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Recent climate change is creating hotspots of butterfly increase and decline across North America

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Abstract

Some insect populations are experiencing dramatic declines, endangering the crucial ecosystem services they provide. Yet, other populations appear robust, highlighting the need to better define patterns and underlying drivers of recent change in insect numbers. We examined abundance and biodiversity trends for North American butterflies using a unique citizen-science dataset that has recorded observations of over 8 million butterflies across 456 species, 503 sites, nine ecoregions, and 26 years. Butterflies are a biodiverse group of pollinators, herbivores, and prey, making them useful bellwethers of environmental change. We found great heterogeneity in butterfly species' abundance trends, aggregating near zero, but with a tendency toward decline. There was strong spatial clustering, however, into regions of increase, decrease, or relative stasis. Recent precipitation and temperature appeared to largely drive these patterns, with butterflies generally declining at increasingly dry and hot sites but increasing at relatively wet or cool sites. In contrast, landscape and butterfly trait predictors had little influence, though abundance trends were slightly more positive around urban areas. Consistent with varying responses by different species, no overall directional change in butterfly species richness or evenness was detected. Overall, a mosaic of butterfly decay and rebound hotspots appeared to largely reflect geographic variability in climate drivers. Ongoing controversy about insect declines might dissipate with a shift in focus to the causes of heterogeneous responses among taxa and sites, with climate change emerging as a key suspect when pollinator communities are broadly impacted.

KEYWORDS
biodiversity, cropland, insect conservation, pollinators, species traits

1 | INTRODUCTION

There is little question that conversion of natural lands to agriculture, and other large-scale human disturbances, has dramatically altered insect communities (Dirzo et al., 2014). Nonetheless, recent declines among European honey bees (*Apis mellifera*) and other pollinators make it clear that subtler, ongoing changes to insect populations can bring additional harm to natural and managed ecosystems (Biesmeijer et al., 2006; Carvalheiro et al., 2010; Potts et al., 2010). Particularly troubling are recent reports that some broad groups of insects, particularly, but not only, in Europe are experiencing sudden, often dramatic, decreases in abundance and biomass

(Conrad et al., 2006; Hallmann et al., 2017). These trends suggest that rapid change in environmental drivers such as land use, climate change, light pollution, pesticide applications, or other human-induced changes (Goulson et al., 2015; Owens et al., 2019; Seibold et al., 2019) are pushing insects past a breaking point, endangering the many ecosystem services they provide. At the same time, declines clearly are not uniform. Some insects, even in heavily disturbed sites, appear stable or increasing, even alongside other taxa or groups that are in steep decline (Bell et al., 2020; Macgregor et al., 2019; Roubik, 2001). This same heterogeneity in responses among sites and taxonomic groups has been seen in several syntheses of arthropod abundance trends (Crossley et al., 2020; Outhwaite et al., 2020; van Klink et al., 2020). Out of necessity, efforts to search for broad patterns and possible unifying mechanisms generally must rely on summaries across disparate insect groups sampled at different places and times, monitored in very different ways. This can make contrasting patterns of increase and decline difficult to meaningfully sum, and complicates the extraction of any general, broad-acting mechanisms (Saunders et al., 2020). Uncertain and conflicting findings have led to some skepticism that an "insect apocalypse" is truly underway, or even would be likely (Montgomery et al., 2020; Saunders et al., 2020; Thomas et al., 2019). Most edifying would be data that report consistent sampling of ecologically diverse species over broad spatiotemporal scales, sufficient to capture meaningful variation in the traits of species and landscapes that might underlie wholesale degradation of insect communities.

Here, we examine recent abundance and biodiversity trends for adult butterflies observed during the North American Butterfly Association's (https://www.naba.org) yearly midsummer counts. This remarkable citizen-scientist monitoring effort began in earnest in 1993 and has included substantial sampling at over 500 sites across Canada, Mexico, and the United States (Figure 1). The millions of butterflies observed include ca. 80% of the species expected to occur across these locations. The spatiotemporal coverage of these data presents a unique opportunity to examine recent population trends at a near-continental scale spanning different ecoregions, climates, and levels of human disturbance. The data also represent an important and diverse insect group that was consistently tracked using the same methods. Butterflies are key pollinators, but also serve as food resources for birds and many predators, parasites, and pathogens (Boggs et al., 2003). Butterflies are also often brightly colored and appealing to people, leading them to play important roles in human culture (Hvenegaard, 2016). Therefore, butterflies contribute to a wide array of provisioning, regulating, cultural, and supporting ecosystem services. Like other insects, butterflies of some species and/or at some sites appear to be in steep decline, most clearly in Europe, although some species, communities, and/or sites are relatively stable or even increasing (Breed et al., 2013; Forister et al., 2010; Kuussaari et al., 2007; van Strien et al., 2019; van Swaay et al., 2006; Wepprich et al., 2019). Both species-specific traits such as diet and habitat breadth, and landscape-scale drivers such as loss of natural areas and climate change, have been linked to butterfly declines (Devictor et al., 2012; Habel et al., 2016; Menéndez et al., 2007). Consequently, butterflies may be useful proxies to learn about insect abundance change and its drivers more generally.

While the North American butterfly counts have been used to examine population trends for single butterfly species (e.g., Espeset et al., 2016) and biodiversity patterns in particular regions (Kocher & Williams, 2000; Meehan et al., 2013), they had not before been comprehensively collated and examined as a whole for broad changes in abundance and diversity across the continent. Here, we distill 8,448,945 butterfly observations into 14,159 species × site abundance trends and ask how well abundance trends are explained by butterfly species traits, as well as climate and landscape attributes of the count sites. We also quantify trends in butterfly species
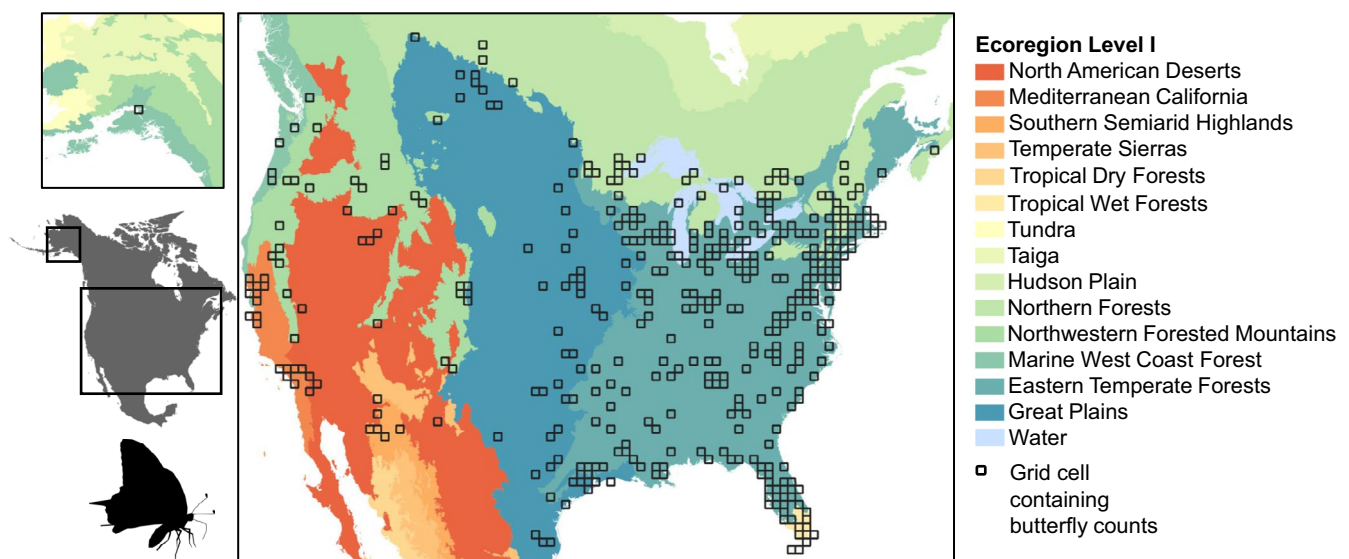

FIGURE 1 Map of butterfly count sites. Squares (N = 418) depict 2500 km^2 grid cells in which abundance trends were estimated. Colors denote Environmental Protection Agency Level I Ecoregions [Colour figure can be viewed at wileyonlinelibrary.com]

richness and evenness and again ask how well biodiversity trends are explained by climate and landscape features. Our analyses reveal broad variability in butterfly abundance and biodiversity change among species and sites, with regional hotspots of butterfly decline and increase. They further suggest recent climate change as an important driver of butterfly species abundance trends, with the greatest declines observed in increasingly dry and hot areas.

2 | MATERIALS AND METHODS

2.1 | Butterfly data curation

Butterfly observational data were obtained from the North American Butterfly Association's Butterfly Count Program, a citizen-scientist monitoring effort that began monitoring butterflies in 1993 throughout Canada, Mexico, and the United States (https://www.naba.org/). Butterfly counts are made within a 15-mile (~24 km) diameter circle, typically in July, and are open to participation from the public. For each count event, the abundances of butterfly species are tallied and the sum of associated party hours (a measure of sampling effort that aggregates the number of hours spent by each observer) is recorded. In total, the raw data contained 388,675 butterfly species × site × date observations and documented a total of 11,950,146 butterflies between 1993 and 2018 (Figure S1A).

Raw count data underwent several curation steps prior to analyses. To obtain species-level records, we removed 15,737 instances of butterflies identified only to genus, and merged counts of subspecies to the species level (affecting 45 species). This species-level dataset contained 387,842 species × site × date observations for 645 species. To minimize bias due to differences among sites in the day of year when butterfly counts were conducted, we limited our analysis to butterfly counts that occurred between June and August. Prior to estimating trends in abundance and diversity, we removed any species × site combinations that had <5 data points and that spanned <10 years (Didham et al., 2020). Remaining sites spanned on average 15.8 ± 0.3 years and a maximum of 26 years. The curated dataset documented a total of 8,448,945 butterflies and comprised 456 species from 503 sites (Figure S1B). Once curation was complete, only sites from the conterminous United States, southern Canada, and Alaska remained in the analysis, limiting our ability to predict changes in some regions, notably Mexico and northern reaches of Canada.

2.2 | Estimating abundance trends

Butterfly abundance trends were estimated on a per-species × site level following the analytical approach of Meehan et al., (2019), which analyzes a highly analogous dataset (the Audubon Christmas Bird Count) using a spatially varying coefficient approach. First, butterfly counts were assigned to 50 × 50 km (2500 km^2) cells on a uniform grid covering North America. Thus, counts from the 503 sites

were assigned to 418 unique grid cells, where the number of count sites per grid cell ranged from 1 to 4 and averaged 1.203 ± 0.023 (SE). Next, expected counts of a butterfly species were modeled as a random variable from a negative binomial distribution and assumed to be a function of (1) cell-specific random intercepts; (2) spatially structured, cell-specific, random slope coefficients for the local effects of sampling effort; (3) spatially structured, cell-specific, random slope coefficients for the year effect; and (4) an exchangeable random effect that accounted for variation in relative abundance among circles (for the formal model equation, see Meehan et al., 2019). We examined overdispersion to test if a negative binomial distribution was justified over a Poisson distribution. Of the 456 butterfly species for which abundance trends were calculated, 415 (91%) had overdispersion parameters >1, suggesting that a negative binomial model was usually justified. The random intercept and slopes for effort and year effects were modeled with an intrinsic conditional autoregressive structure, and their precision matrices were scaled such that the geometric mean of marginal variances was equal to one (Freni-Sterrantino et al., 2018; Riebler et al., 2016; Sørbye & Rue, 2014). Priors for these parameters and for the zero-centered random circle effect were penalized complexity priors, with values UPC = 1 and aPC = 0.01 (Simpson et al., 2017). Bayesian posteriors for model parameters were estimated using integrated nested Laplace approximation (Rue et al., 2009). Prior to analysis, year (y) was transformed according to y − 1993, and party hours were natural log-transformed (Meehan et al., 2019). The estimated year effects were taken as the butterfly abundance trends, which are interpreted as the percent change in abundance per year per party hour of sampling effort (Meehan et al., 2019). We note that we used the linear modeling approach of Meehan et al., (2019), despite the availability of methods that detect nonlinear changes in abundance, such as generalized additive mixed models (Bell et al., 2020) and segmented regression (Macgregor et al., 2019), because the latter approaches do not allow for simple extraction of a rate of change over time and are not as amenable to making broad comparisons among species and sites and then attempting to associate this with trait and environmental variables.

Trends in total butterfly abundance were also estimated using the same spatially varying coefficient approach, except that total abundance (the sum of butterfly counts across all species observed in a site × year) was used as model input. Total abundance trends were estimated with the full complement of species and with a dataset that excluded counts from the two most abundant, and invasive, butterfly species: *Thymelicus lineola* and *Pieris rapae*.

2.3 | Estimating diversity trends

We used species richness and evenness as our measures of diversity and used their rarefied forms for trend estimation. Richness was calculated as the number of species at a given site and year, and was rarefied according to a minimum sample size of 100 butterflies using the *rarefy* function in the "vegan" R package (Oksanen et al., 2019).

Evenness was calculated according to E_{var} (Crowder et al., 2012; Smith & Wilson, 1996):

$$E_{var} = 1 - \left(\frac{2}{\pi}\right) * arctan\left(\sum_{s=1}^{S}\left(\frac{\left\{\ln[x_s] - \sum_{t=1}^{S}\ln[x_t]\right\}}{S}\right)\right),$$

where x_s and x_t are the number of individuals in species s or t, respectively, and S is the number of species. For evenness calculations, species absences at a given site × year were considered implicit zeroes. To calculate rarefied evenness, instead of raw species counts as input to the E_{var} equation, we used the species occurrence probabilities based on a minimum sample size of 100. Note that rarefied richness in a site × year equaled the sum of these occurrence probabilities. We selected a minimum sample size of 100 among a range of examined minimum sample sizes (10, 100, 500, 1000) for rarefaction of richness and evenness because overall trend estimates were relatively robust to sample size and larger sample size requirements greatly reduced the number of sites included in the trend estimation procedure (Figures S2 and S3).

Time trends in rarefied richness and evenness were calculated at a site level (rather than per grid cell) using autoregressive models fit using restricted maximum likelihood (Ives et al., 2010). Any time series with greater than 5 (out of 10) years of missing data were excluded from the analysis (343 sites were retained). Prior to trend estimation, rarefied richness and rarefied evenness were Z-score transformed, and time was transformed according to $y - 1993$ such that trends are interpreted as change in standard deviations per year.

2.4 | Trait and environmental covariates

Butterfly traits that we examined included two continuous variables, adult size (midpoint estimate of wingspan in mm) and larval diet breadth (defined as the number of plant families represented among larval host plants), as well as four categorical variables, larval color (aposematic vs. not), larval hairs (present vs. absent), adult color (aposematic vs. not), and NatureServe conservation status (ranging from secure to critically imperiled; we acknowledge that conservation status might better be termed a "characteristic" and not a trait inherent in a species). Species traits were acquired from a combination of scientific websites and primary literature (see Data Availability Statement). These traits have been predicted to affect response to anthropogenic environmental change through a variety of indirect mechanisms. Larger species (adult size) are often at higher risk for declines or extinction, whether due to lower fecundity, greater vulnerability to predators, or greater resource requirements (Dirzo et al., 2014; Sánchez-Bayo & Wyckhuys, 2019; van Swaay et al., 2006). Specialists (larval diet breadth) are expected to be more sensitive to environmental change than generalists (Cornelissen, 2011; Harrington et al., 1999; van Swaay et al., 2006; Warren et al., 2001), as are threatened (NatureServe conservation status) species

(Franzén & Johannesson, 2007; Wilson & Maclean, 2011). Changes in predator populations from anthropogenic change would presumably affect poorly defended species more than well defended (larval and adult color, larval hairs) species (Laws, 2017).

Climate covariates were mean temperature and cumulative precipitation. Climate data were obtained from CRU TS 4.03 (Harris et al., 2014), which provides monthly climate data from 1901 to 2018. Thus, to obtain a contemporary estimate of mean temperature and cumulative precipitation, we calculated the annual average of monthly values, then took the average of annual values between 1993 and 2018. To differentiate effects of contemporary climate from historic changes in climate over the study period, we calculated trends in temperature and precipitation between 1901 and 2018 using autoregressive models fit using restricted maximum likelihood (Ives et al., 2010), first Z-score transforming climate observations and transforming year according to $y - 1901$. These models allowed estimation of linear trends in precipitation and temperature, whose slopes are interpreted as the change in units of standard deviations per year, while accounting for temporal autocorrelation.

Land cover covariates were proportion cropland, historical trend in proportion cropland, and proportion built ("urban") land cover. Proportion cropland and proportion built land cover were used to represent a suite of potentially impactful land use effects on butterfly populations, whose effects are difficult and unnecessary to isolate within our modeling framework. The amount and fragmentation of natural habitat are expected to decrease and increase, respectively, with increasing proportion cropland and built land cover (Haddad et al., 2015). Effects of insecticides and herbicides, which are detrimental to insects directly by toxicity as well as indirectly via effects on host plants (Pleasants & Oberhauser, 2013), will also tend to be greater with increasing cropland and built land cover (Falcone et al., 2018; Meehan & Gratton, 2016). Lastly, given the rapid and dramatic change in the amount and location of cropland in the United States since the 1800s (Crossley et al., 2021; Waisanen & Bliss, 2002), the historical trend in proportion cropland was included to examine whether legacies of historical cropland expansion show any effects on butterfly abundance trends that are distinct from the amount of contemporary, intensively managed cropland (Foster et al., 2003). Contemporary land cover data were obtained from the North American Land Change Monitoring System (NALCMS; MRLC Consortium, 2020). Historic cropland data were obtained from the Historic Croplands Dataset 1700–1992 (https://nelson.wisc.edu/sage/data-and-models/historic-croplands/index.php; Ramankutty & Foley, 1999). As with climate covariates, we obtained a contemporary estimate of land cover and an estimate of historical trends over the study period (though comparable data on historic built land cover were not available). Because the NALCMS datasets for which there is unified, continuous geographic coverage across North America are limited to 2005 and 2015, we took the average of values from 2005 and 2015 as the contemporary estimate. We estimated the historical trend in cropland cover using the same approach as for climate, including proportion cropland estimates

from available years (1901–1992, 2005, 2015) in the trend estimation procedure.

For models predicting abundance trends, climate and land cover covariates were extracted from the same 2500 km^2 grid cells used to calculate butterfly abundance trends using the "raster" R package (Hijmans, 2020). For models predicting diversity trends, climate and land cover covariates were extracted from 24-km diameter circles corresponding to the area over which butterfly diversity was estimated. Maps depicting climate and land cover covariates across grid cells are provided in Figure S4.

2.5 | Environmental correlation analysis

We examined potential drivers of changes in butterfly abundance using linear mixed-effects models with the "nlme" R package (Pinheiro et al., 2020), hypothesizing that butterfly traits and variation in climate and land cover could explain species × site-level differences in abundance trends. Prior to modeling, we removed any trends associated with species that occupied less than 10% of the 418 grid cells in our study extent (trends for 233 species remained). Trait and environmental variables were then Z-score transformed. We used fourth corner analysis (Dray et al., 2014) to determine which trait-by-environment interactions should be considered in models, limiting analysis to continuous traits (adult size and larval diet breadth). Results from this analysis suggested that correlations among traits and climate or land cover covariates were small (fourth corner coefficients ranging from −0.02 to 0.04; Figure S5). We, therefore, excluded trait-by-environment interactions, greatly reducing the complexity of our model fitting procedure. We included as fixed effects the six butterfly traits (adults color, adult size, conservation status, larval color, larval diet breadth, larval hairs), four climate covariates (precipitation and temperature, as well as historical trends in each), and three land cover covariates (proportion cropland, historical trend in proportion cropland, and proportion built land cover). To account for variation due to taxonomic relatedness, we included as random effects butterfly family and butterfly species nested within family. Because we detected spatial autocorrelation in residuals, we used an exponential spatial error structure in subsequent models. We used the Akaike information criterion (AIC) to compare Gaussian, spherical, and exponential spatial error structure, and the exponential spatial error structure was the best fit. We then constructed 72 models (Table S1) with combinations of factors hypothesized to affect species-level abundance trends, ranging from the null model (random effects only), to the global model incorporating all fixed effects and their interactions between contemporary and historical trend variables (e.g., Precipitation:Trend in precipitation). We identified the best-supported model based on AIC$_c$. Covariates in top model were considered strong drivers of the response variable if their associated 95% confidence intervals did not overlap zero. We confirmed that covariates in top models were not highly colinear using variance inflation factors (VIF <5; Fox & Weisberg, 2019).

We examined the sensitivity of model results to changes in the beginning or end date of butterfly abundance time series, as suggested in Didham et al., (2020) as a way to test for a "false baseline effect." To do so, we first repeated curation of butterfly count data so that counts prior to 1998 were excluded (left-censoring) or so that counts after 2013 were excluded (right-censoring). Species-level abundance trends were then estimated, and trait and environment associations examined as described for the full dataset.

To examine the sensitivity of model results to inclusion of butterfly species traits and environmental variables associated with count sites in one global model, we repeated the analysis of butterfly abundance trends as a function of butterfly traits and environmental variables with separate models. We examined the importance of butterfly traits in explaining variation in butterfly species abundance trends by collapsing abundance trends into a single, median abundance trend for each butterfly species, and included the six butterfly traits as fixed effects and butterfly family as a random effect in a linear mixed-effects model (Pinheiro et al., 2020). We examined the importance of site environmental variables in explaining variation in butterfly species abundance trends by modeling abundance trends for each species separately. Models included as fixed effects climate (contemporary precipitation and temperature, and historical trend in precipitation and temperature) and landscape (contemporary proportion built, contemporary proportion cropland, historical trend in proportion cropland) variables, and included grid cell as a random effect. Species that did not occupy at least 10 grid cells were omitted from this analysis. The importance of each environmental covariate was then assessed by tabulating the distribution of covariate effects across species models.

To visualize hotspots of butterfly abundance increase or decline, we used the best-supported model (which included average cumulative precipitation between 1993 and 2018, average annual temperature between 1993 and 2018, historical trend in temperature between 1901 and 2018, interaction between average cumulative precipitation and historical trend in precipitation between 1901 and 2018, and average proportion built land cover between 2005 and 2015; Table 1; Table S1) to extrapolate species-level abundance trends over North America. We did this using the map algebra tool in ArcMap v10.7.1 (ESRI), calculating the extrapolated abundance trend according to: $\alpha + \beta_{built} \times$ Built $+ \beta_{precipitation} \times$ Precipitation $+ \beta_{temperature} \times$ Temperature $+ \beta_{temperature.trend} \times$ Temperature.trend $+ \beta_{precipitation.interaction} \times$ Precipitation.interaction, where α is the model intercept, Precipitation is the average cumulative precipitation between 1993 and 2018, and $\beta_{precipitation}$ is the estimated effect of average cumulative precipitation on species-level abundance trends according to the AIC$_c$-best model. The resulting map was then colored according to standard deviation bins.

We examined potential drivers of changes in butterfly diversity (rarefied richness and rarefied evenness) using linear models fit using generalized least squares (Pinheiro et al., 2020). Model structure was the same as for abundance trend models, except that butterfly

TABLE 1 Covariate effects on species-level butterfly abundance trends based on the linear mixed-effects model best supported by AIC_c. "Prop. built" refers to the average proportion built land cover within 2500 km² grid cells between 2005 and 2015. "Precipitation" refers to the average cumulative precipitation between 1993 and 2018. "Precipitation trend" refers to the historical trend in precipitation between 1901 and 2018. "Temperature" refers to the average annual temperature between 1993 and 2018. "Temperature trend" refers to the historical trend in temperature between 1901 and 2018. "CI" refers to 95% confidence interval. Model degrees of freedom were 13,919

Variable	Estimate	Standard error	Lower CI	Upper CI
(Intercept)	−0.459	0.153	−0.759	−0.160
Prop. Built	0.044	0.018	0.008	0.080
Precipitation	0.163	0.044	0.076	0.251
Precipitation trend	−0.029	0.042	−0.111	0.053
Temperature	−0.131	0.056	−0.241	−0.021
Temperature trend	−0.113	0.048	−0.208	−0.019
Precipitation × Precipitation trend	−0.081	0.034	−0.148	−0.013
Temperature × Temperature trend	−0.037	0.051	−0.138	0.064

Abbreviation: AIC, Akaike information criterion.

traits were not included because this was a site-level analysis. Based on lowest AIC, we included a spherical spatial error structure to account for spatial autocorrelation. A global model was constructed that included all covariates, and a comprehensive model selection procedure was implemented with *dredge* from the "MuMIn" R package (Barton, 2020). We employed a comprehensive model selection procedure for evaluating drivers of diversity change and not abundance change, because evaluation of the latter was not computationally tractable (i.e., model selection with species × site abundance trends was allowed to run for months on an HP Z800 Workstation without ever finishing). This was because diversity models included 503 site observations, while abundance models included 14,159 species × site observations. We identified important covariates and interpreted their effects using the same procedure as for abundance models.

3 | RESULTS

3.1 | "Hotspots" of decline and increase

Species varied considerably in their responses such that mean abundance change broadly overlapped with zero (Figure S2A), with 48% of species (218/456) exhibiting decreases below −1%/year and 26% of species (119/456) exhibiting increases greater than +1%/year (Figure 2a). Likewise, there was variability in the consistency of abundance trends across sites within individual species. Some species declined at all sites, others increased at all sites, and still others exhibited a mixture of declining, increasing, or unchanged abundances at different sites (Figure 2b). While these species-specific responses were highly heterogeneous (Figure S6B), mapping suggested obvious regional "hotspots" of decline, increase, or relative stability (Figure 3a; Figure S6). Declines were overwhelmingly apparent in the southwestern United States and the Intermountain West, with increases predominant in much of the Southeast and coastal Pacific Northwest (Figure 3a). In general, forested biomes (e.g., temperate deciduous and coniferous forests) showed modest

changes, including many increases, while many grassland (Great Plains), desert, and Mediterranean regions showed broad declines (Figure 3a; Figures S6 and S7).

3.2 | Climate change predicts butterfly abundance trends

Average precipitation and temperature during the sampling period (1993–2018) appeared to be the strongest drivers of this complex mosaic of abundance responses (Figure 3b,c; Figure S8), followed by historical trend in temperature, the interaction between average precipitation and historical trends in precipitation, and the proportion of built land cover in the landscape (Table 1; Figures S8 and S9). While models considering responses of individual species separately highlighted the variability in the magnitude and direction of effects of climate covariates on butterfly abundance trends, median covariate effects were in agreement with global model results (Figure S10). In general, butterfly abundances fell at sites that have recently been increasingly dry or hot, and where temperature has increased since the 1900s, but grew at sites that recently have been relatively wet or cool (Table 1; Figure 3; Figure S8). Estimated declines in drier sites were exacerbated when historical trends in precipitation were also negative (Figure S9), as observed in the southwestern United States. In contrast to the seemingly key role of precipitation and temperature, landscape context and species traits appeared less influential. Among the landscape variables we considered, butterflies were detectably increasing only as the proportion of urban area in the landscape increased (Table 1; Figure S8). However, even this effect was quite weak compared to climate effects, and no other landscape factor was retained in the best-supported model (Table S1).

In an examination of the sensitivity of model results to the beginning (left-censoring to exclude counts prior to 1998) and end (right-censoring to exclude counts after 2013) date of butterfly abundance time series, we found that the majority of butterfly abundance trends maintained their direction of change
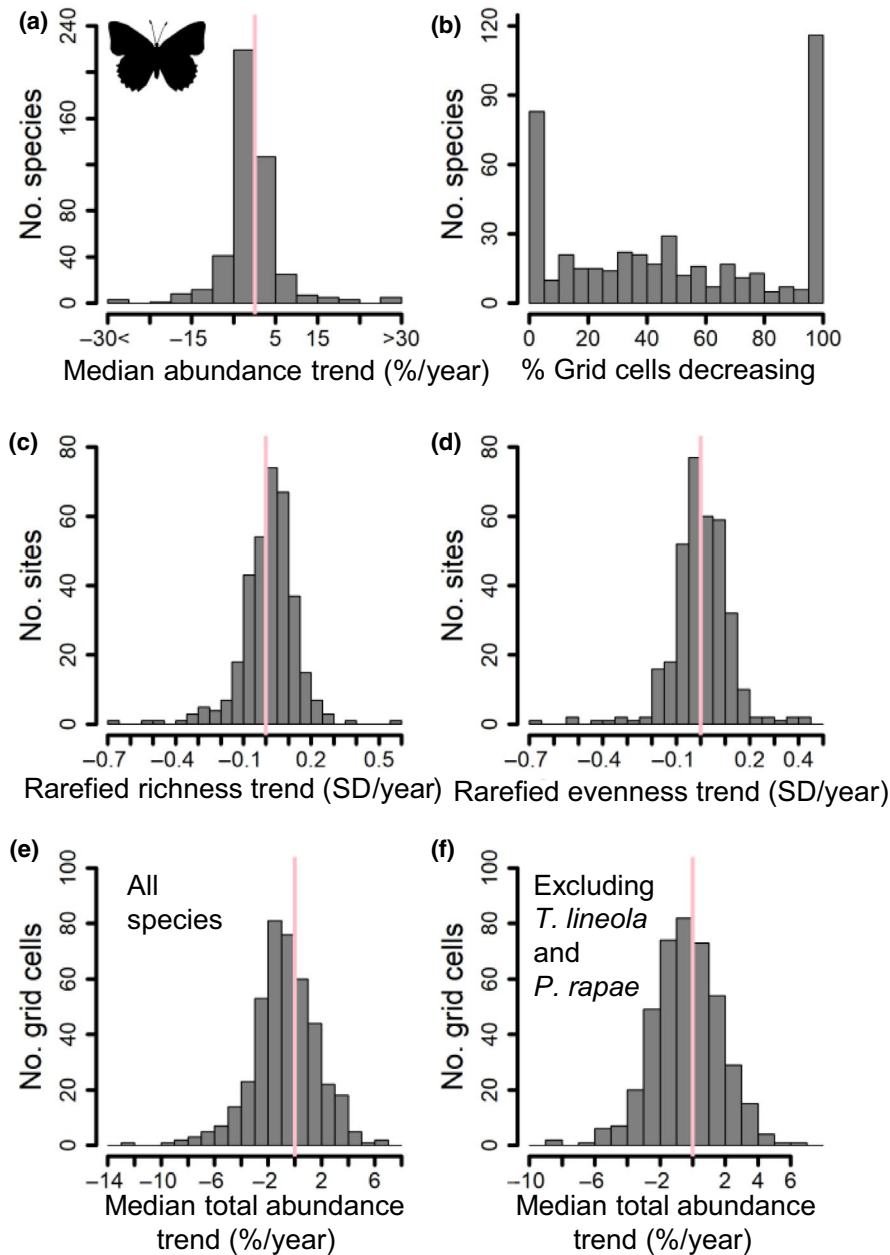
FIGURE 2 Butterfly abundance and diversity trends. (a) Distribution of median abundance trends (%/year) among 2500 km² grid cells (N = 418) per species. (b) Number of species exhibiting abundance declines (<−1% per year) in x% of occupied grid cells. (c) Distribution of rarefied richness trends (standard deviations/year) among sites. (d) Distribution of rarefied evenness trends (standard deviations/year) among sites. (e) Distribution of median total abundance trends (%/year) among grid cells. (f) Distribution of median total abundance trends (%/year) among grid cells, calculated after excluding counts from the invasive species *Thymelicus lineola* and *Pieris rapae* [Colour figure can be viewed at wileyonlinelibrary.com]

across censored and uncensored datasets, while a small but non-negligible portion of trends changed direction from increasing to decreasing, or vice versa, in left-censored (15%) and right-censored (20%) datasets (Figure S11). The AIC$_c$-best model from the full dataset (Table 1) was consistently within 2 AIC$_c$ of the top model in analyses of the left- and right-censored datasets (Table S3). Across censored and uncensored datasets, AIC$_c$-best models all included contemporary precipitation as well as proportion built land cover as significant predictors of (increasing) butterfly species abundance trends (Table S4). Support for other covariates was mixed, but the direction of covariate effects on butterfly abundance trends was consistent among analyses (Table S4). These findings suggest that further characterization of nonlinearity in butterfly abundance trends is worthwhile, but that our analysis of linear, long-term trends using a spatially varying coefficient

approach was relatively robust to the "false baseline effect" described by Didham et al., (2020).

3.3 | Heterogeneous butterfly biodiversity responses

Changes in abundance trajectories among so many butterfly species would be expected to have impacts at the community level. Indeed, different sites showed trends toward increase, decrease, or relative stasis in species richness and evenness (Figure 2c,d; Figures S12–S14). However, net trends broadly overlapped with zero for both biodiversity metrics (Figure 2c,d), and species richness and evenness change was sufficiently variable across the continent (Figure S12) that it did not correlate with any climate or landscape drivers
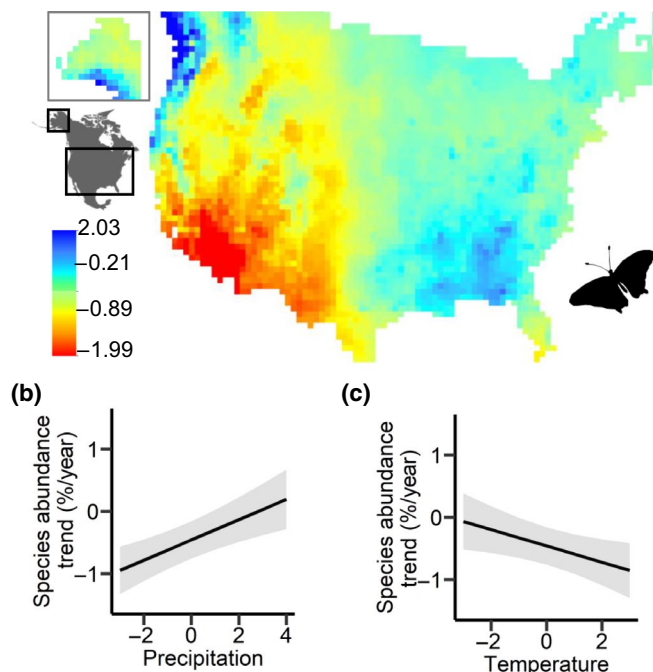
(a) Extrapolated species abundance trend (%/year)

FIGURE 3 Effects of climate and land cover on species-level butterfly abundance trends. (a) Map of extrapolated species × site butterfly abundance trends based on the AIC_c-best model, which included average cumulative precipitation between 1993 and 2018, average annual temperature between 1993 and 2018, historical trend in temperature between 1901 and 2018, interaction between average cumulative precipitation and historical trend in precipitation between 1901 and 2018, and average proportion built land cover between 2005 and 2015 (Table 1; Table S1). Map colors are based on standard deviation bins. (b) Relationship between average cumulative precipitation between 1993 and 2018 and species-level butterfly abundance trends. (c) Relationship between average annual temperature between 1993 and 2018 and species-level butterfly abundance trends. X-axes in (b) and (c) represent Z-transformed values, as used in linear mixed-effects models. Gray shading depicts 95% confidence bands. AIC, Akaike information criterion [Colour figure can be viewed at wileyonlinelibrary.com]

(covariate effects in best-supported models were not significant; Tables S5 and S6).

4 | DISCUSSION

4.1 | Heterogeneous butterfly abundance and biodiversity responses

Through analysis of a long-term citizen-scientist dataset including over 8 million butterflies across 456 species, 503 sites, and 26 years, we found great heterogeneity in butterfly species' abundance trends, aggregating near zero, but with a tendency toward decline. There was strong spatial clustering, however, into regions of increase, decrease, or relative stasis. Recent precipitation and temperature appeared to largely drive these patterns, with butterflies generally declining at

increasingly dry and hot sites but increasing at relatively wet or cool sites. We note that patterns of butterfly decline during drought are well documented for North American butterfly species and regional communities in western North America (Ehrlich et al., 1980; Forister et al., 2018; Thogmartin et al., 2017), although we know of no equivalent reporting for the southeastern and northwestern edges of the continent where counteracting increases were apparent (Figure 3a). We suspect that butterfly declines detected in our analyses might reflect falling availability and/or nutritional quality of food or nectar plants with increasing drought (Ehrlich et al., 1980; van Bergen et al., 2020), and/or growing physiological stress to the insects themselves due to water stress (Hawkins & Porter, 2003) which might, in turn, increase parasite or pathogen loads (McKay et al., 2016). Conversely, butterflies that are increasing in abundance might be benefiting from locally improved food resources or reduced stress in areas that have become wetter.

In contrast to climate variables, landscape and butterfly trait predictors had little influence, though abundance trends were slightly more positive around urban areas. It is perhaps surprising that butterflies might see any benefit from increasing amounts of urbanization, as anthropogenic land use has generally been shown to degrade, rather than enhance, insect populations (Blair & Launer, 1997; Clark et al., 2007). One intriguing possibility worth exploring is that greater environmental awareness is leading to new butterfly-friendly policies and practices in cities and suburbs (Öckinger et al., 2009; Snep et al., 2006). Likewise, butterfly species traits exhibited surprisingly little influence, whether environmental variables were included in models (Table S1) or not (Table S2). There is a large body of evidence that butterfly species that are relatively slow-developing or specialized, are migratory, or face attack by non-native natural enemies, are particularly susceptible to decline (Brower et al., 2012; Kuussaari et al., 2007). However, we did not find any association among species traits and abundance change (Table S1). Overall, it is possible that at the large scale of these data, the broad-acting climate effects simply overwhelmed any finer influence of landscapes or species attributes.

Given the biodiversity and ubiquity of butterflies in terrestrial ecosystems, and their many connections to other species as important pollinators, herbivores, and prey, any decline in North American butterfly biodiversity might broadly harm ecosystem functioning (Salcido et al., 2020). While it may seem reassuring, then, that there was no clear degradation in butterfly biodiversity, we suggest several reasons for caution. First, the general trend toward abundance decline in much of western North America, if it continues, would be expected to eventually lead to species being lost from sites alongside growing imbalance in species' relative abundances. For example, European butterflies appear to imperfectly track their preferred thermal niches as temperatures are warming, leading to biodiversity decline through time as climate mismatches intensify (Devictor et al., 2012; Menéndez et al., 2007; Parmesan et al., 1999; Warren et al., 2001). Second, changes in the identities of abundant versus rare species can change food web structure and function, even when broad biodiversity metrics like richness and evenness show no net change (Salcido et al., 2020).

Most efforts to search for patterns of recent insect decline must, out of necessity, rely on historical datasets collected for other reasons. Often, total insect abundance and/or biomass is the only community-level metric that is recorded, and thus available for analysis and comparison. For the North American butterfly count data, total butterfly abundance (summed across species) showed a general decline, falling ca. −0.72%/year (Figure 2e). This rate of decrease is consistent with the findings of a study including arthropods in German forests (Seibold et al., 2019) and a global meta-analysis for terrestrial insects (van Klink et al., 2020). Total butterfly abundance in the North American butterfly counts, though, was dominated by the invasive Essex skipper (*T. lineola*, which feeds primarily on non-native grasses) and the small cabbage white (*P rapae*, a worldwide agricultural pest), together representing ca. 28% of all individuals. One might expect that butterflies exhibiting the greatest increases would be "weedy" species, that is, those well adapted to human disturbance and global environmental change, while rarer species with more narrow niches decline. However, both invasives were strongly declining, such that their removal nearly halved the rate of total abundance decrease (to −0.42%/year; Figure 2f). That is, drops in the two invasive butterflies disproportionately contributed to overall abundance declines. Indeed, changes in evenness at many sites did not appear to reflect a broad rebalancing of communities in favor of human-associated species. Instead, changes in evenness reflected mixed shifts in rarity or dominance of rare as well as common species (Figure S15), consistent with a broad driver like climate change. Regardless of its magnitude or composition, decline in overall abundance might, for example, represent fewer prey available to generalist predators like birds, and so have ecological impacts beyond butterfly communities.

4.2 | Caveats associated with these citizen-scientist data

The North American Butterfly Count data bring considerable strengths in elucidating drivers of declines because they were collected with standardized methods at a broad spatiotemporal scale. However, there are limitations that must be acknowledged. First, the counts occur roughly midsummer and only consider adult butterflies, such that substantial declines among larvae or overwintering adults, or trends seen at other times of year, might be missed (Brower et al., 2012; Pleasants et al., 2016). For example, early-spring-emerging species are unlikely to be adequately documented by these data, and recent climate-change-induced shifts in phenology might have moved the activity period of some species outside of the sampling window (Didham et al., 2020). Like all citizen-science efforts, observers often differ widely in their skill at species identifications (Meehan et al., 2019), and observer numbers fluctuated broadly at many sites from year to year. While it is possible that the citizen scientists were more likely to detect larger and more colorful species, variation in observer effort was included in models used to estimate abundance trends. Additionally, while the locations of butterfly counts generally

exhibited a higher proportion of built land cover and cropland than North America as a whole, they represented a broad range of heavily modified and relatively unmodified landscapes, and sampling effort did not broadly vary with the amount of cropland or built land cover at a site (Figure S16). Lastly, the broad scale (2500 km^2) over which we associated butterfly abundance and biodiversity trends with environmental drivers likely resulted in missed effects of more local variables such as host plant availability or microclimate that are nonetheless important but difficult to measure at the continental extent of our synthesis. Despite these limitations, data collection by citizen scientists may be the only way to monitor insects at the vast spatiotemporal scales needed to understand broad drivers of population change, and historical data of many types have limitations and biases. We note that our predicted changes in butterfly abundance (Figure 3a) are supported by several studies, primarily in western North America (Espeset et al., 2016; Forister et al., 2018; Wepprich et al., 2019; Westwood & Blair, 2010).

5 | CONCLUSION

When considering insect declines, there is an understandable desire to calculate a net percentage change through time for particular insect taxa, functional groups, or world regions. This allows a simple extrapolation of accumulating change into future years, and eases communication with the general public when intervention is urgent. However, our findings suggest reasons for caution. For example, consideration of only the western or eastern halves of North America would flip net trends from decline to increase, even for many of the same wide-ranging butterfly species (Figure S2). Likewise, our own estimates of net total abundance decline are almost certainly too dire, because they were disproportionately influenced by invasive species of limited conservation value and included little data from the northeastern corner of North America where increases are predicted (Figure 3a). Likewise, southwestern North America suffers from periodic, multi-decadal droughts (Seager et al., 2005) that, if reversed, might entirely rebalance net butterfly declines across the continent toward increase. In general, we suggest that a focus instead on understanding the drivers of heterogeneous insect increase and decrease responses might be more fruitful. This brings the added benefit of providing site-specific conservation recommendations. For example, in North America, butterfly conservation efforts might be more impactful in the Southwest than Southeast (Figure 3a). More broadly, the apparent scale dependence of net change estimates might explain why prior syntheses of insect decline have reached different conclusions (Crossley et al., 2020; van Klink et al., 2020).

A consensus opinion of the scope and reach of recent insect declines may be beginning to emerge. First, broad heterogeneity in population trends across taxa and landscapes appears to be common (Breed et al., 2013; Crossley et al., 2020; Forister et al., 2010; Kuussaari et al., 2007; Outhwaite et al., 2020; Seibold et al., 2019; van Klink et al., 2020; van Strien et al., 2019; van Swaay

et al., 2006; Wepprich et al., 2019), although our findings suggest that this mosaic of responses does not necessarily mean that different mechanisms are at work. Second, the habitat that an insect community inhabits appears to be crucially important, with aerial species, in particular those with large home ranges, perhaps more likely to be harmed by broad drivers like climate change and intensified land use than aquatic species, which may respond more directly to relatively local water-quality conditions (Outhwaite et al., 2020; van Klink et al., 2020; but see Stepanian et al., 2020). Third, it can bring insight to look at species separately whenever possible (Didham et al., 2020), as broad indicators such as total abundance might mask broadly variable responses among native and introduced species. Finally, a focus on understanding variation in insect population change may help prevent the public from losing interest in critical insect conservation needs, which might otherwise fall away among competing, confusing claims for total global "insect apocalypse" versus no change at all. Overall, it is increasingly clear that climate change is dramatically reshaping global pollinator communities (Parmesan et al., 1999; Soroye et al., 2020). Heterogeneity in response to these changes can result from the degree to which interactions with plants are disrupted or enhanced (Rafferty & Ives, 2011), and can also be due to the relative weighting and direction of the impacts of precipitation and temperature change (Parmesan et al., 1999; Soroye et al., 2020). A key next step will be to further detail how these changes are impacting pollination and other insect-delivered ecosystem services, and how this varies by region and taxon.

AUTHOR CONTRIBUTIONS

Jeffrey Glassberg collected butterfly count data; Michael S. Crossley, William E. Snyder, and Matthew D. Moran conceived the idea for the paper, and Michael S. Crossley, Olivia M. Smith, and Amanda R. Meier conducted analyses; All authors assisted with additional data collection and curation; Michael S. Crossley, William E. Snyder, and Matthew D. Moran primarily wrote the paper, although all authors contributed to the final manuscript.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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