

**Citizen science data reveal correlations in
changes of phenology and abundance in
Massachusetts butterflies under climate
change**

An Honors Thesis for the Department of Biology

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Abstract

Organisms throughout the world are responding to climatic shifts in various ways. Range shifting and phenological responses to increased temperatures have been recorded across temperate regions. Lepidoptera as a taxon are uniquely subject to thermal changes and serve as a popular, diverse clade of organisms making them excellent to study the effects of climate change. Using citizen science monitoring data from 1991 to 2017 from the Massachusetts Butterfly Club, we examined species phenology and community composition. Using quantile regression, an underappreciated technique in the study of insect phenology, we revealed changes in the emergence and diapause timing of butterflies and significant differences between univoltine and multivoltine species. Measures of phenology were also compared to trends in abundance which were derived using the list length method. Multivoltine species not only extended their flight period but also increased in abundance relative to univoltine species, indicating that some species are likely adding another generation in the year due to the extended growing season. One southern species, the Zabulon Skipper *Poanes zabulon*, appears to be regularly adding a generation and subsequently greatly increasing in abundance as the state becomes more thermally suitable. Northern species; however, have generally experienced population declines over the time period, corroborating patterns of range shifts that have been observed in other systems. The utility of citizen science data is enhanced by innovative statistical techniques which can reveal significant patterns in phenology and abundance with the capacity to inform both science and conservation.

Introduction

Climate change has been shown to affect the phenology and distribution of species throughout the world (Lindén, 2018; Walther et al., 2002). Due to rising global temperatures, many species are temporally shifting life-stage events. Although the relationship between temperature and phenology has been thoroughly explored in the literature (Visser and Both, 2005), we have a disproportionately weaker understanding of how these changes affect both demography and abundance (Ramula et al., 2015). Phenological changes have been documented in plants (Fitter & Fitter, 2002; Cleland et al., 2007; Feehan et al. 2009), birds (Tøttrup

et al., 2006; Parmesan, 2007) and other species, including insects (Menendez, 2007; Visser and Both, 2005). We see among these studies documenting shifts in phenology, only some have related such shifts to changes in populations and viability (Both et al., 2006; Saino et al., 2010; Møller et al., 2008; Ramula et al., 2015). Although understanding the effect of changing global temperature on species' phenology reveals important information about behavior, explaining how those changes may affect survival, reproduction, fecundity etc. is critical to identifying threatened species.

We understand that phenological changes have the capacity to alter species' demography and populations, though these effects are likely as varied as species' phenological responses themselves. The magnitude and direction of phenological changes is not uniform across species (Møller et al., 2008; Rubolini et al., 2017) especially because the effects of climate change are disparate throughout the world (Walther et al. 2002). Generally, among studies that have investigated both phenology and demography, research has shown that species advancing their phenology or tracking changes in climate, outperform those that do not (Cleland et al. 2012; Willis et al., 2008). Species in temperate zones have evolved such that their habitats are temporally suitable for specific times or certain seasons within the year; species emerging earlier are now tracking temporal changes in habitat suitability to best match preindustrial temperature stimuli. Species emerging earlier in the spring may take advantage of vegetative, floral or other resources which might themselves be appearing earlier due to advanced phenology (Fitter and Fitter, 2002). Lepidoptera altering their flight period might also be better able to

synchronize with mutualists, reduce intraspecific competition or potentially even fit another generation within the growing season (Cleland et al., 2012; Rathcke & Lacey, 1985; Van Dyck et al., 2014). Species incapable of tracking changes with temperature in tandem with associated species or changing habitat may experience population crashes (Stenseth and Mysterud, 2002). Examples of such phenological mismatches include those of predator-prey coincidence (Both et al., 2006), habitat crypsis (Post & Forchhammer, 2007) or migration (Møller et al., 2008). Abundance is also likely to change due to climate-warming related range shifting which has been recorded both altitudinally (Dirnböck et al., 2011) and latitudinally (Deutsch et al., 2008). At the community level, populations existing in the northernmost extents of their species' range are more likely to cope with the changes in climate (Parmesan & Yohe, 2003; Breed et al., 2012) than those positioned southernly in their species' distribution.

Butterflies are a highly diverse and easily identifiable clade of species, making them excellent candidate organisms to study (Pollard, 1988). Lepidoptera, as small ectothermic animals, rely on temperature cues to trigger life stage events across different climates (Roy & Sparks, 2000; Stefanescu et al., 2003). Butterflies are also diverse in their overwintering life stages, their host plant specificity and their reproductive cycles, all of which may interact with changes in temperature. Studies have shown generally advancing butterfly first appearance and peak appearance (Forester & Shapiro, 2003; Stefanescu et al., 2003; Menzel et al. 2006; Roy & Sparks, 2000), though measures of phenology appear to vary in both magnitude and direction for different species (Kharouba et al. 2013; Forester &

Shapiro, 2003; Roy & Sparks, 2000 ;Menzel et al. 2006). These studies have primarily focused on early phenology, measuring the effects of temperature on timing throughout warming periods in the spring. There are, however, considerably fewer studies examining changes in the end of flight period, including diapause timing (Zipf et al., 2017; Gallinat et al., 2015). Studying the end of the flight period is more difficult for a variety of reasons. Systematically observing the last occurrence of a species is more difficult than measuring first arrivals since last occurrences require continuous monitoring after that last observation to ensure that no more occur. Last occurrences are also subject to complex interactions of both environmental and ecological factors making them potentially more difficult to attribute to any driver (Zipf et al., 2017). Nevertheless, measuring both the beginning and the end of the flight period is significant as the end of flight signals the end of the breeding for many species and therefore has the potential to affect demography and populations into their overwintering stages.

The value in understanding butterflies' phenological response to climate change is limited when we cannot draw meaningful conclusions about the population, demographic or community-level effects of this behavioral response. In this study, changes in phenology were related to changes in relative abundance of Massachusetts butterflies using citizen science data. Data were obtained from the Massachusetts Butterfly Club, a group of experienced citizen scientists who have recorded sightings from across the state for over a decade. Such citizen science groups are vital to research of North American butterflies as there are no government-funded butterfly monitoring schemes like those present in Europe

(Stefanescu, 2003; Roy & Sparks, 2000). Citizen science data, however, are generally less systematically collected and more opportunistic than that produced by more rigorous scientific monitoring studies. The analytical approach conceived by Franklin (1999) and built upon by Szabo, Vesk, Baxter and Possingham (2010) increases the utility of citizen science data by using the list of observed species for a given trip as a proxy for search effort. This method is best suited when measuring the presence of species, rather than the number of individuals, and how their presence may change over time. The list length approach, in this instance, may a better measure of search effort than person-hours, person-miles etc. for determining the likelihood of detecting any individual species since more individuals or time searching does not necessarily increase the likelihood of detecting that species. It has been used in a variety of systems including birds (Szabo et al., 2011; Boakes et al., 2017) and insects (Rapacciuolo et al, 2017). List-length analysis determines the change in probability of observing a species on any trip in a given year. This limits the practical use of the analysis but provides meaningful comparisons in relative trends of abundance for each species. This list-length approach is a robust measure or relative abundance as it controls not only for search effort but also for daily weather variations and the conspicuity of certain species since it looks exclusively at the presence of any given species relative to all others in trips over each year of the study period. Breed, Stichter and Crone (2012) performed this analysis with earlier versions of the Massachusetts Butterfly Club data and found that northern species were significantly declining when compared to southern species which were increasing in relative abundance. Corroborating their findings will prove

important to determining whether this trend continues and how the composition of Lepidoptera communities has and may continue to change under a warming climate. Using the list length method, we can also relate species' abundance trends to life history traits or patterns of phenology we observe as well.

Studies of phenology often focus on the mean of the flight period, but we argue that this method is not representative of the changes occurring across all species of butterfly. Because the growing season extends both earlier into spring and later into autumn, measuring the mean day of year on which a species is likely to be seen may not demonstrate changes should the species be both emerging earlier and entering diapause later as we hypothesize for multivoltine species. In this case, a species not changing their phenology and a species expanding in both directions (earlier in the spring and later in the fall) equally would both demonstrate no change in the mean despite undergoing clearly different phenological patterns. Measuring the mean is understandable for species tracking changes in phenology which generally shift the life history or distribution of sightings in one direction (e.g. migration) (Visser & Both, 2005). Instead of modeling the occurrence of species sightings using linear regressions, which capture the change in the mean day of year through time, we use quantile regressions, measuring low and high quantiles and their difference to determine the change in emergence, diapause and flight period length respectively. Quantile regression is an underused statistical approach in ecology (Cade & Noon, 2003) and is especially applicable to measuring phenology. Modelling the slope change of different quantiles' values using a dataset over multiple years enables researchers to determine the trend of different quantiles (i.e.

different portions of a response distribution) over time. Quantile regression is used to model the change in quantiles by minimizing the weighted sum of absolute errors of the day of year variation for that quantile over the years. A quantile regression of the 0.1 quantile e.g. measures the change at which the 10th percentile of a response over the extent of the explanatory variable (Cade & Noon, 2003) and therefore can represent the change in the day of year of any quantile e.g. the earliest, median and latest sightings. The difference between the slope coefficients of the earliest and late quantiles also provides an estimate of the change in the flight period. Coefficients derived from quantile regressions are also more robust to potential changes in population size than first appearance, last appearance and range of sightings as it is not as strongly influenced by changes in population size or interannual variation.

Measures of phenology likely differ between species, especially those with different patterns of voltinism. Should species take advantage of the elongated growing period, there are predictable correlations between the measures of phenology and relative abundance; species emerging earlier, delaying diapause and generally increasing their flight period within the extended growing season should theoretically have higher relative abundance (Roy & Sparks, 2000). Under the same conditions, species not tracking changes in temperature would have relatively lower abundance. We explore the relationship between voltinism, phenology, abundance and species range distribution.

Methods

Data

Data were collected statewide by members of the Massachusetts Butterfly Club (MBC), an experienced group of citizen science observers. Observations include those made in organized group trips and opportunistic outings with records reviewed and vetted for quality before entering a formal database (See Appendix 1). A total of 84 species were considered. Certain species weren't included due to taxonomic realignments or outbreaks uncharacteristic of overall population trends. Others were not included because there were too few sightings throughout the study period (Table 1); a minimum of 15 sightings prior to 2000 was used as a cutoff to consider a species' trend over the span of the study period. Species were also grouped based on shared traits for a given ecological factor (Table 3). Range, overwintering stage, host plant availability, and habitat preference classifications used the same categorical assignments made by Breed, Stichter and Crone (2012) and the Massachusetts Butterfly Atlas (MBA: Leahy). The voltinism behavior for species also drew from assignments taken from Breed, Stichter and Crone (2012) but were corroborated by visually examining plots of year and day of year over the study period (See Supplementary Material); some species appeared to be misclassified based on the timing of observations and were therefore reclassified into two groups: obligate univoltine species and other (multivoltine, bivoltine etc.).

We compiled sighting data from 1991 through 2017 as throughout this period with a relatively consistent number of yearly sightings (827 sightings in 1991, with each year greater than the first; 128851 sightings altogether). This data

was also used in a previous study (Breed et al., 2012), allowing for comparisons and expansions of their findings. Breed, Stichter and Crone (2012) established that southern species were increasing in abundance relative to more northerly species; we carried out this analysis again, this time examining species' change in relative abundance in response to climate change as well.

Sightings were arranged into trips for which there are records for all species. A trip is defined as a sighting or group of sightings which occurred at the same location, on the same date and by the same person/group of people. Trips were compiled for each species and each contained all trips made by the group across the entire study period and whether the species was present (1) or absent (0) for each of the trips. For further information refer to Supplementary Material, Table S-III.

Abundance List-Length

Relative abundance of a species was measured as the proportion of trips on which a species was seen over a given year using the list length analysis conceived by Szabo, Vesk, Baxter and Possingham (2010). This was done only with trips that had a list-length greater than 5 (i.e. more than 5 species were seen on that trip) to ensure that the probability of detecting a species is accurate relative to other species. Because some species are more conspicuous, rare or recognizable, they may be more frequently reported in single-species observations which less accurately represent all species that may be present at that site at that time and would likely inflate the probability of detecting that conspicuous species. Although this phenomenon still exists in trips with longer list-lengths, the model detects differences from a sort of baseline detectability of each butterfly across all trips in

a year. A generalized linear mixed model was generated using the lme and bbmle packages in R (R development Core Team). For each species using both year and list-length as predictors to the proportion of trips on which a species was present. A random effect of year was also included in the model to better account for any random background variation of abundance across years. The same method for measuring change in abundance was used in previous study (Breed et al. 2012). The slope coefficient of year in each species' model demonstrates its trend in abundance relative to other species through time.

Phenology Quantile Regression

Phenology was examined using four metrics: (1) 0.1 quantile, (2) mean, (3) 0.9 quantile, (4) Flight period length. The change in the mean was calculated using linear regression and the change in the 0.1 quantile, 0.9 quantile and flight period were calculated using quantile regressions. One can determine the change in both emergence and diapause by performing a quantile regression on the early and late quantiles (e.g. 0.1 and 0.9 respectively) from the set of all sightings for all the years of interest. Quantile regression does this exactly by fitting a line which minimizes the weighted absolute deviations from values less than or equal to the proportion of sightings at each level of the predictor (Cade and Noon, 2003).

In our case, for the 0.1 Quantile regression we generate a line which effectively demonstrates the change in the day of each year at which the 10th percentile of butterfly sightings had occurred. This change in the earliest sightings demonstrates the annual change in days in which butterflies are emerging. Earlier emergence in the spring would result in a negative slope coefficient since the

numerical day of year values decrease. For the 0.9 quantile, which effectively generates a line modeling the change in the 90th percentile day of year values (i.e. before the last 10%). Positive slope coefficients would demonstrate species extending flight into summer/fall since numerical day of year values are increasing over time. The change in the flight period was calculated as the difference in the slopes of the quantile regression models for each species (0.9 quantile slope – 0.1 quantile slope). All quantile regression models were generated using the ‘quantreg’ package in R (R development Core Team). The mean measure of phenology was calculated using simple linear regression models with the ‘lmer’ package (R development Core Team) tracking the change in the mean numerical day of year over time across the length of the study period. Like the quantiles, positive values demonstrate delayed mean flight date over time while negative values demonstrate advancing mean flight date.

Relationships between Abundance, Phenology and Ecological Groupings

The association between the change in abundance and each measure of phenology for all species altogether was calculated using Pearson’s Correlation Coefficient. These demonstrate the strength and direction of the trend of a species’ relative abundance and its measure of phenology over the time period.

Multiple ANOVAs were calculated to determine whether trends in phenology or abundance were correlated with any of the environmental or ecological factors by which the species were grouped (voltinism behavior, overwintering stage, host plant availability, habitat preference and range location relative to Massachusetts). An ANOVA was carried out using the 0.1 quantile, 0.9 quantile, flight period and

trend in relative abundance with the classifications outlined in Table 3. Tests that meet a ($\alpha \leq 0.05$) p value threshold were then tested using Tukey's Honestly Significant Difference Test to reveal which groups significantly differed and in which direction.

Results

Phenology and Abundance

The change in the mean day of year sighting across all 84 species is significantly negative (one-sample t-test, $t = -4.445$, $df = 83$, $p < 0.0001$). The significantly negative value demonstrates that butterfly species across Massachusetts are generally advancing the average sighting date over the years studied. The change in the 0.1 quantile is significantly negative ($t = -5.686$, $df = 83$, $p < 0.0001$) while the 0.9 quantile is neither significantly positive nor negative ($t = -0.6602$, $df = 83$, $p < 0.5109$). The change in the 0.1 quantile, being significantly negative, demonstrates that across species there is generally advancing emergence phenology in the spring. The change in the 0.9 quantile, which describes the change in diapause timing over the study period, does not differ significantly from the null meaning there are no general trends in late-season phenology that can be applied across all species. The change in flight period is significantly positive ($t = 3.777$, $df = 83$, $p < 0.0003$) meaning species are generally elongating the number of days during which they are active over the years.

Pearson's Product Moment Correlations were calculated between the trend of relative abundance and each measure of phenology. There is a significant negative

correlation between the trend in relative abundance with the change in the 0.1 quantile ($r = -0.3681$, $p < 0.0006$) and positive correlation between relative abundance and the 0.9 quantile ($r = 0.2167$, $p < 0.0477$). This suggests that species that emerge earlier in the spring are increasing in abundance relative to other species. It also suggests that species entering diapause later in the fall are increasing in abundance relative to species. There was also a positive correlation between the change in abundance and the flight period ($r = 0.4698$, $p < .0001$) (Figure 1). This reinforces the results from the former two tests, suggesting that species elongating their flight period are increasing in abundance relative to species that are not. There is no significant correlation between abundance and the mean day of year ($r = 0.1093$, $p = 0.3222$). Although species are increasing their mean day of year, changes in parts of the distribution other than the central tendency better correlate to the changes in abundance among species.

Analysis of Variance

Analyses of Variance were conducted on measures of phenology and relative abundance with groups based on ecological and environmental factors. Obligate univoltine species had significantly smaller flight period changes (ANOVA, $df = 1$ and 82 , $F = 7.745$, $p < 0.0067$) (Figure 1) and smaller changes in diapause timing (ANOVA, $df = 1$ and 82 , $F = 7.6$, $p < 0.0072$) over the study period with no significant difference among the 0.1 quantile changes (ANOVA, $df = 1$ and 82 , $F = 0.2347$, $p < 0.6294$). Subsequent Tukey HSD tests revealed that obligate univoltine species had significantly smaller changes in the 0.9 quantile as well as the flight period than multivoltine and other species. Univoltine species also had

weakly significantly lower abundance relative to other species (ANOVA, $df = 1$ and 82 , $F = 3.454$, $p < 0.0667$) with univoltine species having lower rates of abundance.

ANOVA revealed significant differences between the abundance of Northern, Core and Southern range species (ANOVA, $df = 2$ and 82 , $F = 6.4908$, $p < 0.0024$). Species whose ranges are listed as south of Boston had significantly higher relative abundance compared to species whose core ranges are north of Boston (Tukey $p < 0.0016$). Species whose core ranges are considered to be at or around the latitude of Boston did not differ significantly from Northern species ($p = 0.3312$) or Southern species ($p = 0.8976$). These results corroborate Breed, Stichter and Crone (2012) which found southern species to increasing in population relative to northern species, suggesting that such species are shifting northward due to climate change.

There was no significant difference among species with different habitat, overwintering stages, host plant availability across the state (See Supplementary Material S-IV)

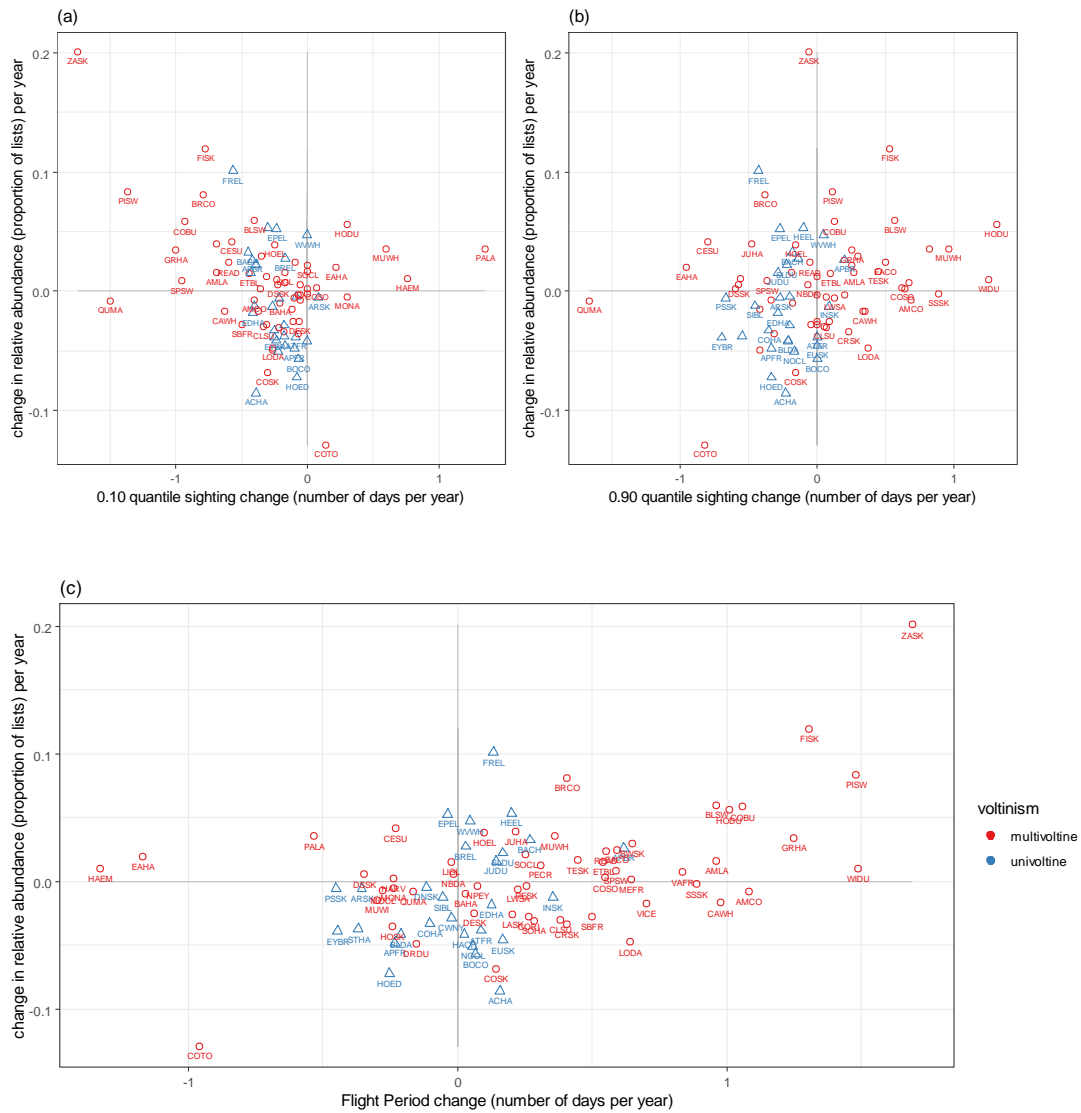


Figure 1. Annual changes in flight period and changes in relative abundance between strictly univoltine and multivoltine species: Each point represents a species plotted by some measure of phenology (a. 0.1 quantile; b. 0.9 quantile; c. flight period) against change in the relative abundance of the species (i.e. the change in the proportion of lists on which the species was recorded). Points greater than 0 on the x axis demonstrate species that are delaying (a and b) or increasing (c) their phenology. Points above the line 0 on the x axis represent species increasing

relative abundance. Obligate univoltine species are labeled as blue triangles and multivoltine/other species are labeled as red circles.

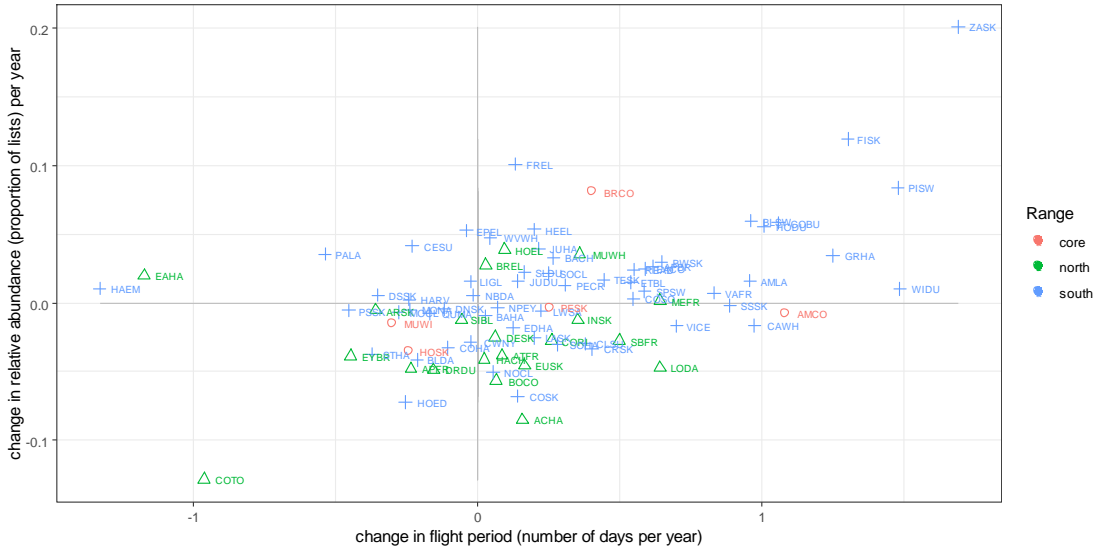


Figure 2. Annual change in flight period and change in relative abundance between species of different ranges: Each point represents a species plotted by the flight period change as a measure of phenology against the change in the relative abundance of the species. Core range species are represented as green circles, northern range species are represented as red triangles and southern species are represented as blue crosses.



Figure 3.

Sighting dates of the Zabulon Skipper (*Poanes zabulon*) from 1991 to 2017: Each point represents the dates of sightings of the Zabulon Skipper (ZASK) by the MBC. The date is described as the numerical day of year (days after the beginning of the year, where January 1st = 1). Points are slightly jittered for visibility.

Discussion

Various global biological changes that have been observed in recent decades can be attributed to climate change. Species have been observed both expanding their range northward and emerging earlier in the year in temperate zones in response to increased temperatures. Butterflies are a clade which have annual life cycles regulated in part by temperature and are therefore affected by the gradual warming climate (Roy & Sparks, 2000). Our results support findings which reveal that butterflies are significantly changing their emergence patterns (Forister & Shapiro, 2003; Roy & Sparks, 2000) but also demonstrate that such phenological patterns may affect species' populations and community composition.

Phenology in butterflies is often measured as changes in the first sighting date, some measure of central tendency, peak abundance date and or the range of sightings in a year (Forester & Shapiro, 2003; Menzel et al. 2006; Stefanescu et al., 2003). We use changes in quantiles as they provide a more robust estimate of early and late sightings. Quantiles also more precisely represent changes in early and late phenology than measures of central tendency including the mean. The 0.9 quantile and the flight period changes based on quantile regression are significantly correlated with species' changes. The change in the 0.1 quantile was not and neither was the change in the mean day of year. Additionally, estimates from quantile regression provide more robust results than changes in first sighting date and the range of sighting dates since quantile regression uses multiple sighting dates in a year for multiple years to represent population trend. Studies of first sighting date

and the range of sighting dates in a population that is increasing or decreasing over time may be more biased or fluctuate due to the changes in population. Because the data we use is structured as describing whether species are present or not, we did not measure peak abundance date or any similar measure of phenology.

Studies of insect phenology often examine the effects of climate change on spring emergence while comparably few have focused on the extended flight period in autumn (Gallinat et al., 2015; Zipf et al., 2017). Despite being less often reported, our results suggest that changes in butterflies' end of the flight period is consequential; the correlation between changes in both early and late sightings with changes in abundance are significant. Gallinat, Primack and Wagner (2015) have suggested, in advocating for the study of late-season phenology, using multiple species and multiple-day events to study the effects of climate change on autumn phenology. By examining the trends in quantiles for each species in Massachusetts we can reveal correlations with both early-season and late-season phenology trends across the community, identify species and groups of species that have different trends in abundance and phenology, and suggest why such changes are occurring.

Quantile regression estimates suggest that most butterflies (72 species) are advancing their emergence timing (Fig. 1a). Trends in the timing of diapause do not reveal a similarly uniform trend (only 35 species appear to be delaying diapause) (Fig. 1b). Both changes in emergence timing and diapause timing are; however, significantly correlated with the changes in abundance. Species advancing emergence earlier into the spring have significantly higher abundance relative to other species. And species delaying diapause later into autumn have

higher relative abundance relative to other species. Generally, species with increased flight periods have increased their relative abundance over the study period. This is consistent with predictions and findings which suggest that species capable of adapting to climate change will outperform those that do not (Cleland et al., 2012). Species emerging early and entering diapause later may be capable of avoiding competition in certain parts of the growing season. The potential also exists among species tracking changes concurrently with food resources for deleterious mismatching with host plants (Miller-Rushing et al., 2010) which could cause cascades within a population or the species.

There appears to be a consistent trend for earlier emergence across all butterfly species but there is no such significant trend for earlier or later diapause timing. This discrepancy between consistent early and inconsistent late phenology may, to some extent, be the result of differing life-history strategies. A difference in voltinism, the number of across species is one potential cause for this inconsistency in the late season phenology. Obligate univoltine species with single generations affected by changing local temperatures may be more likely to advance their entire phenological cycle; such species will be triggered to emerge earlier and complete their adult life stage for the year earlier as well. Species that have multiple generations within a single year may have comparable emergence time advances. These multivoltine species; however, may enter diapause later as they are not as strictly limited to the reproduction of a single generation and may be triggered to enter diapause by some other environmental cue. Our comparison between obligate univoltine and multivoltine species changes at the 0.9 quantile (Fig 1b) reveals that

there are significant late-season differences between the two life history strategies. There exist no such differences in 0.1 quantile where both obligately univoltine and multivoltine species appear to be advancing. These results suggest do that there is some developmental or behavioral difference between multivoltine and univoltine species in how they enter diapause, such that multivoltine species persist longer into the late flight season.

Variation in abundance between univoltine and multivoltine species may be due to benefits of increased multivoltinism in response to the expanded growing season. Few studies of Lepidoptera have managed to document increased multivoltinism in individual species (Pöyry et al. 2010) or across entire taxa (Altermatt, 2009) in recent years. Since development and phenological timing in insects are often regulated by interactions and changes in ambient temperature and photoperiodism (Bradshaw & Holzapfel, 2007; Pöyry et al., 2011) it is difficult to determinately claim that increased multivoltinism, when it occurs, is due to climate changes. Based on our results it appears that at least one species, the Zabulon Skipper *Poanes zabulon*, is increasingly multivoltine in its reproductive behavior over the years in Massachusetts. The Zabulon Skipper (ZASK) is primarily known to be a warm-temperate and subtropical species not often observed in Massachusetts (MBA: Leahy). Over the 26 year period of study, it has increased its flight period more than any other species, an estimated 1.69 days year⁻¹ (Table 1). The species appears to have both advanced its emergence timing and delayed its diapause timing, but also appears to have regularly fit another generation in the growing season from ca. 2008 onward (Fig. 3). It now reproduces a second time

and thus has two generations in a year. Under the same period, the Zabulon Skipper also experienced the greatest increase in abundance primarily by advancing its early flight (Fig. 1a) where the first generation now occurs. Non-mutually exclusive potential explanations for these trends include the following: (1) the ability to successfully colonize more of the state due to its more suitable thermal conditions as the Zabulon Skipper was formerly known as a vagrant species (MBA: Leahy) (2) While it was formerly common to see autumn generations, which may have been the offspring of individuals that successfully overwintered in more southerly locations, moved and then reproduced further north, the species might be overwintering more successfully within the state which would explain why we now observe more regular bivoltine behavior with a spring generation in addition to the fall (Fig. 3).

Other species capable of multivoltine behavior may be adding generations later in the season as opposed to earlier. Since increased temperatures are known to cause faster rates of growth and development in insects and in Lepidoptera specifically (Bale, 2002), some species with the ability to produce an extra generation may if environmental conditions remain suitable. Fitting more generations into a single year may provide fitness benefits to a population since reproducing once more could facilitate evolutionary processes in adapting to climatic changes. This benefit might confer a relative advantage over univoltine species which lack the capacity to evolve as quickly to the changing climate. This; however, may not always be the case, since populations fitting another generation may inadvertently enter a developmental trap. Van Dyck et al. (2014) describe how

population's response to warming could be potentially maladaptive if the added generation fails to reach its overwintering stage prior to the onset of winter. These butterflies would not be able to successfully reproduce and would therefore suffer a decline in population. This could be the mechanism by which some butterflies, like the Long Dash, extend their flight season later into autumn and still experience declines in abundance (Fig. 1b).

Understanding the proximate mechanisms of how species cope with warming climates will help make predictions about species' responses to climate change (Moritz and Agudo, 2013). The ability to track climate change, however, may have a phylogenetic component (Willis et al., 2008). Plasticity of voltinism, rapid evolution and an evolutionary mechanism for phenological variation of have previously been documented in Lepidoptera (Levy et al., 2015). Expanding our understanding of the genetic mechanisms which determine seasonal life stage timing will allow us to more easily identify whether a species is threatened from continued climate change. Understanding the role of phylogeny in these systems may allow us to draw inferences on species ability to survive continued climatic warming. Future studies of phenology should seek to understand both the mechanisms that drive such changes and the population dynamics that result.

Insects have variable responses to thermal changes that have the capacity to affect population dynamics (Bowler and Terblanche, 2008). We see evidence of variable abundance of Massachusetts butterflies in response to climate change in from Breed, Stichter and Crone (2012). Consistent with their findings, we see that species whose ranges were centered south of Boston in terms of latitude appear to

be supplanting species with ranges centered north of Boston. The relative abundance of southern species is increasing over the study period compared to those of northern species which are declining suggesting species are moving northward to regions that are more thermally suitable in response to climate change. Such range changes have been well documented across insects and in lepidoptera specifically (Robinet and Roques, 2010).

The majority of southern species increased (35) rather than decreased (23) in relative abundance while the majority of northern species decreased (16) as opposed to increased (5) in relative abundance. The butterfly that experienced the greatest decline, the Compton's Tortoiseshell, is classified as a northern butterfly and is common in forests in states north of Massachusetts. The Massachusetts Butterfly Atlas (MBA: Leahy) explains that due to unfavorable climate, individuals from the north may immigrate and establish populations that might die out especially when there is low emigration. For species where breeding and stable populations were once common in Massachusetts, it may be becoming more often a sink for northern and near arctic butterfly species.

Although range expansions have been documented in ecological literature (Thomas, 2010), examples of range retractions are relatively rare. Although species are often reported as increasing the northern limits of their range, contractions at the southern limit are more difficult to detect over a coarse resolution range especially when there exist other potential factors (Thomas et al. 2006). Nevertheless, our results suggest that northern species are declining across the state of Massachusetts. For such species as the Compton Tortoiseshell or Acadian

Hairstreak the southern limit of their range may be moving north past Massachusetts where conditions are still relatively thermally suitable. Local extinction is a process that often manifests over multiple generations (Tilman et al., 1994) and so there may be an extinction debt among northern range species within the state of Massachusetts that may be in the process of disappearing. Further monitoring is necessary to evaluate the continued viability of species and to make conclusions about the status of certain species in Massachusetts.

Conclusion

Because North America lacks the long-term government-funded observation programs that are present in Europe we rely on the work done by citizen scientists to monitor Lepidoptera. Members of the Massachusetts Butterfly Club have been monitoring butterflies in the state since 1986. Although citizen science projects like this one are relatively opportunistic relative to other monitoring schemes, using the List Length analysis first implemented by Szabo et al. (2010) we were able to determine the relative abundance of species over time. This measure of abundance was related to observed changes in phenology, measured using quantile regression, which revealed that species generally expanding their flight period were outperforming species that did not. Furthermore, patterns of phenology and abundance appear to be influenced by voltinism behavior as species with the capacity for multiple generations both appear to have extended their flight period further into the spring and increased in abundance relative to univoltine species. As the community of Massachusetts butterflies changes, we see more southerly species supplanting northern species as climate change appears to press

the limits of species ranges northward. Such factors as the ones studied here are important when considering how best to conserve the communities of Lepidoptera though more work should be done to investigate the causal mechanisms involved in species' responses to changing climate

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Supplementary Material

Appendix I

Abundance analyses involved shortening species observations to those trips with minimum number of 5 species observed. Abundance was modelled using a generalized linear mixed model with the presence of a species on a trip as a response and the year of the trip and the list length (the number of species observed on the trip) as fixed predictors with and a random effect of year. Presence is a binomial response (0 or absent, 1 for present) and as such the model gives the slope of the proportion of trips on which the species is present. The year is a basic predictor variable while the list length also acts as a predictor and a proxy for search effort. It acts as a predictor because the more species seen on any trip, the greater the search effort and the more likely any given species is observed. This is true across all species, though this varies across individual species depending on their flight timing relative to all other species. Each species has a unique baseline level detectability at the outset of the study. This baseline is unique to each species, based on different factors affecting detectability including conspicuity and weather conditions during flight in addition to any other factor that regularly affects whether a butterfly is seen on trips throughout the year. Because this baseline is specific to each species, the values for each species themselves have no biological significance when compared directly. The change in each; however, demonstrates trends in the proportion of trips on which each species can be observed and this is comparable across all species because it describes a change from the baseline. For example, particularly large and conspicuous species like some Nymphalidae may be seen very often on trips throughout its flight and therefore cannot be compared to a smaller and more cryptic species like some Hesperiidae which may not be as often seen during its flight period. Deviations from these baseline probabilities of observation in trips throughout a year; however, may reveal meaningful differences between the species as to whether they are increasing or decreasing.

$$\text{probability of observing a species on a trip} = \alpha_1 + \alpha_2 * \text{year} + \alpha_3 * \text{list length}$$

Above is a simple structure of the model where α_1 is the baseline detection, where α_2 is the change in the probability of observance over time, the coefficient representing abundance, and α_3 the effect of the length of the list length on the probability of observing a single species. Not represented is the random effect of year which is expected to vary throughout years due natural fluctuations to precipitation, temperature etc. All models will run using the `glmer()` function.

Quantile regression analyses represented the change in each quantile of the response over the period of study. The change in the 0.1 and 0.9 quantile (i.e. the 10th and 90th percentile respectively) numerical days of the year across the study period were calculated. Quantile regression does this by minimizing the sum of weighted absolute deviations for the model's chosen quantile at each level of predictor, in our case year, for the line generated (i.e. a straight line is fitted through each 0.9 quantile observation across each year). Quantile regression functions similarly to least squares regression but does not assume a normal error distribution around the quantiles like least squares regression does around the mean. Quantile regression is useful exactly in cases where one would expect portions of the response distribution that are not the mean to change, in our case the lower and upper quantiles of sightings. It can theoretically be done for any number of quantiles across a response variable.

$$\text{numerical day of year of quantile}(\tau) = \beta_1(\tau) + \beta_2(\tau) * \text{year}$$

Above is a simple structure of the models where τ represents the quantile of interest, β_1 describes the intercept, the sighting day of year in year 1991 and β_2 describes the slope coefficient of the day of year quantile with every year.

Table S-1: Species codes, Common names, Latin names, whether species were included or excluded from the study (or explanation for exclusion), total number of sightings across the study period. Too few observations under Included may describe total observations or a species with fewer than 15 observations prior to the year 2000.

Code	Common Latin	Latin Name	Excluded
ACHA	Acadian Hairstreak	<i>Satyrium acadia</i>	Included
AMCO	American Copper	<i>Lycaena phlaeas</i>	Included
AMLA	American Painted Lady	<i>Vanessa virginiensis</i>	Included
AMSN	American Snout	<i>Ligytheana carinenta</i>	Too few observations
APFR	Aphrodite Fritillary	<i>Speyeria aphrodite</i>	Included
APBR	Appalachian Brown	<i>Satyroides appalachia</i>	Included
ARSK	Arctic Skipper	<i>Carterocephalus palaemon</i>	Included
ATFR	Atlantis Fritillary	<i>Speyeria atlantis</i>	Included
BACH	Baltimore Checkerspot	<i>Euphydryas phaeton</i>	Included
BAHA	Banded Hairstreak	<i>Satyrium calanus</i>	Included
BLDA	Black Dash	<i>Euphyes conspicua</i>	Included
BLSW	Black Swallowtail	<i>Papilio polyxenes</i>	Included
BOCO	Bog Copper	<i>Lycaena epixanthe</i>	Included
BOEL	Bog Elfin	<i>Callophrys lanoraieensis</i>	Too few observations
BWSK	Broad-winged Skipper	<i>Poanes viator</i>	Included
BRCO	Bronze Copper	<i>Lycaena hyllus</i>	Included
BREL	Brown Elfin	<i>Callophrys augustinus</i>	Included
CAWH	Cabbage White	<i>Pieris rapae</i>	Included
CGAZ	Cherry Gall Azure	<i>Celastrina serotina</i>	Taxonomic Realignment
CTSW	Canadian Tiger Swallowtail	<i>Papilio canadensis</i>	Cryptic Species
CHWH	Checkered White	<i>Ponntia protodice</i>	Too few observations
CLSU	Clouded Sulphur	<i>Colias philodice</i>	Included
CESU	Cloudless Sulphur	<i>Phoebis sennae</i>	Included
COSK	Cobweb Skipper	<i>Hesperia metea</i>	Included
COBU	Common Buckeye	<i>Junonia coenia</i>	Included
CCSK	Common Checkered-Skipper	<i>Pyrgus communis</i>	Too few observations
CORI	Common Ringlet	<i>Coenonympha tullia</i>	Included
ROSK	Common Roadside-Skipper	<i>Amblyscirtes vialis</i>	Too few observations
COSO	Common Sootywing	<i>Pholisora catullus</i>	Included
CWNY	Common Wood-Nymph	<i>Cercyonis pegala</i>	Included
COTO	Compton Tortoiseshell	<i>Nymphalis vaualbum</i>	Included
COHA	Coral Hairstreak	<i>Satyrium titus</i>	Included
CRSK	Crossline Skipper	<i>Polites origenes</i>	Included
DESK	Delaware Skipper	<i>Anatrytone logan</i>	Included
DISK	Dion Skipper	<i>Euphyes dion</i>	Too few observations
DRDU	Dreamy Duskywing	<i>Erynnis icelus</i>	Included
DNSK	Dun Skipper	<i>Eyphyes cestrus</i>	Included
DSSK	Dusted Skipper	<i>Atrytonopsis hianna</i>	Included
EAHA	Early Hairstreak	<i>Erora laeta</i>	Included
EACO	Eastern Comma	<i>Polygonia comma</i>	Included

EPEL	Eastern Pine Elfin	<i>Callophrys niphon</i>	Included
ETBL	Eastern Tailed Blue	<i>Cupido comyntas</i>	Included
ETSW	Eastern Tiger Swallowtail	<i>Papilio glaucus</i>	Cryptic Species
EDHA	Edwards Hairstreak	<i>Satyrium edwardsii</i>	Included
EUSK	European Skipper	<i>Thymelicus lineola</i>	Included
EYBR	Eyed Brown	<i>Satyroides eurydice</i>	Included
FISK	Fiery Skipper	<i>Hylephila phyleus</i>	Included
FREL	Frosted Elfin	<i>Callophrys irus</i>	Included
GISW	Giant Swallowtail	<i>Papilio cresphontes</i>	Too few observations
GSFR	Great Spangled Fritillary	<i>Speyeria cybele</i>	Included
GRCO	Gray Comma	<i>Polygonia progne</i>	Too few observations
GRHA	Gray Hairstreak	<i>Strymon melinus</i>	Included
GUFR	Gulf Fritillary	<i>Agraulis vanillae</i>	Too few observations
HAEM	Hackberry Emperor	<i>Asterocampa celtis</i>	Included
HACH	Harris' Checkerspot	<i>Chlosyne harrisii</i>	Included
HARV	Harvester	<i>Feniseca tarquinius</i>	Included
HEEL	Henry's Elfin	<i>Callophrys henrici</i>	Included
HEHA	Hessel's Hairstreak	<i>Callophrys hesseli</i>	Too few observations
HIHA	Hickory Hairstreak	<i>Satyrium caryaevorus</i>	Too few observations
HOED	Hoary Edge	<i>Achalarus lyciades</i>	Included
HOEL	Hoary Elfin	<i>Callophrys polios</i>	Included
HOSK	Hobomok Skipper	<i>Poanes hobomok</i>	Included
HODU	Horace's Duskywing	<i>Erynnis horatius</i>	Included
INSK	Indian Skipper	<i>Hesperia sassacus</i>	Included
JUHA	Juniper Hairstreak	<i>Callophrys gryneus</i>	Included
JUDU	Juvenal's Duskywing	<i>Erynnis juvenalis</i>	Included
LASK	Least Skipper	<i>Ancyloxypha numitor</i>	Included
LODA	Long Dash	<i>Polites mystic</i>	Included
LOSK	Leonard's Skipper	<i>Hesperia leonardus</i>	Too few observations
LIGL	Little Glassywing	<i>Pompeius verna</i>	Included
LWSA	Little Wood-Satyr	<i>Megisto cymela</i>	Included
LIYE	Little Yellow	<i>Pyrisitia lisa</i>	Single year outbreak
LTSK	Long-tailed Skipper	<i>Urbanus proteus</i>	Too few observations
MEFR	Meadow Fritillary	<i>Boloria bellona</i>	Included
MITO	Milbert's Tortoiseshell	<i>Aglaia milberti</i>	3 year outbreak
MONA	Monarch	<i>Danaus plexippus</i>	Included
MOCL	Mourning Cloak	<i>Nymphalis antiopa</i>	Included
MUWI	Mulberry Wing	<i>Poanes massasoit</i>	Included
MUWH	Mustard White	<i>Pieris oleracea</i>	Included
NBDA	Northern Broken-Dash	<i>Wallengrenia egeremet</i>	Included
NOCL	Northern Cloudywing	<i>Thorybes pylades</i>	Included
NPEY	Northern Pearly-eye	<i>Enodia anthedon</i>	Included
SOHA	Oak Hairstreak	<i>Satyrium favonius</i>	Too few observations
OCSK	Ocola Skipper	<i>Panoquina ocola</i>	Too few observations
ORSU	Orange Sulphur	<i>Colias eurytheme</i>	Too few observations
PALA	Painted Lady	<i>Vanessa cardui</i>	Included
PECR	Pearl Crescent	<i>Phyciodes tharos</i>	Included
PESK	Peck's Skipper	<i>Polites peckius</i>	Included
PSSK	Pepper and Salt Skipper	<i>Amblyscirtes hegon</i>	Included
PEDU	Persius Duskywing	<i>Erynnis persius</i>	Too few observations
PISW	Pipevine Swallowtail	<i>Battus philenor</i>	Included
QUMA	Question Mark	<i>Polygonia interrogationis</i>	Included
READ	Red Admiral	<i>Vanessa atalanta</i>	Included

RSPU	Red-spotted Purple	<i>Limenitis arthemis astyanax</i>	Taxonomic Realignment
RSAD	Red-spotted Admiral	<i>Limenitis arthemis</i>	Taxonomic Realignment
SACH	Sachem	<i>Atalopedes campestris</i>	Too few observations
SBFR	Silver Bordered Fritillary	<i>Boloria selene</i>	Included
SIBL	Silver Blue	<i>Glaucopsyche lygdamus</i>	Included
SLDU	Sleepy Duskywing	<i>Erynnis brizo</i>	Included
SSSK	Silver-spotted Skipper	<i>Epargyreus clarus</i>	Included
SPAZ	Spring Azure	<i>Thorybes bathyllus</i>	Cryptic
STHA	Striped Hairstreak	<i>Satyrium liparops</i>	Included
SUAZ	Summer Azure	<i>Celastrina neglecta</i>	Change in reporting
TAEM	Tawny Emperor	<i>Asterocampa clyton</i>	Too few observations
TESK	Tawny-edged Skipper	<i>Polites themistocles</i>	Included
TISW	Tiger Swallowtail	<i>Papilio glaucus</i>	Cryptic Species
TSSK	Two-spotted Skipper	<i>Euphyes bimacula</i>	Included
VAFR	Variegated Fritillary	<i>Euptoieta claudia</i>	Included
VICE	Viceroy	<i>Limenitis archippus</i>	Included
WVWH	West Virginia White	<i>Pieris virginiensis</i>	Included
WHAD	White Admiral	<i>Limenitis arthemis arthemis</i>	Taxonomic Realignment
WMHA	White-M Hairstreak	<i>Parrhasius m album</i>	Too few observations
WIDU	Wild Indigo Duskywing	<i>Erynnis baptisiae</i>	Included
ZASK	Zabulon Skipper	<i>Poanes zabulon</i>	Included

Table S-2: Species Codes and measures of Relative Abundance and Phenology. Values represent annual changes (i.e. the slope coefficient of the lines fit those data values). Relative Abundance derived from the list length analysis demonstrates the change in the proportion of lists on which the species was seen averaged across years (Δ proportions of list per year). Mean day of year was derived from the Least Squares Regression model illustrating the annual change in the day of year value for sightings of each species (days per year). 0.1 quantile demonstrates the annual change in the sighting date for the 10th percent of that species' sightings across years (days per year) and the 0.9 quantile demonstrates the same change for the 90th percent of that species' sightings across year. The flight period, derived as the difference between the 0.9 and the 0.1 quantiles, demonstrates the annual change in the number of days butterflies were seen between both quantiles (days per year).

species code	relative abundance	mean day of year	0.1 quantile	0.9 quantile	Flight period
ACHA	-0.08551	-0.16127	-0.38889	-0.23077	0.15812
AMCO	-0.0075	-0.14925	-0.4	0.681818	1.081818
AMLA	0.01607	-0.14143	-0.69231	0.266667	0.958974
APBR	0.026315	-0.12981	-0.41667	0.2	0.616667
APFR	-0.04807	-0.12046	-0.1	-0.33333	-0.23333
ARSK	-0.00555	-0.35328	0.083333	-0.27273	-0.35606
ATFR	-0.03844	-0.06524	-0.08696	1.78E-15	0.086957
BACH	0.032588	-0.18368	-0.45	-0.18182	0.268182
BAHA	-0.0096	-0.19398	-0.21053	-0.18182	0.028708
BLDA	-0.04162	-0.13319	4.01E-15	-0.21053	-0.21053
BLSW	0.059777	0.163763	-0.4	0.5625	0.9625
BOCO	-0.05688	-0.01663	-0.06667	-2.53E-15	0.066667
BRCO	0.081006	0.771063	-0.78947	-0.38462	0.404858

BREL	0.027359	-0.26031	-0.16667	-0.13636	0.030303
BWSK	0.029818	-0.13265	-0.34783	0.3	0.647826
CAWH	-0.01663	-0.19843	-0.625	0.35	0.975
CESU	0.041294	-0.45461	-0.57143	-0.8	-0.22857
CLSU	-0.02977	-0.04862	-0.33333	0.047619	0.380952
COBU	0.058363	-0.42596	-0.93333	0.125	1.058333
COHA	-0.03294	-0.28273	-0.25	-0.35294	-0.10294
CORI	-0.02762	-0.3058	-0.30769	-0.04545	0.262238
COSK	-0.06816	-0.2203	-0.3	-0.15789	0.142105
COSO	0.002872	0.708865	0.066667	0.615385	0.548718
COTO	-0.12879	-0.76164	0.142857	-0.81818	-0.96104
CRSK	-0.03376	-0.05591	-0.17647	0.227273	0.403743
CWNY	-0.02852	-0.2855	-0.17647	-0.2	-0.02353
DESK	-0.02513	-0.0557	-0.0625	-1.52E-15	0.0625
DNSK	-0.0046	-0.05429	-0.08333	-0.2	-0.11667
DRDU	-0.04906	-0.31978	-0.26667	-0.42105	-0.15439
DSSK	0.005503	-0.37835	-0.22222	-0.57143	-0.34921
EACO	0.02466	0.202043	-0.09091	0.5	0.590909
EAHA	0.01989	-0.14323	0.214286	-0.95652	-1.17081
EDHA	-0.01828	-0.26383	-0.41176	-0.28571	0.12605
EPEL	0.052664	-0.50448	-0.23529	-0.27273	-0.03743
ETBL	0.015017	-0.17429	-0.44444	0.095238	0.539683
EUSK	-0.04578	-0.11594	-0.16667	-1.44E-15	0.166667
EYBR	-0.03894	-0.3723	-0.25	-0.69565	-0.44565
FISK	0.119292	0.105263	-0.77778	0.526316	1.304094
FREL	0.10104	-0.22496	-0.5625	-0.42857	0.133929
GRHA	0.034381	-0.78879	-1	0.25	1.25
HACH	-0.0414	-0.23359	-0.23529	-0.21053	0.024768
HAEM	0.010518	0.558597	0.764706	-0.5625	-1.32721
HARV	0.002368	-0.12921	-0.36	-0.6	-0.24
HEEL	0.053461	-0.28423	-0.3	-0.1	0.2
HODU	0.055819	0.263006	0.304348	1.3125	1.008152
HOED	-0.07234	-0.38469	-0.08	-0.33333	-0.25333
HOEL	0.038677	-0.32946	-0.25	-0.15385	0.096154
HOSK	-0.03534	-0.30681	-0.07143	-0.3125	-0.24107
INSK	-0.01248	-0.34666	-0.26667	0.086957	0.353623
JUDU	0.015856	-0.50129	-0.42857	-0.28571	0.142857
JUHA	0.039431	-0.30537	-0.69231	-0.47619	0.216117
LASK	-0.02535	-0.03715	-0.11111	0.090909	0.20202
LIGL	0.015617	-0.17132	-0.16667	-0.19048	-0.02381
LODA	-0.04739	-0.0711	-0.26667	0.375	0.641667

LWSA	-0.00579	-0.07855	-0.1	0.125	0.225
MEFR	0.001722	0.202243	-2.23E-15	0.642857	0.642857
MOCL	-0.00704	-0.80532	-0.05556	-0.33333	-0.27778
MONA	-0.00493	0.32757	0.304348	0.066667	-0.23768
MUWH	0.035468	0.417333	0.6	0.96	0.36
MUWI	-0.01479	-0.25012	-0.11765	-0.41667	-0.29902
NBDA	0.005661	-0.01934	-0.05263	-0.06667	-0.01404
NOCL	-0.05056	-0.20703	-0.22222	-0.16667	0.055556
NPEY	-0.00327	-0.04498	-0.07143	-7.91E-16	0.071429
PALA	0.035447	0.272205	1.352941	0.818182	-0.53476
PECR	0.012763	-0.28784	-0.30769	-6.33E-16	0.307692
PESK	-0.00335	0.122834	-0.05556	0.2	0.255556
PISW	0.083673	0.246681	-1.36842	0.111111	1.479532
PSSK	-0.00558	-0.25254	-0.21429	-0.66667	-0.45238
QUMA	-0.0079	-0.4176	-1.5	-1.66667	-0.16667
READ	0.024076	-0.15536	-0.6	-0.05	0.55
SBFR	-0.02763	-0.43169	-0.5	2.68E-15	0.5
SIBL	-0.01236	-0.49579	-0.4	-0.45455	-0.05455
SLDU	0.022228	-0.27216	-0.38889	-0.22222	0.166667
SOCL	0.021599	-0.07015	-3.55E-15	0.25	0.25
SOHA	-0.03046	-0.159	-0.21739	0.066667	0.284058
SPSW	0.008626	-0.23173	-0.95652	-0.36842	0.588101
SSSK	-0.00215	0.2403	5.40E-16	0.888889	0.888889
STHA	-0.03739	-0.24492	-0.17647	-0.54545	-0.36898
TESK	0.016665	0.246216	2.73E-16	0.444444	0.444444
VAFR	0.007226	0.168218	-0.16667	0.666667	0.833333
VICE	-0.0169	-0.10491	-0.36842	0.333333	0.701754
WIDU	0.010185	0.204481	-0.23529	1.25	1.485294
WVWH	0.047141	-0.30536	-1.30E-15	0.045455	0.045455
ZASK	0.201037	-0.85596	-1.75	-0.05882	1.691176

Table S-III. Ecological Groupings. of all butterfly species included in the analysis as outlined in Table 1. Species were assigned based on Breed et al (2013) with the MBA (Leahy). Voltinism was corroborated by examining species specific plots of day of year and year of study (see Fig. 3 of ZASK for example).

Species code	Voltinism	Range	Habitat	Host Plant Availability	Overwintering Stage
ACHA	univoltine	north	wetland	widespread	egg
AMCO	multivoltine	core	disturbed	widespread	pupa
AMLA	multivoltine	south	generalist	widespread	adult
APBR	univoltine	south	open	widespread	larva
APFR	univoltine	north	closed forest	patchy distribution	egg

ARSK	univoltine	north	open forest	widespread	larva
ATFR	univoltine	north	closed forest	widespread	egg
BACH	univoltine	south	open	patchy distribution	larva
BAHA	multivoltine	south	open forest	widespread	egg
BLDA	univoltine	south	wetland	patchy distribution	adult
BLSW	multivoltine	south	open	widespread	pupa
BOCO	univoltine	north	bog	patchy distribution	egg
BRCO	multivoltine	core	wetland	widespread	egg
BREL	univoltine	north	closed forest	widespread	pupa
BWSK	multivoltine	south	wetland	widespread	larva
CAWH	multivoltine	south	disturbed	widespread	pupa
CESU	multivoltine	south	generalist	rare	pupa
CLSU	multivoltine	south	disturbed	widespread	larva
COBU	multivoltine	south	generalist	widespread	adult
COHA	univoltine	south	closed forest	widespread	egg
CORI	multivoltine	north	open forest	widespread	larva
COSK	multivoltine	south	generalist	widespread	larva
COSO	multivoltine	south	open forest	widespread	larva
COTO	multivoltine	north	closed forest	widespread	adult
CRSK	multivoltine	south	generalist	widespread	larva
CWNY	univoltine	south	open forest	widespread	egg
DESK	multivoltine	north	open forest	widespread	larva
DNSK	univoltine	south	wetland	widespread	larva
DRDU	multivoltine	north	open forest	widespread	larva
DSSK	multivoltine	south	generalist	widespread	larva
EACO	multivoltine	south	closed forest	widespread	adult
EAHA	multivoltine	north	closed forest	widespread	pupa
EDHA	univoltine	south	open forest	widespread	egg
EPEL	univoltine	south	closed forest	widespread	pupa
ETBL	multivoltine	south	generalist	widespread	larva
EUSK	univoltine	north	disturbed	widespread	egg
EYBR	univoltine	north	open forest	widespread	larva
FISK	multivoltine	south	disturbed	widespread	larva
FREL	univoltine	south	open forest	patchy distribution	pupa
GRHA	multivoltine	south	open forest	widespread	pupa
HACH	univoltine	north	open forest	widespread	larva
HAEM	multivoltine	south	open forest	patchy distribution	larva
HARV	multivoltine	south	open forest	unknown	pupa
HEEL	univoltine	south	open forest	widespread	pupa
HODU	multivoltine	south	open forest	widespread	larva
HOED	univoltine	south	generalist	widespread	pupa

HOEL	multivoltine	north	open forest	rare	pupa
HOSK	multivoltine	core	open forest	widespread	adult
INSK	univoltine	north	open forest	widespread	larva
JUDU	univoltine	south	open forest	widespread	larva
JUHA	multivoltine	south	closed forest	widespread	pupa
LASK	multivoltine	south	generalist	widespread	adult
LIGL	multivoltine	south	generalist	widespread	pupa
LODA	multivoltine	north	generalist	widespread	larva
LWSA	multivoltine	south	open forest	widespread	larva
MEFR	multivoltine	north	open forest	widespread	larva
MOCL	multivoltine	south	closed forest	widespread	adult
MONA	multivoltine	south	generalist	widespread	adult
MUWH	multivoltine	north	closed forest	rare	pupa
MUWI	multivoltine	core	wetland	patchy distribution	adult
NBDA	multivoltine	south	open forest	patchy distribution	larva
NOCL	univoltine	south	open forest	widespread	larva
NPEY	multivoltine	south	closed forest	widespread	larva
PALA	multivoltine	south	open	widespread	pupa
PECR	multivoltine	south	open forest	widespread	larva
PESK	multivoltine	core	open forest	widespread	pupa
PISW	multivoltine	south	open forest	rare	pupa
PSSK	univoltine	south	closed forest	widespread	larva
QUMA	multivoltine	south	open forest	widespread	adult
READ	multivoltine	south	generalist	widespread	adult
SBFR	multivoltine	north	wetland	widespread	larva
SIBL	univoltine	north	open forest	rare	pupa
SLDU	univoltine	south	open forest	widespread	larva
SOCL	multivoltine	south	generalist	widespread	pupa
SOHA	multivoltine	south	open forest	widespread	egg
SPSW	multivoltine	south	closed forest	widespread	pupa
SSSK	multivoltine	south	open forest	widespread	pupa
STHA	univoltine	south	open forest	widespread	egg
TESK	multivoltine	south	generalist	widespread	pupa
VAFR	multivoltine	south	open forest	widespread	larva
VICE	multivoltine	south	open forest	widespread	larva
WIDU	multivoltine	south	open forest	patchy distribution	larva
WVWH	univoltine	south	open forest	widespread	pupa
ZASK	multivoltine	south	open forest	widespread	adult

Table S-IV. ANOVA results for comparisons between the slope trend of different measures of phenology (derived from quantile regression) and relative abundance (derived from list length method) with difference ecological groupings as outlined in Table S-III. Results significant at the $\alpha \geq 0.05$ level are bolded.

	0.1 quantile	0.9 quantile	Flight period	Relative abundance
Voltinism	0.6294	0.007192	0.006684	0.06669
Range	0.2596	0.5867	0.09574	0.002429
Habitat	0.5944	0.2172	0.1048	0.5291
Host Plant Availability	0.9598	0.3297	0.4234	0.2204
Overwintering Stage	0.2479	0.2479	0.4234	0.2204

Appendix II

Data processing occurred over multiple steps. The Massachusetts Butterfly Club went on regular trips annually from the period 1991 to 2017 (Table S-V). Files were compiled by year with each row of data containing the following information about a butterfly sighting: species name, the date, the number of individuals of that species observed, the location of the sightings, and the names of the observers. In Excel, butterflies of each species were assigned the same 4 letter codes as seen in Table S-1. After reviewing the data and ensuring each row was properly formatted, it was ready to be regrouped. Regrouping the data involved retroactively assigning each sighting to trips based on three variables from the original dataset. Each trip is defined as a collection of sightings of different species which occurred on the same day, in the same place and by the same people. The data were reordered from being organized from files of all sightings within a year into files arranged by all sightings of species from different trips. Rows of the new data files were based on all trips that occurred over the study period. Each trip was assigned a unique trip id based on the place, timing and observers and occupied its own row in each data file.

Regrouping of the data was done in R and used a modified function originally designed by Breed, Stichter and Crone (2013). This function fits and reorganizes the data into new lists with a different file for each species. Values were assigned to the rows of the new data files for each species, iterated over all the original data files from all the years: species code, list length, presence, species quantity, year, day of year and location. Species code was taken from the original files, was the same for all rows in the file and corresponds to species as described in Table S-1. List length is the sum of the number of unique species observed on a trip. Presence of a species was a binary value, describing whether the species of interest (for that specific file) was observed on the trip. Species quantity was the number of individuals of the species observed on that trip if any and though it was not used for any analysis of abundance (number of individuals seen is subject to search effort). The year and day of year were taken from the dates of each trip. Lastly, the location of each sighting was recorded as well by assigning numeric values based on the township of each trip. Location in the original datasets were name locations of different places in Massachusetts including parks, individuals' properties etc. although townships or municipalities were included in nearly all of the records. A reference list of all locations listed in the data in Massachusetts and corresponding numerical identifications was used to assign location values to the new data files. Every new file therefore contained the complete list all trips over the study period and for each trip how many species were seen, whether the species of interest in that particular file was present, how many individuals of that species were seen, the year, the day of

year and the location of the trip. These files were then analyzed to reveal the patterns of relative abundance using the list length method and the measures of phenology using quantile regression as discussed in Methods and Appendix I.

Table S-V. The number of times all unique species were observed on trips by the Massachusetts Butterfly Club. All species were observed across all years and this includes the number of

Year	Number of Species Sightings
1991	827
1992	1128
1993	2037
1994	4141
1995	4964
1996	3806
1997	1055
1998	6123
1999	7247
2000	5678
2001	6274
2002	4627
2003	5861
2004	5342
2005	5023
2006	5310
2007	6083
2008	5643
2009	5594
2010	5860
2011	4841
2012	5801
2013	5422
2014	4698
2015	4827
2016	4723
2017	5911

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