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Insect declines, population variability, and the consequences for insectivorous birds

A Dissertation submitted in partial satisfaction of the
requirements for the degree Doctor of Philosophy in Biology

by

Graham Allen Montgomery

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ABSTRACT OF THE DISSERTATION

Insect declines, population variability, and the consequences for insectivorous birds

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Professor Morgan Winn Tingley, Chair

Recent reports of widespread insect declines have sparked conservation concern for both insects and insectivorous bird populations in North America and beyond, since the magnitude of declines and their effects remain unclear. Here, I present research that aims to inform population trends and linkages for these closely connected groups, by bringing together data from biological resurveys at local scales, and large scale literature synthesis and time-series datasets. In Chapter 1, I first present an overview of insect declines, which focuses on key knowledge gaps and challenges for understanding insect declines. Next, I present research proposing that insect monitoring efforts can benefit from increased methods alignment with other programs, helping multiply the usefulness of data and forming the basis for insect monitoring networks. In Chapter 2, I bring together 4000+ insect population time series to demonstrate that insect population variability is higher than that in vertebrate taxa. I then characterize patterns in this population variability across geographic traits (latitude and biome), time series traits (duration and start date) and species size, finding higher variability at higher latitudes, for smaller species, and for older, shorter time series, which can help inform population trend estimation and extinction risk assessments. In Chapter 3, I present results from a paired, bird-insect biological resurvey from Great Smoky Mountains National Park, TN, U.S.A., where myself and others revisited sites originally surveyed in the late 1940s to collect data on bird and insect community change. Because this protected area serves as a refuge from some anthropogenic pressures (e.g., habitat loss and light pollution), but is still vulnerable to others (e.g., invasive pests and climate change), it serves as a useful natural laboratory for evaluating community change. Using Bayesian n-mixture modeling to account for imperfect detection, I find that populations of many bird species have declined markedly since the 1940s, and that insect communities have declined at some sites but increased at others. Changes in the two communities are correlated, and likely driven by the combination of habitat change and climate change.

The dissertation of Graham Allen Montgomery is approved.

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DEDICATION

This dissertation is dedicated to my little brother, Daniel.

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Co-authors have contributed valuably to each chapter. Chapter 1 consists of two parts; the first is a reprint of an perspective piece on declining insect populations published in Biological Conservation, with co-authors Robert Dunn, Richard Fox, Eelke Jongejans, Simon Leather, Manu Saunders, Chris Shortall, Morgan Tingley (MT), and David Wagner (DLW). The dissertation author (GM) was the primary researcher and author of this material and all authors contributed to iterations of the writing. The second part is a reprint of a review of insect monitoring methods to promote insect monitoring methods published in Frontiers in Ecology and Evolution. GM and MT conceived the idea for the manuscript and proposed the initial outline. GM. and Michael Belitz led writing of the first draft. All authors contributed critically to drafts and gave final approval for publication.

Chapter 2 was led by GM and supervised by MT. Authors contributed to multiple components of the research, but Eliza Grames, Chris Elphick, and DLW informed study design and facilitated data collection. GM and the illustrious finch itch team of Jake Jacobsen, Ethan Kahn, Amanda Leyel, Mia Rosati, and Qiyuan Wu collected data, GM and MT performed the analysis, GM wrote the first draft of the manuscript, and all authors contributed to revisions.

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SELECTED PUBLICATIONS AND PRESENTATIONS

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Chapter 1: Is the Insect Apocalypse upon us? How to Find Out

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Abstract

In recent decades, entomologists have documented alarming declines in occurrence, taxonomic richness, and geographic range of insects around the world. Additionally, some recent studies have reported that insect abundance and biomass, often of common species, are rapidly declining, which has led some to dub the phenomenon an “Insect Apocalypse”. Recent reports are sufficiently robust to justify immediate actions to protect insect biodiversity worldwide. We caution, however, that we do not yet have the data to assess large-scale spatial patterns in the severity of insect trends. Most documented collapses are from geographically restricted studies and, alone, do not allow us to draw conclusions about insect declines on continental or global scales, especially with regards to future projections of total insect biomass, abundance, and extinction. There are many challenges to understanding insect declines: only a small fraction of insect species have had any substantial population monitoring, millions of species remain unstudied, and most of the long-term population data for insects come from human-dominated landscapes in western and northern Europe. But there are still concrete steps we can take to improve our understanding of potential declines. Here, we review the challenges scientists face in documenting insect population and diversity trends, including communicating their findings, and recommend research approaches needed to address these challenges.

Introduction

Declines of insect abundance, biomass, and range are being reported worldwide, from the arctic to the tropics, across insect orders, and from a spectrum of ecological guilds (e.g., Fox 2013, Hallmann et al. 2017, Loboda et al. 2018, Lister & Garcia 2018, and reviews by Sanchez-Bayo & Wyckhuys 2019, Wagner 2017, 2019b). Though fewer than 100 insect species are documented as extinct (IUCN 2019), more recent extinctions have assuredly occurred on islands and deforested tropical regions. One important aspect of many recent studies is the decline of formerly common species, not just rare taxa (Conrad et al. 2006, Van Dyck et al. 2009, Fox et al. 2015), with the realization that such losses likely come with changes to ecosystem connectivity and function (Gaston & Fuller 2007, Dirzo et al. 2014). Some studies have reported dramatic declines: Hallmann et al. (2017) found a 75% decrease in flying-insect biomass over a three-decade period from 63 preserves in northwestern Germany. Declines are also reported from many western and northern European countries, representing a suite of different insect orders (e.g., Conrad et al. 2006, Shortall et al. 2009, Schuch et al. 2012, Van Strien et al. 2019, Hallmann et al. 2019; see also reviews by Sanchez-Bayo & Wyckhuys 2019, Wagner 2017, 2019b). Two of the studies that drew worldwide media attention (Lister & Garcia 2018, Sanchez-Bayo & Wyckhuys 2019) not only ignited discussion of insect declines among scientists and lay people alike, but also received substantial criticism—their methods, results, and extrapolations are much contested (Komonen et al. 2019, Mupepele et al. 2019, Simmons et al. 2019, Thomas et al. 2019, Wagner 2019a, Willig et al. 2019; see Saunders 2019 for a review of the datasets informing this discussion).

Many insect taxa are unequivocally in decline across many regions of the planet, and we know enough to take conservation action (Basset & Lamarre 2019, Janzen & Hallwachs 2019, Forister et al. 2019). However, important aspects of the insect decline phenomenon remain largely unknown. Most importantly, we need to understand how quickly populations are trending upward or downward. Annual declines of 1-2% for species in densely human-populated areas are unfortunate but relatively unsurprising, while >3% annual declines in areas far removed from most human activities would be stunning. Failure to make such distinctions can lead to untenable extrapolations, e.g., that 40% of the world’s insects will be extinct in a few decades, as posited in

Sanchez-Bayo & Wyckhuys (2019). Next, are the rates of population change of insects roughly on par with those of plants, birds, and mammals, as found generally by Dirzo et al. (2014)? If so, then the apocalypse is one suffered by all species. An answer to this question could also point to the drivers. If insects are declining at rates appreciably faster than vertebrates and plants in the same regions, it may be prudent to focus research on stressors like that especially impact insects (e.g., insecticide use), or it may be an indication of what is to come for other taxa. Finally, with so few data from outside Europe, it is difficult to gauge how widespread the phenomenon is, especially in the tropics (Basset & Lamarre 2019, Janzen & Hallwachs 2019), where more 85% of all insect species occur (Stork 2018), and in temperate regions of the southern hemisphere. Many studies show that there are winners as well as losers in recent insect biodiversity change (Brooks et al. 2012; Boyes et al 2019) and that net loss of insect abundance/biomass has not been reported from all study locations (Shortall et al. 2009; Valtonen et al. 2017; Herrera 2019). Overall, although progress is being made, attempts to answer questions regarding the magnitude, and in many cases even the existence, of insect declines face many challenges. Here, we outline these challenges, but focus on research recommendations, from increased monitoring, to community science and pleas for more rigorous methodologies and meta-analyses. We also touch on matters of unexplored data streams, reporting bias, and funding needs.

Challenges

The Insect Side

The greatest challenge to studying insect trends, in diversity, abundance, range, occurrence or other metrics, is the paucity of baseline data (Cardoso et al. 2011, Eisenhauer et al. 2019, Wagner 2017, 2019b, Cardoso & Leather 2019): we lack robust records of past insect populations and diversity. Traditionally, entomological collections have been focused on documenting species diversity rather than abundance, often for a narrow range of taxa, and as such, yield little information about population numbers and survey effort, rendering many historical collection events essentially non-replicable. The geographic distribution of haphazardly distributed baseline data is also a problem – those data that do exist come mostly from “anthroposcapes,” or human-altered ecosystems. While these data are useful for evaluating direct human effects on insects, they are not useful for drawing conclusions about insect populations in areas with modest human activity and wildlands (Wagner 2019b). The temporal distribution of available baseline datasets is also an issue. Many of the baseline data that do exist post-date the onset of purported drivers of insect declines, for example, the UK Butterfly Monitoring Scheme, a flagship long-term insect monitoring effort, began in 1976, after agricultural intensification was well underway (Pollard & Yates 1994).

Additionally, large natural fluctuations in invertebrate populations from year to year, and sometimes even within a single year, make drawing conclusions from demographic studies of insects challenging (Fox et al. 2019). This large interannual population variation is dependent on many intrinsic and extrinsic factors (Hanski 1990), including myriad natural enemies (Turchin et al. 1999) and the vagaries of weather (Wolda 1983, Nelson et al. 2013). This is especially problematic for the interpretation of “snapshot” surveys where population data from one period are compared with population data from another period, without data from intervening years (Habel et al. 2019).

Entomologists and those reliant on sound insect identifications also face an enormous taxonomic impediment (Samways 1993, Habel et al. 2019), especially in tropical regions. It is difficult to know what we are losing when 80% of insect species (representing, conservatively, four million species) remain undescribed and their natural histories unknown (Stork 2018). High insect species diversity compounds this problem; identification of every insect even in a small sample in an area with low alpha diversity can be time- or cost-prohibitive. Declines in insect identification expertise further degrade the ability to determine biodiversity and population trends for most insect lineages (Hopkins & Freckleton 2002); growing sources of identification knowledge through community science, machine learning, and genetic barcoding are helpful, but cannot compensate the continuing loss of professional taxonomist expertise. Using indicator taxa can be an effective approach to sidestep aspects of the taxonomic impediment problem but doing so often results in inadequate knowledge and compromised measures of interest (McGeoch 1998, Thomas 2005).

There are many consequences of this shortfall of insect biodiversity knowledge, when combined with a general lack of baseline population data. One illustration can be seen in the number of insects with global conservation statuses evaluated by the International Union for Conservation of Nature: only 8,355 insect species have been evaluated, and 2,104 of those are "data deficient" (IUCN 2019), out of an estimated 5.5 million insect species worldwide (Stork 2018).

The Human Side

Scientific, public and political interest in insect population declines and conservation is encouraging and has led to new research programs, redoubled interest in sampling methodologies, catalyzed interest in analyses of historical data sets, led to biodiversity-friendly government initiatives, and increased funding for the study of insects. Several high-profile studies finding large declines in insect populations or biomass have spurred massive media attention and generated unprecedented public interest in insects and their ecosystem services. Unfortunately, some media reports of insect declines have made extrapolations that have leapt beyond credible evidence, though there are examples of more balanced coverage (e.g., Yong 2019). Exaggerated claims can sometimes trigger complex feedback loops between scientists, institutions, media and the public (Ransohoff & Ransohoff 2001, Bubela 2006, Caulfield & Condit 2012). To avoid such claims from being made, it is incumbent upon scientists to continue presenting thoughtful, critical assessments; the risks of false positives are high. Because global insect populations have such importance, and also because of the enormous data gaps and potential biases, it is especially important to commit to elevated standards of study design, evidence, and communication.

Human psychology also poses challenges for understanding the insect decline phenomenon, and we should be aware of human tendencies that affect this field. For example, humans tend to view insects as one homogeneous group, which masks the complex and variable effects occurring across taxa and guilds (Habel et al. 2019). Older people recall seeing more moths in headlights (“the moth snowstorm”), summer nights filled with fireflies, and splatted insects on their windshields. Such anecdotes are valuable, but only rarely can be substantiated. On the other hand, younger people may not notice what has been lost as a result of shifting baseline syndrome (Pauly 1995, Soga & Gaston 2018). However, it is also true that a generational shift in where people live has also occurred, with broad shifts toward cities and hence the experience of the subset of species that thrive in cities. Confirmation bias, the tendency to interpret data to support existing hypotheses (Nickerson 1988), could creep into experimental design and analyses, especially in ecological studies where many effects interact weakly. Publication bias is also no doubt at play, where statistically significant results are selected for publication more often than studies with non-significant results (Rosenthal 1979). How large a problem might it be that studies documenting losses are more likely to be written, reviewed, and accepted for publication than studies showing little change? Indeed, studies of insects in general are less likely to be published than studies of other taxonomic groups (Leather 2009), another form of publication bias. There is also a tendency for the most extreme results to be published and cited (Ioannidis 2005) - this may be especially relevant for a topical issue like insect declines. While most scientists are already aware of these issues, it is important to regularly remind ourselves of them.

Research recommendations

Determining the scale and severity of declines in insect diversity, abundance, and range must be among the most urgent global research, conservation, and legislative priorities going forward. But what research will be most effective? Entomologists have unique opportunities in this moment of heightened public awareness.

Monitoring

First, we need to establish insect monitoring networks on a global scale. By using repeatable sampling methods, new monitoring programs can augment pre-existing ones, and help determine population trends, identify drivers of trends, and serve to engage the public through community science (Lewandowski & Oberhauser 2017). We advocate for large-scale programs to monitor abundances, biomass, and species diversity using standardized, effort-based methods such as Malaise trapping, pitfall trapping, suction trapping, light trapping, count surveying, and new methods such as the modified window traps of Knuff et al. (2019) or smart insect cameras (Hogeweg et al. 2019). Although biomass is an imperfect estimator of diversity because it can be sensitive to changes in abundances of large species (e.g., Shortall et al. 2009), it is a valuable metric from the ecosystem perspective. Determining biomass trends also does not require fine-scale taxonomic knowledge, which is often limited to individuals with specialized training. We advocate this approach with necessary caveats; it is often impractical to attempt monitoring all insect species from any community with appreciable diversity (though meta-barcoding and other genetic approaches can help).

Long-term monitoring should consider the relative economic and ecological costs and benefits; although regular lethal trapping may not have major impacts on insect communities (Gezon et al. 2015), the economic costs of sampling and identification of large volumes of many taxa may be prohibitive (Tepedino et al. 2015; Drinkwater et al. 2019). Better-known taxa like butterflies, macromoths, orthopterans, and some bees and beetles can serve as indicator or substitute species for other insect groups, but only when carefully validated (Henry et al. 2019). Effective long-term monitoring takes many forms, including complex spatial designs with many observers and single-observer designs with temporally intensive data from fewer sites (Pocock et al. 2015). Continuous, or at least multi-year, time-series are especially valuable for insects, where year-to-year population variation can be high. Although longitudinal time-series (e.g., Wepprich et al. 2019) provide better inferential power, “snapshot” surveys are useful for taxa or regions limited by a lack of continuous historical data, if scientists control for variation in effort and changes in methods – whether through strong data filtering or direct statistical modeling (Tingley 2017) – and can replicate previously conducted surveys on a broad geographic scale. Though existing long-term monitoring programs are relatively rare, programs that do exist provide invaluable data and can be used as models for new monitoring efforts. A non-exhaustive list of such programs include the Wijster Biological Station pitfall program (NL; Den Boer & van Dijk 1994), the Rothamsted Insect Survey (UK; Storkey et al. 2016), the Krefield Entomological Society surveys (DE; Hallmann et al. 2017), the United Kingdom, Dutch & Catalan Butterfly Monitoring Schemes (UK; Pollard & Yates 1994, NL; Van Swaay et al. 1997, ES; Melero et al. 2016), midwestern butterfly surveys (US; Swengel et al. 2011, Wepprich et al. 2019), and the Shapiro butterfly surveys (US; Forister et al. 2011). Collectively, these programs form the basis for a large part of what we know about long-term diversity and population trends in insects – the next step is expanding and complementing these schemes on a global scale, while continuing to support existing programs.

Surveying across space

Surveys across light pollution, agricultural intensification, pesticide use, plant invasion, urban heat island, human density, or other gradients could provide insight into what factors are contributing to insect declines and their relative importance. There is an urgent need to gather demographic data from tropical sites—while not wholly surprising, it is ironic that we know the least about the Earth's most species rich and ecologically diverse entomofaunas (Stork 2018). In addition, surveys that substitute space for time can serve as an imperfect substitute for baseline data. This survey strategy is commonly used in ecology when time-series data are lacking (Blois et al. 2013) and can prove particularly powerful when tested against experimental data and, for the subset of sites for which they are available, time-series data (Lahr et al. 2018).

Making time-series data available

We also need to make baseline data more open and accessible. Continuous or nearly continuous time-series of insect abundance and diversity have been collected by observers outside of insect conservation and ecology circles. For example, changes in lady beetle populations have been monitored using control plots at experimental farms (Alyokhin & Sewell 2004). Vertebrate ecologists studying insectivores that also collect insect (prey) abundance data have the potential to contribute much to our knowledge of insect population trends (e.g., Harris et al. 2019).

Data collected by agricultural and silvicultural monitoring, land-management agencies, insect collectors, and nature enthusiasts can all be useful. These datasets, like datasets from traditional ecological sources, should be made available and posted to online repositories like Dryad (datadryad.org), BioTIME (biotime.st-andrews.ac.uk; Dornelas et al. 2018), or the Global Biodiversity Information Facility (gbif.org) when possible. We recognize that there are social and financial barriers to contributing data sets to online repositories that still need to be addressed, and care needs to be taken to protect the intellectual property rights of ongoing long-term surveys to ensure their continuity (Pearce-Higgins et al. 2018).

Community science

Some of the best long-term monitoring data comes from community or citizen scientists. The biomass declines reported by Hallmann et. al. (2017) in Germany are based on the work of the Krefield Entomological Society, an organization of knowledgeable entomologists, most of which commit their free time to insect research. Beyond already existing community science efforts, the current moment is also an opportunity to reach new audiences with a message of insect conservation on a global scale (see Pocock et al. 2018). Concerned community scientists can be recruited to re-sample “snapshot” surveys on a large geographic scale. Similarly, enlisting school classrooms to participate in insect monitoring can provide useful data (e.g., the School Malaise Trap Program in Canada: Steinke et al. 2017, and Saunders et al. 2018). Live pitfall and LED UV-light traps are inexpensive to set up and monitor and can mitigate ethical concerns sometimes associated with specimen collecting, especially by the public. Taxa such as caterpillars, larger beetles, and wasps can be imaged (and identified) with cell phones, offering myriad possibilities. School monitoring programs also have the potential to be expanded to larger geographic scales.

Such community science efforts simultaneously serve to educate, raise awareness about the importance of insects, and provide opportunities for invertebrate conservation (Lewandowski & Oberhauser 2017). Error and bias due to variation in the expertise of the participants is a recognized issue (Gardiner et al. 2012) and designing protocols that account for or minimize this is important (see Dennis et al. 2017); training projects such as BioLinks (https://www.fscbiodiversity.uk/projects/biolinks) can play important roles. There are many successful insect-related community science projects that collect useful data on insect abundance, diversity, or distribution that can serve as models. Examples include The Monarch Larva Monitoring Project, National Moth Recording Scheme, Caterpillars Count, Bumble Bee Watch, Lost Lady Bug Project, Firefly Watch, Wild Bee Garden Count, Western Monarch Thanksgiving Count, Australia's Wild Pollinator Count, UK Pollinator Monitoring Scheme, iNaturalist.org, and BugGuide.net.

Reporting and synthesizing results

Once insect trend data have been collected, they need to be shared, and well-designed insect demography studies should be published or otherwise made available. To combat publication bias, researchers, reviewers, and journal editors alike need to publish reports of increasing and stable trends, in addition to documenting declines. Reports of where insects are not declining are as important as reports of where they are declining, since this heterogeneity can help elucidate key threats. Unbiased reporting will also reduce systematic biases in the literature, which is helpful for researchers performing systematic reviews and meta-analyses. These forms of evidence synthesis can effectively provide a means of evaluating the scale and severity of insect declines and their potential drivers when they follow question formulation tools like PICO (Richardson et al. 1995) and reporting guidelines like ROSES (Haddaway et al. 2018). We recommend projects such as the EntoGEM systematic mapping project (Grames et al. 2019; https://entogem.github.io), a community-driven effort to assimilate global literature and data sets relevant to insect population and diversity trends.

Under-exploited datasets

Beyond these steps, however, complementary approaches are needed to fully evaluate the mechanisms, pattern, and consequences of insect declines, especially to provide alternative baseline data. For example, NEXRAD is a network of weather radars in the United States that are used to monitor birds (Dokter et al. 2018); data from these radars could also provide estimates of aerial insect biomass flows over the last 25 years (Hu et al. 2016). The use of museum collections to estimate insect trends (e.g., Cameron et al. 2011, Bartomeus et al. 2013, Boyle et al. 2019) is becoming more powerful with new statistical methods. Caution is required when using data that were not collected for this purpose (e.g., see Wepprich 2019), including spatiotemporal bias (Ries et al. 2019), and abundance trends do not always correlate positively with occurrence (range) data (Dennis et al. 2019). However, museum collections can be used to infer trends and drivers of trends (e.g., Scheper et al. 2014, Meineke et al. 2019), and effort data can sometimes be extracted from species-list length in a time or place (Van Strien et al. 2013). Continued digitization efforts (e.g., iDigBio, LepNet, SCAN) are necessary to bring collection data to bear on the issue of insect declines, since current numbers of digitized specimens are not enough to draw conclusions about trends in many cases (Ries et al. 2019). Stored samples from monitoring projects are also available and have been utilized to some extent (Shortall et al. 2009, Hallmann et al. 2017) — most are available for further work. In some cases, data for insectivorous taxa may exist where baseline data for insects do not, perhaps allowing inferences about insect diversity and population levels (English et al. 2018, Wagner 2019b). Such insectivorous taxa can also provide insect data directly, through DNA sequencing diet samples or feces (e.g., Krauel et al. 2018). Entomologists should also think broadly and creatively about new technologies and "Big Data" streams that could be used to study insects, from passive acoustic monitoring (Zilli et al. 2014), smart insect cameras, and eDNA (Mächler et al. 2014) to LIDAR (Simonson et al. 2014), and social media (Alvaro et al. 2015).

Funding

Few of these research priorities will be feasible without funding. There needs to be a recognition by research funding agencies, foundations, and individuals that entomological survey and monitoring work should receive a step-change in funding. Funding should more closely reflect abundance, diversity, and ecological importance of taxa, not their perceived charisma (Clark & May 2002). Crowdsourcing may draw in some funds, but what is required is stable, substantial funding that will allow existing and future international collaborations to flourish. For this to happen, we need to convince funders, and society, to support insect conservation as much as insect control. Long-term monitoring studies can be unappealing to funders and yet are the main lens through which we understand the rapid changes in biological systems; in this way they are akin to public health surveillance, essential and yet radically underfunded compared to studies of medical interventions.

Conclusion

Insects are in trouble, and we must take conservation actions now, rather than wait for biologists to provide exhaustive demographic data, measure all drivers, and attempt to quantify population trends across thousands of individual lineages. But the many data gaps presently in the insect decline literature do matter, and it remains to be seen if some recent alarming results are indicative of global-scale insect declines that would trigger losses of ecosystem function. The drivers of declines are many, from habitat loss, agricultural intensification, and climate change, to invasive species, pesticides, and light pollution, but much remains unknown, including the scope and severity of insect declines. Despite the challenges faced by researchers studying trends in insect diversity and demography, it is urgent that we fill these crucial data gaps and use rigorous science to do so. It is time to get to work.

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Chapter 2: Standards and Best Practices for Monitoring and Benchmarking Insects

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Abstract

Benchmark studies of insect populations are increasingly relevant and needed amid accelerating concern about insect trends in the Anthropocene. The growing recognition that insect populations may be in decline has given rise to a renewed call for insect population monitoring by scientists, and a desire from the broader public to participate in insect surveys. However, due to the immense diversity of insects and a vast assortment of data collection methods, there is a general lack of standardization in insect monitoring methods, such that a sudden and unplanned expansion of data collection may fail to meet its ecological potential or conservation needs without a coordinated focus on standards and best practices. To begin to address this problem, we provide simple guidelines for maximizing return on proven inventory methods that will provide insect benchmarking data suitable for a variety of ecological responses, including occurrence and distribution, phenology, abundance and biomass, and diversity and species composition. To track these responses, we present seven primary insect sampling methods – malaise trapping, light trapping, pan trapping, pitfall trappings, beating sheets, acoustic monitoring, and active visual surveys – and recommend standards while highlighting examples of model programs. For each method, we discuss key topics such as recommended spatial and temporal scales of sampling, important metadata to track, and degree of replication needed to produce rigorous estimates of ecological responses. We additionally suggest protocols for scalable insect monitoring, from backyards to national parks. Overall, we aim to compile a resource that can be used by diverse individuals and organizations seeking to initiate or improve insect monitoring programs in this era of rapid change.

Introduction

"The best time to plant a tree is 20 years ago. The second best time is now."

-*Unattributed proverb*

The threat of widespread insect declines, supported by accumulating evidence across the globe (Conrad et al., 2006; Forister et al., 2011; Hallmann et al., 2017; van Klink et al., 2020), has sparked broad and outspoken concern. But even this general pattern of insect decline is heterogeneous in time and space, and drivers of declines in particular taxa and locations remain unclear, though they are likely myriad (Fox, 2013; Wagner, 2020). To better understand insect declines in the face of data gaps and other challenges (Didham et al., 2020), researchers need more systematic and long-term monitoring of insect abundance and diversity. Though many monitoring schemes already exist, relatively few have been operating long enough to draw robust, independent conclusions about insect populations and diversity over time (e.g., Shortall et al., 2009), and these monitoring schemes are necessarily limited in their geographic and taxonomic coverage. As scientists, we can and should lament our severely limited data on insect declines – long-term monitoring efforts should have been underway long before now, but were prevented for many reasons, including a lack of funding, motivation, and organization. Given increased societal interest in insects, there is the potential for widespread, long-term monitoring at the scale necessary to benchmark and track insect trends moving forward.

Many new monitoring efforts have been recently initiated, motivated by reports of insect declines. Researchers, managers, and community scientists are currently increasing efforts to document insects, whether photographing insects at porch lights, counting pollinators on transects, or establishing structured malaise trap programs. These efforts are a crucial first step toward broadly tracking trends in insect abundance and diversity. To maximize the information gain from these largely independent efforts, we recommend integration with established insect monitoring methods to coordinate sharing data that are accessible and interoperable. As much as possible, new monitoring efforts should align methods, metadata, and data access with those that already exist to increase explanatory power, streamline analysis, and facilitate the development of a global insect monitoring network. This network is already beginning to form through the efforts of organizations like PollardBase (Taron and Ries, 2015), the National Moth Recording Scheme (Fox et al., 2011), the Global Malaise Program (Geiger et al., 2016), as well as regional efforts, taxon-specific programs (e.g., for monarch butterflies and lady beetles), and even groups of Twitter users organizing nights to check their porch lights for insects[1]. Recently, Woodard et al. (2020) took the important step of proposing a national bee monitoring network in the United States. However, the urgency of insect declines requires even more rapid development and integration in an era of purported "insect apocalypse".

To reach the goal of a long-term monitoring network on a global scale, we will need data that, through standardization and well-defined metadata, can be integrated across monitoring efforts. Without standardized data and metadata collection, researchers will assemble datasets that are difficult or impossible to integrate, hindering synthesis. In other words, the efforts of thousands working independently are most valuable when those efforts can be assembled into a collective whole.

To meet this challenge, our aim here is to inform new monitoring projects with standardized data collection and metadata collection practices, facilitating future integration. We present a standardized toolbox for monitoring methods and metadata practices, aimed as a

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[1] https://www.anecdata.org/projects/view/738

starting point for non-specialists and a reference point for specialists. Specifically, we provide: (1) overviews of common insect monitoring methods, including malaise, light, pan, and pitfall trapping, beating sheet, and audio and active visual surveys; (2) specific recommendations for how to carry out each method in the field; (3) an overview of metadata considerations; (4) recommendations for standardized metadata collection for each method (Table 1); and (5) a forecast of emerging methods that can complement and extend existing methods.

Our audience is anyone interested in insect monitoring, from community members motivated to contribute to science, to entomological specialists who want to make their data more broadly useful. We especially hope these recommendations will aid those interested in insect monitoring but are not sure where to start. Workers can choose monitoring methods from the toolbox we present, then modify as needed for their goals and systems. We make these recommendations with scalability in mind – the methods we discuss are generally low cost, field-tested, and can be performed by a single individual. We generally organize these methods by following the framework presented by Ferro and Summerlin (2019), while our summaries and recommendations are especially influenced by Southwood and Henderson (2009), Samways et al. (2010), and previous efforts to advocate for sampling alignment for bees (Droege et al., 2017) and birds (Ralph et al., 1993). Along these lines, we do not advocate for existing monitoring networks to change their methods even if they are not easy to integrate with other efforts.

Though methodological standardization is ultimately a goal, we pragmatically advocate as much for *alignment* with and among existing monitoring efforts as we do for standardization. In the following sections, we outline recommended methods for sampling a given set of insect taxa for monitoring purposes. These methods are generally suitable for a variety of key benchmarking goals, including the measurement of occurrence and distribution, phenology, abundance and biomass, and diversity and species composition (Box 1). This is not a guide for conducting exhaustive species inventories (e.g., BioBlitzes or site lists), which often emphasize maximizing species counts, nor is it a guide for maximizing insect catches. This guide also does not aim to eliminate bias – no method is free of bias, but if methods and metadata are documented carefully and are consistent over time, then bias can largely be estimated and controlled. Additionally, monitoring insects in sites with rare and endangered species also requires unique considerations that must be site- and species-specific, and we do not cover the complexities of those considerations here, nor do we go into details of how to analyze data once collected. Finally, we do not recommend these sampling methods for entomologists with highly specific taxonomic goals; the class Insecta is simply too diverse in its niches and behaviors to be comprehensively assessed by one or even a few sampling methods. Here, we attempt to create a balance between being too general or too specific, by presenting a variety of methods for sampling broad taxa and guilds, each with its own strengths and weaknesses (Figure 1). If you find yourself wanting to monitor more specific insect groups, your sampling methods may need to be modified from those discussed here or may not be covered.

Box 1. Measurement goals of benchmarking studies

The goals of benchmarking and monitoring studies typically aim to measure change in at least one of the following: (1) occurrence and distribution, (2) phenology, (3) abundance and biomass, or (4) diversity and species composition. The seven monitoring methods we highlight can be used with the goal of measuring changes in as many of these responses as desired. Each of these four categories of response is important for different reasons, requires a different minimum spatiotemporal scale of sampling, and is currently used to study how insect populations and communities change over time.

Occurrence and distribution: Changes in occurrence and distribution are important indicators of how shifts in underlying processes affect organisms. Occurrence can also sometimes serve as proxies for abundance (Royle and Nichols, 2003). Estimating occurrence and distribution requires, at minimum, the formal identification of a taxon at a location (i.e., a presence), but the addition of data on what taxa were not present (i.e., an absence), allows for a more powerful analysis of occurrence. For insects, occurrence and distribution monitoring is perhaps the most widespread benchmarking method (e.g., Chen et al., 2009; Boyes et al., 2019; Outhwaite et al., 2019), especially for invasive species and in the context of shifting ranges due to climate change.

Phenology: Shifts in phenology can indicate changes in the factors governing the timing of insect life cycles, from temperature and precipitation patterns, to flowering periods in plants. Shifts in insect phenology can cause mismatches with other taxa in their communities, from plants to birds, and can have demographic consequences for those taxa (Visser and Gienapp, 2019). Estimating phenology typically requires, at minimum, presence data for a taxon at a location repeatedly over a short time span (i.e., a “season”), but presence and absence data together allow for stronger inference. Changes in insect phenology are poorly documented in most taxa, but recent interest in the effects of climate change has spurred a larger focus on insect phenology in monitoring efforts (Gimesi, 2012).

Abundance and biomass: Changes in abundance and biomass, both measures of ecosystem function, are important for understanding the health of the ecosystem as well as for conservation and management. Estimating abundance and biomass typically requires presence and absence data in addition to accurate counts of individuals of each taxa. This form of monitoring is historically rare but has been perhaps the most influential in spurring recent interest in insect declines (Hallmann et al., 2017; Wepprich et al., 2019).

Diversity and species composition: Changes in measures of biodiversity, such as species diversity and composition, indicate how communities respond to environmental change. Estimating diversity and species composition typically requires presence and absence data for multiple taxa in a community, with some expectation that sampling is equally likely across taxa. Monitoring insect diversity and composition is relatively common compared to abundance, biomass, and phenological monitoring (e.g., Brooks et al., 2012; Valtonen et al., 2017).

Standardized monitoring practices for different taxa and methods

Malaise trapping

Overview

Malaise traps (Malaise, 1937) are large tent-like structures made of netting meant to funnel insects to a common area (Figure 2A). In essence, an insect flies into a vertical wall of netting, responds by flying upwards, then is gradually funneled by sloped netting into a collecting vial. This vial is then checked and emptied periodically over days or weeks. The Townes-type malaise trap is the most common style used, but at least four other types – Gressitt malaise, Schact malaise, Sea, land, and air malaise (SLAM), and Cornell malaise – are also in use (Matthews and Matthews, 1983; van Achterberg, 2009). For detailed accounts of history and methodology, see van Achterberg (2009). Exemplar malaise trapping programs include the School Malaise Trap Program in Canada (Steinke et al., 2017) and the Swedish Malaise Trap Program (Karlsson et al., 2020). For those interested in joining an existing network, the Global Malaise Trap Program/BIOSCAN (Geiger et al., 2016) is accepting new members.

Taxonomic considerations

Malaise trapping is only appropriate for monitoring flying insects (Figure 1). Many flies (Diptera) and some wasps, flying ants, bees (Hymenoptera), bugs (Hemiptera), moths (Lepidoptera), and semi-aquatic taxa are effectively sampled by malaise traps (Matthews and Matthews, 1970; Noyes, 1989; Campbell and Hanula, 2007; Fraser et al., 2008; Mazon and Bordera, 2008; Diserud et al., 2013; Schmidt et al., 2019). Within these groups, malaise trapping is especially appropriate for Tenthredinidae, Ichneumonoidea, Scelionidae, Mymaridae, and other hymenopterans with similar life histories, as well as Cicadellidae and Cercopidae (Hemiptera), microlepidopterans (Lepidoptera), and the semi-aquatic orders Plecoptera, Ephemeroptera, and Trichoptera – if traps are placed alongside aquatic habitats. It is important to note that malaise trap efficacy for a taxon can depend on habitat. For example, bees (Apoidea) are sampled well in some habitats, like tallgrass prairie (Geroff et al., 2014), but pan-trapping is generally more effective for sampling this superfamily (Campbell and Hanula, 2007). The narrower the taxon of interest, the more necessary it is to customize these recommendations to your own system.

Methodological considerations

Location*:* Spatial placement is extremely important for malaise trapping; it is critical to document the trap's exact position and microhabitat by photograph, written description (particularly for habitat), and precise coordinates (see Table 1 for additional metadata needed). Choice of placement will vary based on the particular taxon of interest, but malaise traps should generally be placed along natural flight corridors (e.g., streams or gaps between bushes) to maximize catch. Amount of wind exposure should also be recorded, as wind can limit efficacy. The vertical panel of netting (i.e., the interception area) that insects hit should be oriented to be perpendicular to the expected movement corridor.

Design*:* We recommend Townes-type malaise traps due to their broad efficacy and already widespread use. Multiple sizes are available, with a 165x110cm interception area being most common. The vertical wall of netting is commonly black to reduce visibility, while the dome of the tent is white to increase insects' propensity to fly upwards (i.e., toward "the sky"), which increases catch. We recommend 95% ethanol (as is used by BIOSCAN) as a killing agent that preserves DNA, but lower concentrations (down to 80%) can be used if evaporation or cost prohibits use of 95%. Alternative approaches to collection include cyanide (hazardous to humans), ethyl acetate (destroys DNA), and live collecting (needs to be checked daily, and specimens are often damaged). Ethanol, however, does remove scales from taxa like lepidopterans. Mesh size and shape are also important to note: holes that are too wide are less effective at sampling small flies, wasps, and other microfauna, but large mesh sizes can better sample groups like stinging hymenopterans (Darling and Packer, 1988). Some insects, such as many beetles, drop after hitting the mesh screen, rather than trying to escape by flying higher. To take advantage of this, pans with collecting liquid can be placed underneath the mesh wall, creating what is called a flight-intercept trap (traditional malaise traps are a specialized flight-intercept trap that only samples upward-moving insects). If this is done, pan color should be recorded.

Scalability: Commercial malaise traps can be expensive (usually > US $230). Costs can be reduced by constructing home-made malaise traps (e.g., Blackmon, 2010). Mosquito netting can be used for the interception area (Lamarre et al., 2012), but mesh size and shape should be considered. Setup effort is generally low (up to 1 hour the first time). Sampling effort is minimal once a malaise trap is set up (10 minutes per week once at the site): the sample vial simply needs to be emptied into a storage vial. Post-sampling effort can be high, however, since malaise trapping can yield large numbers of insects (e.g., up to 10,000 specimens per week depending on the site). DNA metabarcoding of the sample is a faster post-sampling identification method for measuring diversity (though abundance is lost), and nondestructive methods to sample from fixative fluids show promise (Marquina et al., 2019; Nielsen et al., 2019; Zizka et al., 2019). Although metabarcoding lowers the time costs off post-sampling identification, metabarcoding does come with increased costs related to DNA sequencing and additional genetic expertise is needed. See Hausmann et al. (2020) for a recent example of a malaise trap study employing metabarcoding. Finally, because malaise traps are sensitive to microhabitat variation – like most stationary sampling methods – multiple traps at a site are better than a single trap.

Light trapping

Overview

Light traps are one of the most common and efficient methods for surveying insect that fly at night. At their most basic, light traps simply consist of a light attractant and a viewing surface, often a bedsheet (Figure 2B). More structured light traps commonly consist of a funnel, vanes (which deflect insects toward the funnel), and a collection container, which together are used in conjunction with the light source to form a structured trap. In either case, light-attracted insects fly toward the light source, hit a surface or vanes surrounding the light, and can then be observed and recorded or sampled and collected. Common styles of vaned light traps include Robinson traps and Heath traps (Macgregor et al., 2017). Light traps provide an opportunity to gather standardized and comparable data, but many factors influence the abundance and composition of light trapped insects, including trap type, season, time of day, lunar phase, duration of sampling, and light attractant (Jonason et al., 2014). Consequently, these details are all important to track (Table 1). Mercury vapor bulbs are the most commonly used attractant and have consistently caught a higher abundance and diversity of insects than other standard bulbs due to the powerful low-wavelength light emitted (Jonason et al., 2014; White et al., 2016). Other commonly used bulb types include UV, metal halide, and LED (Ferro and Summerlin, 2019). Although many commercial light traps are available and can be deployed in remote locations, light trapping can be as simple as documenting the moths that are attracted to your porch light. Individuals interested in joining the Discover Life's Mothing project can join a network of people working to photograph and identify moths that come to their porch light (Pickering, 2015). Exemplar long term light-trapping programs include the Hungarian Light-trap Network (Szentkirályi, 2002) and the Rothamsted Insect Survey (Macgregor et al., 2019), both of which have been surveying phototactic insects for over 50 years.

Taxonomic considerations

Light trapping is appropriate for monitoring phototactic (i.e., light-attracted) night-flying insects in both terrestrial and aquatic habitats and is used for surveying a wide range of insect taxa (Figure 1), including flies (Diptera), true bugs (Hemiptera), beetles (Coleoptera), caddisflies (Trichoptera), parasitic wasps (Hymenoptera, and moths (Lepidoptera), among other groups.

Light trapping is especially appropriate for moths (Lepidoptera) (Macgregor et al., 2019), caddisflies (Trichoptera) (Waringer, 2003), and many beetle taxa (Coleoptera) (Liu et al., 2007).

Methodological considerations

Location*:* Spatial placement is extremely important for light trapping. Although light traps can attract insects from the surrounding environment, insects are rarely attracted at distances greater than 30 meters (Truxa and Fiedler, 2012). Therefore, the microhabitat of the trap location will influence what organisms are trapped, making it important to describe the trap location in field notes and record the precise coordinates of the trap location (Table 1). Light pollution can decrease the flight-to-light behavior of moth populations (Altermatt and Ebert, 2016), so light sensors (low quality light sensors are available as smart phone apps) should be used to note the lumens/m^2 of light pollution at the trap location.

Design*:* The wavelength and brightness of light attractants differs dramatically among different light bulbs and are important to consider when designing light trapping projects. If the goal is to sample the greatest abundance and diversity of insects, then we recommend using mercury vapor bulbs, as these are consistently found to attract the most moths (Jonason et al., 2014; White et al., 2016). However, mercury vapor traps may not be the optimal tool because of their cost and the logistics required to deploy them (e.g., an outlet or automotive battery is needed). Therefore, low-cost, light-weight, and easy to deploy light traps offer convenient alternatives and facilitate insect trapping at more sites and in more diverse settings (White et al., 2016). If light traps can be checked early in the morning, insects can be trapped alive by having traps lined with egg cartons to provide areas for the insects to hide (Jonason et al., 2014). Live specimens can be photographed in the field or later in the lab, after cooling in a refrigerator and then released the following night (Ford et al., 2020). If observation alone is undesirable, light trap containers can be lined with pest strips (18.6% dichlorvos [2,2-dichlorovinyl dimethyl phosphate]) or filled with ethanol.

Scalability***:*** Commercial light traps can be expensive (between US $75 and US $500). Additionally, commercial light traps often require outlets or car batteries, making carrying them into remote locations challenging. Homemade light traps can be inexpensively constructed and can greatly reduce weight by running efficient LED strips using small 12V batteries (White et al., 2016). Effort required for field sampling can be high if insects are live trapped and identified in the field or transferred to jars to be photographed. If insects are lethally trapped, sampling effort can be low, with just a few minutes spent setting the light trap each sampling event and a few minutes spent collecting the specimens the following morning. However, post processing costs can be high, as light traps can yield a high diversity and abundance of insects. Technological advances in “smart light traps”, where insects attracted to lights are automatically photographed throughout the night, offer great promise to increase the scalability of light trap surveys (Hogeweg et al., 2019).

Pan trapping

Overview

Pan traps (Moericke, 1951) are trays filled with liquid set out to collect insects. Pan traps often rely on color as an attractant and are effective primarily because insects mistake them for food resources. An insect flies to a pan, attempts to land, then becomes trapped in the liquid solution – often soapy water, propylene glycol, or saline (Figure 2). Pan traps can be made from nearly any object that holds liquid – i.e. a disposable plate filled with water and a few drops of dish soap – and this accessibility has made them more popular than more training-intensive methods that may sample more diversity (e.g., standardized sweep-netting; Cane et al., 2000). Like all sampling methods, there is no doubt that pan traps have considerable sampling bias for certain taxa (Portman et al., 2020). For detailed accounts of history and methodology, see Droege et al. (2017), LeBuhn et al. (2003), Vrdoljak and Samways (2012), and Southwood and Henderson (2009). An exemplar pan trap monitoring networks is the UK Pollinator Monitoring Scheme, and a data-recording scheme designed for bee monitoring can be found in LeBuhn et al. (2003).

Taxonomic considerations

Pan trapping is appropriate for monitoring flying insects (Figure 1C). It is effective at sampling aphids (Hemiptera), thrips (Thysanoptera), bees and parasitic wasps (Hymenoptera), flies (Diptera), some beetles (Coleoptera), and even some grasshoppers (Orthoptera) (Evans and Bailey, 1993; Westphal et al., 2008; Vrdoljak and Samways, 2012). Trap efficacy for each taxon varies strongly with pan color (Vrdoljak and Samways, 2012). Yellow is most commonly used, as yellow traps often collect the largest catches and highest total insect diversity, but other common colors include blue, white, red, and green. As with other monitoring methods, habitat and geographic region can affect the trap efficacy for a given group (Vrdoljak and Samways, 2012; Saunders and Luck, 2013). For those with broad taxonomic interests for their monitoring programs, we recommend what has become a common standard: yellow pan traps in conjunction with white and blue pan traps (Vrdoljak and Samways, 2012; Sircom et al., 2018), as is done in the UK Pollinator Monitoring Scheme. If needed, traps can be painted using colors defined by the Bee Inventory Plot program (LeBuhn et al., 2003).

Methodological considerations

Location: Pan traps are typically placed in open areas where they can be seen by target insects. Traps can be placed together as close as 5m – the minimum distance at which they do not influence each other (Droege et al., 2017). Although a large diversity of spatial arrangements exist, we recommend one of two methods. The first method, used by the UK Pollinator Monitoring Scheme, places 1 trap per square km, and is suitable for sampling large geographic regions. The second method, from the Bee Inventory Plot (LeBuhn et al., 2003), uses 15 traps in a single array, each separated by 5m and placed in two perpendicular lines forming an “X”. This arrangement is suitable for targeted monitoring, with two arrays (30 traps) demonstrated as being adequate for sampling local bee diversity (Shapiro et al., 2014).

Design*:* For discussion of pan trap color, see *Taxonomic considerations*. Pan traps can be placed on the ground (most common), elevated above the ground, or placed flush with the substrate (i.e., essentially modified pitfall traps). Elevated pan traps sometimes yield larger numbers of specimens (Tuell and Isaacs, 2009), and pan traps flush with the ground can also attract ground-dwelling species (Ernst et al., 2016). Trap size may not affect catch (Gonzalez et al., 2020), so small pan traps are desirable to minimize costs; circular pans with a 7 cm diameter are common. In arid areas, the trap solution may evaporate too quickly between visits, so larger pan traps can be used, for example, 2-gallon buckets. The amount of liquid in a trap can affect trap efficacy and should be recorded when setting up and checking traps. We recommend premixing the liquid solution recipe of LeBuhn et al. (2003): 1 part dish soap to 750 parts water (approximately 1 teaspoon soap for a gallon of water).

Because pan color is the main attractant, it is important to maintain trap color through frequent cleaning and eventual trap replacement when color fades. Scented water like rose water can be used to increase catches for some taxa (Laubertie et al., 2006) but since maximizing the number of individuals caught is not necessarily a goal of standardized monitoring, we recommend against using scents or baits for benchmarking. Small amounts of preservative chemicals can be added to prevent fungal growth when the time between visits is necessarily long, but chemical safety precautions should be taken.

Scalability*:* Pan traps are low cost but require frequent (often daily) trap visits and maintenance. For an estimated time budget for a 24-pan transect, see Droege et al. (2017). Specimen processing times can be high depending on target taxon abundance. A typical pan in a field could yield only a few specimens over 24 hours, but even with low abundances, numbers can rise quickly if using multiple traps over long time periods. Sieving with nylon mesh (e.g., an aquarium net) is a common practice that speeds up specimen processing, but can damage small, fragile taxa such as aphids.

Pitfall trapping

Overview

Pitfall traps (Hertz, 1927) are containers placed flush with ground level to capture ground-dwelling (epigeic) insects. In essence, an insect walks to the trap edge, loses balance, and falls in (Figure 2D). The container is then checked, the catch collected or documented, and reset. Several recent reviews have discussed pitfall trapping (Skvarla et al., 2014; Brown and Matthews, 2016; Hohbein and Conway, 2018), and standardized traps have been proposed by Brown and Matthews (2016). Like any insect sampling method, pitfall traps produce taxonomically biased samples (Topping and Sunderland, 1992; Lang, 2000), but are inexpensive and popular for monitoring. For detailed methodological accounts, see Southwood and Henderson (2009), Brown and Matthews (2016), and Hoekman et al. (2017). Existing pitfall trap monitoring networks include the US National Ecological Observatory Network (NEON; Hoekman et al., 2017), and the UK Environmental Change Network (Brooks et al., 2012).

Taxonomic considerations

Pitfall traps are most appropriate for sampling ground-dwelling beetles (Coleoptera) – especially Carabidae and Staphylinidae – and ants (Hymenoptera: Formicidae) (Baars, 1979; Skvarla et al., 2014). They may incidentally collect flying taxa, especially if the trap is roofless and white or yellow (Buchholz et al., 2013), but are not an effective sampling method for most other groups (Figure 1).

Methodological considerations

Location*:* Pitfall traps can be placed nearly anywhere with suitable substrate for digging. There is some controversy over how far apart traps should be placed; some studies have found that traps provide independent samples even when only 1m apart (Ward et al., 2001), while others recommend 10m (Hohbein and Conway 2018). NEON, which conducts standardized trapping across North American sites, separates traps by at least 25m. Digweed et al. (1995) found that population depletion occurs when traps are separated by 10m or less, but not if separated by distances of greater than 25m. Until there is more consensus, a 25m distance between traps should be adequate to ensure independence of samples.

Design*:* Pitfall traps can be made of glass, plastic, or metal, but disposable plastic cups have become perhaps the most widespread trap container. The container should be placed with its lip flush with the soil surface. As might be expected, the diameter of the trap affects catch (Abensperg-Traun and Steven, 1995). Collecting fluid should generally be used to avoid damage to specimens from other trapped insects and to prevent escapes, but the type of collecting fluid used can affect the taxa attracted (Skvarla et al., 2014). Ethylene glycol has been traditionally used but is toxic for wildlife if consumed and can be easily substituted with propylene glycol, which we recommend for most uses. Propylene glycol evaporates more slowly than ethanol and adequately preserves most DNA, at least over the short-term (Nakamura et al., 2020). Traps with baits will be more readily disturbed by vertebrates (Vandenberghe, 1992), and should be avoided. Fences, or guidance barriers that direct insects towards the trap, can increase catch (Boetzl et al., 2018) but require more effort to set up. Pitfall color affects taxonomic composition of the catch (Buchholz et al., 2013) and should be recorded; we recommend using transparent containers as described in Brown and Matthews (2016). Using funnels increases catch efficiency while simultaneously reducing vertebrate bycatch (Radawiec and Aleksandrowicz, 2013), although low roofs also reduce vertebrate bycatch (Hoekman et al., 2017). Roofs also prevent rain from diluting the collecting fluid and appear to not influence the composition or magnitude of insect catch (Buchholz and Hannig, 2013). Containers should be nested to allow fast and easy removal of samples. Disturbance from trap placement can affect catch, so a latent period of one to two weeks before trap monitoring begins should be observed if possible (Greenslade, 1973). Calls for pitfall trapping standardization have a longer history than other monitoring methods (Brown and Matthews, 2016), and we recommend alignment with existing programs. Given the broad extent of NEON, we recommend that new monitoring programs (at least those in North America) adopt the NEON pitfall trapping protocol when practical (Hoekman et al., 2017). This protocol involves nested clear plastic cups (diameter: 11 cm, depth: 7 cm, volume: 473 mL) and a roof made of hard plastic raised 1.5 cm above the trap entrance. Each trap is filled with 150 mL of an equal ratio of propylene glycol to distilled water. Traps are placed in arrays of 4, arranged in a square with sides 25m long.

Scalability*:* Pitfall trapping using disposable plastic cups is relatively cheap and easily scalable. Set-up can be labor intensive depending on the design (and the inclusion of fences), but under the NEON protocol is limited to simply digging an appropriately sized hole and placing the trap and roof. Checking traps is also a low time commitment, especially when using a nested cup design, which allows for easy removal.

Beating sheets

Overview

A beating or beat sheet is a piece of fabric supported by a frame, which is placed below a substrate of interest (e.g., a tree branch). An insect rests or feeds on the substrate, which is then shaken or hit ("beat"), dislodging the insect so that it falls on the sheet where it can be collected or recorded (Figure 2E). This active sampling method is often used in conjunction with an aspirator to suck up fast-moving taxa. Currently, the most common design is two pieces of wood or PVC pipe forming an "X", with a piece of white fabric (e.g., bedsheet) stretched behind. Alternative designs include simply placing a sheet on the ground, or even using an umbrella. Beating sheets are cheap, easy to build, and straightforward to use. Insects can be recorded visually or collected for further identification depending on project goals. The Caterpillars Count! citizen science program (Hurlbert et al., 2019) is an example of a beating sheet monitoring network in North America.

Taxonomic considerations

Beating sheets are appropriate for sampling tree and shrub dwelling insects, such as caterpillars (Lepidoptera), some true bugs (e.g., aphids and scale insects; Hemiptera), some beetles (Coleoptera), and other plant-feeding insects (Figure 1). It is not a good method for sampling flying insects; they will often fly away when the branch is hit, or hit the sheet, then quickly escape.

Methodological considerations

Location*:* Beating sheets can be used anywhere vegetation is found for beating: typically shrubs and trees, but also groundcover in some cases.

Design*:* The standard size and shape for a beating sheet is a square with sides of about 90 cm (3 feet), using two pieces of PVC or wood 1.3m (51 inches) long for crossbars. A cloth can then be stapled or glued to the crossbars. White cloth should be used to maximize visibility of insects that fall on the sheet. The object used for hitting the substrate can vary, but dimensions should be recorded; a stick of about 2.5 cm (1 inch) diameter and 60 cm (2 feet) long works well. The surveyor should strongly hit the branch 10 times, but not so strongly that the plant is damaged. Because many insect species have some degree of host specificity, substrate type (e.g., tree species) strongly predicts insect species diversity and abundance. This will affect sampling decisions depending on your goals; sampling plants of only one species or of multiple species are both reasonable. Either way, we strongly recommend always recording the plant species (Table 1). If collecting specimens, using an aspirator helps capture fast-moving or flying insects.

Scalability*:* A simple beating sheet can be constructed in less than 15 minutes using materials that cost less than US $10 [2]. As an active sampling method, using beating sheets can be more time consuming than passive methods, but usually not prohibitively so. Sampling a substrate and collecting the specimens can take less than 5 minutes. Visual surveys can be substituted for specimen collection to reduce time spent on post-sampling identification, but at the likely cost of taxonomic resolution. Only one beating sheet is needed per person sampling. Some research suggests that three plants of the same species is the minimum necessary to accurately estimate insect abundance (Harris et al., 1972).

Acoustic monitoring

Overview

Acoustic monitors provide a passive, non-destructive method to detect and identify insects (Ganchev et al., 2007; Mankin et al., 2011). Insects may generate bioacoustic signals as a means of communication (Penone et al., 2013), or as a by-product of locomotion (Kawakita and Ichikawa, 2019). These bioacoustic signals may be captured as sounds with microphones or as vibrations with contact sensors (Figure 2F). Although contact and ultrasonic sensors have been successful in detecting insect pests that live inside agricultural products (Mankin et al., 2011), we focus here on acoustic recording units and their use for surveying the relative abundance and diversity of insects. Many factors influence the efficacy of acoustic devices in identifying and estimating density of insects, including the frequency range, substrate (air or water), type of sensor, the size and behavior of the insect, and the distance between the insects and the sensors

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[2] https://vimeo.com/43932105

(Gibb et al., 2019). These factors should be considered and noted when conducting surveys using acoustic monitoring. Large-scale acoustic monitoring has been successfully coordinated by the French National Museum of Natural History to assess the impacts of anthropogenic stressors on Orthoptera communities (Penone et al., 2013; Jeliazkov et al., 2016).

Taxonomic considerations

Acoustic monitoring is an appropriate method for monitoring insects that use sounds or vibrations in communications. Some of these noises, such as cicada and cricket songs can be detected over long distances. If the bioacoustic signal produced by insects follows a consistent species-specific pattern, it can be extracted from background noise for identification purposes (Ganchev et al., 2007). Therefore, passive acoustic monitoring is particularly well suited for loud terrestrial insects such as Orthoptera or Cicadoidea because they produce species-specific mating calls (Penone et al., 2013) (Figure 1), but may also be useful for a variety of other insects including bees (Galen et al., 2019; Kawakita and Ichikawa, 2019) and aquatic Hemiptera (Desjonquères et al., 2020; Gottesman et al., 2020).

Methodological considerations

Location: The distance at which acoustic signals can be detectable above ambient noise varies depending on the sound's amplitude and frequency, landscape heterogeneity such as topography and vegetation, and weather (Gibb et al., 2019). Additionally, anthropogenic sounds or sounds from other animals can mask target sounds. The precise GPS coordinate of where static sensors are deployed must be recorded and potential sources of sound pollution should be noted (Table 1). Bioacoustic devices can also be used while traveling along transects, but we recommend keeping bioacoustic devices in fixed locations to collect data that is easier to standardize across sites and replicate across visits.

Design: Commercially available acoustic monitors can be flexibly programed to collect acoustic signals and on-board metadata for long intervals across a variety of sampling regimes (Hill et al., 2019). The use of inexpensive components (e.g., microelectromechanical systems microphones) may decrease financial barriers to initiating multisensor surveys but can lower data quality by having lower signal-to-noise ratios and inconsistent frequency response (Gibb et al., 2019). Critical to successful acoustic surveys is the development of efficient pipelines to process sound files and output annotated data. Manually annotating data is time consuming and can be biased by the analyst’s knowledge level. Developing automated machine learning pipelines to process individual sound files – which can each include more than 10 minutes of ambient sound recording – can both increase the efficiency of data processing while also making data processing more reproducible and interoperable.

Scalability: Recent advances in custom built electronics and the lowering costs of small but usable microphones provide novel opportunities to monitor select insect taxa across greater spatial and temporal scales. Passive acoustic monitors can automatically collect data over long periods (e.g. a month), with minimal maintenance needed to replace batteries and digital memory cards (Hill et al., 2019). Typically, they are programmed to record periodically during a window of interest. Recent developments in customizable acoustic devices have dramatically lowered costs closer to US $50 (Hill et al., 2018). Developing automatic identification pipelines using machine learning algorithms is critical to scaling acoustic monitoring and discussed further in section 4.

Active Visual Surveys

Overview

Visual surveys are commonly used to document the abundance and diversity of insects that can easily be visually identified in the field, often with the aid of close-focus binoculars and nets (Figure 2G). These surveys typically involve researchers documenting the presence of a species or counting the total number of individuals of each species observed during a standardized survey. The most frequently used methods include (1) transects, (2) point counts, and (3) area counts. Although mark/recapture is another frequently used visual survey technique to document insect population dynamics, we do not consider that a viable benchmarking technique as it takes enormous effort and would not be tractable to do simultaneously for large numbers of insect species.

All three of the commonly used methods have extensive histories of standardized protocols. Transect counts use visual identification while searching along predefined transects with specified search distances. Pollard walks are a commonly used transect method used in butterfly research, in which an observer visualizes a box that extends 5m ahead and 5m to the sides as they walk a transect counting butterflies (Pollard, 1977). Point counts, where an observer stands still and identifies and counts the number of individuals of the target taxa around them during a set period of time, provides an alternative to transects in sites that are difficult to walk in or where habitats are fragile or at-risk (Henry et al., 2015). Distance sampling techniques, where observers note their distance from the observed insect, can be implemented with both transects and point counts to estimate densities (Isaac et al., 2011; Henry et al., 2015). By incorporating imperfect detection, distance sampling allows for density and absolute population size to be estimated in closed populations (Buckland, 2001). Area counts, such as the North American Butterfly Association's count circle (Taron and Ries 2015), consist of surveyors counting each species within a delimited study plot during a certain time period. Insects that are challenging to identify quickly or in flight can be netted and transferred into vials and placed in a cooler to chill until the end of the survey period (Loffland et al., 2017). Photos of chilled individuals can then be taken for later identification before releasing these individuals. Exemplar visual survey programs include multiple butterfly monitoring schemes (BMS) such as the UK BMS, the Dutch BMS (Schmucki et al., 2016), and the Ohio Lepidopterists BMS (Wepprich et al., 2019).

Taxonomic considerations

Visual surveys are only appropriate for large insects that can be easily detected and identified or photographed in the field. Butterflies (Papilionoidea), dragonflies and damselflies (Odonata), and large bees (Apidae) such as bumblebees are effectively sampled using visual surveys (Figure 1). When species cannot be identified, individuals can be netted and then identified or photographed (Loffland et al., 2017; Holtmann et al., 2018). However, not all species can be identified in the field; for some species, microscopic examination of the genitalia and abdominal appendages is necessary for identification. Visual surveys generally focus on generating a complete list of species observed (with or without counts), and therefore, visual surveys must focus on a select target group of insects (e.g., butterflies or bumblebees).

Methodological considerations

Location*:* The location of the visual survey is important as many insects are habitat specialists. After selecting sites for visual surveys, multiple transects, points, or areas should be randomly selected to ensure sampling across the heterogeneity of a site. It is important to document the coordinates of the survey location and note the habitat type. Visual surveys occurring in difficult terrain or in at-risk ecosystems may consider choosing point counts to limit trampling or allow for more flexible walking routes.

Design*:* Care should be taken when selecting the location of visual surveys, as we recommend these locations remain fixed to enable surveys to be compared from year to year. Transect surveys should be at least 1 km in length, although visual survey methods allow for the correction of survey effort by adjusting by the length of the transect or by time of survey (Taron and Ries, 2015). Thus, detailed information must be documented on the length of transects and the start and end times of surveys (Table 1). Consistent and repeated surveys are needed to capture the seasonal abundance of individual species and to fully capture the diversity of the community. Therefore, surveys should begin before the first adult individuals of the target group are presumed to be active and terminate after the final adult activity. During this period of activity, visual surveys are recommended to occur weekly when conditions meet the time of day and weather criteria suggested by Pollard and Yates (1993). Surveys should occur between the midday hours of 1000 and 1700 when air temperature exceeds 13°C (although this may be reduced to 11°C in polar, upland areas) and there is at least 60% sun or 17°C in any conditions, providing it is not raining and wind speeds are below a six on the Beaufort scale (Pollard and Yates, 1993).

Scalability*:* Visual surveys can require extensive field effort with the potential of a single survey taking multiple hours complete. Due to the field effort required to complete visual surveys across numerous sites, many successful visual survey programs rely on the dedication of numerous trained volunteers (Wepprich et al., 2019; Schmucki et al., 2016). Critical to the success of visual surveys is a rigid observer training protocol, as untrained observers tend to have biased distance estimates and observer experience can significantly affect detection functions (Buckland, 2001). Visual surveys generally have limited post-sampling effort, with the main effort being transcribing field notes and data collection sheets. This process can be further enhanced by using GPS handheld tablets to record data in the field (Hackett et al., 2019).

General Methodological Considerations

Replication

Four types of replication are especially important when sampling: spatial, inter-annual, intra-annual, and within-sample replication. All types of replication are important and broaden the inferential scale of any monitoring program while also expanding the analytical options and flexibility. We caution, however, that when sampling lethally, large-scale replication (particularly, spatially and temporally intense sampling at a local scale) could theoretically lead to abundance declines, especially perhaps in rare taxa (Minteer et al. 2014, but see Gezon et al. 2015). Lethal sampling should only be done when scientifically and ethically justified (Drinkwater et al. 2019).

The required amount of spatial replication for accurate and precise monitoring is still unknown for many insect monitoring methods, and contentious for others. We provide specific discussion in each method section, but in general, the more spatial replication, the more accurate and precise the estimates of measured responses. One way to increase the degree of spatial replication without increasing individual effort is to join an existing monitoring network, thereby increasing the network's degree of spatial replication.

A high degree of inter-annual replication is important for monitoring of most taxa (Wauchope et al., 2019), but is especially important for measuring insect abundance, where large year-to-year fluctuations are common (Didham et al., 2020). Failure to account for high inter-annual variability has led to disagreements over whether some insect populations are truly declining or not (see Willig et al., 2019 in response to Lister and Garcia, 2018).

A high degree of intra-annual replication is also important because insect phenology is complex and variable. For example, the week of peak abundance for a species one year could be different the next year, and even the number of generations produced by a species can vary across years. Even if only interested in studying occurrence or abundance, intra-annual variation in phenology of insect activity and generations can lead to strong biases in these responses if samples are only collected once per year (i.e., the "groundhog effect"; Didham et al., 2020). To account for this, we strongly recommend that monitoring efforts be carried out for the entire season of activity for the taxon of interest, allowing easier comparison across years.

Finally, within-sample replication – that is, multiple samples of a response at a single site during a period when the occurrence and abundance of target taxa are assumed to be constant – can be important for the statistical analysis of trends when trying to account for imperfect detection of individuals and species, such as with occupancy modelling (MacKenzie et al., 2006). Within-sample replication can be achieved either through spatial sub-samples – for example, using "array" designs, as discussed above for pitfall and pan traps – or temporal sub-samples – such as conducting visual or acoustic surveys at the same location multiple days in a row. In general, the ability to collect within-sample replication of monitoring data depends on the design and scalability of a chosen method. Although within-sample replication can substantially increase effort of monitoring, the ability of increased samples to account for sampling noise can be extremely powerful when detection probabilities of target taxa are low. For recent examples of occupancy modelling using some means of sampling replication for insects, see Isaac et al.

(2014), Loffland et al. (2017), Outhwaite et al. (2019), Szewczyk and McCain (2019), and Powney et al. (2019).

Curation of specimens

Many of the monitoring methods discussed require collecting insect specimens for subsequent identification. After identification, it is generally up to the scientist whether specimens should be kept or discarded, although vouchering of representative taxa can be key to the long-term value of datasets, particularly given taxonomic revisions and new technologies. To that end, great care should be taken to ensure specimens are preserved properly, if kept. For an overview of insect specimen storage, see Heraty et al. (2020). It is becoming increasingly common to preserve specimens in 80-95% ethanol to better preserve DNA. Regardless of the preservation method, it is worth developing a plan for deposition and cataloguing of specimens prior to beginning a monitoring project. If discussed ahead of time with university and museum insect curators or collection managers, specimens that are properly preserved and curated should be donated. Optimally, archival deposition should include all survey notes, along with specimens, to enhance long-term re-use value.

Curation of data and metadata

Just like physical specimens, data are valuable resources for future science. Just as important as data are metadata, that is, the collective information about how the monitoring data were collected. Each method of insect monitoring has its own unique set of critical metadata (Table 1). Monitoring programs should strive to meet FAIR data principles to ensure their data and metadata are: findable, accessible, interoperable, and reusable (Wilkinson et al., 2016). Findable and accessible data will require that collected data are digitized and uploaded to websites or online databases that are constructed to hold data about the collecting method. There is much work on this topic that needs to be done, but some resources are developing rapidly.

Interoperable data may be the most challenging aspect of FAIR principles, given that each monitoring program often develops its own reporting standards, even for the same monitoring methods, which ultimately places the burden on downstream users to reintegrate, often with loss of key information. Recent efforts have called for unified, global monitoring standards, such as the Humboldt Core metadata standard (Guralnick et al., 2018). While it is unlikely that one data standard will fit all insect monitoring, the Humboldt Core provides a typology of different survey and inventorying processes, such as restricted or open searches, along with key definitions of taxonomic, spatial, and temporal scopes, that strongly aid in discovery of monitoring datasets. More specific metadata describing particulars of different monitoring schemes can and should be accommodated (Table 1). We argue that rather than assume an improbable utopia of full data integration, monitoring programs should work in federations and take seriously the production of detailed metadata, and, as much as possible, develop standardization for metadata that can be as easily linked as possible into existing frameworks. The end result will be FAIR data that can most easily be integrated into flexible modeling frameworks that allow statistical integration of well-described data to better answer broad-scale ecological questions.

As with specimens, it is critical that a plan for data management be considered prior to beginning a monitoring project. Data standards are a key part of that plan since monitoring metadata is crucial for generating insights from monitoring outcomes. However, other factors are also critical, including developing local data storage solutions, deciding on a longer-term repository for data, assuring appropriate credit models for those involved with data collection, and licensing and use agreements of data products. Each of these issues deserves its own longer contribution and we point readers to Michener (2015) and Hardisty et al. (2019) for further reading. Here we make two broad recommendations. First, we strongly suggest development of a coherent data storage and sharing plan that has community buy-in. A best-case approach is development of an internal content management system that provides tools for data access and curation for program participants along with a broad, coherent, and multipronged, data sharing policy that assures long-term access. One part of this sharing policy should focus on best practices for archiving data in community repositories such as Zenodo and Dryad. A second part should focus on publication to aggregators that specialize in biodiversity data mobilization, such as the Global Biodiversity Information Facility (GBIF). The value of publishing to GBIF is enhanced discoverability, since it acts as a single, global access point to biodiversity data and information. However, it can still be challenging to properly publish all survey metadata given GBIF's reliance on standards that were built for incidental records (Guralnick et al. 2018). Finally, we also encourage monitoring programs to explicitly state data collection and review policies, including how individuals within the programs are credited for the work they do. Such credit models may include attribution for use of data, which can be supported by both licensing mechanisms such as creative commons licenses, and data use policies.

We also encourage development of digital tools to support the capture of field data. Digital tools (e.g., phone apps) can limit transcription errors and are sometimes easier to manage in the field. However, physical data sheets still play an important role in most monitoring programs and are a reliable backup over the very long-term. For these, archival-quality paper and ink should be used to maximize longevity. Though the cost and effort are not trivial, undigitized data can be digitized increasingly easily via scanning and optical character recognition (OCR) capture.

Finally, the entoGEM project[3] (Grames et al., 2019) is soliciting unpublished insect abundance and diversity time series for inclusion in a global systematic map and meta-analysis. EntoGEM is a database, not a repository, but can serve as a temporary mechanism for archiving until a suitable repository is found and is a way to increase the utility of your data.

Looking Forward

Traditional survey methods are limited by being labor and time intensive, but ecological monitoring of animals has recently undergone a dramatic transformation with the development of technologies that expand the spatial, temporal, and taxonomic scales possible to monitor biodiversity (Pimm et al., 2015). These technological advances could facilitate the collection and availability of vast quantities of data by reducing the effort and expense of insect monitoring. No single method will be able to monitor multiple different insect groups across diverse landscapes. However, a combination of emerging technologies in surveying methods, processing, and data sharing pipelines will allow insect trends to be extracted at currently unprecedented scales.

We are entering an era where passive automated monitoring is already augmenting the traditional methods discussed above. Passive acoustic monitoring using arrays of acoustic sensors are already being deployed and tested. Such new methods have enormous promise, but also produce enormous volumes of data. A single acoustic recording unit can easily generate hundreds of gigabytes of data, with much of the data consisting of non-target (i.e., non-insect) sounds. Algorithms to automatically locate and identify target sounds within audio recordings are being developed (Gibb et al., 2019), and machine learning approaches can substantially improve

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[3] http://entogem.github.io

detection and classification accuracies by discriminating spectro-temporal information directly from annotated spectrograms. These algorithms have been demonstrated to outperform alternative detection and classification methods in a variety of settings (Fairbrass et al., 2019). Unfortunately, one of the greatest barriers to detecting and classifying species using passive acoustic monitoring is the limited availability of expert-verified sound databases for reference and training data (Gibb et al., 2019). This problem may be especially exacerbated for insects, given their vast diversity, the paucity of audio libraries, and that only 5% of published terrestrial acoustic monitoring research has been on invertebrates (Sugai et al., 2019).

Camera traps are another emerging surveying tool that are being used to monitor a variety of wildlife (Burton et al., 2015). Networks of many camera traps allow for data to be collected across greater spatial and temporal scales (Kissling et al., 2018). Like with acoustic monitoring, deep learning convolutional neural networks are being developed to automatically count and identify wildlife (Norouzzadeh et al., 2018). The relatively small size of insects compared to wildlife typically captured using camera traps provides unique challenges to monitoring insects with cameras. However, recent studies have shown the potential of camera traps to monitor the overall abundance of flying nocturnal insects (Ruczyński et al., 2020). Additionally, a portable computer vision light trap has been developed to attract and identify live moths (Bjerge et al., 2020), and a monitoring network of camera traps that are made with smart image processing has been proposed to monitor light-attracted insects in the Netherlands (Hogeweg et al., 2019). Continued effort into developing camera traps designed to monitor insects has great potential for passive surveying of non-acoustically detected insects at greater spatiotemporal scales.

Environmental metabarcoding is an emerging tool that provides rapid and cost-effective means for taxonomic identification of many organisms in terrestrial and aquatic environments (Piper et al., 2019). These approaches can provide detection/non-detection data for insects collected from a variety of methods, especially if specimens are stored in 80-95% ethanol. Metabarcoding insect feces (e.g., frass) offer another non-lethal surveying tool, as caterpillars have been identified to species by amplifying larval DNA from caterpillar feces (Rytkönen et al., 2019). Unfortunately, most insects have insufficient reference sequences in public archives such as GenBank, making genetically identifying insects challenging. Still, environmental metabarcoding provides a cost-effective and efficient option to identify insects collected in large quantities.

Radar can also create standardized monitoring data for insects at broad spatial and temporal scales (Didham et al., 2020). Filtering insects from meteorological data can provide previously unused datasets to monitor insects through time and have been used to document the decline of burrowing mayflies (*Hexagenia* spp.) across North America (Stepanian et al., 2020). In most cases, species-level identification cannot be accomplished using radar approaches, but specialized entomological radar shows promise in monitoring insects that may migrate in large abundances at heights difficult to monitor using traditional approaches.

New methods do not need to work in isolation nor are they replacements for traditional monitoring methods. Rather, these new approaches are ways to augment existing ones, and to lower costs for onerous activities that may be partially or wholly automated. We envision passive monitoring tools that can be deployed in conjunction with traditional trap or restricted search methods. For example, acoustic monitors and camera-loaded light traps could be controlled by one device and augment, for example, pitfall trapping, to capture a broader spectrum of insects at a single site. If these sensor approaches also have means to easily share data across a network of sensors and people, it may speed up necessary steps to create the most usable data resources for broad-scale insect monitoring.

Conclusion

We live in an era of rapid change that affects nearly all life on Earth. We can only understand this change and its effects on insects by pooling effort, integrating projects, and working together. Methods standardization is a relatively simple first step, but what challenges come next? For one, we urgently have to coordinate our use of these tools. Networks of networks need to be built for data collection. This means incentivizing participation, coordinating new and existing projects, and organizing efforts on a trans-national scale. Large networks should communicate with each other to increase complementarity, and smaller networks should seek to fit in with what is already being done while maximizing the utility of their own data. But coordination is likely not the greatest challenge.

The largest bottleneck for insect monitoring is getting from trap to accessible data – we need to accelerate the time-consuming stage spent processing and identifying specimens and build tools for the efficient capture of all data and metadata associated with an observation. Improving identification is an area where we have immense potential for advancement over the near term. Bringing more automation to this stage will result in much shorter lag times between data collection and analysis and increase scalability of new and existing projects. Tools for automating identification include metabarcoding, computer vision, and machine learning. Efficient expansion of these identification tools will not only facilitate the broader participation of individuals in insect monitoring (e.g., those without specific skills in taxonomy), but the digital nature of automated and semi-automated identification will speed up data accessibility and metadata capture.

We also need analytical advances for integrating data collected by multiple sampling methods. Assimilating data collected using the same benchmarking method into a composite database is the first step, but ultimately, integrating data collected by multiple different means will vastly improve our ability to understand the broader insect community. But even if we arrive at the point where all the necessary data are being collected on a global scale, the best data in the world are useless if they are not made available – where availability means in a digital format that adheres to all of the FAIR principles. Consequently, we also need the infrastructure to aggregate, store, and share data widely –existing databases such as GBIF are paving the way – while also recognizing the importance of attributing credit (e.g., Chavan and Penev 2011) to incentivize participation in the process of infrastructure development and data curation.

Every one of these challenges will require collective action to overcome. In the face of rapid Anthropogenic change, there is an intense urgency to this effort. These are no small tasks, and the timeline for completing them is short. Benchmarking has no point when there is nothing left to benchmark. Appropriate foresight and funding would have developed large-scale insect monitoring long ago, but the second best option is to rapidly build capacity now.

Conflict of Interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Author Contributions

G.A.M. and M.W.T. conceived the idea for the manuscript and proposed the initial outline. G.A.M. and M.W.B. led writing of the first draft. All authors contributed critically to drafts and gave final approval for publication.

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Tables

Table 2.1. Recommended metadata for each of seven methods of insect monitoring. In order for systematic insect monitoring data to be fully used and integrated by future researchers, scientists need information on the methods and conditions underlying data from insect monitoring (i.e., metadata). Metadata fall into a number of general classes, documenting details on: locality, site, temporal, and environmental conditions, and sampling methods. Some metadata will need to be collected every time insect data are collected, while other metadata will only need to be collected once, for example, when traps are first set up. Metadata should be stored alongside insect data (both on paper and digitally) and efforts should be made to include all metadata when contributing survey data to data aggregation projects.

Metadata class	Required metadata	Malaise trapping	Light trapping	Pan trapping	Pitfall trapping	Beating sheet	Acoustic monitoring	Active visual surveys
Locality	GPS Coordinates of sampling location(s)	X	X	X	X	X	X	X
-	Location description	X	X	X	X	X	X	X
-	Photo of trap in situ	X	X	X	X	X	X	X
Site Description	Habitat description	X	X	X	X	X	X	X
-	Photos in four cardinal directions showing habitat	X	X	X	X	X	X	X
-	Description of plant phenology (e.g., leaf-out, flowering, senescence)					X		X
-	Amount of light pollution		X					
-	Sampling substrate (e.g., plant species)					X	X	
-	Substrate size (including number of leaves)					X		
-	Substrate condition (e.g., wetness)					X		
Temporal	Date trap or monitoring established	X	X	X	X	X	X	X
-	Date of data collection	X	X	X	X	X	X	X
-	Time beginning data collection	X	X	X	X	X	X	X

-	Duration of data collection	X	X	X	X	X	X	X
-	Time of detection							X
Environmental	Wind during sampling (Beaufort scale)	X	X	X		X	X	X
-	Temperature during sampling	X	X	X	X	X	X	X
-	Precipitation during sampling		X	X	X	X	X	X
-	Humidity during sampling		X			X		
-	Cloud cover during sampling		X			X	X	X
-	Lunar phase during sampling		X				X	
Sampling description and placement	Trap or sampling equipment type	X	X	X	X	X	X	
-	Trap or sampling equipment photo	X	X	X	X	X	X	
-	Trap or sampling equipment manufacturer and model	X	X	X	X	X	X	
-	Trap or sampling equipment dimensions (e.g., size of capture area)	X	X	X	X	X		
-	Mesh hole size, density, and shape	X						
-	Killing agent	X	X	X	X			
-	Use of scent or bait			X	X			
-	Trap orientation	X						
-	Height from ground	X	X	X		X		
-	Bulb type, wavelength, power, and brightness		X					
-	Amount of liquid evaporation during sampling			X				
-	Trap, pan, or sheet color	X		X	X	X		

-	Collecting method (e.g., aspiration)	X	
-	Number of hits per substrate	X	
-	Object dimensions and weight used for hitting	X	
-	Detection distance		X

Figures

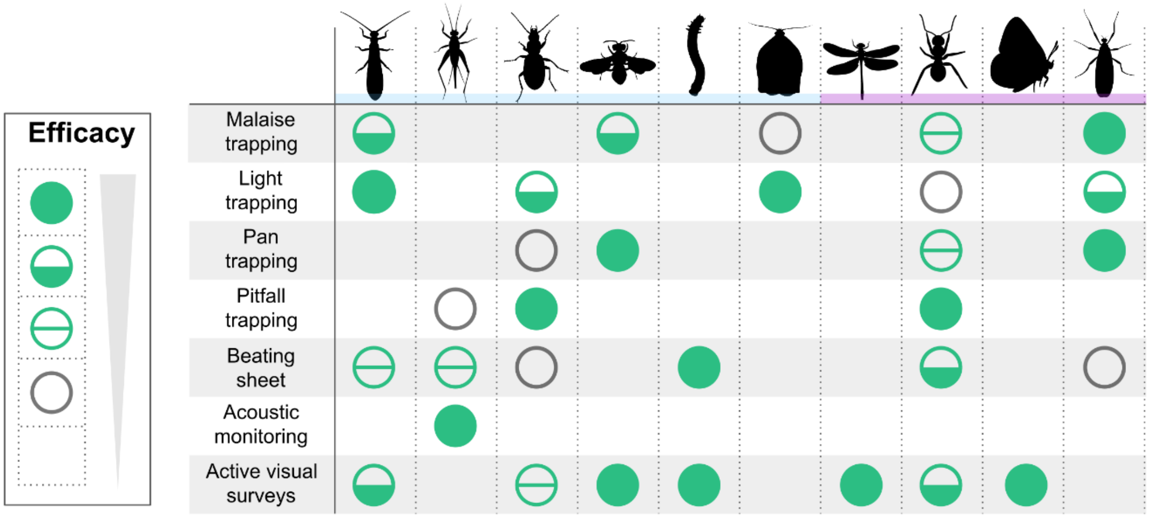

Figure 2.1. Commonly-monitored insect guilds and taxa and the efficacy for each of seven benchmarking methods. Efficacy of each method for a given insect group is scored as follows: filled green circles indicate optimal suitability; half-filled circles indicate possible suitability; divided, unfilled circles indicate marginal suitability; unfilled gray circles indicate bycatch only; and no circle indicates general unsuitability. Insect groupings are defined by ecological traits (blue bar) or taxonomic clades (purple bar). In order by column, insect groupings are: adult semi-aquatic insects (Plecoptera, Ephemeroptera, and Trichoptera); singing insects (Orthoptera & Hemiptera: Cicadoidea); ground-dwelling beetles (Coleoptera: Carabidae and Staphylinidae); non-lepidopteran pollinators (Hymenoptera, Diptera, Coleoptera); leaf-chewing larvae (Lepidoptera and Hymenoptera: Symphyta); night-active moths (Lepidoptera); dragonflies and damselflies (Odonata); ants (Hymenoptera: Formicidae); butterflies (Lepidoptera: Papilionoidea); and flies (Diptera).

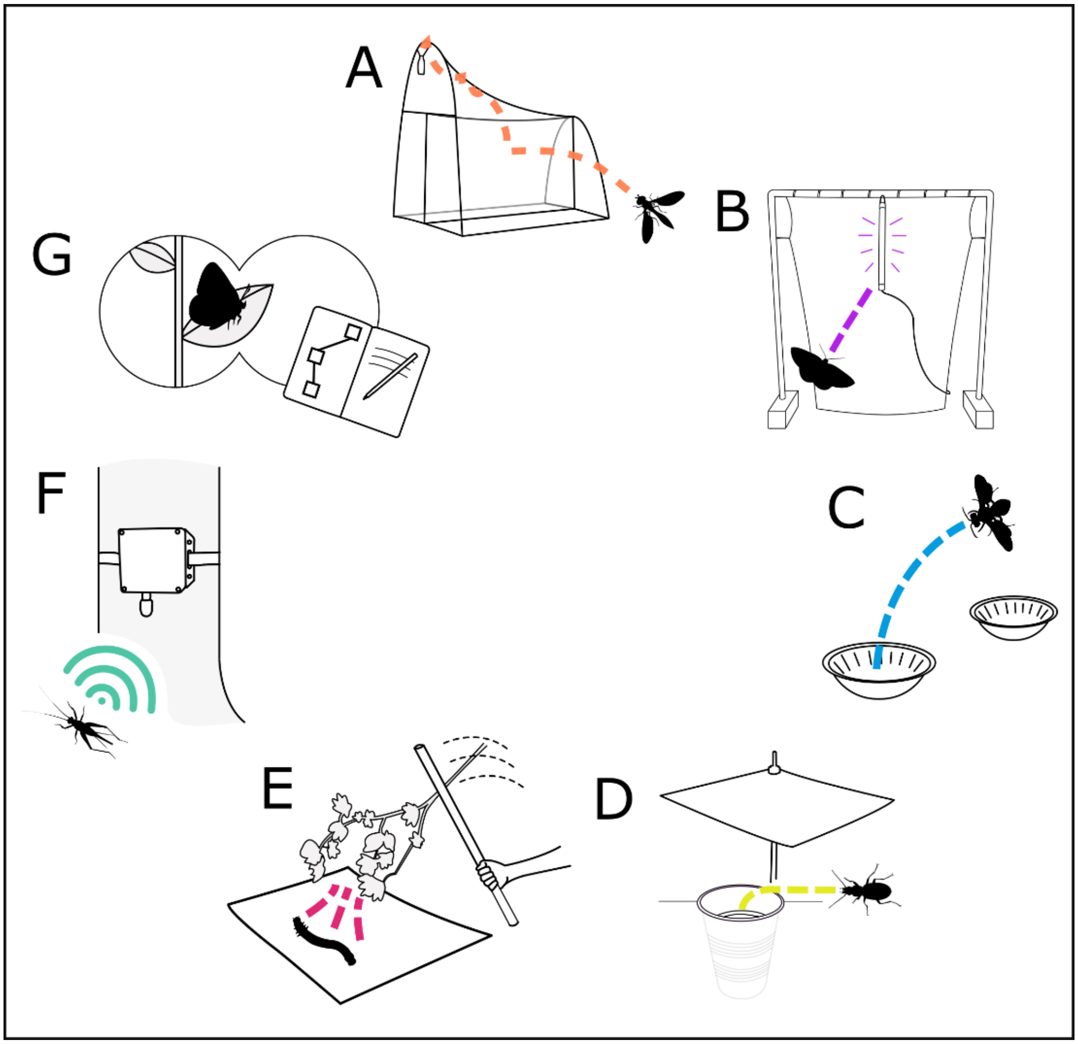

Figure 2.2. A visual overview of the seven insect benchmarking methods summarized here: (A) malaise trapping, (B) light trapping, (C) pan trapping, (D) pitfall trapping, (E) beating sheet, (F) acoustic monitoring, and (G) active visual surveys.

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Chapter 3: Are insect populations inherently more variable? A multi-taxa approach to characterizing interannual fluctuations in insect time series

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Statement of authorship

Authors often contributed to multiple components of the research, but generally, GM conceived of the study idea, EG, CE, MT, and DW informed study design and facilitated data collection, JJ, EK, AL, MR, QW, and GM collected data, GM and MT performed the analysis, GM wrote the first draft of the manuscript, and all authors contributed to revisions.

Abstract

The determinants of population variability across taxa, time, and space are not fully understood, particularly for insects, a group with recent reports of widespread abundance declines. We collated data from new and existing sources to calculate indices of interannual population variability for over 4500 unique insect time series, comprising data from nearly 1500 species. We evaluate whether insects exhibit greater population variability than other types of animals. Our results demonstrate that insects as a group indeed exhibit much greater population variability than birds, mammals, or fish, but that within Insecta, included orders show similar levels of population variability. We also find that population variability in insects is greater at higher latitudes, for species with smaller body sizes, and for shorter, older time series, and varies between biomes. Overall, our findings can inform the interpretation and prediction of insect population trends, fluctuations, and extinction risk in an era of insect decline.

Introduction

Variation in population size is a fundamental parameter for measuring and interpreting ecological change over time. Population variability (i.e., the magnitude of fluctuation) is the result of a complex interplay of endogenous organismal traits and exogenous biotic/environmental traits, and itself varies across taxonomic, spatial, and temporal scales (Lundberg 2000, Bjornstad & Grenfell 2001). It has frequently been suggested that high variability is associated with a high intrinsic rate of population increase (*r*; Spitzer & Lepš 1988, Gaston & Lawton 1988), small body size (Gaston & Lawton 1988, Sutherland & Baillie 1993), short lifespan (García et al. 2008, Májeková et al. 2014), and high abundance (Anderson et al. 1982, Owen & Gilbert 1989). Other patterns, like higher variability at higher latitudes (Hansson & Henttonen 1985, Dallas & Kramer 2022), have been proposed to result from environmental characteristics (Wolda et al. 1992, Gaston & McArdle 1994, Chisholm et al. 2014). Even the traits of time series themselves can have effects on variability: longer time series may possess higher variability (Inchausti & Halli 2005), possibly due to a higher likelihood of capturing longer-term population cycles (Pimm & Redfearn 1988), population trends, and/or rare environmental events (Gaston & McArdle 1994). Despite being a research focus for population ecologists since at least Andrewartha & Birch (1954), considerable uncertainty in the generality of these relationships about population variability persists (Gaston & McArdle 1994, Vázquez et al. 2017). And although recent progress has been made (Dallas et al. 2024), traits and spatiotemporal variables often explain only a small percentage of measured interspecific differences in population variability (White 2019). Thus, the relative influence of these drivers of population variability and their macroecological patterns across time, space, and taxon also remain incompletely understood.

High population variability is common across many taxa, from birds to phytoplankton to trees (Atkinson et al. 2006, Kane 2011, Chisholm et al. 2014), with fluctuations that can span orders of magnitude from generation to generation (e.g., Ives et al. 2008). This poses challenges for accurate population monitoring and conservation in an era of acute global biodiversity loss where climate change is additionally causing increased climatic variability (Thornton et al. 2014). High population variability can obscure long-term trends in abundance and distribution (Magurran et al. 2010, McCain et al. 2016), necessitating more years of data collection to achieve robust inference (White 2019). For populations at similar levels of abundance, it is well understood that higher population variability also increases extinction risk (Leigh 1981, Caughley 1994, Vucetich et al. 2000, Melbourne & Hastings 2008). Thus, estimates of population variability, even in broad terms, are needed to inform long-term population trend estimates, extinction risk analyses, and predictions of the effects of increased climate variability (McCain et al. 2016). This is especially true for taxa – like insects – where population monitoring is difficult and for which data are less often synthesized at large scales. Insect population trends have recently received intense scrutiny, as reports of widespread insect declines are mounting (van Klink et al. 2020), and large fluctuations have been suggested as a barrier to accurately detecting and estimating these declines (Didham et al. 2020, Aldercotte et al. 2022, Weiss et al. 2023).

As relatively small animals with generally short lifespans and high reproductive output, insects are often perceived as inherently having large interannual population fluctuations (Hanski 1990, Didham et al. 2020). While the truth of this supposition has been demonstrated in many cases at small spatial scales (e.g., Gaston & Lawton 1988) and for certain species (Turchin et al.

2003, Nelson et al. 2013), we currently lack robust, generalizable evidence for or against the exceptionality of insect population variability. This lack is surprising, given an extensive history of vigorous discussion on the topic. For example, Connell and Sousa (1983) found no substantial differences in population variability between vertebrates and terrestrial insects, and apparent variability differences (e.g., as found by Schoener 1986 and Ostfield 1988) have been suggested to be artifacts of measurement or design flaws (Gaston & McArdle 1994, Stewart-Oaten et al. 1995). In one recent analysis with contemporary methods, Dallas and Kramer (2022) found that insects as a group did not show significantly higher variability than fish, mammals, or birds. While this could represent a definitive answer, we note that testing insect population variability was not the primary aim of Dallas and Kramer (2022) and that the database used (BioTIME; Dornelas et al. 2018) has substantially greater coverage of vertebrates than insects, which potentially limits the power of their inference on this topic.

Within Insecta, some studies have broadly investigated the relationships between endogenous and exogenous traits and population variability at varying scales (e.g., Gaston & Lawton 1988, Owen & Gilbert 1989, Crowley & Johnson 1992), with findings including an equivocal relationship with specialization (Redfearn & Pimm 1988), greater community-level variability at higher latitude for moths (Antão et al. 2020), and large intrinsic differences between species in carabid beetles (Dallas et al. 2024). However, we also still lack generalizable evidence for macroecological patterns of population variability for insects, including for relationships between population variability and body size, broad taxonomic group, latitude, and environmental stability (Gaston & McArdle 1994, Dallas et al. 2024). Among other factors, this research gap could reflect the scarcity of synthesizable, long-term population data needed to detect small effects. Such long-term insect population datasets do exist, yet they are scattered throughout large and disparate bodies of literature, ranging from agricultural journals to governmental reports on forest pests. Only through recent synthesis efforts have these diverse datasets been brought together and made available for analysis (Grames et al. 2019a, Van Klink et al. 2023).

Here, we examine the generality of hypotheses about insect population variability by leveraging these large, newly-available population time-series datasets to assemble what may be the largest species-level time-series database for insects yet described. We seek to 1) test the hypothesis that insect populations are more variable than other animal taxa and 2) determine what endogenous (i.e., organismal) and exogenous (i.e., environmental or dataset) traits predict variation in population variability within Insecta. Specifically, we first test the prediction that insects display higher population variability than several commonly-studied vertebrate taxa: mammals (Mammalia), bony fish (Osteichthyes), and birds (Aves). Next – within Insecta – we examine the influence of body size, taxonomic order, latitude, biome, times series length, and time series start date on population variability. Consistent with a possible effect of environmental variability on population variability, we predict that population variability will be greater at higher latitudes, and in longer datasets. We also predict strong variation by taxonomic order identity due to differences in life history traits, and strong variation by biome due to differences in climatic variability. Finally, in addition to these analyses, we provide point estimates of population variability for all evaluated taxa, which may help inform estimates of the minimum time series length needed to accurately monitor each taxa.

Methods

Data sources

We collected population time series from multiple data sources. To be included in our database, individual time series had to satisfy several inclusion criteria: five years or greater in length, an inter-annual mean of 10 or more individuals, and identified to the species level (i.e., time series could not combine populations across multiple species). Additionally, counts must directly represent individuals rather than related measures such as biomass or number of colonies. Counts could represent any life stage, as long as the sampled life stage remained the same over time, and subspecies were not treated separately. We manually screened for and removed duplicate time series. We conducted all data standardization and analysis within R Statistical Software (v4.3.2; R Core Team 2023) via RStudio (v2023.6.1.524; Posit Team 2023); we filtered and manipulated data using "tidyverse" R packages (Wickham et al. 2019).

We began assembling our database of species-level population time series with data from NEON (2024), an ecological monitoring network in the United States, using the neonUtilities R package (Lunch et al. 2023). NEON yielded a total of 657 ground beetle (Coleoptera: Carabidae) and mosquito (Diptera: Culicidae) time series that met our inclusion criteria. Next, we incorporated datasets from previously published data aggregations: BioTIME (Dornelas et al. 2018; n = 222 time series), Global Population Dynamics Database (GPDD; Prendergast et al. 2010; n = 1008), US Long Term Ecological Research & Suction Trap Networks (LTER, Crossley et al. 2020; n = 108), and Insect Change (van Klink et al. 2023, n = 2453). We included data from "natural experiments" where population dynamics could be considered representative of dynamics in nature but removed time series – specifically from Insect Change and LTER – with data issues identified by Gaume and Desquilbet (2024) and Welti et al. (2021). Following the same inclusion criteria as for insects, we then included vertebrate population time series from GPDD and BioTIME for birds (n = 332), mammals (n = 720), and bony fish (n = 351).

Finally, we used the Entomological Global Evidence Map (EntoGEM) to identify new, additional insect time series. EntoGEM uses robust evidence synthesis standards, including automated keyword generation (Grames et al. 2019b), a pre-published search protocol, and screening of all sources in duplicate to produce a list of studies containing information on insect community and population change. Working from EntoGEM's list of literature, we used the metaDigitise R package (Pick et al. 2018) to extract 98 additional time series meeting inclusion criteria. This brought the total number of insect time series to 4544, comprising 1491 species. Time series were distributed unevenly across taxonomy, space, and time (Figure 1 presents the six most frequent insect orders, representing 99% of the insect data).

We then matched each time series with taxonomic, size, and biome covariates. To account for taxonomic changes, we harmonized synonymous scientific names using the GBIF taxonomic backbone (GBIF 2023) via the taxadb R package (Norman et al. 2020) and sourced higher taxon names from the full iNaturalist.org (2023) taxonomic tree. A small number of time series with uninterpretable scientific names were removed entirely. For insects, we additionally assigned each species in a family the average size of the family as compiled by Finlay et al. (2006) when the data were available. We assigned each time series to its terrestrial biome (sensu Dinerstein et al. 2017) based on its latitude and longitude using the IUCNN R package (Zizka et al. 2022).

Quantifying interannual variability

We calculated a measure of interannual population variability for each of the 5947 time series. Many indices have been developed to quantify variability in population time series data, such as the standard deviation of logged population counts (*s*; Williamson 1984), the Proportional Variability Index (PV; Heath & Borowski 2013) and the Coefficient of Variation

(CV; Gaston & McArdle 1994). However, these metrics are vulnerable to bias from rare events and zero counts (Hanski 1990, Gaston & McArdle 1994), and/or do not account for the chronological nature of population series (Heath & Borowski 2013). For these reasons, we here use the Consecutive Disparity Index, *D* (Fernández-Martínez et al. 2018, Dallas & Kramer 2022), which numerically accommodates zero counts and incorporates the chronological order of the values. Intuitively, *D* provides a measure of the average rate of change between consecutive values in a time series, following the formula,

$$D = \frac{1}{n-1}\sum_{t=1}^{n-1}\left| ln\left(\frac{p_{t+1}+k}{p_t+k}\right)\right|$$

where p_t is the population value at time t, n is the length of the time series (here, in years), and the constant k is 1% of the max of p_t (to prevent zero denominators). For time series with multiple counts per year, we took the maximum single count as our population index for that year, before calculating *D*. For two databases (Insect Change and LTER), the database versions we used only provide the sum total of repeat counts within each year. In data exploration, we found largely equivocal results whether we used the annual sum or max. Where applicable, we ignored missing data and treated all remaining years as consecutive (per Dallas & Kramer 2022). In utilizing *D*, we assume observation effort from year to year is constant (a fair assumption across the suite of standardized, published datasets that form our database, and with effort made to remove exceptions). Data and code for all data cleaning and analyses are accessible via our Figshare repository (DOI :10.6084/m9.figshare.28602776).

Modeling variability across birds, mammals, fish, and insects

We tested for differences in population variability across birds, mammals, bony fish, and insects using a generalized linear mixed model run in a Bayesian framework. We modeled population variability (*D*) as being drawn from a gamma distribution governed by shape, λ, and rate, λ/e^{μ}, parameters, where we model μ as a log-linear function of fixed effects for (i) taxonomic group (i.e., bird, mammal, fish, or insect), (ii) latitude, (iii) start year and (iv) duration of time series (both logged), and with random intercepts for (v) dataset and (vi) genus.

We additionally ran a second generalized linear mixed model to explore differences in population variability within Insecta. In this model, we also modeled population variability (*D*) as coming from a gamma distribution with fixed effects for (i) taxonomic order within Insecta (for orders with n > 30), (ii) latitude, (iii) start year of time series, (iv) duration, and (v) body size, with random intercepts for (vi) dataset and (vii) genus. Finally, we ran a third generalized linear mixed model replacing latitude with biome as a categorical variable (including biomes where n >30). In all models, continuous covariates were centered and standardized prior to model fitting. Because predictor variables are scaled, each slope result can be read as the expected change in *D* for one standard deviation increase in the predictor.

We fit all models to the data with JAGS (Plummer, 2003) using the Rjags (Plummer 2023) and dclone (Solymos 2010) R packages, with output commands via MCMCvis (Youngflesh 2018). All of our normally-distributed variables came from vague priors with means of 0 and sd of 100,000; shape parameters were drawn from uniform distributions bounded between 0 and 100. We ran four chains of 100,000 iterations with a burn-in of 10,000 and assumed chain convergence when the Gelman-Rubin statistic was less than 1.1 for all parameters

(Gelman and Rubin 1992). Based on our model estimates, we present posterior means and 95% credible intervals (CrI).

Results

Variability comparison between birds, mammals, fish, and insects

We found that insects as a group exhibited higher average population variability (average *D* = 1.12; 95% CrI: [0.94, 1.34]) than birds (*D* = 0.34; 95% CrI: [0.28, 0.42]), mammals (*D* = 0.47; 95% CrI: [0.38, 0.59]), and bony fish (*D* = 0.55; 95% CrI: [0.45, 0.67]) (Figure 2). We also found that D increased with absolute latitude (μ = 0.03, 95% CrI: [0.01, 0.05]) and that D decreased with earlier (log) time series start date (μ = -0.10, 95% CrI: [-0.12, -0.08]) and (log) time series duration (number of monitoring years; μ = -0.04, 95% CrI: [-0.06, -0.02]).

Variability within Insecta

For the six insect orders tested, we found similar levels of population variability, as follows: Coleoptera (*D* = 1.09; 95% CrI: [0.87, 1.33]), Diptera (*D* = 0.95; 95% CrI: [0.75, 1.18]), Hemiptera (*D* = 1.16; 95% CrI: [0.93, 1.42]), Hymenoptera (*D* = 1.32; 95% CrI: [1.03, 1.71]), Lepidoptera (*D* = 1.07; 95% CrI: [0.84, 1.30]), and Orthoptera (*D* = 1.29; 95% CrI: [1.00, 1.65]; Figure 2). We detected a negative relationship between body size and population variability (μ = -0.05, 95% CrI: [-0.08, -0.01]). As in the previous model, we also found that D increased with absolute latitude (μ = 0.06, 95% CrI: [0.05, 0.08]), and that *D* decreased with increased time series duration (μ = -0.06, 95% CrI: [-0.08, –0.04]) and with more recent time series start date (μ = -0.22, 95% CrI: [-0.25, -0.20]) (Figure 3). Finally, in our model investigating the effect of biome on *D* in insects, we found that population variability was lowest in Tropical & Subtropical Moist Broadleaf Forests (μ = 0.80, 95% CrI: [0.62, 1.05]) followed by Temperate Conifer Forests (μ = 1.13, 95% CrI: [0.89, 1.48]), Temperate Broadleaf & Mixed

Forests (μ = 1.17., 95% CrI: [0.92, 1.52]), Tundra (μ = 1.25, 95% CrI: [0.98, 1.65]), Temperate Grasslands, Savannas & Shrublands (μ = 1.28, 95% CrI: [1.00, 1.67]), Deserts & Xeric Shrublands (μ = 1.55, 95% CrI: [0.22, 2.08]), and Boreal Forests/Taiga (μ = 1.60, 95% CrI: [1.22, 2.18]). Through post-hoc evaluations of derived posterior distributions, we observed confident differences (i.e., CrIs not overlapping zero) in the mean D across 16 of 21 pairwise biome comparisons (Table 1).

Discussion

Ecology of population variability

A better understanding of the factors affecting population variability has long been a primary goal for ecology (e.g., Andrewartha & Birch 1954, Connell & Sousa 1983, Gaston & Lawton 1988, Hanski 1990). Organisms like insects, with short lifespans and high reproductive output, are often predicted to exhibit higher population variability compared to large, long-lived organisms like most vertebrates; however, broad evidence for this hypothesis has been lacking. Indeed, most recent comparative studies have found no evidence of consistent differences (Gaston & McArdle 1994, Dallas & Kramer 2022). Here, using an assembled composite dataset focused around insects, our results confirm that insects indeed show markedly higher population variability than major vertebrate groups (Figure 2a).

Within insects, we found no evidence of general differences in population variability between major insect orders (Figure 2b). This is perhaps surprising due to previous findings of strong phylogenetic signal in population variability (Dallas et al. 2024) and the often dramatically different life history strategies employed by each order. For example, modes of development can be either hemimetabolous (Hemiptera and Orthoptera) or holometabolous (Coleoptera, Lepidoptera, Hymenoptera, and Diptera), and some orders exhibit greater degrees of specialization (Lepidoptera and parasitic Hymenoptera), both related to traits theorized to affect population variability (Gaston 1994). However, order is also a broad (and somewhat artificial) taxonomic measure; insect orders can contain a remarkable variety of life history strategies (e.g., Hymenoptera contains vegetarian sawflies, eusocial ants, and parasitoid wasps) and trait diversity, which may overwhelm any contribution of shared evolutionary history at the level of order. Our model includes a random effect for genus, which accounts for any shared variability at the genus level, where population variability can be quite similar (Dallas et al. 2024).

We also found support for several population variability-trait relationships (Figure 3), including body size, latitude, time series duration, and time series start date. Our finding that insects with larger body sizes have more stable populations has not previously been shown in insects, or for most taxa. This effect could be direct, for example if smaller body size physiologically increases susceptibility to environmental variability, but it is more likely acting indirectly through covariation with traits like lifespan or population growth rate (Gaston & McArdle 1994), although such traits can also act in opposing directions to population variability. Body size is typically positively correlated with both species' lifespan – which leads to lower population variability – and reproductive output – which can lead to higher population variability. Longer-lived insects may be more temporally resilient to environmental conditions (e.g., through dormancy), which allows them to better maintain consistent reproductive output by taking better advantage of periods of suitable breeding conditions than short-lived insects, which are more heavily subject to the conditions of the short period in which they find themselves living. Longer-lived species also buffer population fluctuations since, on average, individuals are part of the population for longer (Morris et al. 2008).

We also found that insect population variability increases toward the poles, as has recently been shown for other taxa (Dallas & Kramer 2022). However, compared to other investigated factors, this effect was relatively weak. Precipitation and temperature both covary with latitude, but other geographic factors can exert stronger influences on climate than latitude. A region's biome is by no means independent from latitude, but important differences often exist even at the same latitude; e.g., Mediterranean Scrub, Deserts, and Mixed Broadleaf and Coniferous Forests all occur at 32° N. Each biome experiences different levels of climatic variability, particularly in terms of precipitation, which may strongly influence insect population fluctuations. However, biomes also differ along other axes that could affect population variability. We find evidence for differences in variability between most included biome types (Figure 4). For example, insect populations in the Tropical and Subtropical Moist Broadleaf Forests biome showed substantially lower mean variability for insects, than any other biome. This biome is closer to the equator, with generally more stable temperatures, energy inputs, and precipitation levels compared to temperate broadleaf forests. Though the effects of biome were substantial in some cases (e.g., high mean variability in the deserts and xeric shrublands biome), *D* values still spanned a wide range within each biome (Figure 4). The broader effects of biome may be buffered by the considerable variability within most biomes in the form of habitats and microhabitats. Overall, our finding of a relationship between latitude and population variability, as well as some biome differences, is generally consistent with hypotheses of relating population variability and environmental variability. Other factors, however, could play an important role, such as the latitudinal gradient of diversity acting through the portfolio effect, where communities with higher biodiversity may exhibit decreased variability (Schindler et al. 2015).

Finally, we observed decreasing population variability as time series duration increased, despite the opposite pattern being well-documented (Pimm & Redfearn 1988, Ariño and Pimm 1995, Inchausti & Halley 2002). Our finding could be related to our inclusion criteria: time series with durations less than five years were excluded, which could affect the trend if shorter time series are less variable. This result is also partly the consequence of a few high-leverage time series longer than 40 years in duration – the effect weakened substantially (but did not disappear) when these were excluded.

Implications for insect monitoring and conservation

Population variability can be an obstacle for monitoring species for conservation (McCain et al. 2016). If the goal is to understand insect community health broadly while balancing cost and time constraints, being able to compare the average population variability for insect taxa may help monitoring programs choose which species to monitor. Indicator species with low population variability may be preferable to species with high variability since they require fewer years of monitoring to be confident in the direction of the population trend (White 2019). When such data are lacking for a particular species, focusing on species with larger body size (with generally lower variability) may be a good option. Given an expected population variability (e.g., Supp. Table 2), it is possible to produce an estimate of the number of years necessary to monitor a species to get an accurate trend estimate (Wauchope et al. 2019, White 2019).

Our results specifically confirm the challenge of high population variability for insect monitoring. This affirms that “snapshot” surveys – where a small number of years are sampled after a large time gap – are particularly difficult to interpret, but our results may help inform these types of studies. As has been previously suggested (Didham et al. 2020), such surveys should be examined with proper accounting of the true sample size (in number of years) presented (White 2019). This high population variability also means that researchers investigating insect population trends should take special care to estimate trend reliability and power to detect change (e.g., Dauwalter et al. 2007, Wauchope et al. 2019), both still underused strategies in population time series analysis (White 2019), especially for insects. Considering the pitfalls of trend estimation from short-term monitoring, if insect monitoring on a large scale is to be successful and reliable, special effort and funding need to be made available for insect monitoring on appropriate, long-term timescales, especially in areas where data gaps are most severe. Even now, in an era of insect declines, valuable long-term monitoring programs are still being lost due to lack of funding.

Data and methodological considerations

Gaston and McArdle (1994) identify five common faults in studies examining patterns of population variability. Although we account for these when applicable and possible, our study is subject to important temporal, taxonomic, spatial, and linguistic biases (Figure 1). Although this is not a comprehensive, systematic account of the insect population literature, we can conclude that currently synthesizable time series data in the English scientific literature are mainly available from Europe and North America north of Mexico; relatedly, well over half (3000+) of the time series were collected in a single biome, Temperate Broadleaf & Mixed Forests. Our study includes particularly sparse sampling throughout the southern hemisphere and central Eurasia. Searches in languages other than English would likely help mitigate this and are an important next step. Time series data were also primarily available for more economically-important insect orders and species.

Because we lack data on generation time for most species, we base our estimates of population variability on interannual fluctuations, although variation in sampling rate would ideally be standardized to the pace of life cycles (e.g., generation time). Since we pool annual estimates, and because yearly cycles are biologically important, especially for the regions where most of our data come from, this should not lead to directional biases (Clark & Luis 2020). We also only coarsely examine the effect of body size, using the average size at the family level calculated in Finlay et al. (2006), in large part due to difficulty in acquiring insect species trait data at a large scale. Large trait databases including characters like size and generation time are valuable for answering ecological questions but are uncommon for insects.

Populations can be synchronized in space and time, and this is likely the case for our data, which come from an unevenly distributed patchwork of sites and can include time series of different species from the same site. Such spatial synchrony (i.e., autocorrelation) could effectively lower our sample size for *D*, since time series may not be far enough apart spatially to be considered independent samples. Our dataset may be less susceptible to this spatial synchrony since it includes many times series that do not overlap in time, and we attempt to partially account for it by including database (e.g., InsectChange, NEON, etc.) as a random intercept in our modeling. However, we acknowledge that our conclusions may be limited by not fully controlling for more subtle pseudoreplication. We were also not able to account for differences in detectability between years, although differences should generally not lead to systematic bias.

Next steps for insect population monitoring

Climatic variability itself is hypothesized to correlate with higher population variability (e.g., Le Coeur et al. 2021), and small, short-lived organisms like insects may be particularly exposed to this variability (Morris et al. 2008), but the extent to which this is true in insects at a large scale remains unclear. As newly surfaced and digitized insect population time series data are increasingly available for analysis, studies that explicitly examine species traits and climatic variability directly (as in Dallas et al. 2024), are important for understanding the relative contribution of climatic variability. Because higher climatic variability is also predicted as climate change accelerates, with both positive and negative consequences for populations (Estay et al. 2013, Vázquez et al. 2015), better understanding of this relationship is an important next step for insect conservation.

Insect monitoring is often conducted with the goal of evaluating the overall health of an insect community and its contribution to ecosystem function. Community-level monitoring may be less sensitive to the pitfalls of monitoring individual species populations in isolation. As species-level monitoring increases with increasing conservation concern for specific insect species, pairing species- and community-level data can be valuable when constraints allow for it. Aggregate metrics of ecosystem function (e.g., biomass) can be more stable than population metrics due to compensatory dynamics, where declines in one species can result in increases of others (Gonzalez & Loreau 2009, Zhao et al. 2020). However, community synchrony is also common in some systems (e.g., Stephens et al. 2017), and the degree to which both occur in insect communities is still relatively uncertain (Cottingham et al. 2001, Dallas & Kremer 2022).

Beyond population variability as a nuisance variable, the metric itself (e.g., as D) may also be worthwhile to monitor since increased mean population variability of a community (i.e., lower stability) has been proposed as a consequence of biodiversity loss (Olivier et al. 2020). The estimates of variability we provide for different insect taxa could help inform extinction risk assessments for these taxa (Vucetich et al. 2000, Ovaskainen & Meerson 2010). Species with both high variability and restricted geographic range should be at particularly high risk of extinction (Gaston & Lawton 1988). Although at times a barrier to interpreting trends, population variability is meaningful – high and low points are real, and matter for conservation (Ariño & Pimm 1995). Although linked, the probability of population extinction may ultimately be more relevant than the overall trend, so increased emphasis on extinction risk, in tandem with trend estimation, may help researchers and managers draw conclusions about insect population declines.

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Figures

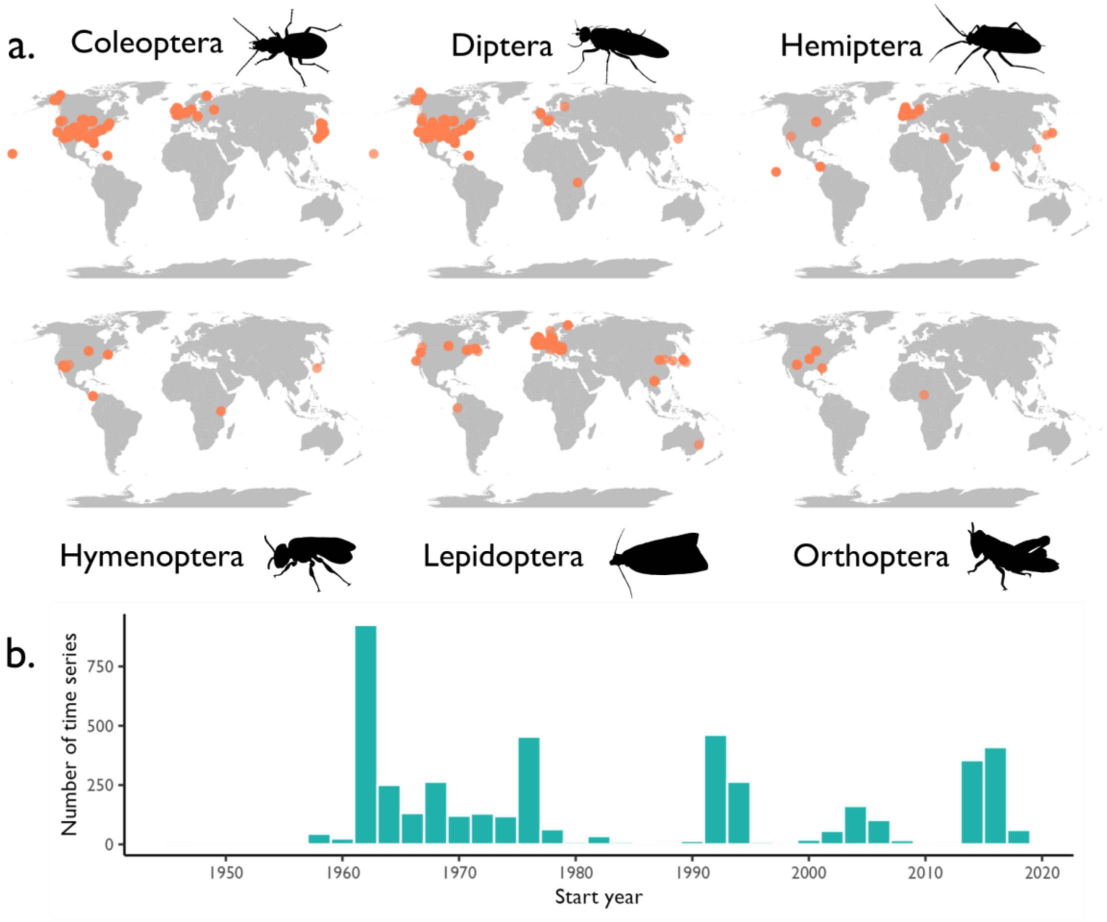

Figure 3.1. Insect population time series (a; with coordinates, n = 4291) primarily come from six taxonomic orders and three geographic regions (eastern Asia, northern Europe, and the United States; each dot represents a single population time series location for a given taxonomic order; note that multiple time series can come from a single location). Time-series start years (b) are widely but unevenly distributed over time (datasets prior to 1945 [n = 120] were excluded from (b) for visualization purposes).

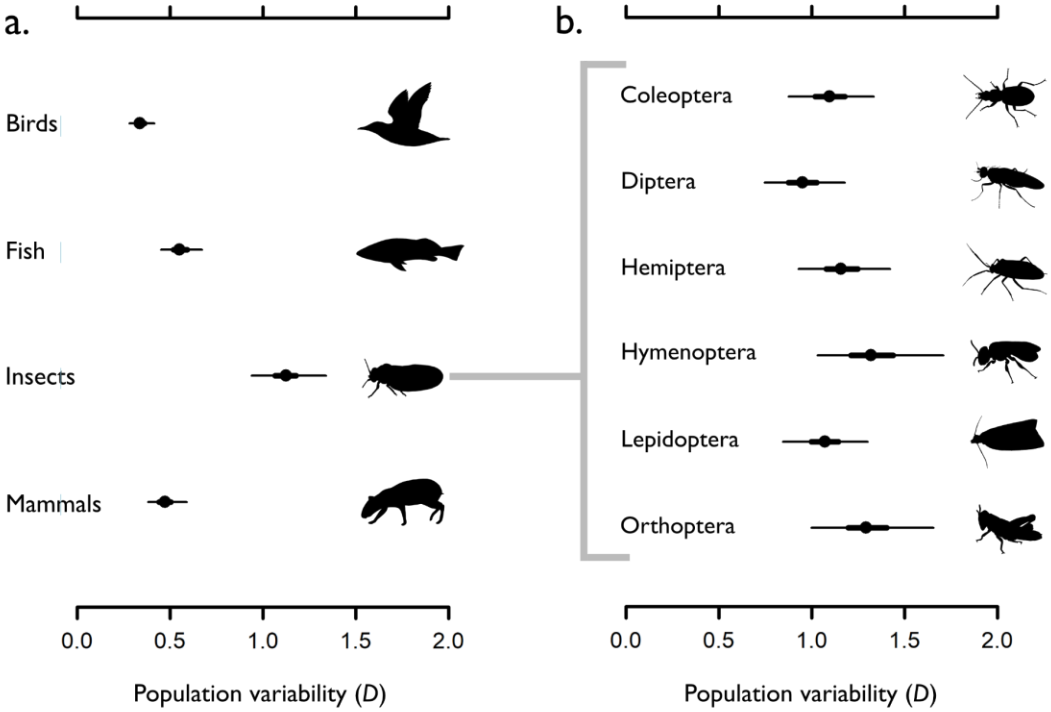

Figure 3.2. Insects showed higher population variability than all three examined vertebrate groups (a). A second, insect-only model (b) found no evidence of consistent differences in population variability between compared insect orders.

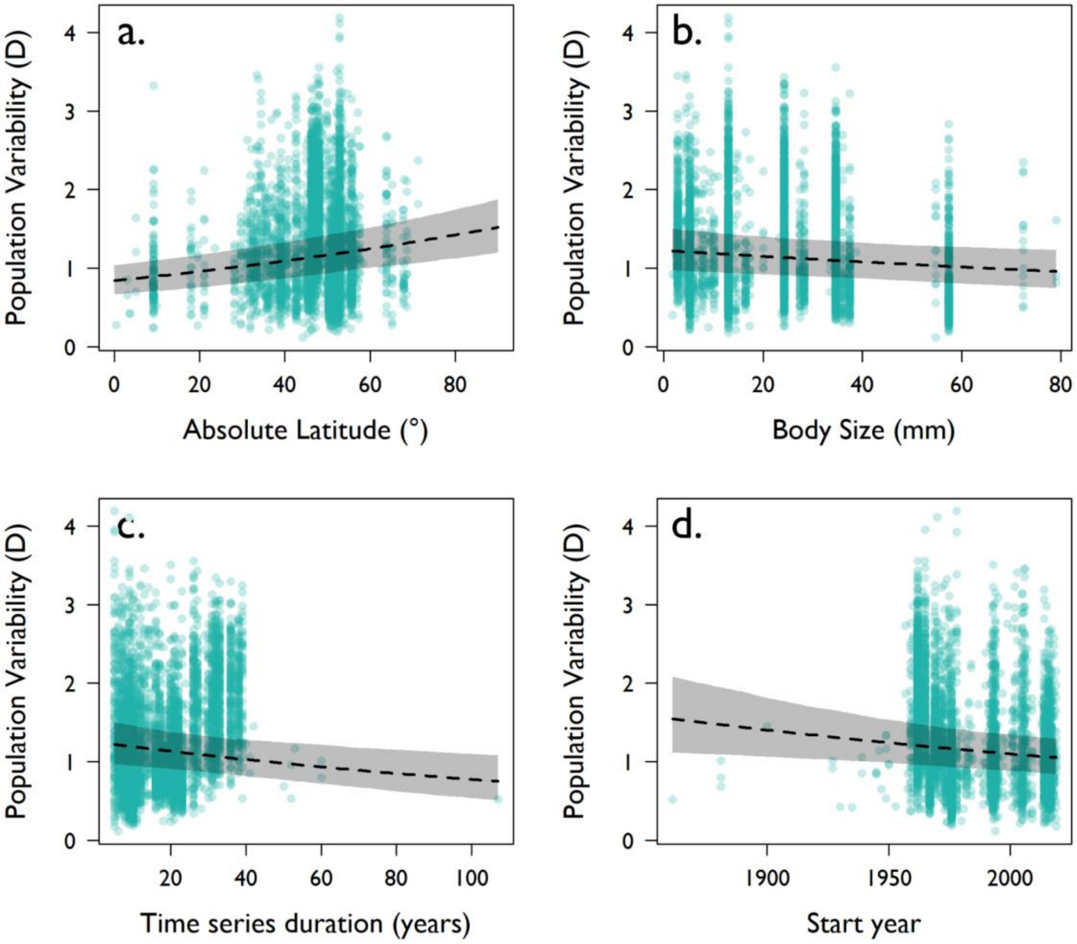

Figure 3.3. Comparing across just insect time series, we found strong evidence (i.e., 95% CrI not overlapping 0) of a positive relationship with absolute latitude (a), a negative effect of family body size (b), a negative effect of time series duration (c), and a negative effect of start year (d) on population variability. Plots show posterior mean (dotted line), 95% CrI (shaded area), and raw time series calculations of D.

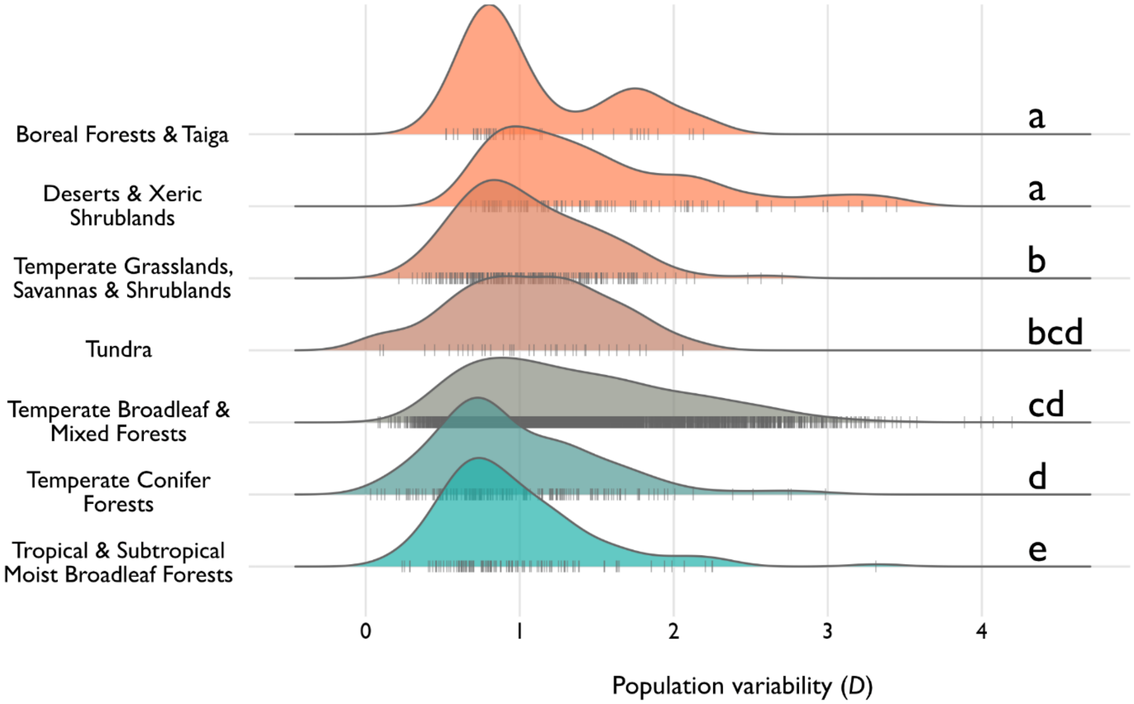

Figure 3.4. Population variability for Insecta differs by biomes, with the lowest D in Tropical and Subtropical Moist Broadleaf Forests and the highest D in Boreal Forests and Taiga and Deserts and Xeric Grasslands. Plots show kernel density plots of values of D, with data rugs showing individual time-series points. Letters indicate pairwise posterior evaluation of differences between biomes conducted on 95% credible intervals (Table S1).

Appendix 2-I: Supplemental tables

Supplemental Table 1. Post-hoc derived with posterior distributions of the pairwise differences in *D* between biomes. 95% CrI that do not cross zero are interpreted as strong evidence in support of a pairwise difference.

comparison	mean	2.5%	97.5%
tukey[1,2]	0.64	0.55	0.76
tukey[1,3]	0.52	0.45	0.58
tukey[2,3]	0.81	0.7	0.94
tukey[1,4]	0.68	0.63	0.75

tukey[2,4]	1.06	0.94	1.2
tukey[3,4]	1.32	1.2	1.45
tukey[1,5]	0.71	0.63	0.79
tukey[2,5]	1.1	0.99	1.25
tukey[3,5]	1.37	1.24	1.53
tukey[4,5]	1.04	0.98	1.11
tukey[1,6]	0.5	0.42	0.59
tukey[2,6]	0.78	0.66	0.94
tukey[3,6]	0.97	0.82	1.15
tukey[4,6]	0.73	0.63	0.85
tukey[5,6]	0.71	0.6	0.82
tukey[1,7]	0.62	0.56	0.69
tukey[2,7]	0.97	0.86	1.1
tukey[3,7]	1.21	1.1	1.34
tukey[4,7]	0.92	0.86	0.97
tukey[5,7]	0.88	0.82	0.95
tukey[6,7]	1.25	1.06	1.46

Supplemental Table 2: Population variability by species. We calculated variability for each unique insect species (columns = species, n, order, family, avg year length; arranged alphabetically by order, family, and species, and categorized into levels of population variability based on quantiles; very low (0-20%), low (20-40%), medium (40-60%), high (60-80%), and very high (80-100%). We caution that results from one population (or several) often can not be generalized to others and possess serious biases, including possible spatial autocorrelation. However, we still find these categories valuable for providing intuition when other data are lacking. Because of the size of this table, we do not include it here, readers interested in using these data are encouraged to access the full dataset and metadata on dryad.

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Chapter 4: Bird population declines and insect community shifts in response to habitat and climate change in great smoky mountains national park, U.S.A.

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Trophic interactions, insect declines, insectivory, community dynamics, ecological monitoring, snapshot surveys

Abstract

Recent reports of widespread insect population declines have raised concerns that insectivorous bird populations are being negatively affected. Here, we used paired bird-insect resurveys in Great Smoky Mountains National Park, TN, USA to investigate bird and insect community change since the late 1940s. We found evidence of population declines in 12/28 bird species, increases in two species, and upslope elevational shifts in 19/28 species. For insects, we found no evidence of consistent abundance or biomass shifts between the survey periods in this protected area. Changes in insect and bird community abundance and biomass were correlated at survey sites with overlapping data. Overall, these results suggest linkage between bird and insect populations at the site level, highlight signatures of the effects of climate change, and emphasize the importance of considering habitat change when examining community change for both birds and insects.

Introduction

Avian population declines in North America have been documented for decades (Wilcove 1988, Holmes and Sherry 2001, Faaborg et al. 2010, Smith et al. 2015), are especially pronounced in neotropical migrant species and aerial insectivores and includes many common species (Schipper et al. 2016, Rosenberg et al. 2019). A suite of complex interacting drivers have been implicated (Norris et al. 2004, Michel et al. 2016, Rushing et al. 2016, Kramer et al. 2018, Stevens et al. 2024), but recent evidence of widespread insect abundance declines (Shortall, et al. 2009, Brooks et al. 2012, Hallmann et al. 2017, Van Klink et al. 2020, Staab et al. 2023) has raised concerns that such declines may be contributing to these trends (Bowler et al. 2019, Spiller and Detmers 2019, Tallamy and Shriver 2021). This is especially plausible since insectivorous bird populations are subject at least in part to bottom-up control (Narango et al. 2018, Grames et al. 2023, Yazdanian et al. 2024) via food resource availability. However, the extent to which insect declines may contribute to bird declines is unclear (Yazdanian et al. 2024), in part because insect trends are still much less well-understood compared to birds.

The magnitude of insect population declines is highly variable across taxonomic, geographic, and temporal scales (Wagner et al. 2022). Although generalizable conclusions about drivers are mostly not yet available, local factors (Van Klink et al. 2020) and species traits (Staab et al. 2023, Van Klink et al. 2023) may be especially important. Declines have been linked to a host of variables (Wagner 2020), including agriculture (Seibold et al. 2019, Outhwaite et al. 2022), light pollution (van Langeveld et al. 2017), nutrient dilution (Welti et al. 2020), and climate change (Harris et al. 2019, Soroye et al. 2020, Forister et al. 2021, Edwards et al. 2025). Most areas, however, lack wild insect population survey data necessary to understand the severity of local insect declines trends, especially outside better-surveyed taxa like pollinators. Although protected areas are clearly important for limiting population declines in many taxa, including insects, the extent to which they can successfully buffer insect populations from more widespread drivers is also unclear (Rada et al. 2019).

Biological resurveys provide an opportunity to investigate such questions of populations and community change over time, especially when conducted across sites with varying characteristics and across multiple trophic levels (e.g., Møller et al. 2019). However, suitable historical datasets for resurvey are typically rare, small in geographic and taxonomic scope, and use sampling designs that preclude the use of recently developed modeling methods like occupancy modeling (MacKenzie 2006).

In 1947, Benjamin Fawver conducted bird surveys across 10 sites in Great Smoky Mountains National Park, TN, USA (Fig. 1; Kendeigh and Fawver 1981). The following year, his graduate school classmate, Robert Whittaker, conducted insect surveys at 13 sites in the Park (Whittaker 1952), including at seven of Fawver's bird survey sites, providing a unique paired snapshot of the Park's bird and insect communities in the late 1940s. Revisiting and resurveying these sites for birds and insects can allow for investigations into how bird and insect communities have changed at these sites over time, and in relation to each other. Indeed, Fawver's bird transects were resurveyed over two years by Wilcove et al. (1988), in 1980–1981, then again in 2012–2013 and 2019–2020. Whittaker's insect surveys were never revisited until our recent resurvey in 2019–2020.

The study area, Great Smoky Mountains National Park, provides an especially useful system for understanding parallel bird and insect community change over time due to its diversity of habitats and elevations (Whittaker 1956, Jenkins 2007), its status as a well-protected conservation area with a history of significant research and monitoring (e.g., Harrod et al. 1998, Smith and Nicholas 1998, Caruso and Lips 2013, Baird et al. 2014), and being subject mosaic of anthropogenic and "natural" changes varying from site to site. For example, sites have been affected variously by hemlock death due to the invasive hemlock woolly adelgid (Krapfl et al. 2011), Fraser fir declines due to invasive balsam woolly adelgid (Smith and Nicholas 1998), burning due to wildfire (Reilly et al. 2022), the effects of increased visitation (Wilcove 1988), simultaneous deer and pig population increases due to the loss of large predators (Harrod 1999), ecological succession due to the removal of grazing pressure from livestock, fire suppression, prevention of logging, and loss of American chestnut (Woods and Shanks 1959, Flatley et al. 2015, Tuttle and White 2016). In addition, sites are also subject to more pervasive effects of air pollution increases and decreases (Shaver et al. 1994, McDonnell et al. 2018, Neufield et al. 2019), nitrification (Welti et al. 2020), and climate change. The Park is thus simultaneously a textbook "protected area" that has been subject to a wide variety of natural and anthropogenic disturbances and forces that likely have resulted in ecosystem change over the last 80 years.

Here, we present results from our paired bird-insect resurvey. To provide modern data for comparison to the 1940s-era surveys, we revisited the original survey sites (Figure 1) and replicated survey methods in three study periods 1) 1982-1983 (birds; Wilcove 1988), 2) 2012-2013 (birds), and 3) 2019-2020 (both birds and insects). We use these population- and community- level resurvey data to investigate 1) the degree to which avian and insect abundance and biomass changes are occurring in Great Smoky Mountains National Park and 2) if change in avian abundance and biomass is predicted by a) degree of insectivory and b) site-level insect community abundance and biomass change.

Methods

Bird surveys and modeling

Benjamin Fawver's 1947 bird surveys (Fig. 1; Table S1) made use of a "spot-mapping" survey method (Kendeigh and Fawver 1981). This effort-intensive technique involves estimating distance and bearing to birds along a transect and revisiting each site several times. At each survey point of a transect, all birds seen or heard were counted and distance and bearing estimated. Surveys were conducted in the morning (from 30 minutes pre-sunrise to approximately 10 am) in good or fair weather and basal area by tree species and estimates of tree, shrub, and ground cover within plots were also recorded. The authors resurveyed these sites in 1982-1983 (led by DSW), 2012-2013 (led by MWT), and 2019-2020 (led by GAM), yielding a series of snapshots of avian abundance and diversity. In order to be sure that sites were being revisited accurately, Wilcove communicated with Fawver in the 1980s and set up transects matching elevations along stable, established trails. Tingley visited sites with Wilcove in 2012 prior to survey initiation, worked with historical maps to re-find sites of Fawver's that were skipped by Wilcove, and digitized transects with GPS coordinates to easy revisitation by

Montgomery and others. All resurveys of Fawver's original work replicated his methods, conducting 4–10 replicated spot map transects per site per year. To examine phenological differences between eras quantitatively, we used modeled temperature data from PRISM (PRISM Climate Group 2024) to calculate accumulated growing degree days for each survey date and location at a 10°C threshold.

We surveyed sites repeatedly during each survey season, allowing for a multispecies n-mixture modeling framework (MacKenzie et al. 2019) which produces more accurate abundance estimates by accounting for imperfect detection. This class of models concurrently calculates the probability of occupancy (ψ) of a site by an organism, its abundance, and the probability of detection (p) for that organism in a one-step mathematical process. We modeled historical and resurveyed sites by combining all sites by time period (resulting in four distinct "eras") and fitting single-season n-mixture models that allowed abundance to change between time periods as a species-specific shift in the intercept by time period. We described detectability with covariates for era (i.e., observer), and the linear and quadratic effects of day of year (centered and normalized) and modeled occupancy as a linear function of survey era. An overly simplified assumption of this model is that the elevational distribution for each species remains constant over time, which may not be the case in this system. Because we lack the necessary data to perform n-mixture modeling on Fawver's maps, and because Wilcove (1988) found no evidence of substantial avifaunal changes between 1947 and 1982 (except for a few species associated with clearcuts like Prairie Warbler), we treat the 1982-1983 time period as equivalent to Fawver's era (1947-48) in our analysis.

We conducted all analyses within R statistical software (v4.3.2; R Core Team 2023) and RStudio (v2023.6.1.524; Posit Team 2023); we filtered and manipulated data using "tidyverse"

R packages (Wickham et al. 2019). We implemented an n-mixture modeling framework in a Bayesian context using JAGS (Plummer, 2003), via the Rjags (Plummer 2023) and dclone (Solymos 2010) R packages. We provided uninformative priors for hyperparameters, and ran three parallel chains of 50,000 iterations each with a burn-in period of 10,000. We summarized and visualized model outputs in R with MCMCvis (Youngflesh 2018) and assessed convergence by ensuring visually that chains mixed well and verified that diagnostic Gelman-Rubin values (Gelman et al. 2004) for all parameters were less than 1.1.

To investigate specific hypotheses, we extracted species mass data from AVONET (Tobias et al. 2022) to estimate species- and community- level avian biomass. For regional- and national-level abundance comparisons, we derived annual trends from the Breeding Bird Survey (Smith et al. 2015) for the survey period, and we derived estimates of insectivory from the Avian Diet Database (Hurlbert et al. 2021).

Insect surveys and modeling

Robert Whittaker's 1947 insect surveys for foliage-dwelling insects were conducted at 13 sites in the Great Smoky Mountains (Figure 1; Table S1), yielding 31,721 total specimens (Whittaker 1952). He visited each site three times and collected using a detailed and repeatable sweep-netting protocol, including information on net design and sweeping effort. Whittaker surveyed at each site by conducting 5 rounds of sweep-netting from a central point, each 50 paces long, sweeping with a four-foot arc. Each of the three vegetation strata (herb, shrub, and low tree) at a site was sampled this way, and each site was visited twice more over the course of June and July, yielding a total of 2,250 sweeps per site across three total visits. All insect specimens were identified to order, and most were identified to family, with many also being identified to genus and species, often by taxonomic experts, such as Kathryn Sommerman

(“Psocoptera”). Unfortunately, although a small percentage of his specimens survive at the Great Smoky Mountains National Park biological collection, most have been lost.

We digitized Whittaker’s written data archive from these surveys, held at the Cornell University library. The hand-written survey sheets include taxonomically-verified (he worked with several experts) tables of every specimen that was collected on each site survey, specific to sweep-net section and strata (e.g., Figure S1). For analysis, we excluded sites he visited outside the Park boundary, specimens collected incidentally with inconsistent effort, and extraneous rounds of sampling. At one site (Double Springs Gap), Whittaker combined shrub and tree strata when sampling. We attempted to match this in the analysis by taking 2 sets from our shrub stratum and 3 from our tree stratum, since the tree stratum was slightly more dominant at the site. Occasionally, Whittaker’s taxonomic names could not be assigned to a modern taxon due to unknown acronyms and misspellings. In these cases, it was treated in our database as a member of the lowest taxon that could be unambiguously ascertained. Whittaker also assigned some taxa to morpho-species (e.g., *Atheta* sp. 8), but without surviving specimens or more information, we do not fully know the taxonomic authority or concept used to identify them as such. Therefore we assign these to the genus level, rather than treating each as a separate species. After digitization, we harmonized subsequent taxonomic changes with names from the GBIF backbone taxonomy (GBIF 2024) and the taxadb (Norman et al. 2020) R package.

For present-day insect resurveys (2019-2020), we replicated Whittaker’s sampling methods and visited the same sites, but as with bird surveys, started earlier in the season in an attempt to account for expected phenological advancement since 1947 due to climate warming. All 2019–2020 collected specimens are stored in ethanol and loaned to the Smithsonian Institute for storage, although they remain property of the National Park Service. To produce estimates of insect biomass for both historical and modern datasets in the absence of a widely applicable insect trait database, we assigned each specimen a length from a database of average family-level data (Finlay et al. 2006) based on taxonomic identity, then calculated consumable biomass by using the class-level allometric relationship provided by Straus and Avilés (2018). A century of taxonomic progress and identification resources have made modern-day identification easier for some taxa, but significant barriers remain for others. Identifications were made to at least order level by GAM and exemplar specimens are designated to document species concepts used in identification. Taxa requiring specialist knowledge or dissection to identify were left at broader taxonomic levels.

We derived several metrics from these data. To calculate biomass change, we treated the maximum biomass at a site visit in a year as the metric of comparison to allow for "peak" biomass to vary as phenology has advanced. Separately, we also used modeled temperature data from PRISM (PRISM Climate Group 2024) to calculate accumulated growing degree days for each survey date and location at a 10°C threshold, then took only the phenologically "closest" values for comparison.

Results

Avian population and community change

Seven total years of survey data across three 'eras' yielded over 18,000 individual bird detections distributed across 80 species. Of the 28 species included in the model based on a sample size threshold of at least 5 occurrences on different visits to one or more sites, 12 species showed strong evidence for directional temporal trends in abundance (Figure 2, Table 1). Of these, we detected negative trends for 11 species: Acadian Flycatcher (μ = -0.06, 95% CrI: [-0.08, -0.03]), Black-capped Chickadee (μ =-0.07, 95% CrI: [-0.04,-0.02]), Blue-headed Vireo (μ

= -0.03, 95% CrI: [-0.02,0.00]), Black-throated Blue Warbler (μ = -0.02, 95% CrI: [-0.03, -0.01]), Canada Warbler (μ = -0.03, 95% CrI: [-0.04,-0.01]), Dark-eyed Junco (μ = -0.03, 95% CrI: [-0.05, -0.02]), Hairy Woodpecker (μ = -0.04, 95% CrI: [-0.07,-0.01]), Ovenbird (μ = -0.04, 95% CrI: [-0.05, -0.03]), Veery (μ = -0.02, 95% CrI: [-0.03, -0.00]), Winter Wren (μ = -0.02, 95% CrI: [-0.04, -0.01]), and Wood Thrush (μ = -0.04, 95% CrI: [-0.06,-0.01]). The two positive trends observed were for Hooded Warbler (μ = 0.03, 95% CrI: [0.01,0.04]) and Indigo Bunting (μ = 0.02, 95% CrI: [0.00, 0.04]). Across all sites, Acadian Flycatcher showed the largest negative trend. Although the modeling framework accounts for differences between them, we examined detectability and did not observe substantial differences between eras (Figure S2), except for potentially lower detectability in the second era, when more observers contributed to surveys.

Overall, regional- and national- level trends from BBS were not informative for predicting population change in the Great Smoky Mountains (Figure 3). Many populations exhibited a considerably greater change in the Smokies (positive or negative). Species showing relatively large increases in the Park also compared favorably to their national trend (Hooded Warbler, Tufted Titmouse, and American Robin). More species were performing worse in the Great Smoky Mountains compared to how they were faring nationally (17/25). More species increased their mean elevation at detection than decreased (20/25; Figure 4), with Black-throated Blue Warbler showing the largest increase in mean elevation detection.

Insect population and community change

Despite moving sampling dates for modern insect surveys forward in anticipation of phenological change, accumulated growing degree days at a 10°C threshold were still substantially higher during the modern era than during Whittaker's era (1947; Figure 5).

Precipitation was also greater in the modern era, which frequently precluded insect sampling when vegetation was wet.

Across both eras, the most commonly observed insect families identified to the family level or lower were Cicadellidae (Hemiptera), Hybotidae (Diptera), and Drosophilidae (Diptera) (Table 2) and the most common species were *Anaspis rufa* (Coleoptera: Scraptiidae), *Forcipata loca* (Hemiptera: Cicadellidae), and *Eupteryx flavoscuta* (Hemiptera: Cicadellidae) (Table S2). Averaged across all visits in the two eras and measured in terms of the difference between the maximum number of specimens (n) and the difference in maximum biomass observed per sample, per year, with the two modern sampling maximums averaged together. Abundance increased at six of ten sites included in analysis, and biomass increased at seven of ten sites. Both abundance and biomass showed the largest decline at the heath bald at Brushy Mountain (-70 specimens between maximum sample counts; -3,412.9 mg between maximum sample biomasses; Figure 6) and the largest increase in beech forest at Double Springs Gap (+192 specimens). Biomass showed sensitivity to differences in the biomass calculation method used, and moved in a different direction from abundance at one site (Trillium Gap).

Bird species population trends in Great Smoky Mountains National Park were not related to their degree of insectivory measured by average percent insects in summer diet (Figure 6). For sites with overlapping insect and bird data, two out of seven sites showed swings in the same direction (positive in both or negative in both): Brushy Mountain and Rocky Springs Gap. Across these seven sites, changes in insect community abundance and bird community abundance were positively correlated ($r^2 = 0.658$), as were changes in insect community biomass and bird community biomass ($r^2 = 0.765$).

Discussion

Using resurveys of bird and insect communities in Great Smoky Mountains National Park, we find: 1) evidence of population declines in 11 of 28 bird species and population increases in only two species; 2) no clear evidence that change in avian abundance and biomass is predicted by degree of insectivory; but 3) that bird and insect community abundance and biomass change moved in the same direction (positive in both or negative in both) at five of eight sites with overlapping data. We also find 4) that insect abundance declined at high elevation sites, but not necessarily biomass, while both biomass and abundance increased at lower elevation sites. Based on these patterns, we suggest that an ongoing interplay between habitat change and climate change in the Great Smoky Mountains is contributing to differences between eras in both bird and insect communities. We also propose that in this system, trends may be more influenced by site-level factors rather than pervasive landscape-level factors, which may help inform studies investigating parallel insect and bird declines.

Population size is the result of a mosaic of factors that affect demographic parameters. Anthropogenic factors can modulate “natural” population drivers and introduce new ones, creating both winning and losing species (Dornelas et al. 2019). And in any given system, it can be expected that some species will decline and others will increase (White 2019) due to stochasticity. For the 28 bird species included in our model, we find that 11 species declined, two species increased their population, and 16 species exhibited no detectable trend (i.e., with credible intervals overlapping zero) across all sites. The relative uniformity of species trends as either stable or decreasing is skewed more negatively than might be expected due to random chance, with dramatic declines for many species, and very few “winners.” In addition, this may represent an overly optimistic set of trends for the avian community in the Park, since our model also only describes abundance changes for the subset of species that show substantial population density during at least one time period (28 species of the 80 observed during sampling). Our model therefore can not provide information about species that are already rare in the Park, which are at higher risk of extirpation, such as Swainson's Warbler or Yellow-billed Cuckoo.

Declining species in our model included common species (e.g., Dark-eyed Junco), habitat specialists (e.g., Acadian flycatcher), high elevation species (e.g., Veery), species with more northerly distributions (e.g., Black-throated Blue Warbler), neotropical migrants (e.g., Canada Warbler), and ground-nesters (e.g., Ovenbird). Six of the twelve most common species in our sample showed declines, including four of the five most common: Dark-eyed Junco, Black-capped Chickadee, Blue-headed Vireo, and Black-throated Blue Warbler. Dark-eyed Junco and Black-throated Blue Warbler in particular showed the largest absolute declines in abundance, contributing disproportionately to the overall community abundance decline due to their relative abundance. While common species may be at less risk of immediate extirpation, population declines in common bird species are well-documented (Rosenberg et al. 2019) and concerning since common species often make large contributions to ecosystem function (Winfree et al. 2015, Baker et al. 2019).

The common but declining Dark-eyed Junco and Black-throated Blue Warbler have different historical abundance trends in the Park. Dark-eyed Junco is a species that was only recorded at a few sites in the 1940s, but had expanded considerably by the 1980s, becoming one of the most common species in the Park (Wilcove et al. 1988). Black-throated Blue Warbler has always been abundant in the Park but has generally shown a steady downward population trend across its global range over the past 50 years, including in the southern Appalachians (Lewis et al. 2023, Gaya & Chandler 2025). Both species are relatively "cool-adapted" at the southern edge of their breeding range in the southern Appalachians (Gaya & Chandler 2025), and both shifted their elevational distributions substantially upslope as a possible consequence of climate warming. Overall, we observed upslope elevational shifts expected with rising temperatures in 20 out of 25 species, including in most declining species. The sole “winners” in our model, Hooded Warbler and Indigo Bunting, are both at the core of their ranges, but showed strong differences in their elevational shifts. Hooded Warbler is expanding its global range northward (Melles et al. 2010) and shifted its elevational distribution upslope in the Park, at a potential competitive cost to its declining congener, Black-throated Blue Warbler, which prefers a similar vegetation stratum.

Indigo Bunting, however, shifted its elevational distribution downslope more than any other species, contrary to expectations due to climate change alone. Compared to the southeastern US broadly, the southern Appalachians have experienced a relatively small mean temperature increase since 2000 (Lewis et al. 2023). Although this increase likely has profound effects on abundance and elevational distribution, habitat change may be just as important, or more so, for many species, like Indigo Bunting and many of the declining species. The Indigo Bunting’s downward shift is likely related to the large increase in successional habitat at middle and lower elevations due to wildfire and hemlock death in recent years. Since the 1980 study period, Eastern hemlock mortality due to the invasive hemlock woolly adelgid has led to dramatic changes in forest composition (Krapfl et al. 2011). Hemlocks facilitate a unique, shaded microhabitat at low- to mid-elevations in the Park, especially on cool, north-facing slopes, and host a unique insect fauna (Buck III 2004). Several bird species are often associated with hemlocks in the eastern US, including at least seven species in the Park: Black-throated Green Warbler, Dark-eyed Junco, Black-throated Blue Warbler, Winter Wren, Acadian Flycatcher, Wood Thrush, and Canada Warbler (Shriner 2001). All declined substantially in our study, except Black-throated Green Warbler, which is also associated with second growth in the Park (Shriner 2001). Although it has never been common in the Park, Blackburnian Warbler is also a hemlock specialist (Tingley et al. 2002) with habitat flexibility and may have avoided population declines by utilizing higher-elevation second growth habitats. The effects of habitat change and climate change can interact as well; the increasingly common Hooded Warbler, expanding upslope, also reaches its highest densities in continuous forest with dense shrub understory, and has been associated with successional forest after hemlock death (Tingley et al. 2002).

Species associated with high elevations in the Park include Dark-eyed Junco, Veery, Winter Wren, and Golden-crowned Kinglet (Shriner 2001), all of which overlap substantially with hemlock-associated species. The high elevation spruce-forest these species inhabit has historically been dominated by Fraser fir, another tree species that declined during the study period due to an invasive insect pest (Smith and Nicholas 1998) and is now beginning to recover (Kaylor et al. 2017). Despite this change, some species avoided declines, counter to expectations in the face of both climate change and habitat change due to fir loss and recovery. For example, Golden-crowned Kinglet specializes on high-elevation spruce-fir forests, which are possibly subject to more extreme effects of climate change than other sites in the form of reduced snowpack, but did not exhibit large declines. Despite the increase in successional forest across the study area due to wildfire, hemlock loss, and other disturbances, there were no observable abundance increases for most bird species that specialize in successional forest (e.g., Eastern Towhee), although species richness did increase at those sites due to small numbers of edge species now present, like Yellow-breasted Chat.

Declining insect abundance has been hypothesized to be connected to bird declines broadly, and evidence for this connection has been found in some systems (Møller 2019, Yazdanian et al. 2024). Here we find no evidence of differences in bird species trends due to their degree of insectivory (Figure 7). The low variability in summer diet among our sample of songbirds could contribute to this finding, since the diets of most songbird species during breeding season approaches 100% insects (Hurlbert et al. 2021). Bird and insect community changes (abundance and biomass) also only occurred in the same direction at two of the seven sites with both bird and insect data. However, changes in total abundance and biomass for bird and insect communities were highly correlated across seven sites (Figure 8), suggesting either causal linkage, or similar community responses to underlying site-level changes. The apparent discrepancy between the directionality of the change, despite the strong correlation between the two groups, could be due to methodological biases (e.g., in insects) where the direct comparisons of absolute numbers are subject to bias, but the relative changes are (e.g. methods are consistent within time periods). To that end, a strong correlation here indicates that there may well be credence to a link between birds and insects. If these changes are linked, sites with stable or increasing insect community trends could help offset bird community losses due to climate or habitat change.

We also did not find evidence of large insect declines, at the community level (i.e., not examining species-specific trends), across our sites. Overall, we observed insect abundance declines at four sites, and increases at six sites. The overall lack of a stark, consistent decline in the Great Smoky Mountains National Park insect community is not necessarily surprising given its protected status and relative insulation from what are likely the worst anthropogenic drivers of insect declines (light pollution, agricultural intensification, and habitat loss; Wagner 2020).

Higher precipitation in the modern survey years (2019 and 2020) could also have affected insect community trends positively. Water stress is an important source of mortality for insects, with resulting consequences for populations (Janzen & Hallwachs 2019), and many species population increases are associated with wetter years (Lamarre et al. 2022). Precipitation at survey sites was higher in the modern era than the historical surveys (Figure 5), which may be the consequence of a longer-term trend towards higher interannual variability in precipitation in the southern Appalachians (Lewis et al. 2023). Although insects may benefit in years with higher precipitation, they may conversely decline in dry years, with unknown consequences for the overall trend.

Climate warming and site-specific habitat change are likely important contributors to the varied insect trends we observed in different habitats across the Park. We observed abundance declines at two high-elevation sites, Brushy Mountain (1496m) and Rocky Springs Gap (1794m), but marked increases at two other high-elevation sites, Double Springs Gap (1684m) and Silers Bald (1696m). Of these, only the heath bald habitat at Brushy Mountain, an isolated peak, has remained relatively stable between the study eras. Rocky Springs Gap is the highest-elevation site, and has been dominated by fir-spruce forest throughout the study period, but much of its mature Fraser firs have been lost (Smith and Nicholas 1998) and replaced by red spruce. Declines at high elevations could be linked to warmer winter temperatures and the loss of insulating snowpack could expose insects to lethally low temperatures (Harris et al. 2019), but this stressor may be outweighed by habitat change. For example, the Silers Bald and Double Springs Gap are no longer subject to grazing pressure and have shown considerable increases in green biomass since 1948. Similarly, green biomass in the sampled vegetation strata has also increased (and species composition has changed) at lower elevation sites in the face of hemlock loss and recent wildfire. This has resulted in succession at these sites, warmer temperatures, and markedly different microhabitats. Although abundance may have increased at the site of a former hemlock forest (Trillium Gap), the modern entomofauna is likely more homogenous and less unique compared to the original fauna (Buck III 2004). Few insect species observed in the historical insect surveys were confirmed to be entirely lost in the modern era, but we observed several new, non-native species like *Eristalis tenax* (Diptera: Syrphidae), *Stomoxys calcitrans* (Diptera: Muscidae), *Japananus hyalinus* (Hemiptera: Cicadellidae), *Harmonia axyridis* (Coleoptera: Coccinellidae), and *Graphopsocus cruciatus* (Psocodea: Stenopsocidae).

We primarily focus here on insect *community* trends rather than species population trends because insect populations can exhibit extreme interannual population variability (Montgomery et al. in review). Given this high variability, “snapshot” surveys with small effective temporal sample sizes, like this one (n = 3 years), can be susceptible to random species population fluctuations. This phenomenon obscures trends (White 2019) and has been recognized as a barrier to understanding insect declines (Didham et al. 2020). Community-level metrics like total community abundance and total biomass, however, are less variable than individual species populations due to portfolio effects (Dallas and Kramer 2022), and may allow for more robust interpretation, provided other sources of variability (e.g., weather conditions) are minimized. We attempted to limit the influence of this variability in several ways: 1) by repeat sampling within a year, we are able to increase our confidence that our samples accurately reflect the year’s conditions and account for phenology; and 2) by repeat sampling within sites, we are able to average totals across multiple samples, reducing the relative importance of sample-level stochasticity, producing a relatively high level of accuracy and precision across our nearly 1000 insect samples. Although bird populations are less variable than insects (Montgomery et al. in review), they can still show substantial year-to-year variation (e.g., Black-throated Green Warbler). Thus, for birds, we also employ n-mixture modeling, enabled by repeat sampling, which produces more accurate estimates of abundance. This method also takes into account possible differences in detection probability between observers.

Resurveys often seek to limit the number of confounding variables at play by carefully revisiting locations to ensure they replicate sampling in space. However, communities and populations occur in both space and time, and failing to account for phenological change in the face of systematically rising temperatures could produce non-replicate data points that sample different points on the phenological curve. For example, the growing season in Great Smoky Mountains National Park during 2019/2020 was nearly three weeks ahead of where it was in 1947 (Figure 5). By tracking communities phenologically, we can better track changes and isolate covariates, even if each individual species does not react equally. Our resurvey study design attempted to account for possible differences in three ways, by 1) beginning repeat surveys earlier, 2) using accumulated growing degree days as a means of better matching comparable samples, post-collection, and 3) using maximum counts, rather than means, as a metric of insect abundance, to reduce sensitivity to missing a peak phenological period of insect abundance. Even so, samples in the modern era generally occurred later in terms of accumulated growing degree days.

As a protected area in the US National Park system, a primary goal of Great Smoky Mountains National Park is to protect species that inhabit it, be they birds, insects, or other taxa. Over half of the modeled species populations appeared to remain stable over the study period. Despite declines in 11 out of 28 species, we found that many nationally-declining species were still common. For some species, declines were less severe than when compared to regional- and national-level species trends (Figure 3; Smith and Edwards 2020), although there was considerable variability. This suggests that despite pervasive habitat change and climate change, the Park continues to serve as an important source for some species populations, such as Black-and-white Warbler and Golden-crowned Kinglet. However, other species, especially the biggest "losers" in our model – which tend to be those species at the southern edge of their range and associated with hemlocks – performed more poorly in the Great Smokies. Although we only have insect data from a small number of years, we can be hopeful that Great Smoky Mountains National Park may also be conserving insect abundance and biomass, at least at the community level, as insect declines occur regionally and nationally.

Habitats are rarely static and unchanging, even in conservation areas relatively buffered from direct human modification. Our study system is subject to myriad disturbances, from non-native species introductions to climate change. For example, wildfires have created abundant second growth at three sites, likely contributing to increases (or smaller decreases compared to other sites) in bird and insect abundance, biomass, and species diversity. At other sites, previously dominant hemlocks have been lost entirely, with little resulting change in insect abundance or biomass, but large effects on avian species composition and abundance. All sites have also gradually been less affected by acid rain and ozone pollution in recent decades. Indeed, habitats at only 5 of 37 sites remain relatively "unchanged" since their previous survey period (e.g., the heath bald at Brushy Mountain). Resurveys often seek to limit the number of confounding variables by choosing habitats that are relatively unchanged (Forister et al. 2023), but this can come at the expense of the examination of habitat change itself. Habitat change is a common mechanism by which drivers like climate change or invasive pests impact populations, despite being perhaps the most proximate way that organisms interact with their environments.

The effects of relatively “natural” habitat change can be underrated despite being profound and pervasive (e.g., via succession, afforestation, etc). In the Great Smoky Mountains, shorter-term habitat change due to invasive pests could be just as predictive a driver as longer-term, but more pervasive effects of climate change, at least for mobile, endothermic taxa like birds.

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Figures

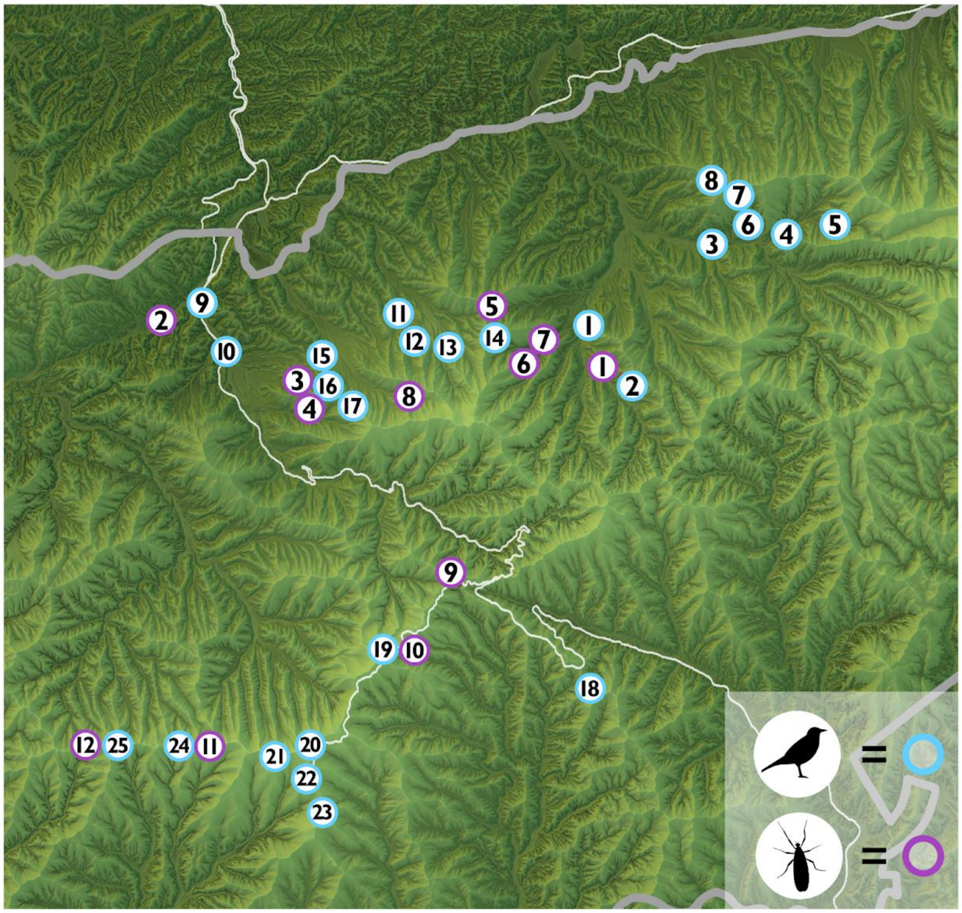


Figure 4.1. Bird and insect survey sites in Great Smoky Mountains National Park.

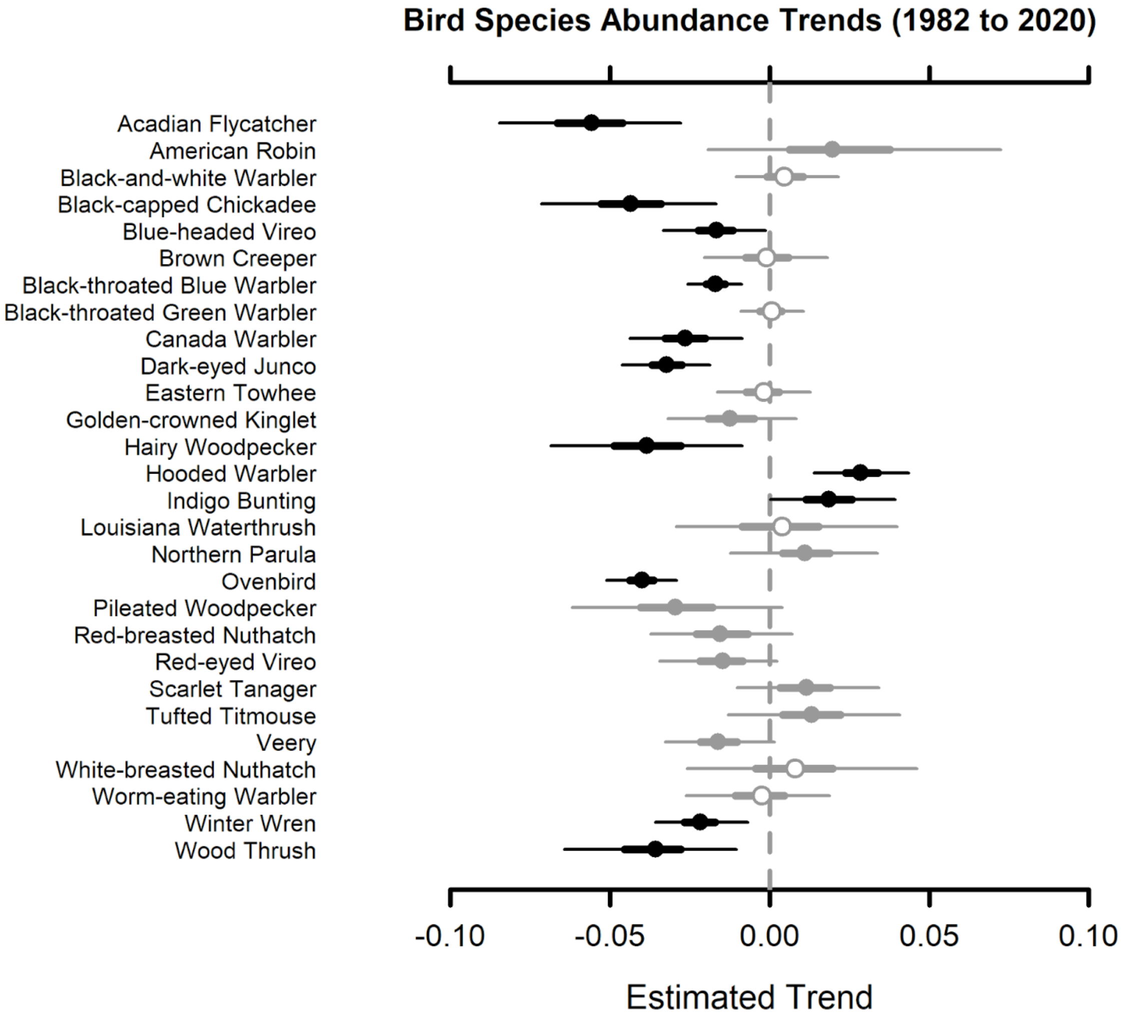


Figure 4.2. The x-axis represents the slope of the population trend, i.e., the average annual change across the time period from 1982 to 2020. Few bird populations increased between time periods, and some decreased, like Dark-eyed Junco, Blue-headed Vireo, and Wood Thrush. Hooded Warbler and Indigo Bunting were the only species that increased in abundance.

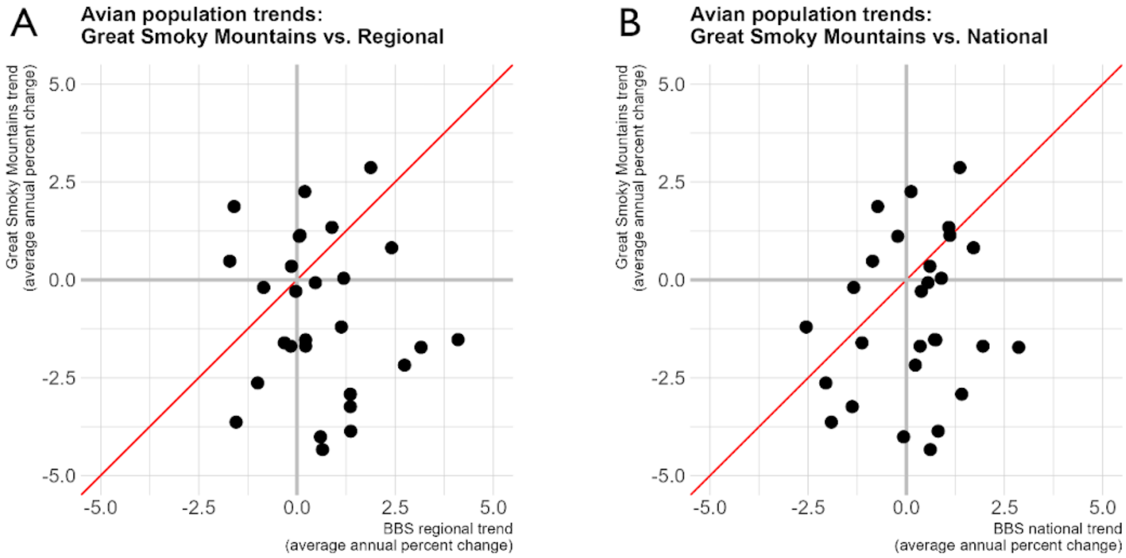


Figure 4.3. Bird populations in Great Smoky Mountains National Park either increased or decreased to a greater degree than the regional or national population trends. Species above the 1:1 line are doing better in the Park than they are at the larger scale, while species below the line are doing less well. See Figure S3 for species labels.

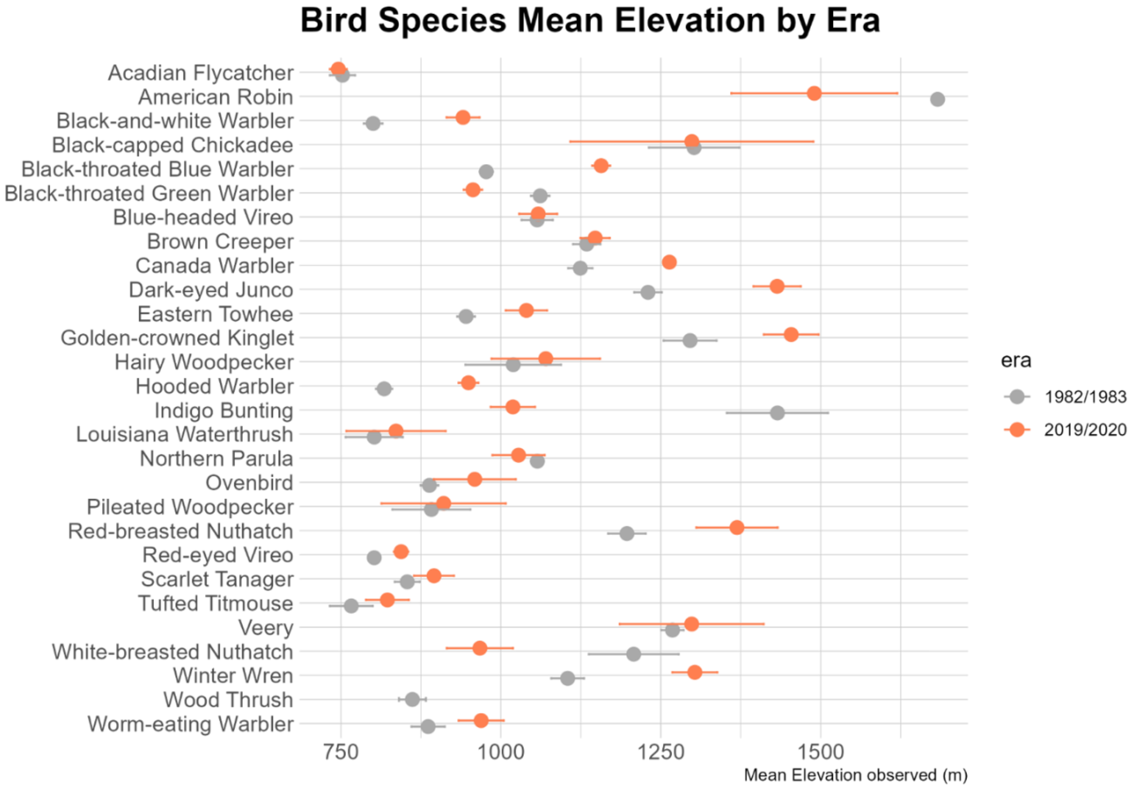


Figure 4.4. The average elevation at which a bird species was detected increased for most species when considering only sites surveyed in both 1982/1983 and 2019/2020; non-overlapping sites were excluded to prevent bias from site sampling. Error bars represent standard errors.

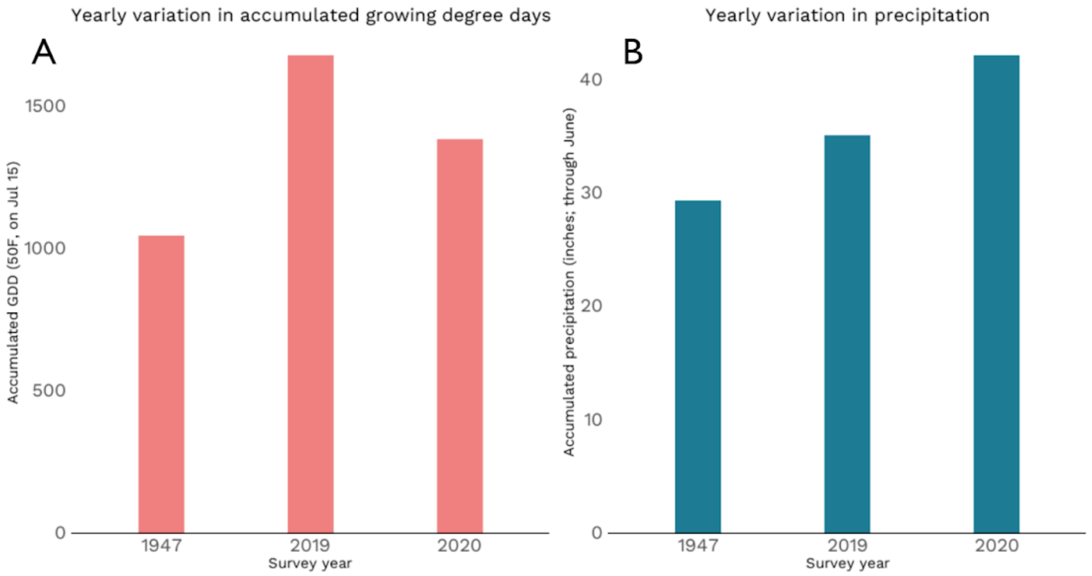


Figure 4.5. Precipitation and accumulated growing degree days varied considerably from year to year, but accumulated growing degree days (AGDD) at the survey season midpoint were higher in the modern era. Because our earlier sampling effort did not completely account for change in AGDD, we use maximum count as a metric of insect abundance, rather than mean, to be less sensitive to missing a peak phenological period of insect abundance.

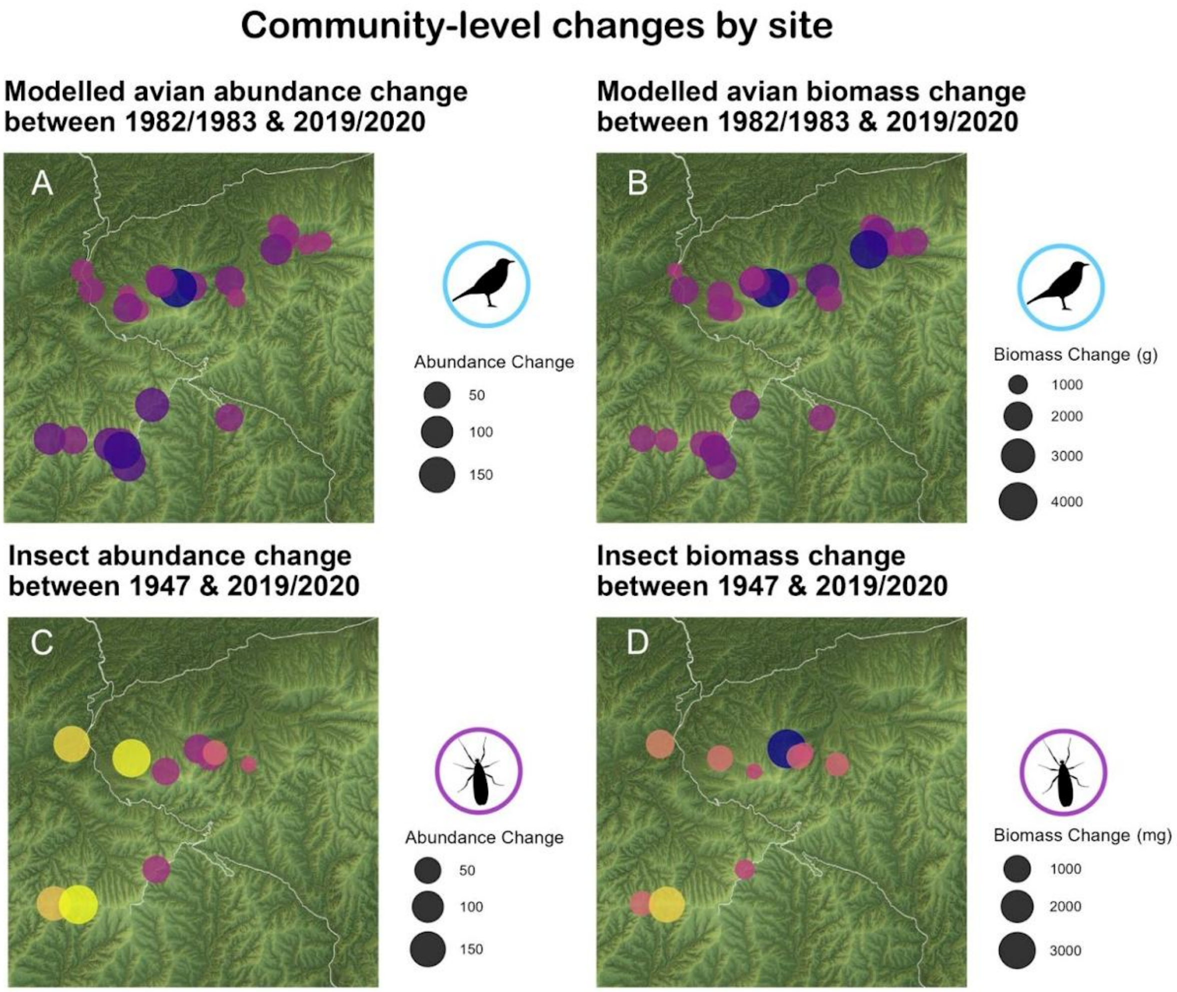


Figure 4.6. Magenta to purple colors represent negative changes, while pink to yellow colors represent positive change. Insect and bird community changes only moved in the same direction (positive or negative) at two sites.

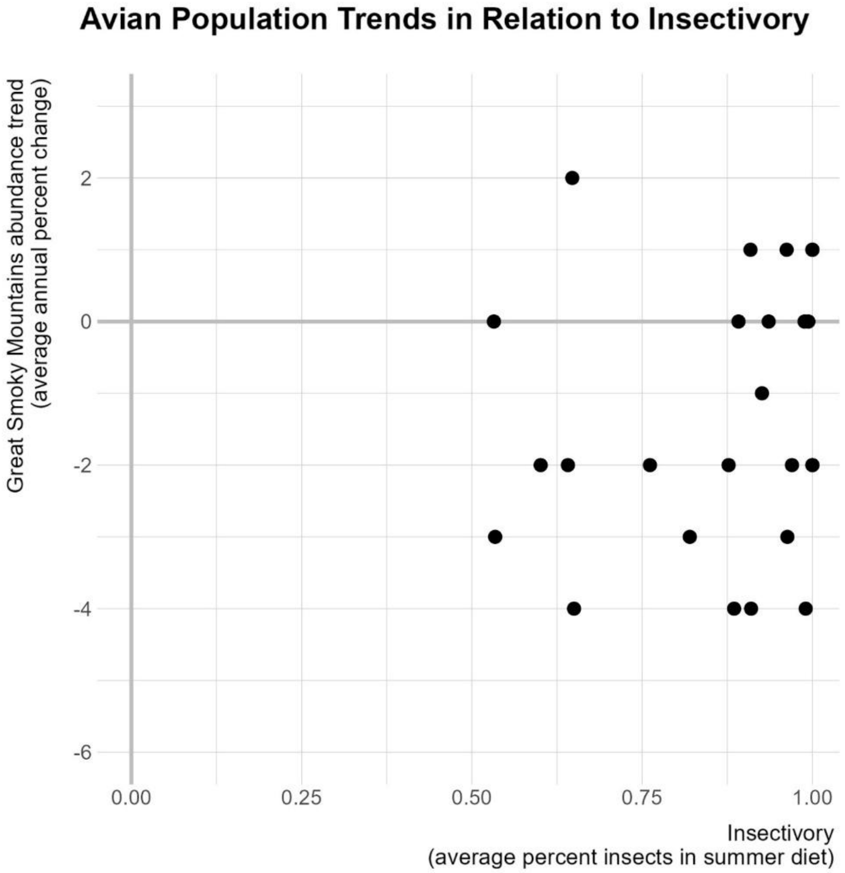


Figure 4.7. Modelled estimates of population change did not appear to be strongly related to the degree of insectivory, calculated as the average percent insects in summer diet for each species.

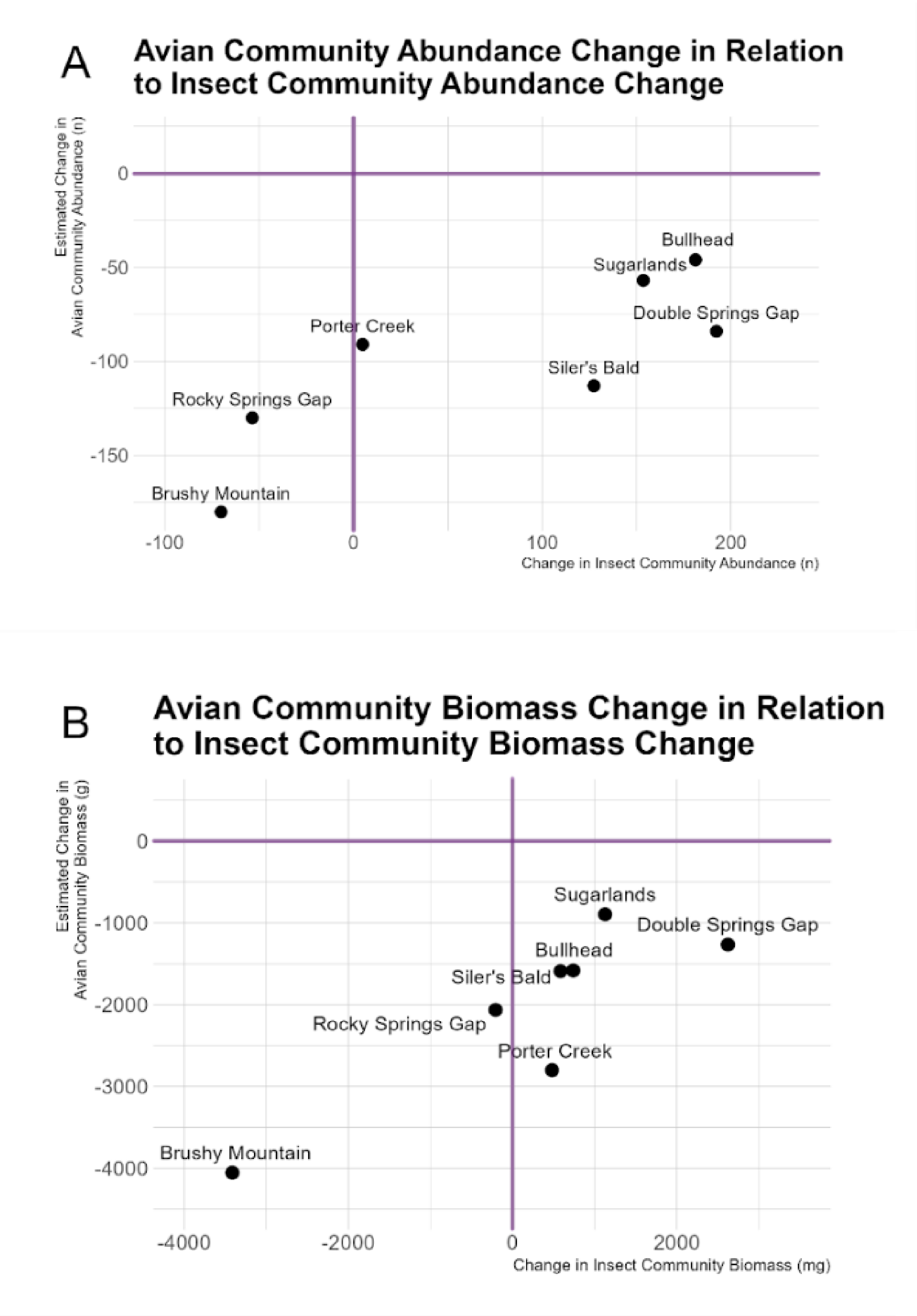


Figure 4.8. Of the seven sites where both birds and insects were surveyed, insect and bird community abundance and biomass changed together in the same direction (positive or negative) at only two sites. Despite this, we observed strong correlations between bird and insect community change when measured by both total abundance and total biomass.

Tables

Table 4.1. N-mixture model: selected parameters and metrics

Species	Annual trend	SD	2.5%	50%	97.5%	Rhat	N.eff
Acadian Flycatcher (ACFL)	-0.06*	0.01	-0.08	-0.06	-0.03	1.00	600
American Robin (AMRO)	0.02	0.02	-0.02	0.02	0.07	1.01	940
Black-and-white Warbler (BAWW)	0.00	0.01	-0.01	0.00	0.02	1.01	600
Black-capped Chickadee (BCCH)	-0.04*	0.01	-0.07	-0.04	-0.02	1.00	496
Blue-headed Vireo (BHVI)	-0.02*	0.01	-0.03	-0.02	0.00	1.01	634
Brown Creeper (BRCR)	0.00	0.01	-0.02	0.00	0.02	1.00	600
Black-throated Blue Warbler (BTBW)	-0.02*	0.00	-0.03	-0.02	-0.01	1.00	540
Black-throated Green Warbler (BTYW)	0.00	0.00	-0.01	0.00	0.01	1.00	1890
Canada Warbler (CAWA)	-0.03*	0.01	-0.04	-0.03	-0.01	1.00	700
Dark-eyed Junco (DEJU)	-0.03*	0.01	-0.05	-0.03	-0.02	1.00	549
Eastern Towhee (EATO)	0.00	0.01	-0.02	0.00	0.01	1.01	600
Golden-crowned Kinglet (GCKI)	-0.01	0.01	-0.03	-0.01	0.01	1.00	669
Hairy Woodpecker (HAWO)	-0.04*	0.02	-0.07	-0.04	-0.01	1.00	600
Hooded Warbler (HOWA)	0.03*	0.01	0.01	0.03	0.04	1.00	624

Indigo Bunting (INBU)	0.02*	0.01	0.00	0.02	0.04	1.00	561
Louisiana Waterthrush (LOWA)	0.00	0.02	-0.03	0.00	0.04	1.00	600
Northern Parula (NOPA)	0.01	0.01	-0.01	0.01	0.03	1.00	617
Ovenbird (OVEN)	-0.04*	0.01	-0.05	-0.04	-0.03	1.00	556
Pileated Woodpecker (PIWO)	-0.03	0.02	-0.06	-0.03	0.00	1.00	604
Red-breasted Nuthatch (RBNU)	-0.02	0.01	-0.04	-0.02	0.01	1.01	600
Red-eyed Vireo (REVI)	-0.02	0.01	-0.03	-0.01	0.00	1.01	428
Scarlet Tanager (SCTA)	0.01	0.01	-0.01	0.01	0.03	1.01	554
Tufted Titmouse (TUTI)	0.01	0.01	-0.01	0.01	0.04	1.00	600
Veery (VEER)	-0.02*	0.01	-0.03	-0.02	0.00	1.00	690
White-breasted Nuthatch (WBNU)	0.01	0.02	-0.03	0.01	0.05	1.00	858
Worm-eating Warbler (WEWA)	0.00	0.01	-0.03	0.00	0.02	1.00	802
Winter Wren (WIWR)	-0.02*	0.01	-0.04	-0.02	-0.01	1.00	600
Wood Thrush (WOTH)	-0.04*	0.01	-0.06	-0.04	-0.01	1.00	706

*****Trends with 95% credible intervals not including zero are marked with an asterisk.

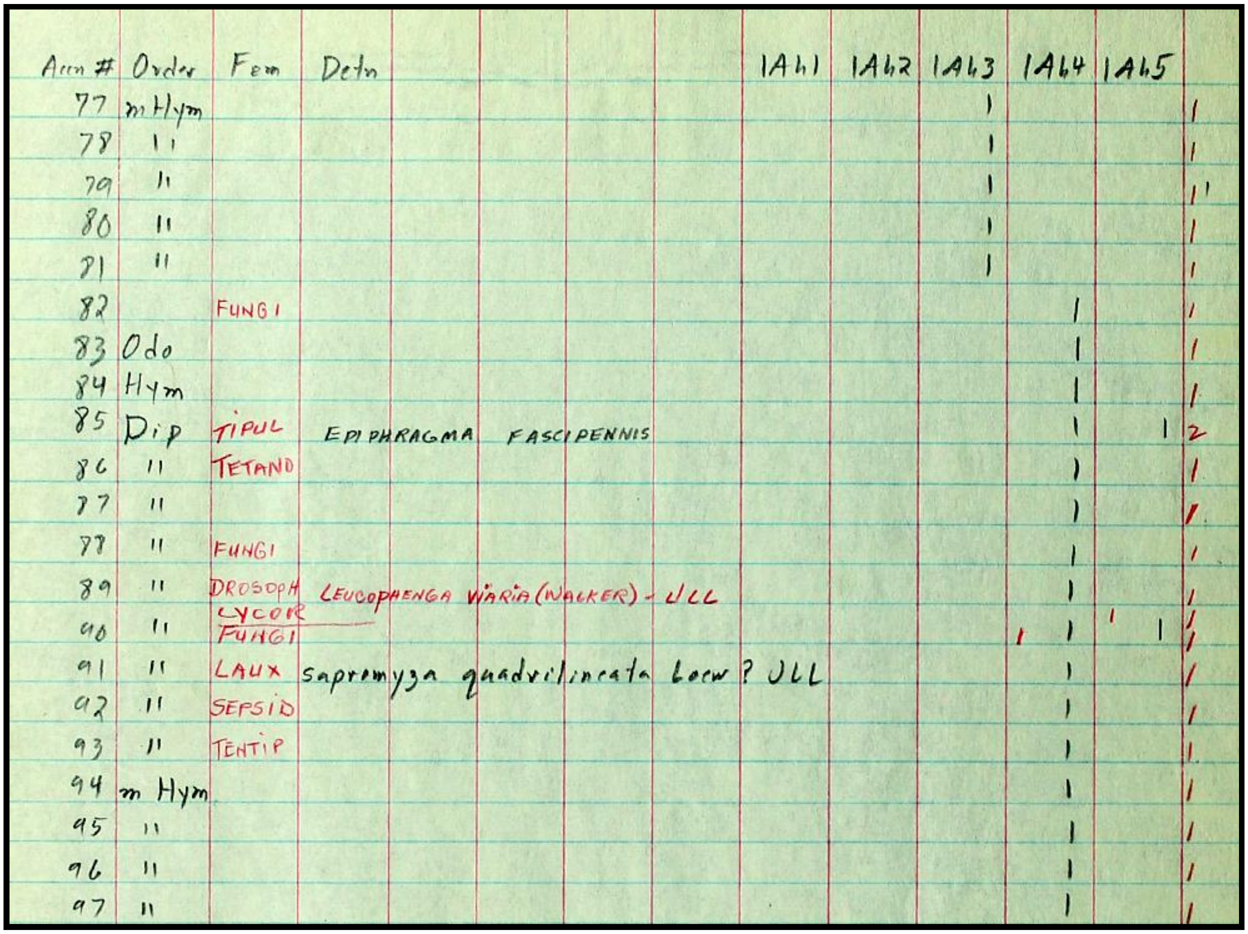
Table 4.2. 20 most commonly-detected insect families (across all samples; descending order)

Order	Family

Hemiptera	Cicadellidae
Diptera	Hybotidae
Diptera	Drosophilidae
Coleoptera	Chrysomelidae
Coleoptera	Scraptiidae
Hemiptera	Miridae
Diptera	Muscidae
Psocodea	Caeciliusidae
Diptera	Empididae
Hemiptera	Psyllidae
Diptera	Limoniidae
Diptera	Chloropidae
Diptera	Lauxaniidae
Psocodea	Amphipsocidae
Coleoptera	Cerambycidae
Coleoptera	Staphylinidae
Hemiptera	Lygaeidae
Coleoptera	Kateretidae

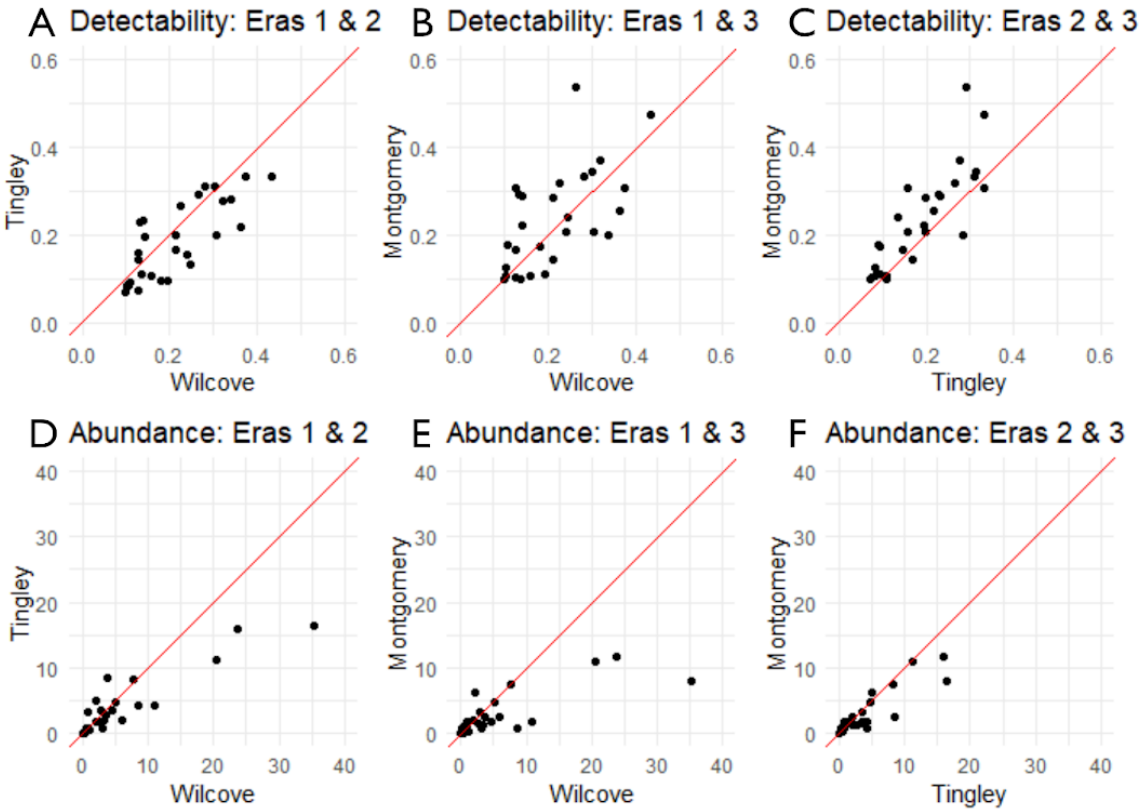
Diptera	Tipulidae
Diptera	Simuliidae
Diptera	Rhagionidae
Coleoptera	Nitidulidae
Hemiptera	Tingidae
Coleoptera	Mordellidae
Diptera	Dolichopodidae
Mecoptera	Panorpidae
Coleoptera	Elateridae
Diptera	Milichiidae
Hemiptera	Delphacidae
Psocodea	Psocidae

Appendix 4-I: Supplemental figures

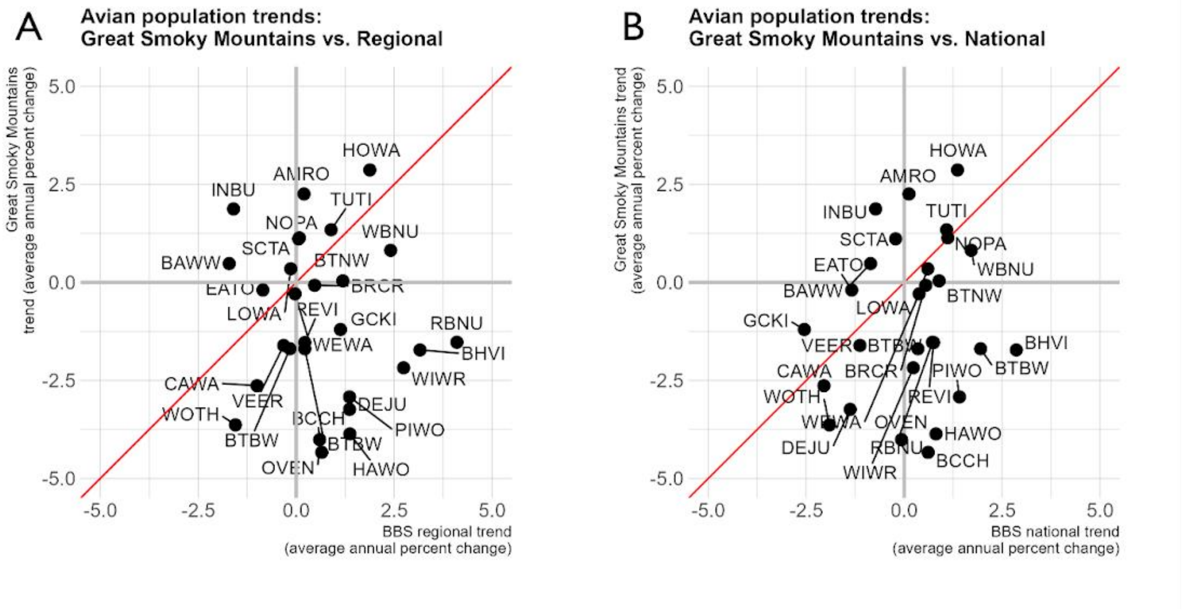


Accn #	Order	Fam	Detn	1Ah1	1Ah2	1Ah3	1Ah4	1Ah5	
77	m Hym					1			1
78	"					1			1
79	"					1			1
80	"					1			1
81	"					1			1
82		FUNGI					1		1
83	Odo						1		1
84	Hym						1		1
85	Dip	TIPUL	EPIPHRAGMA FASCIPENNIS				1	1	2
86	"	TETANO					1		1
87	"						1		1
88	"	FUNGI					1		1
89	"	DROSOPH	LEUCOPHENGA VARIA (WALKER) - JLL				1		1
90	"	LYCOR FUNGI					1 1	1 1	1 1
91	"	LAUX	sapromyza quadrilineata Loew ? JLL				1		1
92	"	SEPSID					1		1
93	"	TENTIP					1		1
94	m Hym						1		1
95	"						1		1
96	"						1		1
97	"						1		1

Supplemental Figure S4.1. Robert Whittaker’s datasheets for his 1948 insect survey, archived at the Cornell University Library and now digitized, provide a thorough accounting of his sampling scheme.



Supplemental Figure S4.2. A-C) Detectability remained relatively constant across all eras, and did not generally increase, suggesting that higher detection in modern eras did not bias abundance estimates. D-F) Estimated abundance declined markedly for several species, with Dark-eyed Junco showing the largest total decline in terms of numbers of individuals lost.



Supplemental Figure S4.3. Avian population trends compared to regional and national trends (see Figure 3), with species labeled with banding codes referenced in Table 1.

Appendix 4-II: Supplemental tables

Supplemental Table S4.1. Bird and insect survey site locations and elevations

Bird survey sites

Site #	Site name	Latitude	Longitude	Elevation
1	Porter Creek (lower)	35.68053	-83.397	725
2	Porter Creek (upper)	35.66792	-83.391	908
3	Ramsey Creek (lower)	35.70323	-83.3537	657
4	Ramsey Creek (mid)	35.70705	-83.3248	909
5	Ramsey Creek (upper)	35.70894	-83.3111	1105
6	Greenbriar Chestnut Oak	35.70829	-83.3422	939
7	Greenbriar Red Oak	35.71492	-83.344	1245

8	Greenbriar Pinnacle	35.71985	-83.3502	1311
9	Sugarlands	35.68802	-83.5349	445
10	Quiet Walkway Trail	35.6737	-83.526	485
11	Spruce Flats	35.68189	-83.4625	946
12	Lower Roaring Fork	35.67932	-83.4603	988
14	Brushy Mountain Trail	35.67541	-83.4459	1200
15	Brushy Mountain Bald	35.67652	-83.4317	1483
13	Bullhead (lower)	35.67067	-83.4927	843
16	Bullhead (middle)	35.66098	-83.4924	1208
17	Bullhead (upper)	35.6594	-83.4819	1295
18	Thomas Divide	35.58144	-83.3973	1419
19	Rocky Springs Gap	35.59069	-83.4695	1793
20	Kuwohi	35.56296	-83.4986	2024
21	Mt. Buckley	35.56211	-83.5085	1956
22	Andrews Bald	35.54788	-83.4918	1741
23	Forney Ridge Trail	35.55787	-83.4975	1889
24	Double Springs Gap	35.5652	-83.543	1684
25	Silers Bald	35.56622	-83.5651	1696

Insect survey sites

1	Porter Creek	35.66667	-83.3833	1141
2	Bullhead (upper)	35.66314	-83.4923	1125
3	Bullhead (lower)	35.67121	-83.4927	836
4	Fighting Creek	35.68149	-83.5486	465
5	Brushy Mountain	35.67799	-83.4303	1496

6	Trillium Gap	35.67215	-83.4192	1225
7	Trillium Gap Pines	35.67516	-83.4147	1063
8	Rainbow Falls	35.66162	-83.4607	1385
9	Indian Gap	35.61078	-83.4453	1650
10	Rocky Springs Gap	35.59065	-83.4696	1794
11	Silers Bald	35.56603	-83.5653	1706
12	Double Springs Gap	35.5652	-83.5425	1679

Supplemental Table S4.2. Most frequently detected and identified insect genera and species across (across all samples; descending order)*

Order	Family	Species
Coleoptera	Scraptiidae	*Anaspis rufa*
Hemiptera	Cicadellidae	*Forcipata loca*
Hemiptera	Cicadellidae	*Eupteryx flavoscuta*
Diptera	Drosophilidae	*Scaptomyza terminalis*
Hemiptera	Cicadellidae	*Balclutha sp.*
Hemiptera	Cicadellidae	*Evacanthus interruptus*
Psocodea	Caeciliusidae	*Valenzuela sp.*
Diptera	Muscidae	*Coenosia atrata*
Psocodea	Amphipsocidae	*Polypsocus corruptus*
Diptera	Hybotidae	*Hybos slossonae*
Hemiptera	Psyllidae	*Psylla carpinicola*
Hemiptera	Cicadellidae	*Graphocephala coccinea*
Hemiptera	Lygaeidae	*Kleidocerys resedae*
Hemiptera	Miridae	*Monalocoris filicis*
Coleoptera	Chrysomelidae	*Altica sp.*
Coleoptera	Cerambycidae	*Pidonia aurata*

Hemiptera	Cicadellidae	*Oncopsis sp.*
Coleoptera	Staphylinidae	*Atheta sp.*
Diptera	Hybotidae	*Chelipoda sp.*
Diptera	Lauxaniidae	*Minettia lupulina*
Coleoptera	Kateretidae	*Brachypterus urticae*
Coleoptera	Chrysomelidae	*Odontota dorsalis*
Hemiptera	Cicadellidae	*Typhlocyba sp.*
Hemiptera	Cicadellidae	*Thamnotettix confinis*
Diptera	Hybotidae	*Leptopeza compta*
Hemiptera	Cicadellidae	*Empoasca sp.*
Diptera	Simuliidae	*Simulium parnassum*
Hemiptera	Cicadellidae	*Agalliopsis novella*
Diptera	Lauxaniidae	*Sapromyza sp.*
Hemiptera	Cicadellidae	*Graminella nigrifrons*
Coleoptera	Chrysomelidae	*Pachybrachis tridens*
Diptera	Hybotidae	*Platypalpus sp.*
Diptera	Hybotidae	*Leptopeza ruficollis*
Hemiptera	Miridae	*Neolygus belfragii*
Coleoptera	Nitidulidae	*Brassicogethes aeneus*
Diptera	Limoniidae	*Austrolimnophila toxoneura*
Hemiptera	Cicadellidae	*Erythroneura sp.*
Diptera	Empididae	*Rhamphomyia sp.*
Coleoptera	Chrysomelidae	*Xanthonia decemnotata*
Diptera	Hybotidae	*Platypalpus mimus*
Diptera	Chloropidae	*Thaumatomyia pulla*
Diptera	Drosophilidae	*Scaptomyza graminum*
Hemiptera	Cicadellidae	*Agalliopsis sp.*
Hemiptera	Cicadellidae	*Agallia quadripunctata*

Hemiptera	Cicadellidae	*Eupteryx vanduzei*
Coleoptera	Chrysomelidae	*Syneta ferruginea*
Diptera	Tipulidae	*Dolichopeza carolus*
Mecoptera	Panorpidae	*Panorpa nebulosa*
Diptera	Chloropidae	*Parectecephala eucera*
Diptera	Drosophilidae	*Scaptomyza sp.*

* Note that more common insect species could have been present in the sample without being identified to genus or species level.

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