Abstract

* Butterflies as a useful model of phenological change
* Limited understanding of phenological change in the SE US

Methods:

Introduction to system

* We used observational butterfly sighting data from the *Butterflies of North Carolina* (29th Approximation) (LeGrand and Howard 2021). The database was first created in 1993 and covers North Carolina’s 177 known butterfly species. It is updated yearly and included 232,779 records from 1899 to 2020. The data is collected opportunistically, in which participants may submit sightings from any time or location. It covers all North Carolina counties. Each entry lists the common name, date, observer name, number of individual butterflies observed, and the county of sighting. We selected just Triangle observations. We used data collected from 1990 to 2020, as the large majority of the observations were made in this interval. Within this interval, we also selected those species which had at least 10 years with at least 10 records and are not significantly migratory in the Piedmont ecoregion, resulting in 42 focal species (Supplemental Table 1).

Subsetting species and observations

* Selected Triangle observations
  + These are the top three counties in terms of number of records
* Parameters used to select species and observations
* Non migratory in the Triangle region, using xx sources
* At least 10 “good species years”
  + What this means

Calculating temperature

* Temperature from PRISM climate group
  + Description of the data
* Selected 4 month window (March – June)
* Rasterized in R using x programs.

Defining earlydate

* Date associated with first 10% of individuals.

Earlydate versus temp or year

* Remove outliers using cooksd

Species traits analyses

* Testing for phenological signal?

Results

Diagram, schematic

Description automatically generated

**Figure 1.** Violin plots illustrating the distribution of slope values by species traits. Red dots indicate the mean, and error bars indicate the standard deviation. A) Distribution of earlydate versus temperature and B) year by overwintering stage. C) Distribution of earlydate versus temperature and D) year by voltinism. The slopes for species with 3.5 and 5 voltinism are not displayed because there is a single value for each.

Chart

Description automatically generated

**Supplemental Figure 1.** A) A map of North Carolina counties, with NC Counties indicated in light green and Triangle counties (Durham, Orange, Wake) indicated in purple. B) Non-cumulative number of Triangle butterfly observations records per year and yearly fluctuations in mean temperature from March to June between 1990 and 2020. Map compiled using ArcGIS Version 10.6.1. County shapefile obtained from the US Census Bureau. Temperature data obtained from PRISM Climate Group (Oregon State University 2022).

**Supplemental Table 1.** Summary of species and species traits included in analysis.

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| Family | Species | Voltinism | Overwintering stage | Reference |
| Hesperiidae | *Ancyloxypha numitor* | 3 | larvae | LeGrand and Howard 2022 |
| Hesperiidae | *Atalopedes campestris* | 3 | larvae | LeGrand and Howard 2022, NABA North Jersey Chapter 2017 |
| Hesperiidae | *Epargyreus clarus* | 2 | pupae | LeGrand and Howard 2022, Hall 2008 |
| Hesperiidae | *Erynnis horatius* | 3 | larvae | LeGrand and Howard 2022, BAMONA 2022 |
| Hesperiidae | *Erynnis juvenalis* | 1 | larvae | LeGrand and Howard 2022, BAMONA 2022 |
| Hesperiidae | *Euphyes vestris* | 2 | larvae | LeGrand and Howard 2022, BAMONA 2022 |
| Hesperiidae | *Lerema accius* | 1 | pupae | LeGrand and Howard 2022, Burgess 2018 |
| Hesperiidae | *Nastra lherminier* | 2 | larvae | LeGrand and Howard 2022, NABA North Jersey Chapter 2017 |
| Hesperiidae | *Polites origenes* | 2 | larvae | LeGrand and Howard 2022, BAMONA 2022 |
| Hesperiidae | *Pompeius verna* | 2 | larvae | LeGrand and Howard 2022, Alabama Butterfly Atlas 2022. Note possible main change |
| Hesperiidae | *Pyrgus communis* | 3 | larvae | LeGrand and Howard 2022, BAMONA 2022. Note possible name change |
| Hesperiidae | *Thorybes bathyllus* | 2 | larvae | LeGrand and Howard 2022, BAMONA 2022. Note possible name change |
| Hesperiidae | *Wallengrenia otho* | 2 | larvae | LeGrand and Howard 2022, Burgess 2018. Note name change |
| Lycaenidae | *Calycopis cecrops* | 2 | larvae | LeGrand and Howard 2022, Hall and Butler 2019 |
| Lycaenidae | *Celastrina ladon* | 1 | pupae | LeGrand and Howard 2022, Alabama Butterfly Atlas 2022 |
| Lycaenidae | *Celastrina neglecta* | 3 | pupae | LeGrand and Howard 2022, BAMONA 2022 |
| Lycaenidae | *Cupido comyntas* | 4.5 | larvae | LeGrand and Howard 2022, BAMONA 2022 |
| Lycaenidae | *Strymon melinus* | 3 | pupae | LeGrand and Howard 2022, BAMONA 2022 |
| Nymphalidae | *Asterocampa celtis* | 2 | larvae | LeGrand and Howard 2022, Hall and Butler 2021 |
| Nymphalidae | *Chlosyne nycteis* | 3 | larvae | LeGrand and Howard 2022, BAMONA 2022 |
| Nymphalidae | *Cyllopsis gemma* | 3 | larvae | LeGrand and Howard 2022, BAMONA 2022 |
| Nymphalidae | *Hermeuptychia sosybius* | 3 | larvae | LeGrand and Howard 2022, Tan and Lucky 2016 |
| Nymphalidae | *Lethe anthedon* | 2 | larvae | LeGrand and Howard 2022, Alabama Butterfly Atlas 2022 |
| Nymphalidae | *Lethe appalachia* | 2 | larvae | LeGrand and Howard 2022, Alabama Butterfly Atlas 2022 |
| Nymphalidae | *Libytheana carinenta* | 2 | adults | LeGrand and Howard 2022, Hall and Butler 2021 |
| Nymphalidae | *Limenitis archippus* | 3 | larvae | LeGrand and Howard 2022, Wisconsin Pollinators |
| Nymphalidae | *Limenitis arthemis astyanax* | 3 | larvae | LeGrand and Howard 2022, Hall and Butler 2019 |
| Nymphalidae | *Megisto cymela* | 1 | larvae | LeGrand and Howard 2022, BAMONA 2022 |
| Nymphalidae | *Phyciodes tharos* | 4.5 | larvae | LeGrand and Howard 2022, Alabama Butterfly Atlas 2022 |
| Nymphalidae | *Polygonia comma* | 2 | adults | LeGrand and Howard 2022 |
| Nymphalidae | *Polygonia interrogationis* | 2 | adults | LeGrand and Howard 2022 |
| Nymphalidae | *Speyeria cybele* | 1 | larvae | LeGrand and Howard 2022, Alabama Butterfly Atlas 2022. Note possible name change |
| Nymphalidae | *Vanessa virginiensis* | 3.5 | adults | LeGrand and Howard 2022, Hall 2021 |
| Papilionidae | *Battus philenor* | 3 | pupae | LeGrand and Howard 2022, Illinois Department of Natural Resources 2017 |
| Papilionidae | *Eurytides marcellus* | 3 | pupae | LeGrand and Howard 2022, Hall and Butler 2020 |
| Papilionidae | *Papilio glaucus* | 2 | pupae | LeGrand and Howard 2022, BAMONA 2022. Note name change |
| Papilionidae | *Papilio polyxenes* | 3 | pupae | LeGrand and Howard 2022, BAMONA 2022 |
| Papilionidae | *Papilio troilus* | 2 | pupae | LeGrand and Howard 2022, BAMONA 2022 |
| Pieridae | *Abaeis nicippe* | 3 | adults | LeGrand and Howard 2022, Florida Museum 2021 |
| Pieridae | *Anthocharis midea* | 1 | pupae | LeGrand and Howard 2022, BAMONA 2022 |
| Pieridae | *Colias eurytheme* | 4.5 | pupae | LeGrand and Howard 2022, BAMONA 2022 |
| Pieridae | *Pieris rapae* | 5 | pupae | LeGrand and Howard 2022, BAMONA 2022 |

This is the write-up from 2016:

Phenological changes in North Carolina butterflies using an opportunistic dataset

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ABSTRACT Recent trends show that species are undergoing a widespread shift in the timing of life history events in accordance with climate change. Butterflies typify this effect because they are ectothermic and therefore sensitive to changes in temperature. Multiple studies indicate that spring appearance dates in butterflies have been occurring earlier with rising temperatures. In this study, we use an extensive citizen science dataset to examine changes in the flight dates of 56 butterfly species in North Carolina between 1990 and 2016. We also examine changes in the date of first appearance at the regional level by comparing the mountains, Piedmont and coastal regions. Finally, we explore whether certain species-specific traits correlate with early flight date. There was a trend of earlier appearance dates over time, with an average advancement of 0.51 days for each year. There was also a trend of earlier appearance dates in years with higher temperatures, with an average advancement of 1.62 days for every 1°C increase in mean temperature. However, species differed in whether year or temperature was a more effective predictor of early date. There were few significant differences in the advancement of early flight date between North Carolina’s three main geographical regions. Model averaging indicated that voltinism and diet breadth were important predictors of early date in most models. These results point to possible further shifts in butterfly arrival date as temperatures are projected to rise in the southeastern US and the potential for using citizen science data to observe widespread phenological shifts.

**Introduction**

Mounting evidence indicates that species are undergoing significant changes in seasonal timing and distribution on a global scale in response to climatic change (Walther et al. 2002, Parmesan and Yohe 2003). While species can have varied responses to changing temperatures due to variation in physiology and range, distinct patterns have emerged. Firstly, species have generally shifted their ranges both towards the poles and upwards in elevation (Parmesan et al. 1999). Secondly, spring events have advanced, largely occurring earlier over time (Parmesan and Yohe 2003). These patterns have repercussions for individual fitness, community interactions, and the continued persistence of certain species (reviewed in Parmesan 2006, Møller et al. 2008). Therefore, as global temperatures rise, it is increasingly crucial to study the consequences of changes in temperature on seasonal timing and biological processes.

Spring phenology is an informative measure for examining how species respond to changing temperatures, and is consequently used in numerous reports of climate change response (IPCC 2007, Parmesan 2007). Butterflies are a useful model organism for studying changes in spring phenology because they have predictable and readily observable life events (Roy et al. 2001). Additionally, butterflies have long been a popular subject for naturalists and hobbyists, which has allowed for the persistence of long term datasets of butterfly observations and museum specimens (Thomas 2005, Eskildsen et al. 2015). As ectotherms, they are also sensitive to changes in temperature (Pollard et al. 1993). As temperatures increase, the date of spring emergence has advanced in many butterfly species, as observed in California (Forister and Shapiro 2003), the Mediterranean Basin (Stefanescu et al. 2003), England (Diamond et al. 2011; Roy and Sparks 2000), and Ohio (Diamond et al. 2014).

Many traits may be involved in shaping species’ response to changing temperatures. For butterflies, these traits may include voltinism (the number of generations per year), overwintering stage, geographic range, and the breadth and composition of the larval diet (Altermatt 2010a, Diamond et al. 2011). Examining diet breadth as an indicator of seasonal timing changes can be complex because host plants are also undergoing temporal changes under climate change (Visser and Holleman 2001). However, studying phenology and diet breadth can give insight into how mutualistic relationships will be affected because of climate change. For example, species with a narrow diet breadth may be more susceptible to changes in seasonal timing than those with a broad diet breadth because their range and phenology is dependent on a limited number of plant species (Diamond et al. 2011). Additionally, species that primarily feed on woody plants may experience a more drastic shift in life cycle events because the leaves of woody plants are only palatable during the early spring (Altermatt 2010a).

While there have been multiple studies of changes in butterfly spring phenology from around the globe (Roy and Sparks 2000, Forister and Shapiro 2003, Stefanescu et al. 2003, Diamond et al. 2011, Diamond et al. 2014), our understanding of this phenomenon in the southeastern United States is unclear. This region is noteworthy because it has not experienced the same clear upwards trend in temperature observed on a global scale. Rather, the southeastern US experienced a slight cooling trend over the 20th century (Portmann et al. 2009). This designates the southeastern US as a climatically unique region with the potential to shed light on how species interactions may be altered in this region as temperatures are projected to rise (US Global Change Research Program 2014).

In this study, we use a database of butterfly observations collected opportunistically throughout North Carolina by citizen scientists to determine whether butterflies have shifted their spring appearance dates over the past twenty years and whether temperature plays a role in these shifts. We also examine this at the regional level by comparing North Carolina’s three geographically distinct regions- the mountains, the Piedmont, and the Coastal Plain- to understand whether there is a localized influence on changes in phenology in North Carolina butterflies, as these three regions differ in elevation and growing season length. To mitigate the potential biases presented by data sourced from citizen science, we test the robustness of different proxies for early flight date prior to analysis. Finally, we also explore how species-specific traits relate to changes in first appearance dates in North Carolina butterflies, focusing on voltinism, overwintering stage, diet breadth, and diet composition. When examining voltinism, we expect those species with higher voltinism to experience a greater advancement in early flight date because warming has been shown to be associated with an increase in the number of generations per year in butterflies (Altermatt 2010b). We hypothesize that species which overwinter as adults will experience a greater advance because the adults are more mobile, and may more readily respond to temperature changes. We expect butterflies with a narrower larval diet breadth to have a greater advance in early flight date because they are required to conform to the phenology of their host plants. Finally, we expect those species that feed primarily on woody plants in their larval stage to experience a greater advance in early flight date because the leaves of woody plants tend to be palatable for a narrow length of time (Altermatt 2010a). Examining a geographically and climatically diverse region like North Carolina will give further insight into how the local environment can influence species’ responses to climatic change, and how the timing of butterfly lifetime events might be expected to change in these areas in the coming years.

**Methods**

***study system and data set***

We used observational butterfly sighting data from the *Butterflies of North Carolina* (24th Approximation), a database compiled yearly by Dr. Harry E. LeGrand at the North Carolina Department of Natural Resources (2016). The database was first created in 1993 and covers North Carolina’s 177 known butterfly species. It is updated yearly and now includes 169,400 records from 1938 to 2014. The data is collected opportunistically, in which participants may submit sightings from any time or location. It covers all North Carolina counties, and has good representation of the mountains, Piedmont and Coastal Plain regions (LeGrand and Howard 2015). Each entry lists the common name, date, observer name, number of individual butterflies observed, and the county of sighting. We used data collected from 1990 to 2016, as the large majority of the observations were made in this interval.  Within this interval, we also selected those species which had at least 500 entries in the database to ensure sufficient data for analysis, ultimately choosing 56 butterfly species comprising 125,928 observations. All statistical analyses were performed using R (version 3.3.3).

***Early flight date***

Using the first record of appearance as a proxy for early flight date can be a biased estimate and is heavily subject to outliers and influence by variation in sampling effort or population size (van Strien et al. 2008). We therefore tested different alternative proxies for date of early flight to determine which was the most robust against differences in sampling effort for use in the rest of the analyses. These alternative proxies included using the date by which 10% of that year’s individuals had been observed, the date by which 25% of that year’s individuals had been observed, the date on which the 10th individual of that year was observed, and the date on which the 25th individual of that year was observed. These proxies were chosen based on a study by van Strien et al. (2008), which used hypothetical data to test the robustness of different estimates of early flight date against bias from sampling effort.

To test the different estimates of early flight date, we chose the year with the most records for a particularly abundant species, which was the 2006 data for *Papilio glaucus*, comprising 469 records. To examine how early flight date estimates varied with sample size, we randomly sampled the records for this *P. glaucus* in 2006 to create subsamples of the data consisting of 10, 20, 50, 100, 150, 200, and 250 individuals. The early flight date was estimated for each sample using each proxy. This was done 1000 times and averaged for each subsample to examine how it compared to the best estimate of early flight date, which is the early flight date calculated for all of 2006. A relatively robust estimate of early flight date was indicated by whether the average early flight date determined from smaller subsamples was similar to the best estimate of early flight date (Figure 1). Based on this test, the date by which 10 percent of the individuals for that year had been observed was determined to be the most robust against sampling effort, and was used for all subsequent analyses as the proxy for early flight date. For the analyses of the mountains, Coastal Plain, and Piedmont regions, early flight was determined using only observations from within each region (Figure 2).

***Temperature***

For each species, the average month of appearance was determined by averaging the early flight date for each species from 1990 to 2016 (Roy and Sparks 2000). We measured temperature as the mean monthly temperature for North Carolina averaged over the 8 months prior to the mean arrival month for each species for each year. For the analyses of the mountains, Coastal Plain, and Piedmont regions, we used the mean temperatures of the all the counties in the region, rather than the whole state. If the average arrival date of a species landed before the first 15 days of a month, then the previous month was used as the starting point for calculating average temperature. If the average arrival date for a species landed on or after day 15 of a month, then that month was used as the starting point for calculating temperature. We chose this eight-month interval because of the importance of winter and spring temperatures in dictating the variation in the timing of insect emergence (Forister and Shapiro 2003, Dell et al. 2005). Temperature data was obtained from the PRISM Climate Group at Oregon State University.

***Phenology analysis***

For each species, the change in early flight date over time was examined using linear regression analysis with year and temperature as the covariates. Linear regression analysis was also used to examine the relationship between early flight date and both year and temperature as fixed effects within each of the three regions. Of the 56 species, 6 were excluded from the regional analysis because they were not observed sufficiently in all three regions. We used a one-way ANCOVA to compare whether there was overall difference in the changes in early flight date for the remaining 50 species between the mountains and the Coastal Plain regions in comparison to the Piedmont. We also used a one-way ANCOVA to compare the Coastal Plain to the mountains.

***Species Traits***

We examined four species-specific traits as factors: voltinism, diet breadth, diet type, and overwintering stage. Voltinism was defined as the number of generations per year for populations in North Carolina. Diet breadth was defined as diversity of the larval host plant species, and comprised four categories: single species, single genus, single family, and multifamily (Peterson and Denno 1998). Diet type was defined as whether the larvae eat only woody plants, only herbaceous plants, or a mixture of both. Overwintering stage was reported as whether a species overwinters as larvae, pupae, adults, a mix of larvae and pupae, or a mix of pupae and adults. The butterfly *Wallengrenia otho* was not included in the overwintering analysis because its overwintering stage is unclear. Information on voltinism, diet breadth, diet composition, and overwintering stage were obtained from the website for Butterflies and Moths of North America (BAMONA), and from the 24th Approximation of *Butterflies of North Carolina* (Table 1).

Early flight date was tested as a response to species-specific variables using both linear and mixed-effects models in R, using early flight date as the response variable and species as a random effect. Year, temperature, overwintering stage, voltinism, diet breadth, diet type, and the interaction term between either year or temperature and all the species traits were used as predictor variables. Mixed-effects models were analyzed using the nlme package in R (Pinheiro et al. 2015). Model averaging was also performed on our full model using the MuMIn package in R (Barton 2015) and the non-conditional results for the full model averaging were examined.

**Results**

***Phenology analysis***

Between 1990 and 2016, 14 out of the 56 species tested experienced a significant correlation between early flight date and year. Of those 14 species, 2 had a positive correlation between early flight date and year, and the remaining 12 had a negative correlation (Figure 3a, Table 3). Overall there were 40 negative and 16 positive slopes, a much higher proportion of negative slopes than the expected equality (binomial test, *p*<0.0001). Across all species, there was an average advance of 0.51 days for every year.

Using temperature as the predictor variable, 5 out of the 56 species tested experienced a significant correlation between early flight date and temperature. Of those 5 species, 4 had a negative relationship and 1 had a positive relationship (Fig. 3b, Table 3). Out of the 56 species, there were 35 negative slopes and 21 positive slopes, which was again a much higher proportion of negative slopes than expected (binomial test, *p*<0.05). Across all species, there was an average advance of 1.62 days for every 1°C increase in mean temperature.

Of the 56 species tested, there were no species for which both year and temperature were significant predictors of early flight date. However, there were 23 species for which both year and temperature had a non-significant negative relationship with early date.

***Phenology analysis- regions***

For the effect of year on early flight date, 11 of the 50 species had a significantly different slope when comparing the mountains to the Piedmont, all of which had a smaller or more negative slope in the mountains (ANCOVA). When comparing the Coastal Plain to the Piedmont, 6 species had a significantly different slope, 5 of which were smaller or more negative in the Coastal Plain. When comparing the Coastal Plain to the mountains, 8 species had a significantly different slope, 7 of which were smaller or more negative in the Mountains. In all three regions, the majority of species had negative slopes for early flight date versus year (Table 4).

For the effect of temperature on early flight date, 3 species had a significantly different slope when comparing the mountains to the Piedmont, all of which were more negative in the mountains (ANCOVA). When comparing the Coastal Plain to the mountains, only *Lerema accius* had a significantly more negative slope in the mountains. No species were significantly different between the Piedmont and the Coastal Plain. Again, in all three regions the majority of species had negative slopes for early flight date versus temperature (Table 5).

***Species Traits***

From an ANOVA on the full linear model, early flight date varied strongly by diet type (F2,37=7.7313, p=0.0016, Figure 4, Table 2) and voltinism (F5,37=6.4586, p=0.0002, Figure 4, Table 2).

Using model averaging on the full model, voltinism was an important predictor of early flight date in 103 of the 106 models tested (97%). Diet type was an important predictor in 89 of the 106 (84%) of the models tested.

**Discussion**

The results of the state-wide phenology analyses are consistent with trends in advancement of early flight date in butterflies, as demonstrated by previous studies of long-term butterfly data (Diamond et al. 2011; Roy and Sparks 2000, Forister and Shapiro 2003, Stefanescu et al. 2003), and with a well-established trend of the influence of temperature on insect spring phenology (Forister and Shapiro 2003, Dell et al. 2005). However, it is noteworthy that none of 56 species tested shared both year and temperature as a strong predictor of early flight date. It is also notable that more of species experienced a strong negative correlation when year was used as covariant than when temperature was used. This is unusual because the relationship between higher temperatures and earlier flight dates is well-established, and it would be expected that temperature would have a significant effect on early flight date.

For those species for which temperature was not a strong predictor of early flight date, it is likely that an environmental variable besides mean temperature may be important. For example, photoperiod is a more effective predictor of phenology for some insects (Bale et al. 2002, Valtonen et al. 2011). In California, winter precipitation was also found to be an effective predictor for phenology (Forister and Shapiro 2003). Butterflies are varied in their life history traits, so they are likely to be affected differently by different seasonal cues. Insects in seasonal environments in particular benefit from having life history events which are synchronous with their specific host plants, which in turn have evolved to respond to different cues (van Asch et al. 2007). Indeed, in an analysis of the effect of species traits on early flight date we found that diet type was important in 89/106 (84%) of the models tested, pointing to the potential importance of host plant type in shaping phenology.

Another potential reason that temperature was not a widely effective predictor of phenology is that North Carolina is part of a climatically unique region which has experienced an atypical warming pattern compared to the rest of the world. This region- sometimes termed the “warming hole”- describes a region of the southeast where changes in temperature have not risen as consistently as they have globally (Folland et al. 2002, Portmann et al. 2009). This may have repercussions on the strength of the correlation between early flight date and year parameters in this analysis, as butterflies in North Carolina have not experienced a warming trend for as long as most other regions. We found no significant correlation between mean temperature and year for the 26-year interval used in this study.

In the regional data, only a very small proportion of the species tested experienced significantly different changes in early flight date between the three regions. However, when comparing the mountains to the other two regions, there were 23 instances in which species’ slopes differed significantly, 22 of which were more steeply negative in the mountains. The reason for this is unclear. Butterflies may be adapted to local climate at different elevational gradients, which may allow species in this region to better track seasonal changes.

There are many potential biases from working with data generated by citizen science. For example, sampling effort was highly variable between species, years, and regions. Although the proxy analysis sought to minimize the effect of sampling bias, there may have been an effect between regions, where sampling effort tended to be greater in the Piedmont than in either the Coastal Plain or the Mountains. In addition, it is possible that observers were more likely to go out to observe butterflies when temperatures were warmer, possibly influencing when butterflies were first sighted in a year. Despite these limitations, this dataset demonstrates the usefulness of citizen science data in phenological studies, which often require tracking diverse species over a wide geographical area over many years.

Average temperatures in the southeastern US are projected to climb (US Global Change Research Program 2014). This analysis therefore points to the potential for continued changes in early flight date as temperatures continue to warm. This could have repercussions for survival at both the individual and species level (reviewed in Parmesan 2006, Møller et al. 2008). For a more cohesive model of predicting phenological change in butterflies, additional analyses should account for climatic variables such as precipitation and photoperiod in addition to temperature.

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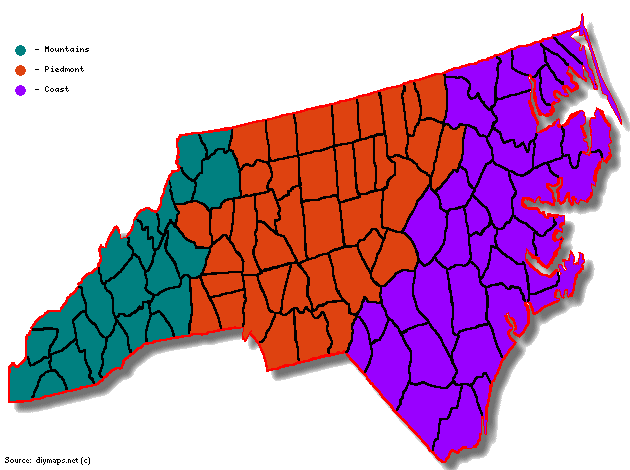
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**Tables and Figures**

**Chart, line chart

Description automatically generated**

**Figure 1:** Calculated flight dates using hypothetical subsample of data and different proxies of early flight date.



**Figure 2.** The three regions used for analysis. From left to right: Mountains, Piedmont, and Coastal Plain.

(a)

**Chart, histogram

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(b)

Chart, histogram

Description automatically generated

**Figure 3.** Histograms of the distribution of values of the slopes for all 56 species in a linear regression analysis. Red vertical lines indicate the average slope. (a) Distribution of slope values for early flight date vs. year. The average slope is an advance of 0.51 days for every one year. (b) Distribution of slope values for early flight date vs. temperature. The average slope is an advance of 1.62 days for every 1°C rise in temperature.