A hierarchical perspective on the diversity of butterfly species' responses to weather in the Sierra Nevada Mountains

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Abstract. An important and largely unaddressed issue in studies of biotic–abiotic relationships is the extent to which closely related species, or species living in similar habitats, have similar responses to weather. We addressed this by applying a hierarchical, Bayesian analytical framework to a long-term data set for butterflies which allowed us to simultaneously investigate responses of the entire fauna and individual species. A small number of variables had community-level effects. In particular, higher total annual snow depth had a positive effect on butterfly occurrences, while spring minimum temperature and El Niño-Southern Oscillation (ENSO) sea-surface variables for April–May had negative standardized coefficients. Our most important finding was that variables with large impacts at the community-level did not necessarily have a consistent response across all species. Species-level responses were much more similar to each other for snow depth compared to the other variables with strong community effects. This variation in species-level responses to weather variables raises important complications for the prediction of biotic responses to shifting climatic conditions. In addition, we found that clear associations with weather can be detected when considering ecologically delimited subsets of the community. For example, resident species and non-ruderal species had a much more unified response to weather variables compared to non-resident species and ruderal species, which suggests local adaptation to climate. These results highlight the complexity of biotic–abiotic interactions and confront that complexity with methodological advances that allow ecologists to understand communities and shifting climates while simultaneously revealing species-specific variation in response to climate.

Key words: *Bayesian hierarchical model; butterfly fauna; climate change; Donner Pass, California; ENSO; long-term data; monitoring; weather.*

INTRODUCTION

The study of organisms interacting with their environments is central to our understanding of the natural world. Ecologists have sought to link variation in weather with temporal variation in densities of plants and animals (Andrewartha and Birch 1954, Roy and Sparks 2000, Serreze et al. 2000, Coulson et al. 2001, Stenseth et al. 2002, Thomas et al. 2004, Dennis and Sparks 2007). The goal of understanding the influence of weather on organisms has gained renewed importance as long-term changes in the climate have become apparent. In some cases, general hypotheses have been derived from these data sets that transcend individual species and communities (Parmesan and Yohe 2003, Beaumont et al. 2007, Grosbois et al. 2008). For example, high-

latitude and upper-elevational range limits are advancing with warming temperatures (Pounds et al. 1999, Root et al. 2003, Walther et al. 2005, Wilson et al. 2005, Parmesan 2006, Lenoir et al. 2008, Poyry et al. 2009, Forister et al. 2010). The search for generalities linking species to climate raises an important issue regarding the consistency of species-specific responses. When considering closely related species or species living in similar habitats, to what extent should we expect a common suite of responses to fluctuations in weather? The answer to that question is perhaps readily apparent in the extremes: Droughts and other extreme examples of natural climatic variation can have lethal effects across species (Shapiro 1979, Ehrlich et al. 1980, Easterling et al. 2000, Meehl et al. 2000). When considering more subtle or long-term variations in weather, we have to conclude that the question of consistency of response across taxa is understudied. Long-term data sets are becoming available that provide opportunities for addressing this issue (Magurran et al. 2010). In addition, analytical advances, such as hierarchical models (Dixon

and Ellison 1996, Ellison 2004, Kery 2010) offer new perspectives on the diversity of biotic responses to climate (Pearson et al. 2004, Amano et al. 2010, Lahoz-Monfort et al. 2013).

The use of hierarchical models addresses an important problem in community ecology: Our most widely used statistical tools have been well suited for either analyses of single species (e.g., fluctuations in abundance) or analyses of whole communities (e.g., variation in richness or eveness), but not both simultaneously. Analyses of single species produce richly detailed results that can be difficult to generalize (e.g., Forister et al. 2011a), while analyses of community richness or diversity sacrifice biological detail in exchange for results that are easier to interpret and extrapolate (Currie et al. 2004). Hierarchical models can estimate effects at the community and species level simultaneously, and provide an opportunity to study full assemblages of species without sacrificing the biological detail of species-specific dynamics (Royle and Dorazio 2008, Mutshinda et al. 2011, Diez et al. 2012). Bayesian implementations of hierarchical models have been particularly powerful for field data and ecological applications because of their ability to handle heterogenous and unbalanced data (Ellison 2004, Gelman et al. 2004, McMahon and Diez 2007, Fordyce et al. 2011).

Here we took advantage of a long-term, observational data set coupled with a hierarchical Bayesian framework for generalized linear models. The data consist of the presence and absence of 106 butterfly species recorded every other week during the butterfly season for 38 years at a single study site, Donner Pass, in the Sierra Nevada Mountains of northern California. Donner was chosen as the focal point for the current study because (1) the high species richness at the site provides an interesting opportunity to explore the diversity of biotic responses to fluctuations in climate, and (2) the relatively short, high-elevation flight season for most species also means that there is great variation among taxa in the number of days present within years, and also the number of years a species is present across the whole data set. This kind of variation in sample size among taxa is something that hierarchical Bayesian models deal with efficiently.

We used the 38 years of butterfly observations at Donner to ask the following questions. First, are there weather variables that have detectable or strong effects at the community level? Second, do species respond in similar ways to patterns of interannual variation in weather? Given the diversity of species studied, an expectation of consistency of response to weather would be naive (Sparks et al. 2006). Instead, we designed analyses to ask which weather variables are associated with a more or less consistent response across species. For example, spring precipitation could affect host and nectar resources and have a positive effect across a majority of species, while another factor such as annual variation in minimum temperature would have a more varied effect depending on the phenologies and life

histories of particular species. Similarly, regional weather variables could have a stronger effect on migratory species relative to the effect of more localized temperature and precipitation. Addressing these issues is important for the study of biotic responses to climate change because climate is complex and multifaceted and ecologists need to know which elements of the climate can be most usefully tracked and modeled. Consequently, and to further refine our understanding of consistency of response to weather, we asked if differences among species in their responses to weather can be understood in the context of several aspects of butterfly biology and ecology.

MATERIALS AND METHODS

Data collection

Data on the presence and absence of butterflies at Donner Pass were collected from site visits every two weeks as part of a long-term monitoring project. The Donner Pass site, at 2000–2200 m elevation, is a high-montane site that includes areas of subalpine vegetation. The Donner Pass butterfly fauna includes a large number of butterfly species and is one of the richest faunas in the United States (Shapiro 2011). Further details of data collection have been described elsewhere (Forister and Shapiro 2003, Thorne et al. 2006, Forister et al. 2010, 2011b, Shapiro 2011). We used the data collected from 1973 to 2010, a total of 38 years. The presence of a particular species during a site visit was recorded and we used the number of "day positives" as our response variable (i.e., the number of site visits for which a particular species was observed). The list of 119 species recorded at Donner Pass from 1973 to 2010 was trimmed by eliminating species that were present in only one or two years. Thus, the data set we considered here included 106 total species (Appendix B: Table B1). These species were monitored during 601 site visits (mean = 15.8 site visits/year), and the data consist of 11 711 day positive records for these 106 species.

Climatological covariates

We examined the response of individual species and the community as a whole to variation in climate using data for 13 variables (Table 1). These weather variables included measures of precipitation, maximum and minimum temperatures, total annual snowfall, and monthly sea-surface temperatures. Quarterly precipitation and temperature records were obtained from the Central Sierra Snow Laboratory (049998) and represent the meteorological "water year" from October of the preceding year to September of the current year. Thus, these climate variables were chosen to include climate factors likely to influence the butterfly flight season for each year. Because previous studies have clearly indicated that snow has a direct impact on insects (Boggs and Inouye 2012), total annual snowfall (snow depth) data were obtained from the Central Sierra Snow Laboratory, which is located within the Donner Pass

TABLE L.   Results of hierarchical analyses of single weather variables (plus year).

Variable	β coefficient (95% CI)	ESS	τ coefficient (95% CI)	ESS	ΔDIC
Winter minT	0.044 (−0.053 to 0.148)	3 515.4	47.3 (10.2–1130.8)	2065.1	11 813
Snow depth	**0.026 (0.002 to 0.050)**	3 665.5	672.8 (196.6–2757.6)	1308.0	11 798
Winter precipitation	0.023 (−0.006 to 0.051)	5 137.1	314.2 (103.4–1780)	1075.0	11 782
Spring precipitation	0.010 (−0.024 to 0.044)	3 038.9	431.2 (111.5–2215.2)	1056.4	11 798
ENSO May–Jun	−0.024 (−0.048 to 0.002)	4 335.5	553.5 (170.0–2479.7)	1325.3	11 804
ENSO Dec–Jan	−0.024 (−0.055 to 0.009)	19 565.2	93.1 (53.6–178.6)	7522.7	11 811
ENSO Mar–Apr	−0.025 (−0.055 to 0.006)	16 272.6	110.8 (61.6–239.2)	4471.1	11 879
ENSO Jan–Feb	−0.025 (−0.058 to 0.007)	20 317.9	89.50 (51.90–171.9)	7457.1	11 848
ENSO Feb–Mar	−0.028 (−0.060 to 0.003)	18 981	96.12 (55.16–187.8)	5983.2	11 839
ENSO Apr–May	**−0.040 (−0.070 to −0.012)**	12 050.8	161.8 (77.70–480.7)	2034.8	11 811
Spring maxT	−0.044 (−0.121 to 0.036)	1 337.2	163.2 (23.9–1723.3)	670.2	11 784
Winter maxT	−0.103 (−0.225 to 0.012)	1 388.3	178.9 (19.10–1844)	2590.2	11 780
Spring minT	**−0.112 (−0.187 to −0.037)**	860.3	298.9 (40.02–2150)	708.1	11 774

Notes: Variables are listed by magnitude and sign of their estimated standardized regression coefficient (β). Point estimates for β and τ are medians of the posterior distributions. Values of β whose 95% equal-tailed credible interval (95% CI) does not include zero are indicated in boldface type. Effective sample sizes (ESS) are reported for β and τ coefficients. The ΔDIC scores compare the fit of the models where all species were constrained to have the same β (constrained model) to models in which species were allowed to have unique β's (unconstrained models) (i.e., ΔDIC was calculated as DIC$_{constrained}$ − DIC$_{unconstrained}$). Abbreviations are: ENSO, El Niño-Southern Oscillation; maxT, maximum temperature; and minT, minimum temperature

study site. 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 online*;[7] Wolter and Timlin 2011). These covariates were included because of clear linkages between sea-surface temperatures and synoptic climate and ecosystem responses in North America (e.g., Mochizuki et al. 2010). The multivariate ENSO index values were averaged across two-month periods (i.e., ENSO January–February; Table 1). Initial exploration of the influence of weather variables indicated that variables associated with winter and spring were most important, while fall and summer variables did not produce strong or interesting patterns (data not shown). Consequently, we focused on 13 variables encompassing winter and spring weather (Table1).

The year in which butterfly data were collected was also included in the models (i.e., a "year" effect) to account for other factors influencing species' occurrences besides the climate covariates described above and to assess trends over time. All covariates were standardized using *z*-transformation. To examine relationships among the weather variables, we calculated correlation coefficients among all the variables and plotted them in R using the *corrplot* package (R Development Core Team 2012). These correlations were used in the interpretation of patterns revealed in analyses of single climate covariates.

Natural history categories

To explore observed differences among species in their responses to weather, we constructed a series of hierarchical models to examine how butterfly natural history characteristics shaped species' responses. Each of these natural history groups was modeled separately. These models grouped species into natural history categories using the data from Shapiro (2011) (Appendix B: Table B1). We examined four aspects of natural history, each with species grouped by categorical predictors: (1) Resident status; species were grouped by whether they maintain year-round breeding populations, at least for some of the 38 years (resident), or do not breed at the site (non-resident). (2) Diapause stage (or overwintering mode); species were grouped by overwintering life stage: egg, larva, pupa, or adult. Two non-diapausing species (*Brephidium exile* and *Leptotes marina*) were omitted from this analysis. (3) Number of generations per year; species were grouped as single, double, or multiple generations per year. The semivoltine *Oeneis chryxus ivallda* was omitted from this analysis. (4) Ruderal status; species were grouped by whether they are associated with disturbed areas (ruderal or "weedy" species) or undisturbed habitats (non-ruderal or "not weedy" species). Ruderal species have a higher dispersal capacity and exhibit less localized population dynamics than non-ruderal species. Assignment to the categories of ruderal and non-ruderal were made prior to the analyses described here (e.g., Forister et al. 2010). These natural history categories were not chosen with the aim of providing a comprehensive investigation. Instead, these categories serve as a tractably short list that is sufficiently varied to shed some light on the mechanisms that might be associated with a diversity of biotic responses to weather. The investigation of the diversity of biotic–abiotic relationships was our primary goal.

Statistical analyses

We asked if species at Donner Pass have diversified responses to a suite of climate variables and if these diversified responses might be explained by features of

[7] http://www.esrl.noaa.gov/psd/enso/mei/table.html

their natural history. We used generalized linear regression models in a Bayesian, hierarchical framework to address these questions. "Day positives" (DP), the number of days during a year that a species was detected, was modeled using the binomial distribution with the number of trials equal to the number of visits to the Donner site for each year. Previous analyses at other transect sites have demonstrated that the fraction of day positives is highly correlated with absolute count abundance, and thus, represents a reasonable metric of the response of species to a variety of variables (Forister et al. 2011*b*, Casner et al. 2013). A generalized linear model with a logit link function that incorporated effects of one or more climate variables and the effect of years was fit to these data using a hierarchical Bayesian approach implemented in the BUGS language (Gilks et al. 1994, Lunn et al. 2000) using JAGS (version 3.2.0; Plummer 2003) and run in R using the *rjags* package (R Development Core Team 2012). These models can be referred to as either logistic or binomial regression models.

Our hierarchical models consisted of species ($n = 106$) nested within the Donner Pass community, or within natural history groups (see previous section). We modeled the response DP_{ij} (day positives for species i for year j) as:

$$DP_{ij} \sim \text{Binomial}(p_{ij}, \text{Visits}_j)$$

where Visits_j is the number of site visits per year j, and p_{ij} is the probability of occurrence for species i in year j (i.e., proportion of site visits for which a species was detected or present). The linear model was connected to the response variable, DP_{ij}, using the inverse logit function:

$$p_{ij} = 1/(1 + \exp(-\alpha_{ij}))$$

where

$$\alpha_{ij} = \mu_{\text{species}_i} + \beta_{1\text{species}_i} \times \text{covariate}_{1_{ij}}$$
$$+ \beta_{2\text{species}_i} \times \text{covariate}_{2_{ij}} + \ldots$$
$$+ \beta_{K\text{species}_i} \times \text{covariate}_{K_{ij}}$$

and K equals the number of covariates included in the model. Species-specific intercepts, μ (the mean logit of probability of occurrence for species i) and β coefficients were modeled hierarchically as:

$$\mu_{K\text{species}_i} \sim \text{Normal}(\mu_\mu, \tau_\mu)$$

$$\beta_{K\text{species}_i} \sim \text{Normal}(\mu_{\beta_K}, \tau_{\beta_K})$$

The species-level coefficients for each covariate were assumed to be drawn from a common Normal distribution with a mean (μ_{β_K}) and precision (τ_{β_K}), which we equated to community-level coefficients. Thus, the "community-level response" is characterized by the mean of the Normal distribution from which the species-level responses are drawn. Similarly, the precision parameter, which is the inverse of the variance, measures the variation among species. A high precision (larger value of τ_β) indicates greater similarity in species' responses to the covariate. We used uninformative hyperpriors for the community-level means and precisions as follows:

$$\mu_\mu \sim \text{Normal}(0, 0.0001)$$

$$\mu_{\beta_K} \sim \text{Normal}(0, 0.0001)$$

$$\tau_\mu \sim \text{Gamma}(0.1, 0.001)$$

$$\tau_{\beta_K} \sim \text{Gamma}(0.1, 0.001)$$

Posterior probabilities for model parameters were estimated using Markov chain Monte Carlo (MCMC) simulations in JAGS (version 3.2.0; Plummer 2003).

Initial analyses examined the effect of each climate covariate separately along with a year effect. These analyses were performed to survey species responses and to identify covariates that exhibited a strong (i.e., positive or negative) community-level response. These analyses assess whether species exhibited similar or diverse responses to each climate variable. For each climate covariate, a second model was analyzed that constrained all species to have the same response (i.e., all species have the same β_K). Deviance information criterion (DIC) scores were calculated for unconstrained and constrained models, and ΔDIC scores were used for model comparison (Spiegelhalter et al. 2002). Thus, we used two approaches to address the question of whether species respond in similar ways to weather patterns, or alternatively, exhibit a diversity of responses: (1) We examined the community-level precision parameters (τ), which directly measure variability in species' responses (with higher values of τ indicating less variation among species); and (2) DIC scores were used to compare the constrained and unconstrained models (i.e., strong evidence in favor of the unconstrained model is indicative of a diversity of responses among species). These two approaches facilitate a thorough examination of the diversity in species' responses. (An example of model specifications in the BUGS language is included in Appendix A). To illustrate species-specific changes in the probability of occurrence (p) over the course of the study, we used the binomial modeling approach described here to estimate p with no climate covariates and plotted these probabilities for the 38 years over which the data were collected.

We also explored a model that included all of the climate variables and accounted for correlations among them. For this analysis, we reduced the dimensionality of the 13 variables using principal components analysis (PCA). We used the scores of the first three principal components (PC; which explained 78% of the variance, see *Results*), plus year in a hierarchical model. This approach allowed us to account for the correlational structure among variables where the PC's constitute orthogonal, linearly uncorrelated variables. As with the models incorporating single covariates, we examined the diversity of species responses with the community-level precision parameter (τ). We also compared the fit of this model with species allowed to vary in their responses (unconstrained model) to the performance of an alternative model with species responses constrained to be identical (constrained model). DIC scores were used for model comparison.

We then asked if differences among species can be attributed to differences in various aspects of their natural history. We fit models using the three covariates with nonzero β coefficients at the community level and three other covariates with large β coefficients (see *Results*) to subsets of species grouped by natural history categories (see *Natural history categories* and Appendix B: Table B1). Each analysis examined the effect of a single covariate plus a year effect. Each group within the natural history categories was analyzed with a hierarchical model that included a group-level mean and precision for the β coefficients. These models were otherwise identical to the unconstrained models for the entire fauna. Our strategy was to model each grouping of species (categorical predictor) within a natural history category separately. We chose to use these simple models, rather than a more complex, multilevel model (i.e., "pooling"; Gelman and Hill 2007), because numbers of species within each grouping were relatively large and this model was computationally more efficient. A multilevel model might be more appropriate when sample sizes within groups or categories are small and there is a real possibility of overfitting the data (Gelman and Hill 2007); however, this was not the case with the Donner data.

For each model and analysis, posterior distributions for all parameters were estimated using MCMC in JAGS. For all models, including single climate covariates plus year (with either all 106 species or species grouped by natural history categories), as well as the multivariate model using three principal components plus year, two MCMC chains with different initial values were used, and each chain included at least 50 000 MCMC samples, with 5000 discarded as burn in. To confirm that the MCMC algorithm sampled the stationary distribution, diagnostic tests were performed for each analysis, including an examination of MCMC chain history, and calculation of effective sample size (ESS) and the Gelman and Rubin convergence diagnostic (Gelman and Rubin 1992, Brooks and Gelman 1998).

All diagnostics were performed in R using the *coda* package (R Development Core Team 2012). Posterior distributions for species-level and community-level parameter estimates and 95% equal-tail credible intervals, as well as DIC scores, were also calculated in R.

RESULTS

Thirteen weather variables were investigated for their potential influence on the population dynamics of 106 species of butterfly. In general, hierarchical models performed well and we were able to estimate regression coefficients for weather affecting individual species and for the entire community with models that achieved reasonable sampling of stationary distributions (Table 1). Examination of the Gelman and Rubin convergence diagnostic and plots of chain histories, and calculation of effective sample sizes, indicated satisfactory performance of all MCMC chains. Analyses were conducted both for individual weather variables and for a multivariate model containing transformed variables in the form of the first three principal components of all 13 variables. The community-level details from analyses with single weather variables are given in Table 1, where variables are ranked from the most positive standardized β coefficients to the most negative.

Coefficients shown in Table 1 are for the community-level response. In other words, Table 1 presents the standardized regression coefficients estimating the effect of particular weather variables on all of the species considered collectively; regression coefficients for individual species are estimated in the same analyses (Appendix C: Tables C1 and C2). Most weather variables have coefficients whose credible intervals overlap zero (Table 1). Three weather variables were identified as important at the community level, specifically: snow depth, spring minimum temperature, and ENSO for April–May. The last two of those variables had negative effects, while snow depth had a positive effect, such that winters with a deeper snow pack were followed by butterfly seasons characterized by higher probability of occurrence, or more days with positive observations across species. Three other variables also had large coefficients, though their credible intervals for the community level overlapped zero: winter minimum temperature, spring maximum temperature, and winter maximum temperature (Table 1).

Year was used as a covariate in all models to account for linear change through time in the butterfly populations that might be causally unrelated to weather variables (see Appendix C: Table C3). We also plotted the probability of occurrence for all species across the 38 years of the study to illustrate these interannual trends (Appendix C: Fig. C2). In general, year had a highly consistent, negative effect in all analyses with a standardized regression coefficient of approximately −0.14 (−0.2 to −0.09; posterior median and 95% credible interval), indicating an overall decline in the probability of detection across species over time. Exploration of
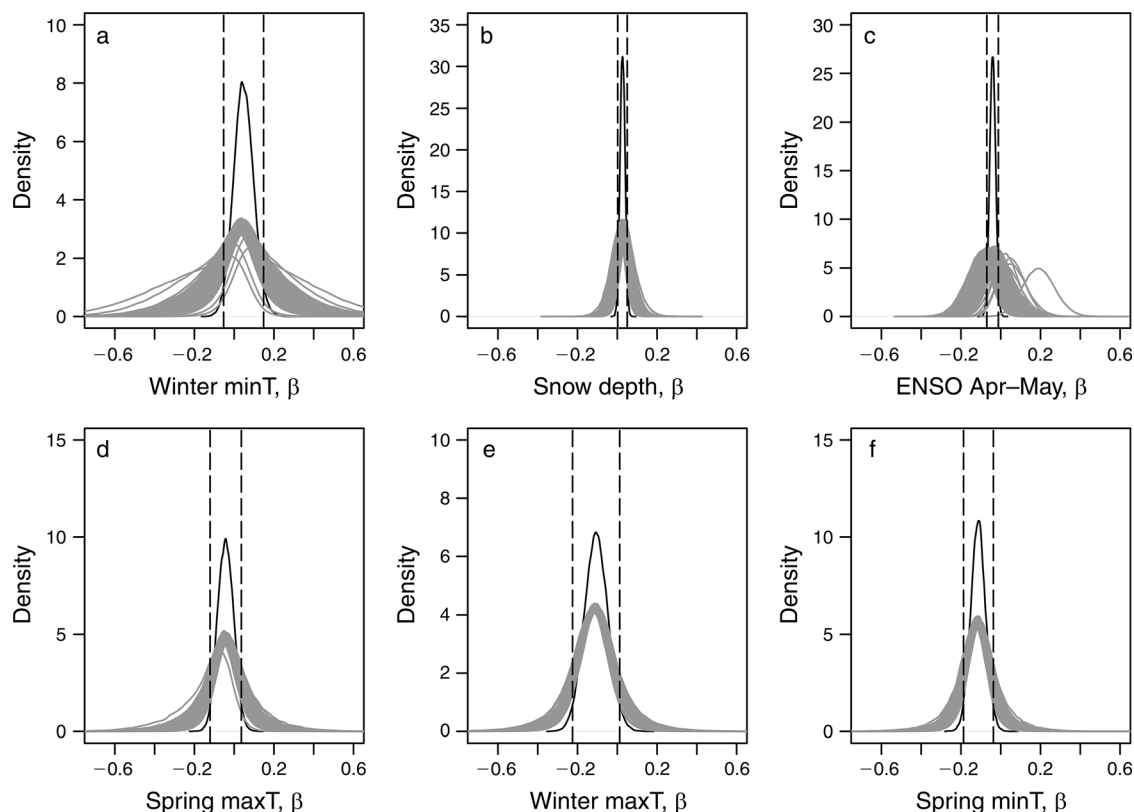
FIG. 1. Posterior densities for estimates of standardized β coefficients. Densities of species-level β's are shown as gray lines. Community-level β's are shown as solid black lines. Boundaries of the 95% equal-tailed credible interval (i.e., a 95% credible interval) for the community-level β are shown as dashed lines. Abbreviations are: ENSO, El Niño-Southern Oscillation; maxT, maximum temperature; and minT, minimum temperature.

curvilinear models with higher order polynomial functions of year produced no evidence of more complicated relationships or trends over time (data not shown). In addition, the very low precision values for year effects in the single variable models supports the notion that species have strong, individualistic responses across years (Fig. 3; Appendix C: Table C3, Fig. C2).

Beyond the estimation of community-level β coefficients, one of the advantages of the hierarchical approach is the ability to ask if the response to a particular predictor variable is better modeled with all species constrained to have similar responses or with an unconstrained, diversity of responses. We conservatively considered ΔDIC scores >10 to indicate clear differences in the fit of models being compared (Spiegelhalter et al. 2002, Fordyce et al. 2011). For all weather variables, the unconstrained models were a better fit to the data (Table 1).

There was extensive variation in the diversity of species responses to the various climate variables. The precision values or τ's (defined as the inverse of the variance in species-level coefficients) in Table 1 summarize this facet of our results, with higher values of τ corresponding to results where species tended to have a

more similar or less diverse response for a given weather variable. Fig. 1a, b also illustrates this variation, with the largest diversity of response to winter minimum temperature, and a relatively constrained response to snow depth (Table 1). It is important to note that the diversity of individual species-level responses is not constrained by the strength of the community-level response. In other words, a community-level response that is different from zero does not necessarily imply a consistency of responses from individual species. Moreover, a simple test of correlation between standardized β coefficients and τ's from Table 1 does not suggest any relationship between diversity of response and strength of community-level response ($r = -0.143$, $P = 0.641$).

Because weather variables have some correlational structure (Appendix C: Fig. C1, Table C6), it is useful to consider the behavior of a model which estimated β coefficients for principal components for all weather variables. Results of the PCA of the 13 weather variables are presented in Table 2. The first three PC axes explained 78.0% of the variance. The multivariate analysis of these three PC axes (plus year), provided a negative and nonzero community-level response for PC2 (Table 3). As with previous analyses, the unconstrained

TABLE 2. Results of principal components (PC) analysis of the 13 weather variables.

Variable	PC1 (38.7%)	PC2 (25.4%)	PC3 (13.9%)
Eigenvalues	5.027	3.306	1.813
Snow depth	0.11600	−0.40916	0.35145
Spring precipitation	0.09295	−0.34382	0.32694
Spring maxT	−0.10938	0.47988	0.01987
Spring minT	−0.01487	0.45374	0.16943
Winter precipitation	0.10239	−0.06071	0.60807
Winter maxT	−0.0622	0.36223	0.11336
Winter minT	0.06151	0.28552	0.53567
ENSO Dec–Jan	0.40427	−0.00281	−0.15627
ENSO Jan–Feb	0.41995	−0.01518	−0.11992
ENSO Feb–Mar	0.42854	0.01240	−0.08652
ENSO Mar–Apr	0.42823	0.09885	−0.10567
ENSO Apr–May	0.40037	0.15972	0.02224
ENSO May–Jun	0.28366	0.16138	0.11401

Notes: Column headings provide the proportion of variance explained for each principal component. Loadings for each of the weather variables are reported in each column.

model was a much better fit to the data (ΔDIC = 11 853). Considering the loadings for PC2 (Table 2), the negative β indicates that years with more precipitation, cooler temperatures, and more negative ENSO patterns (especially from March to June) resulted in more days with observations across species. In general terms, this interpretation of the effects of weather variables from the multivariate analysis parallels the single-variable analyses: Precipitation variables were associated with positive β coefficients, while ENSO and temperature variables, especially spring minimum, spring maximum, and winter maximum temperatures, had negative β coefficients (Table 1). The exception is winter minimum temperatures, with a positive β coefficient (Table 1).

Considering the diversity of responses to weather, our final set of analyses investigated the possibility that some of that diversity might be understood in the light of butterfly natural history. In Fig. 2, species-level variation in response to six weather variables is illustrated with respect to four aspects of natural history: resident status, overwintering mode, number of generations, and ruderal status. There are clear differences among species in different natural history categories for certain weather variables. For example, non-resident species have a much wider range of responses than resident species (Fig. 2). This pattern is also evident in the estimates of precision (τ) for the groups (Tables 4 and 5).

DISCUSSION

The study of abiotic effects on organisms is as old as the science of ecology, and has received renewed interest in the light of changing global climate associated with anthropogenic influence (Burrows et al. 2011, Chen et al. 2011). Early successes in the field of global change biology focused on a few patterns that were recurrent across different groups of organisms in different places, such as shifting spring phenology and poleward range shifts (Sparks and Carey 1995, Parmesan 2006). More recently, researchers have opened up new avenues of complexity in biotic–abiotic interactions by investigating, for example, abiotic influence on trophic interactions which might be disrupted by differential phenological response among interacting species (Yang and Rudolf 2009, Sheldon and Tewksbury 2011). Here, we have focused on a different axis of complexity, addressing the diversity of biotic responses to weather variables among a large suite of butterfly species at a single study site. Using hierarchical, Bayesian models appropriate for complex ecological data, we found considerable variation at Donner Pass in response to weather variables. More important, we found that certain variables were associated with a more unified response across species relative to other variables associated with a greater diversity of response (Fig. 1, Table 1).

In our model comparisons, the unconstrained models were a better fit for the data than models with all species constrained to have the same response, clearly demonstrating variation among species in response to weather. The hierarchical precision parameters (τ's) in the models describe the range of variation among species within the whole community or within natural history categories. For example, variation in species' responses ranged from very similar for the snow depth covariate (which had the highest estimate of precision of all 13 weather variables), to a highly diverse response to winter minimum temperature (which showed the lowest precision among weather variables; Fig. 1a, b, Table 1).

These differences in response to weather variables can be at least partly understood by differences in ecology and natural history. For example, double- and multiple-brooded species tended to have a greater diversity of responses (lower τ) compared to species with a single brood per year (Tables 4 and 5, Fig. 2). Resident species as a whole showed nonzero responses to the three

TABLE 3. Results of hierarchical multivariate model with species allowed to vary in their response to the first three principal component variables and year.

Covariate	β (95% CI)	ESS	τ (95% CI)	ESS
PC1	−0.011 (−0.026 to 0.003)	19 330.0	449.4 (259.3–863.9)	7 458.6
PC2	**−0.017 (−0.032 to −0.003)**	4 692.8	1481.7 (553.7–4099)	2 670.7
PC3	0.012 (−0.010 to 0.034)	7 329.5	395.6 (160.6–1555)	1 739.7
Year	**−0.138 (−0.190 to −0.086)**	24 267.9	21.7 (14.2–33.4)	19 141.5

Notes: Effective sample sizes (ESS) are reported for β and τ coefficients. Values of β whose 95% credible interval (95% CI) does not include zero are indicated in boldface type.
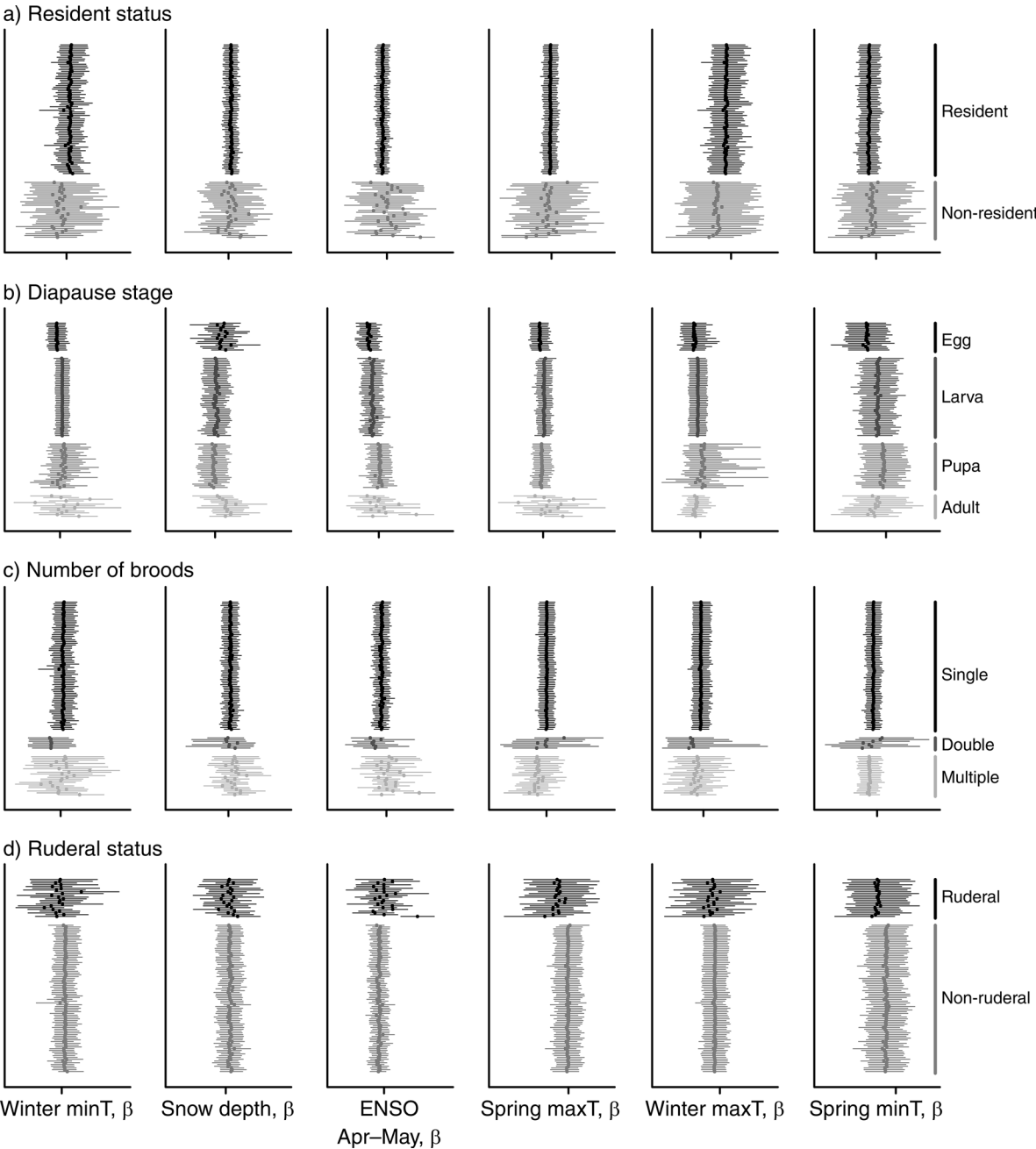
a) Resident status

b) Diapause stage

c) Number of broods

d) Ruderal status

Winter minT, β   Snow depth, β   ENSO Apr–May, β   Spring maxT, β   Winter maxT, β   Spring minT, β

Fig. 2. Median values (points) and 95% credible intervals (lines) for species' responses to four weather variables estimated as standardized β coefficients. Species are grouped by natural history category. Community-level β's and sample sizes are provided in Tables 4 and 5.

weather variables with nonzero community-level coefficients (snow depth, ENSO April–May, and spring minimum temperature). Also, non-resident species have a considerably greater amount of variation in response to weather than do resident species. These results are interesting and perhaps suggestive of local adaptation to climatic conditions (including climatic variability), with the permanent residents at Donner Pass being characterized by a more consistent relationship with weather.

This pattern parallels that observed for ruderal species, which had substantially lower precisions than non-ruderal species. In contrast, the different overwintering modes did not show marked differences with respect to diversity of responses, though they differed in their median response (Tables 4 and 5, Fig. 2).

The idea that certain weather variables are associated with a more or less diverse response from the species at our study site suggests that a consideration of this

diversity could be crucial to understanding the influence of climate on natural communities. Indeed, joint consideration of variability among species (as estimated by τ) and the sign and magnitude of the standardized regression coefficients (as estimated by β) might offer insights. Consider the three weather variables that we found to have a substantial impact at the level of the entire community. We learned that greater snow pack has a positive impact on butterflies with relatively little variation among species, while warmer spring minimum temperatures and greater values for the ENSO index for April–May have negative and much more diverse effects across species. In fact, spring minimum temperatures had the largest effect of all weather variables, with an intermediate precision (τ), while ENSO April–May had a modest and more diverse impact on species.

Greater snow pack might benefit species directly by increasing the probability of overwinter survival (Matter et al. 2011). Alternatively, snow pack might have an indirect, positive effect on host plants and nectar resources (Boggs and Inouye 2012). In the context of long-term trends associated with climate change, the effect of snow pack appears to be a potentially important factor. Snow depth has been observed to be decreasing in the Sierra Nevada in recent decades, particularly at higher elevations, as a consequence of lower snowfall amounts and earlier melting (Johnson et al. 1999, Coats 2010, Kapnick and Hall 2012). In the Donner data analyzed here, there was no relationship between snow depth and year (i.e., no trend over time; Appendix C: Fig. C1, Table C6), but our snow covariate is a coarse measure of snow accumulation over the total winter season and we do not have the temporal resolution to distinguish changes in accumulation vs. increasing spring warming and consequent earlier melting over time. However, winter and spring temperatures, minimums and maximums, are positively correlated with year. While the 38-year record analyzed from this one site is not sufficient for definitive analyses of regional weather patterns, the trends in these climate variables suggest that increasing temperatures and earlier spring melting might have significant consequences for snow depth. Warmer average low (overnight) temperatures in the spring (spring minimum temperature) might have a negative effect through desiccation of overwintering life history stages, or warmer low temperatures might reduce snow cover via melting and reduce the associated insulating effect or have adverse effects on host or nectar resources.

One of the major contributing factors to decreasing snowpack in the Sierra Nevada and other western North American mountain ranges is increasing spring temperatures that shift the balance from snow accumulation to melting (Kapnick and Hall 2012). For the Donner Pass climate variables, warmer spring temperatures are strongly, negatively correlated with snow depth (Appendix C: Table C6, Fig. C1), which might indicate that the negative effect of warmer spring temperatures is not
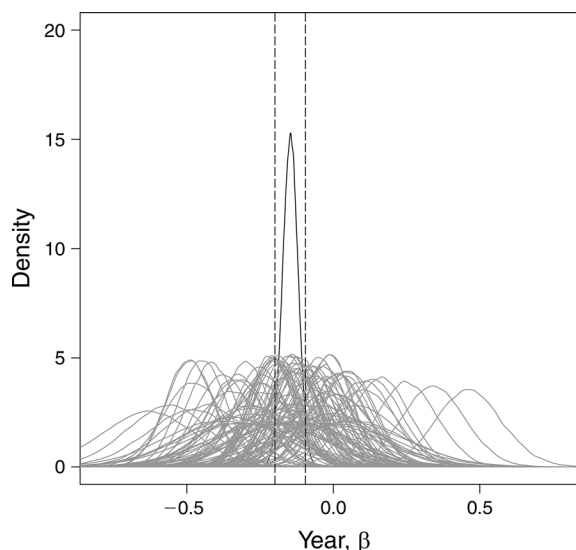

FIG. 3. Posterior densities for estimates of standardized β coefficient for the year effect from the single-variable plus year model for snow depth (see Table 3). Densities of species-level β's are shown as gray lines. The community-level β is shown as a solid black line. Boundaries of the 95% equal-tailed probability interval (i.e., a 95% credible interval) for the community-level β are shown as dashed lines.

a direct effect, but rather is mediated by the resulting decrease in snow depth due to melting. As the regional warming trend continues, lower accumulations and earlier melting are forecast. Not only could this have an effect on the butterfly fauna by reducing the positive aspect of snow depth, it also has the potential for shifting emergence phenologies. This could create phenological mismatch, or exacerbate mismatch, between butterfly species and resources (Thomas et al. 1996, Singer and Parmesan 2010, Boggs and Inouye 2012), possibly leading to further declines.

Interestingly, winter minimum temperatures were observed to have the opposite effect compared to spring minimum temperature, although the variation among species was much greater for winter minimum temperature (the 95% credible interval for the community-level β for this covariate includes zero; Table 1, Fig. 1a). Warmer winter temperatures that are still below freezing, especially overnight low temperatures, might contribute to greater snow accumulation when relative humidity is higher, although winter temperatures have less of an impact on snow depth than temperatures in the spring months (Kapnick and Hall 2012). It might also be that the impact of winter temperatures on butterfly occurrence is unrelated to effects of snow depth. Warmer average overnight temperatures in winter generally have a positive impact on butterfly species. This might be directly related to adverse physiological effects of extreme low temperatures on overwintering stages for resident species (Matter et al. 2011).

TABLE 4. Results of unconstrained hierarchical models with species grouped according to natural history categories.

Climate variable	Winter minT	Snow depth	ENSO Apr–May
Resident status β			
Resident ($n = 74$)	0.077 (−0.028 to 0.185)	**0.027 (0.002 to 0.053)**	**−0.053 (−0.079 to −0.027)**
Non-resident ($n = 32$)	−0.120 (−0.403 to 0.200)	0.024 (−0.065 to 0.115)	0.016 (−0.097 to 0.124)
Resident status τ			
Resident ($n = 74$)	79.20 (13.11 to 1519)	945.1 (271.9 to 3453)	872.4 (248.0 to 3263)
Non-resident ($n = 32$)	11.47 (2.36 to 695.4)	58.47 (16.34 to 560.8)	25.68 (10.36 to 68.54)
Diapause stage β			
Egg ($n = 17$)	−0.098 (−0.320 to 0.128)	0.054 (−0.013 to 0.117)	**−0.104 (−0.165 to −0.043)**
Larva ($n = 47$)	0.069 (−0.070 to 0.210)	0.009 (−0.028 to 0.047)	**−0.066 (−0.106 to −0.027)**
Pupa ($n = 27$)	0.094 (−0.136 to 0.368)	−0.011 (−0.065 to 0.042)	0.008 (−0.047 to 0.064)
Adult ($n = 13$)	0.153 (−0.225 to 0.600)	**0.084 (0.009 to 0.162)**	0.022 (−0.099 to 0.146)
Diapause stage τ			
Egg ($n = 17$)	194.8 (14.24 to 2030)	264 (40.57 to 2038)	526.8 (93.53 to 2742)
Larva ($n = 47$)	274.3 (29.49 to 2205)	642.7 (148.2 to 2877)	502.4 (117.4 to 2534)
Pupa ($n = 27$)	17.62 (2.79 to 941.0)	531.8 (101.1 to 2684)	446.9 (80.13 to 2524)
Adult ($n = 13$)	3.13 (0.89 to 14.50)	206.5 (31.17 to 1854)	34.32 (10.65 to 112.6)
Number of broods β			
Single ($n = 75$)	0.065 (−0.044 to 0.182)	0.02 (−0.008 to 0.048)	**−0.055 (−0.084 to −0.025)**
Double ($n = 7$)	−0.237 (−0.682 to 0.218)	0.014 (−0.187 to 0.153)	−0.132 (−0.284 to 0.043)
Multiple ($n = 23$)	0.053 (−0.228 to 0.359)	0.055 (−0.013 to 0.133)	0.033 (−0.058 to 0.125)
Number of broods τ			
Single ($n = 75$)	117.7 (15.23 to 1585)	904.4 (245.8 to 3288)	688.5 (187.2 to 2892)
Double ($n = 7$)	111.5 (3.47 to 1770)	126.3 (9.235 to 1685)	141.7 (8.559 to 1820)
Multiple ($n = 23$)	5.92 (1.79 to 83.61)	112.8 (28.36 to 1079)	42.92 (15.60 to 135.49)
Ruderal status β			
Ruderal ($n = 22$)	−0.070 (−0.325 to 0.208)	0.021 (−0.042 to 0.086)	0.002 (−0.092 to 0.094)
Non-ruderal ($n = 84$)	0.078 (−0.024 to 0.179)	**0.028 (0.001 to 0.055)**	**−0.053 (−0.081 to −0.024)**
Ruderal status τ			
Ruderal ($n = 22$)	10.47 (2.22 to 624.0)	205.2 (42.53 to 1686)	44.44 (15.42 to 143.2)
Non-ruderal ($n = 84$)	107.7 (13.95 to 1483)	816.6 (216.2 to 3219)	541.9 (152.2 to 2529)

Notes: For each natural history category, models were fit for each of the three weather variables and year. Standardized β's (medians of posterior distribution) and precision parameters (τ's) are reported for each weather variable. Samples sizes (n) are indicated for each natural history group. Values of β whose 95% credible interval (95% CI) does not include zero are indicated in boldface type. Standardized β's and precision parameters (τ's) for the year effect in each model are reported in Appendix C: Tables C4 and C5.

Our finding of a negative impact of warmer springs is inconsistent with other studies of Lepidoptera (Dennis and Sparks 2007). These studies have found positive effects of warmer temperatures during the spring season. However, this negative effect is associated specifically with overnight low temperatures (spring minimum temperatures) and might be more related to effects on snow cover rather than direct effects on the physiology of the butterflies. We speculate that the reversed relationship might also be a function of the relatively high elevation of our study site (Roy et al. 2001), and the relatively short flight season there. The spring months (March, April, and May) constitute a relatively cool season at Donner Pass, during which snow cover is persistent. The median adult flight interval for species at Donner Pass is short, just 23 days (Appendix C: Fig. C3). The persistence of snow in the spring months, and the short flight period at Donner Pass, might explain why we found a negative effect of warmer spring temperatures compared to other studies. Warmer temperatures might reduce snow by melting, and thus make overwintering larvae and pupae more susceptible

to bacterial or fungal infection, or disrupt butterfly phenologies (Thomas et al. 1996, Singer and Parmesan 2010, Boggs and Inouye 2012).

Examination of species grouped by natural history categories provides more insight to the diversity of responses to weather variables. For example, the positive community-level response to increasing snow pack appears to be mainly mediated by positive responses of permanent residents, species that overwinter as adults, and non-ruderal (non-weedy) species (Tables 4 and 5, Fig. 2). The overall negative response to increasing spring minimum temperatures seems largely mediated by negative responses of resident species, those overwintering as eggs and those species with multiple generations per year. Both ruderal and non-ruderal species responded negatively to increasing spring minimum temperatures. For ENSO April–May, species that overwinter as eggs and larvae have a generally more negative association than species that overwinter as pupae or adults. Pupae and adults might be relatively insensitive to these early-spring conditions.

TABLE 5. Results of unconstrained hierarchical models with species grouped according to natural history categories, continued from Table 4.

Climate variable	Spring maxT	Winter maxT	Spring minT
Resident status β			
Resident ($n = 74$)	−0.027 (−0108 to 0.055)	−0.082 (−0.217 to 0.047)	**−0.113 (−0.192 to −0.039)**
Non-resident ($n = 32$)	−0.089 (−0.358 to 0.217)	−0.227 (−0.545 to 0.117)	−0.057 (−0.278 to 0.203)
Resident status τ			
Resident ($n = 74$)	318.6 (41.88 to 2254)	167.66 (13.60 to 1861)	319.3 (43.18 to 2254)
Non-resident ($n = 32$)	7.54 (1.94 to 319.5)	52.93 (3.55 to 1508)	34.4 (3.75 to 1277)
Diapause stage β			
Egg ($n = 17$)	−0.104 (−0.318 to 0.118)	−0.167 (−0.443 to 0.113)	**−0.235 (−0.417 to −0.056)**
Larva ($n = 47$)	0.030 (−0.092 to 0.152)	−0.073 (−0.0248 to 0.101)	−0.1 (−0.208 to 0.017)
Pupa ($n = 27$)	−0.046 (−0.212 to 0.124)	0.073 (−0.198 to 0.505)	−0.034 (−0.191 to 0.126)
Adult ($n = 13$)	0.157 (−0.255 to 0.606)	−0.139 (−0.337 to 0.071)	−0.137 (−0.333 to 0.068)
Diapause stage τ			
Egg ($n = 17$)	189.0 (14.37 to 1923)	115.8 (5.56 to 1740)	199.7 (15.77 to 1978)
Larva ($n = 47$)	189.7 (20.72 to 1908)	225.8 (21.60 to 1959)	233 (21.68 to 2000)
Pupa ($n = 27$)	159.5 (12.97 to 1904)	34.38 (1.41 to 1272)	169 (15.34 to 1865)
Adult ($n = 13$)	3.18 (0.89 to 13.66)	88.32 (6.59 to 1612)	83.98 (6.486 to 1517)
Number of broods β			
Single ($n = 75$)	0.005 (−0.082 to 0.095)	−0.067 (−0.199 to 0.071)	**−0.087 (−0.172 to −0.001)**
Double ($n = 7$)	−0.006 (−0.503 to 0.576)	−0.290 (−0.872 to 0.474)	−0.124 (−0.607 to 0.482)
Multiple ($n = 23$)	**−0.202 (−0.391 to −0.013)**	−0.180 (−0.464 to 0.114)	**−0.183 (−0.346 to −0.014)**
Number of broods τ			
Single ($n = 75$)	338.5 (43.87 to 2294)	215.45 (23.55 to 1916)	301.0 (37.74 to 2262)
Double ($n = 7$)	8.92 (0.84 to 876.2)	66.71 (0.70 to 1596)	9.99 (0.790 to 900.1)
Multiple ($n = 23$)	36.85 (5.23 to 1208)	22.78 (2.27 to 1170)	184.5 (15.76 to 1937)
Ruderal status β			
Ruderal ($n = 22$)	−0.159 (−0.605 to 0.035)	−0.152 (−0.433 to 0.145)	**−0.174 (−0.344 to −0.003)**
Non-ruderal ($n = 84$)	−0.009 (−0.090 to 0.075)	−0.098 (−0.229 to 0.0320)	**−0.093 (−0.175 to −0.008)**
Ruderal status τ			
Ruderal ($n = 22$)	40.36 (5.51 to 1324)	22.38 (2.37 to 1213)	160.3 (12.62 to 1866)
Non-ruderal ($n = 84$)	264.07 (29.64 to 2087)	214.8 (19.38 to 1974)	244.6 (31.52 to 2006)

Notes: For each natural history category, models were fit for each of the three weather variables and year. Standardized β's (medians of posterior distribution) and precision parameters (τ's) are reported for each weather variable. Samples sizes (n) are indicated for each natural history group. Values of β whose 95% credible interval (95% CI) does not include zero are indicated in bold. Standardized parameters for the year effect in each model are reported in Appendix C: Tables C4 and C5.

Across weather variables, there were trends for some variables and groups of species. For example, permanent residents and non-ruderal (i.e., non-weedy) species showed positive responses to increasing snow depth, cooler spring maximum temperatures, and lower values of the ENSO index for April–May. Non-residents, ruderal species, and species with more than one generation per year tended to show much less consistent responses as captured by lower estimates of the precision parameters (τ's; Tables 4 and 5). When considering these results, it is important to recognize that the natural history categories are not independent (Appendix B: Table B1). For example, many of the resident species are also non-ruderal species. This nonindependence is inherent in ecological traits, but does not invalidate inferences drawn from analyses within natural history categories.

The ability to formulate hypotheses on the diversity of responses to climate and explore potential underlying mechanisms for a community with high species richness is encouraging. However, the results from the hierarchical models suggest that considerable caution is warranted when interpreting patterns from such long-term data: Because a variable is important at the level of an entire community does not mean that it has an impact that is consistent in magnitude or even sign across all species. The community-level response to the ENSO April–May covariate was distinctly negative, yet most species show regression coefficients whose credible intervals overlap zero (Fig. 1c; Appendix C: Tables C1 and C2). Similarly, the spring minimum temperature community response was negative, yet individual species' β coefficient credible intervals include zero. Thus, while there are substantial effects at the level of the community that can be partly explained by examination of different groups of species based on natural history characteristics, effects at the level of individual species are subtle and rarely discernibly different than zero. This finding suggests that studies of individual species responses might fail to identify climate variables that are important at the community level. This challenge might be most acute at high-elevation or high-latitude sites with narrow flight windows and relatively less information per species, at least compared to locations with

longer flight windows and more observations per year per species.

The greatest diversity of species' responses was observed for the year effect, describing linear trends through time (Fig. 3). This is not attributable to a systematic change in site visits; there is no correlation between the number of site visits to Donner and year (see Forister et al. 2010: Fig. S3). The magnitude of this year effect was greater than the effects of most weather variables, which highlights how much there is yet to be learned and provides a baseline for future studies of factors affecting the Donner Pass butterfly fauna. In all analyses, the β coefficient for year was strongly negative at the community level, indicating a relatively strong decline in species' abundances over the 38 years of the study. However, at the species level, we observed substantial variation as demonstrated by the low precision value for year, which was the lowest of all covariates (Fig. 3; Appendix C: Table C3). While most species showed a negative trend over time, some species appear to be declining rapidly. Eighty-eight species (83% of the Donner fauna) have negative point estimates of the standardized regression coefficient, and 35 species (33% of the fauna) have negative β values with credible intervals that do not contain zero. These declining species represent an eclectic mix that includes high-altitude endemics, such as *Plebejus shasta*, *Thorybes mexicana nevada*, and *Hesperia nevada*, as well as much more widespread species such as *Nymphalis antiopa*, *Vanessa annabella*, *Pieris rapae*, and *Danaus plexippus* (Appendix C: Tables C1 and C2). Thus, high montane species and ruderal species that commonly fly up to Donner Pass from the Central Valley of California are declining, suggesting multiple phenomena are at work. These results are consistent with Forister et al. (2010), who detected sharp declines in species richness at low-elevation sites (including species demographically connected to higher elevation sites), as well as declines for a small number of alpine-specialist species associated with the highest elevations.

The ecological and taxonomic breadth of the species within these groups, especially the declining species, coupled with the rather low explanatory power of the climate covariates, suggests that there is much left to understand in terms of determinants for the Donner Pass butterfly fauna. Examining these trends in the context of natural history categories, we find that declines are the rule for all categories except pupal diapausers and bivoltine species, which, as groups, show no trends (Appendix C: Fig. C4, Tables C4 and C5). It seems likely that much of the explanation for these patterns in various species over time might involve specific ecological interactions (i.e., specialized natural enemies or larval food resources), regional effects, including declines in source populations for migrants, or with altitudinal or latitudinal range shifts (Parmesan 1996, Parmesan and Yohe 2003).

The results of our hierarchical, Bayesian modeling of the responses of butterfly species demonstrates the capacity of this approach to estimate community- and species-level effects simultaneously for a relatively rich community where windows of detectability for individual species are relatively short. This appears to be a powerful approach for analyses of long-term data. Future applications might include an examination of consistency of patterns across multiple sites, the correlation or connectedness among sites, or even a search for commonalities among different data sets. Do snow depth and spring minimum temperatures exhibit strong community-level responses in other montane sites or at high latitudes? Are regional-level variables, such as ENSO sea-surface variables similarly important at different sites? These investigations might also include dissecting patterns using other categorizations of species. For butterflies and other invertebrates, these might include host range (diet breadth), range size, and other factors. Alternatively, patterns of species richness through time in response to climate change could be examined with hierarchical models that include natural history and ecological species groupings within the entire community as a means by which various contributing factors might be parsed. While our modeling of the Donner butterflies was a modest beginning, our conclusions with respect to the utility of the hierarchical approach potentially have far-reaching consequences. In particular, researchers should consider the possibility that community-level responses to global change might or might not encompass the responses of substantial numbers of organisms within the community, and that this effect will be dependent on the natural histories of the individual species. This study gives strong support to a Gleasonian interpretation of communities as aggregates of individualistic species and their adaptations to the environment, subject to disassembly and reassembly in the face of climate change. It suggests that future butterfly faunas at Donner Pass might have no analogues in the Sierra Nevada of today (Bennett 1997).

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SUPPLEMENTARY MATERIAL

Appendix A

Example of BUGS code (*Ecological Archives* E095-191-A1).

Appendix B

Listing of study species and natural history categories (*Ecological Archives* E095-191-A2).

Appendix C

Supplementary Results: tabulation of standardized coefficients for species and year effect, analyses of correlations among weather variables, and analyses of butterfly flight windows and probabilities of occurrence (*Ecological Archives* E095-191-A3).