Insects and recent climate change

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Edited by David L. Wagner, University of Connecticut, Storrs, CT, and accepted by Editorial Board Member May R. Berenbaum October 26, 2020 (received for review March 9, 2020)

Insects have diversified through more than 450 million y of Earth's changeable climate, yet rapidly shifting patterns of temperature and precipitation now pose novel challenges as they combine with decades of other anthropogenic stressors including the conversion and degradation of land. Here, we consider how insects are responding to recent climate change while summarizing the literature on long-term monitoring of insect populations in the context of climatic fluctuations. Results to date suggest that climate change impacts on insects have the potential to be considerable, even when compared with changes in land use. The importance of climate is illustrated with a case study from the butterflies of Northern California, where we find that population declines have been severe in high-elevation areas removed from the most immediate effects of habitat loss. These results shed light on the complexity of montane-adapted insects responding to changing abiotic conditions. We also consider methodological issues that would improve syntheses of results across long-term insect datasets and highlight directions for future empirical work.

Anthropocene | climate change | population decline | extinction | extreme weather

From invasive species to habitat loss, pesticides, and pollution, the stressors of the Anthropocene are many and multifaceted, but none are as geographically pervasive or as likely to interact with all other factors as climate change (1, 2). For these reasons, understanding the effects of anthropogenic climate change on natural systems could be considered the defining challenge for the ecological sciences in the 21st century (3). It is of particular interest to ask how insects will respond to contemporary climate change because they are the most diverse lineage of multicellular organisms on the planet and are of fundamental importance to the functioning of freshwater and terrestrial ecosystems. The issue also has new urgency in light of recent and ongoing reports of insect declines from around the globe (4). Insects and climate change have been discussed elsewhere (5–8), and our goal here is not to cover all aspects of the problem. Instead, we focus on recent discoveries and questions inspired by continuous long-term monitoring of insect populations. Although other sampling designs can of course offer important insights (9), we focus on long-term monitoring as being uniquely powerful for understanding the influence of climatic fluctuations on animal populations because of the ability to decompose complex temporal trends into effects driven by different factors (10, 11).

In the sections below, we compare climate change with other stressors and examine multifaceted impacts in terms of climate means, limits, and extremes. We then discuss the geography of climate change with particular focus on the responses of montane insects, with a case study from the butterflies of Northern California that illustrates the value of long-term observations that span a major gradient of land use intensity. Two areas that we do not cover in detail are the theoretical foundations of climate change research (12) and community-level consequences, including altered trophic interactions (13). As a qualitative survey of the state of the field, we have gathered insect monitoring studies that are from relatively undisturbed

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Author contributions: A.M.S. designed research; A.M.S. performed research; J.H.T. and D.P.W. processed data; C.A.H., J.A.F., C.C.N., and M.L.F. analyzed data; and C.A.H., J.A.F., C.C.N., J.H.T., D.P.W., and M.L.F. wrote the paper.

The authors declare no competing interest.

This article is a PNAS Direct Submission. D.L.W. is a guest editor invited by the Editorial Board.

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This article contains supporting information online at https://www.pnas.org/lookup/suppl/doi:10.1073/pnas.2002543117/-/DCSupplemental.

Published January 11, 2021.

locations or that span a land use gradient. We only include studies that encompass at least 10 y of continuous sampling, examine 10 or more species, and analyze climatic data in some fashion (Table 1 and *SI Appendix*, Table S1). It is important to note that 10 y is a useful minimum cutoff, but we acknowledge that it might not be sufficient to separate population fluctuations from long-term trends in many cases (14–16). Table 1 provides a summary of the monitoring programs that met our criteria, while *SI Appendix*, Table S1 breaks these out further by publication and includes an abbreviated summary of findings.

On the Relative Importance of Climate Change and Other Stressors

Although anthropogenic stressors must ultimately be understood as an interacting suite of factors (17, 18), it is useful to start by asking: How will the consequences of climate change compare with other stressors? Over the last three centuries, the global percentage of ice-free land in a natural state (not intensively modified by human activity) has shrunk from 95 to less than 50% (19), with consequences that include the extirpation and extinction of plants and animals (20). Although habitat loss (including degradation through pollution and numerous other processes) continues, it is possible that we are living through a period of transition where the importance of changing climatic conditions could begin to rival the importance of habitat loss as shifting climatic means and extremes stress individuals and populations beyond historical limits (21, 22).

An empirical understanding of the effects of climate change in comparison with other stressors depends in large part on long-term observations from protected areas or from gradients of land use that will let us directly compare the effects of different factors. In Great Britain, both land use and climate change have been important for explaining the decline of 260 species of macromoths and an increase of 160 species (of a total of 673 species) (23). The signal of habitat loss is seen in widespread species, which have declined in regions with increased intensity of human land use. At the same time, the role of climate can be seen in the decrease of more northern, cold-adapted species and the simultaneous increase of more southern, warm-adapted species (23). A cross-taxa study including insects and other organisms from central Europe found that temperature was a stronger predictor than habitat association for understanding trends in terrestrial organisms (24). Less multifaceted signals of global change can be found in smaller areas sheltered from direct effects of habitat loss. For example, beetle incidence in a protected forest in New Hampshire, United States, has decreased by 83% in a resampling project spanning 45 y, apparently as a function of warmer temperatures and reduced snow pack that insulates the diverse

Table 1. Monitoring studies of at least 10 insect species and at least 10 y from land use gradients or protected areas that have been used to examine weather in relation to insect populations

Location	Source	Years	Species	Taxa	Method
Australia	Gibb et al. (79)	22	106	Ants	Pitfall traps
California, United States	Shapiro Transect (33, 56–58)	47	163	Butterflies	Modified Pollard walk
Colorado, United States	Iler et al. (80)	20	20	Syrphid flies	Malaise traps
Costa Rica	Tritrophic Interaction Monitoring in the Americas (39)	22	1,724	Lepidoptera, Parasitoids	Collect and rear
Ecuador	Neotropical fruit-feeding nymphalid trap studies (77)	10	137	Butterflies	Fruit traps
Europe	Bowler et al. (24)	19	—	Many (includes insects)	Standardized surveys
Europe	Bowler et al. (34)	19	448	Many (includes insects)	Many
Europe	Devictor et al. (81)	19	—	Butterflies (and birds)	Various monitoring schemes
Europe	Jourdan et al. (28)	32	—	Benthic invertebrates	Surface water survey
Finland	Finnish Moth Monitoring Scheme (49)	14	334	Moths	Light traps
Finland	Hunter et al. (26)	32	80	Moths	Light traps
Germany	Baranov et al. (14)	42	125	Mayflies, stoneflies, and caddisflies	Emergence trap
Germany	Krefeld Entomological Society (82)	27	—	Flying insects	Malaise traps
Germany	Voigt et al. (29, 71)	24	1,041	Arthropods	Pitfall trap, sweep net
Greenland	Greenland Ecosystem Monitoring BioBasis program (36)	19	16	Arthropods	Pitfall traps
The Netherlands	Dutch Butterfly Monitoring Scheme (41)	15	39	Butterflies	Pollard walk
The Netherlands	Hallmann et al. (83)	26	—	Many insect orders	Pitfall traps, lighted sheet counts
Russia	Chronicles of Nature (84)	40	19	Many (includes insects)	Traps
Spain	Catalan & Andorran Butterfly Monitoring Schemes (30)	17	169	Butterflies	Pollard walk
Spain	Stewart et al. (85)	10	10	Butterflies	Pollard walk
United Kingdom	Hassall et al. (73)	30	215	Syrphid flies	Malaise traps
United Kingdom	Rothamsted Insect Survey (15, 35, 40, 68, 72)	51	345	Aphids, moths	Suction trap, light trap
United Kingdom	UK Butterfly Monitoring Scheme (16, 40, 42, 68, 74)	45	55	Butterflies	Pollard walk
United Kingdom	UK and Ireland Garden Moth Scheme (86)	11	50	Moths	Light trap

For studies with multiple associated publications, only a few are listed here; a more complete list is in *SI Appendix*, Table S1. Numbers of species and years are shown based on the literature that met our criteria and may not represent the total numbers of years or species from associated datasets; also, numbers are not shown if, for example, specimens were not identified to species.

overwintering beetle fauna during the coldest months (25). In a headwater stream in a German nature preserve that has been isolated from other anthropogenic stressors (other than climate change and possible indirect effects of land use change in the region), community shifts have been dramatic over 42 y of monitoring, with the abundance of common macroinvertebrates declining by 82% and overall species richness increasing (14). It is important to note that a strong signal of climate driving population trends has not been found in all long-term insect studies, even those from protected areas, perhaps as a result of buffering of high-quality habitat or other ecological factors. For example, in a subarctic forest in Finland, negative associations with a warming climate were detected for subsets of the moth fauna; however, populations were primarily stable or increasing for a majority of species (26). It can also be noted that the literature on long-term responses of insect populations to climate is neither taxonomically nor geographically broad, which is an important conclusion from Table 1, where it can be seen that most studies come from northern Europe and Lepidoptera are disproportionately represented, as others have noted (4).

Beyond the direct effects of climate change, we can ask: How will changing climatic conditions interact with habitat loss, invasive species, pesticide toxicity (27), and other factors? This is an area that is ripe for experimental work (10), but the number of potentially interacting factors that could be tackled in an experiment is daunting, which is why experiments will profitably be inspired and focused by observational results. Multiple studies from Table 1 have compared the effects of climate in different land use types, and such studies have discovered higher climate impacts in areas of disturbance (28–30). A notable example of modeling interactions in the context of global change comes from a recent study of British insects, where researchers found that the most successful model for poleward range shifts included habitat availability, exposure to climate change, and the interaction between the two (31).

On Changing Maxima, Minima, Means, and Variance

Climate change is of course not one phenomenon, and axes of change include shifts in limits (maxima and minima), average conditions, and variance, which can all be measured at different temporal and spatial scales. The multifaceted nature of climate change is illustrated by the fact that nighttime temperatures are warming faster than daytime conditions (32). The consequences of this for insects are poorly understood but potentially serious, including reduced time for recovery from daytime heat stress and indirect effects through plants, which are all areas where additional experimental work is needed (32). In the mountains of California, rising average daily minimum temperatures had some of the most dramatic negative effects on insects, especially in combination with drier years (33). Rising minimum temperatures in particular seasons might impact insects through effects on critical overwintering and diapausing stages. In central Europe, warmer overwintering temperature is associated with increased abundance in the following year for terrestrial organisms in a large-scale study that included insects (34). In the United Kingdom, the annual population dynamics of moths are affected by overwintering temperature and precipitation (35). In this case, winter precipitation has a negative association with moth abundance, while winter temperature has a positive association (35). In Greenland, changes in the structure of arthropod communities over 18 y have been influenced by warming summers and falls and fewer freeze–thaw events, with the most negative associations observed for surface detritivores (36). On the other side of the temperature spectrum is maximum temperature, which has been shown to be the variable most associated with local extinctions in a global survey of insects and other taxa (37).

While our understanding of biotic response to warming means and limits improves, the greater challenge of changing variance is now upon us. Increased climatic variance is often considered in the context of extreme events; however, changing variance can also negatively impact an organism by subjecting it to nonoptimal conditions or combinations of conditions, even if mean temperature and the number of extreme events remain the same. That said, predictions for many parts of the world do include an increased frequency of extreme weather events, which might include maximum or minimum temperatures outside of a historical range, more intense precipitation events or droughts, or combinations of these phenomena (38). We have few studies on this topic from which to draw conclusions; only six studies in Table 1 explicitly investigated extreme weather events (refs. 28, 33, and 39–42 but also see ref. 43). In the few cases where biotic response to extreme events has been examined, the results are as we might expect: extreme events are extreme population stressors. Large, synchronized population swings of Lepidoptera in the United Kingdom are associated with extreme climate years, and responses to these years were negative in five of six cases (40). On a continental scale, a recent resurvey of 66 bumblebee species across two continents points to temperatures outside of historical ranges as a major driver reducing occupancy across the landscape (44). Salcido et al. (39) report an increase in extreme flooding events as one of the factors contributing to the loss of parasitoids and Lepidoptera in a Costa Rican forest, which includes the disappearance of entire genera of moths (minimum temperatures also had strong negative effects, consistent with results discussed above). The complex and apparently disastrous effects of climate change at low latitudes, including the drying of cloud forests and loss of associated insects in another protected forest in Costa Rica, are discussed further in another paper (45).

On the Geography of Biotic Response to Climate Change

An important test of our understanding of ectotherm response to abiotic conditions is the extent to which we can understand and predict responses of insects living in different biomes or climatic regions (46). Current warming is not evenly distributed across the globe, with regions at higher latitudes and elevations experiencing the most severe increases, which could be expected to disproportionately impact populations (positively or negatively) (47). In the United Kingdom, for instance, population dynamics at range margins for many butterflies now more closely resemble core populations (48), and in Finland, rising temperature is associated with increasing moth multivoltinism (49). It has also been suggested that tropical insects are more sensitive to warming conditions because tropical regions have historically experienced less climatic variability, both within and between years, and thus, insects in those regions are already closer to detrimental thermal maxima relative to temperate insects (50, 51); however, with relatively few tropical monitoring datasets, this is a critical area for further investigation (52). A related issue is the effect of climate change along elevational gradients, and at least a few expectations align to suggest that montane insects could fare better in climate change scenarios as compared with insects in less topographically complex environments (53). First, montane insects have the opportunity to track analog climate conditions to buffer against rapid change, which might include shifts to higher elevations, into valleys, or to poleward aspects of slopes. Second, montane insects have access to a greater diversity of thermal environments, which might differ in mean conditions or rates of warming and could allow for behavioral thermoregulation even without changes in elevational range (54). Third, relative to lowlands that are degraded in many parts of the world (because of the concentration of agriculture or urban areas), insects on mountains will often find a greater diversity of plant resources, which (at least for herbivorous insects) should provide some buffer against climate-induced changes in the plant community. Are these expectations borne out by long-term monitoring of insect populations? The answer to that question has applied relevance because it affects how we think about land protections and whether or not mountains can be climate refugia during the upheavals of the Anthropocene (55).

Few insect monitoring programs encompass extensive elevational gradients, but one exception is the Shapiro Transect across Northern California: 10 sites and 163 species of butterflies over more than 2,500 m of elevation, including a severe gradient in land use, from the intensely modified Central Valley to above tree line in the Sierra Nevada (Fig. 1 *A* and *B*). Observations have been taken every 2 wk during the butterfly flight season for between 32 and 48 y, depending on the site; details of data collection have been described elsewhere (56–58).

Previous modeling work has highlighted the complexity of population response to weather in this diverse fauna (56) and has documented an array of factors impacting populations along the elevational and land use gradients. At lower elevations, the loss of open spaces, warming summers, and pesticide application have been associated with widespread declines (57, 59), while the impact of climate change and an extreme drought have been more apparent at higher elevations (33). Here, we revisit the question of climate change impacts in this system (with an additional 3 y of data), with an emphasis on understanding species-specific traits that predict persistence in the mountains. We also revisit a previously described upslope shift (58) with an additional 13 y of data to ask if elevational dynamics were impacted by the megadrought of 2011 to 2015.

Butterflies in the mountains and the Central Valley have, on average, followed downward population trajectories (Fig. 1 *C* and *D*). Populations at low elevations have been trending downward for a greater span of years, while montane populations appear to have been relatively steady through the 2000s but were severely impacted following 2011 (the start of a megadrought). Roughly speaking, this comparison is between populations affected by all of the major Anthropocene stressors (in the Central Valley) and populations affected primarily by a changing climate (in the mountains). The mountains are not without some land conversion and incursions of invasive plants along roadways, but for the most part, our sites are in undisturbed natural areas. Thus, it is noteworthy that the montane declines have reached almost one-half of a standard deviation away from the mean (relative to the long-term average), matching roughly the depth of decline in the Central Valley.

The density plots in Fig. 1 *C*, *Inset* and *D*, *Inset* reflect the distribution of demographic trends in the two regions: the bulk of coefficients (associated with years in regression models) is negative (reflecting downward population trajectories) in both cases, but not all species are in decline. With respect to the mountains, it is of interest to ask if species with better performance are species that have been observed with greater frequency at the highest elevations, which would be consistent with a bioclimatic (upslope) niche-tracking model. We have updated (in Fig. 1*E*) an earlier analysis (58) from before the megadrought years and confirm that butterflies were on average being observed at slightly higher elevations in later (2002 to 2010) vs. earlier (1977 to 1985) years; the distribution of those elevation changes in Fig. 1*E* is positive and upslope. A shift in average elevation of occurrence (or change in central tendency of elevational range) is consistent with vegetation dynamics observed in another California mountain range (60). In contrast, when the early vs. late comparisons encompass the drought years in a recent (Fig. 1*F*) or broader span of years (Fig. 1*G*), it can be seen that the elevational changes are more evenly balanced with both upslope and downslope shifts. This is not unlike the complexity of upslope and downslope responses observed in other taxa in the same mountain range (61, 62).

The severe declines of the drought years in Northern California have in effect cancelled out the earlier upslope signal, which leaves us with the question of whether or not success (or failure) in the mountains in recent years can be predicted based on species-specific traits. We took a constrained ordination approach (redundancy analysis) to understand montane butterfly populations over time in the context of potential predictors that include voltinism (number of generations per year), habitat association, overwintering biology, sensitivity to specific weather variables, and other traits (Fig. 2). Focusing on the west slope locations (relevant to our measure of elevational population dynamics in Fig. 1 *E*–*G*), we see that the most successful montane species can be characterized as mostly resident (reproducing at our sites), univoltine species with earlier emergence, and also as species with positive responses to precipitation and average minimum daily temperatures (Fig. 2). The converse is that declining montane species (in the lower half of Fig. 2) have a negative association through time with minimum temperatures, which is consistent with a previous analysis, focused on species richness (33), that hypothesized rising minimum temperatures as a driver of declining montane butterflies. The association with precipitation sensitivity suggests that a successful subset of the montane fauna not only persists with warming nights but is able to take advantage of the highly variable precipitation of the region (33).

Declining populations in the mountains (in the lower half of Fig. 2) tend to be weedy, multivoltine habitat generalists with broad geographic ranges (although they can be locally rare). This result is perhaps superficially surprising given the resilience of generalist species in other contexts (63, 64) but was predicted 10 y ago for the montane Northern California fauna (58), and it has been seen for multivoltine butterflies in another seasonally hot and dry Mediterranean climate (65). For most species, the warm season at higher elevations is not long enough to support true multivoltinism (66); thus, species with many generations per year depend on demographic contributions from lower elevations, where populations have been failing for at least two decades (Fig. 1*D*). It is also possible that warming temperature and drought are acting indirectly and interactively, causing late season vegetation to dry earlier in the year, which could impact late season butterflies, including multivoltine species (67). It is interesting to note that having multiple generations per year, however, conveyed the opposite effect at the lowest elevations during an extreme weather event, where we observed that multivoltinism combined with early springs allowed populations in the Central Valley to reach higher densities during the drought years of 2011 to 2015, which can be seen in Fig. 1*D* (33).

These results, which encompass between 100 and 142 butterfly species (depending on the analysis), challenge some of the expected patterns of biotic response to climate change. First, the

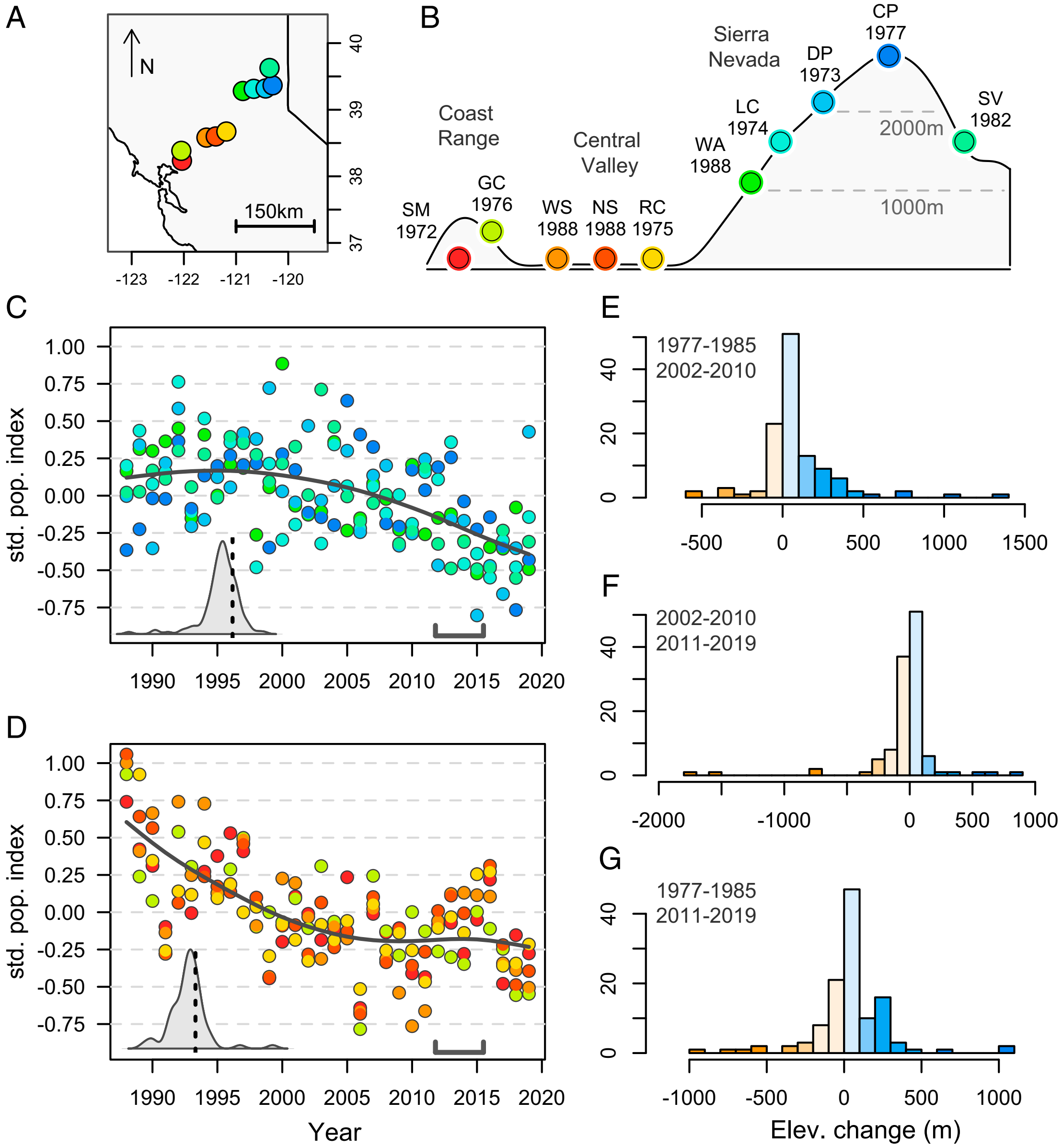

Fig. 1. **Overview of geography and major trends for the Northern California case study. (*A*) Map of Northern California with focal sites, also shown in elevational profile in *B* with two-letter site abbreviations and the year when continuous sampling started at each site (SM, Suisun Marsh; GC, Gates Canyon; WS, West Sacramento; NS, North Sacramento; RC, Rancho Cordova; WA, Washington; LC, Lang Crossing; DP, Donner Pass; CP, Castle Peak; SV, Sierra Valley). (*C* and *D*) Standardized population indices (means across species by site) for mountain sites (*C*) and low-elevation sites (*D*), with site colors the same as in *B* and brackets above *x* axes to indicate major drought years from 2011 to 2015. Density plots in *C*, *Inset* and *D*, *Inset* show the distribution of year coefficients across species in the two regions (high and low elevations), with vertical dotted lines marking zero, such that observations to the left of the line represent species with negative trends across time. (*E*–*G*) Histograms summarize changes in elevation between different 9-y windows of time; for example, *E* is the change in mean elevation per species between the earliest years (1977 to 1985) and years immediately before the megadrought (2002 to 2010). Colors in histograms are for visualization, with darker orange corresponding to more negative (downward) shifts and darker blue being more positive (upslope) shifts (*SI Appendix*, Fig. S1 shows additional details). Mean shifts (in meters; with SEs) and results from one-sample *t* tests (against the null of mean elevational shift being zero) are as follows: (*E*) 85.5 (±22.4), $t_{116} = 3.82$, $P < 0.001$; (*F*) −40.9 (±25.6), $t_{116} = -1.59$, $P = 0.12$; and (*G*) 38.1 (±23.4), $t_{118} = 1.63$, $P = 0.11$.**

ability of montane microclimatic heterogeneity to buffer against climate change might be limited and context dependent, especially when considering extreme regional events. Overall, our montane locations have tended to show more variation in population indices among sites (*SI Appendix*, Fig. S2), which could be consistent with montane microclimatic heterogeneity. However, declines in the mountains following the megadrought are comparable with declines in the Central Valley (Fig. 1 *C* and *D*), and both multivoltine species (with demographic connections to lower elevations) and resident species with fewer generations per year have suffered in the mountains (*SI Appendix*, Figs. S3 and S4). These results highlight the power of long-term data to quantify climate sensitivities along with natural history when understanding population trajectories under climate change. These results also bring into focus the complexities faced by organisms when traits (such as voltinism) confer different advantages and disadvantages at

https://doi.org/10.1073/pnas.2002543117

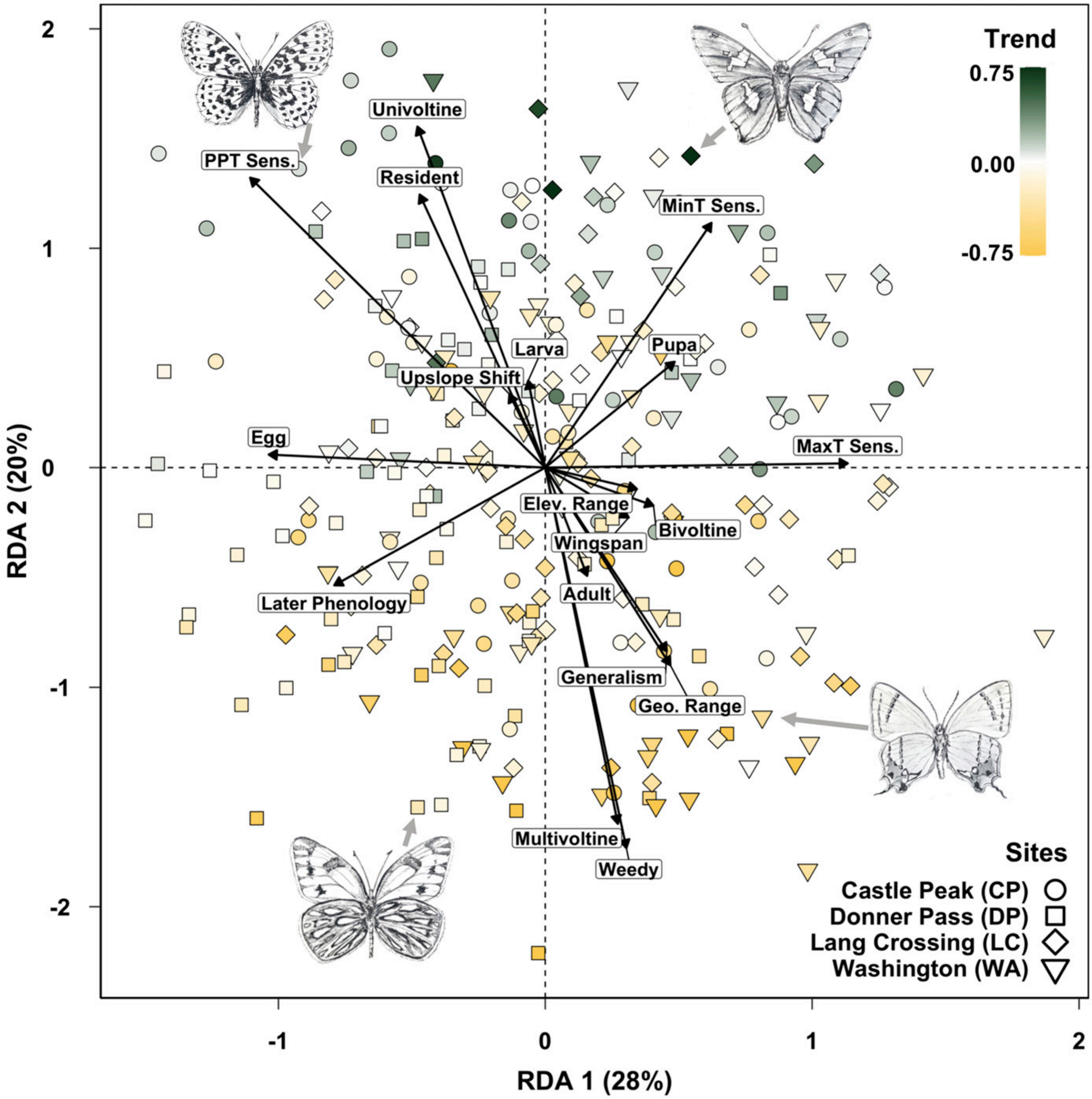

Fig. 2. Traits associated with population trends at four montane monitoring sites. Points represent a species at a site (any individual species can have between one and four points), and those in the top half are generally increasing, while bottom half points are generally declining. Points are colored according to coefficients associated with years (i.e., "trend" or change through time), and those coefficients as well as climate sensitivities were estimated in separate Bayesian models. Traits represented include life history traits and sensitivities to climatic variables, specifically precipitation (PPT Sens.), average daily maximum temperatures (MaxT Sens.), and average daily minimum temperatures (MinT Sens.). Life history traits include overwintering states, geographic range (Geo. Range), phenology (average date of first flight), elevational range (Elev. Range), elevational shift (as in Fig. 1 *E–G*), voltinism, body size (wingspan), breadth of habitat association (generalism), and weedy status (the text and *SI Appendix* have more details). Percentage of constrained variation explained is shown in parentheses after each axis label. Four species are illustrated (clockwise from the upper left): *Boloria epithore*, *Epargyreus clarus*, *Strymon melinus*, and *Pontia occidentalis* (Illustrations credit: M.L.F.). RDA, redundancy analysis.

locations that are potentially within dispersal distance but separated by elevational, climatic, and habitat differences.

Conclusions and Practical Lessons

Reports of insect declines from monitoring programs across the world have been staggering and reflect the multifaceted challenges facing insects in the Anthropocene. Given these declines and the utility of monitoring studies for parsing different stressors, it is worth asking: what lessons have we learned so far about the impacts of climate change, what are the most pressing current questions, and what responses can be expected as we progress further into the Anthropocene? Contemporary climate change is having positive effects on some species and negative effects on others (68, 69), and in some cases, the balance (of positive and negative effects) can be determined by geographic factors such as latitudinal position (23, 50) or species-specific traits (6, 7). In previous periods of change, we know from the paleontological record that individual beetles have relocated across continents (70), and distributional change is a commonly observed response among insects today (47). Some of the studies from Table 1 discuss traits that predict positive or negative responses to climate change, including whether an insect is terrestrial or aquatic (24, 34), its trophic position (14, 28, 29, 68, 71), its functional group (14, 28, 36), and its voltinism (33, 42, 72–74). Many of these studies find support for greater climate sensitivity in higher trophic levels and positive responses to warming for multivoltine species (relative to univoltine species); however, as can be seen from the case study (Fig. 2), trait effects can vary over relatively short distances. The impact of extreme weather events or prolonged stretches of weather outside of historical conditions will have more consistently negative effects across species (4, 75), although this is an area where additional research is urgently needed. Finally, altered biotic interactions will likely have large impacts on population responses to climate change, given that trophic position and degree of specialization are common predictors of success or decline (13, 14, 28, 29, 68, 71, 76).

Perhaps the clearest finding is the fact that we found relatively few studies that matched our search criteria, which were focused on monitoring studies as uniquely useful for revealing impacts of climate change. Even more important, only two of those studies are from tropical areas (39, 77), where the majority of insects live, which thus represents a major gap in our understanding of terrestrial biodiversity in the Anthropocene. Our reading of the literature also suggests a few methodological issues that could be better aligned across future studies. Results from analyses of weather and insect populations should be reported as standardized beta coefficients to facilitate comparisons among studies. Further, population dynamics should be predicted by weather at both seasonal and annual scales (although not necessarily in the same model), and finer scales may be appropriate for certain questions or datasets. Whenever possible, year or time as a variable should be included in models with weather explaining insect population or community data. Conditioning on year strengthens the inference of causation, especially when variables (insects and climate) are known a priori to be characterized by directional change. When year and weather variables are highly correlated, rather than simply excluding year from the model, researchers might consider methods of trend decomposition or variance partitioning, where unique and shared components of explained variance by years and climatic data can be examined (11).

In summary, the relevant scientific literature is of course not perfect but is growing rapidly, and we know enough now to say that the combination of climatic effects with other anthropogenic stressors will certainly have interacting consequences (43, 58). The modernization of agriculture has removed natural habitat and increased pesticide exposure, urbanization has paved previously open lands and introduced novel thermal and light pollutants, and tropical deforestation is destroying habitat in the most diverse regions on Earth (4). The rising threat of climate change will test the resiliency of populations already facing such threats, especially in the context of the increasing frequency of extreme weather events, which could be particularly detrimental in diverse tropical areas (39, 45). Nevertheless, we believe that the studies reviewed here offer some tangible hope. In all but the most severe cases, there are some species that manage to take advantage of anthropogenically altered conditions (69). Unlike animals with larger home ranges and greater per-individual resource requirements, insects are remarkable in the speed with which they respond to a bit of hedgerow improvement or even a backyard garden. In our own experience, we have been surprised by the resilience of the low elevations of Northern California (33). Some of these places are far from land that you might spot as a target for protection: rights-of-way, train tracks, levees, or drainage ditches. Yet, it was the butterflies in those places that proved to be the most robust during the megadrought. Of course, the butterflies at low and high elevations in California still continue on downward population trajectories, of which climate plays no small part, but if other stressors could be alleviated, it might be the case that many insects, even in close proximity to human development, will continue to do what insects do best: survive.

Methods

The literature search was performed on Web of Science in February 2020 using the search terms TS (topic) = (insect* OR lepidoptera* OR hymenoptera* OR diptera* OR hemiptera* OR coleoptera*) AND TS = (climate OR weather) AND TS = ("long term" OR "long-term" OR monitor*), which identified 2,264 studies. To be included in Table 1, a study had to have examined at least 10 insect species for at least 10 y and include an analysis of climate. Data had to have been collected continuously (at an annual frequency or better) at one or more sites, which could be part of a larger monitoring network. This excludes studies that use museum specimens or resampling efforts, which are of course valuable in their own right but make different assumptions and provide different insights (especially regarding geographic ranges). Additionally, studies must have either been restricted to a protected area or span a gradient of land use types (e.g., from developed to protected), and by "protected," we mean relatively isolated from land conversion rather than any legal or political designation. This was determined by reading methods sections and looking for terms such as "preserve," "undisturbed," "natural," or other similar labels. We supplemented the Web of Science search with ad hoc searches using Google Scholar focused on individual monitoring schemes.

Analyses of Northern California butterfly data involved visualization of population trends averaged at the site level, estimation of population trends at the species level, calculations of changes in mean elevation of occupancy per species, and ordination of interannual population variation in association with natural history traits. Full details on all methods are given in *SI Appendix, Supplementary Methods*, but in brief, our visualization of populations (in Fig. 1 *C* and *D*) was based on z-transformed probabilities of observation that we have shown to be indices of abundance (78). Estimation of coefficients summarizing population change over time (*Insets* in Fig. 1 *C* and *D* and shading of points in Fig. 2) is based on hierarchical Bayesian binomial models as presented in previous work with these data (56). Changes in average elevation per species (Fig. 1 *E*–*G*) used sample-based (or visit-based) rarefaction to impose an equal number of simulated visits to a site in repeated resampling to calculate differences between time windows. The specifics of time windows were motivated by a desire to understand change before, during, and after a millennium drought (2011 to 2015), which was the single most impactful climate event (during our study) on the montane populations. Finally, redundancy analysis combined many lines of information into one picture of population-specific change over time with respect to population-specific traits (Fig. 2).

Data Availability. Butterfly presence/absence data have been deposited in Art Shapiro's Butterfly Site at the University of California, Davis (http://butterfly.ucdavis.edu/query).

Acknowledgments

Thanks to David Wagner for organizing the Entomological Society of America symposium where much of this paper was originally presented; Trevor Faske for discussion of the redundancy analysis; the authors of the papers in Table 1 who provided feedback, especially Juha Pöyry; and two anonymous reviewers and Toke T. Høye for their feedback and suggestions. M.L.F. was supported by a Trevor James McMinn professorship.

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