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SHORT COMMUNICATION

Insect diversity over 36 years at a protected Sierra Nevada (California) site: towards an evaluation of the insect apocalypse hypothesis

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Abstract. 1. Recent authors have suggested that declines of insect abundance or diversity, documented first for particular insect taxa of high interest (e.g., butterflies, bees), may apply to insect diversity more generally. This has led to an urgent call for analysis of additional longitudinal datasets to examine trends in general insect diversity.

2. Here we present a dataset gathered from 1982 to 2018 by advanced undergraduate students and graduate students enrolled in a taxonomy course that involved collecting as many insect families as possible over a 5-week period at a high-elevation protected forested site in the Sierra Nevada, California, USA.

3. The data do not support any consistent gain or loss of family-level richness between 1982 and 2018 (no linear trend); a non-linear model suggested a possible small decrease in family-level richness collected between 1986 and 1990, followed by a gradual increase from 1990 to 2018. Neither weather variables nor collector experience or skill appeared to explain among-year variation in collected insect diversity.

4. We urge caution in attempting to draw conclusions from single-site, longitudinal datasets like this one; a definitive answer to the hypothesis of a broad, global decline of insect diversity will require the joint analysis of many datasets like the one we share here.

Key words. Diversity declines, insect declines, insect conservation.

Introduction

Insects play essential ecological roles in natural and managed settings and provide human societies with several important ecosystem services. Thus, reports of declining populations of some groups of well-studied insects, including in particular bees and other pollinators (Potts *et al.*, 2010) as well as butterflies and moths (Thomas *et al.*, 2004; Forister *et al.*, 2010), have been alarming. More recently, published studies have suggested for the first time that these declines may be more generalised, involving insect diversity more broadly, even in protected areas [Hallmann *et al.*, 2017; Lister & Garcia, 2018 (but see Willig *et al.*, 2019); Rada *et al.*, 2019; Didham *et al.*, 2020; van Klink *et al.*, 2020; Wagner, 2020]. Such declines might threaten terrestrial food webs, and in particular might result in decreasing populations of birds, amphibians, non-avian reptiles and mammals that depend on insect prey.

The possibility of a generalised decline in insect populations has attracted widespread attention in the popular media, which has dubbed the phenomenon an 'insect apocalypse' (Jarvis, 2018). As noted by Goulson (2019) and Wagner (2020), however, data needed to evaluate the hypothesis are currently sparse. Although initiating new studies incorporating long-term monitoring of insect populations would seem to be a priority, such studies will require many years to provide answers; in the short-term, we need to seek out datasets, including those that may have been gathered for other reasons but that can be repurposed, to shed light on long-term changes in insect diversity. Our goal in this report is to contribute a dataset on long-term trends in insect diversity at a protected site in California's Sierra Nevada. We test the hypothesis of a long-term drop in insect diversity, while recognizing that our dataset will need to be combined with many other datasets to produce a definitive answer to the question of where and under what conditions insect declines are occurring.

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Materials and methods

Our dataset was assembled by advanced undergraduate students ($n = 100$), graduate students ($n = 39$) and participants coming from outside our university ($n = 3$) enrolled in a 5-week intensive summer course in insect diversity (ENT109 Field Taxonomy and Ecology). The class was taught during approximately the last 2 weeks of June and the first 3 weeks of July (see File S1 for details) at the University of California Natural Reserve System's Sagehen Creek Field Station every other year from 1982 to 2018 by PSW; only in 1988 was the class not offered. An introductory entomology course and experience collecting insects was a prerequisite for participation. Each student was tasked with assembling an insect collection with as much family-level richness as possible.

The Sagehen Creek Field Station is a 3642 ha parcel in the high-elevation (1800–2650 m; main facilities at 1943 m) central Sierra Nevada (39.43, −120.24). The station has extensive forest stands (*Pinus contorta* Douglas, *Pinus jeffreyi* Balf., *Abies concolor* (Gordon) Lindley ex Hildebrand, *Abies magnifica* A. Murray, and others), brush fields (*Ceanothus velutinus* Dougl. ex Hook, *Arctostaphylos patula* Greene, *Artemisia tridentata* Nutt., and others), mountain meadows and fens. Average annual precipitation at 1943 m is 88 cm of rain and 515 cm of snow. Students also collected at four additional locations during day field trips to the following sites in northern California: (i) Lang Crossing and vicinity, 1425 m (39.32–120.66), mixed coniferous forest and chaparral; (ii) 8 km NW Quincy, 1030 m (40.00–120.98), mixed coniferous forest and meadow; (iii) Hallelujah Junction, 1440 m (39.78–120.07), sagebrush; and (iv) Carson Pass, 2680 m (38.68–119.99), alpine meadow. In addition, there were field trips to Great Basin desert in adjacent Nevada, to (i) Sand Springs Dune, 1200 m (39.29–118.42), and (ii) either Pyramid Lake, 1140 m (39.83–119.45; 1982–1998) or Fort Churchill State Historic Park, 1280 m (39.29–119.27; 2000–2018). Students invested approximately (8 hours/day) × (6 days/week) × (5 weeks) = (240 hours/student) × (142 students) = 34 080 total hours of effort collecting, curating and identifying adult insects to family level, using dichotomous keys in three successive editions of an entomology textbook widely used in North America (Borror *et al.*, 1981, fifth edition for 1982–1986; Triplehorn *et al.*, 1989, sixth edition for 1990–2004; and Johnson & Triplehorn, 2004, seventh edition for 2006–2018). Because the allocation of collection effort to different locations was stable across years, and because each class represented a fresh set of collectors, we think a null hypothesis of no trend in family-level richness is a reasonable expectation for this data set.

Students used a variety of methods to collect insects, including hand-collecting, use of aerial nets and sweep netting. A single Malaise trap and two blacklights (an ultraviolet light suspended in front of a white sheet) were also run during the duration of the class; the Malaise trap was emptied every day and the catch made available to all students, who could sort the material to locate novel families for their collections. Students were free to visit the blacklight to hand-collect specimens. Leaf litter samples were also collected each year and processed in Berlese funnels (1982) or Winkler extractors (1984 onwards) to generate additional specimens.

At the end of the class, the instructor (PSW) and a graduate student teaching assistant checked all submitted collections and excluded any misidentified specimens. The number of misidentified specimens in each collection was recorded in years 1986–2018 (data not recorded for 1982 and 1984), and we use these data to evaluate possible longitudinal trends in collector quality. Our primary response variable was insect diversity, defined as the number of different, correctly identified insect families collected (family-level richness).

The transitions between successive editions of the textbook (5th–6th between 1986 and 1990; 6th–7th between 2004 and 2006) created a possible bias in the data, as changes in taxonomy resulted in gains and losses of family-level taxa. For the 201 families that were most frequently found in student collections, we estimate that the 5th–6th edition transition was associated with approximately 6 family gains and 5 family losses, for a net change of just +1 families (see File S2). For the 6th–7th edition transition, gains (3 families) and losses (11 families) were less well balanced, with a net change of −8. Thus, prior to performing statistical analyses we corrected total family diversity counts for students using the 5th and 6th textbook editions by subtracting 7 and 8, respectively, so that they would be comparable to diversity estimates obtained with the 7th edition. These corrections are approximate, as we do not know which families were present in each collection, and it was therefore impossible to implement a precise correction for taxonomic changes.

Central California has a Mediterranean climate, and rainfall during the 5-week summer collecting period was generally minimal; total precipitation of the winter months, combined with winter and spring temperatures, determine when the snowpack melts off, influencing plant and animal phenology and general soil water availability during the summer collecting period. Although Sagehen Creek Field Station currently houses a weather station, the history of data collection is too shallow to be useful for this analysis. Sagehen Creek is located near the centroid of the region formed by combining Nevada County and Sierra County; therefore, to evaluate the possibility that interannual variation in climate might be correlated with insect diversity, we used average temperature and rainfall for these two counties during the 12 months preceding the class (July–June), as reported by the United States National Oceanic and Atmospheric Association (https://www.ncdc.noaa.gov/cag/; see File S3). Students collected over a wide area and elevational range within the Sagehen Creek basin, as well as at the various day trip sites; by averaging over Nevada and Sierra Counties, we hoped to include some of that variation.

Linear mixed-effect models were fit to examine linear effects on insect diversity (response variable, *families*) of the following predictors: year (*year*); student status as an undergraduate, graduate or student from outside the University of California Davis (*student status*); mean temperature and precipitation during the preceding year (*temperature*, *precipitation*) and a random effect for each class (*classID*), to account for possible non-independence of different students' collections due to shared collecting efforts (e.g., shared Malaise and blacklight samples). A linear mixed-effect model was also used to examine influences on the total number of misidentified specimens of *year*, with a random effect for *classID*, using the *lme4* package in R (Bates *et al.*, 2015). To accommodate the possibility of non-linear relationships between insect diversity and predictors, data were also analysed with a generalised additive model (GAM) using the *mgcv* package (Wood, 2019) in R, with the same set of predictors examined (*year*, *student status*, *temperature*, *precipitation*) and a random effect for each class (*classID*).

Results and discussion

Students collected and correctly identified an average of 179.2 ± 29.7 (SD) different insect families during their 5-weeks of sampling effort, with graduate students collecting, on average, ca. 24 more families than did undergraduates (File S4). A linear model failed to identify any linear trends in family-level insect diversity collected over the full 36-year period of sampling [coefficient: -0.406 ± 0.366 (SE), $P = 0.22$, n.s.; Fig. 1]. The non-linear GAM model revealed a significant effect of year on the number of families collected (Fig. 2, $P = 0.0135$); family-level diversity was greater by approximately 20 families during the three earliest classes (1982–1986) than in the immediately following years, followed by a gradual, partial recovery from 1990 to 2018. Insect diversity collected was not associated with the previous year's mean temperature or precipitation in either the linear or non-linear model ($P > 0.4$; File S4).

In a longitudinal study like this one, it is important to consider the consistency over time of data collection methods. Although the collection sites and methods were similar over time, a different student was responsible for each of the 142 diversity estimates analysed here. We analysed the total number of specimens that were misidentified to ask if there were any long-term trends (1986–2018) in the level of student expertise; the total number of misidentified specimens [mean = 15.1 ± 10.6 (SD)] did appear to function as expected for an index of collector expertise, since it was inversely associated with the number of families collected [coefficient = -0.585 ± 0.219 (SE), $P = 0.008$]. However, the number of misidentified specimens did not change significantly from 1986–2018 [coefficient = -0.121 ± 0.11 (SE), $P = 0.25$]. Thus, insofar as the number of submitted but misidentified specimens is an accurate measure of student capability, we see no evidence that changes in student ability over time might explain long-term trends in the number of insect families collected.

It is important to recognise the limitations of attempting to track insect diversity through a family-level measure of richness. This is neither a measure of insect abundance, nor a measure of species-level richness, which are the two metrics most commonly used to evaluate insect decline hypotheses. As with any measure of richness, including species-level richness, our metric will be relatively insensitive to changes in abundance of the most common taxa. For instance, at our study site, some insect families are species-rich and contain many quite abundant species (e.g., flies in the family Asilidae, wasps in the family Tenthredinidae, and moths in the family Geometridae). Such families are likely to be collected in a 5-week intensive effort, even if overall abundance of the group dropped substantially; furthermore, many species could disappear entirely without having a meaningful influence on the likelihood of collecting some representative of the family. A family-level measure of richness will, instead, be responsive to changing abundance of the relatively rare taxa, which often represent a large proportion of all families (e.g., Carpio *et al.*, 2019). Family-level richness may also be important in its own right, as families may reflect functional diversity. Furthermore, insect families are

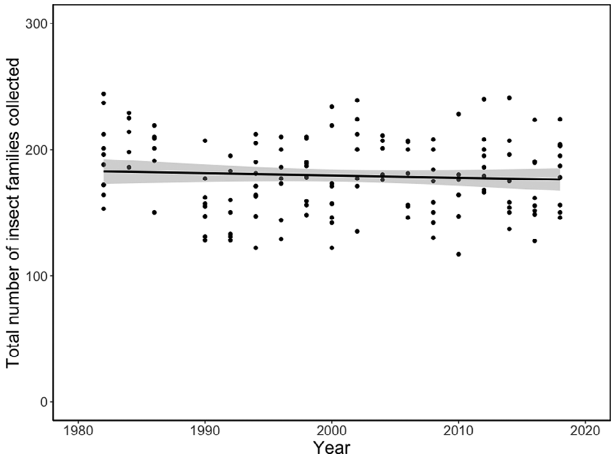

Fig. 1. Simple bivariate linear regression of the influence of *year* on total insect family-level richness collected (number of families collected by each student) during a 5-week period of intense collecting at the Sagehen Creek Field Station in the Sierra Nevada, California from 1982 to 2018.

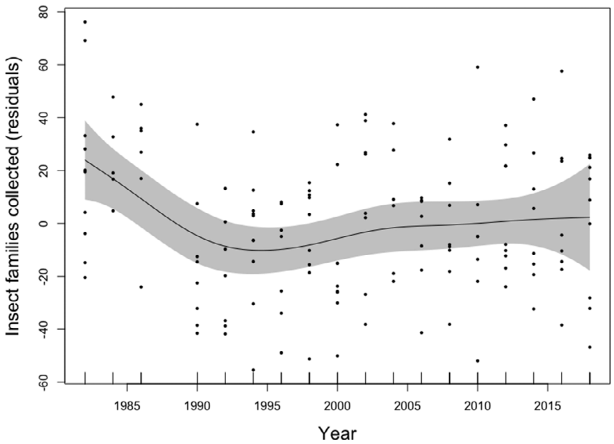

Fig. 2. Insect family-level richness (number of families collected by each student) during a 5-week period of intense collecting at the Sagehen Creek Field Station in the Sierra Nevada, California from 1982 to 2018. The solid line is the smooth from the GAM model, and shows the partial residuals after correcting for (i) differences between undergraduate students, graduate students, and non-UC Davis students, as well as (ii) the (nonsignificant) effects of temperature and precipitation during the preceding 12-month period; the shaded region is the 95% confidence interval.

typically clades that have been evolving for at least 100 million years (Grimaldi & Engel, 2005; Misof *et al.*, 2014), and thus family-level richness captures this higher-level lineage diversity, which has its own merits as a measure of biological diversity. Finally, as noted by Timms *et al.* (2013) in their review of arthropod biodiversity studies in temperate or boreal forests, if we wish to obtain a broad taxonomic view of biodiversity, including groups for which taxonomic knowledge may be limited, then use of higher-level taxonomy (at the level of genus or family) may be a useful compromise, and one that preserves the signal of anthropogenic impacts.

What the underlying cause(s) might be of the among-year variation in insect diversity collected in our study (Fig. 2) is unclear. There have been no obvious changes in land use, no major habitat destruction, and only very limited logging activity in the Sagehen Creek watershed or in the immediately surrounding areas; none of the logging was in the area near the field station, where most of the insect collecting occurred (https://sagehen.ucnrs.org/home/about-us/land-use-history-in-the-sagehen-basin/). Climate has varied between 1982 and 2018, but the most obvious anomaly was a cluster of warm and dry years that occurred between 2012 and 2015 (Forister *et al.*, 2018; see File S3), which does not coincide with the periods of greatest changes in family richness in our data (1986–1990). Pesticide use in Nevada and Sierra Counties is minimal (https://www.cdpr.ca.gov/docs/pur/pur17rep/tables/table3.htm). Although atmospheric transport and deposition of pesticides from California's Central Valley, where pesticide use is heavy, remains a possibility (e.g., Smalling *et al.*, 2013), the eastern edge of the Central Valley lies ca. 110 km to the west of Sagehen Creek. We conclude that only by combining our dataset with many other datasets, collected at diverse locations, and placed in the public domain regardless of whether they reveal positive, negative or no significant trends in insect abundance or diversity over time, so that an unbiased set of studies can be assembled (Didham *et al.*, 2020; van Klink *et al.*, 2020; Wagner, 2020), will we be able to evaluate rigorously the hypothesis of a general decline of insect diversity.

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Data availability statement

The data that support the findings of this study are openly available in DRYAD at https://doi.org/10.25338/B8FG9R.

Supporting Information

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

File S1. Data on family-level diversity collected at Sagehen Creek, California, and vicinity, 1982–2018, with associated temperature, precipitation and a measure of misidentified specimens.

File S2. Families gained and lost over three successive editions of the textbook used by student collectors.

File S3. Temperature and precipitation data for Nevada and Sierra Counties, California, 1981–2018.

File S4. GAM model of factors associated with family-level diversity collected.

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