

ARTICLE

Climate Ecology

Long-term declines in insect abundance and biomass in a subalpine habitat

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Abstract

Recent reports of insect declines have caused concern among scientists and the public. Declines in insect abundance and biomass are ubiquitous across many climatic zones and have been largely attributed to anthropogenic land use intensification and climate change. However, there are few examples of long-term continuous data in relatively undisturbed environments, as opposed to agricultural landscapes. We sampled insects weekly from 1986 to 2020 in a protected subalpine meadow in Colorado, which is embedded in an undisturbed natural landscape. During the study period, summers became warmer, while winters became drier. Insect biomass declined by ~47% and abundance declined by ~61.5% over the last 35 years. Insect declines occurred in concert with changes in climate, as some climate factors were correlated with insect abundance and biomass. Specifically, insect abundance was lower during years with less summer precipitation and winter snowfall, and to a lesser degree with warmer temperatures. In subalpine systems, changes in precipitation and warmer temperatures are expected to continue under climate change; thus, continued insect declines might be expected even in relatively undisturbed habitats.

KEYWORDS

climate change, Diptera, Hymenoptera, insect abundance, insect biomass, insect decline, long-term study, Malaise trap, Rocky Mountain Biological Laboratory, subalpine

INTRODUCTION

Recent studies have suggested that insect biomass, abundance, and diversity have declined by 20%–75% over the last few decades in many taxonomic groups and ecosystems (Dennis et al., 2019; Hallmann et al., 2017; Seibold et al., 2019; Shortall et al., 2009; Stepanian et al., 2020;

van Klink et al., 2020a, 2020b; Wepprich et al., 2019). These reported declines are alarming, because insects are vital for numerous ecosystem processes, including pollination, nutrient cycling, and pest control, and as food for many insectivores. The continued loss of insect biodiversity and biomass may thus have ecological and economic consequences (Forister et al., 2019; Losey & Vaughan, 2006). Several factors have been suggested as causes for insect declines (Mupepele et al., 2019;

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Sánchez-Bayo & Wyckhuys, 2019), including habitat fragmentation (Wagner et al., 2021), agricultural intensification (Raven & Wagner, 2021), pesticide application (Frampton & Dorne, 2007), and changes in land use (Seibold et al., 2019), light pollution (Owens et al., 2020), nutrient dilution (Welti et al., 2020), and climate change (Soroye et al., 2020); our understanding of these potential causes is incomplete (Wagner et al., 2021).

Reports of declines in insect biomass and abundance have multiplied in the last few years, yet there are still few long-term continuous studies in relatively undisturbed habitats (Baranov et al., 2020; Hallmann et al., 2017; Shortall et al., 2009; van Klink et al., 2020a, 2020b; Wepprich et al., 2019). Studies based on incomplete time series (e.g., historical vs. contemporary comparisons) and short time series should be interpreted with caution, as insect populations can have large interannual fluctuations (Boggs & Inouye, 2012; Palmer et al., 2017) or show multiyear cycles (Welti et al., 2020). Testing for declines in natural areas is particularly important for informing expectations under future climate change, as undisturbed habitats have fewer nonclimate reasons (notwithstanding pesticide drift from nearby agricultural areas) for declines than more human-dominated landscapes.

Our study is one of few, systematic, long-term continuous studies of insect populations in a landscape with few human impacts. We determined the extent to which insect biomass and abundance declined from 1986 to 2020 and assessed potential environmental drivers of these declines, including winter snowpack, summer temperature and precipitation, floral abundance, and lagged effects of the previous year's conditions. Winter snowpack could have direct effects on overwintering insects, as low snowpack could reduce insulation from extreme cold, while winter snow and summer precipitation are important drivers of plant growth via their effects on soil moisture. Summer temperatures could have either positive or negative effects on insect abundance, depending on how mean temperatures compare to thermal optima for most species. If mean temperatures are currently below most species' thermal optima, warmer temperatures may increase insect abundance; conversely, if mean temperatures are near or above current thermal optima, warmer temperatures are likely to be associated with declines in abundance. Temperature might also have contrasting effects at different timescales, with short-term increases in insect catch rates if warmer temperatures lead to higher activity levels, but lower long-term abundances if warmer temperatures negatively affect reproduction. Our sampling site (an 11-ha meadow) is protected from all human uses other than ecological research and is embedded in a landscape of undeveloped US National Forest and land protected by conservation easements.

METHODS

We used a Malaise trap to sample insects in an 11-ha subalpine meadow (Research Meadow) at the Rocky Mountain Biological Laboratory (RMBL) in the West Elk Mountains in Colorado, USA (38°57'31" N, 106°59'15" W, elevation: 2895 m), from 1984 to 2020 (Appendix S1: Figure S1A). Vegetation in this meadow is a diverse mixture of forbs and grasses; aspens, willows, and conifers surround the meadow, and a few individual trees grow within it. Naturally occurring forest-meadow ecotones in this region can be spatially static over long periods (Schauer et al., 1998). Based on archived photographs, the extent of this meadow and vegetation in it have not changed appreciably in at least 70 years, and in our 53 years of personal observation (DWI), the meadow has not undergone notable succession or other changes. Additionally, the meadow has been fenced to exclude cattle for over 35 years. The growing season at the RMBL begins in May or June once the snow melts (mean date: May 19; range: April 23–June 19) and ends in September or October. During our sampling period, average snowfall was 1045 ± 269 cm (mean $\pm$ SD). The mean summer (defined here as May–August) temperature during the study period was $11.27 \pm 0.69^\circ\text{C}$ and total summer precipitation was 16.62 ± 5.44 cm (mean $\pm$ SD).

Insect sampling

Malaise traps are commonly used for passively sampling aerial insects; this method thus captured only a subset of insects in this meadow. We set up a Malaise trap (BioQuip Model No. 2875A/AG) every year in the same location (38°57'24.8" N, 106°59'08.0" W), using a permanent metal stake to support the trap's central pole (Appendix S1: Figure S1B). We placed a collection jar that contained a small piece of Hotshot No-Pest Strips (2,2-dichlorovinyl dimethyl phosphate) on top of the Malaise trap for approximately two days (mean $\pm$ SD: 2.05 ± 0.41 , range: 1–7 days) each week over the course of the growing season (mean $\pm$ SD weekly samples per growing season: 11.0 ± 3.6 , range: 6–19) from 1984 to 2020 ($n = 406$ samples). All other days (approximately five per week), the Malaise trap was open at the top and no insects were captured. The model of the Malaise trap that we used has a relatively small opening (19 mm) for the collection jar; thus, we did not collect large aerial insects such as most butterflies. After sampling ended each week, we brought the insect collection jar into the laboratory and allowed the insects to dry at room temperature for approximately 72 h. We sorted the insects into coarse taxonomic groups (e.g., Diptera, Hymenoptera, and others), counted individuals, and weighed the dried insects

within each group using an Ohaus Dial-O-Gram 310 g balance (precision 0.01 g). Our data for Hymenoptera consist almost entirely of asocial species (mostly predatory or parasitoid wasps), as bumblebees can avoid the Malaise trap, there are no honeybees in the area, and vespids wasps are rare.

To confirm that our repeated lethal sampling was not inadvertently reducing local insect populations over time, we used an identical Malaise trap to sample an additional site approximately 7 km away (Washington Gulch: 38°56'11.3" N, 107°01'13.6" W, elevation: 2978 m) in a subset of years, from 1990–1996, 1998, and 2019 ($n = 65$ samples). If our lethal sampling were affecting insect biomass and abundance, we would have expected the insect population at this site to decline from 1990 to 1996 and then rebound between 1998 and 2019, but this was not seen. We did not detect any differences between insect biomass and abundance between RMBL and Washington Gulch (personal observation) and concluded that our sampling did not contribute to the declines we detected at the RMBL (similar to findings for native bees at the RMBL in Gezon et al., 2015).

We began sampling insects in 1984; however, the results presented in the main text begin in 1986, as 1984 and 1985 had unusually high Diptera biomass and abundances (Appendix S1: Figure S2A,D). We took a conservative approach to assess insect decline because we could not confirm that 1984 and 1985 were preceded by years of similarly high insect abundance, for example, a “false baseline effect” (Didham et al., 2020). Observations by DWI suggest that fly abundances were generally high in the decade preceding 1984 and that a fungal epidemic was responsible for mass mortality of muscoid flies in 1986, which have failed to return to high abundances, but systematic samples prior to 1984 are not available. Although the results in the main text exclude these two years, we repeated analyses described in the main text with the full dataset (1984–2020) and present the results in Appendix S1: Tables S1–S8. We were unable to locate data on insect abundance from 2007, and it is therefore not in our current analysis.

Weather records

We accessed publicly available climate data on winter and summer precipitation and temperature at and near the RMBL. We used two snow climate variables: total snowfall (in centimeters) and date of snowmelt in a reference $1 \times 1 \text{ m}^2$ plot at the RMBL, which are collected by Billy Barr, a community scientist and permanent resident of the RMBL (<http://www.gothicwx.org/long-term-snow.html>). We retrieved daily temperature (in degrees Celsius) and precipitation (in centimeters)

data from the Crested Butte weather station (38°52'25.7" N, 106°58'37.9" W), which is 9.5 km south of the RMBL (<https://www.ncdc.noaa.gov/cdo-web/datasets/GHCND/stations/GHCND:USC00051959/detail>). We calculated average weekly and seasonal summer temperatures (May–August) (in degrees Celsius) and weekly and cumulative summer precipitation from these daily temperature and precipitation records.

Flower data

Because some of the insects at the RMBL require flowers and/or seed heads to complete their life cycle, we included the total number of nongraminoid open flowers between May 8 (median first day of collection) and the end of August as a proxy for potential resources. We recorded the number of open flowers (capitula or umbels for Asteraceae and Apiaceae, respectively) in twenty-three $2 \times 2 \text{ m}^2$ plots around the RMBL ($n = 140$ species) approximately every other day over the full span of the growing season. For more information on these methods, see CaraDonna et al. (2014) or metadata archived at <https://osf.io/jt4n5/>.

Anthropogenic impact data

Although the meadow where the Malaise trap is located was not altered and does not seem to have undergone any successional changes, tourist visitation to the region has increased in recent decades. We present three datasets on possible anthropogenic change in this region (Appendix S1: Figure S3); however, we were unable to resolve unambiguously how land use or human impacts influence insect biomass and abundance in our study as we only have a single sampling site and limited data on human impacts spanning our full time series. We thus used a continuous “year” term in all of our models, recognizing that some aspects of anthropogenic activity have increased over time (Appendix S1: Figure S3), along with potential changes in mean climate. The Crested Butte, CO Chamber of Commerce, provided data on the total number of summer visitors to the Mt. Crested Butte Visitors Center from 2010 to 2020. We retrieved public data from Gunnison County, CO Public Works, on the total acreage platted for subdivisions from 5 to 10 km south of RMBL from 1984 to 2020; all other land closer to and around the RMBL is undeveloped US National Forest or undeveloped private grazing land used seasonally by cattle and under conservation easement. Finally, we accessed publicly available annual nitrogen deposition (in kilograms of N per hectare) from the National Atmospheric Deposition

Program's (NADP) National Trends Network (NTN) site at the RMBL (CO10) (<https://nadp.slh.wisc.edu/sites/ntn-co10/>).

Data accessibility

All metadata, data files, and R scripts are available at: <https://doi.org/10.17605/OSF.IO/S9F76>.

Analyses

We analyzed changes in insect biomass and abundance in the RMBL Malaise trap samples in three ways. First, we used weekly insect data and environmental data for the week of sampling, for a total of 390 biomass and 376 abundance measures (supplemental analyses including 1984 and 1985: 406 biomass and 392 abundance samples). Second, we repeated this analysis for shorter subsets of the data to explore the importance of the length of time series. Third, we analyzed data summarized on a yearly basis, using 35 years (supplemental analyses have 37 years), to test lagged effects of the previous summer's environmental variables. We chose a lag of one year as many of the insects in our samples are univoltine, with individuals that are larvae in one summer being adults the following year (personal observation). In addition to total insect biomass and abundance, we analyzed data separately for three partitions: Diptera, Hymenoptera, and all other insects. We completed all analyses in R version 3.6.2 (R Core Team, 2019).

For analyses of weekly insect biomass and abundance, we standardized the number of days the trap was open. We next assessed how our weekly samples of biomass (in grams per day) and abundance (number of insects per day) changed over time using linear mixed models. Our models used three environmental variables as covariates, calculated from data for seven days preceding the last day of each sample (mean daily temperature [in degrees Celsius], cumulative precipitation [in centimeters], and mean daily floral abundance [number of flowers]), and included the number of days after the year's snowmelt and days after snowmelt², calculated from the final day of each sampling period. We included interaction terms between year and all fixed effects and a random effect of year (as a factor) to help account for repeated sampling and other differences among years. To reduce collinearity and aid interpretation, we standardized all predictor variables by subtracting their mean and dividing by their sample SD. We square-root-transformed the response variables to satisfy model assumptions. We generated all mixed model *p* values with the lmerTest

package (Kuznetsova et al., 2017), with the Satterthwaite approximation for degrees of freedom. We then repeated this using smaller subsets of our time series, including the most recent 10, 15, 20, and 35 years, and the full 37 years of data.

For the analyses of yearly insect biomass and abundance, we needed to account for the timing of sample collection, which varied among years relative to seasonal phenology. We used days past snowmelt to standardize seasonal phenology across years instead of a calendar date. At this strongly seasonal site, the timing of snowmelt is the most important driver for the phenology of most species (e.g., CaraDonna et al., 2014; Prather et al., 2023; Stemkovski et al., 2020). Therefore, we used all years of weekly data to model square-root-transformed insect biomass or abundance as the response variables, and days after snowmelt, days after snowmelt², weekly mean temperature, and weekly cumulative precipitation as explanatory fixed effects. This provided an average expected value of insect biomass or abundance for each day past snowmelt, with mid-season peaks in abundance and biomass. We then calculated the mean residual from this regression for each year to estimate whether insect biomass and abundance were higher or lower than the long-term average for the whole dataset; this mean residual thus accounts for different sampling dates within each year. We used these annual mean residuals as the response variable in linear regressions against year, with standardized measures of summer (May–August), mean temperature, cumulative precipitation, floral abundance, and total snowfall of the preceding winter. We also included one-year lags (indicated by the subscript $t - 1$) for the environmental variables and interactions between year and precipitation and snow (including lagged variables). We removed year $\times$ precipitation and year $\times$ floral abundance interactions from our models due to variance inflation factors that were above a conservative threshold of 3 (James et al., 2013). We weighted the annual mean residuals in our models by the square root of the number of weekly samples in a year, which gives years with more weeks of sampling effort greater influence. We then selected best fit models using bidirectional stepwise selection based on Akaike information criterion (AIC) values, as we consider these to be hypothesis-generating analyses to explore which environmental factors are most strongly related to changes in annual insect biomass and abundance. We also ran models with and without data from 2015 (Appendix S1: Tables S11 and S12), because floral abundance was extremely high in that year, which had exceptionally high summer precipitation (2015: 261,2672 flowers, range all years except 2015: 21,509–119,590). Global, stepwise selected, and candidate model AIC scores are reported in Appendix S1: Table S13 for the reduced (1986–2020) and full dataset (1984–2020).

RESULTS

We found changes in some environmental variables at and near the RMBL from 1986 to 2020. Mean summer temperature increased by $0.031 \pm 0.010^\circ\text{C}$ per year and total snowfall declined by 9.15 ± 4.06 cm/year (mean $\pm$ SE; Appendix S1: Figure S4). Cumulative winter snowfall, summer precipitation, and total floral resources were highly variable and did not show significant directional change over this time (Appendix S1: Figure S4 shows values for 1983–2020, as we used 1983 data for analyses with lagged variables).

After accounting for precipitation, temperature, and floral abundance during the week of sampling, we found a $\sim 47\%$ decline in mean insect biomass and $\sim 61.5\%$ decline in mean weekly abundance since 1986 (Figure 1; Appendix S1: Table S1). We excluded 1984 and 1985 from

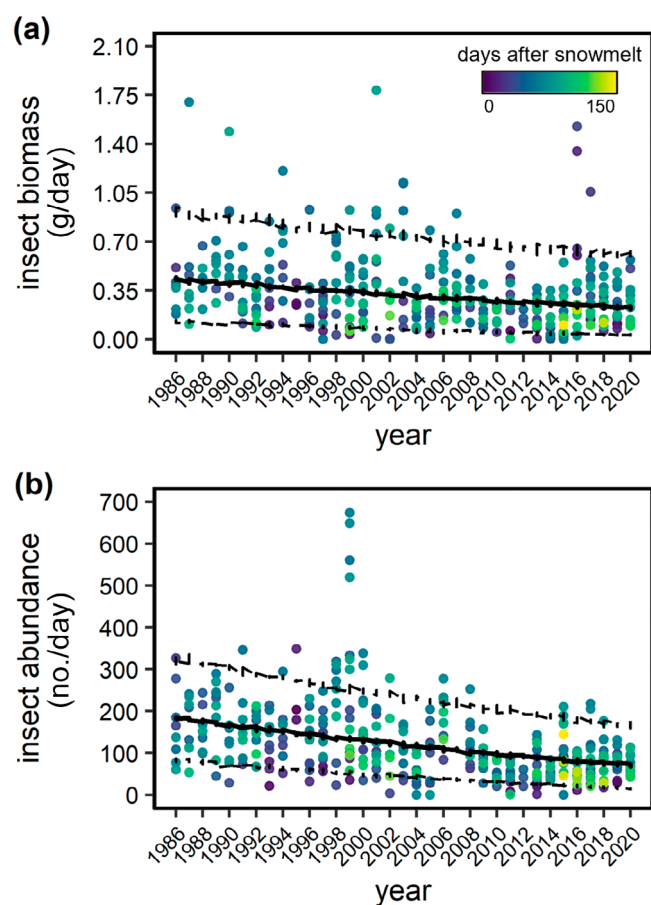


FIGURE 1 Insect biomass and abundance over time. (a) Total insect biomass and (b) abundance collected at the Rocky Mountain Biological Laboratory in Colorado, USA, between 1986 and 2020. Each point represents a weekly sample and is colored according to the number of days after snowmelt that the sample was collected. Prediction lines from the generalized linear mixed models (GLMMs) are solid and 90% CIs are dashed. The GLMM prediction line appears discontinuous due to including year as a random effect as well as a continuous variable.

this analysis because they were outliers with high counts of Diptera; including those years makes estimated declines even more dramatic (Appendix S1: Table S2, Figure S5). When we partitioned total insect biomass and abundance into coarse taxonomic classifications, we found trends for decreasing Diptera biomass and abundance and Hymenoptera abundance, but not for the combined other taxa (Appendix S1: Figure S2, Tables S3–S8). We generally found that the climate covariates correlated with daily insect biomass and abundance were of similar importance for predicting Diptera and Hymenoptera and other insect abundance and biomass (e.g., temperature and days after snowmelt) (Appendix S1: Tables S3–S8). On average, more insects were collected in weeks with warmer temperatures; however, the effect of warmer weeks was reduced in later years, which themselves tended to be warmer on average (negative year $\times$ temperature interactions; Appendix S1: Table S1).

While the decline in insect biomass and abundance is readily apparent in the full dataset, shorter time series would not have revealed this decline. Within our data, short runs of years with increasing insect biomass and abundance are common; using only the 10 most recent years of data would indicate a significant increase in insect abundance ($p = 0.02$), and no significant change in biomass ($p = 0.29$; Appendix S1: Figure S5). On average, both responses have increased slightly since 2011. Using the 20 most recent years of data, we would have been able to report significant effects of temperature (higher biomass and abundance caught in weeks with higher temperatures) and a year $\times$ temperature interaction for biomass, but the declines in insect biomass and abundance since 2000 are not statistically significant ($p = 0.10$ and 0.23 , respectively).

The analyses of yearly insect biomass estimates for 1986–2020 showed declines over time (annual mean residuals decreased over time, $p = 0.056$; Appendix S1: Figure S6). We know of no reason to exclude one outlier that affects the statistical significance of abundance, which also declined. However, these substantial reductions in insect biomass and abundance at the RMBL over the last 35 years could largely be explained by changes in climate (Figure 2; Appendix S1: Tables S9 and S10 for results from full dataset). Several variables, including lagged variables, were retained in the final models. Insect abundance was positively correlated with cumulative summer precipitation ($p < 0.001$) and weakly correlated with total snowfall in the previous winter ($p = 0.06$) (Figure 3), which provides early-season soil moisture. Total insect biomass tended to be higher in years with more precipitation in the previous summer ($p = 0.069$). Both insect abundance and biomass tended to be slightly lower in years with high floral abundance (abundance: $p = 0.078$; biomass: $p = 0.081$);

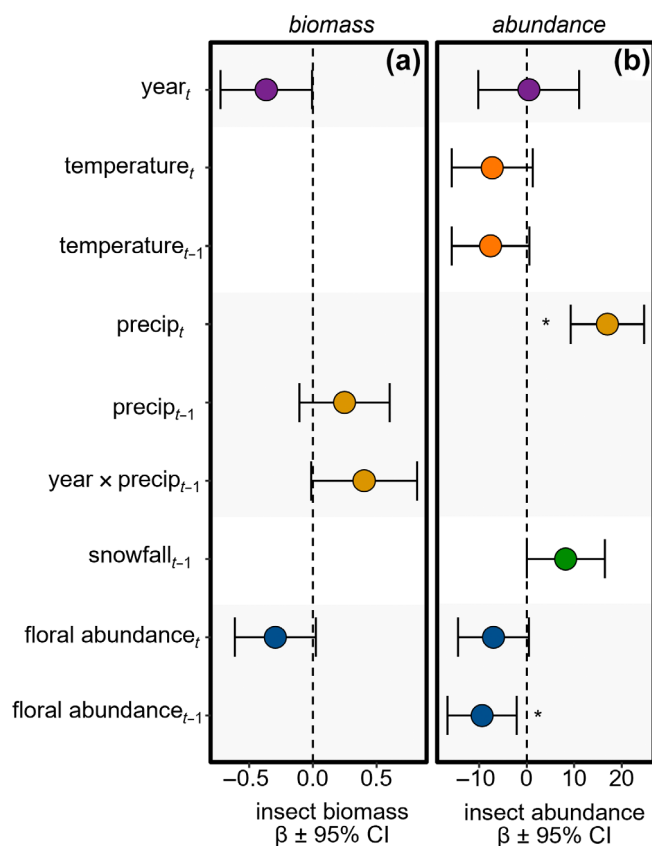


FIGURE 2 Weather and floral abundance affect insect biomass and abundance. Estimated regression coefficients (β) and 95% CIs from best fit multiple linear regressions of environmental correlates (year, summer temperature, cumulative summer precipitation, cumulative summer snowfall, and annual floral abundance) on summed residual annual insect biomass and abundance. Significant factors ($p \leq 0.05$) are annotated with an asterisk. Subscripts indicate either the year of sampling (t) or the year prior to sampling ($t - 1$) as a test for lagged effects of climate on larvae that may manifest in the subsequent year's sampling of flying adults.

however, this result was strongly influenced by the one year (2015) that was an outlier with extremely high flower counts (Appendix S1: Tables S11 and S12). Otherwise, floral abundance was not retained as an important factor affecting insect abundance or biomass.

DISCUSSION

We found clear evidence of declines in insect abundance and biomass at a site with few potential anthropogenic impacts beyond climate change. Importantly, these declines would not have been apparent in shorter time series (Didham et al., 2020), even series as long as 20 years, yet very few long-term records of insect abundance or biomass are available for any habitats. We found that declines were associated with changes in climate

variables, even climate up to a year prior to data collection. Our data thus support the idea that insect declines occur in pristine subalpine habitats and are likely related at least in part to changes in climate.

Precipitation, which affected insect biomass and abundance (Figures 2 and 3), could act through both direct and indirect mechanisms. Winter precipitation is extremely important in subalpine systems. The snowpack acts as an insulation layer for many overwintering insects; a reduction in snowfall might lead to soil freeze-thaw cycles, negatively altering overwintering energetics through exposure to severe temperatures (Williams et al., 2015) (minimum air temperatures at the RMBL during the study period were $-10.44 \pm 0.40^\circ\text{C}$ (mean $\pm$ SD) between October and May, minimum: -40°C). Furthermore, winter precipitation provides critical soil moisture for the plant community in the spring and mediates the effects of frost on both leaves and flowers, as early snowmelt can expose developing flower buds to frost effects (Inouye, 2008; Inouye et al., 2002; Pardee et al., 2019). We have observed frost to kill the first flush of aspen leaves, likely affecting a variety of herbivorous insects (D. W. Inouye, personal observation). If snow accumulation is low, plant abundance and floral resources are likely to be reduced in the early spring (Inouye, 2008), potentially affecting higher trophic levels. In addition to dry winters, drier summer conditions in this system also lead to significant changes in the plant biomass and floral resources (Ogilvie et al., 2017). Though precipitation seems to be an important driver of changes in insect abundance and biomass in this system, warmer temperatures had only a weak negative association with insect abundance ($p = 0.107$). As insect development and metabolism can be very sensitive to the thermal environment, temperature could have adverse impacts on insect abundance through phenological mismatches with host plants, range shifts, or changes in population dynamics (Lehmann et al., 2020; Robinet & Roques, 2010). However, at our high-elevation sample location, temperatures may not have surpassed the thermal optima of insects, making precipitation more influential than temperature in driving insect abundance under current climate conditions.

Although we are unable to parse apart all possible drivers of climate and nonclimate effects on insect populations because we had only a single site, we did examine additional anthropogenic factors surrounding the RMBL. The landscape immediately surrounding the RMBL is relatively pristine; we think it is unlikely that most anthropogenic changes that have occurred contribute to the insect declines we observed (Appendix S1: Figure S3). The meadow (~11 ha) surrounding the Malaise trap is owned by the RMBL, is used only for ecological research, and has not undergone any noticeable successional changes for several decades. The surrounding

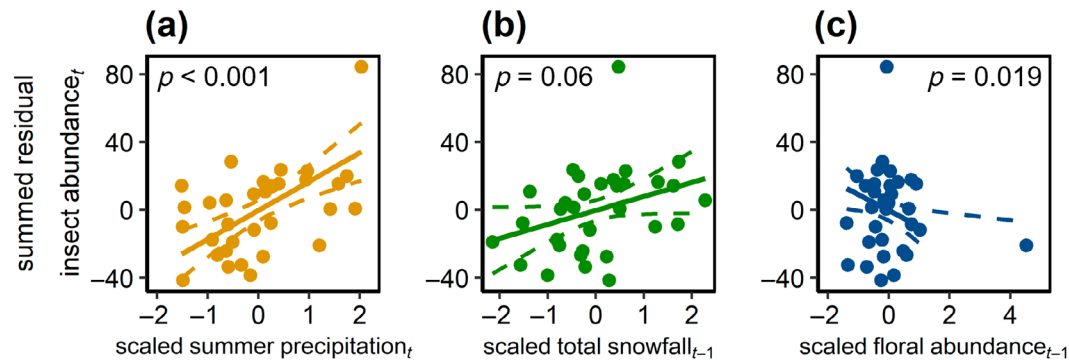


FIGURE 3 Precipitation and floral abundance affect insect abundance. The relationship between summed residual total insect abundance in year_t and scaled (a) summer precipitation in year_t, (b) total snowfall in year_{t-1}, and (c) floral abundance in year_{t-1} from the selected multiple regression. Prediction lines are solid and 95% CIs are dashed.

landscape within 5 km is a patchwork of meadows and forest (aspen and spruce-fir) owned by the US National Forest Service and private grazing land under conservation easement and thus undeveloped. The surrounding Forest Service land is lightly grazed by cattle in the late summer and fall, but the meadow we sampled is fenced to exclude cattle, and grazing pressure in this region has not changed appreciably over the course of our study. Forest Service land is also used for recreation (e.g., hiking, biking, and hunting). While no long-term data are available for those specific uses, there has been an increase in tourism to the Crested Butte area since at least 2010 (as far back as data are available; Appendix S1: Figure S3A), which likely correlates with more recreation in the sampled valley. However, the closest heavily traveled trail is 1.2 km away, and the dirt road that serves the valley is ~260 m away, making large impacts on the sampled meadow unlikely. Light pollution has been implicated in insect declines in other studies (Owens et al., 2020), but the closest lit structures to our trap are seasonally occupied researcher cabins ~200 m away and out of view from the Malaise trap. The number of buildings and associated light sources have remained relatively constant; therefore, any change in light pollution is likely quite limited. Development of the nearest towns (Mt. Crested Butte and Crested Butte, 5–10 km distant from the Malaise trap) increased but then leveled off around 2006 (Appendix S1: Figure S3B). Light from regional development is unlikely to influence insects in our meadow because of its isolation; local topography blocks sightlines from the meadow toward Mt. Crested Butte and Crested Butte. Nitrogen deposition (Kurze et al., 2018) and increases in atmospheric CO₂ (Welti et al., 2020) have also been suggested as influencing insect declines. Due to its location on the western slope of the Rocky Mountains, anthropogenic nitrogen deposition near the RMBL is minimal (Elser et al., 2009) (Appendix S1: Figure S3C).

Atmospheric CO₂ concentrations have increased globally and may affect insects via altered plant productivity and nutrient dilution (Welti et al., 2020); because we lack local data on CO₂, we could not examine this factor explicitly.

We found significant declines in insect biomass and abundance in a relatively undisturbed subalpine meadow habitat over the last 35 years, particularly under drier winter and summer conditions. The decline in insect biomass that we observed is less than the maximum magnitude of decline in some reports; Hallmann et al. (2017) found 75% decline in insect biomass over 27 years, and Seibold et al. (2019) found that insect biomass decreased by 67% in grasslands and 41% in forested areas over just nine years. However, the declines we observed are within the range of other estimates in a recent meta-analysis (van Klink et al., 2020a, 2020b). The fact that we observed any decline is troublesome because our data come from a site that is relatively pristine, as opposed to integrating data from sites in both natural and human-dominated landscapes (Hallmann et al., 2017; Seibold et al., 2019). Recent literature has suggested that large declines in insect populations are mainly in landscapes dominated by agriculture (Uhler et al., 2021; but see Halsch et al., 2021), where pesticide use may have been increasing. Our results suggest that declines in insects could largely be driven by regional environmental dynamics, which may be exacerbated under future climate change. Global factors, such as increased levels of wind-borne anthropogenic chemicals (pesticides, fertilizers, endocrine disruptors, “forever chemicals,” etc.), could also be affecting insect physiology and demography. Understanding the sensitivity of insect diversity, rather than biomass and abundance alone, to changes in climate will be vital for making predictions and conservation planning under future climate change.

AUTHOR CONTRIBUTIONS

Michael E. Soulé and David W. Inouye began the study and conceptualized the project. Rebecca M. Dalton, Brian D. Inouye, and Nora C. Underwood analyzed the data and created visualizations. Rebecca M. Dalton wrote the first draft of the manuscript. Rebecca M. Dalton, Michael E. Soulé, Brian D. Inouye, Nora C. Underwood, and David W. Inouye collected data and edited drafts.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data and R scripts (Dalton et al., 2023) are available from the Open Science Framework: <https://doi.org/10.17605/OSF.IO/S9F76>.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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