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REPORT

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Specialized flower visitation in montane butterflies is associated with positive population trajectories over time

Tara Christensen[1] | **Christopher A. Halsch**[1,2] | **Lee A. Dyer**[1] | **Angela M. Smilanich**[1] | **Arthur M. Shapiro**[3] | **Matthew L. Forister**[1]

[1]Program in Ecology, Evolution, and Conservation Biology, Department of Biology, University of Nevada, Reno, Nevada, USA

[2]Department of Biological Sciences, Binghamton University, Binghamton, New York, USA

[3]Center for Population Biology, University of California, Davis, California, USA

Correspondence
Tara Christensen
Email: tara.c9@gmail.com

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Abstract

Insect biodiversity is under threat from multiple stressors, including climate change and extreme weather. For butterflies, nectar resource use is an understudied trait in relation to population trajectories and responses to global change. Here, we characterize nectar breadth for 50 species of montane butterflies occurring in the Sierra Nevada mountains of California and Nevada. These species displayed a wide spectrum of nectar use, including relative specialists and extreme generalists. Further, we examined how nectar breadth and other species traits, including latent variables indicating ecological flexibility and dispersal potential, were indicative of long-term population trajectories and responses to an extreme drought event from 2011 to 2015. Species that were more nectar-generalized were more likely to be declining, but nectar breadth did not predict how a species responded to extreme drought. Greater ecological flexibility, as reflected in other traits, was positively associated with population performance, while dispersal potential was negatively associated with population trajectories. Drought response was strongly associated with flight period, where species that fly later in the season are more susceptible to the negative effects of drought. Our study highlights the importance of considering butterfly nectar breadth in predicting population resilience and challenges assumptions about dietary generalism as a buffer against environmental change.

KEYWORDS
butterflies, butterfly ecology, diet breadth, nectar plants, plant–pollinator interactions

INTRODUCTION

We are confronting a global biodiversity crisis which has been called Earth's sixth mass extinction event (Dirzo et al., 2014). However, not all taxa are equally vulnerable to extinction or population declines, and it has been proposed that susceptibility is partly linked to specific biotic traits (Koh et al., 2004). The extent to which observed traits can successfully predict population trajectories is unclear, as many analyses have found weaker than expected relationships between traits and changes to populations through time (Tordoff et al., 2022; Wepprich et al., 2019). For insects, Earth's most diverse multicellular taxon, recent evidence points to regional declines in abundance and species richness (Hallmann et al., 2017; van Klink et al., 2020). The causal factors behind this have been extensively studied in recent decades and are primarily attributed to habitat loss and fragmentation, agricultural intensification, pesticides, invasive species, and climate change, with the last as a primary driver in arid lands, tropical communities, montane communities, and polar regions (Van Dyck et al., 2009; Wagner et al., 2021). Lepidoptera are the best-monitored insect group and have consistently shown signals of decline, though trends are mixed among taxa (Salcido et al., 2020; Wagner, 2020).

Within Lepidoptera, butterflies are facing numerous global threats. Due to their popularity among researchers, several high-quality, multi-decadal butterfly monitoring programs exist, and studies from North America have found extensive declines in butterfly diversity and abundance (Edwards et al., 2025; Wepprich et al., 2019). Butterflies in the Western United States are experiencing substantial losses over recent decades (Forister et al., 2021). For montane populations inhabiting the Sierra Nevada mountains, causal factors influencing declines include warming and drying conditions, especially in winter (Halsch et al., 2024). Furthermore, an extreme drought event between 2011 and 2015 resulted in precipitous declines in population density in the region (Forister et al., 2018), implicating extreme weather as a distinct threat.

Ecological traits related to ecological flexibility, or the ability to persist in a wide range of environmental conditions, as well as greater dispersal ability, are expected to be advantageous to species experiencing anthropogenic stressors (Buckley & Kingsolver, 2012; Öckinger et al., 2010). Most often, traits are treated as single or independent predictors, but there are suites of traits associated with ecological flexibility, including greater habitat breadth and larval diet breadth, which have been associated with population resilience for Lepidoptera (Kotiaho et al., 2005). Similarly, dispersal ability has been predicted to positively predict population performance in periods of environmental change, as it allows species to escape unfavorable conditions more readily (Sunde et al., 2023), and this trait has typically been estimated by other variables like range size and wingspan. However, single traits have had limited success as predictors of susceptibility to environmental change (Tordoff et al., 2022). Concepts such as ecological flexibility and dispersal ability may be best understood through multiple traits; for example, multivariate methods have found that combinations of traits indicating greater ecological generalism are associated with better population performance over recent decades (Dapporto & Dennis, 2013; Eskildsen et al., 2015).

In phytophagous insects, associations with host plants (Dapporto & Dennis, 2013) and nectar plants (Boggs & Inouye, 2012) can influence how populations fare under anthropogenic stressors. For example, dietary generalism may be advantageous as specific plant species experience changes in density or geographic ranges (Schweiger et al., 2008), or in phenology leading to a mismatch of trophic interactions (Kudo & Ida, 2013). However, for adults, nectar resource breadth is seldom studied, which is notable given that nectar limitation has been linked to declines in butterflies (Wallisdevries et al., 2012) and can be expected to worsen under drought conditions (Suni et al., 2023). The importance of nectar for butterflies is evident; many are obligate nectarivores, and nectar is a source of water and vital nutrients including carbohydrates, amino acids, and salts (Nicolson, 2022). Nectar availability and quality can influence longevity (Lebeau et al., 2016), reproductive fitness (King & Schultz, 2024), migration success, and overwintering survival (Brower et al., 2006). Therefore, it follows that nectar resource breadth could play a role in population dynamics and response to anthropogenic change to a similar extent as larval diet and habitat breadth.

In western North America, a unique effort consisting of up to 53 years of continuous monitoring (Shapiro transect) has yielded high-resolution data on species-level trends in the abundance of butterflies in the Central Valley and Sierra Nevada mountains of California (Forister et al., 2021; Halsch et al., 2021), as well as their responses to an extreme drought event from 2011 to 2015 (Forister et al., 2018). This drought event was estimated to be the worst in the last 1200 years in the region as reflected in the Palmer drought severity index (PDSI) and as inferred from climate records reconstructed using tree ring data (Griffin & Anchukaitis, 2014). Here, we used nectar association data to better understand population trends and drought responses derived from the aforementioned monitoring data. We estimated nectar breadth of 50 butterfly species from monitored locations and compiled natural history databases and expert observations from Arthur M. Shapiro to quantify additional species traits including mean date of last flight, ecological flexibility, and dispersal potential. Ecological flexibility and dispersal potential are treated as latent variables designed to reveal underlying ecological attributes that are indicated by measured variables. Mean date of last flight was chosen as we know that hot and dry conditions in late summer and fall are particularly detrimental to these populations (Forister et al., 2021). We predicted that species utilizing more nectar plants would be more resilient to population declines and fare better during the extreme drought period. Furthermore, we expected that species displaying greater ecological flexibility and dispersal potential would be more resilient to population declines and negative effects of the extreme drought.

METHODS

Butterfly species trends and drought responses

The Shapiro butterfly monitoring data are a temporally intensive dataset that consists of between 37 and 53 years of biweekly (every 2 weeks) observations along transects at each of 10 sites that include the California Central Valley and Sierra Nevada mountains. Each site visit was comprised of a walk along a fixed route, and the observer (Arthur M. Shapiro, Christopher A. Halsch, or Matthew L. Forister) recorded the presence and absence of all butterfly species seen. Previous work using these data has found that repeated presence/absence records summarized at an annual level are an effective index of annual abundance (Casner et al., 2014; Halsch et al., 2024). Here, we used the Shapiro data from the montane sites to estimate trends over time using a hierarchical Bayesian model that estimates a beta coefficient for each species both within each site and across all monitoring sites that represents the change in the probability of observation of the species throughout the time series (Appendix S1: Figure S1a). Additionally, we calculated an index for response to an extreme drought event (Appendix S1: Figure S1b).

Butterfly nectar breadth and other natural history traits

To estimate nectar breadth for butterfly species in our dataset, we utilized data collected through photographic observations by Christopher A. Halsch and Tara Christensen, and from iNaturalist obtained from the Global Biodiversity Information Facility (GBIF). GBIF observations were located by drawing a rectangular polygon bounding our study sites (N: 39.645, S: 39.307, E: −119.900, W: −120.673). All photos used in the current study documented butterflies contacting flowers. Both butterflies and flowers were identified to species wherever possible (see Appendix S1: Section S1 for details on species identification). In total, 613 photographs from personal observations (collected during 2018–2022) and 607 from iNaturalist (2005–2022) were eligible (1220 photos total). Pairwise observations of diet breadth were positively correlated between the two data sources (Pearson's product-moment correlation: $r = 0.45$, 95% CI = [0.04, 0.7], $t = 2.26$, df = 20, $p = 0.035$).

Data analysis

All statistical analyses were performed in R version 4.2.3 (R Core Team, 2023). Nectar breadth was calculated as the number of unique plant species each butterfly species was observed on. To address unequal sample sizes between species, we employed both extrapolation and rarefaction approaches. Only data for species with at least 10 photographic observations were retained (50 species). First, we calculated asymptotic nectar breadth for each species using the Chao1 index to estimate "true" nectar richness (Chao, 1987). We calculated rarefied nectar breadth by repeatedly sampling to a common sample size of 10. Both Chao1 richness and rarefied nectar breadth were calculated using the "vegan" package (Oksanen et al., 2022). Asymptotic richness was used to explore potential true nectar breadth of species and make use of all available data, while rarefied nectar breadth was used in the models predicting population trends and drought response in order to attain equal sample sizes of observations among species. Extrapolated nectar breadth and rarefied nectar breadth values were strongly positively correlated (Spearman's rank correlation: $\rho = 0.67$, $p < 0.001$, Appendix S1: Figure S2). Other natural history variables were compiled from various natural history sources that are detailed in Appendix S1.

All continuous predictor variables underwent *Z*-score transformations before being used in models. Exploratory factor analysis was performed using the "psych" package in R using the "minres" method (Revelle, 2022). Exploratory factor analysis is a method aimed at reducing variables to common factors, or latent variables, that help resolve correlations among measured variables (Cudeck, 2000; Floyd & Widaman, 1995). An initial factor analysis was run using all available ecological trait variables including nectar breadth, abundance, geographic range, ruderal status (i.e., affinity for disturbed or weedy habitats; see Appendix S1: Section S1 for detailed description), larval diet breadth, and wingspan. Two factors were selected to reflect a trade-off between over-specification (three-factor model) and high root mean square error of residuals (one-factor model). Rarefied nectar breadth was subsequently removed from the factor analysis, as it did not strongly load onto either factor (loadings < 0.4), with 84% of its variance being unique or error variance ($h^2 = 0.16$). A Bayesian structural equation model (SEM) was implemented to explore the effects of the two factors as well as the measured variables for nectar breadth and date of last flight on population trajectories and drought response. The specification of latent variables was separated from the structural model to distinguish between defining latent constructs and testing causal hypotheses, to improve interpretability, and to reduce the influence of individual indicators on model inference. Model structure was based on a priori hypotheses using previous knowledge of the study populations, and comparisons among ecologically relevant models were conducted via leave-out-one cross-validation (Vehtari et al., 2017; see supporting information methods section for model details and comparison; Appendix S1: Figure S3). Probabilities of effects (PE) were calculated as the proportion of posterior distributions that are greater than or less than zero for a given path coefficient (McElreath, 2020). Additionally, an analysis was done using the original measured traits on population trends and drought response to compare it to the latent variable approach (supporting information for details; Appendix S1: Figure S4).

RESULTS

Distributions of nectar breadth and larval diet breadth

In total, of the 1220 images representing 96 butterfly species, we had sufficient data (at least 10 photos) to calculate extrapolated and rarefied nectar breadth for 50 species. Based on the asymptotic estimation of nectar breadth, adult butterflies in this community displayed a wide spectrum of nectar use (Figure 1a; min = 1, median = 14.6, max = 72) with 19 species in the lowest third of nectar breadth, 15 in the intermediate, and 16 in the highest third. For larval diet breadth, we had plant species-level data for 77 butterfly species, and found that larval diet breadth was highly specialized both at the plant species (Figure 1b; min = 1, median = 9, max = 127) and at the plant family level (Figure 1b; min = 1, median = 1, max = 19). *Euphilotes battoides* displayed the highest degree of nectar specialization (Figure 1a,d), being observed on a single flower species, *Eriogonum umbellatum*. The most nectar generalized butterfly was *Phyciodes mylitta* (Figure 1d), with an estimated asymptotic nectar richness of 72.

Exploratory factor analysis

The variables of abundance, ruderal status, and larval diet breadth loaded strongly onto Factor 1 (Figure 2a; loadings: abundance = 0.85, ruderal status = 0.96, and larval diet breadth = 0.45). We hereafter call this factor "ecological flexibility" as the measured variables that indicate greater flexibility in resource use (diet breadth), association with disturbed habitat (ruderal status), and greater abundance are expected to provide resilience to environmental change (Mair et al., 2014). Geographic range size and wingspan had loadings onto Factor 1 of 0.19 and −0.10, respectively. In contrast, wingspan and geographic range size strongly loaded (0.48 and 0.88, respectively) onto Factor 2. We will call Factor 2 "dispersal potential" as wingspan and geographic range size have been shown to correspond to dispersal ability (Nieminen, 1996; Sekar, 2012). Abundance, ruderal status, and larval host breadth had loadings onto Factor 2 of 0.00, −0.15, and 0.34, respectively. Together, Factors 1 and 2 encompassed 64% of the standardized variance.

Structural equation model

The best fitting SEM included the exogenous latent variables of "ecological flexibility" and "dispersal potential" using the scores from the factor analysis, along with measured variables for rarefied nectar breadth and mean date of last flight (Figure 2b). Ecological flexibility was positively associated with trends over time (path coef. = 0.51, 95% CI = [0.07, 0.93], PE = 97%) and with nectar breadth (path coef. = 0.44, 95% CI = [0.06, 0.82], PE = 99%). Nectar breadth was negatively related to trends over time (path coef. = −0.23, 95% CI = [−0.56, 0.08], PE = 94%). Dispersal potential was negatively related to trends over time (path coef. = −0.51, 95% CI = [−0.96, −0.10], PE = 99%), and positively related to the date of last flight (path coef. = 0.22, 95% CI = [−0.08, 0.51], PE = 93%). The date of last flight was negatively related to drought response (path coef. = −0.42, 95% CI = [−0.79, −0.05], PE = 98%).

DISCUSSION

The literature on trait-based analyses of population trends reveals considerable complexity as reflected in heterogeneous associations between individual traits and population trajectories (Burner et al., 2021; Tordoff et al., 2022). For butterflies, there has been a focus on larval diet, as most adult butterflies are assumed to be opportunistic nectar generalists (Lebeau et al., 2017; Subedi et al., 2021). Nevertheless, nectar availability at the community or landscape level likely affects butterfly population dynamics (Crone et al., 2024; Wallisdevries et al., 2012), and we expect differences in nectar breadth could mediate this relationship. Our results show that montane butterflies in our area of the western United States display a wide spectrum of nectar breadth (Figure 1a) with some species displaying relative nectar specialization (Figure 1d), which is not unprecedented (Altermatt & Pearse, 2011; Lebeau et al., 2017), and few displaying extreme generalism. We also found that nectar-specialized butterflies are less likely to be declining (Figure 2b). Compared with

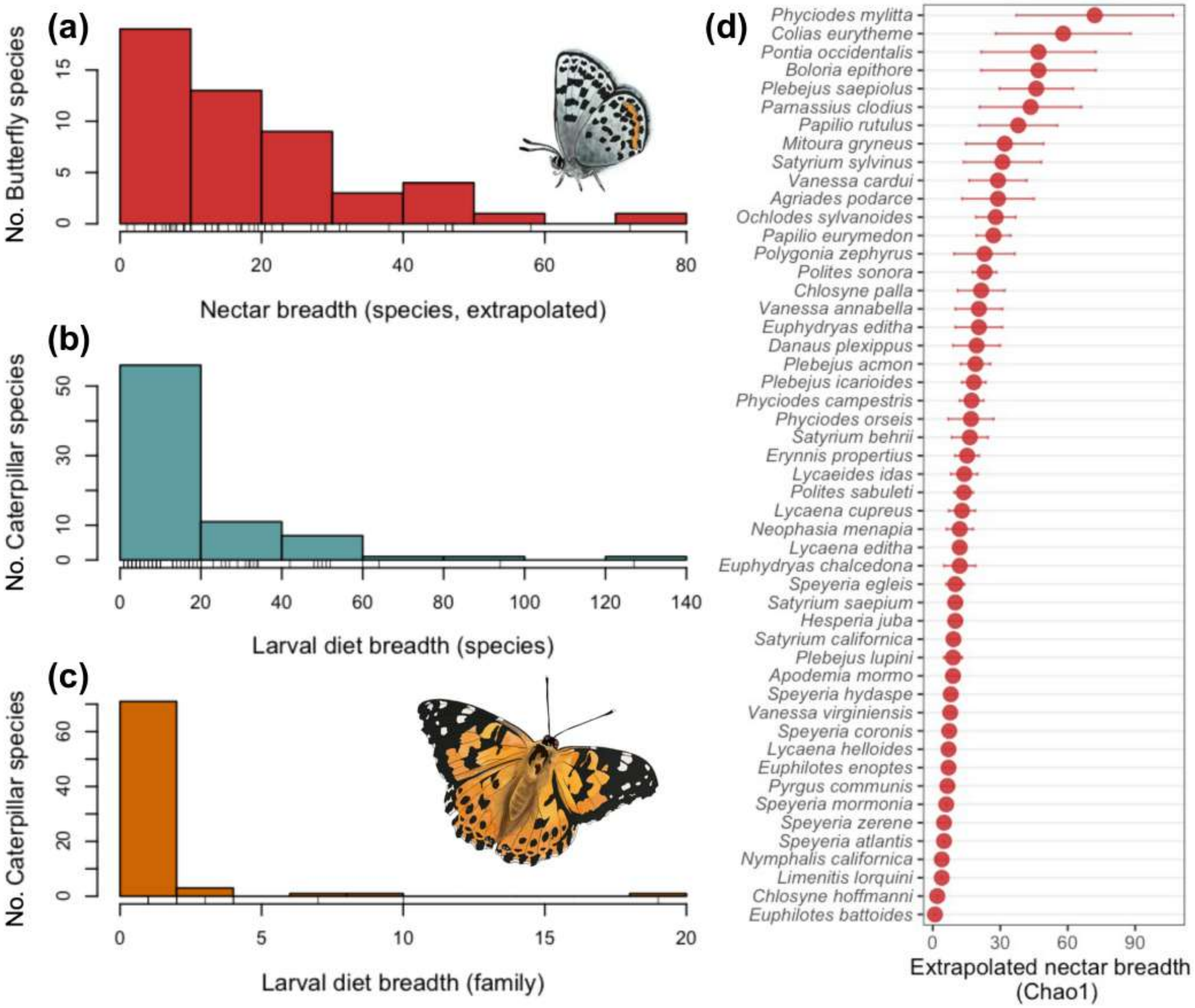

FIGURE 1 (a) Histogram of nectar breadth values for 50 species of Sierra Nevada butterflies. The *x*-axis shows extrapolated nectar richness for each butterfly species based on Chao1 estimates, and the illustration is of *Euphilotes battoides*, the most specialized nectar feeder (Chao1 = 1). Larval diet breadth of 77 butterfly species at the host plant species level (b), and host plant family level (c), with an illustration of *Vanessa cardui*, the species displaying the greatest larval generalism. (d) Extrapolated nectar breadth (Chao1 asymptotic richness) for 50 species of butterflies indicated by the dots, with SEs for estimates shown by horizontal lines. Butterfly illustrations were drawn by Tara Christensen.

nectar breadth, larval diet displays higher specialization (Figure 1b,c), with the majority of larvae feeding only on a few plant species, or within one or two families, which aligns with global patterns of larval diet breadth (Forister et al., 2015). Larval diet breadth alone did not influence population trajectories (Appendix S1: Figures S4a and S5a).

Despite heterogeneity in the ability of trait-based analyses to identify the causal factors that influence susceptibility to decline in insects, previous work has shown that ecological flexibility through generalism in resource use as well as dispersal potential confers an advantage to taxa experiencing environmental stressors under anthropogenic change (Buckley & Kingsolver, 2012; Warren et al., 2001). We found that species at our sites with greater dispersal potential are faring worse over time, which is consistent with previous work on these populations from Halsch et al. (2021). The authors posited that many wide-ranging species observed at the montane sites are dependent on migration from low-elevation sites experiencing multi-decadal declines associated with increasing pesticide use and land-use change (Forister et al., 2016). In our models, later dates of last flight were negatively associated with drought

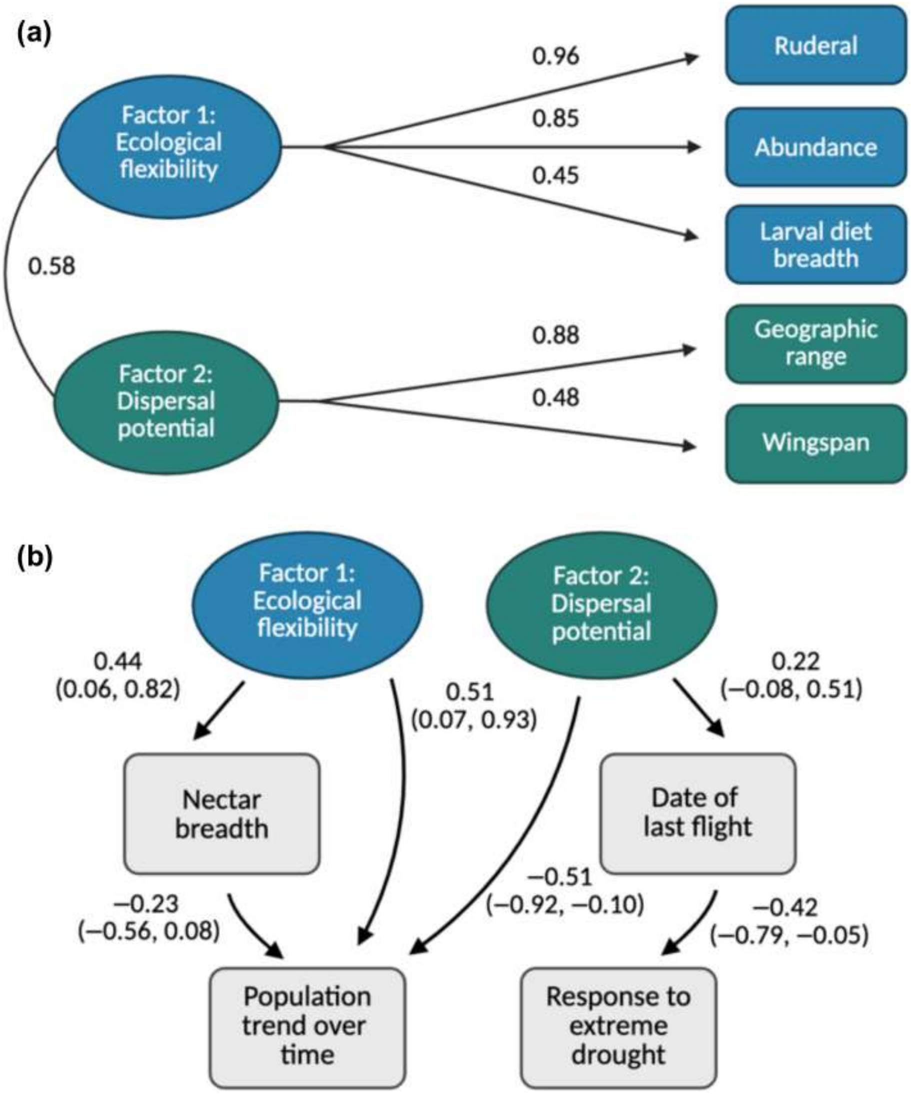

FIGURE 2 (a) Two factors were identified to represent the latent constructs of "ecological flexibility" and "dispersal potential" (variance encompassed = 0.64). Variables describing associations with weedy habitats ("ruderal"), abundance, and larval diet breadth had strong, positive loadings onto Factor 1 ("ecological flexibility"), while geographic range and wing span loaded strongly onto Factor 2 ("dispersal potential"). The correlation between factors is 0.58. (b) Modeled relationships between variables from the SEM. Path coefficients are indicated for individual paths, with 95% credible intervals given in parentheses. Population trends for butterflies were strongly positively related to "ecological flexibility" and negatively related to "dispersal potential," while species with greater nectar breadth had more negative population trajectories. Dispersal potential was positively associated with later dates of last flight, which were negatively associated with response to an extreme drought event.

response, perhaps due to limited nectar availability in the late summer during drought years or decreased nutritional value of host plants due to drought stress (Scriber, 1977).

Our findings indicate that species with greater ecological flexibility tend to perform better over time (Figure 2b), and that species deemed more ecologically flexible are also more likely to display increased nectar breadth. However, there was a negative direct effect of nectar breadth on population trends. This contrasts with conventional thinking on the relationship between dietary specialization and population trajectories amidst anthropogenic change, as well as empirical evidence from specific studies (Kotiaho et al., 2005; Palash et al., 2022). However, positive population responses of specialists are not unheard of; a study of British butterflies found that many specialists were expanding their ranges, suggesting resilience to anthropogenic change (Dapporto & Dennis, 2013). One possible explanation for our result is that apparent nectar specialists may be preferentially nectaring on plants that are highly abundant at these sites. For example, *Eu. battoides*, our most extreme specialist, was found nectaring only on *Er. umbellatum*, its larval host plant, which is widespread and abundant across the Sierra Nevada. Species appearing more specialized may depend on a few reliable nectar plants that they are better able to track through changing geographic or temporal distributions, while generalist species might depend on diverse assemblages of nectar resources that have variable responses to environmental change. Our study sought to expand the ecological trait literature by including nectar breadth because availability and quality of nectar resources are expected to change under climate warming (McCombs et al., 2022). For example, a meta-analysis of nectar traits showed substantial heterogeneity in responses to warming treatments (Alquichire-Rojas et al., 2024). Thus, butterfly species-level differences in nectar resource partitioning could influence population resilience if they utilize nectar resources that perform favorably under anthropogenic change. However, we did not find a strong effect of nectar breadth on response to regional drought, indicating that nectar use patterns may be more consequential over the long term than for buffering responses to extreme events.

Our study contributes to the ongoing discussion on the role of ecological traits in predicting species population trajectories under anthropogenic change and in response to climate extremes. While the literature presents a mixed picture regarding the impact of traits such as dietary and habitat specialization on butterfly populations, our findings suggest that increased ecological flexibility offers an advantage to butterfly populations experiencing climate change. Additionally, we found nectar specialists performed better in recent decades, underscoring the importance of considering nectar use when describing butterfly niche space and challenging the assumption that dietary generalism is always beneficial in changing environments. As the global biodiversity crisis continues, our study emphasizes the need to interpret the effects of traits in a nuanced manner, consider understudied traits, and recognize that generalism and specialism can shape resilience in complex ways.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data and code (Christensen et al., 2025) are available in Dryad at https://doi.org/10.5061/dryad.tb2rbp0cg.

ORCID

Tara Christensen https://orcid.org/0000-0002-3237-9049

Christopher A. Halsch https://orcid.org/0000-0003-1381-1905

Lee A. Dyer https://orcid.org/0000-0002-0867-8874

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SUPPORTING INFORMATION

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

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