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Global weather and local butterflies: variable responses to a large-scale climate pattern along an elevational gradient

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Abstract. Understanding the spatial and temporal scales at which environmental variation affects populations of plants and animals is an important goal for modern population biology, especially in the context of shifting climatic conditions. The El Niño Southern Oscillation (ENSO) generates climatic extremes of interannual variation, and has been shown to have significant effects on the diversity and abundance of a variety of terrestrial taxa. However, studies that have investigated the influence of such large-scale climate phenomena have often been limited in spatial and taxonomic scope. We used 23 years (1988–2010) of a long-term butterfly monitoring data set to explore associations between variation in population abundance of 28 butterfly species and variation in ENSO-derived sea surface temperature anomalies (SSTA) across 10 sites that encompass an elevational range of 2750 m in the Sierra Nevada mountain range of California. Our analysis detected a positive, regional effect of increased SSTA on butterfly abundance (wetter and warmer years predict more butterfly observations), yet the influence of SSTA on butterfly abundances varied along the elevational gradient, and also differed greatly among the 28 species. Migratory species revealed the strongest relationships with ENSO-derived SSTA, suggesting that large-scale climate indices are particularly valuable for understanding biotic-abiotic relationships of the most mobile species. In general, however, the ecological effects of large-scale climatic factors are context dependent between sites and species. Our results illustrate the power of long-term data sets for revealing pervasive yet subtle climatic effects, but also caution against expectations derived from exemplar species or single locations in the study of biotic-abiotic interactions.

Key words: biotic-abiotic interactions; butterflies; climate change; El Nino Southern Oscillation (ENSO); elevational gradient; generalized linear mixed model (GLMM); migratory taxa.

Introduction

Large-scale climatic phenomena, such as the El Niño Southern Oscillation (ENSO) and North Atlantic Oscillation (NAO), influence weather patterns around the world and provide an opportunity to evaluate the effects of climatic variation on natural populations (Holmgren et al. 2001, Jaksic 2001, Stenseth et al. 2003, Hallett et al. 2004, Halkka et al. 2006, Roland and Matter 2013). Such large-scale climatic phenomena are of particular interest because they have the potential to homogenize or synchronize biotic patterns of phenology or population abundance across large areas (Post and Forchhammer 2002, Stenseth et al. 2003, Hallett et al. 2004, Halkka et al. 2006). Given that some climate change models predict an increase in the frequency and intensity of these large-scale climatic cycles, the study of heterogeneity in population response is of applied and basic interest because it is important to know if observations can be generalized among species, sites or time periods. This is particularly important when making predictions about long term effects of global climate change on biotic communities (Parmesan and Yohe 2003, Latif and Keenlyside 2009, Blois et al. 2013, Cai et al. 2014, Nice et al. 2014, Srygley et al. 2014).

Previous studies suggest a strong association between insect populations and ENSO. For example, the abundance of a migratory sulfur butterfly (Pieridae) in Panama and a migratory brush-footed butterfly (Nymphalidae) in the United States were closely coupled to ENSO-derived sea-surface temperature anomalies (SSTA; Vandenbosch 2003, Srygley et al. 2010, 2014). Both authors proposed that these relationships were largely due to a tight association between SSTA, precipitation, and host plant productivity. However, these studies were limited to a few species or a single location and it remains to be seen how the effects of ENSO may vary with taxa or habitat. When considering a species rich insect assemblage that exists across a diverse range of habitats, we expect significant variability in the strength of climatic-biotic associations among species and sites (as documented among species at a single one of our study sites by Nice et al. [2014]).

In this study, we investigated the relationship between ENSO-derived SSTA and the abundance of 28 co-
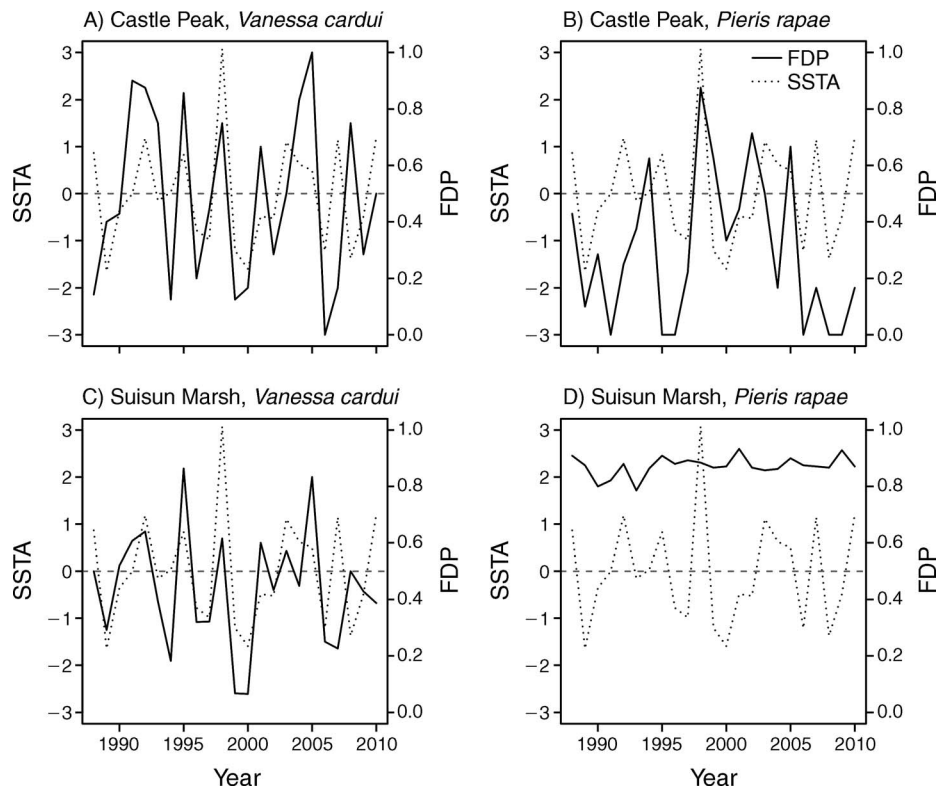
FIG. 1. A time series of the fraction of day positives (FDP, solid lines, right-hand y-axes) and ENSO-derived sea-surface temperature anomaly (SSTA, dashed lines, left-hand y-axes) from 1988–2010 at two sites and for two species used in this analysis. Castle Peak (CP) and Suisun Marsh (SM) were chosen to compare the highest (CP) and lowest (SM) elevation sites in this study.

occurring butterfly species along an elevational gradient (0–2750 m) in the Sierra Nevada Mountains of California in the western United States. ENSO has been shown to influence regional weather patterns in California; in particular, strong ENSO events commonly result in more precipitation across the region (Shang et al. 2011). We wanted to understand if the relationship between butterfly abundance and the global climate cycle, ENSO, is detectable across a diverse assemblage of species and sites, and if so, identify how its influence varies among species and sites along an elevational gradient (see Fig. 1). Using 23 years (1988–2010) of a long-term butterfly monitoring data set we addressed the following questions: (1) Is there a detectable, regional effect of a global climate cycle (ENSO) on butterfly populations across all study sites and species? (2) To what extent does the response to a global climate cycle (ENSO) vary along the elevational gradient and between species? (3) Are ENSO driven patterns across sites different depending on the species (i.e., is there a species by site interaction)? Ultimately, the goal of this study was to explore taxonomic and spatial variability in responses to a large-scale climate pattern, ENSO, using a species-rich butterfly assemblage across a variety of habitats.

MATERIALS AND METHODS

Butterfly data

One of us (A. M. Shapiro) has been monitoring butterflies in California since 1972 by collecting presence/absence data on a biweekly basis for all butterflies at 10 sites across Northern California, including the western slope of the Sierra Nevada Mountains (for a total elevation gain across sites of 0–2750 m). Sites were originally chosen to maximize habitat diversity, butterfly diversity, and proximity to local weather stations (Appendix A: Table A1). Sampling at all sites followed the Pollard walk method, with a fixed route being walked and the presence of all butterfly species noted. The analyses reported here include data collected between 1988 and 2010, and a subset of species that were observed at all 10 sites at least once during the 23 years, which includes 28 species from five butterfly families (Table A2). Butterfly populations were also identified as being resident or non-resident; where a butterfly population is considered a resident if it maintains a breeding population year around at a particular site. The number of observed presences over the 23-year monitoring period for each species at each site is shown in Table A3.

Table 1. Guiding questions and general structures of the four models used in analyses.

Model	Fixed effects	Random effects
1) Are effects of ENSO on the abundance of butterflies detectable across all sites and species?	SSTA + $N_{(t-1)}$ + Precip + MaxT + MinT	$\gamma_{jk}^{(species)} + \gamma_{k}^{(site)}$
2) Do the effects of ENSO on the abundance of butterflies vary among sites along an elevational gradient in California?	(SSTA × Site) + $N_{(t-1)}$ + Precip + MaxT + MinT	$\gamma_{jk}^{(species)}$
3) Do the effects of ENSO on the abundance of butterflies vary among species?	(SSTA × Species) + $N_{(t-1)}$ + Precip + MaxT + MinT	$\gamma_{k}^{(site)}$
4) Are the effects of ENSO on the abundance of butterflies site and species specific?	(SSTA × Site × Species) + $N_{(t-1)}$ + Precip + MaxT + MinT	none

Notes: The notation for random effects follows Hebblewhite and Merrill (2008). The random-effects model structures are $\gamma_{jk}^{(species)}$, random intercept for effect of species; $\gamma_{k}^{(site)}$, random intercept for effect of site, where each butterfly species is represented by j, and each site is represented by k. Other variables are $N_{(t-1)}$, previous year's FDP (the fraction of day positives, i.e., the number of days with positive sightings, weighted by the total number of times that a site was visited during a year); Precip, total monthly precipitation; MaxT, maximum monthly temperature; MinT, minimum monthly temperature; and SSTA, ENSO-derived sea-surface temperature anomaly. Detailed explanations of the variables used in each analysis are provided in *Materials and Methods*.

Local weather data

Monthly values of total precipitation, average maximum temperature, and average minimum temperature were collected from weather stations near each site for years matching the butterfly data (Table A1; also see Forister et al. 2010: Fig. 1 for a site map). Gates Canyon contained several missing monthly data points, so probabilistic principle coordinates analysis (PPCA), in the R package pcaMethods (Stacklies et al. 2007), was utilized to interpolate missing values (Table A1). This method uses an expectation-maximization (EM) approach for PCA with a probabilistic model to calculate the likelihood of a reconstructed value (Tipping and Bishop 1999, Stacklies et al. 2007). Three weather stations (Castle Peak, Rancho Cordova, and Lang Crossing) contained missing values that exceeded 10% of the total data for those stations, so PRISM weather data were used as a replacement (Table A1; data *available online*).[1] The acquired PRISM data were compared to a subset of the local weather station data to evaluate accuracy, and Pearson correlation coefficients between PRISM and available local weather data exceeded 95% in all cases. Yearly averages of total monthly precipitation (Precip), maximum monthly temperature (MaxT), and minimum monthly temperature (MinT) were used in the analyses presented here. The annual time frame corresponds to the precipitation cycle (the water year) that is common in mediterranean climates, which begins in September of the previous year and ends with the following August (e.g., 1988 = September 1987 through August 1988 [Forister et al. 2010]). All weather data were z-standardized prior to analyses. These data were also used to examine relationships between ENSO-derived SSTA and local weather across the elevational gradient.

El Niño Southern Oscillation (ENSO) data

As an indicator of ENSO, we used the sea-surface temperature anomaly (SSTA) from 1988–2010 in the Niño 3.4 region published by the Climate Prediction Center of the National Oceanographic and Atmospheric Administration (data *available online*).[2] The Niño 3.4 SSTA is defined as a departure from the long-term SST mean in the Niño 3.4 region of the eastern tropical Pacific Ocean. According to the Climate Prediction Center (NOAA), sea-surface temperatures in the Niño 3.4 region of the Pacific Ocean have been found to be effective in characterizing ENSO patterns (Srygley et al. 2010). They capture sea surface temperatures near the equator, but are also indicative of temperatures along the coast (Vandenbosch 2003). The mean SSTA of December and January from the current water year were used in analyses; these two months were chosen because they correspond to the peak of ENSO (Vandenbosch 2003).

GLMM and generalized linear model statistical analyses

The fraction of day positives (FDP; i.e., the number of days with positive sightings, weighted by the total number of times that a site was visited during a year) served as our response variable and a proxy for butterfly abundance (Casner et al. 2014) in generalized linear mixed models (GLMM) and generalized linear models (summarized in Table 1). Previous year's FDP ($N_{(t-1)}$) was also included as a covariate in all models. GLMMs were utilized to account for random variation among replicate units (sites and species), which might influence population abundance, and to identify robust relationships with ENSO-derived SSTA across all elevations and species (Pfister and Stevens 2003, Hebblewhite and Merrill 2008, Bolker et al. 2009). A logit link function

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[1] http://www.prism.oregonstate.edu/

[2] http://www.cpc.ncep.noaa.gov/data/indices

specifying a binomial error distribution was used in all models and all GLMM results were fit by Laplace approximation. Prior to building each model, correlations among the variables were investigated (Table A4).

To investigate differences in the strength and variance of butterfly responses to SSTA and local weather, odds ratios (OR) and standard errors (SE) were compared within each model (odds ratios were converted from log odds ratios generated by the models). Models reported here do not include interactions among variables because preliminary investigations during model development revealed that main effects did not differ significantly when interactions were included, but biological interpretation was considerably more difficult. Additionally, our goal was to compare the strength and variance of responses to SSTA and local weather, which was not facilitated by the inclusion of interactions among climatic factors in the models. A type III Wald χ^2 analysis of deviance identified significant variables and interactions within each model (Fox et al. 2014). We quantified the coefficient of determination (pseudo-R^2) for GLMM using methods developed by Nakagawa and Schielzeth (2013). All statistical analyses were conducted in R (version 3.1.1) using the packages lme4 for mixed-effects logistic regressions, car for analyses of deviance, and pscl for generalize linear model pseudo-R^2 calculations. (Bates et al. 2014, Fox et al. 2014, R Core Team 2014, Jackman et al. 2015).

Path analysis

Considering the potential complexity of regional and local weather effects on our focal species, path analysis was utilized to investigate specific mechanistic hypotheses focused on direct and indirect associations between butterfly populations, ENSO-derived SSTA, and local weather. In particular, we wanted to test hypotheses that the effects of SSTA detected in linear models described above could be explained solely through the influence of the regional climate cycle on local weather, or if effects of SSTA on butterflies might be detectable independent of effects mediated through local weather. Any SSTA effects beyond the influence on local weather could be strongest for species with wide-ranging populations or migratory habits, and the regional climatic index of SSTA might be the most useful climatic predictor for those species. The endogenous variable for all models was the number of positive sightings, and models included the number of visits per year as a covariate to account for sampling effort. All variables from the previous models were used in these analyses, with year as an additional variable to account for trends in butterfly populations not explained by weather. Data from all sites and species were used to generate a full path model, then the same path model was performed for each individual species and each individual site to examine how the model support (χ^2) and path coefficients change depending on the species or site. Direct and total indirect effects of SSTA on butterfly abundance were estimated for all species and sites to address hypotheses that SSTA influences butterfly abundance both directly and indirectly via local weather. Path analysis was performed with PROC CALIS in SAS 9.4 (SAS Institute 2013).

RESULTS

Model 1: The effect of ENSO is detectable across all butterflies and sites

Our analysis contained 6440 observations that spanned 23 (1988–2010) years, and included 28 species across 10 sites (0–2750 m). All variables included in the model significantly influenced butterfly abundance in Northern California (Fig. 2, Appendix B: Fig. B1 and Table A5). We detected a positive, regional effect of ENSO-derived SSTA on the butterfly populations (Fig. 2; also supported by the type III χ^2 analysis of deviance, Table 2, Table A5). When all sites and species are considered, the probability of obtaining additional positive sightings per year increased on average by 3% with each degree increase in the SSTA. Across all sites, resident and non-resident populations exhibited dissimilar relationships with ENSO-derived SSTA (Fig. 2, Tables A6 and A7). Based on the odds ratios, the probability of obtaining an additional positive sighting for non-resident taxa increased on average by 6% with each degree increase in SSTA, while resident taxa revealed only a 2% increase. Differences between mountain and valley sites were less substantial (Tables A8 and A9), but valley sites (OR = 1.12, 95% CI 1.102, 1.138) exhibited a stronger and less variable response to SSTA than mountain sites (OR = 1.07, 95% CI 1.047, 1.093).

It has been recognized that SSTA and precipitation are strongly correlated in California, therefore, butterfly associations with precipitation and SSTA were examined to determine if the observed relationships between SSTA and butterfly abundance were comparable to those with precipitation (Fig. 2). Unlike SSTA, precipitation displayed a negative relationship with butterfly abundances for all data sets except the non-residents. Besides maximum temperature, SSTA was the only variable that significantly influenced butterfly populations across all five data sets analyzed and it was a consistent, positive effect (Fig. 2, Fig. B1; results of type III χ^2 analysis of deviance for each of the four separate analyses are reported in Tables A6–A9).

Model 2: The effects of ENSO on butterfly abundance differ between elevations

Butterfly responses to ENSO differed significantly between sites (SSTA by site interaction; Table 2, Table A10). Increased SSTA had a positive effect on butterfly abundance at all ten elevations (Fig. 2), and all effects were significant except the easternmost site, Sierra Valley. Castle Peak, the highest elevation site, exhibited the strongest positive effect of ENSO on butterfly abundance. Linear regressions revealed that odds ratios
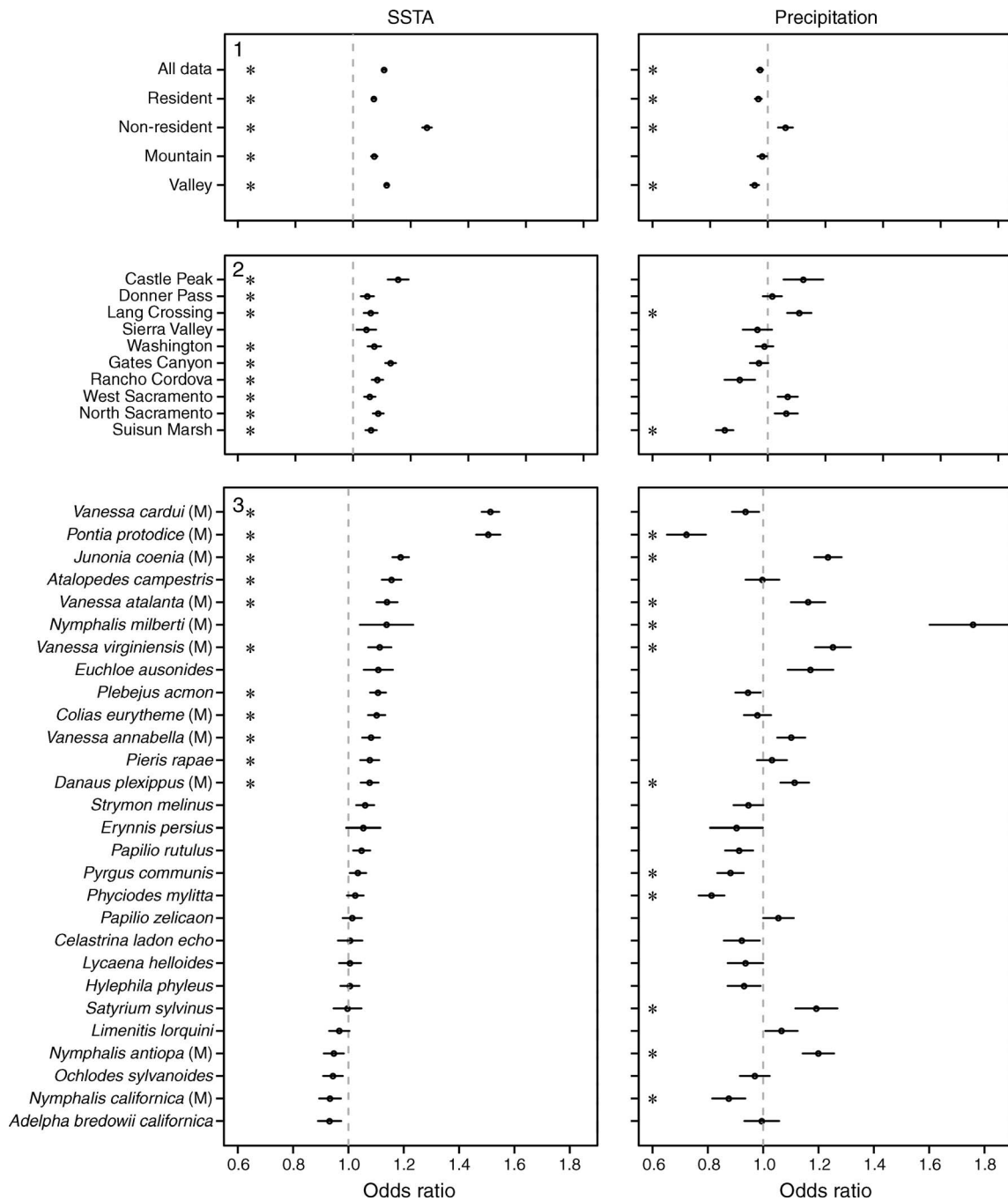
FIG. 2.   Odds ratios and standard errors for SSTA and precipitation variables included in Models 1–3 from Table 1 (panels 1–3 correspond to Models 1–3). Numbers represent the results from each corresponding model. Odds ratios >1 signify an increase in the probability of attaining an additional positive sighting with each unit increase in SSTA and *z*-standardized annual precipitation. A significant effect on the abundance of butterflies is indicated with an asterisk (* *P* < 0.05). (1) Each analysis contained identical fixed and random effects, but were performed with different subsets of the data. All data represents the outcomes from the entire data set (*n* = 6440). The resident analysis contained 4646 observations, while non-resident data contained 1794 observations. Mountain and valley analyses had the same number of observations (*n* = 3220). (2) Results for each site along the elevational gradient. Sites on the *y*-axis are oriented from lowest (Suisun Marsh) to highest (Castle Peak) in elevation. (3) To more easily compare how species responses to SSTA differ from annual precipitation, species in both figures are ordered from highest to lowest SSTA odds ratio. Species marked with "(M)" represent migratory species (i.e., long-distance and elevational). Several other species (e.g., *Pieris rapae* and *Strymon melinus*) also display some degree of seasonal elevational migration, but as individuals and not en masse. Error bars show SE.

TABLE 2. Results from analyses of deviance for each model from Table 1.

Model	Random effects	χ^2	df	$Pr(>\chi^2)$	R^2
1) SSTA	$\gamma_{jk}^{(species)} + \gamma_k^{(site)}$	237.57	1	<0.0001	0.24
2) SSTA $\times$ Site	$\gamma_{jk}^{(species)}$	33.79	9	<0.0001	0.25
3) SSTA $\times$ Species	$\gamma_k^{(site)}$	627.15	27	<0.0001	0.32
4) SSTA $\times$ Species $\times$ Site	none	268.4	243	0.1259	0.62

Notes: Each analysis of deviance was performed in the R package car (Fox et al. 2014). All analyses of deviance are type III. The models correspond to Table 1 and the specific hypothesis that were being tested. Statistics χ^2 and $Pr(>\chi^2)$ represent only the variable or interaction of interest and not the entire model. Conditional R^2 for the first three models (GLMM) were calculated using the methods from Nakagawa and Schielzeth (2013). McFadden's pseudo-R^2 was used for Model 4 from the pscl package in R (Jackman et al. 2015) .

associated with ENSO-derived SSTA did not significantly increase with elevation (slope $\beta = 7.93 \times 10^{-6} \pm 1.21 \times 10^{-5}$ [mean $\pm$ SE], $P = 0.531$). However, variance increased significantly with elevation ($\beta = 4.792 \times 10^{-6} \pm 1.388 \times 10^{-6}$, $P = 0.009$), which indicates that butterfly populations responded more variably to ENSO at higher elevations. Responses to local weather variables, including precipitation, were more erratic across the elevational gradient, and unlike SSTA, no single, local weather variable displayed a consistently positive or negative response across the entire gradient (Fig. 2, Fig. B1).

Model 3: The effects of ENSO on butterfly abundance varies among species

Responses to ENSO differed significantly between the 28 butterfly species (SSTA by species interaction, Table 2, Table A11). Species displayed considerable variability in both magnitude and variance in their response to ENSO-derived SSTA (Fig. 2). The abundances of eleven species increased significantly in response to increased SSTA, while significantly negative responses were not detected for any species. Approximately 10 of the 28 species showed little or no relationship to ENSO across all ten sites and only three species displayed a negative relationship to increased ENSO-derived SSTA. *Vanessa cardui* (Nymphalidae) exhibited the strongest, positive response to ENSO cycles, which is consistent with results reported by Vandenbosch (2003) for the same species. The abundance of *Adelpha bredowii californica* (Nymphalidae) revealed the most negative relationship to increases in ENSO-derived SSTA. The positive, but insignificant associations of the nymphalid, *Nymphalis milbertii* and the pierid, *Euchloe ausonides* might be attributed to low abundances across several sites. Species that displayed significant relationships with SSTA did not match with those that responded significantly to increased precipitation. One of the species most influenced by increases in SSTA, *Pontia protodice*, displayed a strong, negative relationship to increased precipitation across the gradient. This suggests that the different climatic indices (local weather and SSTA) contain different information with respect to

understanding butterfly populations. Butterfly relationships with maximum and minimum temperature were also generally dissimilar from SSTA (Fig. B1).

Model 4: Responses to ENSO are typically not site and species-specific

The SSTA by species by site interaction was not a significant predictor of butterfly abundance (Table 2, Table A12). These results indicate that butterfly populations tend to not respond to ENSO-derived SSTA in a site and species-specific manner. We selected several species that displayed either positive or negative relationships to SSTA in the previous model to understand how site-specific responses to ENSO-derived SSTA relate to the outcome of that model (Fig. 3; site-specific responses to SSTA for the remaining 22 species are displayed in Fig. B2), and some of these species are discussed further here to explore species-specific responses at different sites.

Adelpha bredowii californica displayed the most negative response to SSTA across the elevational gradient, but was not significantly affected at any individual site. Negative relationships to ENSO-derived SSTA were more pronounced at the highest elevations (CP, DP, and LC [see Fig. 1 for site names]), and this species is rarely observed at North Sacramento (NS) and West Sacramento (WS), which may explain the extreme odds ratios and standard errors. Site-specific responses of *Nymphalis californica* indicate that the butterfly's negative relationship to increased SSTA is primarily restricted to the five mountain sites, with the three highest sites (CP, DP, and LC) showing significant negative responses. The significant positive response at WS for *Nymphalis californica* may help explain the lack of relationship in the previous model (across sites) for this species. *Vanessa cardui* and *Junonia coenia* both displayed strong positive associations to ENSO-derived SSTA in the previous model. *Vanessa cardui* exhibited significant positive responses across all ten sites, except the easternmost site (SV), while *Junonia coenia* responded positively to increases in SSTA at three mountain sites and the lowest elevation site (SM).
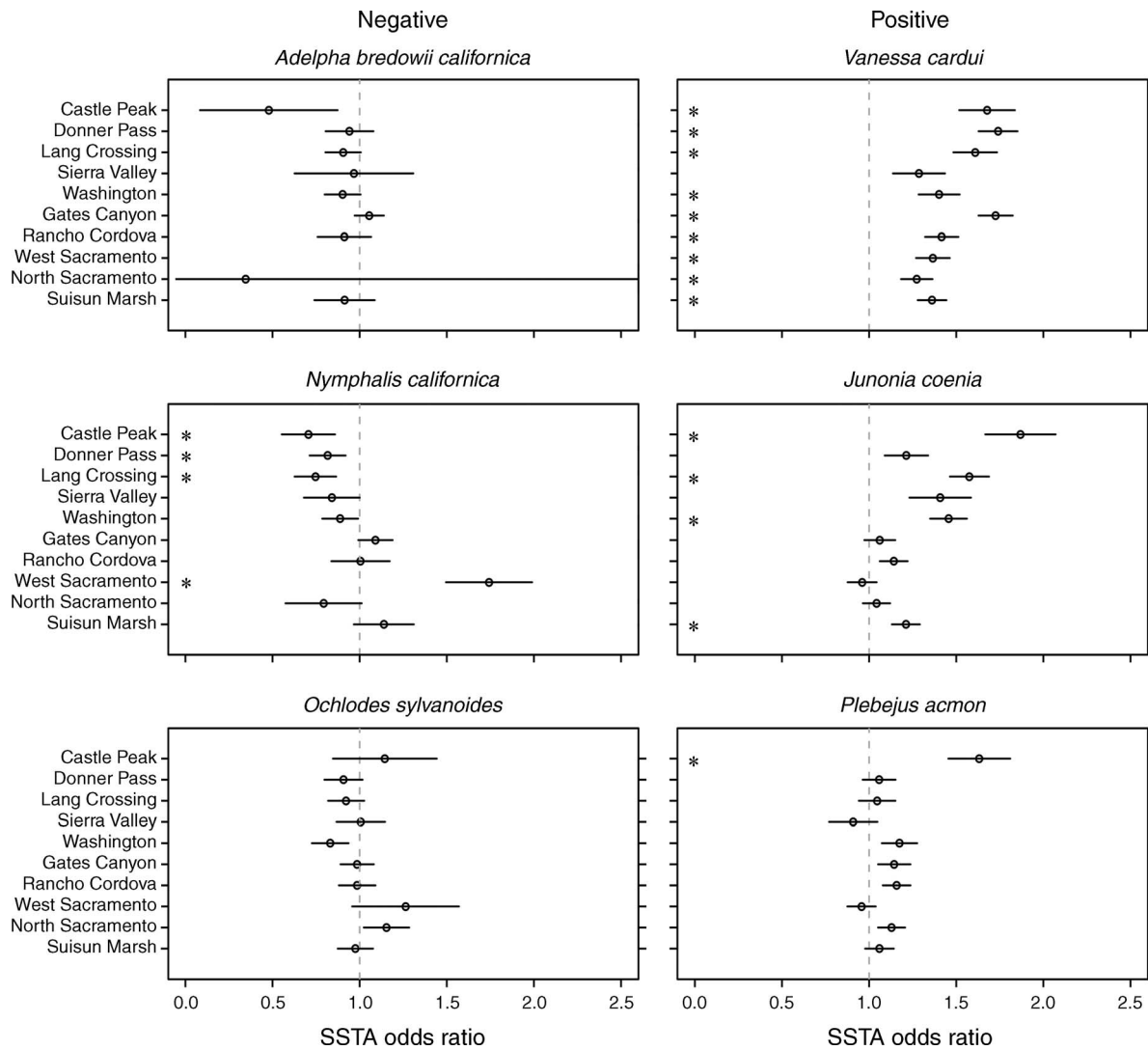
FIG. 3.   Odds ratios and standard errors associated with the SSTA variable from logistic regressions for six of the 28 species. These species were chosen to show site-specific responses of species that displayed either overall negative or positive responses to ENSO-derived SSTA in Model 3 (the other 22 species are shown Appendix B: Fig. B2). Sites on the y-axis are oriented from low to high elevation. Significant effects of SSTA on the abundance of butterflies at each site are indicated with an asterisk (* $P < 0.05$). Error bars show SE.

Path analysis reveals direct and indirect effects of SSTA on butterfly abundance

Path analysis, across all sites and species, revealed both significant direct and indirect effects of SSTA on butterfly abundance (Fig. 4; Table A13). The χ^2 model fit for the full path model was weakly supported (Pr $>$ $\chi_1^2 = 0.07$) and several paths included in the model are not summarized within the path diagram (Fig. 4; all path coefficients and associated standard errors reported in Table A13). The total indirect effects of SSTA on butterfly abundance were negative, while the direct effect was significantly positive. SSTA significantly influences all three local weather variables used in this analysis, but across all sites and species, only maximum temperature has a significant positive effect on butterfly abundance.

The negative path coefficient from Year to No. positive sightings, indicates that butterfly abundances have significantly declined over the last 23 years, consistent with other work on this long-term data (Forister et al. 2010, 2011).

Path analyses for all 28-species were well supported (Pr $> \chi_1^2 = 0.72$). Significant direct effects of SSTA on butterfly abundance were found for seven individual species, and all were positive (Table A14). Species models that included a direct positive path coefficient from SSTA to butterfly abundance were the same species that showed that relationship in our previous analyses. Significant indirect effects of SSTA were revealed in seven species, all but one (i.e., *Adelpha bredowii californica*) being negative. Similar to our

FIG. 4. A path diagram displaying the standardized path coefficients across all sites and species. Lines ending with an arrow represent positive coefficients, while lines ending with a circle represent negative coefficients. The dashed line represents the total indirect effects of SSTA on the abundance of butterflies. To improve coherency of the path diagram, not all paths were included in the figure (see Appendix A: Table A13 for the results for all paths included in the model). Significant path coefficients are indicated with an asterisk (* $P < 0.05$). Abbreviations are Precip, total monthly precipitation; MaxT, maximum monthly temperature; and MinT, minimum monthly temperature.
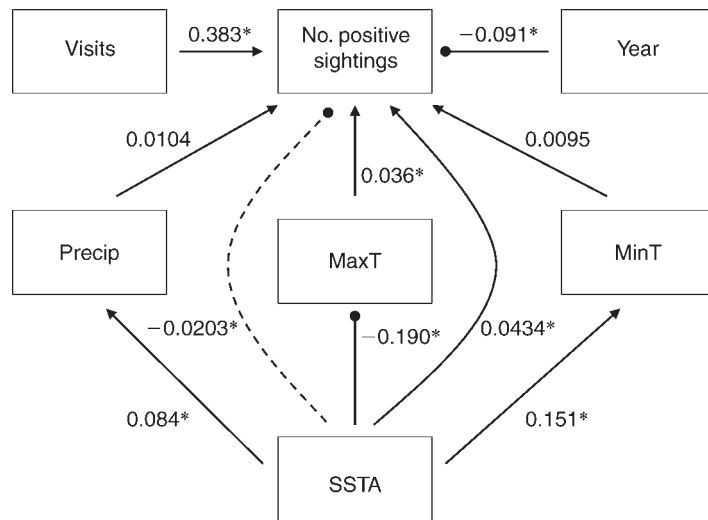
previous models, the abundances of *Vanessa cardui* and *Pontia protodice* were characterized by the most positive direct effect of increases in SSTA. Most path models for individual sites were not well supported (Table A15), which is consistent with our finding that butterfly responses to climate are heterogeneous, even within sites.

DISCUSSION

Previous research has shown that at least some butterfly species fluctuate in association with climatic phenomena that are tied to ENSO indices, and the results presented here support these previous efforts (Vandenbosch 2003, Cleary and Genner 2004, Srygley et al. 2010, 2014). However, previous work has often encompassed small numbers of species or sites, thus the generality of findings to larger spatial scales and for entire communities was unclear. At the regional scale (i.e., across all sites and species), our analysis detected a significant positive association between butterfly populations and ENSO-derived SSTA. Specifically, the probability of obtaining an additional positive sighting per year increased by 3% ± 1.7% with each degree increase in SSTA, and non-resident populations exhibited a stronger response to increased SSTA, compared to residents. This suggests that resident populations, which maintain breeding populations at a site, are less responsive to the global climate phenomenon, ENSO, than non-residents. Across weather variables, Nice et al. (2014) similarly found more variation in the response of non-residents at one of the same study sites (Donner Pass). It is possible that resident and non-resident populations respond to climatic forces that act at different spatial and temporal scales. Non-resident species might be less affected by local weather at individual sites, and thus their dynamics are simply better captured by the regional weather variable (SSTA) that encompasses climatic dynamics at other locations

outside of our study sites (presumably including those where they maintain breeding populations).

Consistent with the possibility of differential impacts of local and regional weather on resident and non-resident species, the path analysis detected both positive (direct) and negative (indirect) effects of SSTA on butterfly abundance. Indirect effects are represented by the total sum of effects of SSTA on butterfly abundance mediated by the local weather variables. The negative indirect effect is driven by the contrasting relationships among SSTA, maximum temperature, and butterfly abundance. Increases in yearly maximum temperature typically result in an increase in butterfly abundance, however increased SSTA characteristically results in lower maximum temperatures for the year (Fig. B3), which has an accompanying negative effect.

It is unclear which particular aspect of ENSO-derived SSTA results in an increase in the abundance of butterflies, but increases in SSTA are often associated with increases in precipitation across Northern California. In arid regions like the Mediterranean climate of California, increased precipitation has been shown to lead to increases in primary productivity, and consumers subsequently respond positively to increased availability of resources (Rosenzweig 1968, Markham and McLain 1977). However, we did not find that local precipitation causes an increase in butterfly abundance when all sites and species are considered (Fig. 2). This suggests that the positive relationship between SSTA and butterfly abundance is complex and involves more than a simple connection between SSTA and precipitation.

While a regional effect of ENSO-derived SSTA on butterfly abundance was detected, we also found that the impact of ENSO varied significantly among elevations and species (Fig. 2). SSTA was the only climatic variable that displayed a positive effect on butterfly abundance across the entire elevational gradient. Local weather variables displayed an unpredictable relationship with butterflies, which is consistent with the idea that large-

scale climate indices offer a more straightforward view of biotic-abiotic relationships of butterflies in Northern California and may predict ecological processes more accurately than local weather (Stenseth et al. 2003, Hallett et al. 2004). The effect of SSTA on butterfly abundance did not significantly strengthen along the elevational gradient, but the associated variance did. The type of precipitation along the elevational gradient may explain the increased variance. Most precipitation in this region of California arrives during the winter, so valley sites receive rain while mountain sites get snow. Thus precipitation could have more variable effects on the mountain populations than valley populations because the flight period and host-plant availability in the mountains depends on the snow depth and timing of snow melt (Boggs and Inouye 2012, Roland and Matter 2013). Years with high snowpack reduce flight periods, while years with low snowpack could reduce plant growth and important nectar and food resources. Conversely, the low elevation sites receive moisture from local precipitation events and additional water from the yearly snowmelt in the mountains, and that combination of rain and runoff from mountain snow could be an inherently less variable process. It will be interesting to learn if this pattern persists in the future, as the elevation of snow levels for winter storms in many mountain ranges in the west is getting higher and more precipitation is falling as rain instead of snow (Diaz et al. 2003, Knowles et al. 2006, Mote 2006, Stoelinga et al. 2010, Svoma 2011).

As with heterogeneity among sites, associations with ENSO parameters differed significantly among the 28 butterfly species. Site was modeled as a random effect, so that we could identify species that show robust relationships to ENSO-derived SSTA across all sites (and generalize to their entire geographic distributions). The abundance of most species displayed positive trends with increased SSTA, but only 11 of those were statistically significant. Of the butterfly species that showed significant positive associations with SSTA across all sites, six are within the family Nymphalidae, which tend to have relatively large wingspans, can travel long distances, and frequently undertake seasonal migrations (across elevations and latitudes). *Vanessa cardui*, *Nymphalis californica*, and *Danaus plexippus* all undergo long distance migrations and reveal strong, but dissimilar relationships with SSTA. Several other species that displayed strong responses to SSTA (e.g., the nymphalids, *Nymphalis californica*, *Nymphalis milberti*, *Vanessa atalanta*, *Vanessa virginiensis*, and the pierid, *Pontia protodice*) undergo elevational migrations and travel up the slope of the Sierra Nevada as the snowline retreats. *Junonia coenia* is a non-resident at sites over 1600 m, but can sometimes reach high densities due to waves of immigrants in the early summer. Both forms of migration appear to have strong influences on the relationship between butterfly abundance and ENSO-derived SSTA in California and support our previous finding that the abundances of non-resident populations are more closely coupled to ENSO-derived SSTA than resident populations (Vandenbosch 2003, Srygley et al. 2010).

Although the SSTA by site by species interaction was not identified as being significant, populations of the same species can respond differently to ENSO parameters at different elevations (Fig. 3, Fig. B2). For example, most of the selected species did not reveal significant relationships with ENSO across their entire elevational range. Instead, significant relationships with ENSO were often restricted to sites located in either the mountains or valleys. With the exception of *Vanessa cardui*, species that showed consistent relationships to SSTA along the elevational gradient were typically those that exhibited little or no overall relationship with ENSO. These results support previous findings that associations with ENSO-derived SSTA are not consistent throughout a species' distribution and that parallel responses among species can occur in similar environments (Vandenbosch 2003). The lack of synchrony with ENSO parameters across all of our sites is potentially due to differences in host plant availability or phenology, natural enemy intensity, or microclimate differences that vary between different habitats, all of which can influence characteristics of population dynamics such as birth, growth, and death rates (Liebhold et al. 2004, 2006, Preisser and Strong 2004). However, we can only raise these possibilities at the current time as avenues for future work.

In summary, the influences of ENSO-derived SSTA on butterfly abundances are regionally detectable; however, these effects vary between elevations and taxa. These results add to a growing literature on the impacts of climate and weather on butterfly populations, and understanding these responses will be important for future predictions on the effects of climate change on natural ecosystems. Some current models predict that ENSO events will become more frequent and more intense and that local weather patterns may be shifting as a result (Latif and Keenlyside 2009, Cai et al. 2014, Srygley et al. 2014). Furthermore, as global levels of SSTA are predicted to increase, these results suggest that migratory butterfly species will be affected more than others, but that these impacts are likely to vary across the landscape. The fact that most populations investigated did not show synchronous responses to ENSO-derived SSTA across the elevational gradient raises the possibility that the extreme habitat heterogeneity provided by the elevational gradient in the Sierra Nevada may increase persistence of lepidopteran species during climate change (Oliver et al. 2010). However, given the variability of response reported here, our results should ultimately raise a note of caution in extrapolating biotic-abiotic relations from studies conducted with single species or over limited spatial extent (Garcia et al. 2014).

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SUPPLEMENTAL MATERIAL

Ecological Archives

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