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Phenological shifts and increases in voltinism within a moth community over a century of anthropogenic change

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Abstract

In temperate ecosystems, warming temperatures can advance spring phenology, extend autumn phenology, disrupt dormancy regulation, result in phenological mismatch across taxa, and even lead to increases in the number of generations per year (i.e., increases in voltinism). Much of what we know about the impacts of global change on species phenology and voltinism comes from recent decades; however, anthropogenic warming began centuries ago. Using light trap datasets from 1889–1892 and 1919–1922, alongside contemporary records, we document long-term changes in phenology and voltinism for 78 moth species, and changes in occurrence for 169 species, in New York, USA. From 1919–1922 to 2019–2024, we found an advance in spring phenology by 0.55 days per decade and an extension of the end of the flight period by 1.18 days per decade. This shift was largely driven by bi- and multivoltine species, which have added generations extending the end of their flight period by 1.58 days per decade compared to an extension of only 0.49 days per decade for univoltine species. We also document the apparent disappearance of 13 species from the region from 1889 to present, whose ranges now tend to be farther north and at higher elevations, possibly due to global change. As this region becomes warmer and wetter with ongoing climate change, more species may extend their active period or add more generations per year, with the potential for rapid adaptation and consequences for ecosystem function as some insect herbivores become more abundant.

KEYWORDS
global change, historical data, historical ecology, light trap, phenology shift

INTRODUCTION

Widespread and rapid environmental changes characterize the Anthropocene, with increasing and accelerating rates of global change after the Industrial Revolution and a second burst of acceleration after World War II (Steffen et al., 2015). Land use change, direct exploitation, pollution, invasive species, and numerous other stressors all contribute to

environmental change; however, increased temperatures due to climate change have been a key factor (Jaureguiberry et al., 2022). Since 1850, there has been a >1.1°C increase in global mean temperature; the rate of warming since 1982 has been more than three times as rapid, with a rate of increase of 0.20°C per decade (NOAA, 2024). Rising global temperatures have been linked to a multitude of biological responses, ranging from changes in species traits and breakdowns of species interactions to population declines and extirpations, to range expansions and contractions, and even extinction (Parmesan & Yohe, 2003). Increasing temperatures lead to phenological shifts across taxa, particularly in poleward regions, by advancing spring phenologies, lengthening the growing season, and reducing the strength of winters (Valtonen et al., 2014). For example, rising spring temperatures can result in earlier leaf out of plants (Polgar & Primack, 2011; Sherry et al., 2007) and emergence from diapause for insect herbivores (Parmesan, 2007). While phenological mismatches have been one hypothesized consequence of temperature change (Van Dis et al., 2023), other demographic consequences may be equally or more important for population dynamics and species interactions (Abarca & Spahn, 2021).

Rising autumn temperatures have been implicated in insect herbivore populations delaying diapause and adding extra generations (Altermatt, 2010; Gimesi et al., 2012; Michielini et al., 2021; O'Neill et al., 2012). Warmer temperatures, particularly during the summer months in temperate ecosystems, can speed up metabolic rates and facilitate rapid development for insects (Zvereva & Kozlov, 2006). This rapid development can result in more generations per year for multivoltine species (those with multiple generations per year), which are able to exploit longer growing seasons to produce more generations per year, thus increasing their intrinsic population growth rate (Altermatt, 2010, Gimesi et al., 2012, Michielini et al., 2021, O'Neill et al., 2012). Multivoltine insect pests may be able to exploit the now longer growing season and add more generations per year, leading to increased host plant herbivory (Schebeck et al., 2024; Tobin et al., 2008; Wepprich et al., 2025). Producing more generations per year not only results in greater abundance, but can also lead to range shifts or expansions (Hällfors et al., 2021), and gives species greater potential for adaptation to changing environments (Knell & Thackeray, 2016) if they can avoid ecological traps (Van Dyck et al., 2015). For example, 190 out of 263 (72%) bi- and multivoltine Macrolepidoptera in Central Europe showed increased population size in second and subsequent generations, while also advancing their spring phenology and emerging from diapause 2.1 days earlier after 1980 compared to prior to 1980 (Altermatt, 2010). The earlier emergence and increasing abundance of multivoltine species under climate change (Pöyry et al., 2011) has also resulted in poleward range expansions (Hällfors et al., 2021; Macgregor et al., 2019). Populations that are strictly univoltine, however, often exhibit negative population trends associated with earlier emergence and increasing temperature (Altermatt, 2010; Macgregor et al., 2019) and may be expected to decline further under future global change.

Datasets documenting phenological shifts in insects have primarily been gathered over recent decades; however, global temperature has been steadily increasing since the start of the Industrial Revolution, and a signal of climate change was detectable as early as 1885 (Santer et al., 2025). Many populations and communities likely began responding to environmental changes decades prior to our current baseline understanding, and thus we may expect to see even stronger phenological responses over longer time periods. Museum specimens can be used to quantify changes in phenology across centuries (Brooks et al., 2014; Maurer et al., 2018); however, the data and analyses are fraught with issues, including inconsistent sampling effort, collector bias, and low rates of museum specimen digitization (Belitz et al., 2023). Alternative data sources such as field notebooks kept by early naturalists and historical scientific publications have the potential to contain historic phenology data (Primack et al., 2023), which could improve our understanding of how global change has impacted insects and other poikilothermic species over time spans that match the Great Acceleration.

Here, we integrate historical and contemporary moth datasets that explicitly tracked species' phenologies in a single location to better understand how phenology has changed over centuries. We compared historical moth phenology from light traps operated in the late 19th and early 20th centuries to contemporary phenology from a light operated by JJD from 2018 to 2024, augmented with participatory science data. We used the contemporary records from JJD along with iNaturalist observations from 2019 to 2024 to measure the current week of first flight and week of last flight, and the number of generations per year for each species. Using this integrated dataset spanning 135 years of moth community sampling, we test the hypotheses that (1) warming temperatures over the last century have advanced spring phenology (i.e., earlier emergence of the first brood), (2) delayed end-of-season diapause has resulted in longer flight durations, and (3) species with plastic voltinism have more generations per year relative to the number of broods historically.

MATERIALS AND METHODS

Historical moth sampling

In 1889 and 1892, M.V. Slingerland operated light traps on the campus of Cornell University in Ithaca, New

York. He described the trap as "an ordinary lantern set on a brick in a common tin pan and these were fastened to a platform on a stake [four feet above the ground]... water was poured into the pan until the brick was covered and then enough kerosene (the killing agent) was used to form a thin film over the water" (Slingerland, 1902). In 1889, six traps were run every night from May 1 to October 15 in the agricultural portion of the campus (Appendix S1: Figure S1); in 1892, only the light trap site at the insectary was run, and for a shorter time window from May 15 to October 1 (Slingerland, 1902). Slingerland reported the count of each species observed in each year, and occasionally also made note of the dates on which they were captured or the species' general flight window.

Thirty years later, W.T.M. Forbes operated a light trap on the Cornell University campus in 1919 and 1922. According to Forbes' notes at the Cornell University Insect Collection, the trap was located "in the south edge of the woods south of Fall Creek Drive west of the filter plant" (Appendix S1: Figure S2), placing it in the same site near the insectary that Slingerland had sampled 30 years earlier. Forbes described the trap as a "two feet cube, with three sides of glass slats adjusted so close as to exclude a few of the larger moths" (Forbes, 1923). In 1919, the bulb was a "strong ordinary tungsten," which was replaced with a 500-W blue tungsten in 1922. The light traps were run from the start of May to the end of October in both years and samples were collected daily, though "in a few cases ... allowed to accumulate three days." Despite sampling daily, Forbes only reported the abundance of each species within each week, using the 1922 calendar year as the standard for weeks of the year beginning on Sundays.

Contemporary moth sampling

To estimate contemporary moth phenology, we used iNaturalist observations from 2019 to 2024. iNaturalist is a participatory science platform where observers can upload photographs documenting species that they have seen, which has been exponentially growing in popularity since it was introduced in 2009 (Di Cecco et al., 2021). We exported all Research Grade, living, adult observations of Lepidoptera in Tompkins County, New York, from January 2019 to December 2024 (i.e., starting 100 years after the first year of Forbes' data collection). Because even iNaturalist Research Grade observations can contain identification errors, we manually screened and verified records that occurred outside the expected flight window. We opted to search all of Tompkins County, which includes the city of Ithaca and the surrounding forested and rural areas, rather than just Cornell University campus because we assume that surrounding populations share similar phenology. To make the iNaturalist records comparable to the weekly records reported by Forbes, we also used the 1922 calendar year as the basis for determining which days fell into which weeks of the year.

iNaturalist records are based on observations, primarily in the form of photographs, and thus are a different method of sampling the moth community than the light traps used by both Slingerland and Forbes. To assess if contemporary iNaturalist phenology records were comparable to a contemporary light trap, we compared them to phenology records collected from a mercury vapor light and ultraviolet light traps run over the same time period in Tompkins County. Since August 2018, JJD has operated this light setup (42.392–76.373) less than 12 km from the historical insectary location (42.451–76.482) nearly every night of the year with favorable weather (i.e., not raining or too cold). The trap is located at the edge of a primary forest, near a creek, and adjacent to open fields. The records from this locality are separated into occurrence during the early, middle, and late periods of each month (approximately 10-day time periods), which are not directly comparable to the weekly historical records taken by Forbes; however, the iNaturalist records are daily, which allows for cross-scale comparisons among the light trap datasets (Appendix S1: Figure S3). We assessed the correlation of the flight periods within the JJD data and iNaturalist data separately for the period of first flight and period of last flight. Because both contemporary datasets were highly correlated (Appendix S1: Figure S3), we proceeded with the estimated phenologies from iNaturalist data, which are comparable to Forbes' historical data grouped by weeks, rather than 10-day periods from JJD which are not directly comparable to Forbes' timescale. We did not attempt a quantitative comparison of phenology to Slingerland, who in many cases reported species' phenology in terms of months (e.g., "May to September") and was inconsistent in the level of detail for species' phenologies, but we do present the Slingerland phenology alongside the other data sources for qualitative comparison (Appendix S2).

Data digitization and cleaning

To make the historical moth data comparable to those from contemporary records, we transcribed the notes associated with each publication reporting results of the Ithaca light traps (Forbes, 1923, 1924; Slingerland, 1902), including species' names verbatim as used by the original authors, counts and dates, number of broods, and miscellaneous notes. Forbes' notes were only for a subset of species, excluding both the rarest and commonest species,

and included weekly phenology charts for many, but not all, of the species in the form of hand-drawn barplots. We digitized each phenology chart using the WebPlotDigitizer (automeris.io) tool. Because hand-drawn figures are imprecise, we treated bars as proportions, with the entire area of all bars summing to one, and multiplied the proportion for each bar by the total count reported by Forbes for each species. We then rounded bars to the nearest whole number and adjusted weekly counts up or down, while consulting the original drawing, until the sum matched the count of individuals Forbes reported in the text. For species with charts combining data across both years (see Forbes, 1923), we digitized open circles as the records for the year not specified and subtracted the total number of circles prior to adjusting counts for the plotted year. In cases where Forbes did not report the total count for a species, we retained the unadjusted, relative weekly proportion of records.

To determine changes in phenology since the historical time period, we limited our analyses to only species which were suitable for inference. Because insect populations fluctuate wildly from year to year, many species were present in only 1 year historically (e.g., a species present in 1919, but not in 1922). These large interannual population fluctuations can introduce bias when comparing historical insect community data to those from contemporary records, especially when only comparing two points in time as we do here (Didham et al., 2020). To minimize this bias, we limited our phenology analyses (Appendix S1: Figure S4) to species that were present in both years of the Forbes dataset (i.e., those that were relatively common historically such that shifts in phenology or occurrence in recent years are less likely to be due to interannual variation). Because we aimed to quantify changes in phenology, we also only included species for which Forbes (1923) included phenology graphs, which were not reported for the most common species. We further excluded species whose flight window was cut short by Forbes' sampling window (i.e., where we could not confirm that the absence of observations historically meant the absence of flight activity or was simply due to lack of sampling effort). We also excluded species that require dissection to distinguish or are otherwise difficult to identify from photographs and would potentially be misrepresented in the iNaturalist records. Finally, we excluded any species with too few observations on iNaturalist to estimate the phenology. We excluded any species with fewer than five observations as a somewhat arbitrary cutoff, as well as any species whose phenology based on the records in iNaturalist seemed to be systematically biased. For example, if a species' phenology in iNaturalist for Tompkins County was drastically different than for Central New York (the broader region including Tompkins County), we excluded it because the subset of records for Tompkins County were likely a biased sample. Similarly, if the species' phenology from iNaturalist was grossly inconsistent with the JJD light trap phenology estimates and it had few observations in iNaturalist, we excluded it for having too small of a sample size to adequately characterize the flight period.

Over the past 135 years, there have been many changes to the taxonomy and nomenclature of the moth species sampled by Slingerland and Forbes. We excluded from all analyses species whose concept had changed (e.g., those that had been synonymized with other species, or split into multiple species), and those which we suspected were likely to have been a mistaken identification in the historical records. To identify the current species names for the historical records for comparisons to contemporary records, we used the Annotated Checklist of the Lepidoptera of North America North of Mexico (Pohl & Nanz, 2023).

In addition to changes in phenology, we used the species records to determine if any species present historically had not been observed in Tompkins County recently. To be included in this analysis, species had to have been present in at least 2 years historically (to avoid introducing bias from vagrants or interannual variation) though not necessarily in the same dataset. For example, a species present in Slingerland's records from 1892 and again in Forbes' records in 1922 (but not in 1889 or 1919) would be included in the analysis. We compared this species list to those observed in iNaturalist and in the JJD records to determine which species had not been observed recently. We did not do any formal analysis for these species; however, we do present the geographic centroid of the five nearest iNaturalist observations for each species.

Voltinism

Because previous theoretical and empirical studies have suggested or found that multivoltine species are able to increase the number of generations per year under warming conditions (Forister et al., 2018; Macgregor et al., 2019; Michielini et al., 2021; Yamamura & Kiritani, 1998), we considered voltinism as a potential covariate to explain changes in species phenology. Forbes reported the number of broods per year for species in his notes, which we used as the estimate of historical voltinism; in cases where he did not make note of the voltinism, we inferred it based on the number of distinct peaks in the historical phenology graphs. To estimate current voltinism, we used the number of clearly distinct peaks in the iNaturalist phenology graphs (i.e., a species with two or more local maxima was treated as bi- or multivoltine, while those with only one were treated as univoltine, see Appendix S2). Because methods of estimating voltinism were imperfect historically (e.g., Forbes often made notes that there were "stragglers" which could be a second brood for

species he considered univoltine) and in iNaturalist (e.g., due to sampling bias), we collapsed our measure of voltinism into those that were strictly univoltine in both time periods, and those that had two or more generations per year in either time period. For this simplified metric, we did not distinguish between bi- and multivoltine species.

Statistical analysis

To test our hypothesis that species were emerging from diapause and flying earlier in the year, we used a paired Student's *t*-test to test if there were significant differences between the week of first flight historically compared to iNaturalist. We used the same analysis to test for differences in the week of last flight. We recognize that testing for differences in extremes can introduce statistical challenges; however, there are constraints when using historical data and we were unable to calculate a more conservative metric (e.g., the 10th and 90th percentiles of the flight distribution) due to the weekly resolution of the historical data. To test whether phenological shifts were associated with voltinism, we used a general linear model. The raw data reported by Forbes were weekly; however, we treated the data as normally distributed because prior to model fitting, we calculated a weighted week of first flight and week of last flight. Weighting was based on the proportion of observations in the first and second weeks of observations for the week of first flight (e.g., for a species with two observations in Week 22 and eight in Week 23, the weighted week of first flight would be 22.8), and for the last and second to last weeks for the week of last flight. This resulted in continuous estimates of phenology rather than integers corresponding to weeks of the year. In our general linear models, we modeled week of last flight in iNaturalist as the response variable, predicted by the week of last flight in the Forbes data, whether a species exhibited bi- or multi-voltinism in either time period or was strictly univoltine, and an interaction between the two predictors. We used the same model structure for week of first flight, though we expected no differences by voltinism for advancing spring phenology. In both models, we allowed for a normally distributed intercept.

RESULTS

Species records

In 1889 and 1892, M.V. Slingerland reported observations for 56 species of moths captured in light traps on the campus of Cornell University; however, many others were not identified (e.g., "large moth") or had not yet been described, and only 37 occurred in both years of sampling. Thirty years later, sampling at the same location, W.T.M. Forbes collected 347 species in total between 1919 and 1922, of which 203 were "rare" (58.5%) and not all of which were identified to species (e.g., *Baileya* spp.). Many of the species reported by Slingerland ($N = 30$, 57.6%) were not reported by Forbes, a third of which are still present in the JJD samples likely due to Forbes' tendency to omit common species from reports ($N = 10$, 33.3%), while others are difficult to identify or had taxonomic issues historically ($N = 7$, 23.3%), and others are among the species that have been lost from the region ($N = 8$, 26.7%). The remaining two species observed by Slingerland but not by Forbes or JJD were *M. americana* (Fabricius, 1793)—an outbreaking species that Slingerland captured 601 individuals of in 1889 and zero in 1892—1889 was presumably an outbreak year—and *Leucania commoides* Guenée, 1852, a species that is still observed in Tompkins County on iNaturalist, but rarely.

Across both datasets, there were 377 species observed historically; however, only 169 were eligible for inclusion in any of our analyses. The remainder were excluded from our analyses because they were rare or only observed in a single year historically ($N = 167$, 44.3%), require dissection or are otherwise difficult to identify ($N = 20$, 5.3%), had major taxonomic revisions ($N = 18$, 4.7%), or had major discrepancies suggesting historical misidentifications ($N = 3$, 0.9%). For our analyses of changes in phenology (Figure 1a,b), a further 91 species were excluded because there were too few observations on iNaturalist in Tompkins County to estimate phenology ($N = 33$, 36.2%), Forbes did not report their phenology ($N = 32$, 35.2%), they were only observed in a single year by Forbes ($N = 15$, 16.5%), or occurred outside the window of time during which Forbes sampled historically ($N = 11$, 12.1%).

Most of the species observed in 1889 and 1892 by Slingerland that were eligible for inclusion in analyses were in the family Noctuidae ($N = 23$, 62.2%), followed by Crambidae ($N = 7$, 18.9%) and Erebidae ($N = 5$, 13.5%), with Pyralidae and Lasiocampidae represented by a single species each. Of the species Forbes observed that were included in any analyses, the plurality of species was in the family Noctuidae ($N = 35$, 23.6%), followed by Geometridae ($N = 34$, 23.0%), Erebidae ($N = 29$, 19.6%), Crambidae ($N = 17$, 11.5%), and Tortricidae ($N = 14$, 9.5%), with four or fewer species from Depressariidae, Drepanidae, Gelechiidae, Gracillariidae, Limacodidae, Notodontidae, Pterophoridae, Pyralidae, Saturniidae, Sphingidae, and Tineidae.

Phenology shifts

The 78 species included in the phenology analyses comparing the Forbes records to iNaturalist showed a moderate advancement in the week of first flight and a

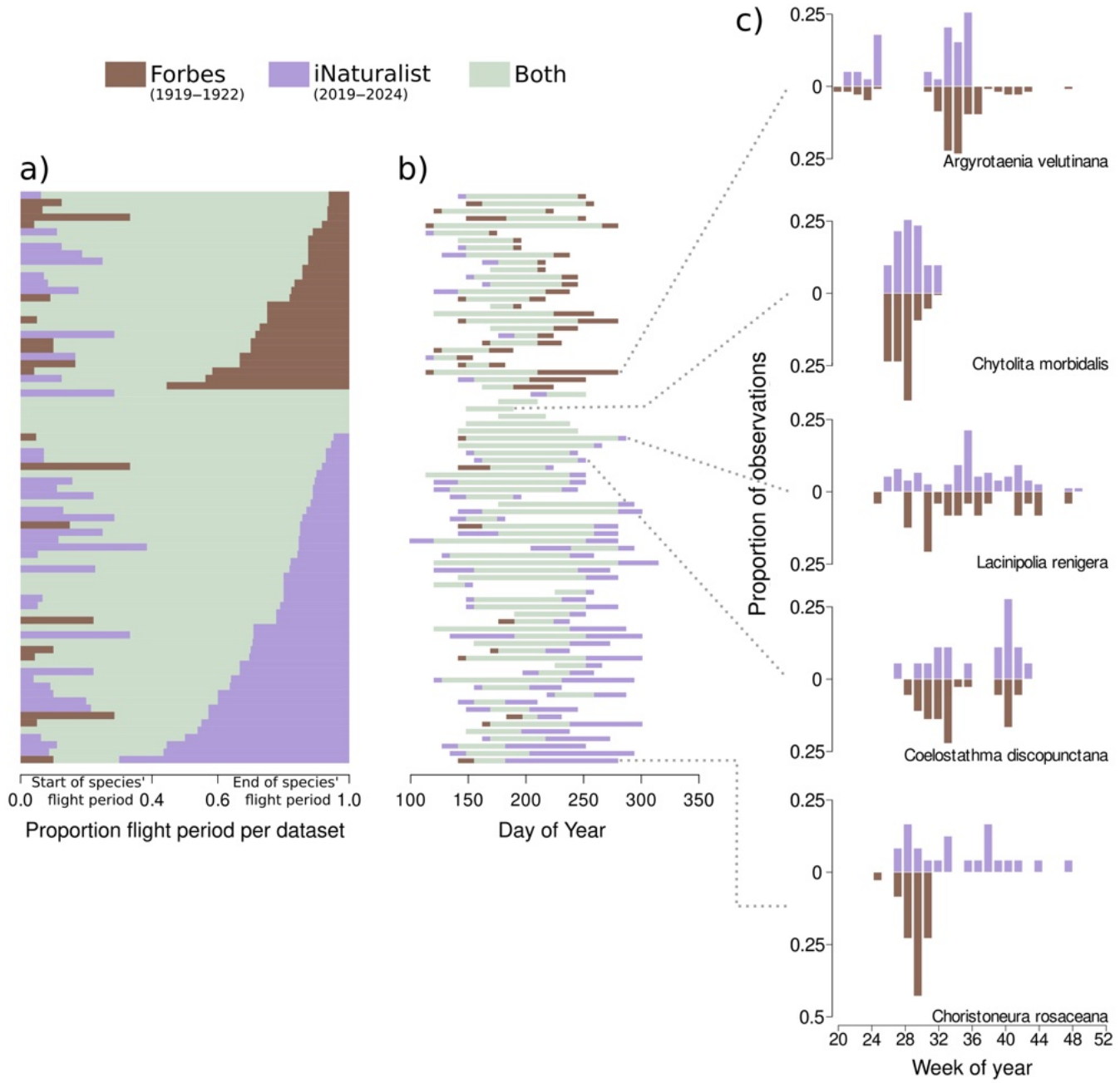

FIGURE 1 Flight periods and phenologies of species included in the phenology analyses. Species flight periods are shown in (a) as the proportion of their total flight period across both time periods in which weeks have records for only the historical period (brown) or contemporary (purple) or shared across both time periods (green); each bar is standardized by the duration of that species' total flight period. Individual species phenologies in relation to the time of year in which they are active are shown in (b), with examples of specific species phenology curves shown in (c). For full species phenology charts, see Appendix S1.

dramatic increase in the week of last flight (Figure 1b). On average, species had advanced their week of first flight by 0.79 weeks ($t_{77} = 3.57$, $p < 0.001$) from the historical time period to the contemporary (Figure 1b). This amounts to approximately an advance of 0.55 days per decade, assuming a linear rate of change in the intervening decades between 1919–1922 and 2019–2024. The mean week of last flight had extended by 1.68 weeks ($t_{77} = 3.64$, $p < 0.001$), an extension of approximately 1.18 days per decade (Figure 1b). When considering strictly univoltine species, the mean week of first flight had advanced by 0.41 weeks but was not statistically significant ($t_{26} = 1.28$, $p = 0.21$), nor was the extension of the week of last flight by 0.70 weeks ($t_{26} = -0.97$, $p = 0.27$). If extrapolated linearly, these amount to an advance of 0.29 days per decade in spring phenology and

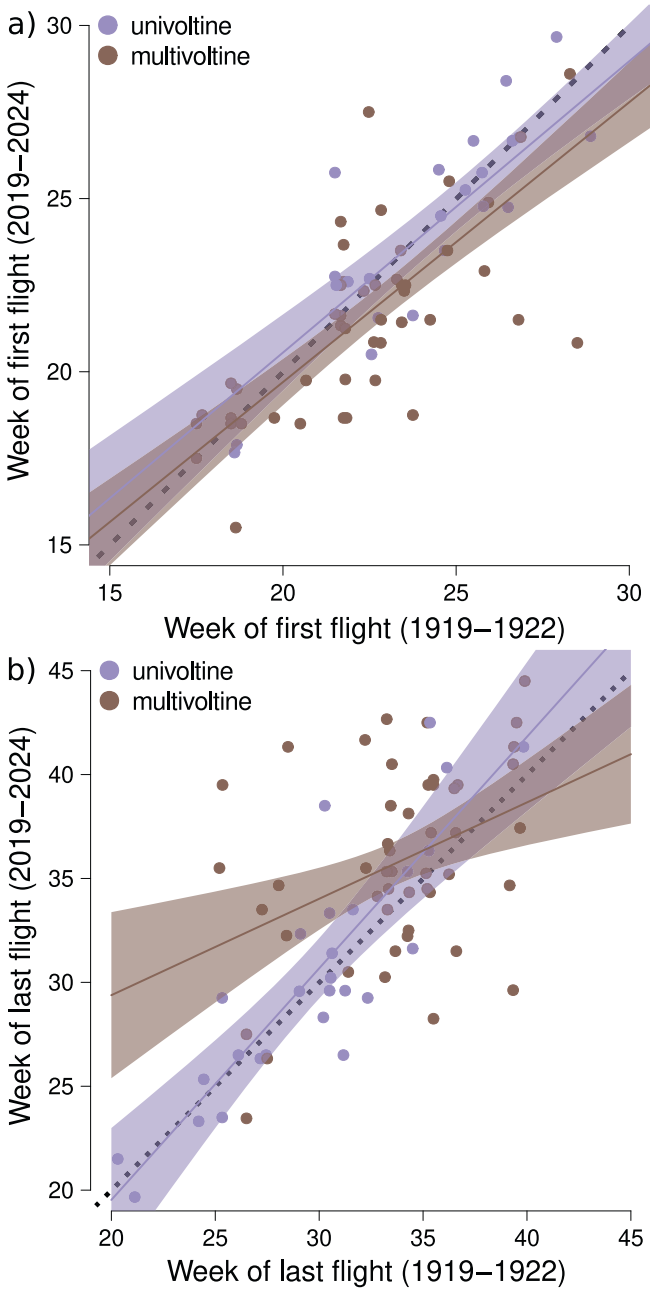

FIGURE 2 Changes in the week of last flight for 78 moth species in Ithaca, New York, from 1919–1922 to 2019–2024 in relation to voltinism. Strictly univoltine species are shown in purple while bi- and multivoltine species are shown in brown. The shaded region indicates the 95% CI from a general linear model and the thick line indicates model fit. The dashed black line indicates the 1:1 line.

extension of 0.49 days per decade for univoltine species, though not significant. For species with plastic voltinism, there were significant differences in the week of first flight which had advanced by 1.0 weeks ($t_{49} = 3.41$, $p = 0.001$) and the week of last flight which was extended by 2.26 weeks ($t_{49} = -3.54$, $p < 0.001$). If extrapolated linearly, these amount to an advance of 0.7 days per decade in spring phenology and extension of 1.58 days per decade for multivoltine species.

In our model examining the relationship between voltinism and shifts in week of first flight (Figure 2a), we found that week of first flight historically was a significant predictor of week of first flight in contemporary records ($\widehat{\beta} = 0.87$, 95% CI = 0.51–1.24), but there was no significant difference for univoltine species ($\widehat{\beta} = -0.18$, 95% CI = −5.67 to 5.29) nor the interaction ($\widehat{\beta} = -0.03$, 95% CI = −0.26 to 0.19). In our model predicting shifts in week of last flight (Figure 2b), we found a similar effect for week of last flight historically ($\widehat{\beta} = 1.76$, 95% CI = 1.05–2.48); however, we also found significant effects of voltinism ($\widehat{\beta} = 22.85$, 95% CI = 9.06–36.66) and the interaction ($\widehat{\beta} = -0.65$, 95% CI = −1.08 to −0.22).

Species disappearance

There were 13 species recorded by Slingerland in both 1889 and 1892 that were absent from iNaturalist and the JJD records. One species (*Alabama argillacea*; Hübner, 1823) is extirpated from all of North America (Wagner, 2009); however, the remaining 12 species are still present in nearby regions and have been recently observed on iNaturalist (Figure 3). We present no formal results for these species disappearances as there are numerous sampling biases present and an analysis would give undue credence to the observed pattern. In lieu of formal analyses, we present the geographic pattern of iNaturalist observations for species that were formerly documented in at least 2 years historically in Ithaca (Figure 3) as a potential explanation for species disappearances.

DISCUSSION

Despite strong evidence of phenological shifts in moth communities over the previous half century, far less is known about changes to populations and communities prior to modern ecological monitoring. Here, we digitize two historical datasets to document changes in moth communities from the late 1800s and early 1900s to present, including advancing spring phenologies and the elongation of flight periods. The elongation of the flight period was driven by the addition of new generations of multivoltine species, including some that have gone from a single generation to two or three generations per year over the past century (Figure 4). We were not able to directly link anthropogenic stressors to changes in phenology and voltinism, and there have been increases in urbanization (Appendix S1: Figure S1) and afforestation in the study region along with climatic shifts; however,

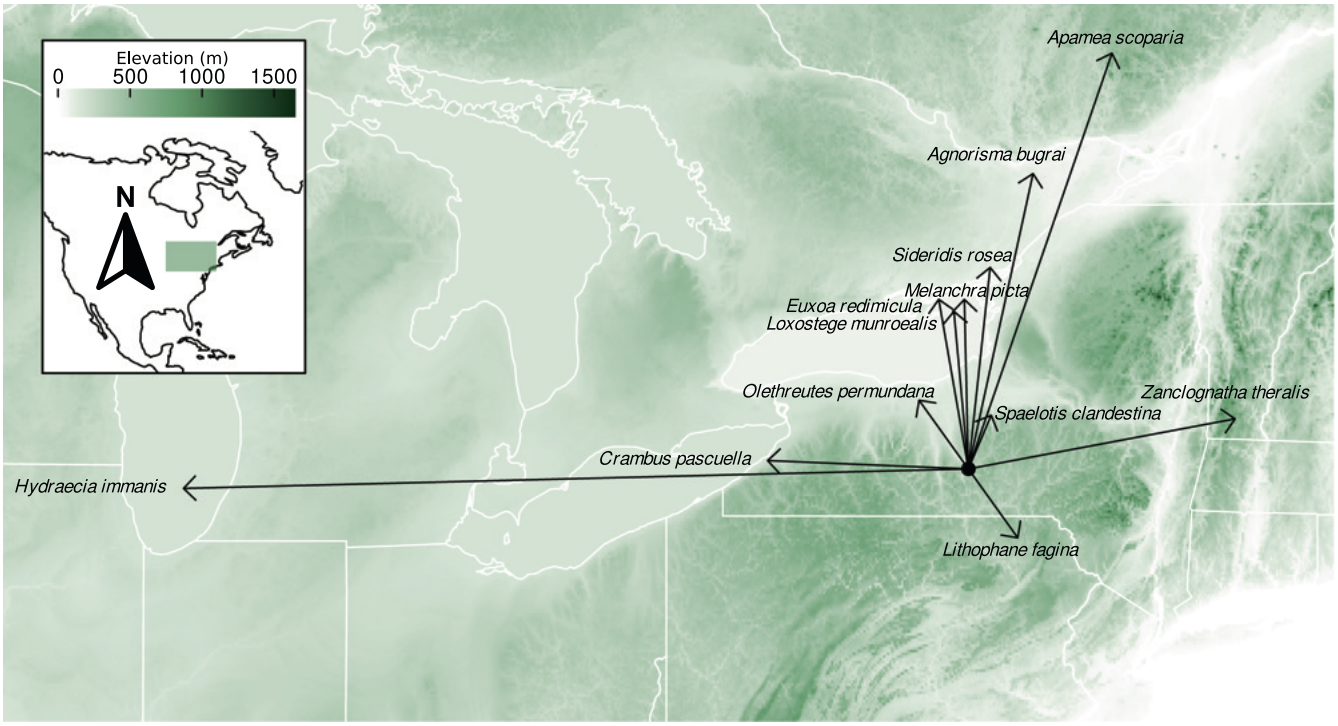

FIGURE 3 Geographic centroid of the five nearest iNaturalist observations for species that were observed in Ithaca in at least 2 years historically but have since disappeared. Arrows indicate geographic centroid for each species; the central location is the location of historical moth sampling in 1889 and 1892 by Slingerland and 1919 and 1922 by Forbes at Cornell University. The base map is elevation based on Danielson and Gesch (2011). Inset shows location of study area relative to North America.

our results are consistent with more recent studies that found a signal of climate change being the primary driver of shifts in voltinism (Altermatt, 2010; Macgregor et al., 2019).

Across the community, many species had a longer contemporary flight period compared to a century ago. This was largely driven by an increase in the number of generations for multivoltine species (Figure 2b), with univoltine species showing relatively similar weeks of last flight across the two time periods. This result is consistent with reports from Europe documenting increased population sizes in second and third generations for 72% of bi- and multivoltine species (Altermatt, 2010). While we were unable to compare population size or trends in abundance due to changes in sampling effort and methods over time (Welti et al., 2021), the phenological pattern is consistent. Diapause initiation in multivoltine insects is often the result of complex gene-by-environment interactions and can involve the integration of both photoperiod and temperature cues (Denlinger, 2002; Emerson et al., 2009). Thus, the observed shifts in voltinism across this time period may be plastic responses to warmer temperatures in autumn. However, genetic adaptation may also be possible as standing genetic variation for photoperiod response traits underlying voltinism allows for fine-scale local adaptation in some Lepidoptera (Levy et al., 2015), and the rapid evolution of diapause regulation has been observed over similar time frames in other insects (Dowle et al., 2020). Plastic responses to voltinism may result in year-to-year variability, which may have been the case for some species with increased voltinism in 1922 compared to 1919. In his notes, Forbes repeatedly remarked on the warm, wet conditions in 1922, which may have resulted in greater abundance of many species in the community. For example, writing of *Idia aemula* Hübner, 1814, Forbes noted that the "Species took advantage of the moist July for an enormous increase; the second brood may have been missed in 1919" (Forbes, 1923). As climatic conditions in the area continue to change and the northeastern United States becomes warmer and wetter (Portmann et al., 2009), we may expect to see even more striking changes to moth community phenology and voltinism. Our results are from a single location due to the limitations of the historical data, and it is also possible that local land use change could explain the shift. The historical traps were located on the campus of Cornell University, which was primarily an agricultural research station when Slingerland sampled it in 1889–1892, and had become more developed by the time Forbes sampled the moths 30 years later (Appendix S1: Figure S1). Tompkins County also developed rapidly from the earliest sampling to present, with the number of people per km^2 growing from 25.92 in 1890 to 27.78 in 1920 and 83.26 in 2020 (Schroeder et al., 2025). This rapid

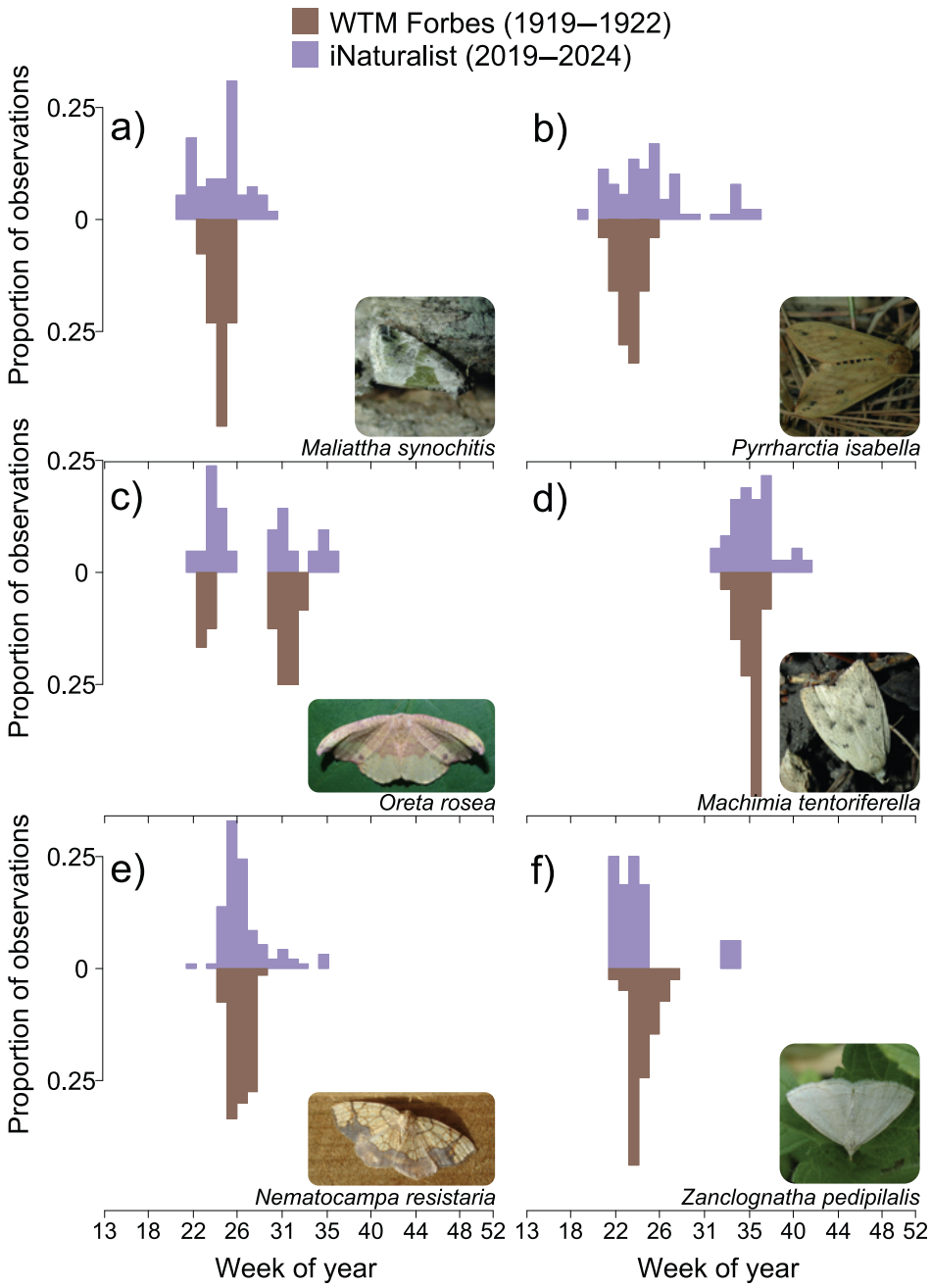

FIGURE 4 Examples of species that have extended their flight periods. (a) *Maliattha synochitis*, (b) *Pyrrharctia isabella*, (c) *Oreta rosea*, (d) *Machimia tentoriferella*, (e) *Nematocampa resistaria*, and (f) *Zanclognatha pedipilalis*. Purple bars show phenology estimates based on iNaturalist observations in Tompkins County from 2019 to 2024. Brown bars represent Forbes' phenology from 1919 to 1922. The height of each bar is the proportion of observations, within each dataset separately, falling within each week of the year (standardized to the year 1922). Photo credits: Jason J. Dombroskie.

population growth and associated urban development could have produced an urban heat island effect that may similarly have changed climatic conditions at a local scale. We find it more likely, however, that land use change in the region contributed to species disappearances, rather than phenological changes.

Despite many reports in the literature of advancing spring phenology as a result of climate change (Forrest, 2016), we saw minimal shift in the week of first flight in the moth community. Diapause development is a multifaceted phenomenon (Koštál, 2006), and the effects of warming temperatures on overwintering and post-winter phases of diapause development may be more complex than those for pre-winter diapause initiation. For many multivoltine species, diapause termination occurs during winter, with insects remaining

quiescent due to the direct effect of cold temperature before resuming development when conditions become physiologically permissive (Denlinger, 2002). The apparent stasis of first flight phenology may represent a balance between contrasting effects of temperature on diapause and post-diapause development rates. Shorter, warmer winters may actually delay diapause termination, while warming spring temperatures would be expected to accelerate phases of post-diapause development. It is also possible that species are advancing their spring phenology but only at certain life stages (Hällfors et al., 2021). Our records are only for adult Lepidoptera (i.e., light traps only catch flying adults), and it is possible that other life stages are shifting their spring phenology but the flight period has not changed. Moreover, spring phenology may be limited by host–plant phenology, with selection acting strongly against insects that develop before either adult or larval food resources are available. Thus, the phenological effects of global change may be difficult to generalize within any group of insects without incorporating species-specific information such as life stage at which species undergo diapause, thermal reaction norms for both diapause regulation and development time, and perhaps even diet breadth (Hällfors et al., 2021; Hickinbotham et al., 2024; Lackey et al., 2023).

Alternatively, it is possible that we missed advancing phenologies as a result of the temporal resolution of the data. Because Forbes reported species' phenologies by week, we were unable to analyze the data at higher resolution. In Britain, Altermatt (2010) documented an advancement in spring phenology, measured as the date of first flight, of 2.1 days after 1980 compared to prior to 1980. An advancement of this magnitude would be unlikely to be captured by our dataset due to the temporal resolution of the historical data, but we find it more likely to be an indication that the rate of phenological change is accelerating over time. From 1995 to 2014, multivoltine Lepidoptera in Britain advanced their phenology by roughly 3 days per decade, while univoltine species advanced by 1.5 days per decade (Macgregor et al., 2019). Similarly, from 1974 to 2009, the first flight date for moths in Ireland advanced by 8.1 days per decade, and the week of last flight extended by 6.4 days per decade (O'Neill et al., 2012). These rates of change in recent decades far exceed those reported in the present study. Our estimated shifts over the 100-year time period, albeit with data only available for two time periods, were 0.55 days per decade in advancing spring phenology and 1.18 days per decade in extension of the week of last flight—substantially less than those of European moths in the past half century. As the rate of climate change accelerates, we would expect to see accelerating phenological changes (Vitasse et al., 2022), and it is entirely possible that the vast majority of phenological change that took place between Forbes' sampling in 1919–1922 and the contemporary records in iNaturalist from 2019 to 2024 was largely during the most recent decades. Without phenological data from the intervening decades, we have no way of knowing when these phenological shifts began, or if and when they accelerated.

We observed the disappearance from the study region of 13 species that were present in at least 2 years historically. One of these, *Alabama argillacea*, is known to be extirpated from all of North America, likely driven by a decline in cotton production in the United States (its host plant) and as a result of intensive pest management targeting this species (Wagner, 2009). Other species are still present, but many appear to have undergone range shifts that may be associated with climate change (Chen et al., 2011; Chowdhury et al., 2025; Hickling et al., 2006; Kiritani, 2006). Several species that were present in Ithaca a century ago are now found farther north or at higher elevation in nearby mountain ranges (Figure 3). We were unable to determine if species that were previously found at more southern latitudes have expanded their range to now encompass the study area, in part because of changes in taxonomy and taxonomic expertise in the region over time, but also because Forbes omitted nearly all of the common species from his reports. This omission also limits our ability to document changes in formerly common species; if patterns are consistent with more comprehensively documented communities (Van Dyck et al., 2009), common species may have changed as dramatically, if not more so, than the rarer species.

The dramatic increase in the number of generations per year, moderate shift in spring phenology, overall elongation of the flight period, and disappearance of species that we report here for moth species over the past century underscores the value of long-term biodiversity studies, participatory science observations, and taxonomic expertise. Were it not for the foresight of entomologists to track the phenology of species, and not simply their presence or absence, such a long-term analysis of the impacts of global change on species traits would not be possible (Appendix S3). As climate change continues to alter temperature and precipitation regimes globally, it is increasingly important to understand how species' phenologies and traits will be affected and what the consequences may be for ecosystem function. It is equally important to contextualize contemporary changes by grounding them in historical records to avoid shifting baselines (Halsch et al., 2025), and seeking out underused historical sampling efforts has the potential to yield incredibly valuable baseline data.

AUTHOR CONTRIBUTIONS

Emma M. Foster: Conceptualization; methodology; validation; formal analysis; investigation; data curation;

writing—original draft; writing—review and editing; visualization. **Jason J. Dombroskie:** Conceptualization; validation; investigation; resources; data curation; writing—review and editing. **Christopher A. Halsch:** Conceptualization; validation; writing—review and editing. **Thomas H. Q. Powell:** Conceptualization; resources; writing—review and editing. **Eliza M. Grames:** Conceptualization; methodology; software; validation; formal analysis; investigation; writing—review and editing; visualization; supervision.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data and code (Grames, 2026) are available in Figshare at https://doi.org/10.6084/m9.figshare.29175902.v1.

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SUPPORTING INFORMATION

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

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