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RESEARCH ARTICLE

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Thirty-six years of butterfly monitoring, snow cover, and plant productivity reveal negative impacts of warmer winters and increased productivity on montane species

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Abstract

Climate change is contributing to declines of insects through rising temperatures, altered precipitation patterns, and an increasing frequency of extreme events. The impacts of both gradual and sudden shifts in weather patterns are realized directly on insect physiology and indirectly through impacts on other trophic levels. Here, we investigated direct effects of seasonal weather on butterfly occurrences and indirect effects mediated by plant productivity using a temporally intensive butterfly monitoring dataset, in combination with high-resolution climate data and a remotely sensed indicator of plant primary productivity. Specifically, we used Bayesian hierarchical path analysis to quantify relationships between weather and weather-driven plant productivity on the occurrence of 94 butterfly species from three localities distributed across an elevational gradient. We found that snow pack exerted a strong direct positive effect on butterfly occurrence and that low snow pack was the primary driver of reductions during drought. Additionally, we found that plant primary productivity had a consistently negative effect on butterfly occurrence. These results highlight mechanisms of weather-driven declines in insect populations and the nuances of climate change effects involving snow melt, which have implications for ecological theories linking topographic complexity to ecological resilience in montane systems.

KEYWORDS
climate change, drought, extreme events, NDVI, phenology, plant–insect interactions

1 | INTRODUCTION

Climate change is driving declines in the abundance of wild organisms across the world (Parmesan, 2006; Sage, 2020; Young et al., 2016). Along with habitat loss and degradation, studies of insects frequently report climate as a primary contributor to reductions in population density (Boggs, 2016; Bowler et al., 2017; Harvey et al., 2022; Wagner, Fox, et al., 2021; Wagner, Grames, et al., 2021; Wilson & Fox, 2021). However, climate change is not one cohesive stressor and is instead a phenomenon composed of changes to mean temperature and precipitation, increased frequency of extreme events, and their interactions, which are all expected to impact individual populations through different direct and indirect processes (Boggs & Inouye, 2012; Filazzola et al., 2021). Additionally, climate shifts are not uniform across space or time, with higher latitudes and elevations experiencing more rapid rates of change and such changes being nonuniformly distributed across seasons (Rangwala & Miller, 2012; Wang et al., 2016). This spatial and temporal complexity makes understanding trends and forecasting future population trajectories difficult as such work requires extensive long-term datasets that are relatively scarce for insects, especially at higher elevations (Halsch et al., 2021). This paucity of information is problematic considering the importance of insects as ubiquitous, crucial components of most natural systems and major components of global biodiversity (Wilson, 1987). In this study, we use 36 years of monitoring data of 94 species to evaluate direct and indirect effects of weather on butterflies and their larval host and nectar plants across three sites along an elevational gradient in the Sierra Nevada mountain range of California.

The direct effects of long-term climate change have been most often observed in phenological responses to temperature, with many examples of temperate zone insect populations advancing their emergence dates to earlier in the year or extending flight activity into later months (Forrest, 2016). As ectotherms, the effects of temperature on insects are far more than just phenological, and events such as heat waves can have direct developmental consequences (Harvey et al., 2020). Rising temperature, however, is just one axis of global climate change, and the disruption of precipitation patterns may be an even greater threat (Wagner, 2020). It appears that precipitation regimes, particularly extreme events, play a significant role in declining insect populations (Forister et al., 2018; Salcido et al., 2020; Stireman et al., 2005). While temperature and precipitation are two different facets of climate, they often covary and specific combinations may be particularly adverse for insects (Dai, 2011; Harvey et al., 2022). For instance, hotter and drier regions in the US are hotspots of butterfly decline, while cooler and wetter regions are seeing increases in abundances (Crossley et al., 2021).

Further complexity derives from the fact that populations are embedded in communities and shifting abiotic conditions are expected to disrupt interactions between co-occurring organisms (Gilman et al., 2010). Like direct effects, these indirect effects have often been explored through a phenological lens. In these cases, climate can have an indirect effect on insect populations by causing a seasonal decoupling of insects and plants where the emergence of a consumer, for example, is no longer aligned with a resource (Forrest, 2016). Much of this work has been focused on the start of the growing season, but the end of the growing season is also important and potentially as consequential (Gallinat et al., 2015; Nielsen et al., 2022; Williams et al., 2012). For instance, sites experiencing warmer temperatures at the end of the adult activity period in late fall experienced the greatest declines in butterfly abundance, and one hypothesis for this effect was stress on late-season plant resources (Forister et al., 2021). Beyond potential mismatches in phenology, climate change will also alter key features of plant communities, such as species composition, nutritional quality, floral resources, natural defenses, and volatiles, which can have positive or negative indirect outcomes on insects (Wilson & Fox, 2021). For instance, drought has been shown to decrease floral resources and volatiles while also decreasing defense against herbivory (Burkle & Runyon, 2016; Rouault et al., 2006), and changes in C:N ratios in leaves have been linked to declines in insect herbivores (Welti et al., 2020). Such indirect effects may prove to be as important as the direct effects; however, studies linking indirect effects to long-term trends are few.

In high-elevation systems, direct and indirect processes are both important for understanding the ways in which insects respond to weather (Mani, 1968). In these landscapes, perhaps no single variable is as important as snow, in the timing of its arrival, the timing of its subsequent melt, and its impact on water availability throughout the following growing season. Population-level data for butterflies have demonstrated the benefit of snow in its protection from extreme winter conditions for both the butterflies themselves (Roland & Matter, 2016) and their host and nectar plants (Boggs & Inouye, 2012). Snow effects can also be long-lasting, as an early melt can cause an early onset of summer water stress in shallow soils (and the plants that utilize these soils) in the following growing season (Blankinship et al., 2014). Of course, while snow is important, weather during the growing season will also influence butterflies directly and indirectly (Murphy & Boggs, 1997; Singer & Thomas, 2002). Summer heat, for instance, may contribute to increased activity and expanded phenology, while also stressing earlier developmental stages and host plants (Forister et al., 2021). In all, the outcomes of montane butterfly populations in response to weather are likely complex, depending on both timing and intensity as well as their own phenology.

Here, we use observations from a temporally intensive butterfly monitoring program in North America to quantify the direct effects of weather and the indirect effects of weather on plant productivity, which affects adults (through quality of nectar sources) and larvae (through abundance and quality of larval food plants) from three sites above 1350 m in the Sierra Nevada (Forister et al., 2010). This dataset contains variation in life histories and landscapes and is ideal for considering the direct and indirect effects of weather and the traits associated with variation in responses to abiotic conditions. We combine these long-term monitoring records with a satellite-derived indicator of plant primary productivity and high-resolution weather data in a modeling framework that incorporates population- and site-specific responses. We first ask how conditions during the winter and the subsequent growing season impact butterflies directly and indirectly, potentially influencing juvenile stages through effects on host plants or impacting adults through changes in nectar resources. We then consider how these effects relate to how populations responded to an extreme, millennium-scale drought (Forister et al., 2018) and the life history traits that mediated drought response. In doing so, we shed new light on how different aspects of climate change covary, the relative importance of different variables, and the pathways through which they impact montane butterflies.

2 | METHODS

2.1 | Overview

Analyses incorporated annually resolved butterfly data, remotely sensed NDVI (Normalized Difference Vegetation Index) data, and weather data from a downscaled regional climate model into a Bayesian hierarchical path analysis to understand direct and indirect effects of weather on butterfly occurrence at three monitoring sites (Figure 1). To do this, we first performed a factor analysis to reduce the dimensionality of the weather data, while still preserving meaningful information with interpretable factors. We then used these weather factors and NDVI data to build two separate Bayesian hierarchical models, one predicting NDVI and another predicting butterfly occurrence (including NDVI as a predictor; Figure 2). These models were interpreted together to build the path analysis. Finally, using daily weather data available at one of the sites, we ran an additional Bayesian hierarchical model describing the effect of warm conditions at the end of winter, an effect of interest based on results from the path analysis.

2.2 | Butterfly data

The butterfly data used in this study are part of a long-term monitoring program that includes observations from 10 sites visited approximately every other week during the adult butterfly season (Forister et al., 2010). These sites cover an elevational gradient in northern California that spans sea level to 2800 m. During each site visit, observers walked a fixed transect and recorded the presence of all butterfly species seen. For this analysis, a population refers to a time series of a species at a site and is not meant to imply genetic structure among sites. We restricted analyses to the subset of species that have been present in at least 10 separate years at a site and that have never been absent more than 5 consecutive years, for a total of 188 populations (Figure S1 for the fauna at each site). These criteria eliminated stray species and those that colonized in the middle of the study. Additionally, since NDVI data were only available beginning in 1984, we further restricted the butterfly data to the years of 1985–2020 (to include a lagged effect of 1984). We then totaled the number of times each butterfly species was seen each year (for each site) and the number of times that a site was visited, which jointly inform the binomial sampling distribution. Intraspecific, annual variation in the probability of occurrence derived from this approach is an established *proxy* for variation in population density, as greater abundance in a year for any particular species is reflected in positive observations on more days throughout the year (Casner et al., 2014). This proxy relationship has been previously investigated with our dataset, where it was found that change through time estimated with individual counts (abundance) and with the number of days present are highly related across the majority of species (Casner et al., 2014). Those analyses were made possible because abundance data are collected (in addition to presence and absence data) at the lower elevation sites of our monitoring program, where the butterfly fauna is less diverse and thus counts

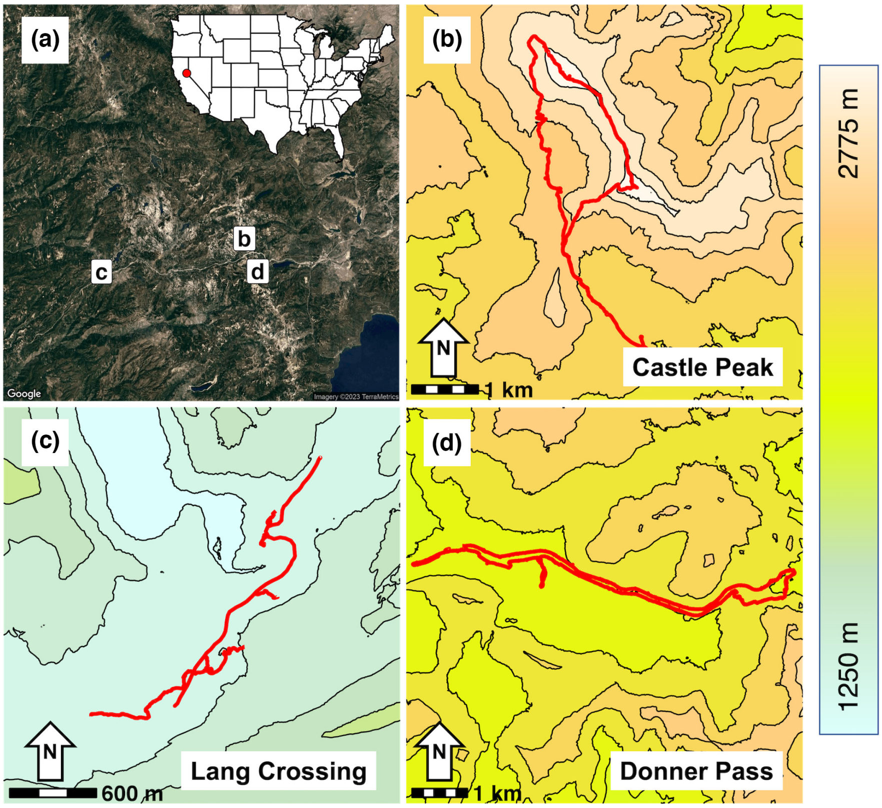

FIGURE 1 Topography of the three butterfly monitoring sites where the route walked is shown in red. (a) Location of monitoring sites in the Northern California Sierra Nevada mountains. (b) The Castle Peak monitoring site which climbs to a summit, follows the ridge, and then descends through two meadows. (c) The Donner Pass site which largely lies at the bottom of a basin. (d) The Lang Crossing site which is also largely at the bottom of a drainage basin and crosses two rivers.

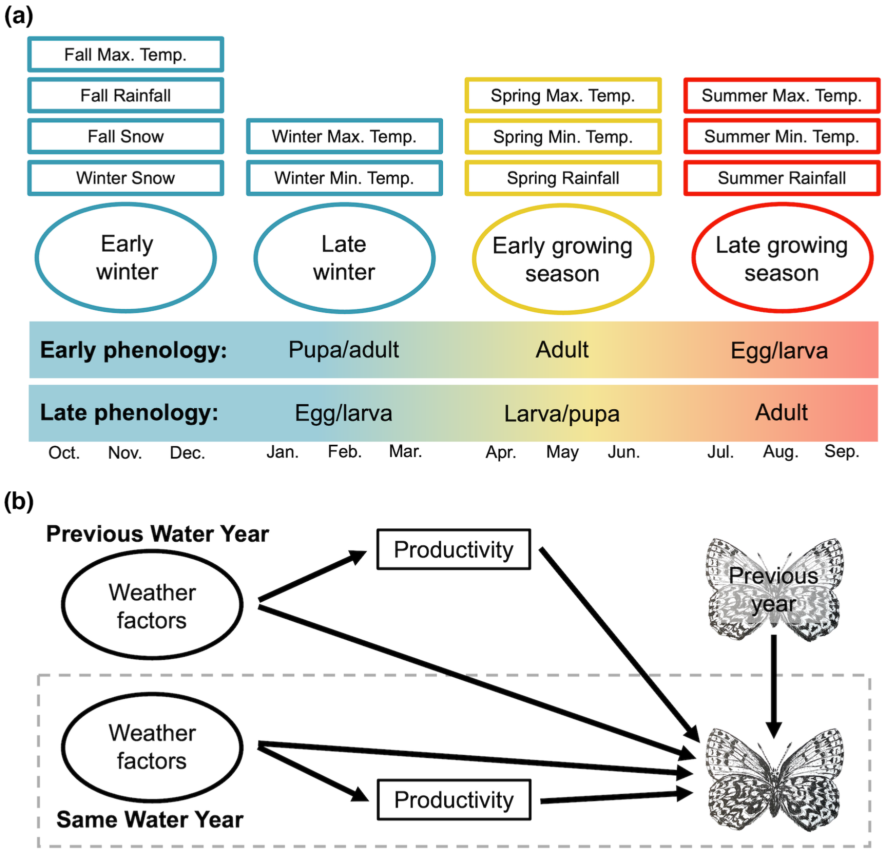

FIGURE 2 Conceptual diagram of the primary analysis. (a) A factor analysis was used to estimate weather covariates where observed weather variables are shown in the rectangles and the weather factors are shown in the ovals underneath them. The relationships between the original variables and the factors can be found in Table S1. The factors are ordered by water year (prior October to current September, shown as months on the bottom). Below the factors are the life stages that a typical early and late phenology butterfly will be in during time periods relevant to these factors. (b) The general structure of the path analysis where butterflies are affected by weather in the same year and from the previous year. We also generate indirect effects of weather mediated by productivity (NDVI) in the same and previous year. Each path is estimated at three levels: a population within a site ($n=188$), a site ($n=3$), and across all sites ($n=1$).

of individuals are more readily recorded. Here, we have revisited this issue with more years of data relative to the previous analysis (Casner et al., 2014), and we again find a clear and positive relationship between the binomial probability previously described and actual abundance (Figure 3).

2.3 | Site descriptions

The three high-elevation sites examined here are Castle Peak, Donner Pass, and Lang Crossing, located in the Sierra Nevada mountain range of California (Figure 1). We selected these sites because they receive substantial percentages of their precipitation as snow, and they remain covered during the winter. We were particularly interested in exploring how the duration of snow pack might relate to the impact of a mega-drought on butterfly populations (Forister et al., 2018). These sites have also remained relatively unchanged compared with the high rates of suburban and exurban development that characterize the lower elevation monitoring sites (Forister et al., 2010). Thus, the primary stressors of butterflies at the three focal montane sites are likely from weather and not from other anthropogenic inputs. Finally, given the known heterogeneity of weather effects across these monitoring sites (Nice et al., 2019), a focus on only a few sites allowed us to more efficiently address the complexity of weather responses among butterflies.

The Castle Peak transect (39.367°N, 120.352°W) is 14.5 km long and spans an elevation range of 2200–2800 m. The route is mostly composed of mixed conifer forest with herbaceous understory but also follows a ridge (above treeline) and crosses two meadows. The landscape is heterogeneous, and snow melt timing is highly variable within a single season, with south-facing sections that melt early and north-facing sections that melt late. The Donner Pass transect (39.367°N, 120.352°W) is 17.75 km long and spans an elevation range of 2000–2175 m. The route is mostly composed of mixed conifer forest with an herbaceous understory but also includes a large meadow and granite rock outcroppings. Most of the route is walked in the bottom of the local drainage and the route itself is mostly flat. The Lang Crossing transect (39.309°N, 120.666°W) is 7.25 km long and spans an elevation range of 1350–1475 m. The route consists of a relatively even distribution of mixed conifer forest, meadows, and xeric rock outcroppings. The route is largely in the bottom of a drainage and crosses both the Bear and Yuba rivers. This route encompasses more topographic complexity than Donner Pass but less than Castle Peak.

2.4 | NDVI data

NDVI is a commonly used spectral index that contrasts the reflectance of red light (which is typically absorbed by healthy vegetation) and near-infrared light (which is typically reflected by healthy vegetation). Thus, NDVI is a holistic indicator of plant community photosynthesis and productivity. We calculated annual NDVI values from Landsat Collection 2 Surface Reflectance

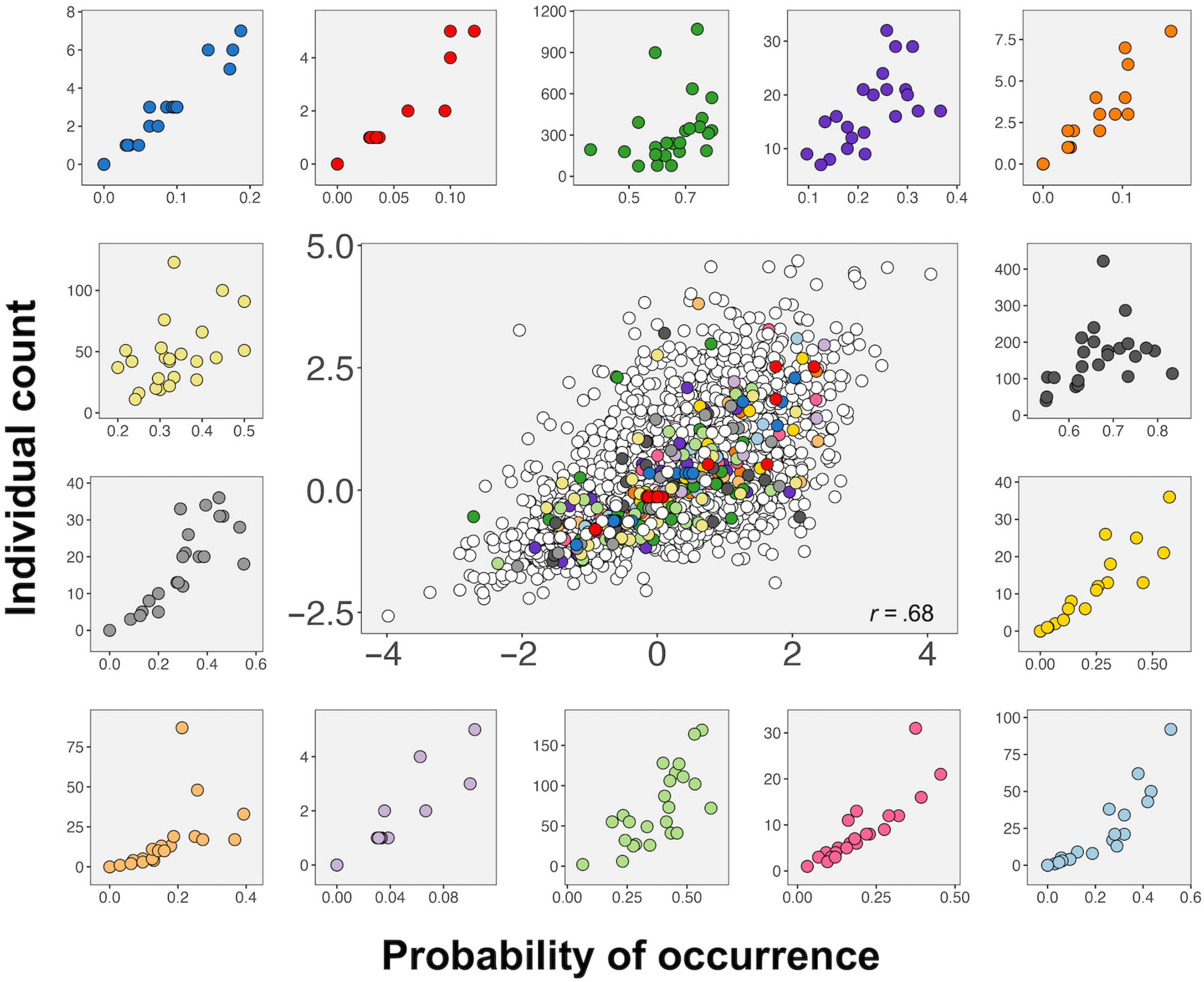

FIGURE 3 Strong positive relationship between the probability of occurrence and annual counts at five lower elevation sites (where counts can be conducted). The center panel show this relationship for 201 populations after *z*-transforming baseline occurrence probability and abundance. Fourteen populations were randomly selected to demonstrate this relationship using the raw data. These are shown in the 14 smaller panels that surround the main figure. Points in all panels are colored by population (white points denote a population that is not shown in the marginal panels).

imagery collected at each of our monitoring sites. To limit the effects of image irregularities in individual Landsat scenes, we used an annual image composite approach as follows. First, we used the CFMask-derived quality assurance band (Foga et al., 2017) to mask pixels with clouds, shadows, water, and snow cover in each Landsat scene that overlapped our study area. For each 30-m pixel and year, we then calculated the 75th percentile NDVI value for all unmasked values in images collected during the typical growing season (i.e., June 1 to September 30), which reflects the overall photosynthetic production within a pixel without being sensitive to outliers. As a result, we developed annual image composites of growing season NDVI for each year in our study period. Within each site, we extracted NDVI data from each year in unforested areas that are representative of annual phenological patterns for herbaceous plants. A single weighted mean NDVI value was then calculated for each year at each site, where a pixel that was completely in an unforested area contributed more than a pixel that was on the edge, with partial forest cover. NDVI values were then centered and scaled (*z*-transformed) prior to analysis.

2.5 | Weather data

Mean monthly values of daytime highs (°C), nighttime lows (°C), and precipitation (mm) were derived from the M3 version of the Parameter-elevation Regressions on Independent Slopes Model dataset (Daly et al., 2008), which provides gridded weather data at 4-km native resolution. These data were spatially downscaled to 270-m resolution (Flint & Flint, 2012) and were then used as inputs for the Basin Characterization Model (BCM), a mechanistic model that balances the water budget on a per-grid cell basis by combining the weather variables with site characteristics, including soil depth, porosity, and bedrock type (Flint et al., 2013; Thorne et al., 2015). The BCM produces additional variables, including runoff, recharge, climatic water deficit, the accumulation and melt of the snow, and the snow water equivalent (SWE). Because the model is mechanistic, it can be calibrated using various ecosystem characteristics. The California version of the BCM has been calibrated and validated for actual evapotranspiration using remote sensing (Reitz et al., 2017), snow water equivalent (SWE) using National Resources Conservation Service (NRCS) Snowpack Telemetry (SNOTEL) stations, and streamflow gauges from the USGS National Water Information System (Flint et al., 2021). We used the path of each transect, buffered by 100 m on either side, to sample the 270 m BCM variables and calculated monthly means for T_{min}, T_{max}, PPT, and PCK (SWE) for each month from 1984 to 2020.

To further explore the role of warm winters in driving butterfly populations, we obtained an additional weather dataset from the Central Sierra Snow Laboratory in Soda Springs, CA, which has maintained a weather station along the Donner Pass monitoring route for the entirety of the monitoring program (Osterhuber & Schwartz, 2021). We used this weather station's daily measurements of maximum temperature, minimum temperature, snow depth, and SWE. To match the temporal window of our factor analysis (discussed below), we summarized both maximum and minimum temperature by taking the mean across the months of January–March. To examine the effects of snow at the end of the cold season, we took the average of SWE (which was >0.95 correlated with snow depth) across the 2 weeks preceding April 1, to account for occasional instances of missing data over that time span. Each of these variables was scaled prior to analysis.

2.6 | Factor analysis

We treated weather as a latent variable by performing a factor analysis on the weather data from the BCM model, with the scores of the factors becoming the covariates used in the path analysis. To do this, we first took seasonal averages of minimum temperature, maximum temperature, precipitation, and SWE, calculated within the water year (i.e., prior October to current September). We then performed a single factor analysis of scaled weather variables across all sites (specifying four factors) using the "oblimin" rotation, which does not force axes to be orthogonal (preserving any correlations that may exist between seasonal weather). By performing one factor analysis across all the weather data, we ensured that the interpretation of factors was consistent across all sites and years. The specification of four factors was chosen based on the results of an exploratory factor analysis where we tried different rotations and numbers of factors to assess fits and interpretations. We then generated factor scores for each site in each year to be used as covariates in subsequent analyses. Finally, factor scores were scaled for use in the subsequent path models. The factor analysis was performed using the psych package (version 2.2.9) in R (Revelle, 2022).

2.7 | Modeling of butterfly populations

The butterfly occurrence and NDVI models were fit as two separate Bayesian hierarchical models, the outputs of which were combined to describe direct and indirect effects. This approach is similar to Piecewise SEM (Lefcheck, 2016), where models are fit separately, but inferences are made using all models. Butterfly occurrences were modeled using covariates for each seasonal weather factor, each seasonal weather factor in the previous year, NDVI, the previous year's NDVI, butterfly density in the previous year, and year (see Figure 2 for schematic of these effects, Figure S2). Butterfly occurrences were treated as binomially distributed where an observation of a species during an individual survey was treated as a "success" and the total number of surveys during a year at that site was the number of "trials." The probability of a success was modeled using a logit link and was predicted by the linear terms in the model. In our hierarchical framework, the coefficients associated with each covariate were estimated at three levels: an individual population within a site (188 estimates per covariate), across all populations within that site (3 estimates per covariate), and across all populations across all sites (1 estimate per covariate). For a small subset of species that only occur early in the year, we removed the effect of the end-of-the-year conditions because this occurs after the adults have completed their flight. NDVI was modeled using covariates for each seasonal weather factor, each seasonal weather factor in the previous year, the previous year's NDVI, and year (Figure 2, Figure S3). The coefficients for each covariate were estimated at two levels: within each site and across all sites. NDVI was treated as normally distributed with a mean that is predicted by the linear terms in the model and a precision estimated from the data. Vaguely informative priors were used for all terms in both models and these prior specifications, along with full model statements, can be found in the supplement (Figures S2 and S3). Both models were run using the jagsUI package (version 1.5.2) in R, which implements Gibbs and Metropolis–Hastings sampling algorithms (Kellner, 2019). Model convergence was evaluated by examining Gelman–Rubin diagnostics and traceplots. Model fit was evaluated using Pareto smoothed importance sampling and posterior predictive checks using the loo (version 2.5.1) and bayesplot (version 1.10.0) packages in R (version 4.4.2; Gabry & Mahr, 2022; R Core Team, 2022; Vehtari et al., 2022).

Once the butterfly and NDVI models were fit, outputs were combined for interpretation. The direct effect of each weather factor on butterflies was inferred from the posterior distribution of each coefficient associated with each weather factor in the butterfly model. The indirect effect of each weather factor was calculated by multiplying points describing the posterior distribution associated with each weather factor in the NDVI model by points describing the posterior distribution of the NDVI effect in the butterfly model. To standardize the coefficients from the butterfly model, which are on a logit scale, we performed a Menard standardization (Menard, 2017). The total effect of each weather variable (whether direct or indirect) was calculated by summing all relevant paths.

In response to the effect of warm winters observed with the path analysis, we ran an additional analysis to understand which traits were most strongly associated with this response at the Donner Pass site (where the most local snow data were available). To do this, we used a Random Forest model; Breiman, 2001) to detect the life history variables that are predictive of how a population responds to a warm winter. In the model, we used larval host breadth, overwintering stage, phenology, wingspan, and range size as predictor variables, with the response variable being the population-specific response to the end-of-winter conditions (i.e., coefficients from the previous path model). This was done with 500 trees with a node size of five using the randomForest package (Breiman et al., 2018). Because they were important features in this Random Forest analysis, we then focused on overwintering conditions and overwintering stages, using a Bayesian hierarchical model and data from the Donner Pass site (Figure S4). For this model, butterfly occurrences were once again binomially distributed (as previously described) and predictors included mean winter maximum temperature, mean winter minimum temperature, SWE, NDVI, year, a multiplicative interaction term between snow and the maximum temperature, and a multiplicative interactive term between snow and minimum temperature. The effect of each predictor on butterflies was estimated at two levels: for each species and for each overwintering stage. We used vaguely informative priors, and a full model statement can be found in the supplement (Figure S4). Full implementation of the model, including sampling, convergence evaluation, and model fit were performed in the same way as the path analysis.

3 | RESULTS

3.1 | Weather factor analysis

We generated four factors that incorporated information from the original 14 temperature and precipitation variables to summarize seasonal covariation in weather (Figure 2a). Two of the factors represented weather during the winter, while the other two represented weather during the growing season (Table S1). The first winter factor largely described early winter conditions, while the other winter factor described the conclusion of winter, particularly temperature at winter's end (Table S1). High values of the early winter factor indicated a cool and wetter onset of winter (including more snow), while high values of the late winter factor indicated a hotter January–March (Table S1). The growing season factors largely split between the first and second half of the adult butterfly season (April–June and July–September, respectively). Higher values for both growing season factors indicated a hotter and drier season (Table S1). Factors were generated with nonorthogonal rotation and are thus correlated, but weakly (Figure S5).

3.2 | Total and indirect effects of weather factors

When looking at the total impact of the four weather factors, summing across direct, indirect, and lagged (previous year) pathways, we found heterogeneous effects on butterfly occurrence. Most of the posterior distributions for both the across-site and the site-level effects were largely overlapping zero, indicating uncertainty in quantifying common responses to weather shared across species at different monitoring sites or even shared across species within a site (Figure 4a, Figure S6). This is despite the weather variables themselves being highly correlated across sites (Figure S7). We did find effects of each of these factors (at an 80% credibility level, equal tail probability interval [ETPI]) at the population level, as shown in Figure 4a and listed in Table 1. Hot and dry conditions in the first half of the growing season have largely negative effects, resulting in reductions in occurrence probability from .13 to .48 per SD of hot spring conditions. We found a reversal of equal magnitude of this effect for many species later in the growing season (Figure 4a, Table 1). We detected both positive and negative responses to winter variables, but a wetter and cooler onset of winter (starting at the end of the previous calendar year) generally increases the probability of occurrence for butterflies in the next year (Figure 4a, Table 1). The end-of-winter conditions affected the most populations, but did so bidirectionally, with populations responding both positively and negatively (Figure 4a, Table 1). When considering indirect effects, we see reversals in the directions of effects as compared to direct effects because NDVI (i.e., higher vegetation productivity) has a negative effect on butterflies, as shown in Figure 4b and Table 1. We found variation in effect sizes by site, but conditions in early winter appear to have the strongest and most general indirect effect, where a high snow year (1 SD above normal) reduces butterfly occurrences indirectly by up to .24. This effect is negative due to it being a positive predictor of NDVI (which itself has a negative association with butterfly populations). We also want to note the negative indirect effect of year: After accounting for seasonal weather variation, there is a residual negative trend over time explained by an indirect relationship with NDVI (Figure 4b, Table 1).

3.3 | Comparing prior and current year weather on butterfly occurrence

The total effects described above are derived from the path coefficients from two different models (including both within-year and lagged effects), whose coefficients can be considered individually. As was the case for total effects, it is the population-specific path coefficients that were more informative; however, we did observe shared variation in responses based upon the site (Figure S8). Within the same year, we saw largely positive responses to wetter

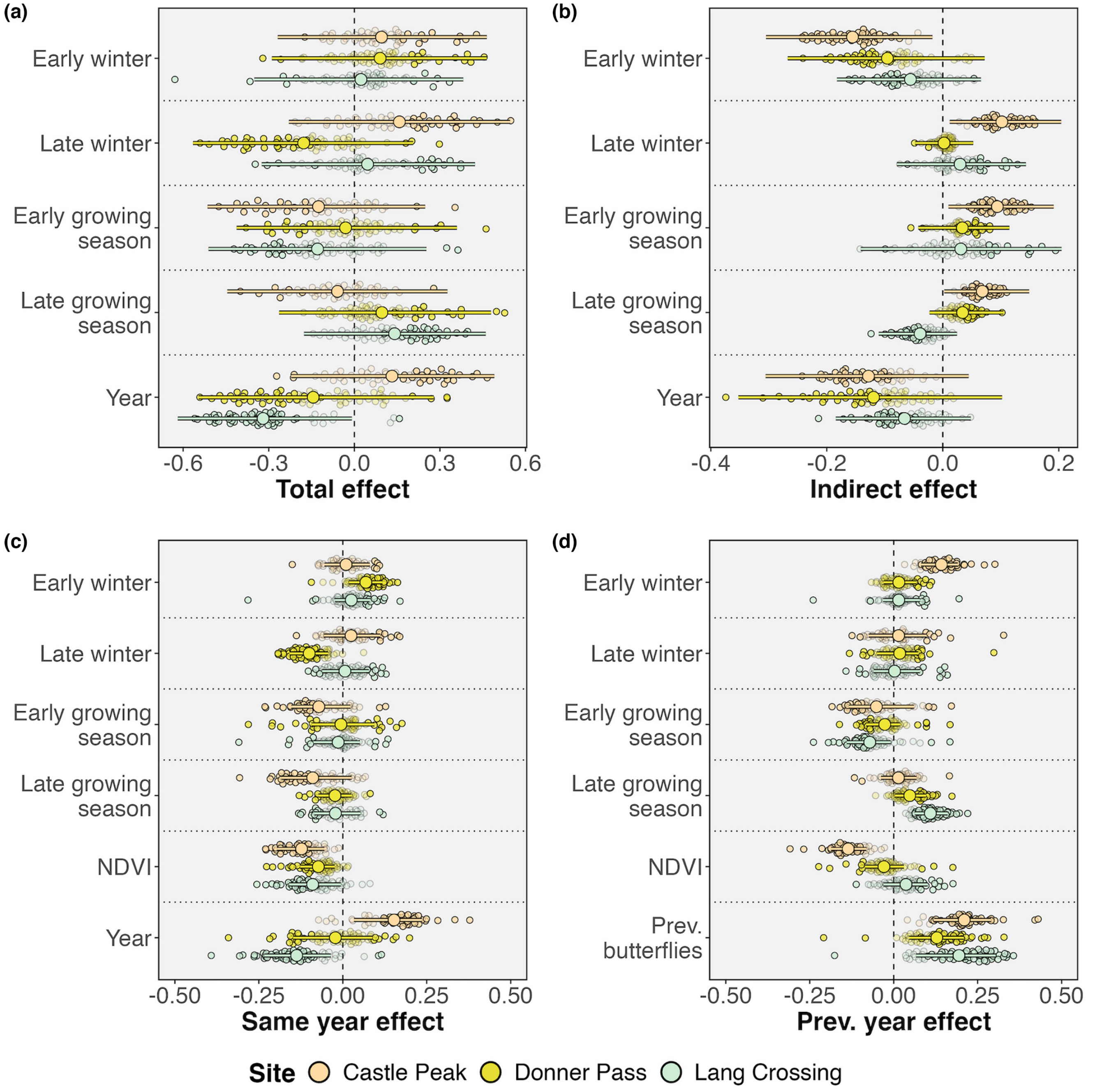

FIGURE 4 Effects of seasonal weather on butterfly populations. For each plot, small colored points show estimates from the lowest level in the hierarchy (a population within a site) and are colored by site (across-site estimates can be found in Figure S6). Points denoting estimates that are credibly different from 0 at a 0.8 level are opaque. Larger colored points with error bars show the site-level estimate with 80% credible intervals. (a) The total effect size (direct + indirect) of each weather covariate. (b) The strength of indirect effects of each weather covariate. (c) The estimated effects of each covariate from the same year butterflies were observed (for instance, butterflies observed in 1980 respond positively to snow accumulation in the 1979–1980 winter). (d) The estimated effects of each covariate from the year before butterflies were observed (for instance, butterflies observed in 1980 respond positively to hot and dry conditions at the end of the 1979 growing season).

early winters and largely negative responses to hot/dry ends to the growing season (at an 80% credibility level, ETPI; Figure 4c, Table 1). We also found strong negative effects of NDVI in the same year, which reduces the probability of occurrences of butterflies between .08 and .26 per SD (Figure 4c, Table 1). When looking at the impacts of weather in the previous year, we again found not only largely positive responses to wet early winters but also largely negative responses to hot/dry early growing season conditions and positive responses to hot/dry late growing seasons (Figure 4d, Table 1). We also found, for most species, a positive effect of butterfly occurrence probability in the previous year affecting observations in the current year. All the parameters in both

TABLE 1 Range of mean positive and negative effect sizes of credible effects at a 0.8 level (the 80% equal tail probability interval does not overlap 0).

Effect type	Predictor variable	Range of positive effect sizes	Range of negative effect sizes
Total	Early winter	0.17–.46 (26)	0.17–.63 (8)
Total	Late winter	0.17–.55 (40)	0.13–.54 (34)
Total	Early growing season	0.21–.46 (9)	0.13–.48 (49)
Total	Late growing season	0.11–.53 (46)	0.18–.40 (6)
Total	Year	0.16–.47 (26)	0.12–.56 (90)
Indirect	Early winter	0.05 (1)	0.04–.24 (110)
Indirect	Late winter	0.05–.16 (62)	0.02–.06 (3)
Indirect	Early growing season	0.03–.19 (83)	0.04–.10 (3)
Indirect	Late growing season	0.02–.11 (76)	0.03–.12 (36)
Indirect	Year	— (0)	0.05–.37 (96)
Same year	Early winter	0.07–.17 (55)	0.08–.28 (5)
Same year	Late winter	0.07–.17 (17)	0.07–.19 (56)
Same year	Early growing season	0.08–.18 (15)	0.08–.31 (42)
Same year	Late growing season	0.08–.12 (3)	0.07–.31 (44)
Same year	NDVI	— (0)	0.08–.26 (93)
Same year	Year	0.09–.38 (47)	0.09–.39 (68)
Prev. year	Early winter	0.06–.30 (63)	0.07–.24 (2)
Prev. year	Late winter	0.07–.33 (25)	0.07–.14 (11)
Prev. year	Early growing season	0.07–.17 (10)	0.07–.24 (66)
Prev. year	Late growing season	0.06–.22 (83)	0.09–.11 (2)
Prev. year	NDVI	0.08–.18 (2)	0.09–.31 (62)
Prev. year	Butterflies	0.09–.43 (145)	0.09–.21 (3)

Note: The number of populations that respond at that level to each predictor variable is indicated with parentheses (out of 188 populations). Effect sizes are the expected change in the probability of occurrence for every 1 SD of change in a predictor variable. Linear relationships for effect sizes from the binomial model were estimated using a Menard standardization (Menard, 2017). “Total” refers to the effects of predictor variables across both same- and previous-year effects. “Indirect” refers to the effects of predictor variables mediated through productivity (NDVI). “Butterflies” (in the predictor variable column) refers to the influence of butterfly density in the previous year (represented by the number of days observed) on observations in the subsequent year.

path analysis models converged and the models were a good fit to the data (Tables S2 and S3, Figures S9 and S10). All parameter estimates and convergence diagnostics can be found in the supplemental materials.

3.4 | Population response to drought

In addition to the impacts of weather, estimated through the models described above, we were also interested in how sensitivity to specific seasonal weather variables could inform our understanding of population responses to a major climatic event. We found that population response to elevated winter temperatures is related to population trajectories during the mega-drought years of 2011–2015 (Figure 5). Populations with an overall positive response to warm end-of-winter conditions maintained higher occupancy during the drought years, which is also related to phenology and overwintering stage (we examined other traits which were found to be less predictive, see Figure S11). Given this result, we next asked how overwintering stage is associated with population response to a warm winter and thus response to the drought. We hypothesized that if the mechanism underlying the relationship to warm winters involves an effect of premature snow melt and a disruption to diapause, then species that overwinter in younger developmental stages will be more vulnerable. Another possibility is that early snow melt reduces water availability at the end of the following growing season, which disproportionately impacts adult butterflies foraging for floral resources that have dried up. In this scenario, an effect of NDVI should be more important, particularly for species that fly late in the season.

We found a positive effect (at an 80% credibility level, ETPI) of higher April 1 SWE on all butterflies, across all overwintering stages (.99 probability of direction [pd]; Figure 6a). For other weather variables, we found that the most credible effects were specific to certain overwintering stages (Figure 6a). For example, we observed a negative effect of elevated minimum temperatures during late winter on populations that overwinter as eggs, larvae, and pupae (.99 pd, .97 pd, and .91 pd, respectively). We also recover the previously detected

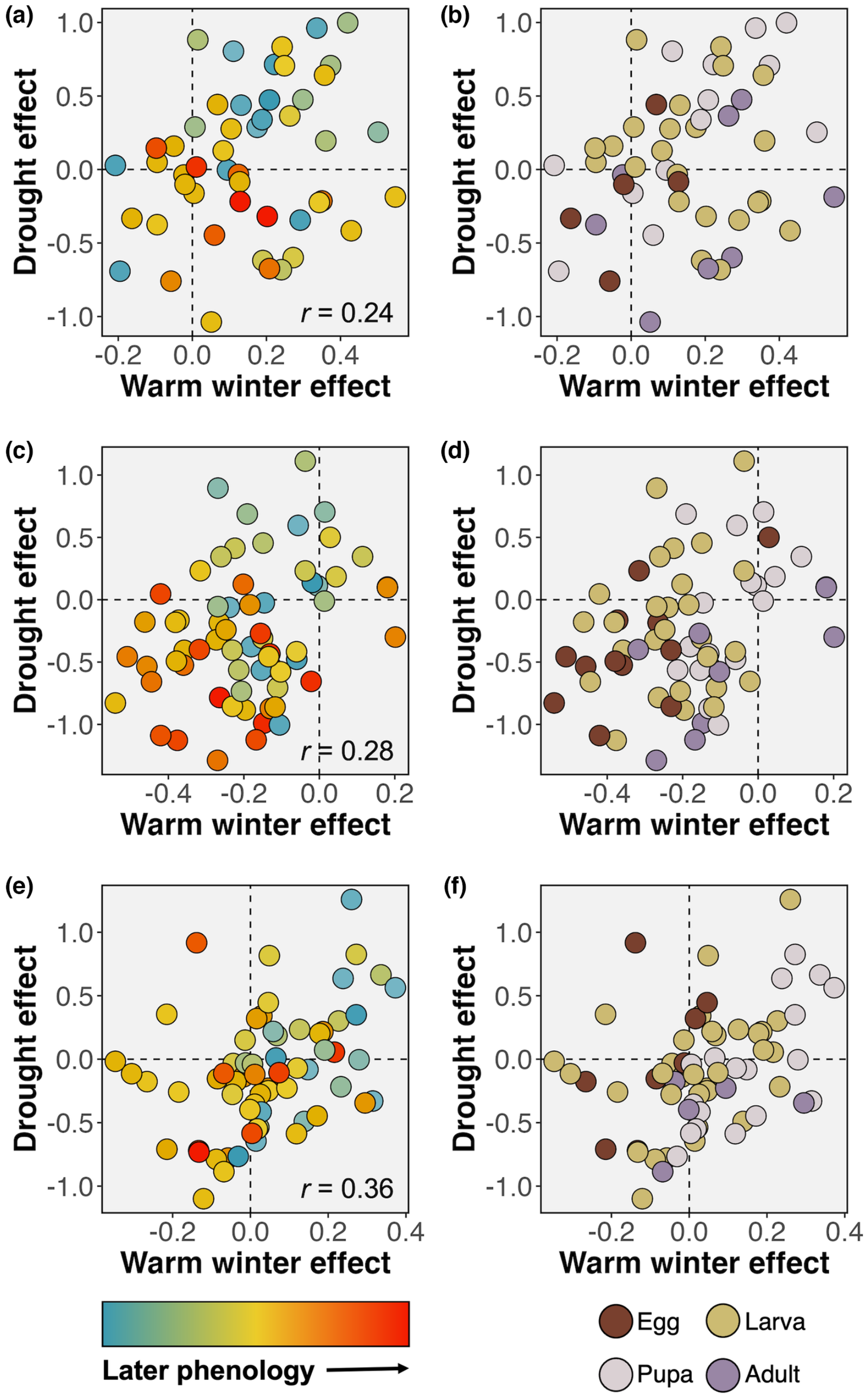

FIGURE 5 Positive relationship between how a species responds to a warmer winter and how a species responded to the 2011–2015 drought at (a, b) Castle Peak, (c, d) Donner Pass, and (e, f) Lang Crossing. Positive values for drought effect indicate that a species did better than its historic average during the years 2011–2015. In panels (a), (c), and (e), points are colored by the average date of when that species has ended its flight at that site. In panels (b), (d), and (f), points are colored by their overwintering stage.

negative effect of NDVI on butterflies, particularly on stages that overwinter as eggs and larvae (.94 pd and .88 pd), that will fly as adults later in the season relative to populations that overwinter as pupae (Figure 6a). Finally, we found support for an interactive effect between April 1 SWE and minimum temperature for populations that overwinter as eggs and larvae (.95 pd and .99 pd; Figure 6a). The interactive combination of both minimum and maximum temperature and April 1 snow (i.e., SWE) is visualized in Figure 6b,c, where years with reduced snow and high minimum temperature greatly reduce the probability of occurrence in the following growing season (Figure 6b), while reduced snow and maximum temperature do not strongly interact (Figure 6c). This is especially informative for the drought, shown with the red point, where the interactive combination of high minimum temperature and low snow reduced the probability of occurrence of juvenile stage overwinter butterflies by over 15% compared with average conditions (Figure 6c). All the parameters in the Donner Pass model converged and the models were a good fit to the data (Table S4, Figure S12).

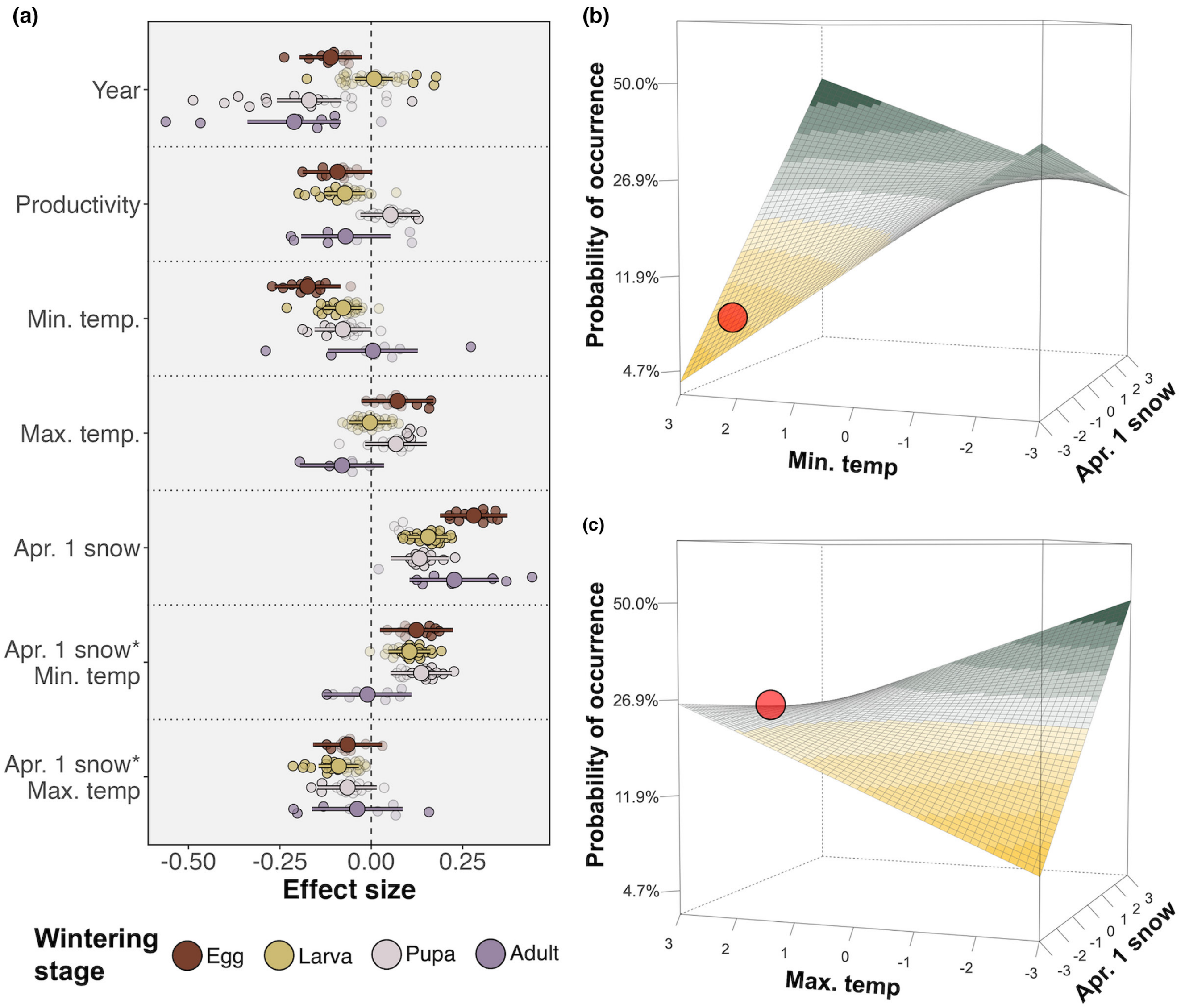

FIGURE 6 Coefficient estimates from the model focusing on Donner Pass. (a) The estimated effect (and 80% credible intervals) of each variable on butterflies. Small colored points show estimates from the lowest level in the hierarchy (a species) and are colored by overwintering stage. Points denoting estimates that are credibly different from 0 at a 0.8 level are opaque. Larger colored points with error bars show the wintering stage-level estimate with 80% credible intervals. (b) Visualization of the interaction between minimum temperature and April 1 snow for eggs and larvae. (c) Visualization of the interaction between maximum temperature and April 1 snow for eggs and larvae. The red point in panels b and c indicates observed conditions during the drought.

4 | DISCUSSION

Butterflies and moths in all landscapes across the world are facing the manifold threats of climate change (Bowler et al., 2017; Harvey et al., 2022; Wagner, Fox, et al., 2021; Wagner, Grames, et al., 2021). Long-term monitoring datasets offer excellent opportunities to better understand the mechanisms underlying population response to shifting and extreme abiotic conditions (Halsch et al., 2021). Here, we found that montane butterfly populations, even those in close geographic proximity to each other, respond in heterogeneous ways to weather (Figure 4). Complex, among-site variation in abiotic effects that are not a simple function of elevation has been observed previously in this system, although using analyses that did not include measures of snow or primary productivity (Nice et al., 2019). In contrast to those heterogeneous effects, we found a strong negative effect of plant primary productivity at all sites and found that many populations respond to winter temperatures (in both the positive and negative direction). The importance of cold season temperatures is consistent with a recent regional analysis of butterflies (Forister et al., 2021), although that study was not designed to disentangle species-specific responses to abiotic conditions. We found that how a population responds to a warm winter predicts how that population fared during a mega-drought, where it appears to be related to the melting of snow, highlighting the importance of the end of winter for montane butterflies (Figures 5 and 6).

A primary motivation behind this work was to explore the role of plant-mediated effects in the decline of butterflies in natural areas. We focused on productivity (as indicated by NDVI), because those data have been collected for a similar length of time to our own butterfly data. This index is imperfect and does not include aspects of plant communities such as shifts in plant composition or functional groups (Pettorelli et al., 2005). Nonetheless, a strong negative effect of NDVI was detected with relative consistency across sites and species (Figure 4). This result is noteworthy given the observed heterogeneity in the responses of individual populations within and among sites to weather conditions. A negative effect of NDVI on animal populations is not without precedent. One of the most important potential effects of climate change on plant–herbivore interactions is that increasing atmospheric carbon dioxide concentrations and temperature will increase C:N ratios in plant tissues, decreasing nutritional quality of leaves (Robinson et al., 2012). Such changing ratios have been demonstrated to be negative for other insect herbivores and are thus a plausible explanation for this result in our data (Welti et al., 2020). Likewise, interannual changes in NDVI may also relate to fluctuations in plant community composition, which, in turn, can affect nutritional resources. In montane meadows of the Sierra Nevada, high NDVI is often associated with greater cover of hydrophilic species such as sedges (*Carex* spp.), which can form dense mats that exclude other plant species such as grasses and forbs (Davis et al., 2020). Interestingly, while NDVI is itself a negative predictor of butterfly population dynamics, it does not have a straightforward relationship to butterflies during the drought years. In fact, primary productivity decreased during the mega-drought so, if anything, butterflies performed even worse during the drought than would be expected given the positive influence of reduced productivity during that period. Given this, it seems likely that multiple processes are at work, and while primary productivity changes may be associated with gradual change, sudden and extreme population disruption is related to other factors or interacts with productivity in ways we do not yet understand.

The effect that was most associated with drought response was how a population responds to warm conditions at the end of winter. We found that elevated temperatures in the months of January to March were broadly associated with changes in the probability of occurrence (both positive and negative) and species that responded the most negatively to those conditions over the long run of decades were also those species that fared the worst during the drought years (Figure 5). This pattern was found at all three sites; however, it was strongest at the two lower elevation sites: Lang Crossing and Donner Pass. Castle Peak, while very close to Donner (<3 km), is a much more heterogeneous landscape, and such topographic variation may buffer populations against warm winters. Our model focusing on Donner Pass suggests that this warm winter effect is most likely due to damaging effects taking place in the winter itself and not a delayed effect realized later in the growing season, although whether this winter stress is on butterflies (especially on juvenile stages), host plants, or both, we cannot determine (Figure 5). The importance of minimum temperature (and not maximum temperature) is particularly insightful as this variable has been linked to direct physiological stress in both butterflies and host plants (Speights et al., 2017). This interpretation is also consistent with other studies that have associated changes in the beginning and end of winter with disruptions of insect populations (Roland & Matter, 2016), particularly in areas where snow cover patterns are shifting from being covered in winter to being exposed (Roberts et al., 2021). Regardless of the mechanism, disruptions to conditions at the end of winter pose a serious risk to overwintering butterflies, particularly those in more uniform landscapes and in early developmental stages.

Climate change encompasses multiple concomitant weather phenomena that vary in space and time. For organisms that have distinct, seasonal life stages, interannual variation in the intensity of climate change is clearly important for understanding which species are most vulnerable (Uhl et al., 2022). Our findings suggest that changing or novel conditions at the end of winter are impactful for montane butterflies, especially those that overwinter in more vulnerable stages such as eggs or early instar caterpillars. However, our results also show that this effect is not universal and that heterogeneous landscapes that contain variation in topography and canopy cover may provide microrefugia capable of buffering some populations from extreme events in a way that is consistent with long-standing ecological theories of resilience in the face of disturbance (McLaughlin et al., 2017), but it is interesting to note how localized and species-specific that effect may be. We also acknowledge that our primary response variable, the binomial probability of occurrence, is derived from repeated presence and absence observations throughout the flight season, and not from counts of individuals. While the probability of observation is a useful proxy for abundance (Casner et al., 2014), it is also intertwined with phenological variation (Forister et al., 2011), and we expect future studies focusing on that interdependency will be productive (Figure 3). Finally, we note that while many of the variables we examined, such as plant primary productivity and the hotness and dryness of fall, are gradually increasing over time (Figure S13), it was an extreme weather event that was the single largest disruptor of populations (Forister et al., 2018). This further demonstrates the importance of extreme weather events, and interactions between temperature and precipitation, in understanding how climate change is impacting populations in natural areas.

AUTHOR CONTRIBUTIONS

Christopher A. Halsch: Conceptualization; data curation; formal analysis; funding acquisition; investigation; methodology; visualization; writing – original draft; writing – review and editing. **Arthur M. Shapiro:** Data curation; investigation; writing – review and editing. **James H. Thorne:** Investigation; writing – review and editing. **Kyle C. Rodman:** Investigation; writing – review and editing. **Adriana Parra:** Investigation; writing – review and editing. **Lee A. Dyer:** Funding acquisition; writing – review and editing. **Zachariah Gompert:** Funding acquisition; methodology; writing – review and editing. **Angela M. Smilanich:** Funding acquisition; writing – review and editing. **Matthew L. Forister:** Conceptualization; data curation; funding acquisition; investigation; methodology; project administration; supervision; writing – review and editing.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data and code that support the findings of this study are openly available in Zenodo at https://doi.org/10.5281/zenodo.10079930.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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