To understand the plight of insects, entomologists look to the past

Plumbing a variety of historical data could offer important insights into trends in insect declines.

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When avian ecologist Nicholas Rodenhouse moved offices a few years ago, he found a potential treasure trove of data buried in some old file cabinets. Piles of forgotten spreadsheets catalogued taxonomic records of beetles collected in the hardwood forests of Hubbard Brook, NH, between 1973 and 1977. The research was originally meant to speak to the diets of local birds. Convinced that the spreadsheets could serve anther purpose, Rodenhouse, now emeritus at Wellesley College in MA, decided to ask his undergraduate mentee, Jennifer Harris, to resample the old research sites. Her work, conducted between 2015 and 2017, would tease a new story from the old data, one that could inform ongoing mysteries about how and why some insects seem to be disappearing (1).

Harris collected beetles the same way the seventies-era researchers had done, using window traps: clear pieces of glass above a small trough of water. Beetles flying low to the forest floor hit the glass and fell into the water, drowned, and were later retrieved. Between 2015 and 2017, the researchers checked window traps at three different elevations twice a week from mid-May through early August and identified beetles to the family level. The mean number of individuals captured between trap checks declined by 83% between the 1970s and 2010s, and

Some insect populations are declining—even ostensibly versatile species such as Central California's large marble butterfly, *Euchloe ausonides*. Researchers are tracking trends through long-term insect count data and using historical data. Image credit: Joyce Gross (University of California, Berkeley).

Specimens such as this bumble bee were part of a huge data set, used in a February study to track population change for 66 species. Natural history and private insect collections offer troves of historical data. Image Credit: Peter Soroye (photographer).

the number of beetle families fell by 39%. Nineteen families had disappeared entirely. Although insect populations normally expand and contract over time, disappearances across whole families are much more unusual. That so many groups disappeared at once suggested the study had found a genuine signal of decline, Harris says.

Few entomologists would disagree that at least some species of insects are declining. A combination of published data and anecdotal evidence point that way for many bees, monarch butterflies, and fireflies, among many other species (2–4). Several reports even suggest that insect declines reach across communities and taxonomic groups, for example, affecting the myriad flying insects that once splattered across car windshields but are now too few to be noticed (5).

Despite the overwhelming sense that something sinister is afoot, entomologists lack clear, comprehensive data on insect abundances over time. So far, a million species have been described and probably another 4.5 million have yet to be discovered (6). Piecemeal or anecdotal evidence shows the broad strokes of what seems to be a general decline, with some exceptions. At times, the narrative seems almost apocalyptic. And yet, some studies do find stable or increasing arthropod populations. To really quantify what's been going on would require long-term monitoring studies tracking insect abundances over decades. Few such datasets exist, however. When they do, they are the gold standard for reconstructing trends.

In the absence of long-term monitoring studies, entomologists have also turned to plumbing other kinds of historical data for signals of insect population change. One approach is to resample sites that were surveyed years ago, as Rodenhouse and Harris did. Another is to dig into museum collections, to track changes in proxy evidence such as insect damage on leaves for the presence or absence of certain insect species over time.

These resources can help fill in some knowledge gaps to quantify the scope, extent, and causes of insect population change. Even so, "for vast numbers of insect species, we just won't have enough data to understand anything about their change," says Robert Guralnick, curator of biodiversity informatics at the Florida Museum of Natural History, part of the University of Florida campus in Gainesville. Still, for select groups, when enough historical data can be cobbled together, he says, looking to the past is already fleshing out the story of shifting insect populations and communities.

The Long View

Talk to any seasoned entomologist today and they're likely to offer their own anecdotes of once-common insects and other arthropods, now notably absent. Art Shapiro at the University of California, Davis, has noticed the vanishing of local orb weaver spiders; there is very little "gossamer floating in the air," he says. And those big green tomato hornworm caterpillars, the voracious pests that local garden columns still warn against, seem to be regionally extinct as well. "It sounds insane," Shapiro says, but "I've seen one caterpillar, I think, in the last five years—extremely strange."

Looking beyond anecdotal observations in his own backyard, Shapiro also helms one of those rare long-term efforts to monitor insect population changes that set the high bar for detecting trends. He has been tracking populations of 159 butterfly species and subspecies at 10 California sites over the last 48 years and has rigorously documented declines in sootywing (*Pholisora catullus)* and large marble (*Euchloe ausonides*) butterflies, among other species. The long-term data tell a tale of dwindling numbers and unexplained disappearances.

The most surprising case, he says, involves the large marble, which has alabaster wings laced with green and black markings. The butterfly was ubiquitous in Central California in the early 1970s, where it laid eggs twice a year, in early and late spring. Because large marbles could switch from feeding on their native host plant to common weedy mustards that cover the state's rolling hillsides and push up through city sidewalk cracks, the butterfly seemed an excellent candidate to thrive in a quickly urbanizing California. Instead, the butterfly began to disappear. From a high count of 93 individuals on transects at five sites in California's Central Valley in 2001, the large marble dwindled to just 12 in total across all transects in 2003, two in 2005, one in 2007, and very few from 2008 onward (7). Across Shapiro's field sites, large marble caterpillars disappeared in a consistent pattern: The late-spring generation winked out first, followed by the early spring brood a few years later. By 2008, the species was all but extinct in the region.

Other once-ubiquitous California butterflies also grew scarce around the same time, including the sootywing, a glossy black species. Sootywings also foraged on weedy plants and were so commonplace that most butterfly collectors didn't bother catching them. "Nobody cared about it, and now it's gone," Shapiro says. His annual count data for sootywings show a fluctuating and declining population curve, with peaks between 105 and 32 individuals across four sites between 1999 and 2003, dropping into the teens and 20s from 2004 to the present, with occasional sharper population dips or spikes.

Half a world away in Great Britain, populations of moths and other insect groups show similar trends. The longest-running standardized daily insect survey in the world, which began on the sprawling Rothamsted Research estate north of London in 1964, reveals the declines. Sampling takes place every morning at 10 AM, when researchers collect insects from a network of 16 towering suction traps, which run continuously both on the green grounds of Rothamsted and throughout England and Scotland. Each suction trap looks like a 30-foot telephone pole with an inverted funnel at the top, possessing the sucking power to draw in small flying insects, including aphids, flies, beetles, and the occasional honey bee or hover fly. The unlucky insects are identified to species, counted, and stored in test tubes in the Rothamsted archives. In addition to the suction traps, a second network of volunteer-operated light traps use 200-watt tungsten bulbs to attract and capture moths and other nocturnal insects on a nightly basis. There are, on average, 80 active traps in a given year spread throughout the United Kingdom. They click on at dusk and off at dawn.

From these samples, researchers first count the collected insects and then attempt to extrapolate the rate of population change over time, explains James R. Bell, head of the Rothamsted Insect Survey. Bell led a 2020 study using data on more than 24 million individual moths and aphids collected between 1969 and 2016 to estimate the rate of population change for both groups (8). The data showed booms and busts over the years, creating population curves with many peaks and valleys. But importantly, Bell says, some periods of decline were followed by phases of partial recovery, during which insects didn't quite bounce back to their historical high numbers. As a result, the overall slope of the curve trended downward.

Moth populations declined precipitously, by 31% overall. Aphid populations fell by a nonsignificant 7.6%, suggesting that their populations were more stable but trending toward decline. Estimating these rates of population change requires standardized and consistent long-term sampling, Bell says. Surveys such as the one at Rothamsted have the protocols and equipment to make those estimates accurately. And the survey evidence thus far doesn't paint a pretty picture. "Scientists don't disagree for the most part that insects are declining," overall, he says; if there is any debate, it's in the scope and rate of declines.

Leaf mining insects, shown here from collections at the University of Connecticut in Storrs, carve distinctive tunnels into leaves that can be traced back to the species or genera level of the miner that made them. Such remnants are one emerging way to track insect population change. Image Credit: Emily Meineke (University of California, Davis).

Presence Counts

Researchers can use other forms of historical data to try to fill in that picture even without records of meticulous sampling across decades. According to a 2020 study investigating long-term biodiversity change in the United Kingdom (9), records that simply document the presence, or occurrence, of a given species at a specific time and place are much more readily found than the so-called abundance data that come from intensive and expensive long-term monitoring. This makes repeat, or resampling, studies such as the one at Hubbard Brook easier to do. It may also offer a way to get insights into insect abundance, information that researchers crave.

Shapiro and colleagues have compared presence and abundance data for 49 butterfly species at four California sites over nine years and found that, for many species, presence–absence data could stand as reasonable proxies for abundance data, Shapiro says (10). The utility of presence data to predict abundance varied with species, but 112 of 151 total butterfly populations showed similar trends on both indices over time. Only a handful of species bucked the trend, with a weak correlation between abundance data and presence data. These cases were explained by the species being so common that their presence was constant all season, even while abundances varied, according to the authors. One limitation of this approach can be inconsistency in sampling methods between the two types of study. And although presence and abundance data are not interchangeable, their typically tight correlation makes resampling efforts one viable way to study insect population changes over the last century.

Presence data together with historical climate records can also shed light on what's been happening in the insect world over time. The Hubbard Brook Experimental Forest, where Rodenhouse and Harris sampled beetles, for example, has more than 60 years of climate data, including changing temperature, rainfall, and snow depth. Multivariate analysis comparing each climate variable with the beetle data revealed that beetle population size is tightly correlated with median winter snow depth (1). That makes sense, Harris says, because beetles burrow underground overwinter and survive insulated by a thick layer of snow. As climate change has warmed the forest, median snow depth has declined, reducing the insulation, which could result in many beetles freezing overwinter. "Our paper is essentially the first one that nails down the cause of decline for a significant group of insects, the beetles," Rodenhouse says. He adds that similar trends are likely occurring for overwintering insects in any temperate zone where snow is decreasing in depth and duration, and the same processes could be at work in higher latitude boreal forests.

Hidden Troves

Researchers are also digging into museum collections and repurposing museum datasets to track insect trends. In a study conducted from 2016 to 2018, for example, ecologist Emily Meineke pored through digitized collections of oak leaves, stored in the archives of the Harvard University Herbaria in Cambridge, MA (11). Many leaves were pocked with small, brown scars—wounds from chewing insects inflicted and healed during the leaves' lifetimes on the tree. Peering down through a microscope, Meineke quantified the extent of insect damage on thousands of oak leaves and several other kinds of leaves, collected between 1896 and 2015 in the Northeastern United States. She was surprised to find that herbivory damage from chewing insects had increased by 12% over the last century, despite documented declines in many insect species in New England. The study further found that the uptick in herbivorous insect damage was associated with increased winter temperatures; some insect populations thrived in milder cold seasons. Identifying exactly which insects are responsible for the damage isn't possible from the oak leaves; one or many insect taxa may drive the pattern of increased herbivory. However, inspired by her previous study, Meineke, now an assistant professor at University of California, Davis, next plans to turn her attention to herbivore damage that can be pinpointed to a single species, such as tunneling leaf miners, which dig distinctive squiggled tracks into leaves.

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Perhaps the ultimate trove of museum occurrence records is a bumble bee dataset built on digitized information from natural history museum insect collections and private collections beginning in 2015 (12). A study published in February used the dataset to model changes in the presence and regional richness of 66 bumble bee species across North America and Europe over the last century (13). Based on about 550,000 georeferenced records, the authors compared the bumble bees' distributions from 1901 to 1974 with their distributions between 2000 and 2014, then asked which environmental factors might drive the declining trends they observed. The study found that climate change—in particular more frequent extremes of temperature and precipitation exceeding the bees' tolerances—were associated with the greatest declines. Losses in such a ubiquitous and agriculturally important group drive home the biodiversity crises that many species now face, says coauthor and ecologist Peter Soroye, a PhD student at the University of Ottawa, in Ontario, Canada.

Although these latest herbaria and museum findings may not offer definitive answers about insect population changes worldwide, they do illustrate the potential of collections to help piece together declines and some of the processes driving them. Guralnick has spent much of his professional life championing the potential of standardized, digitized natural history collections to study global change. When his career began in the early '90s, researchers often had to travel to individual collections to access their data, and what was available online was not standardized across institutions. Collecting presence data on 66 species of bumble bee across North America and Europe just wouldn't have been feasible back then, he says. "With new technologies we can begin to assemble literally billions of historical records that are spatially and temporally located," he says. And with that comes huge potential to study insect global change.

Zooming Out

All of these historical data, whether from long-term monitoring, repeat studies, or museum collections, are helping to put current insect population changes in a broader context, says ecologist Heather Kharouba at the University of Ottawa.

But the trend is hardly as simple as across-the-board declines. Not all arthropod populations are plummeting. "It seems trivial to say that," notes postdoctoral agricultural entomologist Michael Crossley at the University of Georgia, in Athens. "But in the context of this doom and gloom narrative, it's actually worth saying." Crossley coauthored an August study analyzing more than 5,300 time series of arthropod abundance data from 12 US long-term ecological monitoring sites. Assessing multiple measures of diversity, the study found, for example, that 24% of taxa decreased in species richness by more than one standard deviation, 35%

increased by more than one standard deviation, and 41% didn't change by more than one standard deviation (14). The findings somewhat temper the notion of a wholesale insect apocalypse, Crossley says. But widespread fluctuations are also a sign of ongoing change, adds Soroye, who was not involved in the study. "There are winners and losers in this dramatic period of global human-caused change," Soroye explains.

Another recent meta-analysis, based on 166 studies, each running for 10 years or more between 1925 and 2018, and spread across 41 countries, mainly in temperate zones, revealed a mean trend of 8.81% decline in terrestrial insects per decade, and, surprisingly, an 11.33% increase in freshwater insects per decade (15). This finding may reflect clean water reforms, according to the authors. Notably, declines were less pronounced in protected areas, suggesting that urbanization and agricultural development, associated with habitat loss and pollution, may be part of the problem. Indeed, an October study found that pronounced losses in Belgium's wild bees are correlated with agricultural development (16). Presence–absence data for 205 species between 1950 and 2016 revealed a 33% decrease in wild bee occupancy throughout the country. The most dramatic losses over the last 70 years occurred in the 1970s and 1980s. "In Europe, the landscape totally changed between the Second World War and the 1990s," says coauthor François Duchenne, a PhD student in community ecology at the French National Museum of Natural History in Paris. He suspected that postwar agricultural expansion and urbanization drove the bee declines. Statistical analysis confirmed that intensifying farming was tightly coupled with fewer bee sightings for many species. Urbanization, on the other hand, helped some bee species spread; others, meanwhile, fared worse. Surprisingly, Duchenne says, climate warming had an overall positive effect on the Belgian bees, perhaps because many are originally southerly species, suggesting they can tolerate some warming in Belgium's normally temperate climate.

As powerful as long-term monitoring may be, there simply have been too few projects to tease out the taxonomic scope or the causes of changing insect population trends. And those studies that do exist are largely concentrated in North America and Europe, Bell says, because the world's wealthy countries can afford widespread sampling efforts. More work from the tropics, for example, would help clarify the geographic scope of the declines, Kharouba says.

To understand how severe and widespread insect declines really are clearly requires creative approaches to mining existing data. Looking back at historical records is also a reminder of the value of consistent data collection, Kharouba says. For insects not yet in trouble, "it's hard to anticipate which species will go into decline" in the future, she says. "It's a good reason to keep collecting data now."

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