INSECT DECLINES

Fewer butterflies seen by community scientists across the warming and drying landscapes of the American West

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Uncertainty remains regarding the role of anthropogenic climate change in declining insect populations, partly because our understanding of biotic response to climate is often complicated by habitat loss and degradation among other compounding stressors. We addressed this challenge by integrating expert and community scientist datasets that include decades of monitoring across more than 70 locations spanning the western United States. We found a 1.6% annual reduction in the number of individual butterflies observed over the past four decades, associated in particular with warming during fall months. The pervasive declines that we report advance our understanding of climate change impacts and suggest that a new approach is needed for butterfly conservation in the region, focused on suites of species with shared habitat or host associations.

Shifts in the structure and function of ecosystems in the Anthropocene pose numerous and poorly understood threats to wild plants and animals and to human society (*1*). Of the changes being tracked by ecologists, few are as potentially consequential as reductions in insect abundance and diversity (*2*), with the status of pollinators being of particular concern (*3*, *4*). Although debate continues on the magnitude and taxonomic scope of insect declines (*5–7*), there can be little doubt that insects (like most other major groups) are responding to stressors that include habitat loss, climate change, overuse of pesticides, and invasive species (*8*). However, most historical records of insect populations come from parts of the world—in particular, densely populated areas of Western Europe (*9–11*)—where habitat loss and degradation have been pervasive, thus limiting the ability of researchers to separate the signal of climate change from the effects of other stressors. In this work, we addressed this knowledge gap using community scientist and expert-collected data, focusing on a region, the western United States,

that is particularly useful for understanding the effects of climate change on insects because of warming and drying trends (*12*) observed across land-use gradients (from major cities to protected national parks) as well as elevational and latitudinal gradients that contain great habitat and climatic diversity.

The three datasets that we studied are the Shapiro transect from northern California (*13*), the North American Butterfly Association (NABA) network of community scientist count data (*14*), and the iNaturalist web platform (*15*) of contributed observations (Fig. 1). These three sources encompass more than 450 species of butterflies and are complementary in that they represent gradients of geographic coverage, temporal extent, and expertise; the three sources also differ in coverage of urban and agricultural areas. The Shapiro dataset is expert run, the NABA counts are generated by teams of volunteer or community scientists, and the iNaturalist records are contributed by thousands of nature enthusiasts whose identifications are vetted by means of a machine learning algorithm and by at least two human experts. Previous work with the Shapiro data has uncovered pervasive reductions in the density of butterfly populations across a relatively narrow geographic area that includes large urban and agricultural areas (*16*). Whether similar population trajectories would be observed across wildlands and natural areas has been an open question (*17*). Estimating species-specific trends over time,

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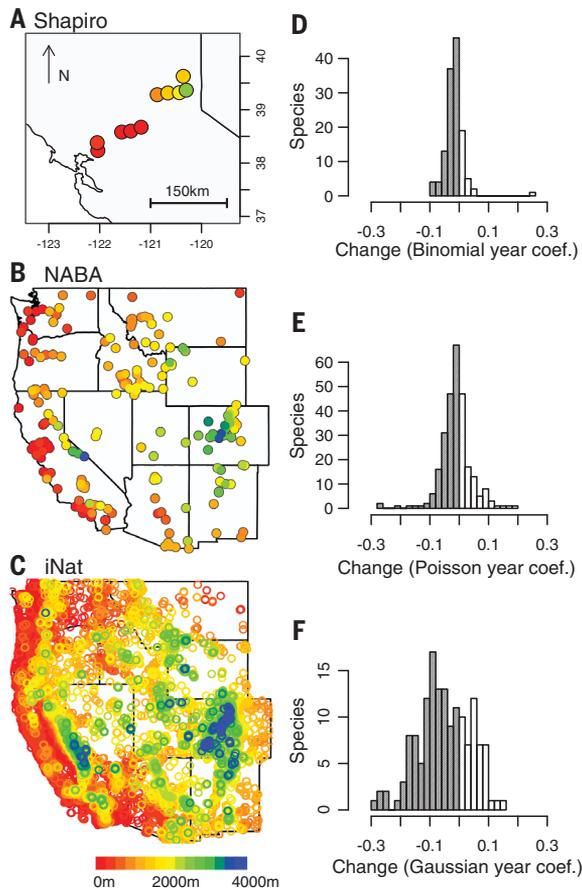
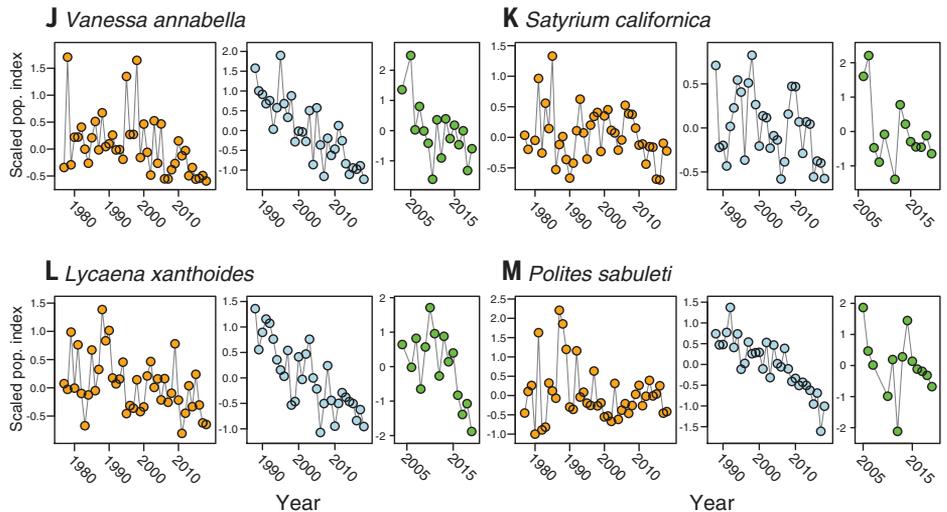**Fig. 1. Three focal datasets and overview of species trends through time.** (**A**) Shapiro northern California data: 10 study sites from the Bay Area to the Sierra Nevada Mountains, with sites color coded by elevation (as in subsequent panels). (**B**) Western NABA locations: all are shown, and a subset (72 sites with 10 or more years of data) was used in many analyses. (**C**) Locations of iNaturalist butterfly records. iNat, iNaturalist. (**D** to **F**) Histograms summarizing species-specific year coefficients (with negative values in gray) for the three datasets: (D) Shapiro, 48 years; (E) NABA, 42 years; and (F) iNaturalist, 15 years. coef., coefficient. The interpretation of year coefficients is not identical across datasets, but in general, negative and positive values indicate decreases or increases in population density or the frequency with which individual species have been observed over time. The means of the three distributions are significantly different from zero (single sample t tests): (D) $t_{130} = -5.6$, $P < 0.001$; (E) $t_{271} = -3.3$, $P < 0.001$; and (F) $t_{160} = -11.8$, $P < 0.001$.
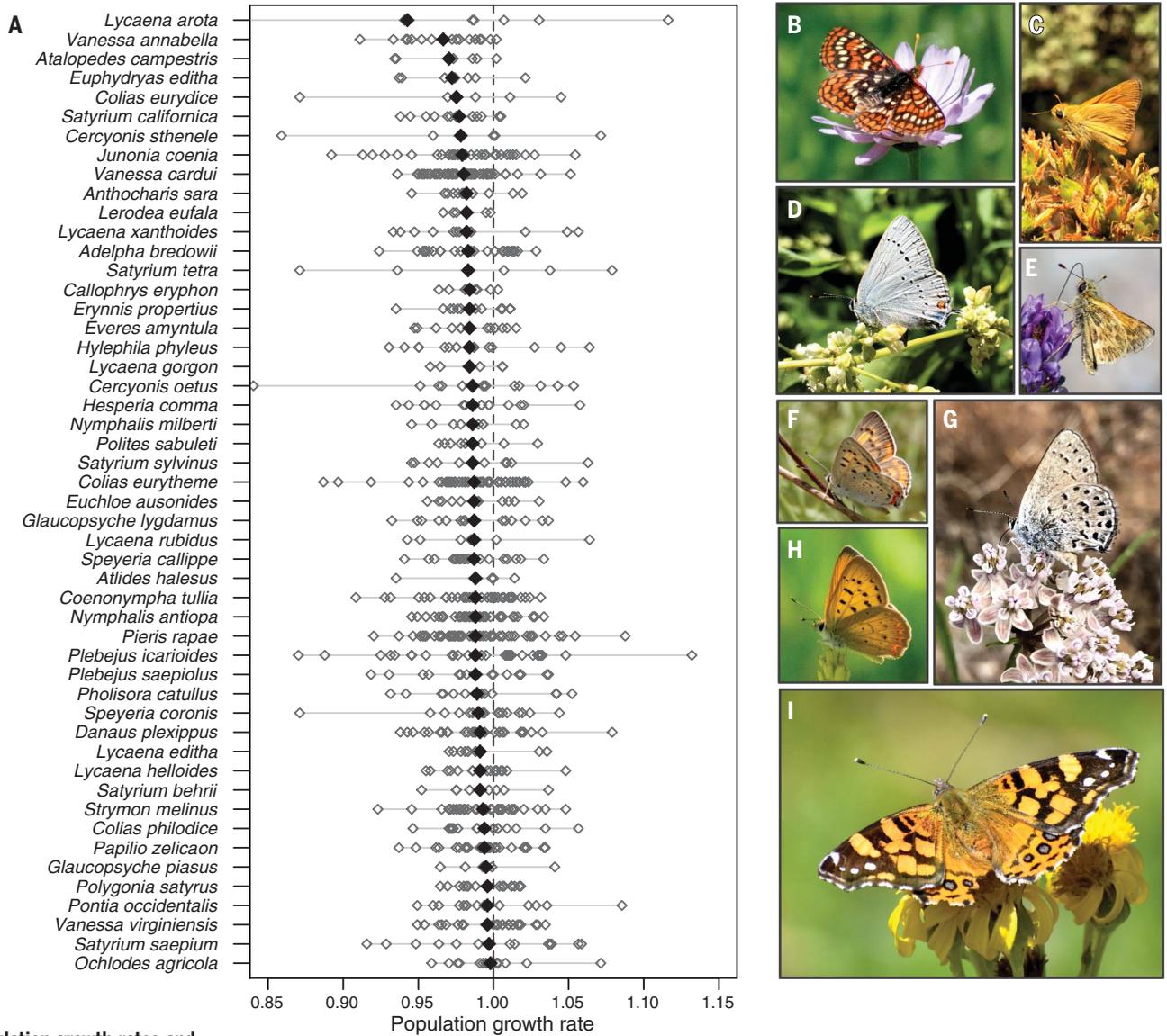
Fig. 2. Population growth rates and example annual trajectories. (**A**) Estimates of population growth rates from NABA counts at the level of species (dark diamonds) and individual locations (open diamonds) for a subset of species; these are 50 species that are estimated to have downward annual trends in at least two datasets (among NABA, Shapiro, and iNaturalist records), but growth rate estimates (shown here) are based only on NABA data, which are well suited for this purpose (see materials and methods). (**B** to **I**) Photos of 8 of the 50 species: (B) *Euphydryas editha*; (C) *Ochlodes agricola*; (D) *Satyrium sylvinus*; (E) *Polites sabuleti*; (F) *Lycaena xanthoides* (J.C.O.); (G) *Satyrium behrii*; (H) *Lycaena helloides*; and (I) *Vanessa annabella*. (**J** to **M**) Time series plots are shown for four exemplar species (see table S2 for other species-specific results), with NABA in orange, Shapiro in blue, and iNaturalist in green; these values are effort corrected and averaged across locations (within each species) and shown as standardized deviations from long-term averages in counts (for NABA) and frequencies of observation (for Shapiro and iNaturalist). pop., population. [Photo credits: (B) C.A.H.; (C) M.L.F.; (D) M.L.F.; (E) C.A.H.; (F) J.C.O.; (G) M.L.F.; (H) C.A.H.; (I) C.A.H.]

Fig. 3. Location-specific changes in butterfly density and associations with climate and global change variables. (**A**) Year coefficients from a hierarchical Bayesian Poisson model predicting total numbers of butterflies at NABA sites (intervals are 95% highest density intervals, which are small and not visible for most locations). Poisson coefficients have been exponentiated and can be interpreted as fractional change per year. The populations are ordered by latitude (more northern at the top) and color coded by elevation (as in Fig. 1). Across all 72 sites (average of 21 years per site), we estimate a coefficient of 0.984, which corresponds to a reduction of 1.6%, with a 95% highest density interval from 0.966 (reduction of 3.4%) to 1.002 (increase of 0.2%); additional details are in supplementary box 2. exp., exponentiated. (**B** to **I**) Posterior probability distributions for the effects of particular variables on the total number of butterflies observed (gray-shaded curves) as well as on the 50 most common species (dark lines) and all other species (dotted lines). max., maximum; summ., summer; temp., temperature. The variables include static descriptions of climate [(B) and (C)], rates of climate change [(D) to (G)], and the fraction of land around sites converted to urban and agricultural spaces [(H) and (I)]. The variance explained (as the square of the observed versus predicted correlation) for the model is 0.39 (see table S4 for detailed results including covariates for spatial autocorrelation). The numbers shown in the upper left of each plot indicate the probability of a positive or negative effect on butterfly abundance; for example, there is an 87% probability that
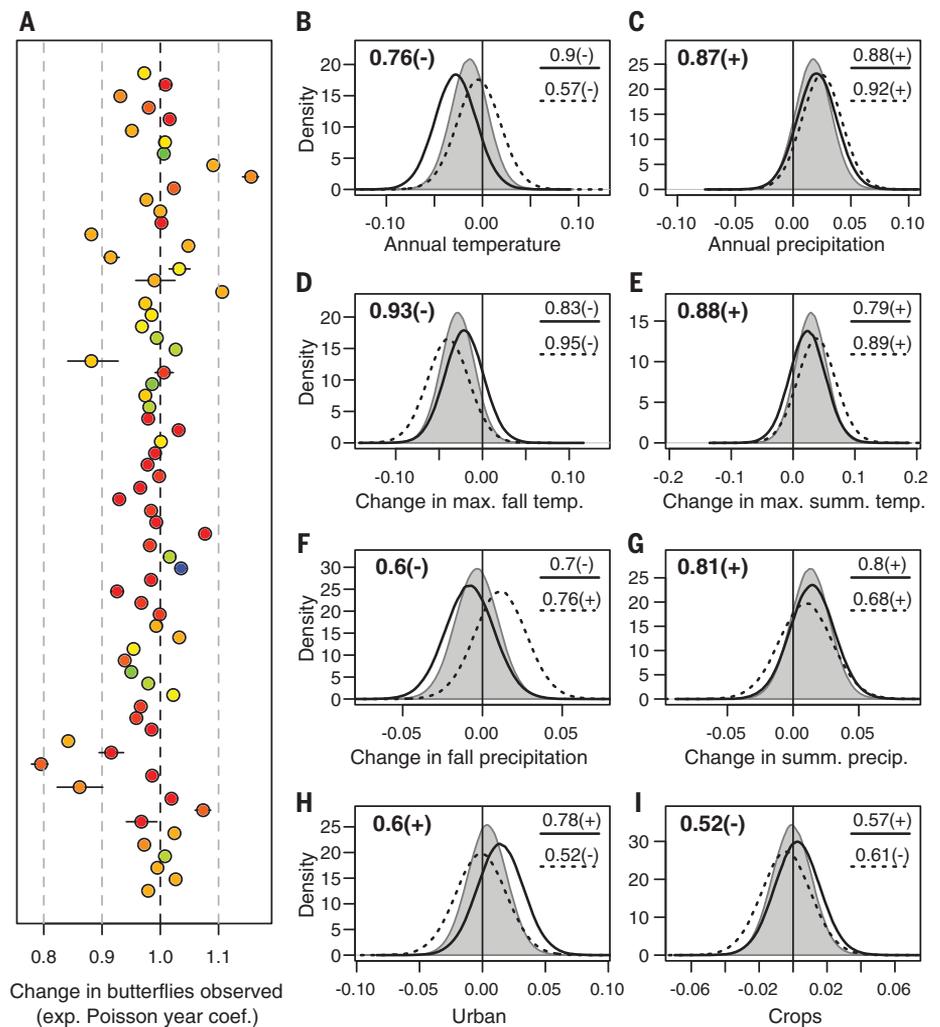

locations with more annual precipitation (precip.) are associated with increases in butterfly counts (C). The values in the upper right of each plot are the same probabilities but from models run separately for common species (solid lines) and all others (dotted lines); for example [also from (C)], there is an 88% probability of a positive effect of precipitation for common species and a 92% probability for all others.

we found that a majority of species in each of the three datasets have downward population trajectories, ranging from slightly downward trending to more severe reductions in abundance (Fig. 1, D to F). Declining taxa include, but are not limited to, wide-ranging species (for example, the west coast lady, *Vanessa annabella*) (Fig. 2J) and butterflies that thrive in disturbed and degraded habitats, such as the introduced cabbage white, *Pieris rapae*, for which decline has been reported from the midwestern United States (*18*). Overall, single-brooded species tend to be in slightly more severe decline, but in general, we found that life history traits (including geographic range size, body size, and host specialization) have little explanatory power (table S3).

Looking beyond individual species, we used the NABA data to investigate the change in the total number of individual butterflies and found

a 96% probability that the total abundance of butterflies is decreasing, with an estimated rate of 1.6% fewer individuals per year. That value was estimated across 72 locations (and 262 species) with 10 or more years of data (Fig. 3A and fig. S1), in total spanning 42 years, from 1977 to 2018 (the average length of time series from individual sites was 21 years) (see table S1). Using the same records to investigate geographic variation in changing abundance, we considered indices of land use and static descriptions of annual climate, as well as season-specific rates of climate change, and found the most influential predictors to be indices of climate change (table S4). Specifically, locations that have been warming in the fall months have seen fewer butterflies over time (Fig. 3D), whereas warming in the summer months is associated with the opposite effect (Fig. 3E). We hypothesize that warm-

ing in the summer influences adult activity times directly and hence increases the probability of detection, whereas fall warming likely induces physiological stress on active and diapausing stages, reduces host plant vigor, or extends activity periods for natural enemies (*19, 20*). The rate of warming is not homogenous across seasons, and warming is greatest in the fall (fig. S2). The difference between fall and summer warming is itself a predictor of changing butterfly densities (Fig. 4). We also saw a positive effect of increasing summer precipitation on butterfly observations (Fig. 3G), which is likely associated with positive effects on nectar plants and larval hosts; the western United States, however, has been drying in recent decades (fig. S2). We have considered the possibility that the results are affected by the abundance of the most common species, but after excluding the 50 most
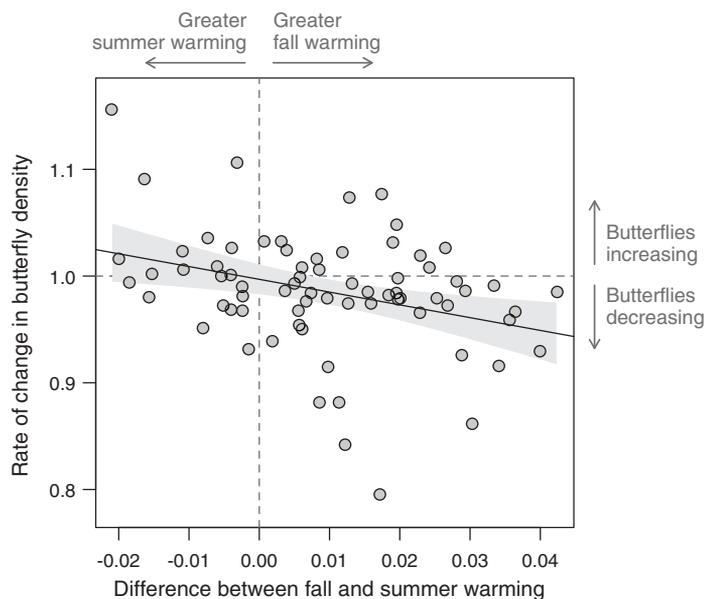
Fig. 4. Differential seasonal warming associated with changes in butterfly density. Rates of change in butterfly density for all sites (as in Fig. 3A) regressed against the difference between fall and summer warming. The fitted line and 95% confidence intervals are from a simple linear regression with slope = −1.2 (standard error 0.41), $F_{1,70}$ = 8.6, P = 0.0046, and R^2 = 0.11.

abundant taxa, we still estimated a decline of 1.8% with 93% confidence (the effects of climate change and other predictors on more and less common butterflies are available in Fig. 3, and a power analysis of overall decline is available in fig. S3).

We did not detect an effect of proximity to either urban development or agriculture (Fig. 3, H and I), despite prior work illustrating that habitat loss and degradation have severe negative effects on insects (21, 22). Pesticide applications in California's Central Valley, in particular, have been implicated in recent declines (16). The NABA sites were not chosen with the goal of providing an unbiased sample of the landscape (and the same can be said of the other datasets), and the median fraction of urban and agricultural land around sites is less than 5% (fig. S4). The NABA sites do, however, include variation in proximity to development, but these factors appear to be less important in comparison with the influence of climate for the sites studied in this work.

In summary, we found that fewer individual butterflies are being observed across the western United States each year, with agreement from expert and volunteer datasets on that conclusion. In contrast to studies—for example, from Western Europe—that have found more straightforward signals of ecological specialization (among other traits) that predict the severity of decline, we have much yet to learn about the species-specific traits associated with population increase and decline in our fauna (23). The taxonomic and

geographic ubiquity of the declines that we report suggest that conservation efforts could profitably target suites of species, potentially defined by commonalities of geography, host plant, or habitat use, instead of conventional conservation and management practices focused on single species. These findings also contrast with a recent report across a number of arthropod taxa in North America that found no overall signal of decline (6). Although the analytical methods in that report are being discussed (24), it might also be the case that either temporally intensive sampling (as with the Shapiro dataset) or highly dispersed geographic sampling (as with the NABA data) have greater statistical power for the detection of directional change through time in highly variable insect populations.

The results reported here have implications for policy and for how society thinks about insect declines (25). The management of developed areas (such as reduction of pesticide use in agricultural margins and urban areas) can have immediate benefits for insect populations (26), but the impacts of climate change cannot be ignored. Society should not assume that the legal protection of open spaces is sufficient without the action to limit the advance of anthropogenic climate change (12). Although our analyses point to warming fall temperatures as an important factor in insect declines, we acknowledge the multifaceted nature of the problem and how much remains to be understood about climate

change interacting with habitat loss and degradation (8, 27).

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Fewer butterflies seen by community scientists across the warming and drying landscapes of the American West

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Warming autumns, fewer butterflies
Many recent studies have revealed sweeping declines in insects over the past few decades. Butterflies are no exception. Forister *et al.* used three different datasets, collected by both experts and community scientists, and found that the number of butterflies has declined over the past 40 years. Although the drivers of decline are complex, the authors found that climate change––in particular, warmer months in the autumn––explain a large portion, even as warming summers actually lead to increases. This work shows that climate change impacts may be insidious and unexpected in their effects.
Science, this issue p. 1042

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