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Beyond annual and seasonal averages: using temporal patterns of precipitation to predict butterfly richness across an elevational gradient

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Abstract. 1. Ecologists often make predictions about community richness and diversity using climate variables that include seasonal precipitation totals and mean daily temperatures. While means and totals can be effective predictors to a certain extent, the complexities of faunal–climate relationships might be over-simplified through the use of coarse-grained variables.

2. The goal of this study was to investigate less commonly studied climate variables, including indices of intra-annual variation in the timing and intensity of precipitation events that might be used to predict butterfly richness across an elevational gradient. Data from a long-term, single-observer dataset at four sites in California were examined with Bayesian model averaging and structural equation modelling. Species-specific responses to climate were compared with community responses at each site.

3. At lower elevations, it was found that the relative importance of climate variables shifted towards temporal patterns of precipitation, including the timing of the first storm event and the annual number of precipitation events. Heterogeneity among sites was apparent in the importance of specific weather variables, and temporal trends (across years) were detected for a small number of variables. Species-specific results paralleled those obtained from analysis of species richness, thus suggesting a commonality of response to climate across site-specific assemblages.

4. Models were improved by inclusion of the Pacific Decadal Oscillation and El Niño-Southern Oscillation indices, indicating that regional variables can profitably be included in faunal–climate relationship analyses. These results emphasise the need for researchers to examine climate variables beyond the most readily summarised means and totals.

Key words. California, El Niño Southern Oscillation, global change, Pacific Decadal Oscillation, phenology, species richness.

Introduction

The impact of a shifting climate on organisms is an issue of primary concern to ecologists and conservation biologists (Walther *et al.*, 2002; Parmesan & Yohe, 2003, 2006; Root *et al.*, 2003), and numerous studies have linked climatic conditions to the distribution and abundance of species (e.g. Thomas & Lennon, 1999; Warren *et al.*, 2001; Perry *et al.*, 2005). Butterflies and moths have been prominent in these studies as well-documented species that are sensitive to climate, both directly and indirectly, through impacts on host species (Dennis, 1993; Pollard & Greatorex-Davies, 1997; Parmesan *et al.*, 1999; Hill *et al.*, 2002; Hanski *et al.*, 2004; Sparks *et al.*, 2006; Powney *et al.*, 2010; Srygley *et al.*, 2010). Most studies of climate change influencing organisms utilise coarse-grained temperature and precipitation variables that are averaged at a seasonal or even annual scale (e.g. Roy *et al.*, 2001; Stefanescu *et al.*, 2004; Schwartz-Tzachor *et al.*, 2008; Forister *et al.*, 2010; Jahner *et al.*, 2012; Swengel & Swengel, 2014). Plants and animals,

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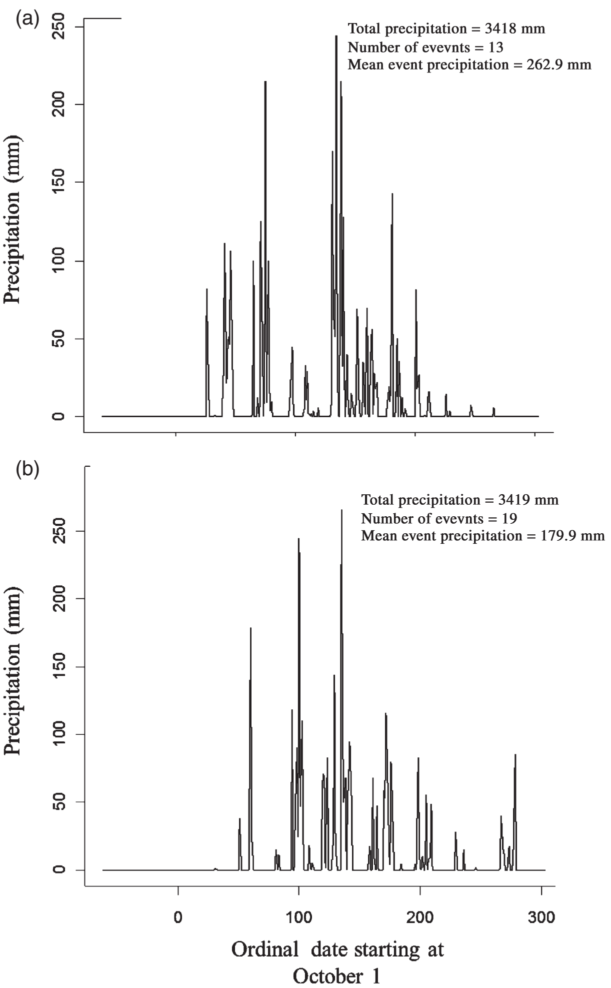

Fig. 1. Examples of the temporal distribution of precipitation in 1973 (a) and 1993 (b) from Suisun Marsh. The total precipitation only differed by 1 mm between the years, but other climate variables differed (e.g. number of events and mean event precipitation).

of course, experience weather daily. Consequently, a focus on coarse-grained variables might overlook key biotic–abiotic relationships (Jentsch *et al.*, 2007; Anderson *et al.*, 2008). For example, total precipitation might be quite similar from one year to another, yet the precipitation patterns underlying these totals can be quite different, as illustrated in Fig. 1 with times series of precipitation from 2 years at one site. Thus, identifying the appropriate temporal and spatial scales at which to study the effects of climate on plants and animals has been highlighted as being of primary importance in the study of global change (Stenseth & Mysterud, 2005).

Temporal patterns of temperature and precipitation, rather than seasonal or annual averages, are probably important to natural populations for numerous reasons (reviewed by Jentsch *et al.*, 2007). The timing of weather patterns can affect vegetation phenology, as individual plants often use temperature and precipitation patterns as cues for when to initiate germination and flowering (e. g. Levine *et al.*, 2008, 2011; Gordo & Sanz, 2010). Additionally, plants might respond to precipitation patterns rather than accumulation over an entire growing season (Knapp *et al.*, 2002; Peñuelas *et al.*, 2004; Sher *et al.*, 2004; Pérez-Camacho *et al.*, 2012), and many small pulses of rain may have a different effect on soil moisture and element cycling than does a single large storm event (e.g. Austin *et al.*, 2004; Huxman *et al.*, 2004). As a consequence, populations of herbivores could be indirectly affected by temporal weather patterns through growth and population dynamics of host plant species (Pollard, 1988; Huberty & Denno, 2004). However, an examination of the impact of temporal patterns in climate variables on butterfly populations has been largely lacking (but see Boggs & Inouye, 2012; Roland & Matter, 2013), which is somewhat surprising considering the interest in linking climate to animal populations.

To address these issues, we utilised a dataset of multi-decadal butterfly observations from multiple sites in northern California spanning an elevational gradient (Shapiro, 2011). Rainfall across the study sites in this Mediterranean climate is highly seasonal (with dry summers and wet winters) and biologically limiting, and thus we can expect that patterns of precipitation might be especially important in this region (Stefanescu *et al.*, 2003). Previous studies using the northern California butterfly dataset have shown that richness has declined in half of the 10 study sites in recent decades, with the greatest decrease in richness at low elevations (Forister *et al.*, 2010; Casner *et al.*, 2014a). Several species have exhibited upward shifts in elevational ranges (Forister *et al.*, 2010), changes in emergence date (Forister & Shapiro, 2003), increased reliance on non-native host plants (Shapiro, 2002; Graves & Shapiro, 2003; Jahner *et al.*, 2011), and rapid declines in population numbers at both low- (Forister *et al.*, 2011) and high-elevation sites (Nice *et al.*, 2014). Taken together, these results indicate that Californian butterflies are responding to ongoing fluctuations in regional climate, potentially including changing precipitation regimes, as well as changes in land-use patterns (Casner *et al.*, 2014a). Consequently, this fauna provides a useful context in which to examine how temporal patterns of precipitation, beyond simple means and totals, might affect butterfly population dynamics.

In this study, we present a detailed analysis of how climate impacts interannual variation in butterfly richness at four sites that had appropriate weather data for our analyses (described further below). We examine rarely utilised variables that describe temporal patterns of precipitation, as well as more commonly utilised variables describing average precipitation and temperature data. Additionally, we explore variables that describe regional climate. We use a model selection approach to select important climatic variables from the larger candidate set examined. Selected variables were then examined more closely in a path analysis framework. Specifically, we address the following questions: (i) do temporal patterns of temperature and precipitation better predict variation in butterfly richness than the more commonly used temperature and precipitation means and totals; (ii) how does the relative importance of climate variables change across low- and high-elevation sites; and (iii) do important climatic variables show any evidence of directional change over the course of the 35 years encompassed by this study? It is important to note that we consider a large suite of predictor variables, and thus we are not performing hypothesis testing or confirmatory analysis (Grace, 2006), but rather an exploration of variables that are not often considered in studies of biotic–abiotic relationships.

Materials and methods

Site description and data collection

Data for the present study were collected as biweekly surveys (every 2 weeks) for the presence and absence of butterfly species along fixed routes at four northern California sites. Species richness for each year was derived from these surveys by counting the number of species that were observed at each site during the sampling period. The four sites are Suisun Marsh, Gates Canyon, Lang Crossing and Donner Pass (hereafter, Suisun, Gates, Lang and Donner respectively). These sites were chosen from the larger dataset of 10 sites, because they have been sampled for more years than other sites and because of the completeness of the weather data at each site (data from many of the local weather stations associated with the other sites were missing large periods of time). All of the sites and associated weather data have been described in detail elsewhere (Thorne *et al.*, 2006; Forister *et al.*, 2010; Shapiro, 2011). At sea level, the plant community at Suisun Marsh is composed of species characteristic of tidally influenced vegetation. Gates is located in the inner Coast Range approximately 70 km from San Francisco (Thorne *et al.*, 2006); the elevation at Gates ranges from <190 to 600 m, with the upper reach dominated by oak woodlands and the lower reach containing riparian communities. At an elevation of 1500–1700 m, Lang is a mid-elevation site with a mix of west-slope Sierran vegetation, including arid-adapted plant species, mesic forest and wet meadow habitat. Donner is the highest site, at an elevation of 2000–2200 m, and spans subalpine-high montane conifer forest (see Table 1 for additional site details).

Climate data

Climate data were collected from four weather stations near transects at individual sites. Near Suisun, a weather station has recorded daily data from 1972 to 2007 (Fairfield station, number 042934 in the US National Weather Service's Cooperative Observer program); at Lang (number 04897) from 1974 to 2010; at Donner (number 049998) from 1974 to 2010; and near Gates from 1976 to 2009. The Gates weather station is located in Vacaville, CA (number 049200), approximately 5.7 km away from the butterfly transect. Because of the distance and differences in topography (which produces orographic effects within Gates Canyon) between the site and weather station, the records of precipitation from the weather station tend to underestimate actual rainfall at Gates. We make the assumption that weather data from the station, which is the closest available, can serve as an index (albeit possibly crude) for weather in Gates Canyon.

Daily weather records were organised into water years, so that the first day of the year was October 1. Due to missing weather data (i.e. extensive gaps in the daily records), 7 years were excluded from Suisun (1977, 1979–1981, 1988, 1996, and 2001), 9 years were excluded from Gates (1978, 1979, 1981, 1985, 1986, 1987, 1988, 1989, and 1990), 8 years were excluded from Lang (1989–1996), and 6 years were excluded from Donner (1979, 1981–1984, and 1986). All precipitation events at Suisun and Gates were considered rainfall (snow is rare at these low-elevation sites). Precipitation events were then identified and quantified for each water year. A single precipitation event was defined as any day, or series of continuous days, with recorded precipitation. Precipitation events were separated by 'gaps', which consisted of the arbitrary increment of at least 3 days of zero precipitation values. Precipitation data were used to create multiple variables, each of which captured differing aspects of within-year precipitation variability (Table 2).

El Niño-Southern Oscillation (ENSO) and Pacific Decadal Oscillation (PDO) indices were also explored as possible predictors of butterfly species richness. Both of these oscillations relate to shifting anomalies in sea surface temperatures that are used in meteorological analyses as indications of trends in regional and hemispheric weather patterns. ENSO generally oscillates on 2- to 10-year intervals, while PDO is longer, at 20- to 30-year intervals (Mantua & Hare, 2002). We used the multivariate ENSO index obtained from NOAA as our approximation of the ENSO (http://www.esrl.noaa.gov/psd/people/klaus.wolter/MEI/). This index is the first principal component generated from a principal components analysis (PCA) of six variables that together describe the ENSO (Wolter & Timlin, 1998). Monthly PDO values were collected from the Joint Institute for the Study of the Atmosphere and Ocean (http://jisao.washington.edu/pdo/PDO.latest). This index consists of the first principal component of a PCA of monthly sea surface temperature anomalies in the North Pacific Ocean

Table 1. Basic description of the four sites included in the analysis. Years sampled is the total number years that were included in the analysis. Richness is the number of species observed in that sampling period.

Site	Years sampled	Habitat type	Elevation (m)	Mean richness	Richness SE	Minimum richness	Maximum richness
Suisun Marsh	29	Tidal community	0	35.5	0.6	26	41
Gates Canyon	25	Oak woodlands/riparian	190–600	57.8	0.8	45	63
Lang Crossing	29	Mesic forest/wet meadow	1500–1700	68.6	1.4	47	85
Donner Peak	30	Montane chaparral/alpine conifer forest	2000–2200	77.4	1.1	63	90

Table 2. Candidate variables examined during Bayesian model averaging (sampling year based on the water year, starting October 1).

Variable name	Definition
Coefficient of variation (CV)	Coefficient of variation of the days without rain recorded for sampling year
ENSO	Averaged monthly ENSO index for the sampling year
ENSO t-1	Averaged monthly ENSO index for the previous sampling year
ENSO t-2	Averaged monthly ENSO index for the sampling year 2 years prior
First event date	Ordinal date of the first recorded precipitation event
First multiday event	Ordinal date of the first recorded multiple day precipitation event
First snow	Ordinal date of the first snow event
Growing degree day (GDD)	Number of growing degree days for winter and spring of water year, base 10 °C
Largest event precipitation	Total precipitation in the largest event
Last snow	Ordinal date of the last snow event of the sampling period
Longest event	Number of days in the largest event
Longest gap	Longest recorded number of days between events
Maximum temperature	Annual average daily maximum temperature
Mean event	Mean number of days per event
Mean event precipitation	Mean precipitation per event
Mean gap	Mean number of non-precipitation days between events
Minimum temperature	Annual average daily minimum temperature
Number of events	Total number of precipitation events
PDO	Averaged monthly PDO index for the sampling year
PDO t-1	Averaged monthly PDO index for the previous sampling year
PDO t-2	Averaged monthly PDO index for the sampling year 2 years prior
Total precipitation	Total precipitation for the sampling year
Visits	Number of visitations to the site by the observer
$Visits^2$	Squared term of the number of visitations to the site by the observer
Year	Sampling year of record

ENSO, El Niño-Southern Oscillation; PDO, Pacific Decadal Oscillation.

(Zhang *et al.*, 1997 for PDO). For each index, monthly values were averaged for each water year included in this study to generate a single value describing the intensity of the oscillation for that year. Additionally, the two water years prior to a particular year were also used in the analysis in order to model a potential lag effect (labelled ENSO t-1, ENSO t-2, PDO t-1 and PDO t-2, respectively).

Other variables examined were annual average daily maximum temperature (‘maximum temp.’) and annual average daily minimum temperature (‘minimum temperature’), both of which have previously been used with this dataset (Forister *et al.*, 2010). Additionally, we calculated the growing degree days during winter and spring of each water year as a measure of thermal accumulation for each site with a base of 10 °C.

Statistical analysis

Species richness was chosen as the primary response variable, as we were interested in community-level effects, as opposed to species-specific responses to climate variables. Previous analyses of the data show that population abundances correlate well with binary presence/absence data from which richness is calculated (Casner *et al.*, 2014b). Once all candidate predictor variables were compiled, the list was narrowed to reduce potential collinearity. Pairwise correlations were examined among all variables. If the correlation coefficient was greater than 0.75, one of the variables was removed from the analysis. Of two competing variables, we retained the one that was inherently more interesting from a biological perspective. In some cases, where the removal of one of the correlated variables could not be biologically justified, a *post hoc* analysis was conducted replacing the correlated variables with each other in a multiple regression analysis and using Akaike information criterion (AIC) and R^2 values to determine which variable was most likely to be important in subsequent modelling. The number of visits per year was included to account for variation in sampling effort among years. In addition, the quadratic component of visits was included, which allows for a relationship between richness and visits that plateaus (i.e. the relationship reaches a point past which more species are not observed with increasing visits; Forister *et al.*, 2010). All variables were treated as fixed effects in the Bayesian linear regression models that were derived.

Model averaging for species richness was done using the Bayesian model selection package (BMS) in R (Feldkircher & Zeugner, 2009; R Development Core Team, 2013). The BMS package was used to calculate the posterior inclusion probability (PIP) and standardised posterior mean coefficient (PMC) for all variables. The prior probability for the model size was set using the default, which uses the median of the number of available parameters and draws from a normal distribution (of the number of possible parameters).

Variables with PIP values >0.5 were further examined using structural equation models (SEMs; Grace, 2006). This allowed us to estimate and examine the regression coefficients associated with each variable and compare direct as well as indirect effects of predictor variables on the response (butterfly species richness). A different SEM was constructed for each site.

Additional variables included in the SEMs were year, visits and visits^2. These additional variables were included without consideration of their inclusion probability. Year was included in models to examine temporal patterns in climate data over the course of the study, and to examine indirect effects that year might have on butterfly richness as mediated through weather variables. SEMs were created in package LAVAAN in R (Rosseel, 2012; R Development Core Team, 2013). Owing to differences in variance among predictor variables, all data were standardised using the *z*-score.

In order to compare community-level results with general trends among individual species, we also examined the species-specific effects of each model variable. For each site, those variables with PIPs > 0.5 were used to examine presence/absence data for each species using a generalised linear model (GLM). This GLM utilised a binomial response consisting of the proportion of presences for a given species out of the total number of site visits made during that year. Rare species (those that appeared fewer than 10 times at a site across the study period) were omitted from this analysis, as they caused the GLM models to separate linearly. For each site, partial regression coefficients for all species were compiled and the mean and variance of those coefficients were calculated. This allowed us to compare the aggregate of species-specific responses to a given weather variable with the observed relationship between that variable and species richness (from analyses described earlier).

Results

A complex suite of climate variables was supported for each of the sites by the Bayesian modelling procedures (Fig. 2). At the two lower sites, Suisun and Gates, the relationship between climate and richness was more complex than at the higher sites, Lang and Donner (Table 2). Regional patterns of climate, indicated by the inclusion of the PDO and ENSO indices, were strongly supported at both Suisun and Gates. Additionally, support for the lagged ENSO effect at Gates, Lang and Donner indicates the presence of legacy climate effects (i.e. carryover from previous years) on butterfly richness. Localised temporal patterns were also well supported at each site. At Suisun, richness patterns were in part driven by the number of events as well as the timing of the first event in a water year, while at Gates, the single greatest precipitation event (i.e. largest event precipitation) and temporal distributions of rain events had a large impact on richness (Fig. 2).

In general, the effect of predictor variables on species richness and on species-specific variation showed similar directionality (Tables 2 and 3). Consistency of response (between effects on richness and species-specific effects) is particularly evident for variables with the strongest effects (e.g. PDO at both Gates and Suisun has a noticeably positive effect on both richness and individual species). In other cases, an effect on richness becomes more complicated when species-specific effects are examined: consider, for example, the largest event precipitation at Gates, which has a strong negative effect on richness, but a weakly negative average effect (with a large variance) across individual species.

Bayesian model averaging

For Suisun, 12 of the 18 variables examined had a PIP > 0.5. These included a combination of all climate variable types (Fig. 2). Of the climate variables, PDO t-1 and PDO had the highest inclusion probabilities, both > 0.99. Year, visits and visits^2 all had PIP values of at least 0.95, indicating strong support for their ability to explain variance in butterfly richness at Suisun. The standardised posterior mean coefficients indicated that year had a strong negative effect on richness with a value of −0.494 and, of the climate variables, PDO had the strongest effect with a value of 0.545 (Table 3).

The BMS analysis for Gates illustrates inherent differences between biotic–abiotic interactions at the two lower-elevation study sites. Seven variables had PIPs > 0.5 (Table 3). PDO and the largest event precipitation had the largest standardised coefficients among the climate variables but the signs of the coefficients were opposite: 0.657 and −0.530, respectively. Unlike at Suisun, year had little support in the Gates dataset (PIP = 0.242 and PMC = −0.021). The latter result is presumably because the fauna at Gates is relatively stable as compared with the butterflies at Suisun, which are part of a regional, low-elevation decline associated with land-use change (Forister *et al.*, 2011).

At Lang, seven variables had PIPs > 0.5 (Table 3). Among the climate variables, the longest event had the largest PIP (0.772), although minimum temperature had the greatest PMC at 0.457. Year had a strong negative effect in the BMS analysis with a PIP of 0.958 and a PMC of −0.861, indicating a strong decline in richness over the course of the study. Like Gates, the relatively large PIP of a lagged ENSO variable indicates potential legacy effects of climatic patterns among years.

Overall, effects of weather on richness were weakest at Donner; only two variables, last snow and visits^2, had PIPs > 0.5, and only four climate variables (last snow, ENSO t-1, ENSO t-2, and PDO t-1) had PMCs > 0.1 (Table 3; Fig. 2). Of the climate variables, last snowfall had the highest PMC, at 0.179. Year had a slight negative effect (PIP = 0.148 and PMC = −0.022).

Structural equation modelling

For Suisun, SEM analysis demonstrated that all variables had significant direct effects on butterfly richness (Fig. 3a). As with the BMS analysis, year had a strong and direct negative effect on butterfly richness (standardised estimate = −0.426, Table S1). Of the climate variables, PDO had the highest regression coefficient (standardised estimate = 0.565). Year had significant direct effects on two climate variables – first event date and minimum temperature – indicating temporal trends in these variables over the course of the study period. The positive regression estimate of year on first event date indicates a shift towards the first event being later in the water year. Additionally, the SEM indicated that Suisun has been warming in terms of minimum temperatures. Year also had a moderate, positive, indirect effect on richness (standardised estimate = 0.293), mediated through the other variables.

Analysis of the Gates data confirmed that all the variables, with the exception of year, had significant direct effects on butterfly richness (Fig. 3b). Among the climate variables, PDO

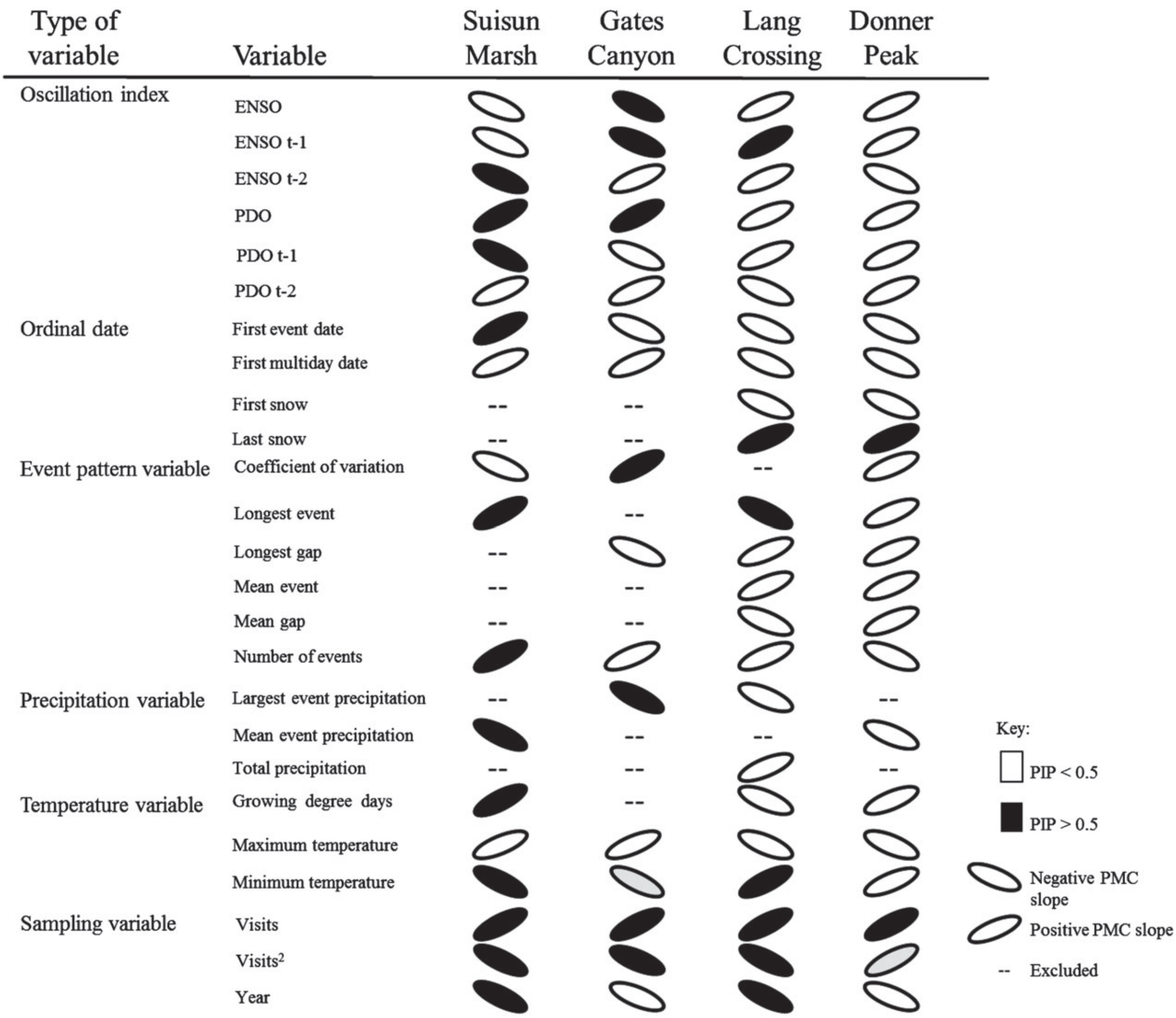

Fig. 2. Across-site comparison of the posterior inclusion probabilities (PIPs) and estimates of standardised posterior mean coefficients (PMCs) for each variable. The variables are separated into six categories: oscillation index, ordinal date, event pattern variables, precipitation variables, temperature variables and sampling variables. Thin bubbles indicate PIPs < 0.5; thick bubbles indicate PIPs > 0.5. Filled-in bubbles indicate positive PMC values; open bubbles indicate negative PMC values. ENSO, averaged monthly El Niño-Southern Oscillation index for the sampling year; ENSO t-1, averaged monthly ENSO index for the previous sampling year; ENSO t-2, averaged monthly ENSO index for the sampling year 2 years prior; PDO, averaged monthly Pacific Decadal Oscillation index for the sampling year; PDO t-1, averaged monthly PDO index for the previous sampling year; PDO t-2, averaged monthly PDO index for the sampling year 2 years prior.

had the highest positive regression coefficient (standardised estimate = 0.695; Table S2). Year had an indirect effect of 0.577, probably mediated through visits and visit^2, as year did not significantly affect any of the climate variables.

Of variables included in the SEM for Lang, only last snow was insignificant for richness (Fig. 3c). Of the climate variables, minimum temperature had the greatest impact on richness with a standardised estimate of 0.317 (Table S3). The positive effect of minimum temperature on richness may help to explain the high indirect effect year had on richness (standardised estimate = 0.803), which was the strongest indirect effect of year across all four study sites. The direct effect of year on richness was also strong, but negative (standardised estimate = −0.799). Among the climate variables, year only had a significant effect on minimum temperature (Fig. 3c).

At Donner, only last snow had a significant effect on richness (Fig. 3d; standardised estimate = 0.323). Unlike Lang, the next highest site, year had a very weak direct and indirect effect on richness at Donner (standardised estimate = −0.009, Table S4). Donner was the only site where visits and visits^2 were not significant variables for the site SEM.

Discussion

Our study highlights the importance of temporal patterns of climate for understanding fluctuations in butterfly species richness

Table 3. Results from Bayesian model averaging analyses for Suisun Marsh, Gates Canyon, Lang Crossing and Donner Pass. Shown are posterior inclusion probabilities (PIPs) and estimates of standardised posterior mean coefficients (PMCs) for each variable. Snow was not observed at Suisun Marsh or Gates Canyon. For variables that do not have an estimation, those variables were removed from the model averaging due to high correlation (> 0.75) with another climate variable.

	Suisun Marsh		Gates Canyon		Lang Crossing		Donner Pass	
Variable	PIP	PMC	PIP	PMC	PIP	PMC	PIP	PMC
Coefficient of variation	0.347	−0.021	0.850	0.423	–	–	0.115	0.013
ENSO	0.279	−0.007	0.912	−0.431	0.397	0.071	0.232	0.042
ENSO t-1	0.195	−0.011	0.769	−0.294	0.585	0.125	0.424	0.121
ENSO t-2	0.533	−0.119	0.320	0.039	0.321	0.092	0.446	−0.149
First event date	0.860	0.342	0.382	−0.125	0.175	−0.021	0.241	−0.037
First multiday event	0.342	0.068	0.334	0.068	0.254	−0.018	0.158	−0.017
First snow	–	–	–	–	0.231	−0.018	0.220	−0.025
Growing degree day	0.842	0.333	–	–	0.284	−0.025	0.186	0.014
Largest event precipitation	–	–	0.948	−0.530	0.287	−0.075	–	–
Last snow	–	–	–	–	0.519	0.117	0.555	0.179
Longest event	0.860	0.367	–	–	0.772	−0.236	0.170	0.002
Longest gap	–	–	0.278	−0.043	0.263	0.048	0.214	−0.015
Maximum temperature	0.255	0.044	0.271	0.041	0.320	−0.063	0.322	−0.083
Mean event	–	–	–	–	0.266	0.003	0.249	0.065
Mean event precipitation	0.705	−0.220	–	–	–	–	0.239	−0.047
Mean gap	–	–	–	–	0.356	−0.043	0.177	0.033
Minimum temperature	0.896	−0.422	0.240	−0.017	0.661	0.457	0.223	0.004
Number of events	0.960	0.428	0.188	0.006	0.274	0.021	0.335	−0.071
PDO	0.991	0.545	0.947	0.657	0.391	0.081	0.165	0.013
PDO t-1	0.996	−0.490	0.445	−0.119	0.212	0.014	0.413	0.143
PDO t-2	0.236	0.038	0.204	0.015	0.336	−0.106	0.239	0.039
Snow fall	–	–	–	–	–	–	–	–
Total precipitation	–	–	–	–	0.271	0.073	–	–
Visits	1.000	4.041	1.000	5.233	0.991	1.529	0.535	0.234
Visits^2	0.998	−3.148	1.000	−4.595	0.503	−0.567	0.462	0.198
Year	0.955	−0.494	0.242	−0.021	0.958	−0.861	0.148	−0.022

ENSO, averaged monthly El Niño-Southern Oscillation index for the sampling year; ENSO t-1, averaged monthly ENSO index for the previous sampling year; ENSO t-2, averaged monthly ENSO index for the sampling year 2 years prior; PDO, averaged monthly Pacific Decadal Oscillation index for the sampling year; PDO t-1, averaged monthly PDO index for the previous sampling year; PDO t-2, averaged monthly PDO index for the sampling year 2 years prior.

among years and sites. We find that biotic–abiotic relationships vary greatly across an elevational gradient, which is likely to be especially true for Mediterranean climates where water stress can play a large role in determining species richness (Stefanescu *et al.*, 2004, 2011). At both the lower sites used in this study (Suisun and Gates), variables that describe temporal patterns of precipitation (e.g. first event date) or regional conditions (e.g. PDO and ENSO) received more support than temperature variables. At Suisun, variables such as the number of events and the first event date were well supported climate variables relating to butterfly richness. Both of these factors may have direct and indirect impacts on butterfly communities. Indirectly, increasing the number of water events throughout the water year may alleviate water stress on host plants, resulting in increased success of developing caterpillars, higher densities of adults and, consequently, greater observed species richness. The first event date is likely to indirectly impact butterfly richness through earlier blooming and increased productivity of host plants (Pitt & Heady, 1978; Levine *et al.*, 2008, 2011). And while the commonly used variable minimum temperature was supported at Suisun, growing degree days was also an important predictor. Recent research has suggested that growing degree days can be useful when modelling insect population dynamics because the accumulation of temperature potentially has a direct mechanistic effect on, for example, specific developmental stages that need a certain number of warm days for successful completion (Cayton *et al.*, 2015).

At Gates, timing of precipitation throughout the year was not nearly as important as the single largest event, which had the largest PIP (PIP = 0.948 and PMC = −0.530) of any climate variable. The average first date of the largest event was January 10 at Gates, ranging between October 9 and February 27. These dates fall during a period before most species have begun flying (Thorne *et al.*, 2006). The negative effect of largest event precipitation could be explained by the timing of these events in relation to development and other life-history stages of the butterflies. Fordyce and Shapiro (2003) demonstrated that smaller *Battus philenor* larvae have higher mortality when developing in cooler temperatures. Prolonged periods of precipitation are associated with higher cloud cover, resulting in lower insolation rates. Large events would produce wetter, cooler conditions than normal, which in turn could increase mortality among butterflies

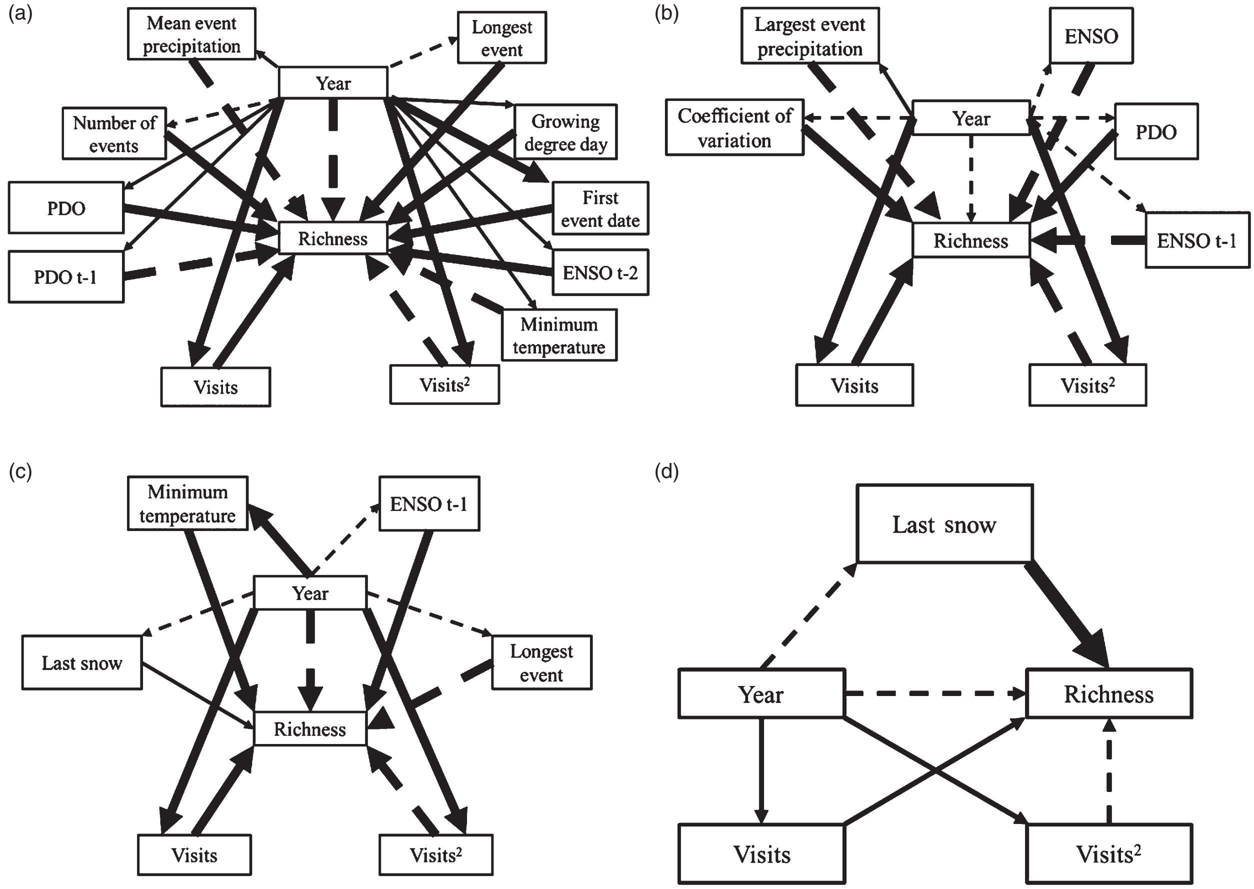

Fig. 3. Structural equation models for butterfly richness at: (a) Suisun Marsh; (b) Gates Canyon; (c) Lang Crossing; and (d) Donner Pass. Solid lines indicate positive relationships; dashed lines indicate negative relationships. The thickest lines indicate paths being significant at $\alpha = 0.05$. Each SEM was constructed using the variables that had a posterior inclusion probability greater than 0.5 from the Bayesian model averaging as well as the visits, visits^2 and year. Note that the covariance among all climate variables was included in each SEM and covariance between 'visits' and 'visits^2' was modelled as well.

still in larval stages. Additionally, large events increase stream flow at Gates and elevate the risk of flash floods or debris flows (A. M. Shapiro, pers. obs.). These disturbance events could also cause higher mortality among caterpillars.

Lang is interesting as it represents the only site where a temperature variable had the highest coefficient for both the BMS and SEM analyses (minimum temperature), although other temporally explicit precipitation variables, including longest event, were significant as well. Higher minimum temperatures may place less thermoregulatory stress on butterflies, whereas the longest event may improve host plant vigour. The importance of both precipitation and temperature variables reinforces the role of these types of climate variables at intermediate elevations, especially at the junction of the Mediterranean and high-montane climates.

At the highest-elevation site, Donner, only last snow had a PIP > 0.5 among climate variables. Last snow may relate to moisture availability for plants, as late snow events could alleviate water stress longer into the summer season. Donner is also interesting as it is one of the most diverse butterfly assemblages in the United States (Emmel & Emmel, 1963); the average yearly richness was 76.2 species at Donner compared with 57.3 at Lang, 57.8 at Gates, and 35.4 at Suisun. The wide range of life-history strategies and the variation in phenology among species present in the Donner butterfly fauna may be behind the apparently weak relationship between richness and climate variables at that site (Nice *et al.*, 2014).

Of the regional climate variables, PDO had a strong association with richness at both Suisun and Gates, with ENSO also receiving support at Gates. PDO and ENSO are known to impact a variety of ecological systems (Holmgren *et al.*, 2001), including those as disparate as Pacific fisheries (Mantua *et al.*, 1997), zooplankton species composition (Keister *et al.*, 2011), rodent outbreaks (Lima *et al.*, 1999), and the timing of flowering in plants in the western United States (Cayan *et al.*, 2001). Other studies have observed significant impacts of both ENSO and PDO on butterfly populations in relation to abundance (Vandenbosch, 2003) and the size of migration (Srygley *et al.*, 2010) for single species. Unlike the other climate variables, PDO and ENSO relate to the regional climate as opposed to localised weather conditions. In northern California, positive ENSO periods are associated with increased winter and spring precipitation

(Preisser & Strong, 2004, but see Schonher & Nicholson, 1989). While increased precipitation may increase host plant growth, negative effects of prolonged precipitation or cloud cover can be associated with negative effects, such as increasing parasitism (Preisser & Strong, 2004). The strong effects associated with PDO potentially reflect the importance of this variable for creating favourable conditions throughout the Central Valley and coastal ranges of California. This may include earlier blooming times and increased run-off (Cayan *et al.*, 2001). Interestingly, PDO t-1 had a significant, negative effect on richness at Suisun, indicating potential lagged effects of climate variables on community dynamics. Favourable conditions in the previous year, as indicated by a positive PDO index, might cause negative density dependence in the following year. Inclusion of both PDO and PDO t-1 reinforces the notion that researchers should investigate ecological data on several scales, not just localised variables.

At all of the sites, year had an overall negative relationship with butterfly richness, with the effect being especially strong at Suisun and Lang. We assume that the downward yearly trend is, in part, driven by factors outside of climate-related variables, such as loss of habitat (Casner *et al.*, 2014a). It is also possible that some effects of a changing climate are not directly affecting butterflies, but rather are affecting host plants (e.g. Boggs & Inouye, 2012). Year had strong direct effects on several climate variables, indicating shifting means for these variables over the study period consistent with the effects of global climate change on this system. Interestingly, year had a positive, and in some instances rather strong, indirect effect (mediated through climate variables) on richness at all four sites.

The results from all four sites suggest that the effect of climate on richness changes across an elevational gradient. Not only does the importance of individual climate variables vary across all four sites, but the number of associated variables also changes across sites. The two lowest sites, Suisun and Gates, had nine and five climate variables with PIPs > 0.5 respectively. This contrasts with the two higher sites, Lang and Donner, where four and one climate variables had PIPs > 0.5, respectively. While several studies have looked at butterfly richness across elevational gradients (e.g. Wilson *et al.*, 2007; Forister *et al.*, 2010; Despland *et al.*, 2012), potential interactions between climate and elevation are less commonly studied. Phenological studies have indicated that flight times vary across elevational gradients (Gutiérrez Illián *et al.*, 2012; Despland *et al.*, 2012), and these studies tend to assume differences in temperature as drivers of phenological variation across elevations. While elevation and weather variables are often highly correlated, we find that climatic effects change in complex ways among the sites we studied, which at least suggests caution in assuming effects of temperature as a sole driver in the context of population dynamics along elevational gradients. We have focused on species richness for simplicity and because it is a simple summary statistic that is of biological interest. However, we have also made a preliminary investigation into species-specific responses (Table 4), which revealed a general consistency (between faunal and species-specific dynamics) but also a degree of complexity that should be addressed in future research.

While it should be noted that we were unable to account for differences in detection probabilities among the sites, this study presents evidence that more traditional variables, such as temperature and seasonally averaged precipitation, may not always be the most effective tools for investigating complex faunal–climate relationships, especially across a range of elevations and topographies. Additional work is needed at other sites and environments to elucidate the role of temporal patterns of precipitation on richness. This is especially true as researchers continue to make predictions about population dynamics in the light of climate change. Although variables such as temperature and seasonal precipitation are clearly still important and may be the only variables that are available for a given study, researchers should explore the role of other weather variables whenever possible.

Table 4. Summary statistics of partial regression coefficients (β) obtained through inputting terms selected through Bayesian model averaging (see Table 3) into site- and species-specific generalised linear models. Coefficients were tabulated from each species on a per-site basis, and mean and variance of those coefficients calculated. Rare species were omitted from these analyses because their inclusion causes models to separate linearly.

Site	Model term	Mean of β	Variance in β
Suisun	ENSO t-2	**−0.002**	0.108
	First event date	**0.002**	< 0.001
	Growing degree day	**0.001**	< 0.001
	Longest event	**0.009**	< 0.001
	Mean event precipitation	**−0.002**	< 0.001
	Minimum temperature	**−0.025**	0.037
	Number of events	**0.032**	0.016
	PDO	**0.134**	0.073
	PDO t-1	**−0.035**	0.177
	Visits	**0.177**	0.105
	Visits^2	**−0.003**	< 0.001
	Year	**−0.029**	0.002
Gates	CV	**0.565**	2.063
	ENSO	**−0.045**	0.247
	ENSO t-1	**−0.190**	0.100
	Largest event precipitation	**−0.000**	< 0.001
	PDO	**0.231**	0.152
	Visits	**0.256**	0.481
	Visits^2	**−0.006**	0.000
Lang	ENSO t-1	**0.096**	0.046
	Minimum temperature	**0.050**	0.038
	Last snow	**0.002**	< 0.001
	Longest event	**−0.004**	0.000
	Visits	**0.132**	0.110
	Visits^2	**−0.005**	0.000
	Year	**−0.017**	0.001
Donner	Last snow	**0.004**	< 0.001
	Visits	−0.03	0.003

CV, coefficient of variation; ENSO, averaged monthly El Niño-Southern Oscillation index for the sampling year; ENSO t-1, averaged monthly ENSO index for the previous sampling year; ENSO t-2, averaged monthly ENSO index for the sampling year 2 years prior; PDO, averaged monthly Pacific Decadal Oscillation index for the sampling year; PDO t-1, averaged monthly PDO index for the previous sampling year; PDO t-2, averaged monthly PDO index for the sampling year 2 years prior.
Values in bold type indicate that the β value had a similar sign to posterior mean coefficients from the Bayesian model analysis.

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Supporting Information

Additional Supporting Information may be found in the online version of this article under the DOI reference: 10.1111/een.12228

Table S1. The estimated regression coefficients for the SEM at Suisun Marsh.

Table S2. The estimated regression coefficients for the SEM at Gates Canyon.

Table S3. The estimated regression coefficients for the SEM at Lang Crossing.

Table S4. The estimated regression coefficients for the SEM at Donner Pass.

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