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Contribution of Urban Expansion and a Changing Climate to Decline of a Butterfly Fauna

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Abstract: *Butterfly populations are naturally patchy and undergo extinctions and recolonizations. Analyses based on more than 2 decades of data on California's Central Valley butterfly fauna show a net loss in species richness through time. We analyzed 22 years of phenological and faunistic data for butterflies to investigate patterns of species richness over time. We then used 18–22 years of data on changes in regional land use and 37 years of seasonal climate data to develop an explanatory model. The model related the effects of changes in land-use patterns, from working landscapes (farm and ranchland) to urban and suburban landscapes, and of a changing climate on butterfly species richness. Additionally, we investigated local trends in land use and climate. A decline in the area of farmland and ranchland, an increase in minimum temperatures during the summer and maximum temperatures in the fall negatively affected net species richness, whereas increased minimum temperatures in the spring and greater precipitation in the previous summer positively affected species richness. According to the model, there was a threshold between 30% and 40% working-landscape area below which further loss of working-landscape area had a proportionally greater effect on butterfly richness. Some of the isolated effects of a warming climate acted in opposition to affect butterfly richness. Three of the 4 climate variables that most affected richness showed systematic trends (spring and summer mean minimum and fall mean maximum temperatures). Higher spring minimum temperatures were associated with greater species richness, whereas higher summer temperatures in the previous year and lower rainfall were linked to lower richness. Patterns of land use contributed to declines in species richness (although the pattern was not linear), but the net effect of a changing climate on butterfly richness was more difficult to discern.*

Keywords: biodiversity, climate, generalized additive model, land use, Lepidoptera, species richness

Contribución de la Expansión Urbana y un Clima Cambiante a la Declinación de la Fauna de Mariposas

Resumen: *Las poblaciones de mariposas por naturaleza son fragmentadas y pasan por extinciones y recolonizaciones. Análisis basados en más de dos décadas de datos sobre la fauna de mariposas del Valle Central de California muestran una pérdida neta en la riqueza de especies a través del tiempo. Analizamos 22 años de datos fenológicos y faunísticos sobre mariposas para investigar patrones de riqueza de especies a lo largo del tiempo. Después usamos 18–22 años de datos sobre cambios en el uso regional de suelo y 37 años de datos de clima temporal para desarrollar un modelo explicativo. El modelo relacionó a los efectos de los cambios en los patrones de uso de suelo, de paisajes de trabajo (granjas y ranchos) a paisajes urbanos y sub-urbanos, y al clima cambiante sobre la riqueza de especies de mariposas. Además, investigamos las tendencias locales de uso de suelo y el clima. Una declinación en el área de suelo para granjas y ranchos y un incremento en las temperaturas mínimas durante el verano y las temperaturas máximas durante el otoño afectaron negativamente la riqueza neta; mientras que el incremento en temperaturas mínimas en la primavera y una mayor precipitación en el verano previo afectaron positivamente la riqueza de especies. De acuerdo al modelo,*

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hubo un umbral entre el 30% y 40% del área de paisaje de trabajo por debajo del cual una mayor pérdida de área de trabajo-paisaje tiene un efecto proporcionalmente mayor en la riqueza de mariposas. Algunos de los efectos aislados de un clima cálido actuaron en oposición para afectar la riqueza de mariposas. Tres de las cuatro variables climáticas que más afectaron la riqueza mostraron tendencias sistemáticas (la primavera y el verano significan temperaturas mínimas y el otoño significa temperaturas máximas). Las temperaturas mínimas en primavera estuvieron asociadas con una mayor riqueza de especies, mientras que las temperaturas más altas en el verano en el año previo y una precipitación más baja estuvieron relacionadas con una riqueza más baja. Los patrones de uso de suelo contribuyeron a la declinación en riqueza de especies (aunque el patrón no fue lineal), pero el efecto neto de un clima cambiante sobre la riqueza de mariposas fue más difícil de discernir.

Palabras Clave: biodiversidad, clima, Lepidoptera, modelo aditivo generalizado, riqueza de especies, uso de suelo

Introduction

Many butterfly species naturally occur in fragmented, local populations in which extinctions and recolonizations are expected (Moilanen & Hanski 1998). This, in turn, means that the composition of any butterfly fauna is dynamic, gaining and losing species over time (Hanski 1998). If local population dynamics become unbalanced through changes in the landscape or other factors and stresses within patches intensify rates of local extinctions will exceed those of recolonization (Wilson et al. 2009).

Like many organisms, butterflies are sensitive to climate (Dennis & Sparks 2007). In climatically favorable years, abundances are regionally high, and there is likely dispersal into nearby habitat that might not normally be occupied. This dispersal elevates species richness of sites throughout the region (Gonzalez & Holt 2002). During unfavorable years, local populations likely survive only in areas where microhabitats provide suitable conditions (Singer 1972). As habitat patches become more disconnected and distant from other population sources and the landscape between patches becomes more unfavorable, rescues and recolonizations occur less frequently (Pulliam 1988). As sites become more isolated, local effects dominate and population persistence can become a site-by-site matter, thus lowering richness locally.

Therefore, the species composition and richness of a site in any given year is a result of weather (Dennis & Sparks 2007), the regional species pool (Caley & Schluter 1997), and the ability of that regional species pool to disperse (Harrison & Cornell 2008). Landscapes are not split dichotomously into habitat and nonhabitat (Dennis et al. 2006); rather, they comprise a spectrum of land uses with varying capacities to support native and naturalized faunas. Permeability and characteristics of areas surrounding habitat patches are important to richness and the composition of the fauna within patches (Öckinger et al. 2012). Agricultural plots (Thomas 1984) and weed lots (Shapiro 2002b) serve as corridors and habitat for many native California butterflies.

California butterfly faunas are subject to 2 potentially conflicting pressures: changing climate, which is shifting geographic ranges, and land-use changes, which are fragmenting and contracting habitat (Forister et al. 2010). When agricultural development began in California's Central Valley in the mid 1800s, land was converted to farms and ranches, and much of the native biodiversity was displaced by agricultural crops and livestock (McGowan 1961). A second transition is currently occurring in which agricultural land is being replaced by suburban development, again changing the composition and richness of plant and animal communities. Additionally, temperatures in California have risen an average of 0.93 °C between 1895 and 2011 and are projected to rise an additional 1.5 °C by 2050 (Moser et al. 2012). We analyzed 22 years of phenological and faunistic data collected for butterflies, 18–22 (depending on the site) years of data on changes in regional land use, and 37 years of seasonal climate data. Long-term data sets are useful for analyzing trends over time and gaining insight into causal relationships.

A number of researchers have used this data set, and their publications provide a broad look into the population dynamics and trends of select populations. Forister et al. (2010) used coarse, county-wide data on land use and annual average temperatures to study the effect of climate and land use on California butterflies. O'Brien et al. (2011) and Thorne et al. (2006) studied inter- and intraannual, respectively, trends in species richness and diversity within single sites. Forister et al. (2011) examined species traits associated with extinction risk among 3 of the 4 faunas that we considered here. At a fine scale, we investigated faunistic trends at 4 sites with varying levels of change in agricultural-urban land use and with variation in climate in space and time. By including site-specific variables for each fauna monitored, we developed a model that addressed the relationships among land use, climate, and species richness. Additionally, because butterflies are seasonal, and the California climate is not expected to change evenly across seasons (Cayan et al. 2008), we considered

responses in butterfly richness to interannual seasonal climate variation and climatic trends. We investigated the consequences of prevailing changes in land use and climate on butterfly richness within a single model so that both the relative and absolute effects of these forces would be apparent. To this end we asked, how does climate affect annual butterfly species richness and does this have implications for richness in a changing climate; is there a relationship between species richness and surrounding land use; and how do these forces influence species richness when acting together?

Methods

Sample Design and Study Area

All field surveys were conducted by one of the authors, AMS, as part of a larger ongoing project studying phenological patterns. The survey at each site was conducted along a fixed transect meant to sample all local habitats at that location. The surveys were all in the Sacramento Valley, the northern portion of California's Central Valley (Shapiro et al. 2003). We focused on 4 site transects: (from west to east) Suisun Marsh (SM), West Sacramento (WS), North Sacramento (NS), and Rancho Cordova (RC). NS, RC, and WS are clustered in or near the city of Sacramento, while SM lies approximately 100 km to the west in a gap of the Coast Range where the Sacramento-San Joaquin Delta, Suisun Bay, and San Pablo Bay intrudes (Fig. 1). Each site had one established transect that passed through a mosaic of vegetation types, each provided habitat for some butterfly species, but no site was suitable for all species. Transects were bound by a natural barrier such as the Sacramento River or SM or a nonhabitat land cover such as a road or industrial area. Transect lengths varied (NS, 8.26 km; RC, 4.57 km; SM, 3.73 km; WS, 5.80 km) to permit sampling of all vegetation types, which were spread out at different sites due to intervening nonhabitat land cover. All study sites were either in flood plains (WS), ecological preserves (SM), or along protected bikeway (NS, WS) and railway corridors (WS). This was considered when the monitoring program was initiated to maintain site continuity indefinitely. All sites are described and mapped in detail at <http://butterfly.ucdavis.edu>. Additionally, these sites support a very similar butterfly fauna and are facing similar anthropogenic pressures, making them suitable for comparison. Monitoring commenced in 1973 at SM, 1976 at RC, and in 1988 at NS and WS. Each site was visited approximately once every 2 weeks throughout the year (average number of visits per year [SD]: NS 27.2 [4.6]; RC 26.9 [3.2]; SM 27.7 [SD 3.6]; WS 28.7 [SD 3.6]) and only during appropriate flying conditions, which represent a constellation of weather variables including recent precipitation, radiation, ambient temperature, and wind. Each species observed was recorded for each visit.

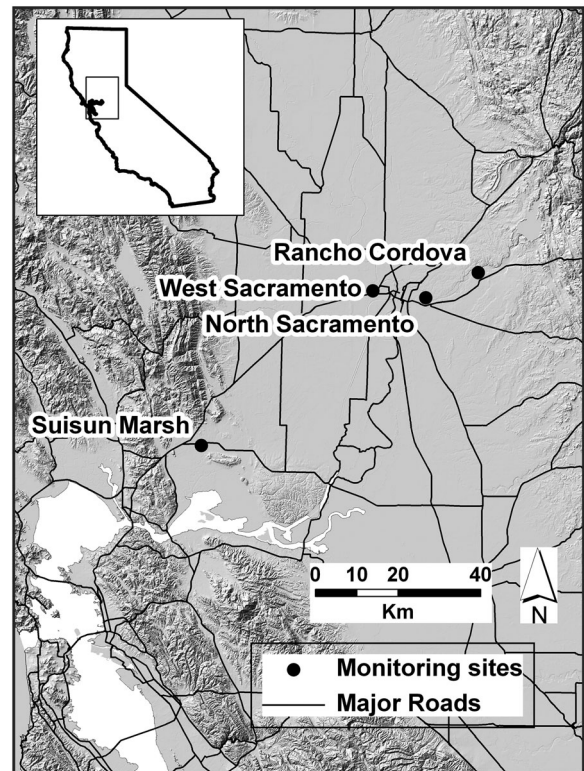


Figure 1. Sites surveyed in study of butterfly species richness. North Sacramento (NS), West Sacramento (WS), and Rancho Cordova (RC) are in the greater Sacramento, California, area. Suisun Marsh (SM) is east of the Coast Range on the Sacramento-San Joaquin Delta. Lines represent major roads, and circles represent sites. The inset image shows the relative location of the sites in California.

Species Richness

To investigate patterns of butterfly richness across all sites over time, we fitted a linear model with annual species richness (number of resident species observed in a single year) as the response variable, and site (categorical), year (continuous), site-by-year interaction, and total annual number of visits to each site (continuous) as the explanatory variables. We used R's stats package for all models unless otherwise specified (R Development Core Team 2012). Coefficients associated with the variable *year* indicate trends in species richness through time. Because monitoring at NS and WS did not begin until 1988, we truncated the RC and SM data sets to the years 1988–2009 so that the trend in regional richness would not be driven by a few sites in early years. Number of visits was included as a covariate to account for small differences in sampling intensity between years and sites. Annual species richness was defined as the number of resident butterfly species observed in a year. Studies on other organisms show that different processes drive richness

of resident and transient species (Magurran & Henderson 2003; Coyle et al. 2013). We excluded transient species by only including those that were present in a minimum of 25% of the years surveyed at each site. We assigned a threshold value in an attempt to minimize inflated richness values, though in doing so we may have excluded very rare or elusive species or species that might have undergone extinction early in the study. We also modeled the trend in richness using all species to ensure that the trends were not significantly different. All models satisfied the assumptions of normality and homogeneity of error variance.

To further understand ecological variables that might be associated with year and therefore might be relevant to trends in species richness, we modeled the response of richness to climate and nearby land uses through time.

Climate and Land Use

Weather data were acquired beginning in 1970. Records from 3 local weather stations were used, each one located within a few kilometers of a study site. The weather station for RC closed mid way through the study, so data from the NS station 26 km away was used as a surrogate. Both current- and previous-year climate may affect oviposition, larval development (Kearney et al. 2010), and host plants (Pollard 1988), so we analyzed the relationship between annual species richness and climate in 5 seasons: previous summer, previous fall, current winter, current spring, and current summer. We defined summer as June through August, fall as September through November, winter as December through February, and spring as March through May. Seasonal averages for minimum and maximum temperature (in °C) and seasonal totals for precipitation (in cm) were developed for a total of 15 climate variables. After examining variance inflation factors (VIF) and collinearity, we excluded 3 temperature variables from further analyses: mean minimum temperature for the current summer (VIF = 8.5), mean minimum temperature for the previous fall (VIF = 7.9), and mean maximum spring temperature (VIF = 7.9).

Land-use data were obtained from the Farmland Monitoring and Mapping Project (FMMP) (<http://www.conservation.ca.gov/dlrp/fmmp>), which has compiled county-wide reports and statistics on land use biannually (every other year) since 1988 for NS, WS, and RC, and since 1984 for SM. At the time of the analysis, land-use data in the form of geographic information system (GIS) polygons with a resolution of 10 acres (4.0 ha) was available through 2006. Our study sites spanned Solano (SM), Yolo (WS), and Sacramento (NS and RC) counties. All study sites were in or close to both urban and agricultural areas. The FMMP delineates 10 land-cover classes, which we generalized into 5 classes for analyses: urban or built-up, grazing land, farmland, water, and other. The other land-cover category included rural residential and com-

Table 1. Climate variables measured at the North Sacramento and Suisun Marsh weather stations with significant trends over time.

| | Coefficient ^a | SE | T | p | Adj R ² |
|--------------------------------|--------------------------|------|-------|-------|--------------------|
| Sacramento Valley ^b | | | | | |
| Summer minimum | 0.03 | 0.02 | 1.86 | 0.04 | 0.08 |
| Winter maximum | 0.06 | 0.02 | 2.56 | 0.01 | 0.12 |
| Fall precipitation | -0.20 | 0.09 | -2.18 | 0.04 | 0.09 |
| Suisun Marsh ^c | | | | | |
| Spring minimum | 0.06 | 0.02 | 2.38 | 0.02 | 0.10 |
| Summer minimum | 0.08 | 0.02 | 3.62 | <0.01 | 0.23 |
| Summer maximum | 0.17 | 0.08 | 2.14 | 0.04 | 0.08 |
| Fall minimum | 0.09 | 0.03 | 3.21 | <0.01 | 0.20 |
| Fall maximum | 0.06 | 0.03 | 2.11 | 0.04 | 0.08 |
| Winter minimum | 0.07 | 0.03 | 2.21 | 0.03 | 0.09 |
| Winter precipitation | 0.45 | 0.22 | 2.02 | 0.05 | 0.07 |

^aFor North Sacramento $n = 39$, and $n = 40$ for Suisun Marsh.

^bData from 1971 to 2009. The Sacramento Valley weather station data were used to represent North Sacramento, Rancho Cordova, and West Sacramento sites.

^cData from 1970 to 2009. Suisun Marsh weather station data represented only the Suisun Marsh site.

mercial lands, vacant or disturbed lands (e.g., mine tailings, gravel operations, undeveloped land within a city), and nonagricultural vegetation (high elevation forests, riparian areas, wildlife refuges). A small amount of natural or seminatural land cover existed in our study area at the beginning of land-use monitoring and was included in the other category. Most of this land is protected and changed little over time. We combined ranchland and farmland into a working landscapes (WLs) category for 2 reasons. First, the classification of a single parcel of land often switches between irrigated farmland and grazing land depending on land idling, primarily due to cessation in irrigation due to water shortages or economic downturns (California Department of Conservation 2008). Second, ranchland and farmland are much more interdigitated than the urban and agriculture front. The increase in urban and built-up land was highly negatively correlated with the decrease in WL (Pearson's product moment, $\text{cor} = -0.83$, $p = <0.01$); therefore, we used changes in WL to also approximate the inverse change in the urban/built-up environment. A 10-km radius area was demarcated around each transect, and land-use changes within this area (hereafter *buffer*) were measured. Ten kilometers was chosen as the buffer distance because it represents an intermediate dispersal distance for members of the studied faunas. Species such as *Satyrium silvinius*, *Satyrium californica*, and *Lycaena xanthoides* exhibit low vagility, not moving far from a single host plant, while other species such as *Pieris rapae*, *Vanessa cardui*, and *Danaus plexippus* disperse tens to thousands of kilometers. The 10-km buffer areas encompassing each of the 4 study sites represented a range in the proportion of WL at the beginning of the study and change in land use through time (Table 3, Supporting Information).

Table 2. Final model relating climate and land-use variables to butterfly species richness ($n = 42$).

| Variable | Slope | s^* | SE | F | p |
|--|-------|-------|------|-------|-------|
| Site level differences (as factor) | | | | 9.27 | <0.01 |
| Previous summer total precipitation | 0.81 | | 0.35 | 5.12 | 0.02 |
| Spring mean minimum temperature | 0.8 | | 0.23 | 11.93 | <0.01 |
| Previous summer mean minimum temperature | | 1.54 | | 9.33 | <0.01 |
| Previous fall mean maximum temperature | -0.54 | | 0.21 | 6.35 | 0.01 |
| Proportion of WL | | 2.31 | | 3.99 | 0.02 |

* Smoothing term for variables with a nonlinear affect on butterfly species richness.

Table 3. Changes in the proportion and number of patches of working landscape (WL) at North Sacramento (NS), Rancho Cordova (RC), Suisun Marsh (SM), and West Sacramento (WS) sites, and the rate of loss (columns 1–3) and results of simple linear regressions relating the proportion of WL within the 10-km buffer^a to richness for each site ($n = 10$ for each site) (columns 4–6).

| Site | Proportion of WL (no. of patches) | | | Richness and working land | | | Richness through time ^b | |
|------|-----------------------------------|------------|----------------------------|---------------------------|----------------|-------|------------------------------------|-------|
| | 1988 | 2006 | rate (km ² /yr) | coef. WL _{SE} | R ² | p | coef. year | p |
| NS | 0.24 (76) | 0.15 (114) | -1.85 | 0.93 _{0.18} | 0.74 | <0.01 | -0.96 | <0.01 |
| RC | 0.13 (50) | 0.10 (29) | -0.5 | 3.66 _{0.98} | 0.59 | 0.01 | -0.85 | <0.01 |
| SM | 0.50 (47) ^c | 0.37 (67) | -1.58 | 1.41 _{0.33} | 0.65 | <0.01 | -0.49 | <0.01 |
| WS | 0.61 (67) | 0.47 (137) | -3.35 | 0.35 _{0.11} | 0.47 | 0.02 | -0.73 | 0.01 |

^aA 10-km radius area around each transect in which land-use changes were measured.

^bResults from Forister et al. (2010). See Supporting Information for relationships between richness and time.

^cFarmland Monitoring and Mapping Program began land cover surveys 4 years earlier in Solano County than in other counties; therefore, initial WL values are reported for 1984 for the SM site.

Transect routes were recorded with global positioning system (GPS) units and digitized to define the linear features in a GIS. We used the 10-km radius buffer around each transect line to demarcate the sampling area for each edition of the FMMP land-use data released every 2 years. We then assessed land cover change, as measured by the FMMP, within the buffer transect areas between years (Table 3, Supporting Information), and the area outside the buffer was ignored. Because the configuration of transects varied between sites, the area encompassed by the 10-km buffer also varied slightly among sites (area in square kilometers and number of 10 acre mapping units [mu], respectively, of each site: NS: 370 km², 9140 mu; RC: 362 km², 8942 mu; SM: 309 km², 7633 mu; WS: 382 km², 9436 mu). Therefore, for comparative purposes, the proportion rather than absolute area of each land-use type was calculated for each site. The biannual proportion of WL was included as a variable to predict species richness. Conversion of WL to urban uses accounts for the greatest (in area) conversion in landscapes in the region (California Department of Conservation 2008). We explored the effect of the number of patches and the edge-to-area ratio with FragStats 3.3. Because dispersal distances vary with species, we used these metrics of fragmentation because they do not require a pre-defined threshold distance within which patches are deemed connected. We investigated additional metrics of habitat patchiness and fragmentation produced by FragStats for every 4 years (4 year periods were due to budgetary constraints), but many of these variables were highly correlated, and they

all had a nonsignificant effect on species richness. The proportion of area of WL and the number of patches occurring in each site's 10-km buffer and a site factor, which accounts for intrinsic differences in sites, were included as predictors of regional species richness.

The general relationship between climate variables and land-use metrics versus species richness was analyzed for all sites collectively with generalized additive models (GAMs) (Hastie & Tibshirani 1990; Wood 2008). Land cover was the limiting variable; biannual data were available for NS ($n = 10$), RC ($n = 10$), and WS ($n = 10$) since 1988 and for SM since 1984 ($n = 12$) (42 observations total). We tested both linear and additive models, but not all independent variables had a linear effect on richness, and the additive model gave a significantly better fit to the data. A GAM is similar to a generalized linear model (GLM) except that GAMs do not require a priori knowledge of the shape of the relationship because the shape is guided by data; thus, fewer assumptions are made about how species respond to their environment (Ferrier et al. 2002). GAMs use nonparametric smoothing functions to link at least some explanatory variables to the response variable. Because they have no equivalent to the GLM slope value, β , these terms' effects are best interpreted graphically.

To identify climate and land-use variables related to annual richness, we fitted the maximal model, considering only main effects, with 12 climate variables, 2 land-use variables (proportion of nearby WL and the number of WL patches), and a site factor, to account for site differences, in the R package *mgcv* (Wood 2006). Because of limited degrees of freedom, interaction terms were included post

hoc for each of the significant weather variables in combination with proportion WL. Our goal was to find a small subset of the variables that explained a large proportion of the variation, so we employed a multistep model selection processes. In all GAM models, smoothed terms were represented by penalized thin plate regression splines. Because we were more interested in general relationships among climate, land use, and species richness, we limited the degrees of freedom associated with each smoothed term to 5. The *mgcv* optimizes the smoothing parameter for each term with generalized cross-validation (GCV) (Wood 2006). We applied a shrinkage smoother to all terms, which heavily penalizes terms to the 0 function, and they were effectively selected out of the model. These factors were then simultaneously dropped from the model (Zurr et al. 2009). Nonsignificant terms still remained, so we used a backwards selection method because it is most consistent with GCV smoothing parameter selection (Wood & Augustin 2002). To confirm the model, we repeated the selection procedure starting each run with a different combination of original variables and degree of smoothing. The same best model was consistently selected, with explained deviance only varying when smoothing was limited.

To examine the effect of land use on richness at the site level, we performed simple linear regressions with species richness as the dependent variable and the proportion of WL as the independent variable. This was done independently for all sites. We also tested additive models, but land use had a linear effect on richness at each site.

Additionally, we tested for local climate and land-use trends. To identify climate trends, we performed simple linear regressions on each of the 12 seasonal climate variables (precipitation, average maximum temperature, and average minimum temperature for each season) over time. The full climate data set, including years between 1970 and 2009, was used to maximize power. To obtain rates of change in WL for each site, we regressed the total area of WL over time.

Results

Species Richness

There was a significant regional decline in species richness over time ($n = 88$) (22 years at each of 4 sites, slope = -0.41 , $p < 0.0001$, SE 0.08, $F = 100.79$, adj. $R^2 = 0.67$), and site differences were also significant ($p < 0.0001$, $F = 27.19$). Differences in sampling intensity between sites and years were not important predictors of annual observed richness (slope = 0.05 , $p = 0.56$, SE 0.09, $F = 0.17$), and the interaction between site and year was not significant ($p = 0.43$, $F = 0.93$). The trend with all species data, including species seen in <25% of the

years, was also significant ($n = 88$, slope = -0.41 , $p < 0.0001$, SE 0.10, $F = 65.28$, adj. $R^2 = 0.53$).

Climate and land use

Climate trends were equivalent at the Sacramento sites (NS and WS), so for simplicity we only report the results for NS. Suisun Marsh (SM), which is approximately 100 km southwest of Sacramento has a different climate from the Sacramento Valley and showed slightly different trends from the Sacramento sites. Of the 12 climate variables tested, 3 showed significant trends in the Valley, and 7 showed significant trends at SM (Table 1).

Of the 12 climate and 2 land-use variables included in the initial model, only 4 climate variables and 1 land-use variable were retained in the final model (total precipitation in the previous summer, the previous summer's mean minimum temperature, the previous fall's mean maximum temperature, the spring's mean minimum temperature, and the proportion of WL within the 10-km buffer) (Table 2). The final model explained 79% of the deviance and had a GCV score of 5.1. Interaction terms raised the GCV score and therefore were dropped. Three of the 4 climate variables affected species richness linearly, so we entered them in the model as linear predictors and calculated a slope for each. Previous fall mean maximum temperature was negatively associated with richness, whereas previous summer precipitation and current spring minimum temperature were positively associated with richness. Previous summer mean minimum temperature was slightly nonlinear with a greater negative effect on richness as temperature increased (Fig. 2). Site-level differences were also significant. The proportion of WL had a nonlinear effect on species richness. The effect of the loss of a unit of WL was not equal among sites (Fig. 2e). Additional loss of WL at sites with an already low proportion resulted in greater losses in richness (Table 3). This was supported by results for within sites as well (Fig. 3). One unit of WL lost at RC yielded a loss of 3.66 species while at WS it was only 0.35 species. Loss of WL at NS and SM had an intermediate effect on richness (0.93 and 1.41, respectively) (Table 3).

Discussion

The 4 butterfly faunas considered in this long-term study are shrinking. A number of species have declined to the point that they no longer occur at some sites, and in some cases they have disappeared regionally (Forister et al. 2010). These local extinctions are occurring more frequently than recolonizations, creating a net loss in richness at all sites through time. Results of our explanatory model suggest that changes in species richness were associated with shifting climatic conditions and a loss of WLs. Spring and summer minimum temperatures

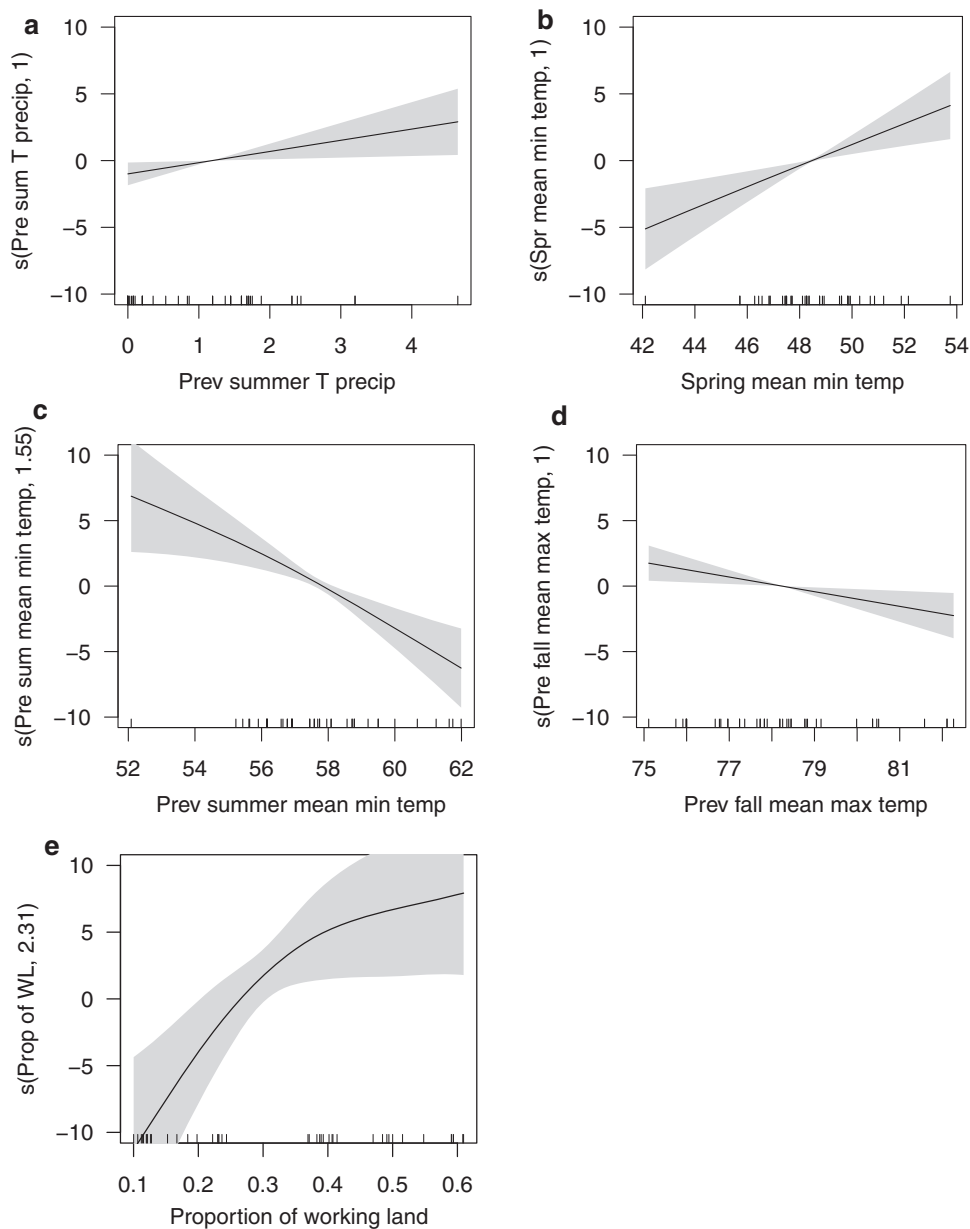


Figure 2. The functional form of the change in butterfly species richness associated with (a) different levels of precipitation during the previous summer, (b) spring mean minimum temperature, (c) mean minimum temperature during the previous summer, (d) mean maximum temperature during the previous fall, and (e) proportion of working landscapes produced from our explanatory generalized additive models (shaded area, 2 SE; hash marks, values of the covariate). The y-axis is the contribution of the smoothing value to the fitted values and is scaled to the linear predictor, but the smoothed values (s) must sum to zero; therefore, s values are mean centered.

were both associated with annual species richness and showed trends through time. The effect of working land on species richness was not linear, and in fact suggested a threshold at 30–40% of the farming and ranching landscape. When WL dropped below this range, additional land conversion resulted in more rapid species loss.

Although habitat requirements differ among butterflies, presence and accessibility of habitat is critical for all butterflies. WLs provide a relatively permeable matrix for dispersal for some species and habitat for others. We do not have records of relative abundance for the northern California fauna preagriculture, though we assume, based on current composition and behavior, that some of the butterfly fauna, pest and nonpest species alike, benefited from the introduction of row crops, fruit orchards, and grazing lands. For example, the native Anise Swallowtail

butterfly, *Papilio zelicaon*, added sweet fennel, poison hemlock, and later citrus (Rutaceae) to its diet of otherwise native apiaceous hosts (Shapiro & Masuda 1980; Shapiro 2002a).

Butterfly habitat is decreasing as the Sacramento region urbanizes. There is a strong positive relationship between the area of surrounding WL and species richness at all sites. Sites with more WL in the early years of the study were developed at a faster rate than those sites that were already more developed, so while loss of species richness per unit of habitat loss was less for sites with more WL, rates of decline were high (Table 3).

Species richness is a relatively insensitive metric by which to measure changes in a fauna because it is not responsive (except indirectly) to changes in population abundance. Local populations must be extirpated

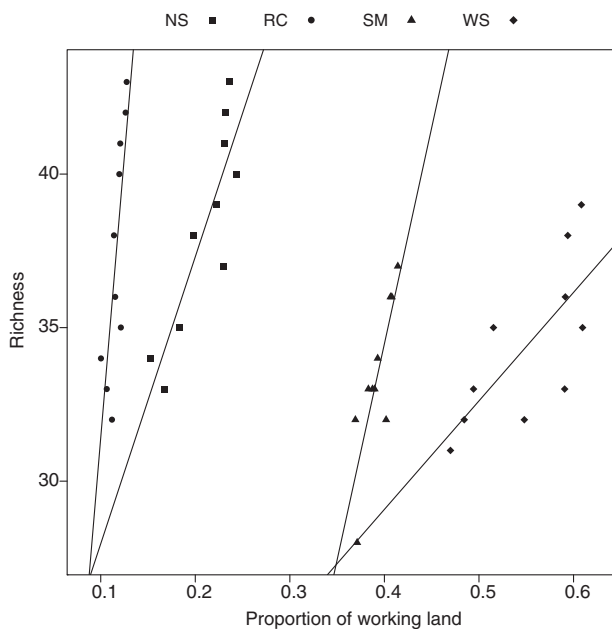


Figure 3. The relationships between the proportion of farm- and ranchland (working land) and butterfly species richness at each site—Rancho Cordova (RC), North Sacramento (NS), Suisun Marsh (SM), West Sacramento (WS).

completely before their decline is registered in species richness totals, so there could be time lags between habitat alteration or loss and species disappearance. Therefore, the 30–40% threshold of WL (Fig. 2e) should be considered a conservative range; the actual tipping point for population decline could be higher and vary among species.

Butterflies are particularly sensitive to climate although the direct and indirect effects of climate on a fauna are complex. For example, the relationship between climate and survival of the California butterfly, *Euphydryas editha*, is mediated by timing of the butterfly's life cycle relative to host and nectar plants rather than direct effects of climate on the butterfly (Parmesan 2003). Additionally, a phenological study of a nearby Sacramento Valley butterfly fauna demonstrated that in rainy years, species richness is reduced through the first half of the year but is greater in the second half of the year (Thorne et al. 2006).

Three of the 4 climate variables that most affect richness showed systematic trends (spring and summer mean minimum and fall mean maximum temperatures), corroborating results of other studies documenting widespread warming (DuVair 2003; IPCC Core Writing Team 2007). Higher spring minimum temperatures were associated with greater species richness, whereas higher summer temperatures in the previous year and lower rainfall were linked to lower richness. Higher spring temperatures had a strong positive effect on richness in the same year, likely

through direct effects on the growth stages of butterflies and through favorable growing conditions for host plants early in the growing season. Species richness was reduced in the year following a particularly warm summer. The same trend was documented by Singer (1972), who found that more than 98% of pre-diapause *E. editha* larvae die as a result of early host senescence, which is perceivable in the low population abundance the following year.

Our results support several other studies that show declines in richness of urban butterfly faunas. Population declines in low elevation ruderal species, including some species in this study, are directly linked to a decline in high elevation populations of the same species that rely on seasonal upslope recolonization (Forister et al. 2010). Urbanization was targeted as the likely cause for the decline in these species at low elevations. A 32-year 4th of July butterfly survey at Willow Slough, less than 16 km from our WS site, found a significant decline in species richness (O'Brien et al. 2011). Likewise, recent studies in the Netherlands (Van Dyck et al. 2009) and United Kingdom (Conrad et al. 2006) revealed similar trends among common, widespread Lepidoptera around urban areas.

Teasing apart the direct and indirect effects of a changing climate across a landscape of fragmented and shrinking habitats is difficult. The sum of the direct effects of climate change on the butterflies and its indirect effects through habitat quality are likely compounded by habitat loss and fragmentation (Clavero et al. 2011). These impacts may be lessened if there is a ready availability of microclimates or if the species have sufficient dispersal capacity to find healthy populations of host plants even in a warmer climate (Weiss et al. 1988). However, as habitat patches become smaller, less diverse, and more difficult to reach, the chances that organisms are able to find adequate habitat to maintain viable populations decline (Murphy et al. 1990). Similarly, the effect of habitat loss and isolation may be accentuated by increasingly adverse climatic conditions in the remaining patches. Areas of intensive urbanization show the greatest warming in California (LaDochy et al. 2007), suggesting that organisms in these regions may experience even higher temperatures due to heat island effects. Habitat quality, especially for larvae, is a key determinant of overall population viability (Thomas 1984; Thomas et al. 2011) and is undoubtedly affected as climate and the landscape are modified.

WLs have often been considered to be at odds with biodiversity and conservation, especially when converted from natural landscapes. Richness and abundance of butterflies are lower in areas surrounded by arable land versus forest in some regions (Berg et al. 2011; Öckinger et al. 2012). We examined trends in species richness associated with a widespread secondary phase of land conversion, from working, arable landscapes to urban landscapes (Brown et al. 2005), for which more studies are

needed (Miller & Hobbs 2002), and found that within this context, habitat surrounded by a greater proportion of working land supported greater butterfly richness. Thus, while Ws are inferior to natural landscapes in terms of habitat quality for most butterfly species, they provide resources for both ruderal and nonruderal species and offer a landscape easier to traverse than urban landscapes.

We focused on the Sacramento Valley, though rates of conversion of agricultural to developed uses are still higher in other parts of California (California Department of Conservation 2008) and other states (Vilsack & Clark 2009). Thus, our most general contribution to the ever-adapting dialog of conservation biology is to add to the growing consensus that Ws are not insensitive to global change, they support a greater richness of species than crops or cattle, and they need consideration and even protection and management along with natural habitats (Polasky et al. 2005).

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Supporting Information

Images showing changes in land use over time at the West Sacramento site (Appendix S1) and a table showing changes in the total area of land types over time for each study site (Appendix S2) are available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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