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Extreme heterogeneity of population response to climatic variation and the limits of prediction

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Abstract

Certain general facets of biotic response to climate change, such as shifts in phenology and geographic distribution, are well characterized; however, it is not clear whether the observed similarity of responses across taxa will extend to variation in other population-level processes. We examined population response to climatic variation using long-term incidence data (collected over 42 years) encompassing 149 butterfly species and considerable habitat diversity (10 sites along an elevational gradient from sea level to over 2,700 m in California). Population responses were characterized by extreme heterogeneity that was not attributable to differences in species composition among sites. These results indicate that habitat heterogeneity might be a buffer against climate change and highlight important questions about mechanisms maintaining interpopulation differences in responses to weather. Despite overall heterogeneity of response, population dynamics were accurately predicted by our model for many species at each site. However, the overall correlation between observed and predicted incidence in a cross validation analysis was moderate (Pearson's $r = 0.23$, SE 0.01), and 97% of observed data fell within the predicted 95% credible intervals. Prediction was most successful for more abundant species as well as for sites with lower annual turnover. Population-level heterogeneity in response to climate variation and the limits of our predictive power highlight the challenges for a future of increasing climatic variability.

KEYWORDS
Bayesian hierarchical model, climate change, long-term data, monitoring, weather

1 | 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, Hill, Ohlemüller, Roy, & Thomas, 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; Sagarin, Barry, Gilman, & Baxter, 1999; Thomas & Lennon, 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, Betancourt, & Brown, 1995) and to population declines (Both, Bouwhuis, Lessells,

& Visser, 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, Roy, Hill, Brereton, & Thomas, 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 (Figure 1, Table S1). This transect, comprised of ten sites, extends from sea level to the east side of the Sierra Nevada Mountains. These sites were visited approximately every 2 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]; Figure 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

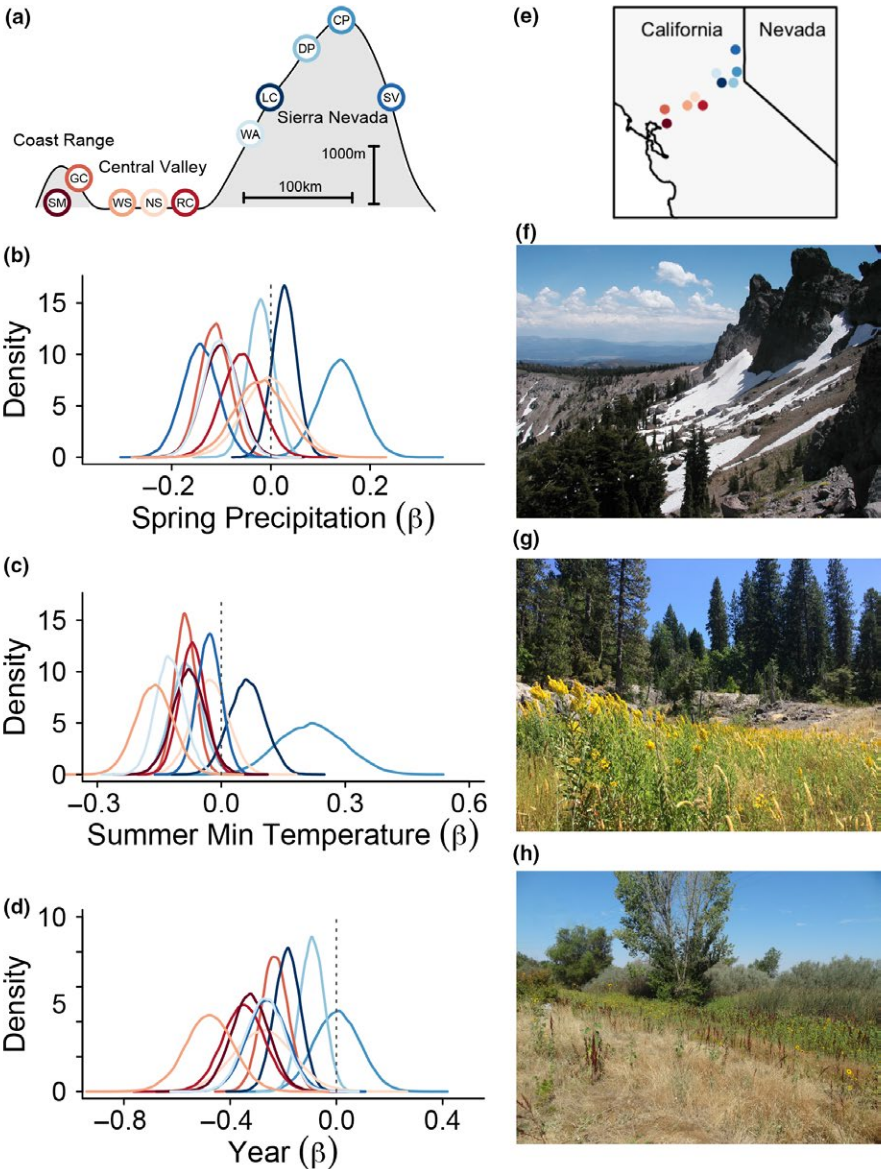

FIGURE 1 Site locations and example probability densities. (a) Butterflies have been monitored for up to 42 years at these 10 sites, which comprise a transect across northern California. (e) The transect covers a diversity of habitats from sea level (Suisun Marsh, SM) to 2,775 m (Castle Peak, CP), and 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

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, Forister, Ram, & Shapiro, 2014b; Forister, Jahner, Casner, Wilson, & Shapiro, 2011) (Supporting Information). The effects of weather variables on day positives can be effectively modeled in a hierarchical Bayesian framework (Harrison et al., 2015; Nice, Forister, Gompert, Fordyce, & Shapiro, 2014) 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) (Figure 1). Here we employ this Bayesian hierarchical modeling approach and focus specifically on site-level parameters that capture the response to climatic variation in the constituent

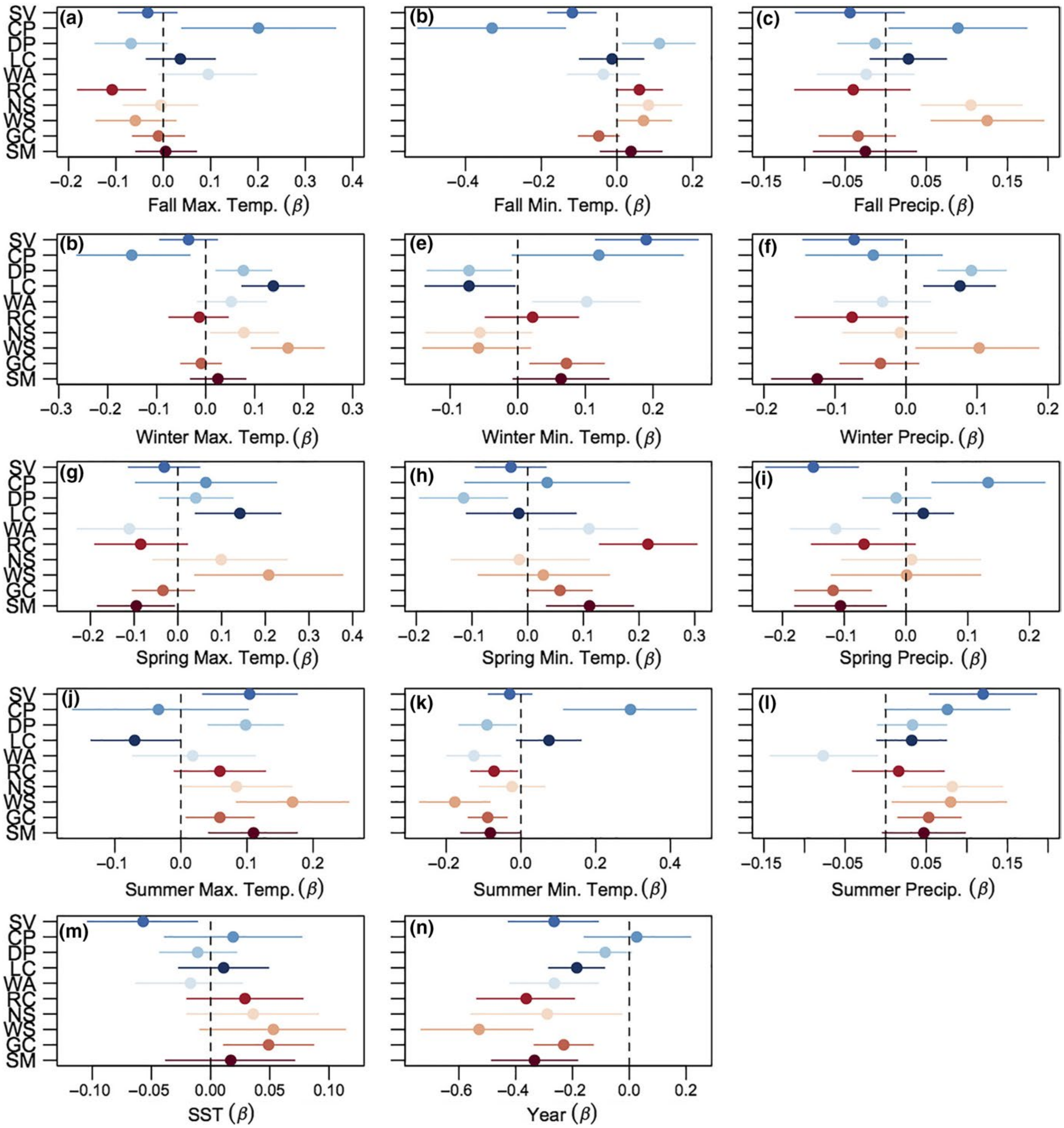

FIGURE 2 The effect of weather variables on butterfly communities. Each panel includes the median values (points) and 95% CIs (bars) for the site-level responses (standardized β coefficients) to weather variables and the year effect. Sites are arranged from west (bottom = SM) to east (top = SV). Colors and site abbreviations are the same as in Figure 1. Note that the scale of *x*-axes varies among panels. Vertical dashed lines represent values of zero

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.

2 | MATERIALS AND METHODS

2.1 | 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 compose a transect across California (Figure 1, Table S1). We used data from 1972 to 2013. These data were pruned to remove any species that was observed less than 5 years at a particular site. Further details of data collection have been described elsewhere (Forister et al., 2011, 2010; Shapiro, 2011). Parts of these data have been used to address a variety of questions about butterfly responses to climate variability (Espeset et al., 2016; Forister et al., 2018, 2011, 2010; Forister & Shapiro, 2003; Harrison et al., 2015; Nice et al., 2014; Pardikes, Harrison, Shapiro, & Forister, 2017; Pardikes, Shapiro, Dyer, & Forister, 2015; Shapiro, 2011; Thorne, O'Brien, Forister, & Shapiro, 2006) 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 (Figures 2 and 3). The population, that is, a particular species at a particular site, is the basic unit of analysis. For example, cabbage white butterflies (*Pieris rapae*) at Donner Pass (DP) constitute a population that is distinct from cabbage whites at SM, or painted ladies (*Vanessa cardui*) at 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 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) database (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.

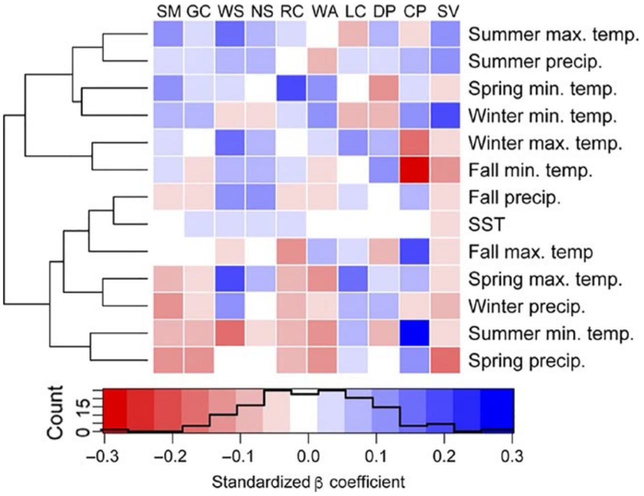

FIGURE 3 Heat map illustrating the patterns of responses of butterfly populations to inter-annual variation in weather at each of the transect sites. Sites are arranged from west to east, site abbreviations are the same as in Figure 1. Weather variables are arranged by similarity of responses. The dendrogram 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

We used a generalized linear model in a Bayesian, hierarchical framework to analyze the butterfly presence/absence data. Day positives, the number of days during a year that a butterfly species was detected at a transect site, were 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 (Casner, Forister, Ram et al., 2014b; Forister et al., 2011). 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, Thomas, & Spiegelhalter, 1994) in R (R Development Core Team, 2012) using the rjags package with MCMC models in JAGS (version 3.2.0) (Plummer, 2003). This Bayesian hierarchical approach has proven to be an effective strategy in other analyses of these data (Harrison et al., 2015; Nice et al., 2014). Our hierarchical model consisted of populations of species nested within each site. Model specification is provided in the Supporting Information. This framework facilitates the 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 CIs 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 (Casner, Forister, Ram et al., 2014b; Forister et al., 2011).

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 CIs 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.

2.2 | 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 10 times dropping different parts of the dataset to generate an entire predicted dataset. We then estimated the correlation between observed and predicted probabilities of occurrence as a global measure of model fit, and we calculated the proportion of the observed day positives that fell within the 95% CI of the predicted day positives as another 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; Forister et al., 2016; Nice et al., 2014; Pardikes et al., 2015), 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 probabilities of occurrence. Specifically, we asked whether the model can predict data from 7 years from 2007 to 2013. These 7 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 (Ehrlich et al., 1980; Shapiro, 1979), we consider these extreme years to be an appropriate test of the predictive power of our hierarchical model. The day positive data for these 7 years were removed from the dataset 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 observed and predicted probabilities of occurrence for each population (site × species) for which the mean number of day positives across years was greater than one. In this case, correlations between observed and predicted probabilities of occurrence were calculated specifically for the 7-year-period from 2007 to 2013. We also counted how often the observed data were contained within the predicted data 95% CI. The model's ability to predict occurrences for these 7 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 occurrences for the years in question.

2.3 | 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, Fordyce, & Fitzpatrick, 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 observed probabilities of occurrence. A positive correlation would indicate that our model performs better when there is greater among-year variation in community composition and evenness, whereas a negative correlation would indicate that our model performs best when communities are more similar, on average, from year-to-year.

3 | RESULTS

The effect of climatic variation on butterfly populations was readily detected and heterogeneous. All weather variables were characterized by varying effects along the elevational gradient, with positive effects (i.e. positive regression coefficients) in some locations and negative effects in others (see Figure 2 and Table S3 for coefficients from the hierarchical model, see Figures S1–S13 and Tables S5–S7 for details of individual climate variables, see Tables S9–S11 for population-level coefficients). Despite transect-wide heterogeneity, adjacent sites in some cases showed similar effects; see, for example the positive effects of increasing sea surface temperatures (El Niño-Southern Oscillation), or spring minimum temperatures at lower elevations and the more negative or neutral effects of these variables at higher elevations (Figure 2). A smaller number of variables show even greater consistency of effect, including the generally positive effects of increasing summer maximum temperatures (warmer daily high temperatures) and the negative effects of spring precipitation (see Figure 3 where variables are clustered by similarity of population-level response). The positive effects of increasing summer maximum temperatures might be a simple consequence of accelerated growth in ectothermal organisms under higher temperatures (Kingsolver, 2000). The negative relationship with spring precipitation is likely a consequence of reduced feeding time during cloudy conditions having a negative impact on butterfly abundance, direct mortality associated with wet conditions, disruption of phenological matching between butterfly and host plants, or indirect effects mediated by changes in host plant quality (Bale et al., 2002; Parmesan & Yohe, 2003; Stefanescu, Penuelas, & Filella, 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, Figure 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 probabilities of occurrence, across the entire dataset was modest (Pearson's $r = 0.23$, *SE* 0.01, Table S8), yet 97% of observed day positives fell within the 95% CIs of the predicted day positives (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, Figure S16). This pattern was evident at the site-level as well: sites with higher mean day positives exhibited greater predictability (Figure 4a). However, resident butterflies were not more readily predicted by our model compared with nonresidents despite resident butterflies having higher occurrences (day positives) than nonresidents (Figure S16).

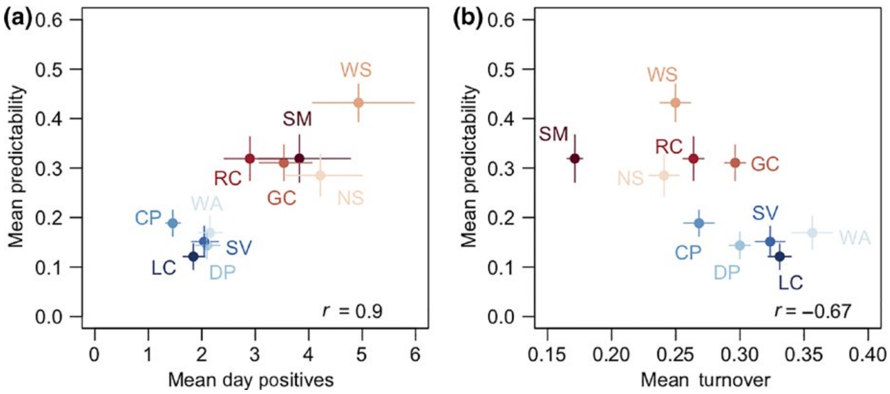

FIGURE 4 Overall site-level predictability increases with increasing mean butterfly occurrences and decreases with year-to-year species turnover and over time. (a) Predictability, defined as the mean correlation between observed and predicted butterfly occurrences (day positives), is lowest for transect 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 Figure 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 1 year to the next

Our ability to predict butterfly occurrences was also lowest for sites with high year-to-year species turnover (Figure 4b). For the Hill numbers we calculated at three orders of q (0, 1, and 2), there was a negative correlation between turnover and predictability (Figure 4b, Figure S15). This negative relationship persisted when the contribution of rare species was down-weighted (Figure 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 negative impact of higher turnover on our predictive ability suggests that habitats with frequent disturbance (e.g., fire prone areas), or high immigration (e.g., mountain top habitats or other islands), will be least predictable, an effect that might be exacerbated if increasing climate variability (Cai et al., 2014; Cubasch et al., 2001; Seneviratne, Donat, Mueller, & Alexander, 2014) causes greater turnover.

Our ability to predict was also variable across time. We asked specifically if parameters estimated from 35 years of data could be used to predict species occurrences during the 7-year-period from 2007 to 2013 that included two severe droughts in California (Supporting Information). We found that butterfly occurrences were extremely difficult to predict accurately for these 7 years (Figure S15c, Table S8). The median predictability for the 2007 to 2013 period was 0.04 and substantially lower than for sets of seven randomly chosen years in which predictability ranged from 0.20 to 0.29 (Table S8). However, the period 1979–1985 was similarly difficult to predict (Figure S15c, Table S8). This suggests that the ability to predict species responses to climatic variation is not obviously tied to extreme weather events such as the recent droughts in California.

In contrast to the generally multifarious responses to climatic variation, the butterfly faunas at all but one of the sites have strong negative associations with year (Table S3, Figure 2). This evidence of decline is consistent with previous reports (Pardikes et al., 2015). The one exception is at the highest elevation (CP), where the local fauna has increased in species richness, apparently as a consequence of colonization and persistence of butterflies that were previously less common or absent from the highest elevation (Forister et al., 2010). We identified several climatic factors that might be important for explaining declining butterfly populations, in particular minimum temperatures. Higher summer minimum temperatures (warmer overnight lows) had a negative impact at most sites (Figure 2); and summer minimum temperatures are rising across many sites (Figure S11, Table S5) and across the state of California (Mazur & Milanes, 2009). Rising minimum summer temperatures negatively impact larval host plants and nectar sources (Kelly & Goulden, 2008). Minimum temperatures in other seasons have a more variable effect, which is presumably due to habitat differences (Table S1). Indeed, habitat heterogeneity might be an important buffer against directional change for mobile organisms (Harrison & Quinn, 1989; Hindle, Kerr, Richards, & Willis, 2015; Oliver et al., 2010; Oliver, Stefanescu, Páramo, Brereton, & Roy, 2014). Winter minimum temperatures, for example, have both strong positive and negative effects across sites and such variation could provide refuges for species with population connectivity. However, the standardized effect of year at most sites is approximately two times larger than the effects measured for weather variables (Figure 2, Table S3). Because the strong year effects were estimated in models that controlled for climatic effects, we infer that nonclimatic factors are influential in the observed declines. These other factors might include interactions with natural enemies and invasive species (Graves & Shapiro, 2003), and availability of food resources (Tylianakis, Didham, Bascompte, & Wardle, 2008), or abiotic factors, such as land use change (Casner, Forister, O'Brien et al., 2014a), pesticides (Forister et al., 2016), and other anthropogenic effects.

4 | DISCUSSION

Unanswered questions remain regarding the causes and consequences of heterogeneous faunal responses to climatic variation. We hypothesize that local idiosyncrasies of topography and microclimate, and their interaction over time, explain much of the variation in butterfly responses (Moritz & Agudo, 2013). These differences among sites might impact butterflies directly through physiological and behavioral mechanisms, or indirectly through microclimatic and topographic effects on other species that interact with butterflies (Ovaskainen et al., 2013; Tylianakis et al., 2008; Van der Putten, Macel, & Visser, 2010). For example, the two highest elevation sites (CP and DPs) are often characterized by disparate responses to climatic variation (Figure 2), and, despite geographic proximity, they contain distinct habitats. DP includes extensive wet and dry meadow complexes, while CP extends to tree line and alpine vegetation. We do not know, however, if disparate butterfly responses at these sites are primarily driven by population differentiation or differences in ecological processes. Intraspecific variation in responses could be correlated with geographic position relative to species' range margins with peripheral populations perhaps being more sensitive to climate variation as has been shown in butterflies (Mills et al., 2017). Furthermore, habitat heterogeneity might strongly influence patterns of dispersal and connectivity among sub-populations of particular species (Warren et al., 2001). Climate change might result in a greater proportion of marginal habitats (i.e., "sink" habitats), although at the same time, such habitat heterogeneity might ameliorate some of the impacts of climate change, especially for mobile organisms that can find refuge in a mosaic of different habitats (Harrison & Quinn, 1989; Hindle et al., 2015; Nadeau, Urban, & Bridle, 2017; Oliver et al., 2010, 2014). This potential benefit of refugial habitats was not supported in a recent analysis of these same sites throughout the major drought years of 2011–2015 (Forister et al., 2018). Those analyses, however, focused on community-level summary statistics and did not analyze species-specific responses; thus much remains to be learned about the interaction between extreme climatic events and heterogeneity of species- and site-specific responses that we report here.

Despite the observed heterogeneity of responses, our overall ability to predict butterfly occurrences was relatively good. While cross validation demonstrated a modest correlation between observed and predicted occurrences, the vast majority (97%) of observed day positives was included in the CIs of predicted occurrences. However, predictability was lower 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 (Figure 4b). Unexpectedly, predictability was not different between resident and nonresident species, despite the incidence of nonresidents being lower. This suggests that rarity is not the only factor determining predictability of species. Further, our ability to predict butterfly occurrences varied over time with no clear trends or patterns associated with climate extremes such as the recent droughts in California (Figure S15c). The links presented here between lower predictability, lower relative abundance, and increasing turnover of species within sites suggest that increasing climate variability (Easterling et al., 2000) should contribute to a decrease in predictive power, but we did not see this in our analysis across time. More investigation, including studies of other communities and other taxa, is required before we fully understand 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 and sites with lower annual turnover. 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 interannual 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.

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AUTHOR CONTRIBUTION

A.M.S. collected the data; C.C.N., M.L.F., J.A.F. J.G.H., Z.G., J.H.T., D.P.W., and A.M.S. designed the study; C.C.N., M.L.F. and J.A.F. conducted statistical analyses and wrote the manuscript with input from the co-authors.

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