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Rapid butterfly declines across the United States during the 21st century

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Numerous declines have been documented across insect groups, and the potential consequences of insect losses are dire. Butterflies are the most surveyed insect taxa, yet analyses have been limited in geographic scale or rely on data from a single monitoring program. Using records of 12.6 million individual butterflies from >76,000 surveys across 35 monitoring programs, we characterized overall and species-specific butterfly abundance trends across the contiguous United States. Between 2000 and 2020, total butterfly abundance fell by 22% across the 554 recorded species. Species-level declines were widespread, with 13 times as many species declining as increasing. The prevalence of declines throughout all regions in the United States highlights an urgent need to protect butterflies from further losses.

The loss of vertebrate and plant species has been well documented (1–3), but recent attention has shifted to losses of the most diverse taxonomic group on the planet: insects (4–7). Insect declines are particularly distressing because of the ubiquitous role that they play in ecological processes—including pollination, cycling of nutrients from dead organisms and dung, and pest control—and as food sources for multiple taxa (4, 8, 9). Despite their considerable diversity and biomass, both of which contribute to their ecological and economic importance, insects are substantially understudied (10). As such, the scope and scale of their declines are poorly documented.

Of all insect groups, butterflies are the most extensively monitored. In the United States (US), butterflies have been the focus of volunteer-based and expert science monitoring programs since 1975, with dozens of local-to-regional programs now monitoring butterfly populations (11). Efforts to analyze these monitoring data have focused on estimating trends within limited geographic regions (typically a single state)

and/or from a single monitoring program (12–17). The patchwork nature of existing studies renders it difficult to determine whether disparities reflect differences in geographic regions or monitoring programs and to identify the extent to which localized species patterns are consistent across their ranges. A unified analysis of trends at a national scale can guide the enormous tasks associated with insect conservation and management and is a necessary first step in pinpointing the causes of broad-scale butterfly declines (18).

We assembled a comprehensive dataset of systematic, decades-long butterfly monitoring within the contiguous US (i.e., the lower 48 states and Washington, DC) from 2000 to 2020 (Fig. 1A). Data sources included every available multi-species butterfly monitoring program of state, regional, and national scale in the contiguous US, as well as several that target individual species, totaling 35 programs (table S1). These monitoring programs differ in their data collection methods, and one of the key challenges that we addressed in our analyses

was integrating the available data while appropriately accounting for heterogeneity across programs. Data for 12.6 million individual butterflies comprising 554 species were accumulated from 76,957 surveys of 2478 unique locations.

Using these data, we (i) calculated the trend in total butterfly abundance across the contiguous US and (ii) estimated species-level trends in abundance for 342 individual species with sufficient data [(19); fig. S1 and table S2]. To account for spatial variation and align with broad-scale conservation decision-making, we aggregated our data into seven geographic regions based on the US Fish and Wildlife Service regions. Using generalized additive models (20), we estimated regional temporal trends in butterfly abundance for 301 species for which we had adequate data (table S3), restricting our analyses to extent-of-occurrence polygons estimated for each species [i.e., species ranges; (21)], and included covariates to account for species phenology (timing of activity; fig. S2) and survey effort. We then calculated range-wide trends using abundance-weighted averages of regional trends. For an additional 41 species, we had insufficient data to parse out variation across regions but sufficient data to fit simpler models. Accordingly, we estimated abundance trends using a single range-wide model for each of these species. To ensure the quality of each species estimate, two or more butterfly experts reviewed data summaries, model predictions, and regional trends; we removed species for which model fits were deemed unreasonable (14 species; initial species-level analyses had included 356 species).

In sum, butterflies are declining

Total butterfly abundance (all individuals of all species) decreased across the contiguous US at a rate of 1.3% annually [95% confidence interval: –2.3%, –0.2%], for a cumulative 22% decline in overall abundance between 2000 and 2020 (Fig. 1B). Of the seven geographic regions, six had declines in total butterfly abundance ranging from 0.2 to 2.3% annually (cumulative 5 to 37% declines) over the two decades (table S4). The Pacific Northwest was the only region with an estimated increase in total butterfly abundance (0.5% annually, cumulative 10% increase), but this increase was driven by the highly irruptive *Nymphalis californica* (California tortoiseshell), which accounted for 8.7% of observations in this region. The removal of this species from the analysis led to effectively constant abundance in the Pacific Northwest (revised estimate: 0.1% annual decline, cumulative 2% decline). By contrast, removing the most prevalent species in every region did not qualitatively alter our estimated decline in total butterfly abundance across the contiguous US (revised estimate: 1.1% annual decline, cumulative 19% decline).

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Our national-scale findings paint the most complete—and concerning—picture of the status of butterflies across the country in the early 21st century. Previously published studies in US states or regions using subsets of the available data have reported similar annual declines of 1.6% in 11 states in the western US (16), 2.0% in Ohio (13), 3.8% in Illinois (15), and 0.72% across the contiguous US using a single data source (17). Only one study found an increase in abundance (1.2% in Massachusetts) over similar time frames (14). Here, we establish the regional and continental patterns of butterfly declines by including data from all the systematic monitoring programs used in these targeted studies, in addition to many other programs. Our results for the US are consistent with declines reported globally (5), and especially in Europe (7, 13).

Declines are common across species, whereas increases are rare

The change in the total number of butterflies between 2000 and 2020 was driven by the rapid decline of many individual species. Thirteen times as many species declined as increased (defined as significant plus or minus change at $P < 0.05$; Figs. 2 and 3). Over our two-decade study period, 33% of individual butterfly species (114 of 342) showed significantly declining trends in abundance ($P < 0.05$; Fig. 2 and table S5). Conversely, only 3% of species increased (nine species with $P < 0.05$). The median species had an annual decline of 2.6%, which resulted in a cumulative decline of 41.5% after two decades. Many species showed extreme declines in abundance: 107 species declined by more than 50%, including 22 species that declined by more than 90% ($P < 0.05$). Despite our expansive butterfly monitoring database, we were unable to conclusively identify abundance changes for many species; we found $P > 0.05$ for all species with cumulative changes in abundance between -42 and +91%. However, when focusing on the magnitude of trends, declines remained far more prevalent than increases. More than two-thirds of all species (245 of 342) had estimated cumulative decreases of more than 10%, whereas only one-fifth of species (65 species) had a cumulative increase greater than 10%. We defined those species with at least plus or minus 10% cumulative change over the study period and $P > 0.05$ as “possibly increasing” (56 species) or “possibly declining” (131 species), respectively (Fig. 2). Declines were present across all butterfly families, with 60 to 75% of species declining or possibly declining within each family (table S6).

Most species present in multiple regions showed geographically variable trends. Of the 192 species for which we estimated more than one regional trend, only 69 had estimated declines across all modeled regions, and only eight had estimated increases across

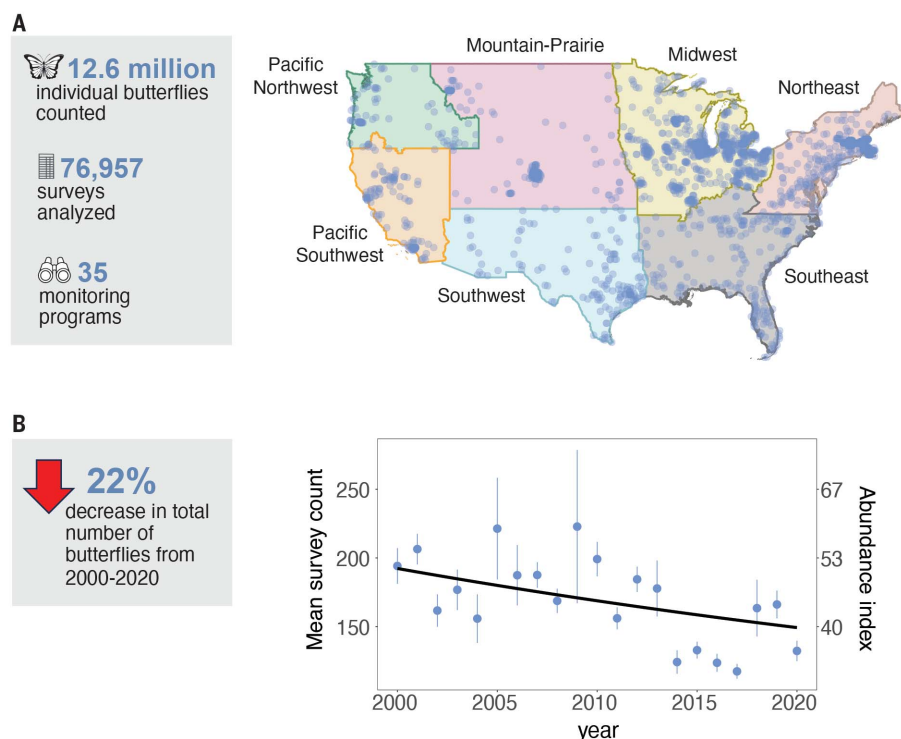
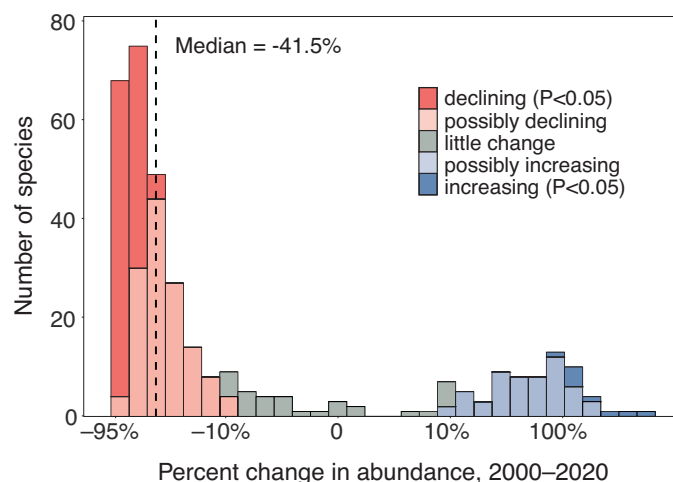


Fig. 1. Data from more than 76,000 monitoring events across the contiguous US reveal a 22% decline in total butterfly abundance from 2000 to 2020. (A) We divided the data into the seven US Fish and Wildlife Service regions, which were used for estimating regional trends. The transparent blue points on the map show the 2478 unique survey locations. (B) Solid blue points show the average number of butterflies recorded per survey for each year of our study; vertical lines show ± 1 SE. The number of surveys per year is available in table S10. The black line shows our estimated abundance index (a relative measure of total butterfly abundance) derived from a fitted generalized additive model of total annual butterfly abundance that accounts for regional variation, seasonality, differences in effort and monitoring program, and site-to-site variation. Targeted surveys (10,511 surveys representing intensive efforts to monitor individual species of conservation concern) were not included in the analysis of total butterfly abundance to prevent overrepresentation of rare and at-risk species.

Fig. 2. Approximately 13 times as many butterfly species declined as increased in abundance across the contiguous US from 2000 to 2020. Species with rates of change that significantly differed from zero ($P < 0.05$) are labeled “declining” and “increasing,” respectively; remaining species that changed by at least plus or minus 10% from 2000 to 2020 were labeled as “possibly increasing” and “possibly declining,” respectively.



The median species declined in abundance by 41.5% across the study period. Percent changes are shown on a log (base 10) scale to improve readability; this scaling “stretches” the plot near 0%, leading to the observed apparent bimodality (see fig. S5 for linear presentation).

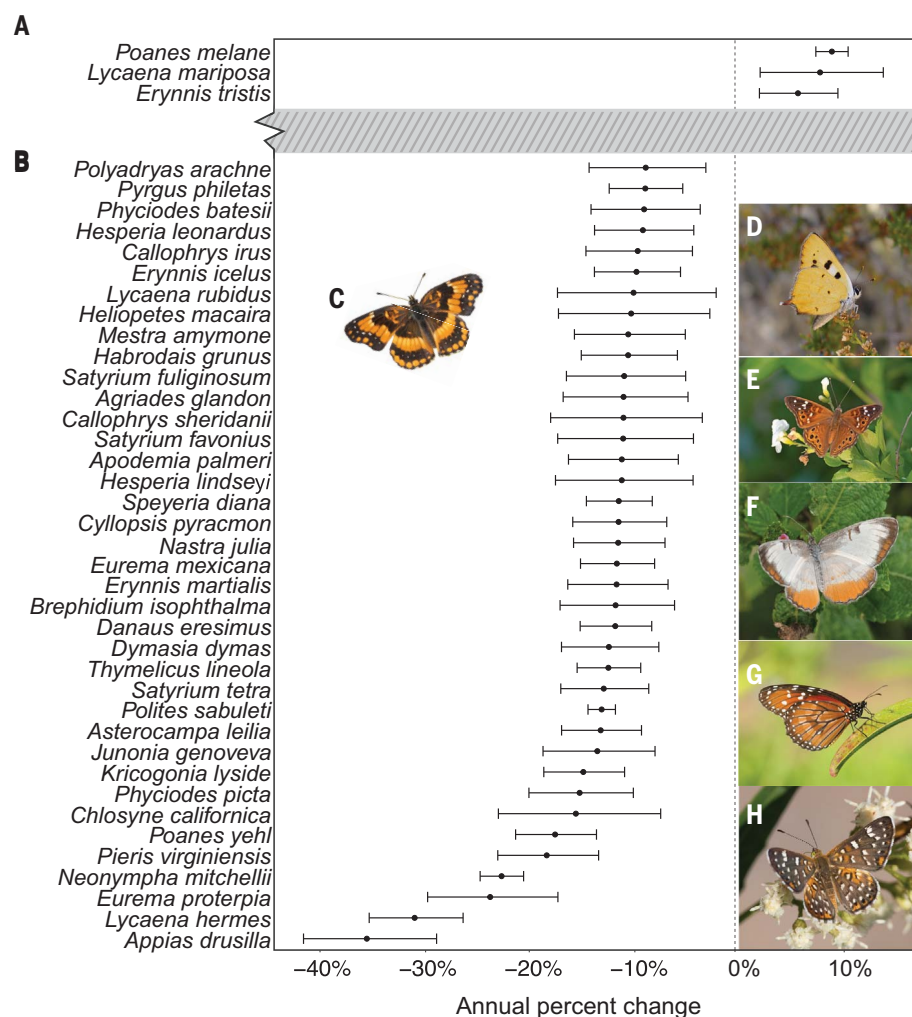


Fig. 3. Species with significant changes in abundance were predominantly declining. Of the increasing and declining species (significant annual change, $P < 0.05$), we show (A) the most extreme one-third of increasers (three of nine species) and (B) the most extreme third of decliners (38 of 114 species). Solid black points show the estimated annual change in abundance; intervals show 95% confidence intervals. The gray bar represents the remaining 301 (of 342) species fit with species-level models (results not shown), which had intermediate growth rates. (C to H) Photos of six of the most rapidly declining species: (C) *Chlosyne californica*, (D) *Lycaena hermes*, (E) *Asterocampa leilia*, (F) *Mestra amymone*, (G) *Danaus eresimus*, and (H) *Apodemia palmeri*. [Photo credits: J.G.]

all modeled regions. In addition to the nine species, 56 species that were not significantly increasing overall had significant increases in one or more regions ($P < 0.05$), which suggests that these species have “refuges” that may prevent range-wide declines, at least in the short term.

If traits were highly correlated with species trends, we could prioritize species groups for conservation action in the absence of species-specific monitoring data. We analyzed seven key traits selected on the basis of their observed relevance to population change in past studies (19). Species with more positive trends were associated with longer wing length [linear mixed effects model, $\chi^2(1) = 7.89$, $P = 0.005$], overwintering in a non-egg life stage [$\chi^2(4) =$

9.54, $P = 0.049$], preferences for moist habitats [$\chi^2(1) = 6.45$, $P = 0.011$], host plant generalists rather than specialists [$\chi^2(1) = 4.27$, $P = 0.04$], and association with human-dominated habitat [$\chi^2(1) = 12.05$, $P < 0.001$] (table S7). The other variables we examined—voltinism and canopy affiliation—had no discernible effects. Despite some significant associations, the examined traits provided limited ability to predict species outcomes. A full model that included all traits explained only 9% of the variation in species trends, and controlling for phylogeny removed any apparent support for the effect of traits (table S8). Our results do not preclude meaningful relationships between traits and trends at a more granular level, for example, across populations in specific landscapes. How-

ever, our findings make clear that at this broad geographic scale and species-level resolution, traits are not an effective proxy for species performance and cannot be used as a replacement for species-specific analyses in national-scale conservation planning.

Species declines are prevalent in all US regions

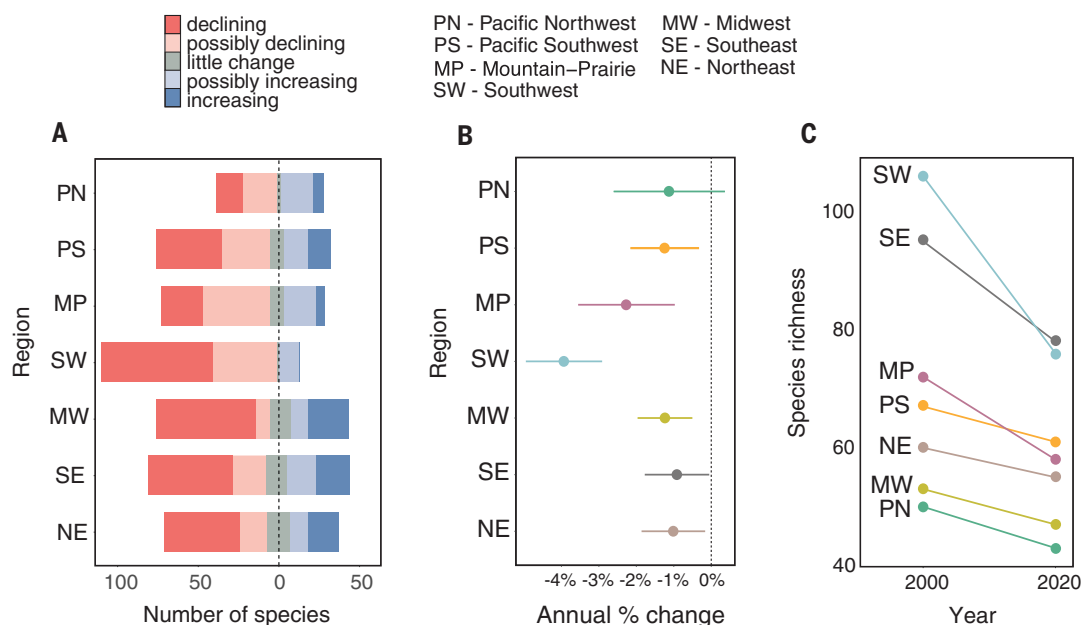
Declines were prevalent across all regions in the contiguous US, with every region containing more declining than increasing species (Fig. 4, A and B, and table S9). The median species annual change in each region (-1.2 to -4.0%) led to cumulative declines of 21 to 55% over the study period. Declines were most severe in the Southwest, consistent with other findings that butterflies in the contiguous US are disproportionately declining in arid and hot climates (16, 17). Among all increasing species, two-thirds had larger extent-of-occurrence areas in Mexico than in the US and Canada combined, and thus our trend estimates primarily characterize the northern portion of these species' ranges.

Between 2000 and 2020, butterfly species richness fell in every region by as much as 28% or 30 species (Fig. 4C). Our measure of species richness is a calculated annual metric of the number of “likely observable” species in each region that accounts for variable monitoring efforts across regions and years [(19); fig. S3]. Our index also accounts for the phenomenon that a sufficiently rare species is unlikely to be encountered even before it declines, whereas a sufficiently common species is still likely to be encountered even after moderate declines.

With climate change, butterfly species in North America may find the southern limits of their ranges becoming too warm while the northern limits of their range become more hospitable (14, 22). We tested this prediction through comparisons of regional trends of species that were present in pairs of regions, one to the north and one to the south, that share a common east-west border. For three out of four region pairs, species had higher trends in abundance in the northern region (Northeast versus Southeast: $F_1 = 15.14$, $P < 0.001$, trend in abundance 0.016 higher in the Northeast; Midwest versus Southeast: $F_1 = 10.18$, $P = 0.002$, trend in abundance 0.015 higher in the Midwest; Mountain-Prairie versus Southwest: $F_1 = 6.86$, $P = 0.012$, trend in abundance 0.017 higher in Mountain-Prairie). We did not see an effect of latitude on the Pacific coast (Pacific Southwest versus Pacific Northwest: $F_1 = 0.04$, $P = 0.848$, trend in abundance 0.001 higher in the Pacific Northwest), possibly because elevational differences play a larger role in determining climate in these regions. Still, improved species performance in more northerly regions was not sufficient to reverse species declines, given

Fig. 4. Declines in individual species abundance and species richness are prevalent across geographic regions.

(A) Species-level trends by region. Species with rates of change that significantly differed from zero ($P < 0.05$) are labeled “declining” and “increasing,” respectively; remaining species that changed by at least plus or minus 10% from 2000 to 2020 are labeled as “possibly increasing” and “possibly declining,” respectively. **(B)** Average species annual percent change for each region and associated 95% confidence intervals were derived from a linear mixed model that included a random effect of butterfly family and weighted species by the inverse of associated uncertainty. **(C)** Changes in the estimated species richness index (i.e., the count of “likely observable” species) from 2000 to 2020 in each region.



that median species trends in northern regions were still negative.

Improved monitoring: A call to action

We conducted the definitive assessment of butterfly trends across the contiguous US for the first two decades of the 21st century and found declines at every scale: reductions in total numbers of butterflies, falling species richness, and large decreases in many individual species. Our continental analysis integrated across monitoring programs in which local or short-lived fluctuations in abundance could be different from regional or continental trends. Our synthesis was made possible because of the many individual datasets collected primarily by volunteer scientists. The combined dataset provides a powerful base for assessing spatially expansive trends and a foundation for future analyses to address key questions about the nature and causes of declines across individual species and butterflies at large.

Of the approximately 650 butterfly species with extent-of-occurrence polygons overlapping the contiguous US, only 85% (554 species) were recorded anywhere in our data and only 53% (342 species) were sufficiently represented for species-level analyses. Even among those analyzed, we lacked the power to detect significant trends for most species. Thus, it is possible that many more butterflies are being lost than is estimable because species with limited data are already rare, with small population sizes living in specialized habitats. Further, whole geographic regions are poorly represented in our data. For example, North and South Dakota together contained only five of our >2000 survey

sites, for an average of one site per 75,000 km² compared with one survey per 340 km² in Illinois. The 11 states for which there are standardized, decades-long monitoring programs provide a template that could be used across other states and around the world (table S1). Digitizing historical butterfly records could also offer new insights by unlocking decades worth of data, because more than 90% of insect collections have yet to be made available for analysis (23). The future of butterflies depends in part on an up-to-date understanding of each species' status, which necessitates the most complete data possible and a coordinated effort to integrate those data into meaningful analyses.

Potential causes of butterfly declines and steps for the future

The scope and scale of butterfly declines suggest multiple and broadly acting threats, including habitat loss, climate change, and pesticide use [(6); fig. S4]. Insecticides have been identified as leading causes of butterfly declines in recent analyses in the midwestern US and California (24, 25). Detailed analyses linking insecticide use to insect mortality can inform regulatory action, including imposing restrictions on neonicotinoid insecticides, as was done in the European Union. Other approaches to reduce pesticide use, such as integrated pest management and diversified cropping, can improve habitats for butterflies and other insects on working lands [e.g., (26, 27)].

Combating habitat loss requires land protection and restoration. Targeted habitat management has successfully reversed the decline

of at-risk butterfly species [e.g., (28)] and has been linked to local increases in abundances for six of our declining species (29). Restoring native landscapes, even in areas where only small spaces are available such as hedgerows, roadsides, and backyards, has great potential for increasing the amount of suitable habitat for butterflies and other insects (30).

Butterfly declines have been linked to rising temperatures and changing climates in the US and other countries (16, 22, 31, 32). Concordantly, we found that species generally had stronger declines in more southern parts of their ranges. Additionally, the two regions with the most negative median species trends—the Southwest and the Mountain-Prairie regions (Fig. 4B)—contain 8 of the 10 driest US states and many of the most rapidly warming climate divisions (33). Slowing climate change necessitates national and international efforts. However, local-scale actions can mitigate the effects of climate change on individual populations. For example, implementing broadly beneficial conservation actions such as native habitat preservation and restoration can increase abundance trends even in the face of climate change (29), and species-specific interventions such as managed relocation (34), genetic rescue (35), and conservation of local variability in habitat structure and type (36) can aid in the protection of highly threatened species.

Butterflies have the potential for rapid population growth under the right circumstances, making species recovery possible—even from very small population sizes (28). Expansive efforts in conservation planning and action for insects could prevent widespread future

losses and create and maintain the environments in which butterflies and other at-risk species can thrive.

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SUPPLEMENTARY MATERIALS

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Materials and Methods

Fig. S1 to S5

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