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Classification: biological sciences; ecology.

**Insects and recent climate change**

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24 **Abstract**

25 Insects have diversified through 400 million years of Earth's changeable climate, yet recent and  
26 ongoing shifts in patterns of temperature and precipitation pose novel challenges as they  
27 combine with decades of other anthropogenic stressors including the conversion and degradation  
28 of land. Here we consider how insects are responding to recent climate change, while  
29 summarizing the literature on long-term monitoring of insect populations in the context of  
30 climatic fluctuations. Results to date suggest that climate change impacts on insects have the  
31 potential to be considerable, even when compared to changes in land use. The importance of  
32 climate is illustrated with a case study from the butterflies of Northern California, where we find  
33 that population declines have been severe in high-elevation areas removed from the most  
34 immediate effects of habitat loss. These results shed light on the complexity of montane-adapted  
35 insects responding to changing abiotic conditions and raise questions about the utility of  
36 temperate mountains as refugia during the Anthropocene. We consider methodological issues  
37 that would improve syntheses of results across long-term insect datasets and highlight directions  
38 for future empirical work.

39

40 **Key words**

41 Anthropocene, climate change, population decline, extinction, extreme weather

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45 **Significance statement**

46 Anthropogenic climate change poses multiple threats to society and biodiversity, and challenges  
47 our understanding of the resilience of the natural world. We discuss recent ideas and evidence  
48 on this issue and conclude that the impacts of climate change on insects in particular have the  
49 potential to be more severe than might have been expected a decade ago. Finally, we suggest  
50 practical measures that include the protection of diverse portfolios of species, not just those  
51 inhabiting what are currently the most pristine areas.

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55 From invasive species to habitat loss, pesticides and pollution, the stressors of the Anthropocene  
56 are many and multi-faceted, but none are as geographically pervasive or as likely to interact with  
57 all other factors as climate change (1, 2). For these reasons, understanding the effects of  
58 anthropogenic climate change on natural systems could be considered the defining challenge for  
59 the ecological sciences in the 21<sup>st</sup> century (3). It is of particular interest to ask how insects will  
60 respond to recent and ongoing climate change, because they are the most diverse lineage of  
61 multicellular organisms on the planet, and of fundamental importance to the functioning of  
62 terrestrial ecosystems. The issue also has new urgency in light of recent and ongoing reports of  
63 insect declines from around the globe (4). Insects and climate change have been discussed  
64 elsewhere (5–8), and our goal here is not to cover all aspects of the problem. Instead, we focus  
65 on recent discoveries and questions inspired by long-term records of insect populations,  
66 discussing other fields (e.g., physiological ecology) where they inform our understanding of  
67 population trajectories under climate change scenarios.

68 In the sections below, we compare climate change to other stressors and examine  
69 multifaceted impacts in terms of climate means, limits and extremes. Then we discuss the  
70 geography of climate change with particular focus on the responses of montane insects, with a  
71 case study from the butterflies of Northern California that illustrates the value of long-term  
72 observations that span a major gradient of land use intensity. Two areas that we do not cover in  
73 detail are the theoretical foundations of climate change research (9), and community-level  
74 consequences including altered trophic interactions associated with shifting phenologies (10).  
75 As a qualitative survey of the state of the field, we have gathered insect monitoring studies

76 (based on a review of more than 2,000 papers) that encompass at least 10 years of continuous  
77 sampling and analyses of climatic data (Table 1). We excluded studies of pest species and  
78 studies from agriculture, as well as projects encompassing fewer than 10 species (as a way to  
79 focus on assemblages of species rather than model systems). In general, we emphasize  
80 monitoring studies as unparalleled opportunities for understanding the influence of climatic  
81 fluctuations on animal populations because of the ability to decompose complex temporal trends  
82 into effects driven by different factors (11, 12).

83

#### 84 **On the relative importance of climate change and other stressors**

85 Although Anthropocene stressors must ultimately be understood as an interacting suite of factors  
86 (13), it is useful to start by asking: how will the consequences of climate change compare to  
87 other stressors? Over the last three centuries, the global percentage of ice-free land in a natural  
88 state (not intensively modified by human activity) has shrunk from 95% to less than 50% (14),  
89 with consequences that include the extirpation and extinction of plants and animals (15).

90 Although habitat loss (including degradation through pollution and numerous other processes)  
91 continues, it is possible that we are living through a period of transition where the importance of  
92 changing climatic conditions could begin to rival the importance of habitat loss (16, 17). That  
93 transition and the rise of climate change as a more severe threat could happen through a number  
94 of related processes. A very partial list would include the inability to disperse quickly enough to  
95 track changing conditions (18), or the phenomenon of dispersal out of previously suitable habitat  
96 into regions where habitat is suboptimal or cannot be found at all (19). There is also the  
97 possibility that abiotic stress associated with changing climatic conditions could simply be the

98 last straw, reducing vital rates below replacement levels as a result of physiological stress in  
99 populations already pushed to the edge by other stressors (5).

100 An empirical understanding of the effects of climate change in comparison to other  
101 stressors depends in large part on long-term observations from protected areas or from gradients  
102 of land use that will let us directly compare the effects of different factors. In Great Britain, both  
103 land use and climate change have been important for explaining the decline of 260 species of  
104 macro-moths and an increase of 160 species (out of a total of 673 species) (20). The signal of  
105 habitat loss is seen in widespread species, which have declined in regions with increased  
106 intensity of human land use. At the same time, the role of climate can be seen in the decrease of  
107 more northern, cold-adapted species and the simultaneous increase of more southern, warm-  
108 adapted species (20). Less multifaceted signals of global change can be found in smaller areas  
109 sheltered from direct effects of habitat loss. Beetle activity in a protected forest in New  
110 Hampshire has, for example, decreased by 83% in a re-sampling project spanning 45 years,  
111 apparently as a function of warmer temperatures and reduced snow pack that insulates the  
112 diverse ground-dwelling beetle fauna during the coldest months (21). In a headwater stream in a  
113 German nature preserve that has been isolated from other anthropogenic stressors (besides  
114 climate change), abundance of macroinvertebrates has declined by 82% over 42 years and mean  
115 emergence is more than two weeks earlier, while species richness has increased (22). It is  
116 important to note that a signal of climate has not been found in all long-term studies of insects,  
117 even those from protected areas. In a sub-arctic forest in Finland, moth populations are primarily  
118 stable or increasing and these trends do not appear to be strongly related to warming  
119 temperatures (23). It can also be noted that the literature on long-term responses of insect  
120 populations to climate is neither deep nor geographically broad, which is an important

121 conclusion from Table 1, where it can be seen that most studies come from Northern Europe and  
122 Lepidoptera are disproportionately represented, as others have noted (4).

123 Beyond the direct effects of climate change, we can ask: how will changing climatic  
124 conditions interact with habitat loss, invasive species, pesticide toxicity (24), and other factors?  
125 This is an area that is ripe for experimental work (11), but the number of potentially interacting  
126 factors that could be tackled in an experiment is daunting, which is why experiments will  
127 profitably be inspired and focused by observational results. The challenge for researchers with  
128 long-term data is to develop statistical models that encompass interactions rather than focusing  
129 only on main effects that might be easier to interpret. A notable example of modeling  
130 interactions in the context of global change comes from a recent study of British insects, where  
131 researchers found that the most successful model for poleward range shifts included habitat  
132 availability, exposure to climate change, and the interaction between the two (25).

133 Our reading of the literature comparing climate to other drivers of change suggests a few  
134 methodological issues that could be better aligned across future studies. Results from analyses  
135 of weather and insect populations should be reported as standardized beta coefficients, and  
136 summarized at both seasonal and annual scales; finer scales may be appropriate for certain  
137 questions or datasets, but those two broader scales would facilitate comparisons among studies.  
138 Whenever possible, year or time as a variable should be included in models with weather  
139 explaining insect population or community data. Conditioning on year strengthens the inference  
140 of causation, especially when variables (insects and climate) are known *a priori* to be  
141 characterized by directional change. When year cannot be included in models because of high  
142 collinearity with weather or other variables, first order differencing or other methods of trend  
143 decomposition should be considered (12).

144

145 **On changing maximums, minimums, means and variance**

146 Climate change is of course not one phenomenon, and axes of change include shifts in limits  
147 (maximums and minimums), average conditions and variance, which can all be measured at  
148 different temporal and spatial scales. The multifaceted nature of climate change is illustrated by  
149 the fact that nighttime temperatures are warming faster than daytime conditions (26), and the  
150 consequences for insects are poorly-understood but potentially serious, including reduced time  
151 for recovery from daytime heat stress, and indirect effects through plants (26). In the mountains  
152 of California, rising average daily minimum temperatures had some of the most dramatic  
153 negative effects on insects, especially in combination with drier years (27). Rising minimum  
154 temperatures in particular seasons might impact insects through effects on critical overwintering  
155 stages. In the UK, the annual population dynamics of moths are affected by overwintering  
156 temperature and precipitation (28). In this case, winter precipitation has a negative association  
157 with moth abundance, while winter temperature has a positive association (28). In Greenland,  
158 changes in the structure of arthropod communities over 18 years have been influenced by  
159 warming summers and falls and fewer freeze-thaw events, with the most negative associations  
160 observed for surface detritivores (29). On the other side of the temperature spectrum is  
161 maximum temperature, which has been shown to be the variable most associated with local  
162 extinctions in a global survey of insects and other taxa (18).

163 While our understanding of biotic response to warming means and limits improves, the  
164 greater challenge of changing variance is now upon us: predictions for many parts of the world  
165 include an increased frequency of extreme weather, which can appear as more intense  
166 precipitation events separated by more prolonged dry periods (30). We have few studies on this



167 topic from which to draw conclusions; only five studies in Table 1 explicitly investigated  
168 extreme weather events (27, 31–34). In the few cases where biotic response to extreme events  
169 has been examined, the results are as we might expect: extreme events are extreme population  
170 stressors. Large, synchronized population swings of Lepidoptera in the UK are associated with  
171 extreme climate years and responses to these years were negative in 5 out of 6 cases (32). On a  
172 continental scale, a recent re-survey of 66 bumble bee species across two continents points to  
173 temperatures outside of historical ranges as a major driver reducing occupancy across the  
174 landscape (35). Salcido et al. (31) report an increase in extreme flooding events as one of the  
175 factors contributing to the loss of parasitoids and Lepidoptera in a Costa Rican forest, which  
176 includes the disappearance of entire genera of moths (minimum temperatures also had strong  
177 negative effects, consistent with other results discussed above).

178

### 179 **On the geography of biotic response to climate change**

180 An important test of our understanding of ectotherm response to abiotic conditions is the extent  
181 to which we can understand and predict responses of insects living in different biomes or  
182 climatic regions (36). It has been suggested that tropical insects are more sensitive to warming  
183 conditions because they are already at their optimal temperatures, and are thus closer to  
184 detrimental thermal maxima relative to temperate insects (37); this is, however, an area of  
185 ongoing investigation (38). A related issue is the effect of climate change along elevational  
186 gradients, and at least a few expectations align to suggest that montane insects could fare better  
187 in climate change scenarios as compared to insects in less topographically complex environments  
188 (39). First, montane insects have the opportunity for upslope shifts in range, and the tracking of  
189 similar environmental conditions in space is potentially the best buffer against changing

190 conditions. Second, montane insects have access to a greater diversity of microhabitats, which  
191 could allow for behavioral thermoregulation even without changes in elevational range. Third,  
192 relative to lowlands that are degraded in many parts of the world (because of the concentration of  
193 agriculture or urban areas), insects on mountains will often find a greater diversity of plant  
194 resources, which (at least for herbivorous insects) should provide some buffer against climate-  
195 induced changes in the plant community. Are these expectations borne out by long-term records  
196 of insect populations? The answer to that question has applied relevance because it affects how  
197 we think about land protections, and whether or not mountains can be climate refugia during the  
198 upheavals of the Anthropocene (40).

199         Few insect monitoring programs encompass extensive elevational gradients, but one  
200 exception is the Shapiro Transect across Northern California: ten sites and 163 species of  
201 butterflies over more than 2500m of elevation, including a severe gradient in land use, from the  
202 intensely modified Central Valley to above tree line in the Sierra Nevada (Fig. 1A and B).  
203 Observations have been taken every two weeks during the butterfly flight season for between 32  
204 and 48 years, depending on the site; details of data collection have been described elsewhere  
205 (41–43).

206         Previous modeling work has highlighted the complexity of population response to  
207 weather in this diverse fauna (41), and has documented the array of factors impacting  
208 populations along the elevational and land use gradient. At lower elevations, the loss of open  
209 spaces, warming summers and pesticide application have been associated with widespread  
210 declines (42, 44), while the impact of climate change and an extreme drought have been more  
211 apparent at higher elevations (27). Here we revisit the question of climate change impacts in this  
212 system (with an additional three years of data), with an emphasis on understanding species-

213 specific traits that predict persistence in the mountains. We also revisit a previously-described  
214 upslope shift (43) with an additional 13 years of data to ask if elevational dynamics were  
215 impacted by the mega-drought of 2011-2015.

216 Montane and valley populations have, on average, followed downward trajectories (Fig.  
217 1C and D). Populations at low elevations have been trending downward for a greater span of  
218 years, while montane populations appear to have been relatively steady through the 2000s, but  
219 were severely impacted following 2011 (the start of the drought years). Roughly speaking, this  
220 comparison is between populations affected by all of the major Anthropocene stressors (in the  
221 Central Valley) and populations affected primarily by a changing climate (in the mountains).  
222 The mountains are not without some land conversion and incursions of invasive plants along  
223 roadways, but for the most part our sites are in undisturbed natural areas. Thus, it is noteworthy  
224 that the montane declines have reached almost one half of a standard deviation away from the  
225 mean (relative to the long-term average), matching roughly the depth of decline in the valley.

226 The inset density plots in Fig. 1C and D reflect the distribution of demographic trends in  
227 the two regions: the bulk of coefficients (associated with years in multiple regression models) are  
228 negative (reflecting downward trajectories) in both cases, but not all species are in decline. With  
229 respect to the mountains, it is of interest to ask if species with better performance are species that  
230 have been observed with greater frequency at the highest elevations, which would be consistent  
231 with a bioclimatic (upslope) niche-tracking model. We have updated (in Fig. 1E) an earlier  
232 analysis (43) from before the mega-drought years, and confirm that butterflies were on average  
233 being observed at slightly higher elevations in later (2002-2010) vs earlier (1977-1985) years;  
234 the distribution of those elevation changes in Fig. 1E is positive and upslope ( $t = 3.82$ ,  $df = 116$ ,  
235  $p < 0.001$ ). A shift in average elevation of occurrence (or change in central tendency of

236 elevational range) is consistent with vegetation dynamics observed in another California  
237 mountain range (45). In contrast, when the early vs late comparisons encompass the drought  
238 years in a recent (Fig. 1F) or broader span of years (Fig. 1G) it can be seen that the elevational  
239 changes are more evenly balanced with both upslope and downslope shifts. This is not unlike  
240 the complexity of upslope and downslope responses observed in other taxa in the same mountain  
241 range (46, 47).

242         The severe declines of the drought years in Northern California have in effect cancelled  
243 out the earlier upslope signal, which leaves us with the question of whether or not success (or  
244 failure) in the mountains in recent years can be predicted based on species-specific traits. We  
245 took a constrained ordination approach (redundancy analysis) to understand montane butterfly  
246 populations over time in the context of potential predictors that include voltinism (number of  
247 generations per year), habitat association, overwintering biology, sensitivity to specific weather  
248 variables, and other traits. Focusing on the west slope locations (relevant to our measure of  
249 elevational population dynamics in Fig. 1 E-G), we see that the most successful montane species  
250 can be characterized as mostly resident (reproducing at our sites), univoltine species with earlier  
251 emergence and positive responses to precipitation and average minimum daily temperatures (Fig.  
252 2). The converse is that declining montane species (in the lower half of Fig. 2) have a negative  
253 association through time with minimum temperatures, which is consistent with a previous  
254 analysis, focused on species richness (27), that hypothesized rising minimum temperatures as a  
255 driver of declining montane butterflies. The association with precipitation sensitivity suggests  
256 that a successful subset of the montane fauna not only persists with warming nights but is able to  
257 take advantage of the highly variable precipitation of the region (27).

258 Declining populations in the mountains (in the lower half of Fig. 2) tend to be weedy,  
259 multivoltine habitat generalists with broad geographic ranges. This result is perhaps  
260 superficially surprising given the resilience of generalist species in other contexts (48, 49), but  
261 was predicted ten years ago for the montane Northern California fauna (43), and has been seen  
262 for multivoltine butterflies in another seasonally hot and dry Mediterranean climate (50). For  
263 most species, the warm season at higher elevations is not long enough to support true  
264 multivoltinism (51), thus species with many generations per year depend on demographic  
265 contributions from lower elevations, where populations have been failing for at least two decades  
266 (Fig. 1D). It is interesting to note that having multiple generations per year, however, conveyed  
267 the opposite effect at the lowest elevations during an extreme weather event, where we observed  
268 that multivoltinism combined with early springs allowed valley populations to reach higher  
269 densities during the drought years of 2011-2015, which can be seen in Fig. 1D (27).

270 These results, which encompass between 100 and 142 butterfly species (depending on the  
271 analysis), challenge some of the expected patterns of biotic response to climate change. First,  
272 montane microclimatic heterogeneity might not be a strong buffer against climate change.  
273 Declines in the mountains are comparable to declines in the Central Valley, which is  
274 experiencing other anthropogenic stressors and contains less climatic variation over short  
275 distances. These results highlight the power of long-term data to quantify climate sensitivities  
276 along with natural history when understanding population trajectories under climate change.  
277 These results also bring into focus the complexities faced by organisms when traits (such as  
278 voltinism) confer different advantages and disadvantages at locations that are potentially within  
279 dispersal distance but separated by elevational, climatic, and habitat differences.

281 **Conclusions and practical lessons**

282 Reports of insect declines in the scientific and popular press have been greeted with surprise,  
283 which could reflect an inherent bias that even scientists have towards assuming that the smallest  
284 and most diverse animals on the planet would somehow be more robust than, for example,  
285 amphibians or birds. Insects have, after all, seen more than 400 million years of climate change.  
286 Can recent and ongoing climate change be that different from others that insects have weathered?  
287 In previous periods of change, we know from the paleontological record that individual beetles  
288 have relocated across continents (52). As can be seen from Table 1, there are relatively few  
289 studies where long-term records of insect populations (with 10 or more continuously-sampled  
290 years) have been analyzed in the context of climatic fluctuations. Even more important, only  
291 two of those studies are from tropical areas (31, 53), where the majority of insects live, which  
292 thus represents a major gap in our understanding of terrestrial biodiversity in the Anthropocene.  
293 Nevertheless, considering results from the studies in Table 1 along with spatial or occupancy  
294 surveys (e.g., 18), conclusions do emerge. Ongoing climate change will have positive effects on  
295 some species and negative effects on others (54, 55), with the balance (of positive and negative  
296 effects) determined in some cases by geographic factors such as latitudinal position (20, 37) and  
297 in other cases by more complex species-specific traits (6, 7), as in the Northern California case  
298 study (Fig. 2). Extreme weather events or prolonged stretches of weather outside of historical  
299 conditions will have more consistently negative effects across species (4, 56), although this in an  
300 area where additional research is urgently needed.

301           Moreover, the combination of climatic effects with habitat degradation will certainly  
302 have interacting consequences (34, 43), which leads to the conclusion that the current crisis is  
303 indeed different than previous periods of Earth history, for the reason that the planet has changed

304 in so many other ways as a result of the increasingly rapid conversion and loss of natural  
305 resources associated with the Anthropocene (13). The modernization of agriculture has removed  
306 the weedy edges, previously open land has been paved (42), and prolonged droughts have  
307 compressed and fragmented tropical cloud forests (56). Nevertheless, we believe that the study  
308 of long-term insect records offers some tangible hope and practical lessons. In all but the most  
309 severe cases, there are some species that manage to take advantage of anthropogenically-altered  
310 conditions (55). Unlike animals with larger home ranges and greater per-individual resource  
311 requirements, insects are remarkable in the speed with which they respond to a bit of hedgerow  
312 improvement or even a backyard garden. In our own experience, we have been surprised by the  
313 resilience of the low elevations of Northern California (27). Some of these places are far from  
314 land that you might spot as a target for protection: rights of way, train tracks, levees, or drainage  
315 ditches. Yet it was the butterflies in those places that proved to be the most robust during the  
316 mega-drought. In the mountains, we have reported success conferred by combinations of traits  
317 that could only have been partly predicted by previous work. Of course, the butterflies at low  
318 and high elevations in California still continue a downward trajectory of which climate plays no  
319 small part, but if other stressors could be alleviated it might be the case that insects even in close  
320 proximity to human development will continue to do what insects do best: survive.

321

## 322 **Methods**

323 The literature search was performed on ISI Web of Science in February 2020 using the search  
324 terms TS=(insect\* OR lepidoptera\* OR hymenoptera\* OR diptera\* OR hemiptera\* OR  
325 coleoptera\* ) AND TS=(climate OR weather) AND TS=("long term" OR "long-term" OR  
326 monitor\*), which identified 2,264 studies. To be included in Table 1, we considered studies that

327 included at least 10 insect species for at least 10 years. Additionally, studies must have either  
328 been restricted to a protected area or span a gradient of land use types (e.g., from developed to  
329 protected); and by "protected" we mean relatively isolated from land conversion rather than any  
330 legal or political designation.

331 Analyses of Northern California butterfly data involved visualization of population trends  
332 averaged at the site level, estimation of population trends at the species level, calculations of  
333 changes in mean elevation of occupancy per species, and ordination of inter-annual population  
334 variation in association with natural history traits. Full details on all methods are given in *SI*  
335 *Appendix* material, but in brief our visualization of populations (in Fig. 1C and D) was based on  
336 z-transformed probabilities of observation that we have shown to be indices of abundance (57).  
337 Estimation of coefficients summarizing population change over time (insets in Fig. 1C and D and  
338 shading of points in Fig. 2) is based on hierarchical Bayesian binomial models as presented in  
339 previous work with this data (41). Changes in average elevation per species (Fig. 1E-G) used  
340 sample- (or visit-) based rarefaction to impose an equal number of simulated visits to a site in  
341 repeated resampling to calculate differences between time windows. The specifics of time  
342 windows were motivated by a desire to understand change before, during and after a millennium  
343 drought (2011-2015) that was the single most impactful climate event (during our records) on the  
344 montane populations. Finally, redundancy analysis (RDA) combined many lines of information  
345 into one picture of population-specific change over time with respect to population-specific traits  
346 (Fig. 2).

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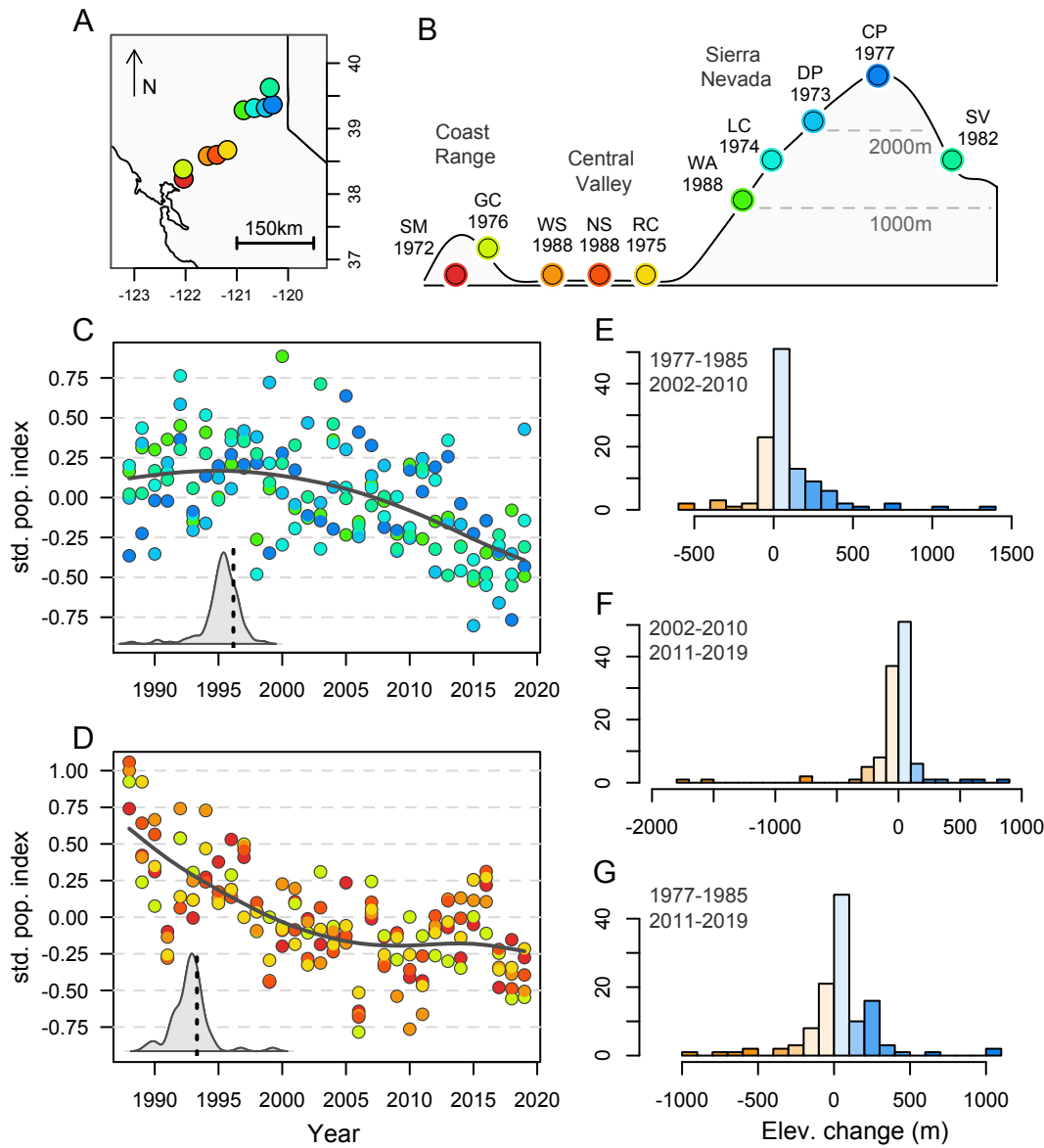
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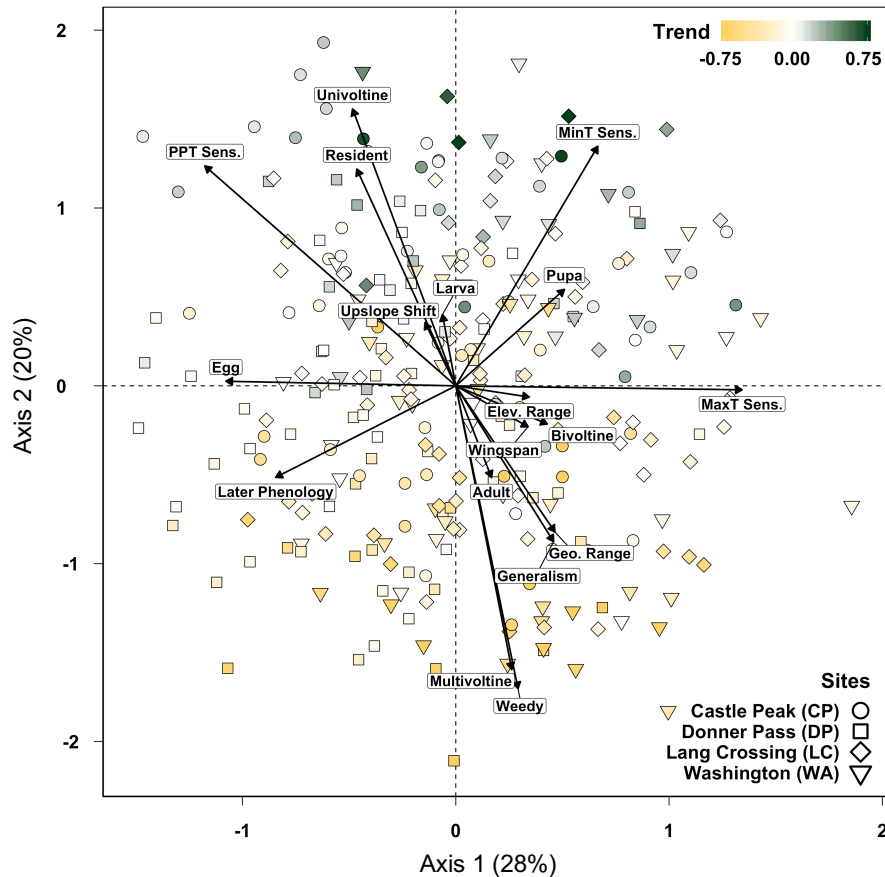
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**Table 1. Monitoring studies of at least 10 insect species and at least 10 years from land use gradients or protected areas that have been used to examine weather in relation to insect populations.**

Location	Source	Years	Species	Taxa	Method
Australia	Gibb et al. (58)	21	106	Ants	Pitfall traps
California, USA	Shapiro Transect (27, 41–43)	47	163	Butterflies	Modified Pollard walk
Colorado, USA	Iler et al. (59)	20	20	Hoverflies	Malaise traps
Costa Rica	Tritrophic Interaction Monitoring in the Americas (31)	22	1724	Lepidoptera, Parasitoids	Collect and rear
Ecuador	Grøtan et al. (53)	10	137	Butterflies	Fruit traps
Europe	Jourdan et al. (60)	32	--	Benthic invertebrates	Surface water survey
Finland	Finnish Moth Monitoring Scheme (61)	13	183	Moths	Light traps
Finland	Hunter et al. (23)	32	80	Moths	Light traps
Germany	Voight et al. (62)	20	1041	Arthropods	Pitfall trap, Sweep net
Germany	Krefeld Entomological Society (63)	27	--	Flying insects	Malaise traps
Germany	Baranov et al. (22)	42	125	Mayflies, stoneflies and caddisflies	Emergence trap
Great Britain	National Moth Recording Scheme (20)	40	673	Moths	Traps
Greenland	Koltz et al. (29)	18	--	Arthropods	Pitfall traps
Netherlands	Dutch Monitoring Scheme (33, 64)	18	40	Butterflies	Pollard walk
Netherlands	Hallmann et al. (65)	28	--	Beetles, Moths, Caddisflies	Pitfall traps
Russia	Chronicles of Nature (66)	40	19	Arthropods	Traps
Spain	Stewart et al. (67)	10	10	Butterflies	Pollard walk
United Kingdom	UK Butterfly Monitoring Scheme (32, 34, 54, 68–73)	45	55	Butterflies	Pollard walk
United Kingdom	Rothamsted Insect Survey (28, 32, 54, 74)	50	345	Aphids, Moths	Light trap
United Kingdom	Hoverfly Recording Scheme (75)	54	215	Hoverflies	Citizen observations



**Fig. 1.** Overview of geography and major trends for 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. (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). Inset density plots in (C and D) 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 nine-year windows of time; for example, panel (E) is the change in mean elevation per species between the earliest years (1977-1985) and years immediately before the mega-drought (2002-2010). Colors in histograms are for visualization with darker orange corresponding to more negative (downward) shifts and darker blue being more positive (upslope) shifts (see *SI Appendix*, Fig. S1 for additional details).



**Fig. 2.** Montane populations through time and population-specific properties that 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.). For example, populations in the upper portion of the ordination are characterized by positive responses to years that are wetter and have warmer minimum temperatures. 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. Each point in the ordination is a population (a species at a site), thus individual species are represented by between 1 and 4 points (depending on their presence at the four mountain sites). Life history traits include overwintering states, geographic range, phenology (average date of first flight), elevational range, elevational shift (as in Fig. 1 E-G), voltinism, body size (wingspan), breadth of habitat association (generalism), and weedy status (see main text and *SI Appendix* for more details). Percent of constrained variation explained is shown in parentheses after each axis label.