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ORIGINAL RESEARCH

Conserved lands unable to maintain butterfly communities in a biodiversity hotspot

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Abstract

The decline in abundance and species richness of insects, including butterflies, have been linked to factors such as habitat loss and climate change. While some butterfly species are increasing, an overall decrease has been frequently observed in both Europe and North America. The objective of this study was to assess trends of butterfly abundances in Mediterranean shrublands of conserved lands in San Diego County, CA, USA. Funding and surveys were focused on the threatened Hermes copper (*Lycaena hermes*), but the abundance of all butterfly species was recorded. Analyses utilized the annual maximum count (Max Count) for each species at each transect during 2010–2022. The 10 most commonly observed species experienced, on average, a 1.4% annual decline in abundance, and 20 less commonly observed species were, on average, found at 5.9% fewer transects each year. The only exceptions to these declines are species (cabbage white [*Pieris rapae*], checkered white [*Pontia protodice*], and white checkered-skipper [*Burnsius albezens*]) that feed on non-native mustards or are more common in disturbed habitats. The Max Count provided an efficient, robust, and stable population index, that can be utilized to leverage funding for focal species to assess the broader community.

Keywords Butterfly conservation · Biodiversity loss · Population trends · Hermes copper (*Lycaena* [*Tharsalea*] *hermes*) · Coastal sage scrub · Urbanization

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Introduction

Insect abundance and diversity have been declining due to a variety of factors including habitat loss and climate change (Hallmann et al. 2017; Montgomery et al. 2019; Sanchez-Bayo and Wyckhuys 2019; Didham et al. 2020a; van der Sluijs 2020; van Klink et al. 2020; Wilson and Fox 2021). These declines will impact ecosystem functions (Oliver et al. 2015) and influence multiple trophic levels across most ecosystems. More specifically, declines in butterflies, a group of insects often used as ecological indicators (Parmesan 2003; Syaripuddin et al. 2015), have also been reported.

Europe has a relatively long history of butterfly monitoring and has documented declines in butterfly population sizes and distribution due to habitat loss and climate warming (Saarinen et al. 2003; Stefanescu et al. 2011). For example, there was a 39% decline in the abundance of 17 grassland butterfly species from 1990 to 2017 across 16 countries (van Swaay et al. 2019). In the United Kingdom, abundance of all butterflies decreased around 50% from 1976 to 2018, with habitat specialist experiencing the larger decline (Warren et al. 2021). But these declines are not ubiquitous across European butterflies as species in open field margins have increased (Kuussaari et al. 2007). Similar declines have been documented in the United States (USA). Butterfly abundance decreased around 33% in Ohio, USA 1996–2016 (Wepprich et al. 2019). Due to drought, butterfly abundances over 40 years have decreased 48% throughout the western USA (Forister et al. 2021). These declines have been more prevalent in areas with low precipitation rates and warmer temperatures such as the southwestern USA (Crossley et al. 2021).

This research, and surveys, were focused on the Hermes copper (*Lycaena hermes*) butterfly, and leverages the associated funding to assess the broader butterfly community. With other studies reporting declines of insect species richness or abundance, assessing multiple species in different geographic locations is important. Hermes copper is endemic to San Diego County, CA, USA, and northern Baja California (Thorne 1963; Marschalek and Klein 2010), and is threatened by urbanization and wildfires (USFWS 2011) and federally listed as threatened (USFWS 2021). Coastal southern California is considered a biodiversity hotspot (Mittermeier et al. 2011), with Mediterranean shrublands associated with a climate of cool, wet winters and hot, dry summers. San Diego County has active and coordinated conservation efforts across a preserve system with many stakeholders (e.g. Greer 2004; SDMMP and TNC 2017).

The Hermes copper inhabits coastal sage scrub and open chaparral vegetation communities with spiny redberry (*Rhamnus crocea*), its only known larval food plant. This plant is relatively well distributed across the lower elevations of coastal California from the San Francisco Bay area south into Mexico (Calflora 2006). In San Diego County, spiny redberry is found in grasslands, coastal sage scrub, and open chapparal vegetation communities. Adults typically fly from mid-May to late June, depending on annual weather, and have a strong preference for feeding on nectar from California buckwheat (*Eriogonum fasciculatum*).

Our primary focus was to determine relative population sizes and trends of the Hermes copper in the San Diego County preserve system, which have been published elsewhere (Marschalek and Deutschman 2008; Marschalek and Klein 2010; Marschalek et al. 2016; several technical reports cited in USFWS 2011, 2021). During all field visits, counts of all other butterfly species (Lepidoptera: Papilionoidea) were recorded to investigate patterns of the broader assemblage. Specifically, our objective was to assess trends in population sizes of summer (May to July) flying butterflies of the coastal sage scrub and open chaparral vegetation communities in San Diego County, CA, USA.

Methods

San Diego County, CA, USA is 1,104 km^2 in size, with elevations rising from sea level at the Pacific Ocean coast to nearly 2,000 m in the mountains of the Peninsular Range. This elevational profile results in different precipitation and temperature profiles for different areas of the county, with vegetation communities changing as well. Surveys for butterfly and skipper (Papilionoidea) species were conducted on conserved lands on the western slopes of the mountains, below 1,160 m in elevation, in 2003–2022 (Fig. 1). These elevations primarily corresponded with grasslands, coastal sage scrub, and chaparral vegetation communities, as well as varying levels of urbanization.

Survey transects were established along dirt roads or trails, with surveys occurring weekly or more frequently in May to July, during periods of appropriate weather (sunny or partly sunny, 20 to 35 degrees C, and modest wind speeds). All individual butterflies vis-

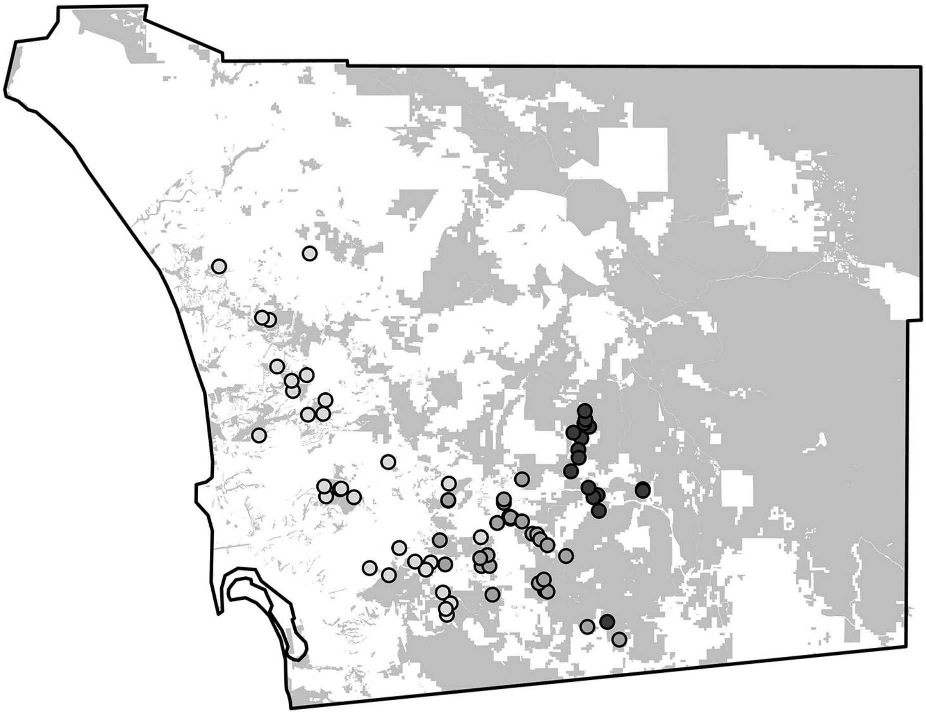


Fig. 1 Butterfly survey transects in San Diego County, CA, USA, with the San Diego County preserve system of conserved land in gray shading (SANDAG 2022). Light gray dots represent sites in Cluster 1 in a more urban landscape at lower elevations, medium gray in Cluster 2 characterized by coastal sage scrub vegetation at intermediate elevations, and dark gray in Cluster 3 characterized by mixed chaparral vegetation at higher elevations. Clusters were determined based on vegetation composition within 500 m of each transect, and elevation (see Fig. 2)

ible from the transect were counted. The length of transects and number of annual surveys varied based on the extent of spiny redberry at each site and yearly objectives, respectively. The annual maximum daily count (Max Count) for each species for each transect and year were used in the analysis. While the Pollard Index is widely used, the Max Count was less sensitive to differing number of annual surveys and likely different timing of surveys each year despite the standardization of sampling summer flying butterflies.

Due to funding obligations, our surveys were focused on detecting Hermes copper butterflies which focused our data in three ways: (1) phenology – summer (May to July) flying species, (2) habitat and range – coastal sage scrub and open chaparral vegetation communities in San Diego County, and (3) sites – yearly objectives changed which resulted in sites changing. Due to variable annual weather conditions, only surveys conducted within 7 days of the first or 7 days after the last Hermes copper adult observation during each year were used in the analysis.

The proportion of each vegetation community type or urban land cover within 500 m of each transect was calculated to estimate relationships between landscape characteristics and the butterfly assemblages. Calculations were made in ArcGIS Pro 3.1 ESRI using the 1995 Holland code classification (City of San Diego et al. 2014). The Holland code has a hierarchical structure which allowed for a coarser grouping of land use categories for this study: urbanization, coastal sage scrub, chaparral, coastal sage scrub-chaparral transition, native grassland, non-native grassland, non-native vegetation, and riparian forest. A 500-meter scale was selected because butterflies should reflect the vegetation within the local area (Pollard 1977; Dennis et al. 2006; Illán et al. 2010; Ribeiro et al. 2012; van Halder et al. 2017; Han et al. 2022) but smaller distances failed to capture the urban land cover which has been shown to be influential in insects within this landscape (Marschalek and Deutschman 2022). To account for the expected change in vegetation communities from the western lower elevation transects to the eastern higher elevations transects, each transect was placed in one of three groups based on adjacent land cover (Fig. 2). Cluster 1 transects were at lower elevations with more urbanization and coastal sage scrub, Cluster 2 transects were at intermediate elevations represented by chapparal, and Cluster 3 transects were at higher elevations with mixed chapparal vegetation communities.

Due to field identification challenges, some butterfly species were grouped for purposes of the analysis. These include checkered (*Pontia protodice*) and cabbage (*Pieris rapae*) whites (white spp.) which are often observed flying so it is hard to see characteristics, especially at a distance of at least a few meters. Acmon (*Icaricia acmon*) and lupine (*Icaricia lupini*) blues are small, have similar characteristics, and occasionally many individuals would be encountered but would take too much time to capture each one. The painted lady (*Vanessa cardui*), west coast lady (*V. annabella*), and American lady (*V. virginiensis*) were generally observed flying and difficult to see wing characteristics. For these three groups of species, we felt the species within each group had similar life histories to make a grouping useful. Many unknown blue butterflies (Polyommatinae) were recorded due to their small size and constant flight. These were not included in the analysis as we felt this group of blue butterfly species did not share similar life histories. Taxonomy follows NABA (2024).

Trends through time were analyzed with generalized linear models. The standard (Gaussian) general linear model (GLM) was used for species richness and the most common taxa. Max Count data were $\log(x+1)$ transformed prior to analysis. Logistic regression was used for less common taxa. Several species with intermediate prevalence were analyzed with

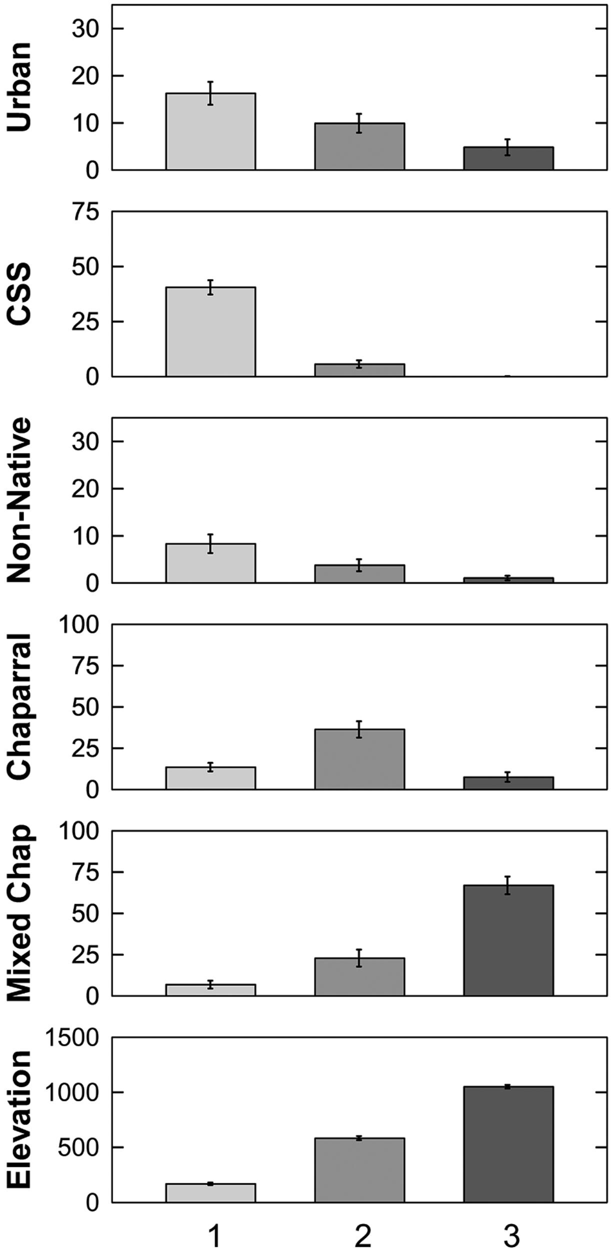


Fig. 2 Cluster analysis of transects based on land cover (vegetation communities and urbanization) within 500 m of each transect, and elevation. The five most common 1995 Holland code classifications are shown (City of San Diego et al. 2014) with 90% confidence intervals (CSS represents coastal sage scrub, Chap represents chaparral). The elevation (meters) of western San Diego County increases from west to east, altering the temperature and precipitation regimes and subsequent vegetation communities

both the GLM and logistic regression. Specifically, the four most abundant taxa (1–4 ranking) were analyzed solely with the standard GLM analysis. For the following six most abundant taxa (5–10 ranking), both techniques were used and compared to assess the sensitivity of the trends to the statistical method used. For the following 15 most abundant taxa (11–25 ranking), only logistic regression was used. Species richness values represent all species observed, not just the 25 most abundant taxa.

All models included year (the independent variable of interest), as well as region (cluster), transect length, and number of annual surveys as covariables. Region (cluster), transect length, and number of surveys were included to avoid confounding spatial variability and within-year sampling effort with change through time. Change through time are reported as slopes for GLMs and as odds ratios for logistic regressions. Significance at $p < 0.10$ and 90% confidence intervals are reported. Analyses were performed in SYSTAT 13.2.

The spatial coverage and intensity of sampling varied among years. Analyses were performed on the full dataset and a subset that was much more balanced. The full dataset included 31% of the possible transect years (all transects across all years) during the study. The balanced subset was based on 14 unique transects that represented 85% of the transect years during the study. Estimates of change through time (slopes from the GLM, odds ratios from logistic regression) were highly correlated across taxa ($r = 0.86$, $r = 0.89$, respectively) between the small group of regularly sampled transects and the full set of transects. Given that the two approaches were consistent, we present the results from the full dataset. We were concerned that 2003 data would be overly influential in determining any trends considering we have little butterfly community data for 2004–2009 (see Didham et al. 2020b for challenges interpreting insect declines). For this reason, these years were excluded from the analyses but results including 2003 data are mentioned in the discussion.

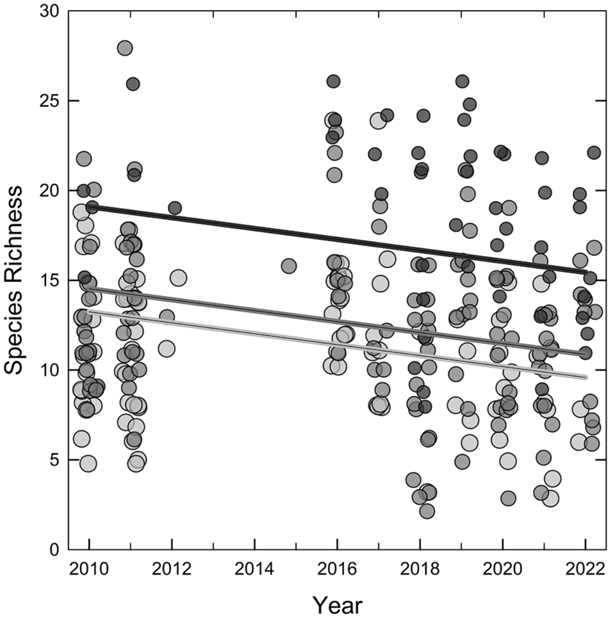
Results

A total of 88 different transects on conserved lands were surveyed in 2010–2022, resulting in 275 transect years, 67 species, and 62,920 butterfly observations. Over the 13-year period, all three regions (clusters) experienced significant declines in species richness (Fig. 3). The rate of decline for species richness across this time period was −0.305 species per year (90% CI -0.395 to -0.214, $p < 0.001$).

Of the ten most abundant taxa, six had slopes that were negative (Fig. 4). The slope was significantly different from zero ($p < 0.10$) in four taxa, all of which had decreased in abundance. The average slope for 10 species analyzed by GLM was −0.014 (1.4% decline per year). A total of 20 taxa were assessed for changes in prevalence (occurrence) across transects each year. Three taxa showed signs of increasing prevalence, two were essentially flat, and 16 declining (Fig. 4). The white checkered-skipper (*Burnsius albescens*) was the only species that exhibited a significant increase, while 11 species exhibited significant decreases in the number of occurrences. The average odds ratio for 20 species analyzed by logistic regression was 0.941 (detected on 5.9% fewer transects per year). For the species analyzed using both techniques, the relative rate of change ($r = 0.96$), rank order of change, and significance were very similar.

Across all species, transect length was a significant indicator of butterfly abundance about 75% of the time and consistently with the most abundant species, while the number of annual surveys was significant about 25% of the time. Significant differences among regions (clusters) occurred about 75% of the time, with the most common pattern being lowest abundance at lower elevations (Cluster 1), intermediate abundance at intermediate elevations (Cluster 2), and highest abundance at higher elevations (Cluster 3), or lower abundances at lower elevations and higher/similar abundances at intermediate and higher

Fig. 3 Species richness of butterfly and skipper (Papilionoidea) species observed during transect surveys in 2010–2022 for three regions of San Diego County. The lightest gray line and circles represent Cluster 1 transects characterized by more urban land cover at lower elevations, dark gray represents Cluster 2 transects characterized by coastal sage scrub vegetation at intermediate elevations, and black represent Cluster 3 transects characterized by mixed chaparral vegetation at higher elevations. Different circle sizes are to assist visualizing overlapping data points



elevations. Including these covariables was important because either one or a combination can be important, depending on the species.

Discussion

We documented robust patterns of decline in species richness, abundances, and prevalence of butterflies of conserved lands in a biodiversity hotspot. Analyzing the Max Count per transect from 13 years of data provided an efficient and powerful method to document changes in common and rare species across an area of 1,104 km^2.

Observed rates of change were variable and a few species appear to be increasing. However, the average rate across the 20 common species was an annual decline in abundance of 1.4% and an annual decline of 5.9% in prevalence. These results are similar to the more extreme declines of butterfly abundances recently published (Crossley et al. 2021; Forister et al. 2021; Warren et al. 2021), but we observed fewer species increasing. Considering that butterflies are widely used and regarded as effective bioindicators (Rosenberg et al. 1986; Erhardt and Thomas 1991; Oostermeijer and van Swaay 1998; Thomas 2005), these declines underscore the need for conservation.

While the reported trends are concerning, the situation may be even worse than we have detailed. We have additional data that goes back another seven years from six sites (Marschalek and Deutschman 2008). Estimates from the expanded dataset result in even steeper declines than those presented in this paper. This earlier period of sampling included a large effort in 2003 while more targeted Hermes copper sampling from 2004 to 2009 had little data from other species. Data from 2003 has very high leverage if it is included in the full analysis. As a result, we focused our analysis on the 13 years beginning in 2010 to ensure that our results were not unduly influenced by a single year.

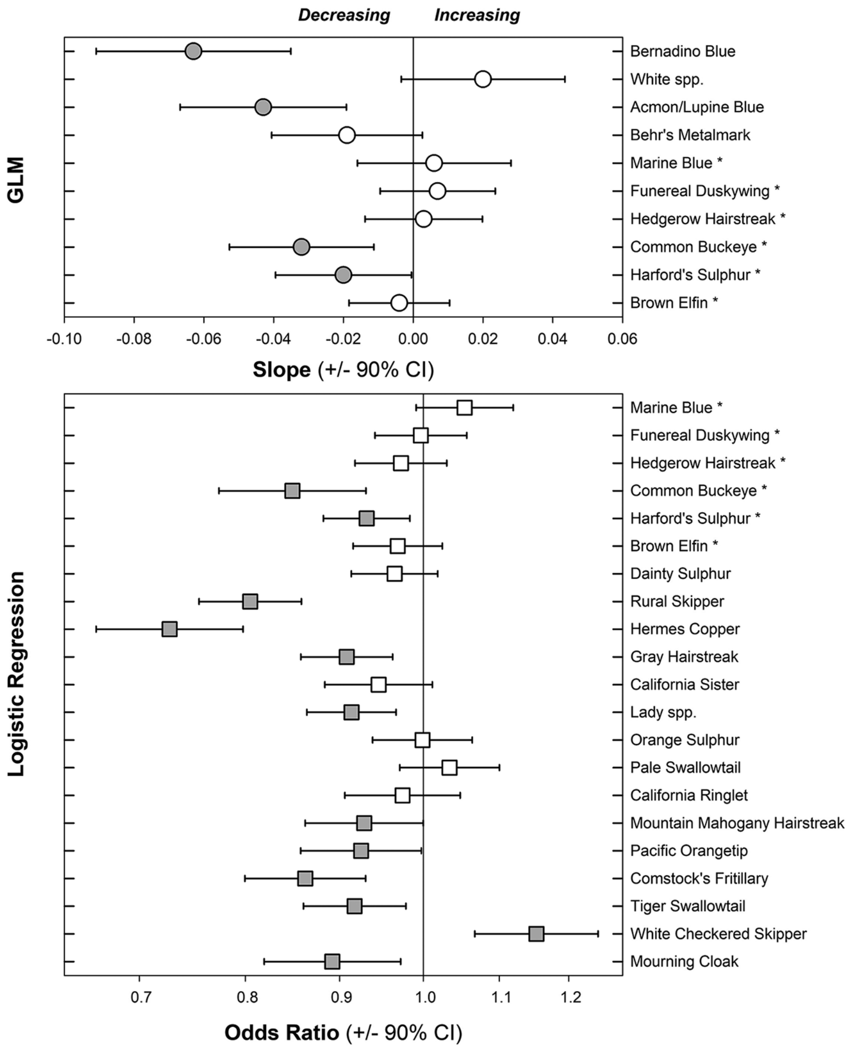


Fig. 4 Taxon specific trends in population size (top panel) and site prevalence (bottom panel). A line for no change is included and significant trends are illustrated with gray shapes. Six species (with an asterisk) are displayed on both graphs to offer a comparison of GLM and logistic regression analyses. Species are listed based on overall abundance, with the most commonly counted species at the top and less commonly counted descending in the list. Species include Bernardino blue (*Euphilotes battoides bernardino*), white spp. (*Pontia protodice* and *Pieris rapae*), Acmon/lupine blue (*Plebejus acmon* or *P. lupini*), Behr's metalmark (*Apodemia mormo virgulti*), marine blue (*Leptotes marina*), funereal duskywing (*Erynnis funeralis*), hedgerow hairstreak (*Satyrium saepium*), common buckeye (*Junonia coenia*), Harford's sulphur (*Colias alexandra harfordii*), brown elfin (*Callophrys augustinus*), dainty sulphur (*Nathalis iole*), rural skipper (*Ochlodes agricola*), Hermes copper (*Lycaena hermes*), gray hairstreak (*Strymon melinus*), California sister (*Adelpha bredowii*), lady sp. (*Vanessa virginiensis* or *V. cardui* or *V. annabella*), orange sulphur (*Colias eurytheme*), pale swallowtail (*Papilio eurymedon*), California ringlet (*Coenonympha tullia california*), mountain mahogany hairstreak (*Satyrium tetra*), Pacific Sara orangetip (*Anthocharis s. sara*), Comstock's fritillary (*Speyeria callippe*), tiger swallowtail (*Papilio rutulus*), white checkered-skipper (*Pyrgus albescens*), mourning cloak (*Nymphalis antiopa*). Taxonomy follows NABA (2024)

Our decision to report significance at $p < 0.10$ and 90% confidence intervals, as well as trends and odds ratios for all species, regardless of significance, represents a conservative approach. Butterfly abundances often vary greatly from year to year which makes it difficult to detect trends at $p < 0.05$, particularly with the less commonly encountered species. For conservation, avoiding false negatives (Type II error) outweighs the risk of false positives (Type I error). False positives would likely lead to increased surveillance or management that may not be needed. That is a significant cost, but it is less costly than failing to take timely action when a species may be in decline and at increased risk of extinction.

Nearly all of the species we observed exhibited declines over the course of this study, either in terms of abundance, prevalence, or both. While trends and patterns in abundance are important, understanding the drivers is important for inform management and conservation efforts. In San Diego County, there were large wildfires in October 2003 and 2007, which may be the reason for greater magnitude declines when including the 2003 data. A "megadrought" occurred during this this study, with 2000–2021 being the driest 22-year period in the last 1500 years (Williams et al. 2020, 2022). Specifically, San Diego experienced historically low precipitation in 2012–2014, however subsequent years had higher precipitation (Western Regional Climate Center 2024).

This research differs from many long-term butterfly studies in the United States because there is limited agriculture (especially row crops) in San Diego County compared to other parts of California and the Midwest (Forister et al. 2016; Crone et al. 2019; Wepprich et al. 2019; Van Deynze et al. 2024). For this reason, pesticide use, including neonicotinoids use should be less of a threat to San Diego butterflies. Habitat loss outside of preserves, and encroachment of non-native species are additional threats. Within the preserve system, management priorities include reducing the risk of fire (fuel load modification) and targeted removal of non-native species, although fires and non-native species are still common in many areas. While there are several threats to these butterflies, quantifying the relative contribution of each is challenging (Rumohr et al. 2023).

There are few publications specifically on long-term trends of butterflies in Mediterranean climates. Data from Catalonia (Spain), described declines in 42% of species during a recent (2021–2022) drought (Stefanescu and Ubach 2021–2022). Previously, habitat specialists were found to have greater rates of decline compared to habitat generalists (Stefanescu et al. 2011). More related to distribution, Numa et al. (2016) conducted a status assessment of butterflies in the Mediterranean Basin (lands adjacent to the Mediterranean Sea), concluding that over 20% of the 463 species are endemic to the region, and 80% of the species threatened with extinction are endemic. Restricted ranges were also described in several species (17 of 41) of the Atlas Mountains of Morocco, although these were not always represented by low abundances (Thomas and Mallorie 1985). Declines in abundance due to drought, restricted ranges for particular butterfly species, and steeper declines for habitat specialists are similar to our observations in southern California.

Despite efforts to specifically find Hermes copper populations, this species exhibited the greatest decline, found at 25% fewer transects each year on average. This species is a specialist (one known larval food plant) and vulnerable to fire (Marschalek et al. 2016). We also detected declines in widespread generalist species such as the common buckeye (*Junonia coenia*) and gray hairstreak (*Strymon melinus*), each with many possible larval food plants and found throughout much of the United States (Brock and Kaufman 2003). Although possibly counterintuitive, more abundant species are often experiencing greater declines than species with smaller abundance (van Klink et al. 2023). Two exceptions to the declines were the cabbage white (*Pieris rapae*) and checkered white (*Pontia protodice*), that were combined for this study, and the white checkered-skipper (*Burnsius albezens*). These species had evidence for the greatest increases. They are also characterized by feeding on non-native mustards (whites) or more common in disturbed habitats (all three species) (Brock and Kaufman 2003). Habitat loss and degradation, exacerbated by fires and drought, could offer an explanation for both the many declines and few increases in species-specific abundances.

Using the Max Count for each species for each transect provided a robust and stable index of abundance, even if a different subset of sites is surveyed each year. While the Pollard Index, a sum of all counts for each species across a season or flight period, is widely used, the Max count could be nearly as effective in detecting changes in abundance (Marschalek and Deutschman 2008). An advantage of the maximum count over a Pollard Index is that it requires less effort, with surveys at the beginning and end of a species' flight season not necessary. While focusing on a specific time period for a focal species may not replicate protocols for butterfly community monitoring, it is common for species of conservation concern (e.g. threatened or endangered species). If there is variation among transect lengths, sampling intensity, or landscape (e.g. elevation and associated vegetation), including these covariable can be important, depending on the species. The template we provide will allow for analyses to be extended to other non-target species in these cases.

There has been some question about the broad claims of global insect declines, including limited geographic coverage (Saunders et al. 2020). However, many areas have experienced levels of habitat loss and degradation that should leave no one surprised that insect abundances are declining for most species and this decline is leading to extirpations and possibly extinctions. Unfortunately, declines can still occur in protected areas including these butterflies of San Diego County. We show that collecting data for other species along with a focal species, and using the annual maximum count, can be a valuable approach to assessing the broader butterfly community and stretch funding to address multiple questions. If replicated, this will provide an assessment of butterfly communities with a greater geographic coverage.

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Author contributions All authors contributed to all aspects of this study. Authors contributed equally to the study conception and design. D.M. was the primary contributor to data collection and D.D. was the primary contributor to analysis but both authors contributed to all of these components. Both authors contributed to the manuscript and all authors read and approved the final manuscript.

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Data availability The datasets generated during and/or analyzed during the current study are available from the corresponding author on reasonable request.

Declarations

Competing interests The authors declare no competing interests.

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