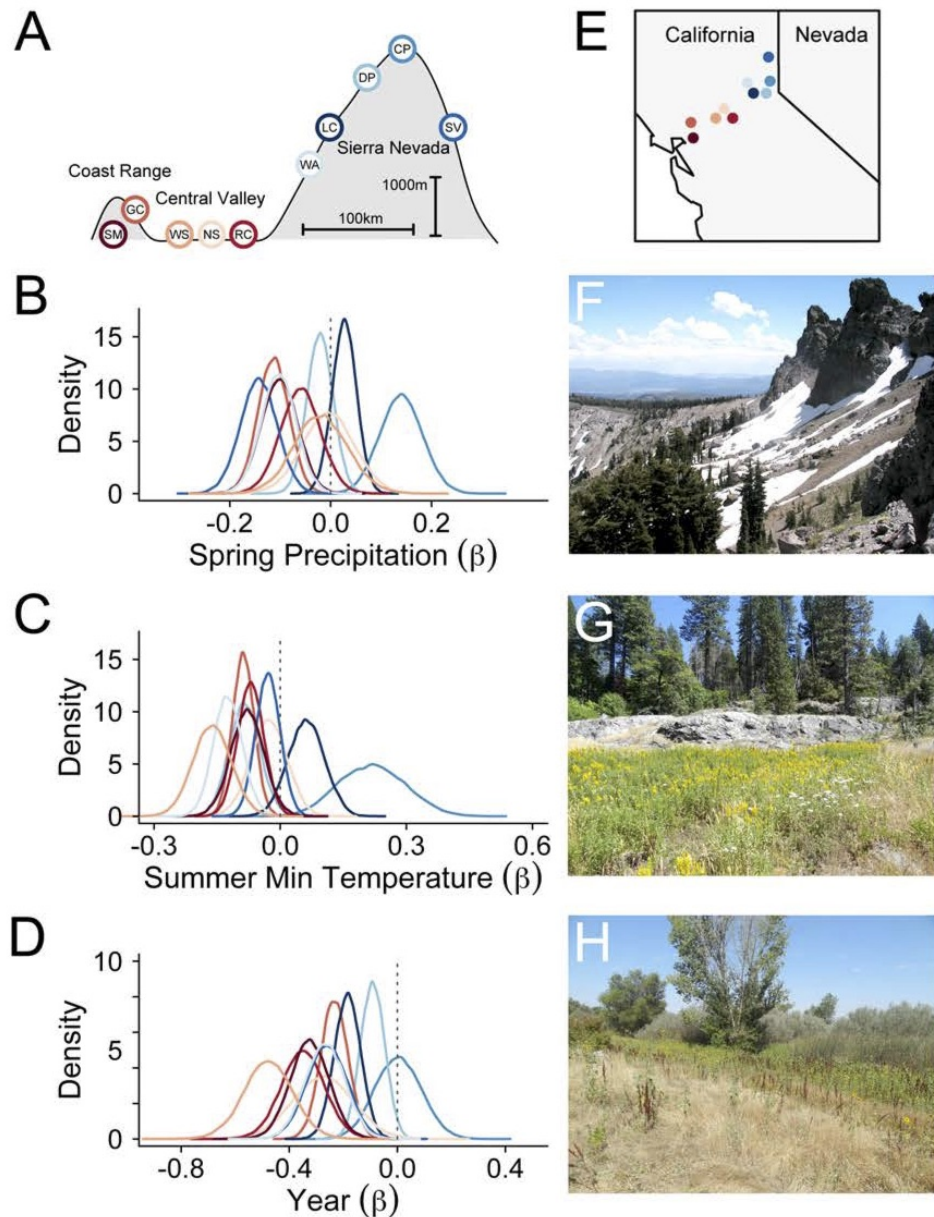
Figure 1: Site locations and example probability densities. A) Butterflies have been monitored for up to 42 years at these 10 sites, which comprise a transect across northern California. (E) The transect covers a diversity of habitats from sea-level (Suisun Marsh, SM) to 2,775m (Castle Peak, CP), and from the Sacramento River delta, to the Coast Range and Sierra Nevada mountains, to the high desert of the western Great Basin. Data for 149 butterfly species were analyzed with a linear, hierarchical model. Model-based probability densities of site-level standardized β coefficients are shown for weather covariates, including: (B) spring precipitation, (C) summer minimum temperature, and (D) the year effect. The vertical, dashed lines in B-D indicate a value of zero. The transect sites span habitat variation including (F) alpine habitat at Castle Peak (CP), (G) montane habitat at Lang Crossing (LC), and (H) low elevation, mixed agricultural and urban habitat in West Sacramento.

Precipitation" is the average daily precipitation for September, October and November for each year). We also used the monthly composite sea-surface temperature and climate data from the El Niño - Southern Oscillation (ENSO) data base (specifically we used the multivariate ENSO index which is the first principal component from six temperature, atmospheric pressure, wind and cloudiness variables available at: http://www.esrl.noaa.gov/psd/enso/mei/table.html) (Wolter & Timlin, 2011). These ENSO variables have been demonstrated to be related to climatic variation and ecological variation in North America (e.g., Mochizuki *et al.*, 2010). The multivariate ENSO index values are averaged across months to provide a yearly average value. The year in which butterfly data were collected was also included in the model (i.e. a "year" effect) to assess trends over time and to account for other factors influencing species' occurrences besides the climate covariates described above (e.g. biotic interactions, pesticides (Forister *et al.*, 2016)). All covariates were standardized using z-transformation.

We used a generalized linear model in a Bayesian, hierarchical framework to analyze butterfly presence/absence data. Day positives (DP), the number of days during a year that a butterfly species was detected at a transect site, was modeled using the binomial distribution with the number of trials equal to the number of visits for each year. This fraction of day positives is highly correlated with absolute count abundance for most species and we use it here as a measure of the response of populations to climate variation (Forister *et al.*, 2011; Casner *et al.*, 2014b). A generalized linear model with a logit link function that incorporated effects of the 13 climate variables (described above) and the effect of years was fit to these data using a hierarchical Bayesian approach implemented in the BUGS language (Gilks *et al.*, 1994) using JAGS (version 3.2.0) (Plummer, 2003) and run in R (R Development Core Team, 2012) using the *rjags* package. This Bayesian hierarchical approach has prove to be an effective strategy in other analyses of these data (Nice *et al.*, 2014; Harrison *et al.*, 2015). Our hierarchical model consisted of populations of species nested within each site. Model specification is provided in the Supporting

Information. This framework facilitates quantification of uncertainty in parameter

estimates in the form of credible intervals (CIs) for each parameter, and uncertainty is

propagated to all levels of the hierarchy. For example, we use day positives as a proxy for

population abundance which undoubtedly introduces uncertainty into the estimation of

population-level parameters which in turn contributes to uncertainty in site-level

parameters. Thus, the credible intervals around parameter estimates are an accurate

accounting of the various kinds of error in these analyses, including the error created by

day positives being an imperfect estimator of abundance (Forister *et al.*, 2011; Casner

et al., 2014b).

Posterior distributions for all parameters were estimated using two MCMC chains

with 30,000 steps each in JAGS. To confirm that the MCMC algorithm sampled the

stationary distribution, diagnostic tests were performed for each analysis (Supporting

Information). Standardized regression coefficients, β coefficients, and 95% equal-tail

credible intervals were calculated for each of the 10 sites and for all 665 populations across

all sites for all 13 climate covariates and year (i.e. there are 10 sites (site level) and 665

species-by-site combinations (population level) for which coefficients were estimated, see

supporting information). The site level is the highest level of the hierarchical model, which

means that each site is modeled independently. Site-level coefficients and CIs were plotted

and population-level values were tabulated. Variation among sites was examined and

illustrated by constructing a heat map for the site-level coefficients for all 13 weather

covariates for all 10 sites in R using the *gplots* package (R Development Core Team, 2012).

To assess whether heterogeneity in response to climate variation among sites was a product

of differences in species composition across the 10 transect sites, we repeated the

hierarchical analysis described above, but restricted this analysis to 18 species which occur

at all sites (Table S2). We then calculated the Pearson correlation coefficient, r, between

site-level parameter estimates from the full model and the parameters estimated from the

limited set of 18 species.

Model Validation and Predictability

We assessed model performance using a posterior predictive check with cross validation that involved dropping out 10% of the data and using the model parameters to predict the missing day positive data. This was done ten times dropping different parts of the data set to generate an entire predicted data set. We then estimated the correlation between observed and predicted data as a global measure of model fit, and we calculated the proportion of the observed data that fell within the 95% CI of the predicted data as an estimate of model precision.

We used the same modeling and posterior predictive check strategy to measure our ability to predict the observed data for different periods of time, for resident species (those which maintain breeding populations at specific sites (Nice *et al.*, 2014; Pardikes *et al.*, 2015; Forister *et al.*, 2016)), versus non-resident butterfly species (which do not breed locally), and for each site. Here we define "predictability" as the correlation between observed and predicted data. Specifically, we asked whether the model can predict data from seven years from 2007 to 2013. These seven years include two major droughts in California from 2007 to 2009 and from 2011 to 2013 (Supporting Information). Given that periods of drought can have dramatic and complex effects on butterfly populations (Shapiro, 1979; Ehrlich *et al.*, 1980), we consider these extreme years to be an appropriate test of the predictive power of our hierarchical model. The day positive data for these seven years were removed from the data set and predicted as in the posterior predictive checks using the remaining 35 years of data. Estimates were obtained from 20,000 MCMC steps. As we did for the posterior predictive checks (above), predictions were assessed by calculating Pearson's correlation coefficient, r, between log transformed observed and predicted day positives for each population (site $\times$ species) for which the mean number of day positives across years was greater than one. In this case, correlations between log transformed observed and predicted day positives were calculated specifically for the seven year period from 2007 to 2013. We also counted how often the observed data was not

contained within the predicted data 95% CI. The model's ability to predict day positives

for these seven years from 2007 to 2013 was compared to the model's predictions for sets of

seven contiguous years replicated as 1972-1978, 1979-1985, 1986-1992, 1993-1999 and

2000-2006, and for seven randomly selected years (replicated five times). For each of these

analyses, separate runs of the model were used to predict day positives for the years in

question.

Species Turnover and Predictability

We examined how variation in butterfly community richness and evenness might covary

with our model's ability to predict butterfly occurrences. Specifically, we examined

sequential turnover in community composition using Hill numbers (Hill, 1973; Jost, 2006,

2007; Marion et $al.$, 2017). Hill number ($^q D$) values vary as a function of the parameter q,

which determines the relative sensitivity to common versus rare species. When q $= 0$, the

measure is analogous to richness, where each species is weighted equally regardless of

abundance. When $q = 1$, species are weighted by their relative abundance as in the

commonly used Shannon's index. When $q = 2$, rarer species are down-weighted in

importance as in the commonly used Simpson's index. Higher orders of q continue to

increasingly down-weight the importance of rare species. β-diversity expressed as Hill

numbers provide the "effective number" of distinct communities in a sample. Pairwise

β-diversity as Hill numbers provides an intuitive summary of community dissimilarity (Hill,

1973; Jost, 2006, 2007; Marion et $al.$, 2017). Here, $^q D \beta$ is constrained between 1 and 2,

where $^q D \beta = 1$ indicates that two community samples are identical (i.e., effectively one

distinct community), and where $^q D \beta = 2$ indicates that two community samples are

completely different (i.e., effectively two distinct communities). Subtracting one from $^q D \beta$

provides turnover, or the expected proportional change from one sample to the next. We

calculated mean sequential turnover across years for orders of q equal to zero, one and two

and examined the correlation between turnover and the correlation between predicted and

206 observed day positives. A positive correlation would indicate that our model performs

207 better when there is greater among-year variation in community composition and evenness,

208 whereas a negative correlation would indicate that our model performs best when

209 communities are more similar, on average, from year to year.

Results

211 The effect of climatic variation on butterfly populations was readily detected and

212 heterogeneous. All weather variables were characterized by varying effects along the

213 elevational gradient, with positive effects (i.e. positive regression coefficients) in some

214 locations and negative effects in others (see Fig. 2 and Table S3 for coefficients from the

215 hierarchical model, see Fig.s S1-S13 and Table S5-S7 for details of individual climate

216 variables, see Tables S9-S11 for population-level coefficients). Despite transect-wide

217 heterogeneity, adjacent sites in some cases showed similar effects; see, for example the

218 positive effects of increasing sea surface temperatures (El Niño-Southern Oscillation), or

219 spring minimum temperatures at lower elevations and the more negative or neutral effects

220 of these variables at higher elevations (Fig. 2). A smaller number of variables show even

221 greater consistency of effect, including the generally positive effects of increasing summer

222 maximum temperatures (warmer daily high temperatures) and the negative effects of

223 spring precipitation (see Fig. 3 where variables are clustered by similarity of

224 population-level response). The positive effects of increasing summer maximum

225 temperatures might be a simple consequence of accelerated growth in ectothermal

226 organisms under higher temperatures (Kingsolver, 2000). The negative relationship with

227 spring precipitation is likely a consequence of reduced feeding time during cloudy

228 conditions having a negative impact on butterfly abundance, direct mortality associated

229 with wet conditions, disruption of phenological matching between butterfly and host

230 plants, or indirect effects mediated by changes in host plant quality (Bale *et al.*, 2002;

Stefanescu *et al.*, 2003; Parmesan & Yohe, 2003).

The heterogeneity in response to climate variation observed among sites was not directly attributable to differences in species composition. The correlation between site-level parameter estimates (standardized β coefficients) from the full data and the restricted data of 18 species (Supporting Information) was high (Pearson's $r = 0.82$), indicating that the observed heterogeneity in response to climate variation is not solely explained by differences in species composition among sites (Table S2, Fig. S14).

Despite the overall high heterogeneity across transect sites in response to climate variation, these responses of butterfly populations were predictable, but to varying degrees. We used a posterior predictive check with cross validation to assess the model's ability to predict the observed data (Supporting Information). Overall, predictability, measured as the correlation between observed and predicted day positives, across the entire data set was relatively high (Pearson's $r = 0.43$, SE 0.01, Table S8) and 96% of observed day positives fell within the 95% credible intervals of the predicted data (Table S8). Predictability was lowest for relatively rare butterflies and there was a generally positive correlation between observed day positives and our ability to predict butterfly occurrences (Table S8, Fig. S16). This pattern was evident at the site-level as well: sites with higher mean day positives exhibited greater predictability (Fig. 4A). Further, resident butterflies were more readily predicted by our model compared with non-residents. This pattern is undoubtedly related to the lower predictability of less common butterflies: on average, resident butterflies had higher occurrences (day positives) than non-residents (Fig. S16).

Our ability to predict butterfly occurrences was also lowest for sites with high year-to-year species turnover (Fig. 4B). For the three Hill numbers we calculated (q=0, 1, and 2), there was a negative correlation between turnover and predictability (Fig. 4B, Fig. S15). This negative relationship was strongest when the contribution of rare species was down-weighted (Fig. 4B), which indicates that the effect of community turnover is important and not simply a product of rare species being more difficult to predict. The
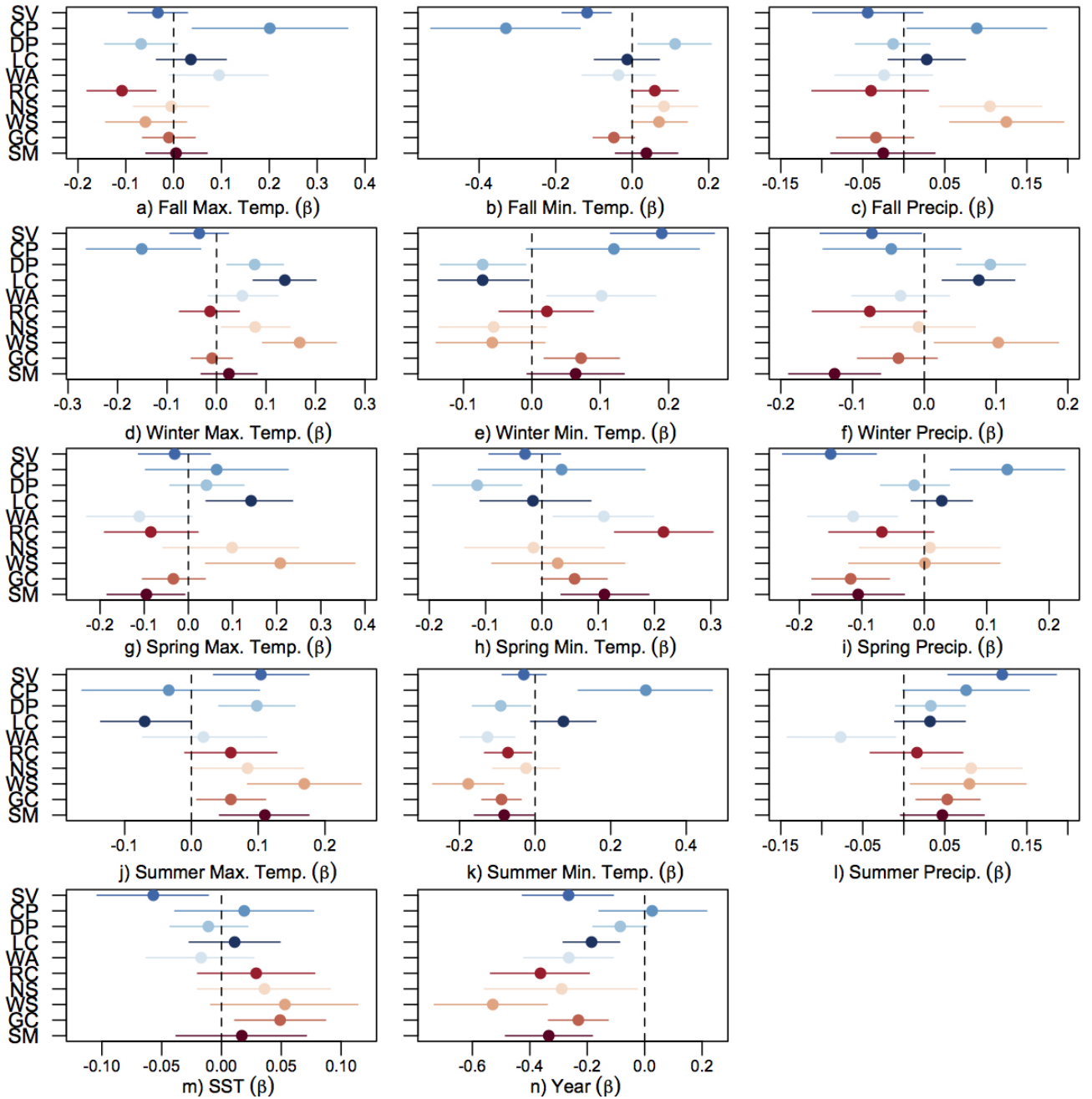
Figure 2: The effect of weather variables on butterfly communities. Each panel includes the median values (points) and 95% CIs (bars) for the site-level responses (standardized β coefficients) to weather variables and the year effect. Sites are arranged from west (bottom = SM) to east (top = SV). Colors and site abbreviations are the same as in Fig 1. Note that the scale of x-axes varies among panels. Vertical dashed lines represent values of zero.
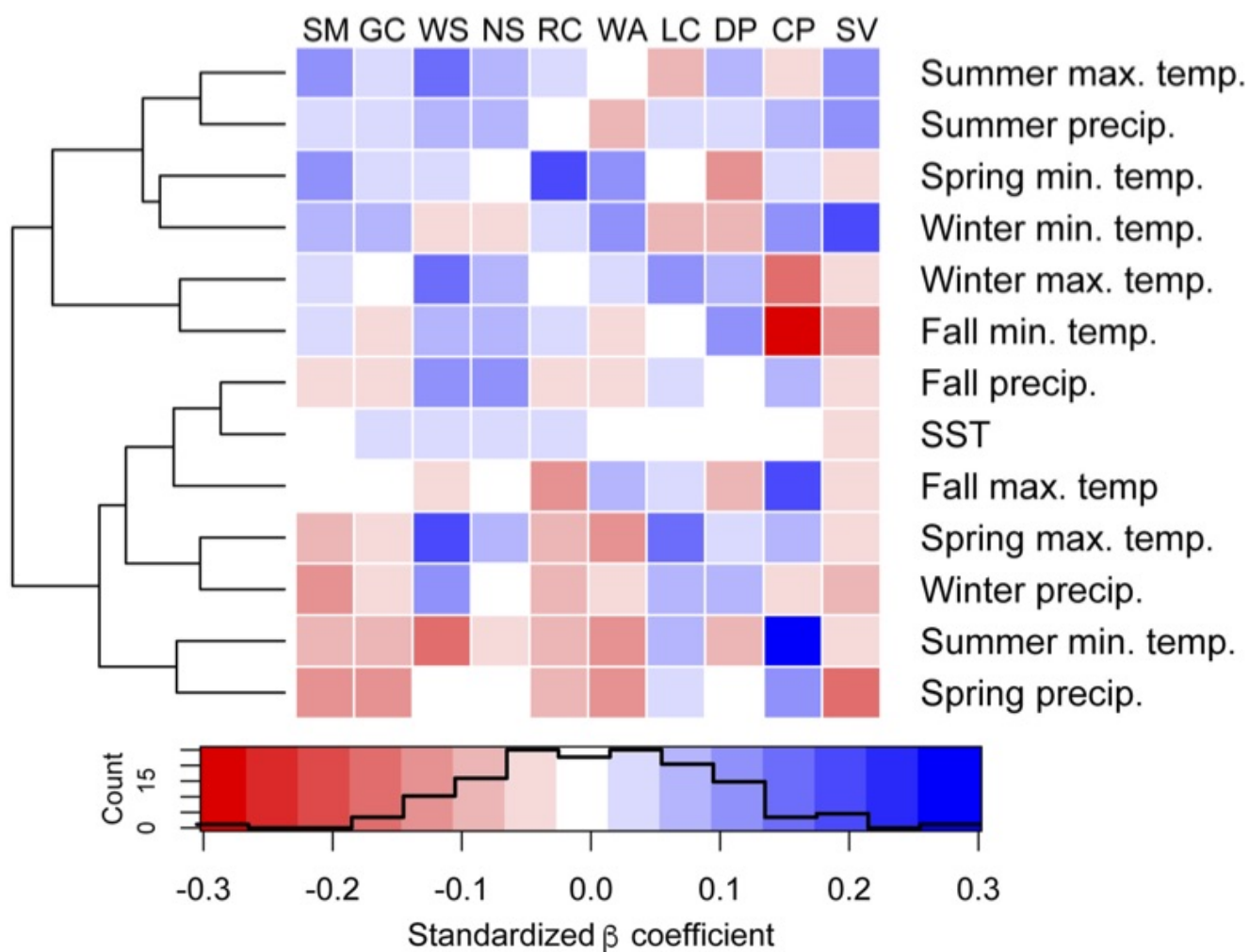
Figure 3: Heat map illustrating the patterns of responses of butterfly populations to inter-annual variation in weather at each of the transect sites. Sites are arranged from west to east, site abbreviations are the same as in Fig 1. Weather variables are arranged by similarity of responses. The dendrogram on the left shows the patterns of similarities among variables and across sites. Sites showed a generally negative response (red squares) to increasing summer minimum temperature and spring precipitation, but showed a generally positive response (blue squares) to increasing summer maximum temperature and summer precipitation. Sites showed highly heterogeneous responses to most aspects of climate variation, especially, for example, variation in spring maximum temperature and winter precipitation. A histogram of standardized coefficients is presented at the bottom of the figure.

²⁵⁸ negative impact of higher turnover on our predictive ability suggests that habitats with

²⁵⁹ frequent disturbance (e.g. fire prone areas), or high immigration (e.g. mountain top

²⁶⁰ habitats or other islands), will be least predictable, an effect that might be exacerbated if

²⁶¹ increasing climate variability (Cai *et al.*, 2014; Cubasch *et al.*, 2001; Seneviratne *et al.*,

²⁶² 2014) causes greater turnover.

²⁶³   Our ability to predict was also variable across time. We asked specifically if

²⁶⁴ parameters estimated from 35 years of data could be used to predict species occurrences

²⁶⁵ during the seven year period from 2007 to 2013 that included two severe droughts in

²⁶⁶ California (Supporting Information). We found that butterfly occurrences were extremely

²⁶⁷ difficult to predict accurately for these seven years compared to other sets of seven

²⁶⁸ contiguous years, or sets of seven randomly chosen years (Fig. 4C, Table S8). The median

²⁶⁹ predictability for the 2007 to 2013 period was 0.09 and substantially lower than for sets of

²⁷⁰ seven randomly chosen years in which predictability ranged from 0.38 to 0.50 (Table S8).

²⁷¹ Not only did the model exhibit its lowest predictive ability for the period 2007 to 2013, but

²⁷² also model predictability declined over time. This suggests that the ability to predict

²⁷³ species responses to climatic variation will become more difficult over coming years as the

²⁷⁴ climate becomes more variable and extreme climate events become more frequent

²⁷⁵ (Easterling *et al.*, 2000).

²⁷⁶   In contrast to the generally multifarious responses to climatic variation, the

²⁷⁷ butterfly faunas at all but one of the sites have strong negative associations with year

²⁷⁸ (Table S3, Fig. 2). This evidence of decline is consistent with previous reports (Pardikes

²⁷⁹ *et al.*, 2015). The one exception is at the highest elevation (CP), where the local fauna has

²⁸⁰ increased in species richness, apparently as a consequence of colonization and persistence of

²⁸¹ butterflies that were previously less common or absent from the highest elevation (Forister

²⁸² *et al.*, 2010). We identified several climatic factors that might be important for explaining

²⁸³ declining butterfly populations, in particular minimum temperatures. Higher summer

²⁸⁴ minimum temperatures (warmer overnight lows) had a negative impact at most sites (Fig.
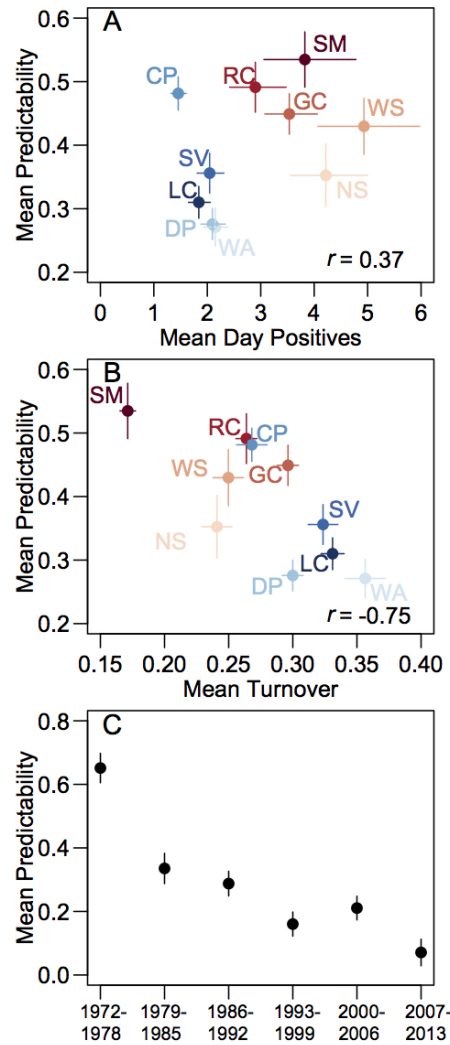
Figure 4: Overall site-level predictability increases with increasing mean butterfly occurrences and decreases with year-to-year species turnover and over time. (A) Predictability, defined as the mean correlation between observed and predicted butterfly occurrences (day positives), is lowest for transect sites with lower mean day positives. Lower elevation sites, with longer seasons and more opportunities to observe butterflies had higher mean predictability compared to higher elevation sites. Colors and site abbreviations are the same as in Fig 1. (B) Transect sites with higher species turnover had lower mean predictability. Year-to-year turnover was estimated with the Hill number (^{q}D) exponent, $q = 2$ (Hill, 1973; Jost, 2006, 2007; Marion *et al.*, 2017) with rarer species down-weighted in importance as in the commonly used Simpson's index (see Supporting Information). Mean turnover is the expected proportional change in the community at a site from one year to the next. (C) Predictability decreased over time and was lowest for the seven years between 2007 and 2013, which is a period that includes two major droughts in California. (It should be noted that the years prior to 1988 do not include observations from all ten sites (see Supporting Information, Table S1)).

285 2), and summer minimum temperatures are rising across many sites (Fig. S11, Table S5)

286 and across the state of California (Mazur & Milanes, 2009). Rising minimum summer

287 temperatures negatively impact larval host plants and nectar sources (Kelly & Goulden,

288 2008). Minimum temperatures in other seasons have a more variable effect, which is

289 presumably due to habitat differences (Table S1). Indeed, habitat heterogeneity might be

290 an important buffer against directional change for mobile organisms (Harrison & Quinn,

291 1989; Oliver *et al.*, 2010, 2014; Hindle *et al.*, 2015). Winter minimum temperatures, for

292 example, have both strong positive and negative effects across sites and such variation

293 could provide refuges for species with population connectivity. However, the standardized

294 effect of year at most sites is approximately two times larger than the effects measured for

295 weather variables (Fig. 2, Table S3). Because the strong year effects were estimated in

296 models that controlled for climatic effects, we infer that non-climatic factors are influential

297 in the observed declines. These other factors might include interactions with natural

298 enemies and invasive species (Graves & Shapiro, 2003), and availability of food resources

299 (Tylianakis *et al.*, 2008), or abiotic factors, such as land use change (Casner *et al.*, 2014a),

300 pesticides (Forister *et al.*, 2016), and other anthropogenic effects.

Discussion

302 Unanswered questions remain regarding the causes and consequences of heterogeneous

303 faunal responses to climatic variation. We hypothesize that local idiosyncrasies of

304 topography and microclimate, and their interaction over time, explain much of the

305 variation in butterfly responses (Moritz & Agudo, 2013). These differences among sites

306 might impact butterflies directly through physiological and behavioral mechanisms, or

307 indirectly through microclimatic and topographic effects on other species that interact with

308 butterflies (Van der Putten *et al.*, 2010; Tylianakis *et al.*, 2008; Ovaskainen *et al.*, 2013).

309 For example, the two highest elevation sites (CP and DP) are often characterized by

310 disparate responses to climatic variation (Fig. 2), and, despite geographic proximity, they

311 contain distinct habitats. DP includes extensive wet and dry meadow complexes, while CP

312 extends to tree line and alpine vegetation. We do not know, however, if disparate butterfly

313 responses at these sites are primarily driven by population differentiation or differences in

314 ecological processes. Intraspecific variation in responses could be correlated with

315 geographic position relative to species' range margins with peripheral populations perhaps

316 being more sensitive to climate variation as has been shown in butterflies (Mills *et al.*,

317 2017). Furthermore, habitat heterogeneity might strongly influence patterns of dispersal

318 and connectivity among sub-populations of particular species (Warren *et al.*, 2001).

319 Climate change might result in a greater proportion of marginal habitats (i.e. "sink"

320 habitats), although at the same time, such habitat heterogeneity might ameliorate some of

321 the impacts of climate change, especially for mobile organisms that can find refuge in a

322 mosaic of different habitats (Harrison & Quinn, 1989; Oliver *et al.*, 2010, 2014; Hindle

323 *et al.*, 2015; Nadeau *et al.*, 2017). Consequences of climate change within the context of

324 habitat-specific responses to climate will likely be complex, and could include an increase

325 in the proportion of marginal (or "sink") habitats. Another possibility is that

326 habitat-specific responses associated with microclimatic and topographic heterogeneity

327 could offer refugia for mobile organisms. This possibility of refugial habitats was not

328 supported in a recent analysis of these same sites throughout the major drought years of

329 2011 to 2015 (Forister *et al.*, 2018). Those analyses, however, focused on community-level

330 summary statistics and did not analyze species-specific responses; thus much remains to be

331 learned about the interaction between extreme climatic events and heterogeneity of species-

332 and site-specific responses that we report here.

333   Despite the observed heterogeneity of responses, our overall ability to predict

334 butterfly occurrences was relatively good. Cross validation demonstrated that the

335 differences between observed and predicted occurrences were generally small and the vast

336 majority (96%) of observed values were included in the credible intervals of predicted

occurrences. However, predictability was lower for non-resident species compared to residents, and for rarer species. Predictability was also lower at sites with higher year-to-year turnover in constituent species and these differences were not solely attributable to rare species (Fig. 4B). Most alarmingly, our ability to predict butterfly occurrences declined over time and was lowest for the last seven years of our data, a period that included extreme droughts in California (Fig. 4C). If the decline in predictability parallels increasing variability in climate and increasing frequency of extreme events, then our ability to predict future butterfly responses might already be largely compromised given predictions of an increasingly variable future climate (Easterling *et al.*, 2000). The links presented here between lower predictability, lower relative abundance, increasing turnover of species within sites, and climate variability suggest a possible mechanism for the decrease in predictive power. However, more investigation is required before we can firmly conclude that increasing climate variability is the cause of the decline in predictability. Studies of other communities and other taxa will provide valuable insights into the the limits of prediction.

While these unknowns should guide future work, the results reported here offer at least four concrete conclusions. First, we should consider among-site heterogeneity when designing long-term studies. The diversified responses to climate variation reported here suggest that among-site habitat heterogeneity might play a critical role in mediating how assemblages of species respond to climate change. Second, strong heterogeneity of faunal response means that global forecasts of biotic effects of climate change will be inaccurate in some cases, such as when changing climate conditions increase population densities in one area and decrease populations in another. Third, a substantial proportion of the variation among sites, and among populations, is not likely to be explained by abiotic factors alone, which suggests a potentially central role for biotic interactions influencing heterogeneity of response. Fourth, despite the heterogeneity of faunal response to climatic variation, prediction of species occurrences was possible, but our ability to predict butterfly

occurrences was highest for more abundant species, sites with lower annual turnover, and for years without extreme climate events, particularly extreme droughts. Given the likely increase of extreme weather events due to climate change (Cai *et al.*, 2014; Cubasch *et al.*, 2001; Seneviratne *et al.*, 2014), these results emphasize the benefits that could be accrued through analyses of predictability of the population dynamics of diverse taxa. The complex variation observed in responses to inter-annual variation in weather, and the limits to our ability to predict those responses, demonstrates that there is much more to learn about mechanistic links between climate change and population dynamics.

Acknowledgments

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